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RESEARCH PAPER

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Food habit divergence between white-spotted charr and masu salmon in Japanese mountain streams: circumstantial evidence for competition

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Abstract The diet and foraging microhabitat of white-spotted charr, *Salvelinus leucomaenis*, were compared between mountain stream reaches where it occurs with (sympatric) and without (allopatric) masu salmon, *Oncorhynchus masou masou*, a potential competitor, to examine the evidence for interspecific competition between these fish, which commonly co-occur in Japanese mountain streams. In three streams examined, the similarity between the diets of allopatric charr and salmon was much greater than that between the diets of sympatric charr and salmon. Both allopatric charr and sympatric salmon intensively utilized terrestrial invertebrates among stream drifts (52%–65% of the diet), whereas this prey category made up only an intermediate portion of sympatric charr diets (11%–29%). Examination of available prey composition in stream drifts showed that the consumption of terrestrial invertebrates by allopatric charr and sympatric salmon was approximately twice as much as that by sympatric charr. The presence of salmon, a potential competitor, may alter the diet of charr in the sympatric reaches. Charr holding focal points closer to the streambed were considered less efficient than sympatric salmon in their utilization of terrestrial invertebrates drifting primarily on the stream surface, although the foraging microhabitat of the charr was not influenced by the salmon. The mechanisms responsible for the dietary divergence between sympatric charr and salmon are probably the consequence of scramble competition over terrestrial invertebrates drifting on the stream surface.

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Key words Scramble competition · Foraging microhabitat · Diet divergence · Stream salmonids · Terrestrial invertebrate

Introduction

In a number of animal guilds, co-occurring species with rather small differences in morphology have often been found to have substantial differences in resource utilization, termed resource partitioning (*sensu* Schoener 1974). Extending the notion that competition can lead to divergence in resource use by similar species, it was argued that resource partitioning provided singular evidence for the operation of competition (Schoener 1974; Diamond 1978). Accordingly, demonstration of the presence of a potential competitor altering resource use by a target species was considered strong support for the operation of competition (Thomson 1980; Wiens 1989). Experimental evidence has documented short-term changes in resource use (i.e., niche shifts) of a target species following manipulative reductions in the densities of potential competitors (Connell 1983; Schoener 1983; Hairston 1989). An alternative method of estimating competitive interactions involves comparison of resource use by a species where it occurs with (sympatry) and without (allopatry) a potential competitor (Grant 1972; Werner and Hall 1976; Dunham 1983; Schmitt and Coyer 1983). Competition is a possible explanation of resource divergence between sympatric species, if similarity between them is greater in allopatry than in sympatry.

Resource use by sympatric salmonids has often been explored within the context of resource partitioning; the approaches have often contrasted the resource use of allopatric and sympatric populations of the same species in both lentic (Nilsson 1965; Andrusak and Northcote 1971; Hindar et al. 1988; Langeland et al. 1991) and lotic systems (Hartman 1965; Glova 1986; Ishigaki 1984; see reviews by Ross 1986; Nakano and Taniguchi 1996). Overall, these studies have demonstrated that salmonids often undergo niche shifts in microhabitat and/or food resource dimensions in the presence of interacting species. Although experimental studies have demonstrated the operation of competition in resource partitioning in sympatry (Everest and Chapman 1972; Fausch and White 1981; Lohr and West 1992; Nakano et al. 1998), addressing competition from strictly nonexperimental data is generally more difficult. Ecological conditions other than the presence of a competitor probably differ between allopatric and sympatric populations and can result in altered resource use (see Holbrook and Schmitt 1989). To ensure that comparisons of such populations are meaningful, it is at least necessary to replicate these comparisons in multiple locations with different resource and habitat bases. The distribution of stream salmonids is often characterized by species replacement patterns along an altitudinal gradient; heterospecifics occur at separate locations, with both species coexisting in intermediate stretches (Vincent and Miller 1969; Rahel and Hubert 1991; Fausch et al. 1994; Taniguchi and Nakano 2000). These situations offer ideal opportunities to test for competition in resource use by comparison of allopatric and sympatric populations, which could be attempted repeatedly within a single drainage by using tributaries as replicates.

