

1 Spatially Varying Trophic Effects of Reservoir-Derived Plankton on Stream

2 Macroinvertebrates Among Heterogeneous Habitats Within Reaches

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18 **Summary**

- 19 1. Dam reservoirs often supply high amounts of plankton to downstream reaches,
20 leading to a critical shift of trophic origins of stream ecosystems from natural
21 sources (e.g. attached algae and terrestrial inputs) to reservoir-oriented plankton.
22 Although this is a widely observed phenomenon, previous studies focused only on
23 lotic habitats (e.g. riffles) rather than lentic habitats such as backwaters and
24 isolated ponds (IP).
- 25 2. Using a stable isotope three-source mixing model, we evaluated trophic
26 contributions of reservoir-derived plankton, epilithon and terrestrial leaves to
27 stream macroinvertebrates at four dam outlet reaches and two reference reaches
28 in the Natori River catchment, Japan. We compared four different habitat types
29 co-occurring within the reaches: lotic habitat (riffle and pool), bar-head (BH) lentic
30 habitat, bar-tail (BT) lentic habitat (backwater) and isolated pond (IP) on sandy
31 bars.
- 32 3. The trophic contributions of reservoir-derived plankton were significantly lower in
33 lentic habitats (BH, 15.4%; BT, 10.4%; IP, 9.1%) than in lotic habitats (mean,
34 27.7%). This was especially notable for filter feeders that feed on suspended fine

35 particulate organic matter (SFPOM). The three-source model analysis indicated a
36 lower biomass proportion of dam plankton in lentic SFPOM (mean, 21.2%) than in
37 lotic SFPOM (mean, 35.6%). This difference in SFPOM composition was reflected
38 in the lower trophic contribution of dam plankton to lentic filter feeders.

39 4. The abundance ratio of filter feeders in the community was decreased in lentic
40 habitats, while the abundance ratios of collector-gatherers, scrapers and
41 shredders were increased. Macroinvertebrates in lentic habitats fed on sources
42 less mixed with reservoir-derived plankton (e.g. benthic coarse particulate organic
43 matter [BCPOM], benthic fine particulate organic matter [BFPOM] and epilithon);
44 therefore, the trophic impact of reservoirs was indistinctive at the community level,
45 indicating that lentic habitats can function as trophic refugia to mitigate the trophic
46 impact of reservoirs.

47 5. Because lentic habitats were decreased in area (accounting for 5.7% of average
48 total area) in the downstream reaches of dams due to riverbed degradation, lentic
49 habitats must be created in order to restore the trophic impact of reservoirs in river
50 ecosystems.

51

52 **Introduction**

53 A key question in the field of food web ecology is how spatial environmental
54 heterogeneity drives diverse food resources and food web structures within a limited
55 space (Wissel & Fry, 2005; Leigh & Sheldon, 2009; Sereda et al., 2012; Kaymak et al.,
56 2018). Riverine reach is a typical template that has large spatial variations in
57 geomorphologic and hydrologic conditions among habitat patches (e.g., riffle, pool,
58 backwater and pond) (Yarnell et al., 2006; Heino, 2013). These morpho-hydrologic
59 variations may influence the patterns of material and energy flow among habitats
60 within reaches, sustaining spatial heterogeneity in the abundance and composition of
61 food sources (Wanner et al., 2002). Assemblage trophic structure varies spatially in
62 association with longitudinal and lateral gradients of geomorphology, environmental
63 conditions and disturbance regimes in rivers (Hoeinghaus et al., 2007; East et al.,
64 2017). Some habitats include highly stored terrestrial detritus and epilithon in
65 backwaters and IPs on sandy bars (Nakajima et al., 2006; Flinn et al., 2008),
66 abundant coarse particulate organic matter deposited in riparian ponds (Langhans et
67 al., 2013), high biomass of phytoplankton in water bodies of medium age (2 to 10
68 days) (Hein et al., 2003) and high biomass of periphyton in lentic habitats (Biggs &

69 Close, 1989). However, little is known about their ecological consequences for food
70 web structure and energy flow at the community's consumer levels.

71 Dam reservoirs may artificially alter the spatial distribution of food sources
72 and community food web structure at dam outlet reaches (e.g. Hoffsten, 1999; Doi et
73 al., 2008; Helmus et al., 2013; Wellard Kelly et al., 2013; Martinez et al., 2013; Murphy
74 et al., 2017; Four et al., 2019). A typical phenomenon often observed below dams is
75 an increased supply of fine particulate organic matter (FPOM) as a consequence of
76 high primary production in reservoirs, which is especially notable in eutrophic lakes
77 (Voelz & Ward, 1996). The high load of FPOM sometimes leads to a critical shift of the
78 main trophic origins of stream ecosystems from natural sources (e.g. attached algae
79 and terrestrial particulate organic matter) to reservoir-derived plankton and also a shift
80 of the functional feeding group (FFG) composition of macroinvertebrates to a
81 structure more dominated by filter feeders (Sheldon and Oswood, 1997; Kobayashi et
82 al., 2011).

83 Although the trophic influence of dam plankton on downstream consumers
84 has been widely tested and validated, previous tests were conducted only in lotic
85 habitats or riffles (e.g. Watanabe & Omura, 2007; Doi et al., 2008; Tagliaferro et al.,

86 2013). To our knowledge, the trophic effect of dams on lentic habitats, such as
87 backwaters and IPs on sandy bars or on riparian terraces, has not been tested
88 (Malard et al., 2002; Takemon, 2007). Therefore, supplementary tests that compare
89 different habitat types in dam outlet reaches may provide better insights into the role
90 of spatial environmental heterogeneity in the formation of spatially varying trophic
91 structures.

