

# Pulsed supplies of small fish facilitate short-term intraguild predation in salmon stocked streams

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## Research Article

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## Abstract

Pulsed supplies of prey organisms generally increase predator food intake. However, whether this holds true when predators and pulsed prey are in same guild (i.e., intraguild [IG] predators and prey) is unclear. IG prey may increase IG-predator food intake by providing a food source, but they may decrease food intake through competition. To test these hypotheses, we compared the food intake of white-spotted charr (*Salvelinus leucomaenis*) (IG predator) in streams that were stocked or unstocked with hatchery-reared masu salmon (*Oncorhynchus masou*) fry (IG prey) in streams in Hokkaido, Japan. One day after stocking, masu salmon fry occupied nearly 60% of the stomach contents by wet weight of white-spotted charr in stocked streams, and mean stomach content weight was six-times higher than in unstocked streams. However, predation of white-spotted charr on stocked fry was rare on other days. Acquisition of predator-avoidance behavior by stocked fry and/or a lack of accommodation by white-spotted charr to the sudden emergence of a new prey source (e.g., the charr in study sites were basically insectivorous, and their foraging behavior might have been ineffective for piscivory) may explain this time-limited intraguild predation. In days other than the first day post-stocking, food intake by white-spotted charr did not differ between stocked and unstocked streams. No effects of interspecific competition on white-spotted charr food intake were observed; this may be due to the body-size advantage of white-spotted charr and/or the low density of stocked masu-salmon fry.

## Introduction

Pulsed supplies of individuals or organs can dramatically affect recipient ecosystems by facilitating predation and competition and altering diets and food intake (Yang et al. 2008). One common example of pulsed supply is masting, in which individuals of one plant species synchronously produce large amount of seeds in the same season, and consumers (e.g., rodents) exclusively forage on the seeds in competition with other consumers (Lobo and Millar 2013; Stephens et al. 2019). Outbreaks of the desert locust (*Schistocerca gregaria*) during great migrations are another typical example: the locust swarms decrease food intake of indigenous herbivores through resource competition, while increasing the food intake of predators (Sánchez-Zapata et al. 2007).

Intraguild (IG) predation occurs when predators (IG predators) prey upon potential competitor species (IG prey) (Arim and Marquet 2004). The occurrence of intraguild predation is affected by the relative density of IG prey and of shared food resources (i.e., the total food availability for IG predators), and pulsed supplies of IG prey or of shared food resources can modify intraguild predation relationships by changing these relative densities (Chacón and Heimpel 2010). For example, Greenville et al. (2014) demonstrated that pulsed supplies of shared food resources (an outbreak of rodents) decreased predation pressure by IG predators (the dingo [*Canis dingo*]) on IG prey (the red fox [*Vulpes vulpes*] and feral cat [*Felis catus*]) in the Australian desert. The effects of a pulsed supply of IG prey, however, are likely to be more complex. Since IG prey function as both competitors and prey for IG predators, a pulsed supply of IG prey may decrease food intake and growth of IG predators through resource competition, while at the same time increasing food intake by boosting the supply of prey resources.

One example of an artificially pulsed supply of organisms is the stocking of hatchery-reared fish into natural environments to boost fisheries resources. The stocking of hatchery-reared salmonid fry, in particular, is frequently conducted in rivers inhabited by other wild salmonids. Because both hatchery-reared and wild salmonids predominantly prey upon aquatic and terrestrial invertebrates, they are often in competition for food resources (Hasegawa et al. 2018). In salmonids, both interspecific competition and competition between hatchery-reared and wild fish are density dependent (Grossman and Simon 2020; Matte et al. 2020). Interference competition, in which dominant (i.e., larger) individuals occupy profitable foraging territories, is the principle competitive mode, and exploitative competition, in which individuals scramble for food resources, are thought to occur simultaneously (Elliott 2002). If multiple salmonid species coexist in the same stream, their dietary niches will be affected by interspecific competition. Diet niche partitioning is sometimes regarded as the outcome of interspecific competition (e.g., one species mainly preys upon drifting terrestrial invertebrates, while another preys upon benthic invertebrates; Nakano et al. 1999; Mookerji et al. 2004). Although high diet-niche overlap is often indicative of intense interspecific competition (Larocque et al. 2021), it may also occur in systems where one type of food item is highly abundant, and fish prey upon them exclusively. In such systems, density-dependent competition may be lacking.