Two native species of stream salmonids, white-spotted charr (*Salvelinus leucomaenis*) and masu salmon (*Oncorhynchus masou masou*), often co-occur in streams throughout much of their geographical range along the Asian side of the North Pacific coast (Kawanabe 1989). Evidence exists that these two salmonids compete for foraging positions in pool habitats of mountain streams (Nakano 1995a). Like most other stream salmonids, both species forage almost exclusively on drifting invertebrates by ambushing them from fixed positions in the water column (Furukawa-Tanaka 1985; Nakano 1994, 1995a,b; Nakano and Furukawa-Tanaka 1994; Inoue and Nakano 1999; Nakano et al. 1999a). In stream reaches where the two species are strictly sympatric, they compete by interference for favorable foraging positions in interspecific, size-structured dominance hierarchies, which depend primarily on individual body size (Nakano 1995a). However, the influences of competitive interactions on their food resource usage have not been examined to date.

In this study, we explored food resource use by white-spotted charr in multiple tributaries of a single drainage. Although charr occurred in sympatry with masu salmon in downstream reaches, the salmon were absent upstream. First, we address whether food resource divergence exists between sympatric charr and salmon. Second, we estimate the mechanisms by which such divergence can be achieved based on comparisons of prey selectivity and foraging microhabitats between allopatric and sympatric populations.

Fish distribution and study area

Fluvial white-spotted charr and masu salmon are distributed either sympatrically or allopatrically throughout most tributaries of the Takahara River basin, a headwater drainage of the Jinzu River system discharging into the Sea of Japan from central Honshu, Japan (Nakano 1995a; Nakano et al. 1996). The abundance of charr and salmon aged one year or older was estimated from single underwater visual counts on one day along each of 73 100-m stream reaches during May to August 1987 (Fig. 1). These age classes, with a fork length (FL) of 9 cm or longer, were easily distinguished from age 0 (FL < 5 cm) during the survey period. The densities of the two species varied among the surveyed reaches, being generally higher in tributaries than in a main stem. The distributions of the species were replaced along altitudinal gradients, charr primarily occupying headwater reaches and salmon extending downstream to the lowermost reaches of the river. Intermediate reaches were characterized by sympatric populations of the two salmonids. We did not conduct research in downstream reaches, the main stem of the Takahara River, because other populations of *O. masou* are released into the main stem. The percentages of charr in the sympatric reaches were surveyed in the Atotsu Stream (mean ± SD, 44% ± 32%; $n = 10$), Sugoroku Stream (36% ± 29, $n = 6$), and Shimosa Stream (29% ± 12, $n = 4$).

Field study on food resource use was conducted during summers in 1987–1989 in three third-order headwater tributaries, the Atotsu, Sugoroku, and Shimosa streams, running through the Hida Mountains (Fig. 1). In all three tributaries, both salmon and charr were sympatric in the downstream reaches, whereas only charr occurred in the headwaters. All of the tributaries were typical mountain streams with stepped-bed morphology and with stream beds composed mainly of gravel, cobbles, and boulders, although the size factor varied among the study reaches (Table 1). The riparian zones of the streams were vegetated by natural deciduous forest, with patches of planted coniferous trees only in the downstream reaches. Water temperatures (12°–16°C; Table 1), which were measured randomly during the fish sampling periods between 05.00 and 19.00 h, were near the preferred range for both species (see Mayama 1992; Takami et al. 1996). A small number of other fish species were observed in the downstream, sympatric reaches: sculpin (*Cottus pollux*) and loach (*Niwaella delicata*) in both the Sugoroku and the Shimosa streams, and these two species together with minnow (*Phoxinus lagowski steindachneri*) in the Atotsu Stream. However, in headwater reaches, only charr occurred.

Methods

Fish and stream drift sampling

In the three streams, six study reaches were surveyed for both fish sampling (thick lines in Fig. 1) and observation of fish foraging microhabitat (asterisks in Fig. 1). The two selected reaches of each stream corresponded to an allopatric and a sympatric reach. Within the region of fish density estimation, we chose these reaches as the site for reducing the impact of artificial constuctions, anglers, and releases of fish (*O. masou*) into the main stem of the Takahara River.