92 Carbon and nitrogen stable isotope analysis is a widely used approach to
93 estimate trophic contributions of different potential food sources to aquatic animals
94 (Phillips et al., 2005; Leberfinger et al., 2011), assuming a monotonic change of
95 isotopic properties through the anabolic process (Rounick et al., 1982; Reid et al.,
96 2008). Autochthonous (e.g. epilithon) and allochthonous (e.g. terrestrial litter) organic
97 matter are the two main sources of trophic contributions in river ecosystems. They
98 have different isotopic signatures due to their different photosynthetic mechanisms
99 and activities (Finlay et al., 2002). In dam outlet reaches, lentic plankton produced in
100 reservoirs could be an additional food source. Dam plankton tends to show distinct
101 isotopic signatures (i.e. low carbon and high nitrogen isotopic signatures) compared
102 with the *in situ* sources produced in rivers (Ock & Takemon, 2014). Based on the

103 reservoir-specific isotopic properties of plankton, several isotopic studies found high
104 trophic contributions of drifting dam plankton to downstream macroinvertebrate
105 communities (Richardson & Mackay, 1991; Monaghan et al., 2001; Watanabe &
106 Omura, 2007; Doi et al., 2008; Mercado-Silva et al., 2009). However, these previous
107 tests were conducted only in riffles, and spatial heterogeneity among different habitat
108 types was out of their focus (but see Ock & Takemon (2014) for the difference
109 between riffle and pool).

110 In this study, using a carbon and nitrogen stable isotope mixing model
111 (Finlay et al., 2002; Reid et al., 2008; Molina et al., 2011; Kominoski et al., 2012), we
112 evaluated the trophic contributions of reservoir-derived plankton, epilithon and leaves
113 to stream macroinvertebrates at four dam outlet reaches in the Natori River catchment,
114 northeastern Japan, along with two reference reaches. We compared the trophic
115 contributions of reservoir-derived plankton among four different habitat types
116 co-occurring within the reaches. Our hypothesis was that differences among habitats
117 in the composition and abundance of food sources induce spatially heterogeneous
118 patterns in the trophic contributions of reservoir-derived plankton. The trophic effect of
119 dam plankton on macroinvertebrates in lentic habitats may be mitigated by low rates

120 of migration of dam plankton and/or accumulation of organic matter of stream origin.

121 By combining data matrices obtained through stable isotope, ecological and GPS

122 analyses, we found overall significant results that support our hypothesis.

123 **Methods**

124 **Study sites**

125 Field surveys and sample collection were conducted in six reaches in two

126 basins in the Natori River catchment in Miyagi Prefecture, northeastern Japan (Fig.

127 S1, Supporting Information). Each basin has one dam in the upstream section, the

128 Kamafusa (K) and Ohkura (O) dams. Four reaches were selected from the

129 downstream (D) reaches of dams (KD1, KD2, KD3 and OD), and two reaches were

130 selected from upstream (U) reaches of the same dams as references (KU and OU)

131 (i.e. no discharge from the dams). The three reaches below the Kamafusa dam are

132 longitudinally located along a corridor with different water distances of 0.6 km (KD1),

133 2.7 km (KD2) and 6.3 km (KD3) from the dam. The Ohkura dam has one downstream

134 study reach (OD) located 2.0 km below the dam. Although there is a small mountain

135 runoff flow into the downstream reaches of the dams, most of the water in the study

136 reaches is discharged from the dam reservoirs. The primary land use types around

137 the six study reaches are agricultural areas and wasteland, and the channels have a
138 complete open canopy. Only OU located in the forest area and the channel is covered
139 by canopy. The Kamafusa and Ohkura dams have 45.5 and 82.0 m vertical and 177.0
140 and 323.0 m wide lengths and water storage capacities of 3.9×10^7 and 2.5×10^7 m³,
141 respectively. High concentrations of phytoplankton are often observed in both dam
142 reservoirs, especially during early summer (June and July).

143 We investigated spatial habitat structure in the six reaches once for each
144 reach at KU and KD2 on 2 July 2008 and at KD1, KD3, OU and OD on 2 October
145 2008. We identified up to four habitat types for each reach: lotic (riffle and pool),
146 bar-head (BH) wando, bar-tail (BT) wando (backwater) and isolated pond (IP) on
147 sandy bars using a high-precision GPS (ProMark3; Thales, France). Geographic
148 positions were recorded at 2-s intervals while walking along contours of the habitat
149 and later post-corrected using base station data to obtain a precision of 0.1 m or less.
150 Water surface area, frequency and shape complexity of each habitat type in a reach
151 were calculated using ImageJ v.1.42 software (NIH, Bethesda, MD, USA). In the field,
152 we also measured current water velocity and water depth in each habitat type using a

153 current metre (VP-201; Kenek, Tokyo, Japan) and a ruler with five replicates per

154 habitat type per reach.

155 We collected quantitative samples of macroinvertebrate communities from

156 each habitat type found in the reaches using a Surber sampler (30 × 30 cm, 250- μ m

157 mesh) with three replicates per habitat type per reach once during July and October

158 2008. The samples were preserved in 99.5% ethanol and separated from detritus and

159 sediment debris in the laboratory under a microscope with 150 \times magnification.