Salmonids of various body sizes also prey on fish to the extent that their gape size allows (e.g., L'Abée-Lund et al. 1992; Daly et al. 2009; Hasegawa et al. 2012). The frequency of this piscivory is determined by various factors. For example, of the three types of habitats inhabited by salmonids (riverine, lacustrine and marine habitats), the occurrence of piscivory is the lowest in riverine habitats due to the high availability of other food items such as drifting aquatic and terrestrial insects (Keeley and Grant 2001; Sánchez-Hernández 2020). Population origins (i.e., genetic backgrounds) also determine whether salmonids become piscivorous or insectivorous (Monnet et al. 2020, 2021), and the two ecotypes differ in some biological traits: for example, piscivores tend to locomote more frequently and have longer gut lengths (Monnet et al. 2020, 2021). However, Hasegawa et al. (2021) reported that riverine salmonids originating from insectivorous populations will still prey exclusively upon stocked salmon fry just after stocking (i.e., when there is an extremely high availability of stocked fry).

Therefore, streams stocked with hatchery-reared salmonid fry are ideal experimental systems in which to test hypotheses regarding intraguild predation and the pulsed supply of organisms. In this study, we conducted field surveys to test two hypotheses: (1) IG prey supplied pulse-wise will compete with IG predators, but (2) intraguild predation will mask the negative effects of competition on IG predators.

## Materials And Methods

### Study systems

A field survey was conducted in 2019 in wadeable tributaries of the Shiribetsu River in Hokkaido, northern Japan (Fig. 1). Stocking of hatchery-reared masu salmon (*Oncorhynchus masou masou*) has been conducted in the Mena River, a large tributary of the Shiribetsu River, since 1915 (Akiba 1986). In our survey year, 900,000 masu salmon fry were stocked in this tributary in total. Four stocked survey sites were established in the Mena River system to detect the effects of stocked fry (Fig. 1, Table 1). All fry stocking in these streams was conducted on 29-May. Masu salmon stocked in the preceding year were rarely observed at these sites. In addition to the four stocked sites, three control sites (no stocked fry) were established in other tributaries of the Shiribetsu River (triangle symbols in Fig. 1). In this study, the stocked fry were treated as IG prey. Potential IG predators across the seven study sites were white-spotted charr (*Salvelinus leucomaenis*), masu salmon and sculpin (*Cottus nozawae*). Of these, white-spotted charr were common to all study sites, and were therefore deemed the target IG predators. Although the white-spotted charr could have preyed on some small fish based on their gape size, they preyed predominantly on insects and did not consume any fish except for the stocked masu salmon fry (see Results). Thus, we assumed that the white-spotted charr in our study sites were of the insectivorous ecotype. Water temperatures in the study sites were typical for streams inhabited by salmonids (Table S1).

### Sampling Procedures

Sampling was conducted once prior to stocking, and at four time points after stocking (Table 1). In stocked streams, sampling was conducted on the day after stocking in late May. To capture fish, a sampler walked upward from the downstream margin of each study site while using a backpack electrofisher (Smith-Root Inc., Vancouver, WA, USA). The numbers of each fish species captured were used as indices of fish density. Although stocked fry in late May were too numerous to count, we confirmed that there were a few thousand fry at each site and that they were obviously more abundant than during other study periods.

Captured fish were anesthetized by using ethyl 3-aminobenzoate methanesulfonic acid, and their fork lengths were measured to the nearest 1 mm. Whereas there were no significant differences in the mean fork lengths of white-spotted charr between study periods or between stocked and unstocked study sites (Table S2), the mean fork lengths of stocked masu salmon fry gradually increased over time (Table S3).

