1 **Title**

2 Flood-induced interspecific interactions in spring-fed tributary as an ecosystem function
3 of heterogeneous river networks

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21

22 **Abstract**

23 Understanding the migratory community dynamics of river networks is important for
 24 maintaining lotic system integrity. River animals migrate to their preferred habitats in
 25 spatiotemporally heterogeneous river environments. Spring-fed habitats are uniquely
 26 characterized by stable temperature and flow regimes, which create suitable spawning
 27 habitats for the chum salmon *Oncorhynchus keta*. *O. keta* exhibits “run up” to its
 28 birthplace for spawning, especially during floods. Because the eggs deposited by this
 29 anadromous fish are nutritious and actively consumed by freshwater animals, the
 30 location and timing of *O. keta* spawning events affect the spatiotemporal accumulation
 31 of mobile consumers. In this study, we examined changes in temporal population
 32 density in spawning *O. keta* and a mobile consumer (juvenile *O. masou masou*) in a
 33 lowland, spring-fed tributary in northern Japan during a 48.5-mm autumn rainfall event.
 34 In both species, population density increased, and then decreased, after the rainfall event.
 35 In *O. keta*, these changes were closely associated with rainfall intensity, whereas in *O.*
 36 *masou masou* the peak was delayed until 3 days after the rainfall event. A comparison
 37 of the gut contents of *O. masou masou* sampled from a spring-fed tributary and an
 38 adjacent non-spring-fed tributary indicated greater consumption of *O. keta* eggs in the
 39 spring-fed tributary. These results suggested that preferential migration of *O. keta* into
 40 spring-fed tributaries for spawning induces subsequent accumulation of juvenile *O.*
 41 *masou masou*, in turn increasing *O. keta* egg consumption. These findings improve our
 42 understanding of community dynamics during floods in a heterogeneous river network
 43 environment.

44 **Key words:** Animal migration, Field ecology, Resource subsidy, Salmonids, Upwelling
 45 groundwater

46 **Introduction**

47 Spring-fed streams, which are maintained by continuous groundwater
 48 upwelling, constitute unique ecosystems with stable temperature and flow regimes
 49 (Mattson et al. 1995; Sear et al. 1999; Lusardi et al. 2016). The narrow range of water
 50 temperature in spring habitats creates refugia for stenothermal glacial relict species
 51 (Reiss et al. 2016; Sun et al. 2020). Stable flow regimes in spring-fed streams are
 52 associated with less sediment runoff during floods than non-spring-fed streams, and the
 53 formation of fine substrates inhabited by abundant detritivorous macroinvertebrates
 54 (Sakai et al. 2020). Thus, the unique habitats of spring-fed streams enhance beta
 55 diversity in river networks (Reiss et al. 2016; Sakai et al. 2020).

56 The chum salmon *Oncorhynchus keta*, an important North Pacific fishery
 57 species, is an anadromous fish. After 2–4 years of growth in the ocean, *O. keta* exhibits
 58 “run up” to its birthplace for spawning from summer to winter (Masuda et al. 1984),
 59 especially during floods caused by rainfall events (Banks 1969). *O. keta* has
 60 preferentially selected upwelling water habitats with a stable warm temperature for
 61 spawning (Kobayashi 1968; Milligan et al. 1984; Geist et al. 2011); these upwelling
 62 springs form egg accumulation zones after rainfall events during the spawning season.

63 *O. keta* eggs are a significant and nutritious food resource for freshwater fishes.
 64 For example, juvenile salmonids rely heavily on eggs deposited by anadromous
 65 spawning salmon, including *O. keta* (Armstrong et al. 2013; Koshino et al. 2013; Bailey
 66 et al. 2019). This marine-derived resource subsidy is available both after floods in
 67 spring habitats, and spatiotemporal heterogeneity in its availability influences the
 68 migration of mobile consumers in rivers containing spawning salmon species (e.g.,
 69 Armstrong et al. 2013).

Understanding migratory community dynamics in river networks is important to preserve lotic system integrity (Ward et al. 1999; Eloisegi et al. 2010); however, direct observation of the migration of lotic animals, particularly fishes, during floods is generally difficult and unsafe. In contrast, spring-fed streams are suitable for investigating community dynamics during flood events due to their high stability. Autumn rainfall can trigger upstream migration of *O. keta* for spawning, which influences the foraging habitats of species that feed on their eggs. This interactional process may represent an additional ecosystem function of spring-fed streams, i.e., structuring biota in river networks. However, substantial gaps in understanding remain regarding the functional role of spring-fed streams in the dynamics of stream fishes during floods.