160 Organisms were identified to the lowest taxonomic level possible (mostly at the

161 species level) based on Kawai and Tanida (2005) and were assigned to one of five

162 FFGs (filter feeders, collector-gatherers, scrapers, shredders and predators) based on

163 the classification of Takemon (2005) modified from Merritt and Cummins (1996) for

164 Japanese freshwater macroinvertebrates.

165 Epilithon (dominated by attached algae), suspended fine particulate organic

166 matter (SFPOM) (< 1.0 mm), benthic fine particulate organic matter (BFPOM), benthic

167 coarse particulate organic matter (> 1.0 mm) (BCPOM) and leaves were collected

168 from three randomly selected locations per habitat type per reach on the same day of

169 collection of macroinvertebrates. Epilithon was collected from stones using a

170 toothbrush, washed in pure water, and filtered onto precombusted Whatman GF/F
171 glass filters (0.7- μm nominal pore size). SFPOM was collected by filtering 1 to 4 litres
172 of surface river water through a 1.0-mm sieve onto a GF/F filter. BFPOM was
173 collected by placing a plastic tube sampler (diameter, 25 cm; depth, 50 cm) on the
174 riverbed, disturbing the benthic material in the sampler by hand, collecting the turbid
175 water and processing the sample by the same pretreatment as for SFPOM. Leaves
176 were collected from several different plant species in each reach. BCPOM was
177 collected using Surber nets together with the macroinvertebrates. Plankton was
178 collected from the reservoirs at three levels (0, 3 and 10 m from the water surface)
179 near the water intakes of the dams and processed by the same pretreatment as for
180 SFPOM in river water. Finally, nine replicates of the epilithon, SFPOM, BFPOM,
181 BCPOM and dam plankton samples were prepared for carbon ($n = 3$) and nitrogen (n
182 $= 3$) isotope analyses and for ash-free dry mass (AFDM) analysis ($n = 3$) (Flinn, 2008),
183 and six replicates of leaf samples were prepared for carbon ($n = 3$) and nitrogen ($n =$
184 3) isotope analysis. All samples were stored at -20°C prior to further processing.

185 **Stable isotope analysis**

186 For stable isotope analysis, macroinvertebrates and potential food sources

187 were acidified with 1 mol l⁻¹ HCl to remove carbonate, and the remaining material was
188 rinsed with distilled water and kept in a freezer (Walters et al., 2007). All samples were
189 freeze-dried and homogenised before stable isotope analysis. The samples, ranging
190 from 0.5 to 1.5 mg dry weight for macroinvertebrates and from 1 to 20 mg dry weight
191 for the potential food sources, were weighted into tin capsules. Carbon and nitrogen
192 isotope ratios (¹³C/¹²C and ¹⁵N/¹⁴N) were measured using an elemental analyser
193 (NA2500; CE Instruments, USA) coupled to a continuous flow mass spectrometer
194 (Finnigan MAT, Delta Plus; Thermo Fisher, USA). Stable isotope ratios were
195 evaluated in δ notation as the deviation from standards (Pee Dee belemnite for δ¹³C
196 and atmospheric nitrogen for δ¹⁵N), calculated as δ¹³C or δ¹⁵N = [(R_{sample}/R_{standard}) - 1]
197 × 10³, where R is ¹³C/¹²C or ¹⁵N/¹⁴N, respectively. Typical precision of the analyses
198 was ± 0.5‰ for δ¹⁵N and ± 0.2‰ for δ¹³C.

199 A Bayesian mixing model of stable isotope analysis in R (SIAR) (Parnell et al.,
200 2010) was used to calculate the relative contribution of each potential food source to
201 the diet of macroinvertebrates. The potential food sources used in the three-source
202 model in the dam outlet reaches were epilithon, leaves and dam plankton. The carbon
203 and nitrogen isotope enrichments in the model were set to + 0.4‰ (McCutchan et al.,

204 2003) and 3.4‰ (Post, 2002), respectively. Before performing the model calculations,
205 we confirmed significant differences in mean isotopic values among the three
206 potential food sources using one-way analysis of variance (ANOVA). In the two
207 upstream reaches of dams (KU and OU), we alternatively used a two-source mixing
208 model (Peterson & Fry, 1987; Molina et al., 2011) to determine the relative
209 contribution of epilithon to the diet of consumers (f) against leaves: f
210 $= [(\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{leaves}}) / (\delta^{13}\text{C}_{\text{epilithon}} - \delta^{13}\text{C}_{\text{leaves}})] \times 100$, where $\delta^{13}\text{C}_{\text{consumer}}$ is the $\delta^{13}\text{C}$
211 of each consumer taxon, and $\delta^{13}\text{C}_{\text{epilithon}}$ and $\delta^{13}\text{C}_{\text{leaves}}$ are the $\delta^{13}\text{C}$ values of epilithon
212 and terrestrial plants. When f was less than 0 in the calculation, 0 was used as f .

213 **Statistical analysis**

214 The mean levels of hydraulic variables (depth and velocity), amounts of the
215 potential food sources (epilithon, SFPOM, BFPOM and BCPOM), trophic
216 contributions of the three sources (dam plankton, epilithon and leaves) to whole
217 macroinvertebrate communities and FFGs, and biomass proportions of the three
218 sources in SFPOM, BFPOM and BCPOM were compared among the four habitat
219 types (lotic, BH, BT and IP) using one-way ANOVA followed by the Tukey–Kramer test
220 for multiple pairwise comparisons. The trophic contributions of dam plankton were

221 also compared among FFGs for each habitat type. Simple correlations between the
222 trophic contributions of dam plankton to macroinvertebrate communities and FFGs
223 and the biomass proportions of dam plankton in SFPOM, BFPOM and BCPOM were
224 tested by ANOVA. All statistical analyses were carried out using SPSS Statistics
225 v.17.0 (SPSS, Chicago, IL, USA).