After measuring the fish for fork length, we sampled the stomach contents of white-spotted charr (up to 17 individuals per study site) by gastric lavage, and of stocked fry (15 individuals per study site) by laparotomy in the laboratory. Stomach

contents and fry were immediately fixed in 70% ethanol. In the laboratory, the wet weight of each diet menu in the stomach contents was determined to the nearest 0.001 g. Diet menu were categorized as follows. All prey fish were identified as stocked masu salmon fry. Invertebrates were separated into terrestrial and aquatic invertebrates, and aquatic invertebrates were identified to the family or genus.

Except for the stocked fry from the laparotomy, captured fish were released to each study site. White-spotted charr were tagged with a banok tag at the time of release, which allowed us to evaluate growth rates by comparing fork lengths between initial and subsequent captures. In addition to the four stocked streams, charr tagging was conducted in the Chiribetsu stream (Fig. 1).

## Data analysis

Diet niche overlaps between white-spotted charr and stocked masu salmon fry were quantified by using a proportional similarity index (PS) (Feinsinger et al. 1981) for each study site where fry were stocked:

$$PS = 1 - 0.5 \sum_{i=1}^m |WC_i - MS_i|,$$

where  $WC_i$  and  $MS_i$  represent the wet-weight proportions of prey category  $i$  (of  $m$  categories) for white-spotted charr and stocked masu salmon fry, respectively. The category "other aquatic invertebrates" was excluded in this calculation. The index ranged from 0 (no overlap) to 1 (complete overlap). Temporal changes of PS were tested by using Friedman's test.

To compare stomach content weights of white-spotted charr between stocked and unstocked study sites, a linear mixed model was constructed as follows:

Stomachcontentweight = studyperiod + stocked/unstocked + studyperiod × stocked/unstocked + studysite

where stomach content weights were specified for each experimental fish. Study periods were treated as a categorical variable. Study site was a random effect.

Specific growth rates (SGRs) of recaptured charr were calculated as follows:

$$SGR = 100(\ln FL_1 - \ln FL_0)/t,$$

where  $FL_0$  and  $FL_1$  are fork length on the days of tagging and recapture, respectively, and  $t$  is the days elapsed between these procedures.

SGRs between late May and mid-June were calculated for 10 charr recaptured at study sites at which masu salmon fry were stocked and for 13 charr recaptured at sites where they were not. SGRs were compared between stocked and unstocked streams with the following linear mixed model:

$$SGR = \text{stocked/unstocked} + \text{studysite},$$

where study site was treated as a random effect.

All statistical tests were performed in SPSS version 24 (IBM Corp., Armonk, NY, USA) with  $\alpha = 0.05$ .

## Results

Whereas the number of stocked masu salmon fry caught by single-pass electrofishing gradually declined over time, the number of white-spotted charr (excluding fry) did not show a noticeable trend (Table 1). Additionally, stocked masu salmon fry vastly outnumbered white-spotted charr in stocked streams throughout the survey (Table 1). The degree of diet niche overlap in late

May was smaller than during other study periods (Friedman's test:  $df = 3$ ;  $\chi^2 = 9.96$ ,  $p = 0.019$ ) (Fig. 2). This means the diet overlap between IG predator and IG prey was smallest when the density of IG prey was highest.

The interaction term between study period and stocked/unstocked was significant for stomach-content weights of white-spotted charr (Table 2). This suggests that differences in stomach-content weight between stocked and unstocked streams varied across study periods. Although stomach-content weights for stocked streams were nearly six times larger than for unstocked streams in late May, the difference between the two stream types were not clear during other study periods (Fig. 3).