Because springs generally provide purified water, spring-fed streams are frequently reserved for use as a human water supply (LaMoreaux and Tanner 2001). Elucidating the ecosystem functions of spring-fed streams would further highlight their value. In the present study, we investigated temporal variation in stream fish dynamics in a spring-fed tributary after a rainfall event. Although access to the surrounding non-spring-fed streams was not feasible during the rainfall event, the spring-fed tributary was relatively calm and could be safely accessed for surveys. We examined the responses of spawning *O. keta* and juvenile *O. masou masou* to the flood event, and associated interspecific interactions related to the consumption of *O. keta* eggs. The findings of this study contribute to our understanding of community dynamics during floods in heterogeneous river network environments.

Materials and methods

94 **Study site**

95 This study was conducted in the Shubuto River basin in Kuromatsunai,
96 Hokkaido, Japan (42.64° N, 140.34° E), which encompasses an area of 367 km² and
97 includes both montane and lowland regions. The region is underlain by sandstone and
98 mudstone, including Cenozoic fossil shells and tuff. The mean annual precipitation
99 between 2009 and 2018 was 1,615.8 mm, and the mean air temperature was 7.5°C,
100 measured at the Kuromatsunai AMeDAS automated weather station located 4 km
101 northwest of the study site. The dominant tree species in riparian zones within the study
102 area are *Salix* species and *Quercus crispula*, and the dominant understory plants are
103 *Sasa kurilensis* and *Reynoutria sachalinensis*. No dams or weirs prevent the migration
104 of fishes in the mainstem of the Shubuto River (Miyazaki and Terui 2016). The Shubuto
105 River system has a perennial spring-fed tributary with significant groundwater discharge
106 (ca. 0.1 m³/s) in the lowland region (Kamiyama River, Fig. 1). This stream has no
107 artificial structures that inhibit longitudinal connections, and stream fishes thus migrate
108 between the spring-fed tributary and mainstem.

109 At this spring-fed tributary, we examined temporal changes in the population
110 density of two *Oncorhynchus* fishes (*O. keta* and *O. masou masou*) during a rainfall
111 event. On October 6–7, 2018, a temperate low-pressure system (formerly the Kong-rey
112 typhoon) released a total of 48.5 mm of rain at the study site. According to our visual
113 surveys performed immediately after the rainfall event, water levels increased
114 substantially in most non-spring-fed streams of the Shubuto River system; however, the
115 study tributary showed no dramatic increase in water level. We collected fish both
116 before (October 6) and after (October 7, 9, and 10) the rainfall event; hereafter, we refer
117 to these collection dates as “before,” “after d1,” “after d3,” and “after d4”, respectively.

118 We also collected the gut contents of *O. masou masou* in an adjacent perennial
 119 non-spring-fed tributary (Utsai River, Fig. 1), for comparison between spring-fed and
 120 non-spring-fed tributaries after the rainfall event. Stream width and water depth were
 121 similar between the tributaries (Table 1); however, the non-spring-fed tributary had a
 122 gravel-dominated streambed with a faster current. *O. keta* rarely migrates to the
 123 non-spring-fed tributary during spawning seasons, but migrates yearly to the spring-fed
 124 tributary; a preference for spring-fed habitats as spawning substrates in this species has
 125 been reported previously (e.g., Kobayashi 1968; Milligan et al. 1986), leading to the
 126 construction of a facility for capturing mature *O. keta* in this tributary. The facility
 127 irreversibly traps mature *O. keta* in an artificial pool, and trapped individuals are
 128 transported to another tributary of the Shubuto River system for egg collection and fry
 129 rearing. Thus, eggs found in the spring-fed tributary are presumed to have spawned
 130 within the tributary, and not drifted from the facility. On October 10 (after d4), when
 131 both tributaries had ordinary flow conditions, we sampled *O. masou masou* gut
 132 contents.