226 **Results**

227 **Habitat structure, hydraulic and food source conditions**

228 Lotic and BH habitats commonly occurred throughout the six study reaches.
229 BT occurred at KU, KD3 and OD, and IP occurred at KD1 and KD3. IP occurred only
230 at dam outlet reaches. Throughout the six reaches, lotic habitat always had the
231 highest proportion of water area in the reaches (88.5% to 96.8%), while lentic habitats
232 (BH, BT and IP) accounted for a minor proportion of water area (1.4% to 11.5%)
233 (Table 1).

234 Mean water depth ($F_{3, 166} = 24.7, P < 0.001$) and mean current velocity ($F_{3, 164} = 105.5, P < 0.001$) (ANOVA) differed significantly among the four habitat types
235 (Table 1). Multiple pairwise comparison tests found significantly higher water depths in
236 the BT (mean, 0.30 m) and the lotic habitat (mean, 0.27 m) than in the BH (0.14 m)
237

238 and IP (0.09 m) ($P < 0.001$, Tukey–Kramer test). The mean current velocity was
239 significantly higher in the lotic habitat (0.51 m s^{-1}) than in the three lentic habitat types
240 (BH, 0.02 m s^{-1} ; BT, 0.01 m s^{-1} ; IP, 0.0 m s^{-1} ; $P < 0.001$, Tukey–Kramer test).

241 Differences among habitats in the availability of food sources were also
242 evident. The mean biomass (AFDM) of potential food sources was significantly
243 different among the four habitat types (SFPOM, $F_{3, 91} = 7.554$, $P < 0.001$; BFPOM, $F_{3, 82} = 19.421$, $P < 0.001$; BCPOM, $F_{3, 58} = 11.717$, $P < 0.001$), except for epilithon ($F_{3, 73} = 2.241$, $P > 0.05$). Multiple pairwise comparison tests found significantly larger mean
246 biomasses of SFPOM, BFPOM and BCPOM in the three lentic habitat types than in
247 the lotic habitat ($P < 0.01$, Tukey–Kramer test). SFPOM biomass was higher in IP and
248 BT than in the lotic habitat ($P < 0.01$, Tukey–Kramer test), and BH was those in
249 between ($P > 0.05$, Tukey–Kramer test). BFPOM biomass was highest in the BT ($P < 0.001$, Tukey–Kramer test), and BCPOM biomass was highest in the IP ($P < 0.01$,
251 Tukey–Kramer test). Three habitat types, but not the IP, showed significant increases
252 in mean SFPOM biomass from the upper to the lower reaches of the dam (lotic, from
253 1.3 to 5.8 mg l^{-1} ; BH, from 2.3 to 16.8 mg l^{-1} ; BT, from 2.3 to 35.5 mg l^{-1} ; $P < 0.05$,
254 t -test). BFPOM biomass increased only in the BT (from 37.9 to 154.2 mg l^{-1} , $P < 0.01$),

255 and epilithon and BCPOM biomass did not change between the upper and lower

256 reaches of the dam.

257 **Macroinvertebrate community**

258 We collected a total of 5547 macroinvertebrates and identified 125 taxa from

259 the 17 habitats among the six reaches (Table 2). The majority of taxa were of the

260 orders Trichoptera (40 taxa), Ephemeroptera (40 taxa), Plecoptera (11 taxa) and

261 Diptera (11 taxa). Taxon richness ranged widely from 11 to 42 taxa among the 17

262 habitats, with significant differences between the lotic (mean, 32.7) and lentic habitat

263 types (IP, 16.0; BT, 16.7; BH, 20.0; $P < 0.05$, Tukey–Kramer test). Total abundance

264 (N) and total biomass (W) were also higher in the lotic habitat than in the lentic habitat

265 types ($P < 0.01$, t -test), except for BH and BT at KU, where *Chironomus* sp. (70 and

266 921 individuals/0.27 m², respectively) were highly abundant, and IP at KB3, where

267 *Cloeon dipterum* (967 individuals/0.27 m²) was highly abundant. Among the 125 taxa,

268 37 and 39 taxa occurred only in lentic or lotic habitats, respectively. *Antocha* sp. were

269 commonly found throughout all 17 habitats with high abundance. The most frequently

270 occurring taxa in the lotic habitats were *Macrostemum radiatum*, *Cincticostella okumai*

271 and *Baetiella* sp., while *Hydropsyche setensis* occurred throughout all six lotic

272 habitats.

273 In the dam downstream reaches, the mean proportional abundance of filter
274 feeders in the macroinvertebrate community was significantly higher in lotic habitats
275 than in lentic habitats ($F_{1,13} = 24.3$; $P < 0.001$, two-way ANOVA), whereas this was not
276 true for the other FFGs. The spatial variation in the proportion of filter feeders among
277 the six lotic habitats was significantly and positively correlated with the variation in
278 SFPOM concentration ($r = 0.954$, $P = 0.003$). We did not detect any other significant
279 correlations between the proportion of FFGs and the biomass of SFPOM, BFPOM
280 and BCPOM in any habitat type.