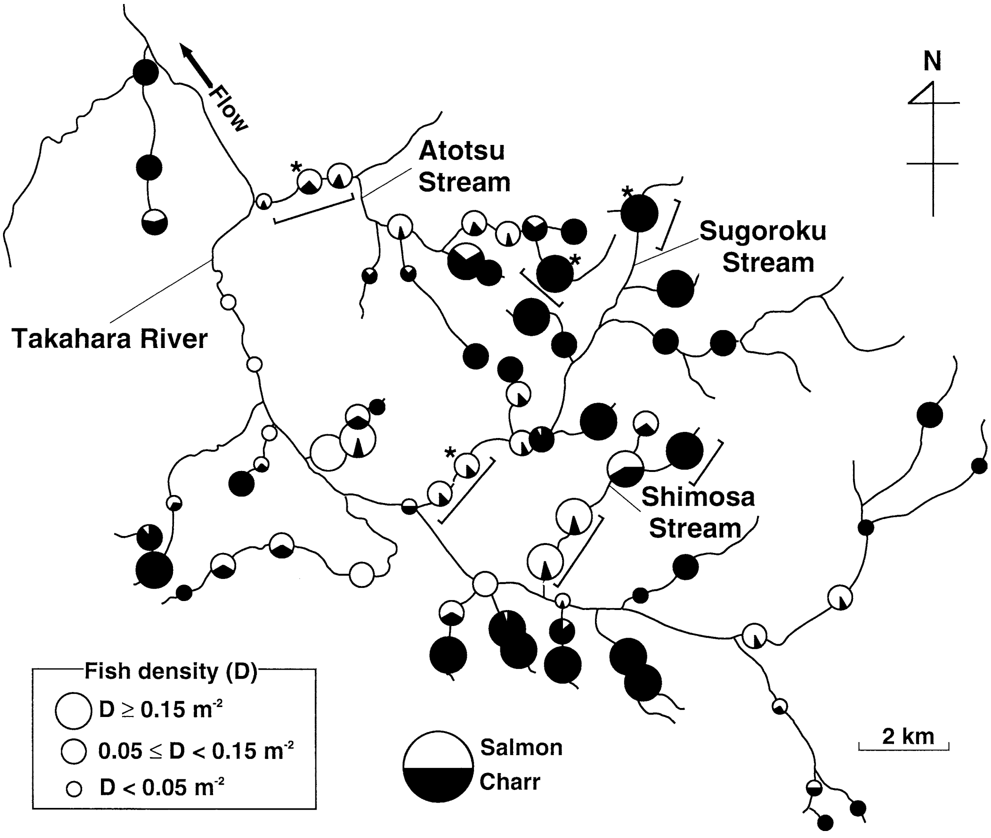

Fig. 1. Map of the study area showing the distributions and densities of white-spotted charr and masu salmon in the Takahara River drainage in central Japan. *Asterisks* represent study reaches where fish foraging microhabitat was observed. *Thick lines* along streams indicate fish sampling reaches

Table 1. Fish body sizes and habitat characteristics of study reaches in the allopatric and sympatric reaches of the Atotsu, Sugoroku, and Shimosa streams[a]

Stream	Fish category	Species	Fish fork length (cm)	Stream width (m)	Water temperature (°C)	Maximum pool depth (cm)	Stream depth[b] (cm)
Atotsu	Allopatry	Charr	14.5 ± 3.6 (20)	4.2 ± 1.7 (10)	14.8 ± 2.8 (10)	42 ± 27 (10)	34 ± 21 (41)
	Sympatry	Charr	16.0 ± 3.3 (34)	10.5 ± 5.8 (10)	13.9 ± 1.9 (10)	64 ± 33 (10)	49 ± 15 (53)
		Salmon	13.8 ± 3.2 (45)				
Shimosa	Allopatry	Charr	15.8 ± 2.7 (23)	5.4 ± 3.0 (10)	13.5 ± 2.0 (10)	42 ± 18 (10)	
	Sympatry	Charr	16.3 ± 2.9 (45)	7.7 ± 2.6 (10)	14.1 ± 2.2 (10)	67 ± 17 (10)	
		Salmon	14.6 ± 3.7 (31)				
Sugoroku	Allopatry	Charr	16.0 ± 2.2 (57)	6.2 ± 2.3 (10)	13.8 ± 1.8 (10)	72 ± 12 (10)	68 ± 33 (68)
	Sympatry	Charr	19.1 ± 2.8 (31)	18.0 ± 4.4 (10)	14.1 ± 3.5 (10)	95 ± 9 (10)	84 ± 33 (80)
		Salmon	19.2 ± 3.6 (26)				