Diet items were classified into 21 categories (including "other aquatic invertebrates") (Fig. 4). In mid-May, the wet-weight percentage of aquatic invertebrates in the diets of white-spotted charr was larger than that of terrestrial invertebrates in both stocked and unstocked streams. From late May to early September (i.e., after fry stocking), the percentage of terrestrial invertebrates exceeded 60% in all streams, with the exception of stocked streams in late May. In stocked streams in late May (i.e., immediately after fry stocking), fish accounted for nearly 60% of the wet weight of white-spotted charr stomach contents in stocked streams, and all fish identified in the stomach contents were stocked masu salmon fry. In fact, 25 out of 42 white-spotted charr examined in stocked streams preyed upon at least one masu salmon fry during this period, whereas only 2 of 172 white-spotted charr did so during other study periods. As with white-spotted charr, the stomach contents of stocked masu salmon fry were mainly occupied by terrestrial invertebrates (Fig. 4). Of the aquatic invertebrates, three categories of mayfly larvae (genus *Baetis*, *Epeorus* and *Drunella*) were dominant in the benthic communities of both stocked and unstocked streams throughout the survey (Fig. S1), and they were also frequently identified in the stomach contents of masu salmon fry and white-spotted charr in both stocked and unstocked streams (Fig. 4).

Specific growth rates of white-spotted charr in stocked ( $n = 10$ , mean  $\pm$  SD =  $0.321 \pm 0.173$ ) and unstocked ( $n = 13$ ,  $0.181 \pm 0.109$ ) streams were not significantly different (Linear mixed model:  $df_{\text{numerator}} = 1$ ,  $df_{\text{denominator}} = 5.615$ ,  $F = 3.490$ ,  $p = 0.114$ ).

## Discussion

Stocked masu salmon fry are a potential competitor of white-spotted charr, as is evidenced by their similar dietary niches, which included terrestrial invertebrates and mayfly larvae. However, the consumption of stocked masu salmon fry by white-spotted charr contributed to an increase in the stomach contents of white-spotted charr. This suggests that the pulsed supply of IG prey can contribute to an increase in the food intake of IG predators, despite the simultaneous interspecific competition for food resources. However, the occurrence of intraguild predation in our study was surprisingly short term.

Even though salmonids are known to exhibit intense density-dependent competition which decrease food intake and/or growth of individuals with increasing density (Grossman and Simon 2020), the peak of stocked masu salmon fry density in late May coincided with the peak of white-spotted charr food intake in our study. Interspecific competition often drives niche partitioning in many salmonids (Nakano et al. 1999; Mookerji et al. 2004), and diet niche partitioning between white-spotted charr and stocked masu salmon was the most noticeable in late May. However, this diet niche partitioning was clearly caused by predation of white-spotted charr on stocked masu salmon fry. Thus, intraguild predation coincided with interspecific competition caused the contradiction if the food intake of white-spotted charr was interpreted based on the outcome of density-dependent competition.

The short-term occurrence of predation on stocked salmonid fry by piscivorous salmonid species has been reported in a previous study (Henderson and Letcher 2003). This short duration could indicate that stocked fry gradually acclimate to stream environments and learn predator avoidance behavior (Mirza and Chivers 2000), and may also be related to the decline in fry abundance over time. Additionally, the white-spotted charr in our study were likely generally of the insectivorous rather than piscivorous ecotype (Monnet et al. 2020, 2021). Thus, their foraging behavior may not have been effective against masu salmon fry except during the short initial period when stocked fry had not acclimated to the stream environment and were drifting downstream in search of suitable microhabitats. Thus, late May (i.e., the day after stocking) might have been the only time when the white-spotted charr could prey on stocked masu salmon fry.

Although stocked masu salmon fry made up a large proportion of the stomach contents of white-spotted charr immediately after stocking, this did not appear to contribute to white-spotted charr growth. As described above, white-spotted charr in our study system are likely to be of the insectivorous ecotype. Monnet et al. (2020) demonstrated that gut lengths of insectivorous salmonids are shorter than those of piscivorous salmonids. This suggests that the insectivorous white-spotted charr in our study are not adapted to effectively digest fish prey. In addition, the active digestive enzymes of fishes are different during insectivorous and piscivorous life stages (Colchen et al. 2020), suggesting that fish may be unable to change their active enzymes in response to rapid shifts in diet. Thus, despite their high consumption of masu salmon fry, white-spotted charr may lack the ability to effectively digest them, meaning that they are unable to convert the energy contained in masu salmon fry into growth.