281 **Carbon and nitrogen isotope signatures**

282 The carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope signatures varied among
283 potential food sources in all habitat types within reaches ($P < 0.01$, ANOVA). Epilithon
284 had the highest $\delta^{13}\text{C}$ ($-22.4 \pm 3.4\text{‰}$) and $\delta^{15}\text{N}$ ($4.1 \pm 2.3\text{‰}$) values, while leaves had
285 the lowest $\delta^{13}\text{C}$ ($-29.8 \pm 1.4\text{‰}$) and $\delta^{15}\text{N}$ ($0.5 \pm 0.2\text{‰}$) values in each habitat. Dam
286 plankton collected from the reservoirs had low $\delta^{13}\text{C}$ ($-28.2 \pm 0.5\text{‰}$) and high $\delta^{15}\text{N}$ (4.9
287 $\pm 0.7\text{‰}$) values. In the dam outlet reaches, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for SFPOM and
288 BFPOM fell within the range of values for epilithon, leaves and dam plankton, allowing

289 the three-source mixing model to be run. All three lentic habitat types had significantly
290 lower mean proportions of dam plankton in SFPOM than the lotic habitat ($P < 0.05$,
291 Tukey–Kramer test) (Table 3). On the other hand, the mean proportion of epilithon in
292 SFPOM was higher in the BH and IP than in the lotic habitat ($P < 0.01$, Tukey–Kramer
293 test). BFPOM had higher proportions of dam plankton only in the IP ($P < 0.05$,
294 Tukey–Kramer test). In upstream reaches of dams, there were no significant
295 differences among habitat types in the proportion of the three sources (epilithon,
296 leaves and dam plankton) in SFPOM and BFPOM.

297 For stable isotope analysis of macroinvertebrates, we selected 91 taxa with
298 > 0.2 mg dry mass. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of macroinvertebrates fell within the
299 habitat-specific ranges among the three potential food sources (epilithon, leaves and
300 dam plankton) in the dam outlet reaches. The trophic contributions of dam plankton to
301 the macroinvertebrate community estimated by the three-source mixing model were
302 significantly different among the four habitat types ($F_{3, 397} = 23.462$, $P < 0.001$) and
303 among FFGs ($F_{4, 396} = 35.695$, $P < 0.001$). Lotic habitats had a significantly higher
304 contribution from dam plankton (mean, 27.7%) than did the BH (15.4%), BT (10.4%)
305 and IP (9.1%) ($P < 0.001$, Tukey–Kramer test). The contribution of leaves in the lotic

306 and BT habitats was significantly higher than that in the BH and IP in the dam outlet
307 reaches ($P < 0.05$, Tukey–Kramer test). Epilithon was estimated to be a principal food
308 source throughout the habitat types downstream from dams.

309 In dam outlet reaches, filter feeders consumed significantly more dam
310 plankton than the other FFGs throughout all habitat types ($P < 0.001$, Tukey–Kramer
311 test). The contribution of dam plankton to filter feeders was higher in the lotic habitat
312 than in the lentic habitats ($P < 0.001$, Tukey–Kramer test with Bonferroni correction),
313 whereas the significant differences were absent for the other FFGs (Fig. 1). In lotic
314 habitats in dam outlet reaches, spatial variation in the contribution of dam plankton to
315 filter feeders was significantly positively correlated with the proportion of dam plankton
316 in SFPOM (Fig. 2), whereas this correlation was not found for lotic habitats and the
317 other FFGs.

318 **Discussion**

319 Our approach to comparing trophic structures among different habitats has
320 provided useful insights into the role of spatial environmental heterogeneity in the
321 formation of food web structures in rivers. Environmental heterogeneity was related to
322 community diversity and food resources of macroinvertebrates on each spatial scale

323 (Boyero, 2003; Boyero & Bosch, 2004; Zilli & Marchese, 2011; Pilotto et al., 2016).

324 However, in previous studies, the relationship between heterogeneity and food webs

325 in macroinvertebrates within habitats was not considered. Using carbon and nitrogen

326 stable isotope analyses, we compared the trophic influence of reservoir-derived

327 plankton on downstream macroinvertebrate communities between lentic and lotic

328 habitats. Our overall results showed habitat-specific patterns of trophic influence of

329 dam plankton, with less influence of dam plankton in lentic than in lotic habitats. This

330 pattern was specifically notable for filter feeders that feed on SFPOM. Although the

331 high trophic influence of dam plankton and dam-derived FPOM on filter feeders has

332 been reported in numerous studies (Doi et al., 2008; Power et al., 2013; Tagliaferro et

333 al., 2013; Four et al., 2019), these earlier observations were limited to lotic habitats,

334 where the strongest impact was observed in this study.

335 We considered the habitat-specific source composition of SFPOM as a

336 potential driver of the reduced trophic impact in lentic habitats. The three-source

337 model analysis of SFPOM indicated a lower proportion of dam plankton and higher

338 proportions of epilithon and leaves in lentic habitats than in lotic habitats. The lower

339 proportion of dam plankton in lentic SFPOM was most likely reflected in the lower

340 trophic impact on lentic consumers through assimilation of SFPOM, especially on filter
341 feeders. This trophic reflection of drifting SFPOM to filter feeders at dam outlet
342 reaches is supported by previous isotopic studies (Doi et al., 2008; Wellard Kelly et al.,
343 2013), although the data from lotic habitats are limited. The habitat-specific
344 composition of SFPOM may be derived from hydraulic and landscape characteristics
345 of lentic habitats. BH located at the leading edges of the bar was not only an area
346 where surface water downwelled into the hyporheic zone but also an area where
347 SFPOM from upstream was accumulated (Boulton et al., 2008). Hence, the
348 contribution of dam plankton in the BH was higher than that in other lentic habitats,
349 but the amounts of epilithon and leaves were higher than in the main stream, resulting
350 in an increase in river-derived SFPOM. It can be inferred that the impact of the dam
351 was moderated. BT located at the downstream end of the bar area where
352 groundwater upwells is an environment where mainstream water and SFPOM cannot
353 easily enter. The biomass of organic matter in the BT is also higher than in the
354 mainstream, and the interaction between hydromorphological and ecological
355 processes may have contributed to mitigating dam effects. On the other hand, it is
356 impossible for dam plankton to flow into the IP when it is disconnected from the