133

134 **Hydrological monitoring**

135 Water level and temperature loggers (HOBO CO-U20L-04; Onset, Bourne,
 136 MA, USA) were fixed on streambeds of the tributaries using metal tubes and wire, and
 137 hydraulic pressure was recorded once per hour. Before the rainfall event started, we
 138 preliminarily recorded water levels at the monitoring points on October 6–7, 2018 using
 139 a folding scale, and devised linear regression models of the relationship between water
 140 level (cm) and hydraulic pressure (kPa). Based on these models, hydraulic pressure data
 141 recorded in the loggers were transformed into water level data. For both study reaches,

the water level at 1:00 A.M. on October 6, 2018 was set at 0 cm, and hydrographs of the ensuing water level changes were created. Hourly rainfall data were obtained from the Kuromatsunai AMeDAS automated weather station.

Fish collection

A 40-m-long study reach was established in the spring-fed tributary to investigate temporal changes in *O. keta* and *O. masou masou* population density during a rainfall event. The Shubuto River *O. masou masou* population includes both anadromous and resident individuals; most females and some males become anadromous after approximately 2 years of growth in the river (Miyazaki 2017). Thus, small individuals collected in the study area were mainly juveniles and resident males. Because the rainfall event occurred during the reproductive period, we classified small *O. masou masou* individuals (standard body length = 60–160 mm) as mature or juvenile based on the presence or absence of nuptial coloration. *O. keta* is anadromous, and generally runs up to the Shubuto River from mid-September, where it spawns until mid-November after 2–8 years of growth in the North Pacific (Miyazaki 2017). Therefore, individuals found in the river during the autumn reproduction season are mature.

We conducted electrofishing using a backpack electrofisher (LR-20; Smith-Root Inc., Vancouver, WA, USA). The upper and lower limits of the tributary study reach were gently partitioned using fishnets to prevent fishes from entering or exiting the reach during collection. Three-pass electrofishing was conducted from lower to upper positions, to collect as many *Oncorhynchus* fish as possible. After collection, the wetted width was measured at five points (10-m intervals) within the study reach, to

166 better represent the surveyed area during each collection (before, after d1, d3, and d4)
167 allow for accurate calculation of fish population density.

168 The population density of *O. masou masou* was estimated using the maximum
169 likelihood method proposed by Zippin (1956), because the number of collected
170 individuals decreased substantially between the first and third removals. The number of
171 collected *O. keta* individuals varied and exhibited no clear pattern. However, we
172 confirmed that each three-pass removal collected all individuals within the reach; this
173 was possible due to their large body size (standard length = 425–801 mm). Therefore,
174 we used the total number of collected individuals to directly estimate population density
175 for this species. The maximum likelihood method was applied using R software (v.
176 3.6.3; R Core Team 2020) with the *FSA* package (Ogle et al. 2020).

177

178 Gut content collection

179 In the early morning and evening of after d4, we collected *O. masou masou* for
180 gut content analysis using a stomach pump; a total of 31 and 11 individuals were
181 collected in the spring-fed and non-spring-fed tributaries, respectively. Each gut content
182 sample was immediately preserved in 70% ethanol. The body size distribution of the
183 collected *O. masou masou* was similar between tributaries. Fish were released into their
184 original habitats after gut content collection. To avoid interference with our population
185 density estimates in the spring-fed tributary, we performed population density sampling
186 in this tributary in the early morning of after d4, prior to gut content collection.

187 Gut contents were sorted and identified using a stereomicroscope (SZ61;
188 Olympus, Tokyo, Japan). Identified gut contents were dried in an oven (FC-610;
189 Advantec, Tokyo, Japan) at 60°C for 24 h and then weighted precisely to within 0.01

190 mg. To test for differences in the gut contents of *O. masou masou* between tributaries,
191 we analyzed the dry weight data using one-way analysis of variance (ANOVA) with
192 permutation tests, which allowed us to deal with unbalanced sample sizes. ANOVA was
193 performed using the R 3.6.3 software with the *anova.lway* function (Legendre 2007).

194

195 **Results**

196 Following the onset of the rainfall event, the water level in the spring-fed
197 tributary declined slightly, but was clearly lower overall than that in the non-spring-fed
198 tributary throughout the monitoring period (Fig. 2). Water levels in the non-spring-fed
199 tributary reflected changes in rainfall intensity, and peaked at 29 cm above the initial
200 water level (Fig. 2). A total of 175 individuals of *O. masou masou* and 35 individuals of
201 *O. keta* were collected in the spring-fed tributary. In both species, population density
202 increased after the rainfall event, but subsequently decreased (Fig. 3); that of *O. masou*
203 *masou* peaked at after d3, whereas for *O. keta* it decreased after d1. All collected *O.*
204 *masou masou* were juveniles, and all *O. keta* individuals were mature and reproductive.