After mid-June, the food intake of white-spotted charr in stocked streams was similar to that in unstocked streams. Predation was rare during this period, and stocked masu salmon fry were more likely to interact with white-spotted charr as competitors than as prey. However, the density of stocked masu salmon fry and/or the difference in food availability for white-spotted charr in stocked vs. unstocked streams may not have been enough to make an impact. Because our study focused on piscivory, white-spotted charr that were too small to prey on stocked masu salmon were not examined. These small charr are likely to have suffered a decline in food intake due to competition with stocked masu salmon fry, because competitive advantages lessen with diminishing body size (Sabo and Pauley 1997).

Our study demonstrates that pulsed supplies of IG prey can increase food intake among IG predators (through prey consumption) rather than decreasing food intake (through interspecific competition). However, any effects of IG prey on IG predator growth were not detected, likely because the IG prey were only consumed during a short period, the prey might have been difficult for the IG predators to digest, and the effects of IG competition were weak during other study periods. In contrast to previous reports, any effects of pulsed prey supply on predators was short lived. In general, prey supplied pulse-wise are not regular food items for predators (e.g., Stephens et al. 2019; Itakura et al. 2021), and predators may be unable to accommodate these prey due to mismatches in foraging behavior or digestive ability.

## Declarations

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**Conflicts of interest/Competing interests** Not applicable.

**Ethics approval** Ethics approval was not required for this study according to the national legislation. The animal law of Japan does not target as fish and invertebrates.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Availability of data** The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

**Code availability** Not applicable.

**Author's contributions** KH conceived the research, conducted fieldwork, analyzed the data and wrote the manuscript. SF collaborated the fieldwork and discussed throughout making a draft of the manuscript.

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## Tables

**Table 1.** Length and mean width measured at 10 points of each study site. Numbers of fry stocked on 29th May and fishes captured by 1-pass electrofishing for each study site and study period are shown (top: stocked masu salmon fry; bottom: white-spotted charr). In late May, the actual numbers of fry were uncountable, but more than 1000 fry were certainly captured.

Study sites	No. of fry stocked ( $\times 1000$ )	Length (m)	Mean width (m)	Number of fishes captured				
				Mid May	Late May	Mid Jun	Late Jul	Ear Sep
				← before stocking		after stocking →		
<Stocked>								
Headstream of Mena riv.	130	128	2.0	- 10	>1000 6	265 11	124 8	36 8
Gunkai stream	30	110	2.0	- 2	>1000 4	339 2	161 4	81 5
Uchiyama stream	30	65	2.0	- 3	>1000 15	117 8	96 15	67 12
Matsumura stream	30	62	2.9	- 15	>1000 17	141 26	111 22	76 16
<Unstocked>								
Shinetsu stream		179	5.2	- 5	- 13	- 14	- 14	- 12
Mumei stream		73	4.0	- 9	- 8	- 10	- 11	- 9
Torii stream		94	2.3	- 10	- 17	- 25	- 38	- 20

Footnotes: Dates for each study period were as follows: Mid May: 13 to 15-May; Late May: 29 to 31-May; Mid Jun: 18 to 20-June; Late Jul: 22 to 24-July; Ear Sep: 3 to 4-September

Table 2. The result of linear mixed model testing the effects of study periods and stocked/unstocked stream, and their interaction term on the stomach content weight of white-spotted charr.

	df <sub>numerator</sub>	df <sub>denominator</sub>	F	p
Study periods	4	329.7	11.58	<0.001
Stocked/unstocked	1	3.451	4.907	0.102
Study periods × stocked/unstocked	4	329.7	7.750	<0.001