357 mainstream during periods of normal water level. After a flood, dam plankton may be
358 left behind in the IP. In addition, the amount of BFPOM in the IP may have increased
359 as a result of plankton production in the water body (Doi, 2009). Therefore, it was
360 suggested that the influence of dam-derived plankton in lentic habitats is due to
361 different hydromorphological and ecological processes. Furthermore, SFPOM derived
362 from allochthonous and autochthonous sources was produced by decomposition of
363 bacteria and relatively dominant scrapers and shredders that inhabited the lentic
364 habitat (Langhans et al., 2008; Treplin & Zimmer, 2012; Halvorson et al., 2015). The
365 high amounts of epilithon, BFPOM and BCPOM observed in lentic habitats can
366 account for these geohydraulic and biological processes, leading to the higher
367 proportions of epilithon and leaves in lentic SFPOM.

368 In addition to the habitat-specific composition of food sources, habitat
369 preference of macroinvertebrates was considered as a potential reason for the
370 reduced trophic contribution of dam plankton in lentic habitats. Filter feeders generally
371 prefer to live in lotic environments with rapid flow and loose stones and gravel of
372 suitable size for their net-spinning behaviour on the riverbed (Georgian & Thorp,
373 1992). Stabilisation of the substrate due to reduced hydraulic and sediment dynamics

374 resulting from dam control is also a driving factor for the abundance of filter feeders at
375 dam outlet reaches (Oswood, 1979; Hoffsten, 1999; Tsydel et al., 2009). In lentic
376 habitats, the substrate is mainly composed of fine materials (silt and sand) and
377 embedded stones with extremely low water flow. Therefore, the abundance ratio of
378 filter feeders in the macroinvertebrate community is reduced in lentic habitats, with
379 increases in the ratios of other FFGs, such as collector-gatherers, scrapers and
380 shredders (Table 2). These other FFGs can feed on sources less mixed with
381 reservoir-derived plankton (e.g. BCPOM and BFPOM) and thus are robust to the high
382 input of dam plankton. As a result of high ratios of these FFGs being potentially robust
383 to the input of dam plankton, the trophic impact on the macroinvertebrate community
384 as a whole may be reduced.

385 Finally, from the conservation viewpoint, the ecologically important role of
386 lentic habitats is worth mentioning. Although the mean proportion of lentic area in the
387 downstream reaches was less than 5.7% in our study, the distinctive hydro-physical
388 and landscape characteristics of the lentic areas led to heterogeneous trophic
389 conditions within the reaches. In general, the amount of lentic habitat in sand and
390 gravel bars decreased in downstream reaches due to riverbed degradation (Brandt,

391 2000; Rollet et al., 2013). In this study, the area of lentic habitat was lower in
392 downstream reaches than in upper reaches, except for KD3. Because KD3 was the
393 most distant reach from the dam, it was believed that the lentic habitat was restored
394 by sediment supplied from the river bank and reduction of the impact of the dam
395 (Rollet et al., 2013). In previous studies, the significance of lentic habitats in the
396 formation of biodiversity was often reported (Taniguchi & Tokeshi, 2004; Tews et al.,
397 2004; Warfe et al., 2008) and was applied to conservation. For example, many river
398 restoration works have created lentic spaces to facilitate spatial heterogeneity of
399 species diversity (Wyżga et al., 2012; Van den Brink et al., 2013) and to supply flow
400 refugia to fishes from flood disturbances (Sedell et al., 1990; Milner & Gilvear, 2012).
401 Creation of lentic habitat was basal idea downstream due to improvement of river
402 morphology, and it was shown that it contributed to mitigation of the trophic impact.
403 Our finding of habitat-specific food resources in lentic spaces and their influence on
404 trophic structures of invertebrate communities expanded the existing idea a little
405 further. Lentic water bodies can help sustain adequate and diverse flows of materials
406 in food webs. In particular, in environments where the main food sources are
407 artificially modified from the natural sources, such as in the dam outlet reaches

408 observed in this study, lentic habitats are expected to act as trophic refugia that can
409 mitigate the trophic impact.

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414 analysis.

415 **Data Availability Statement**

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

418 **Conflict of Interest Statement**

419 The authors declare that they have no competing interests.

420

421 **References**

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- 604
605

606 Table 1. Mean values of hydraulic variables and amounts of potential food sources in

607 each habitat type among six study reaches

608

	Area	Depth	Current	SFPOM [†]	BFPOM [‡]	Epilithon	BCPOM [§]
						(mg	
Habitat	(%)	(m)	(m s ⁻¹)	(mg l ⁻¹)	(g m ⁻²)	cm ⁻²)	(g m ⁻²)
Lotic	93.8 [*]	0.27 [*]	0.51 [*]	4.25 [*]	17.8 [*]	6.3 [*]	3.4 [*]
Bar-head (BH)	4.0 ^{**}	0.14 ^{**}	0.02 ^{**}	11.4 ^{***}	28.9 [*]	10.4 [*]	44.9 [*]
wando							
Bar-tail (BT)	3.2 ^{**}	0.30 ^{**}	0.01 ^{**}	31.8 ^{**}	115.4 ^{**}	15 [*]	50.2 [*]
wando							
Isolated pond (IP)	1.7 ^{**}	0.09 ^{**}	0 ^{**}	21.1 ^{**}	34.8 [*]	6.7 [*]	98.6 ^{**}