205 At after d4, *O. masou masou* in the spring-fed tributary consumed significantly
206 more *O. keta* eggs, whereas those in the non-spring-fed tributary consumed more
207 hemipteran, hymenopteran, and trichopteran insects (Table 2). Due to the large
208 contribution of *O. keta* eggs, the total gut contents were higher in the spring-fed
209 tributary than in the non-spring-fed tributary (Table 2).

210

211 **Discussion**

212 The results showed that increase in population density of *O. keta* immediately
213 after the rainfall event, and the subsequent peak of population density of juvenile *O.*

214 *masou masou* was observed three days after the rainfall event in the spring-fed tributary.
 215 The individuals of *O. masou masou* in the spring-fed tributary consumed more eggs of
 216 *O. keta* compared to those in the adjacent non-spring-fed tributary. These results suggest
 217 that preferential migration of *O. keta* into spring-fed tributaries for spawning induces
 218 subsequent accumulation of juvenile *O. masou masou*, in turn increasing *O. keta* egg
 219 consumption.

220 Typically, lowland spring-fed streams formed by groundwater discharge are
 221 not deep (Sear et al. 1999), and their flow regimes are generally stable (Lusardi et al.
 222 2016). In this study, water levels in the spring-fed tributary did not exhibit the same
 223 marked increase observed in the non-spring-fed tributary during the rainfall event. This
 224 stability creates a valuable opportunity for direct field observation of the dynamics of
 225 aquatic animal communities during floods.

226 Hydrological monitoring indicated that the water level of the spring-fed
 227 tributary decreased following the onset of rainfall. This change may be attributable to
 228 the onset of water transmission into the *O. keta* egg collection facility, because local
 229 fishermen know that this species actively migrates to upstream spawning habitats during
 230 floods (Banks 1969). Our results also indicated that the population density of *O. keta*
 231 peaked immediately after the rainfall intensity peak. The dependence of *O. keta* on
 232 spring-fed habitats for spawning (Kobayashi 1968; Milligan et al. 1984; Geist et al.
 233 2011) may explain the accumulation of this species in the spring-fed tributary during the
 234 flood.

235 Although the population density of *O. keta* was sensitive to temporal changes
 236 in rainfall intensity, the peak population density of *O. masou masou* was delayed until 3
 237 days after the flood. We presume that this temporal increase in *O. masou masou*

238 population density was influenced by two factors: evacuation to flow refugia and
 239 acquisition of *O. keta* eggs as food. Tributaries have been considered as flow refugia for
 240 fishes (Koizumi et al. 2013); thus, some juvenile *O. masou masou* may migrate to
 241 spring-fed tributaries to avoid floods. However, the study reach is located 500 m
 242 upstream of the confluence of the tributary and the mainstem; this distance may be too
 243 long for such evacuations. Makiguchi et al. (2009) reported that a related species, *O.*
 244 *masou formosanus*, endured a massive typhoon event, which induced a 3-m water level
 245 increase, by remaining within their original habitats in the mainstem. Therefore, the
 246 moderate flood observed in this study may not have been a major driver of fish
 247 evacuation to the spring-fed tributary.

248 The eggs of anadromous salmon species are a significant and nutritious food
 249 resource for freshwater fishes (Armstrong et al. 2013; Koshino et al. 2013; Bailey et al.
 250 2019). This food resource is likely targeted by juvenile *O. masou masou* accumulating
 251 in the spring-fed tributary. Our gut content analysis indicated that there were
 252 significantly more salmon eggs in the spring-fed tributary than in the adjacent
 253 non-spring-fed tributary, where *O. keta* rarely migrates. The time lag between the
 254 population density peaks of *O. keta* and *O. masou masou* may be attributable to
 255 differences in their swimming abilities and/or the detection of egg production cues by *O.*
 256 *masou masou*, perhaps related to the timing of *O. keta* sperm release and downward
 257 dispersion. Because the present study lacks information on the redd distribution of *O.*
 258 *keta* in the study streams before and after the rainfall event, whether the consumed eggs
 259 by *O. masou masou* were spawned after the rainfall event or not was unknown.
 260 Grasping the redd distribution can help explain the plausible process proposed here
 261 more clearly.