## Figures

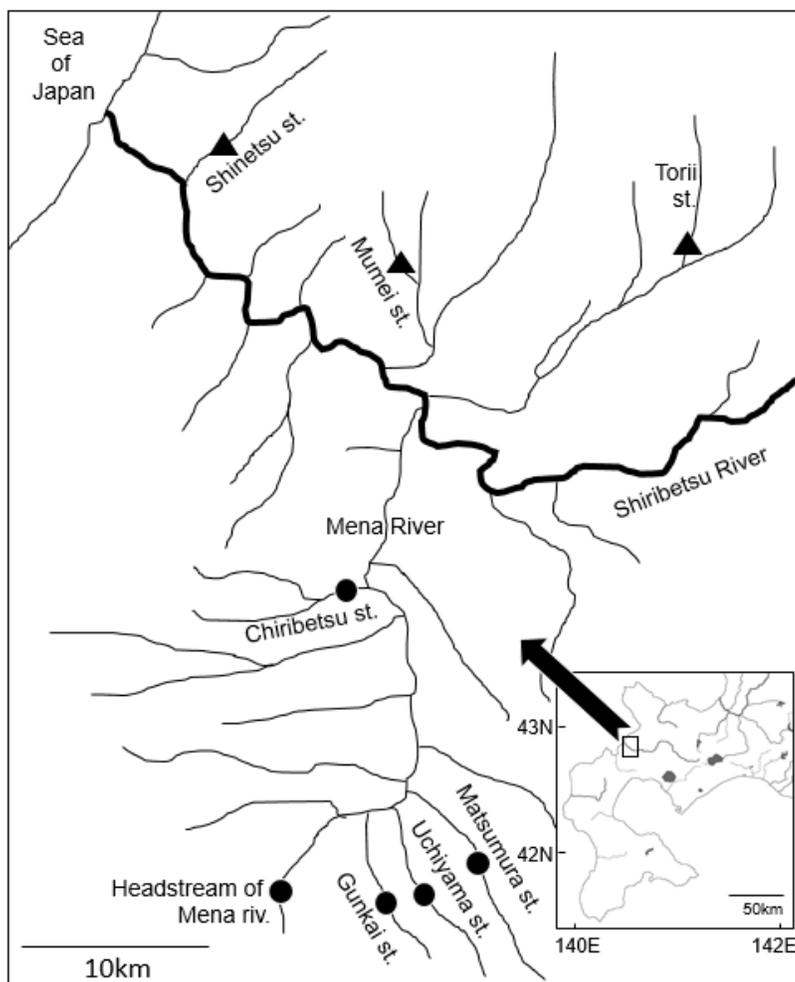
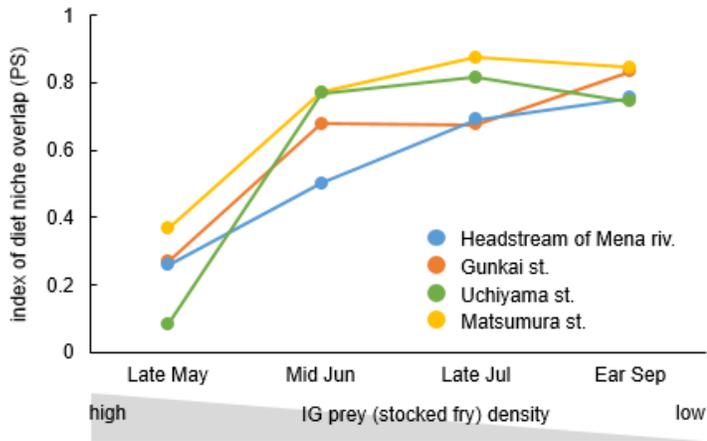


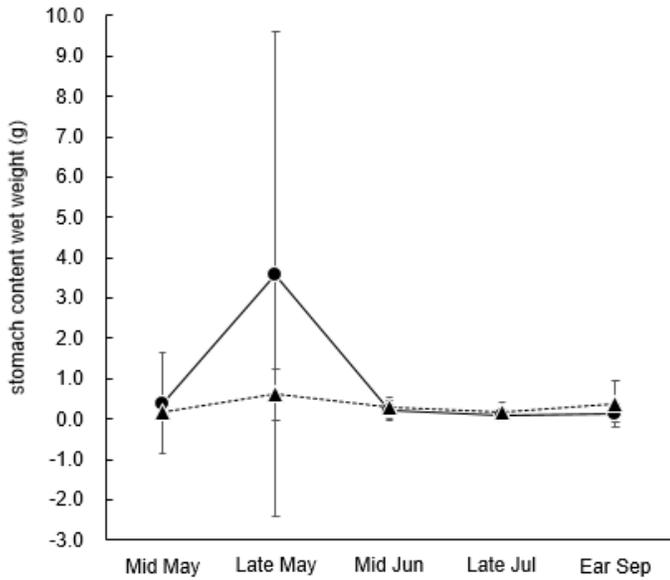
Figure 1

Locations of each study site in the Shiribetsu river system. Circles and triangles indicate study sites for stocked and unstocked streams, respectively.