609 ¹

[†]SFPOM, suspended fine particulate organic matter; [‡]BFPOM, benthic fine

particulate organic matter; [§]BCPOM, benthic coarse particulate organic matter. *,***P* <

0.05, Tukey–Kramer test

610 Table 2. Mean values of species richness, total abundance and total biomass of
 611 macroinvertebrate communities and percentages of functional feeding groups (FFGs)
 612 abundance in each habitat type among six study reaches
 613

Habitat	Total			Relative abundance of FFGs (%)				
	Taxon	abundance	Total biomass	Collect				
	richness	(0.27 m ⁻²)	(mg 0.27 m ⁻²)	Filter feeders	collector-gatherers	Scrapers	Shredders	Predators
Lotic	32.7*	412*	546*	63*	5*	18*	0*	14*
†BH wando	20.0**	148*	237*	24*	20*	19*	3*	34*
‡BT wando	16.7**	435*	260*	26*	28*	25*	1*	22*
§IP	16.0**	586*	442*	2*	44*	48*	1*	6*

614 ²

² †BH, bar-head; ‡BT, bar-tail; §IP, isolated pond. *, ***P* < 0.05, Tukey–Kramer test

615 Table 3. Comparison of mean percentages of trophic contributions of potential food
 616 sources in SFPOM, BFPOM and the macroinvertebrate community among four
 617 habitat types, calculated by two- or three-source mixing models

Habitat	Reference		Dam downstream		
	Epilithon	Leaves	Plankton	Epilithon	Leaves
[†] SFPOM					
Lotic	67.0*	33.0*	35.6*	34.1*	30.3***
[§] BH wando	55.7*	44.3*	23.8*	51.5*	24.9*
[¶] BT wando	50.4*	49.6*	20.5**	37.8***	41.7**
[∞] IP	–	–	19.3**	54.0**	26.8***
[‡] BFPOM					
Lotic	65.3*	34.7*	22.1*	41.6*	36.3*
[§] BH wando	53.7*	46.3*	17.9*	46.3*	35.7*
[¶] BT wando	56.4*	43.6*	17.7*	41.1*	41.2*
[∞] IP	–	–	37.2**	47.6*	15.4**
Macroinvertebrates					

Lotic	90.5*	9.5*	27.7*	46.5*	25.8*
§BH wando	97.1*	2.9*	15.4**	67.9**	16.7**
¶BT wando	88.2*	11.8*	10.4**	58.5**	31.1*
∞IP	–	–	9.1**	73.6**	17.1**

618 ³

³ †SFPOM, suspended fine particulate organic matter; ‡BFPOM, benthic fine particulate organic matter; §BH, bar-head; ¶BT, bar-tail; ∞IP, isolated pond. *,** $P < 0.05$, Tukey–Kramer test.

619 Figure legends

620 Figure 1. Comparison of trophic contributions of reservoir-derived plankton to each

621 functional feeding group (FFG) among habitat types. Letters indicate significant

622 differences among habitat types ($P < 0.001$, Tukey–Kramer test with Bonferroni

623 correction).

624 Figure 2. Relationships between trophic contributions of reservoir-derived plankton to

625 filter feeders and percentage of reservoir-derived plankton in suspended fine

626 particulate organic matter (SFPOM) in the lotic habitat. The regression line indicates

627 significant correlation found in the lotic habitat ($r = 0.574$; $P < 0.001$). The other

628 functional feeding groups (FFGs) while this correlation was not true for lotic habitats

629 and the other FFGs.

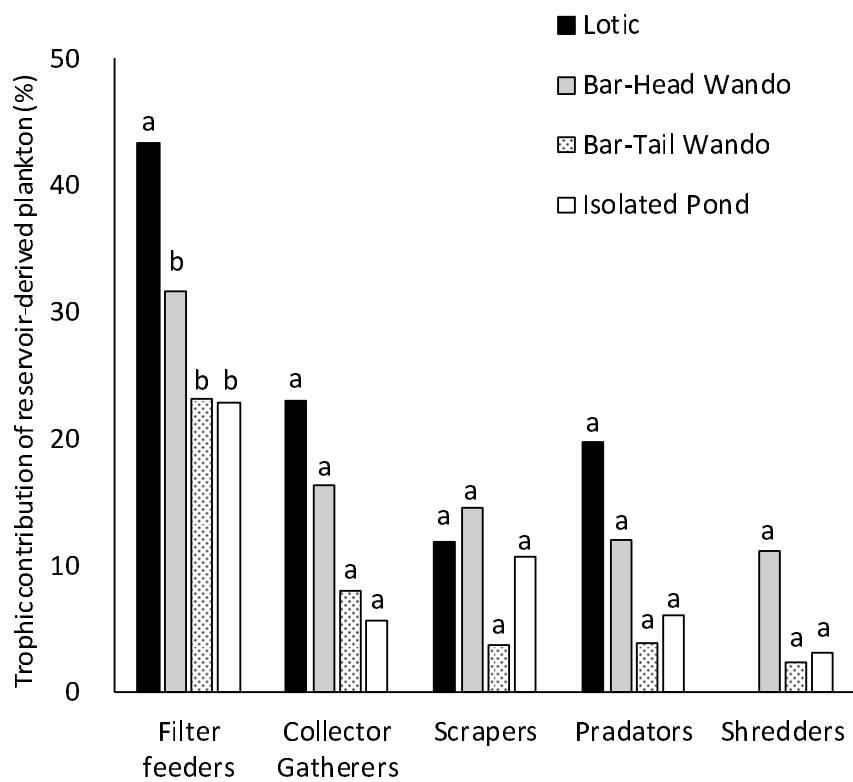
630 Figure S1. Maps of study site (a) and habitats (b). KU, Kamafusa dam upstream;

631 KD1–KD3, Kamafusa dam downstream 1–3; OU, Ohkura dam upstream; OD, Ohkura

632 dam downstream.