Both spring-fed streams and upwelling water habitats function as spawning habitats for *O. keta* (Kobayashi 1968; Milligan et al. 1984; Geist et al. 2011); accumulation of *O. keta* in such habitats can occur during floods (Banks 1969). In this study, we directly observed upward migration of *O. keta* into the spring-fed tributary due to its stable flow regime. Our results indicate that the ecosystem functions of spring-fed streams, with respect to the formation of a unique habitat with stable temperature, provide mature *O. keta* with a suitable habitat and, in turn, provide other species with marine-derived food resources. Interspecific interactions with juvenile *O. masou masou* also occur in such habitats in spring. Thus, it is crucial to evaluate community dynamics in river networks in spatiotemporally heterogeneous environments (Armstrong et al. 2013). A robust sampling design with replications for tributaries and rainfall events, lacked in this study, can unravel the ecosystem function of heterogeneous river networks more clearly. The findings of the present study highlight the importance of enhancing spatiotemporal heterogeneity in spring-fed habitats to maintain interspecific interactions, which have implications for freshwater biodiversity and resource management in river networks.

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361

Table 1 Mean $\pm$ 1 standard deviation of environmental variables in the spring-fed and non-spring-fed tributaries.

Variable	Spring-fed tributary			Non-spring-fed tributary		
	Mean	$\pm$	SD	Mean	$\pm$	SD
Stream width (m)	4.07	$\pm$	0.25	5.13	$\pm$	0.91
Water depth (cm)	15.02	$\pm$	3.60	16.64	$\pm$	4.99
Current velocity (cm/s)	12.43	$\pm$	7.09	23.72	$\pm$	10.35
Fine sediment deposition (%)*	80.63	$\pm$	9.81	22.50	$\pm$	15.92

*cover of fine sediment (< 2 mm) on streambed estimated using the method in Sakai et al. (2013).

Table 2 Mean $\pm$ 1 standard deviation of dry weight (mg) of gut contents in each order and total in the spring-fed and non-spring-fed tributaries.

	Spring-fed tributary			Non-spring-fed tributary			<i>F</i>	<i>P</i>
	Mean	$\pm$	SD	Mean	$\pm$	SD		
Amphipoda	0.52	$\pm$	1.04	0.00	$\pm$	0.00	2.63	0.14
Acari	0.01	$\pm$	0.03	0.00	$\pm$	0.00	0.98	0.35
Ephemeroptera	0.86	$\pm$	2.72	0.68	$\pm$	0.68	0.05	0.82
Plecoptera	0.01	$\pm$	0.04	0.02	$\pm$	0.06	0.49	1.00
Hemiptera	0.00	$\pm$	0.00	1.78	$\pm$	3.75	7.34	0.01
Hymenoptera	0.00	$\pm$	0.00	0.56	$\pm$	1.04	9.27	0.02
Coleoptera	0.00	$\pm$	0.00	0.03	$\pm$	0.11	0.09	0.25
Trichoptera	0.27	$\pm$	1.07	1.35	$\pm$	1.03	8.44	0.01
Diptera	1.22	$\pm$	2.04	0.75	$\pm$	0.70	0.54	0.45
Salmoniformes	9.30	$\pm$	12.78	0.00	$\pm$	0.00	5.73	0.02
Total	12.18	$\pm$	13.72	5.17	$\pm$	4.56	2.72	0.10

Bold characters indicate statistically significant difference between the tributaries, according to one-way analyses of variances with permutation tests ($P < 0.05$).

373 **Figure captions**

374

375 **Fig. 1** Map and photographs of the study tributaries.

376

377 **Fig. 2** Hydrographs and water temperature data for spring-fed and non-spring-fed
378 tributaries during October 6–10, 2018. Circles indicate dates of fish collection for
379 population density estimates in the spring-fed tributary; double circle indicates the date
380 of additional fish collection in both tributaries for gut content analysis.

381

382 **Fig. 3** Temporal changes in the population density of *Oncorhynchus masou masou* and
383 *O. keta* in the spring-fed tributary. Gray band indicates the 95% confidence interval for
384 *O. masou masou*.

385

Fig. 1

Fig. 2

Fig. 3