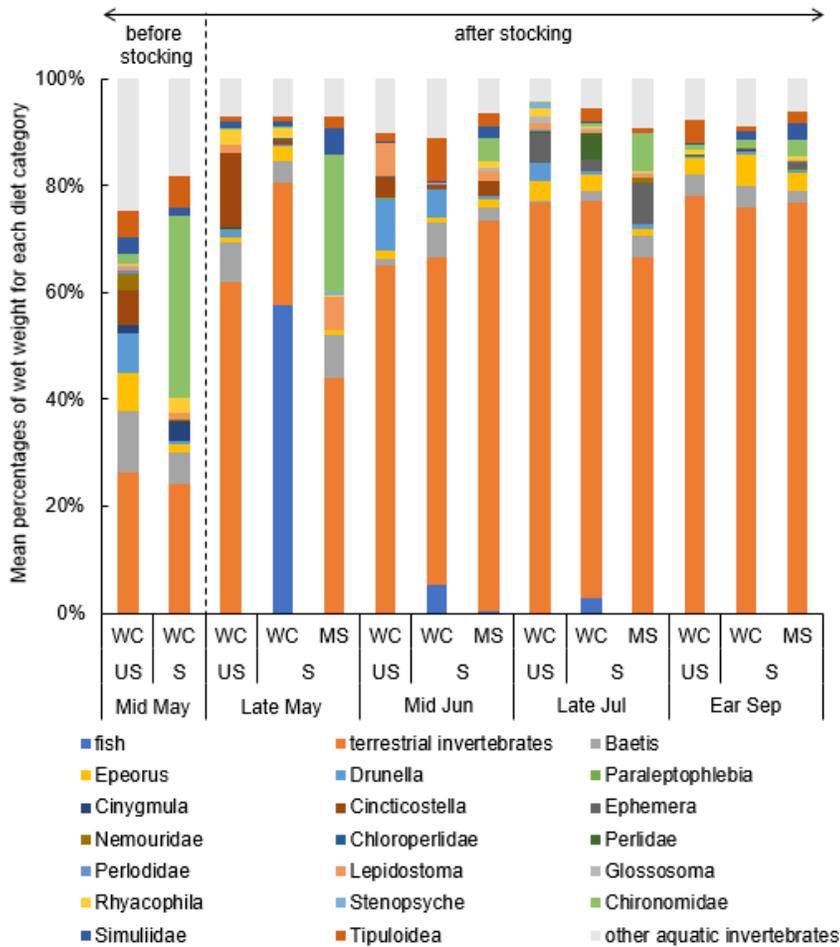
**Figure 2**

Time series of diet-niche overlap between white-spotted charr and stocked masu salmon fry as indicated by the proportional similarity index (Feinsinger et al. 1981). The grey shaded area below the horizontal axis is a conceptual representation of the decline in stocked masu salmon density over time.



**Figure 3**

Comparison of mean stomach-content wet weight of white-spotted charr between stocked and unstocked streams throughout the survey. Error bars indicate standard deviations. Sample sizes are shown in Table S2.



**Figure 4**

Mean percentages of wet weight for each diet category (see legend for category names) in the stomach contents of white-spotted charr (WC) and stocked masu salmon fry (MS) in stocked (S) and unstocked (US) streams throughout the survey. The wet weights of each diet category sampled from each experimental fish were pooled to calculate the percentages for stocked and unstocked streams. Sample sizes of white-spotted charr are shown in Table S2. For stocked masu salmon fry, there were 60 sampled fish (15 fish × 4 study sites) for each study period.

## Supplementary Files

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