633

634

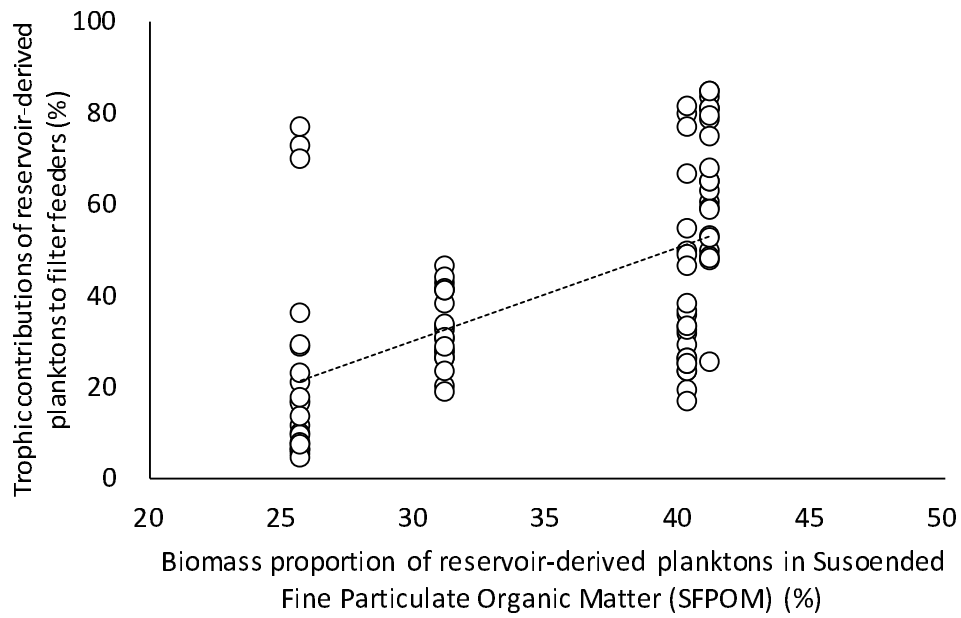


635

636 FIG. 1

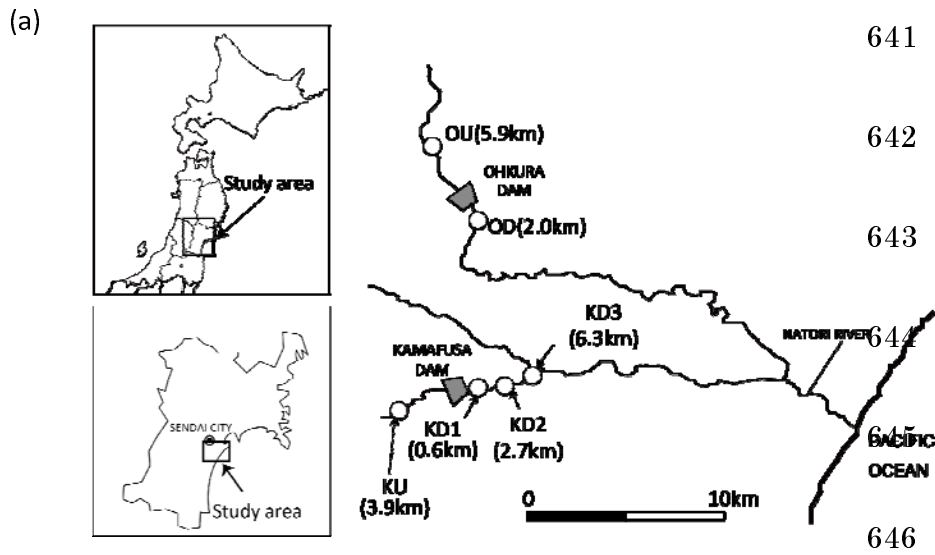
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640 FIG. 2

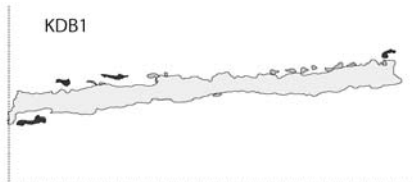


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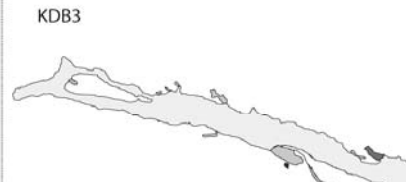
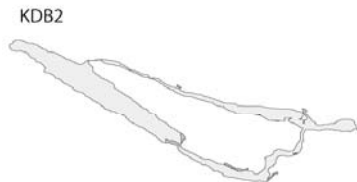
(b)

Main stream
Bar tail wando
Bar head wando
Isolated pool

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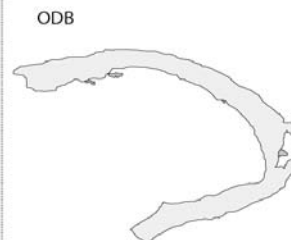


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656 FIG. S1