[a] Values are means ± 1 SD (sample number)

[b] Stream depth was measured at the same location as the fish microhabitat observation

Representative fish specimens were captured within an approximately 1-km-long segment of the allopatric reach and a 2-km-long segment of the sympatric reach of the Atotsu Stream during August 1987, the Sugoroku Stream during June to August 1988, and the Shimosa Stream during July and August 1989, with reaches intended for microhabitat observations (see below) excluded from fish removal sampling (Fig. 1). The specimens were collected randomly by both angling and spearing between 05.00 and 19.00 h during 2- to 7-day periods at each site. On average, 35 individuals of each species were captured in each study reach (312 total), measured (FL to the nearest 1 mm), and had their stomachs removed and immediately preserved in 10% buffered formalin solution.

The body size (FL) of captured fishes in the each tributary differed among the fish categories according to one-way analysis of variance (ANOVA) (Atotsu, $F_{2,96} = 4.24$, $P = 0.017$; Sugoroku, $F_{2,111} = 19.93$, $P < 0.001$; Shimosa, $F_{2,96} = 3.88$, $P = 0.045$; Fig. 1). In both the Atotsu and Shimosa streams, the body size of salmon was significantly smaller than that of sympatric charr ($P < 0.041$ for both by the Scheffé test), with no significant differences for other combinations ($P > 0.266$ for all). The body size of allopatric charr was significantly smaller than that of sympatric charr and salmon ($P < 0.001$ for both), with no significant difference between sympatric charr and salmon in the Sugoroku Stream ($P = 0.994$).

Drifting invertebrates, which are potential food resources for both salmon and charr, were assessed in the fish sampling reaches in the sympatric reach of the Atotsu Stream on 13 and 14 August and in the allopatric reach on 9 and 10 August 1987. We could not collect drift invertebrate samples exactly in both the Sugoroku and the Shimosa streams because of flooding caused by typhoons and muddy water following river improvements. Therefore we excluded drift invertebrate data from the two streams from this study. In each reach, drift nets of 400-μm polyester mesh (20 cm by 20 cm opening, 60 cm long) were set at the surface and bottom layers of five randomly chosen pools (10 nets total) for 30 min, three times between 05.00 and 19.00 h on each sampling day (120 samples total). To estimate the biomass of drifting invertebrates, water velocities were measured at the net openings with a portable current meter (Model-CR7, Cosmo-Riken, Kashihara, Japan). Drift samples were preserved in 5% buffered formalin until they were analyzed.

Observation of foraging microhabitats

Fish microhabitat use was observed underwater during the daytime (05.00–19.00 h) in single study reaches, in which both allopatric and sympatric fish population densities were surveyed in the Atotsu and Sugoroku streams during August 1987 and July and August 1998, respectively (Fig. 1). Both fish species were typical drift foragers, holding focal points in the stream flow and intercepting food items in the drift, with only occasional feeding attempts on the substrate (Nakano 1995b). An observer moved upstream from the lowermost end of the observation reaches, recording the positions of focal points and the distance between the substrate and the fish snout (hereafter called the focal point height) to the nearest 1 cm by reference to a handheld ruler for most of the fish aged one year or more (i.e., >9 cm FL) encountered. The focal point position for each fish was marked with a colored sinker. Immediately following completion of the underwater observations in each study reach, the current velocity at the focal point (focal point velocity) was measured for each marked focal point using the above-described current meter. Subsequently, the stream depth at the focal point was measured to the nearest 1 cm (Table 1). In each study reach, the observations were made three times on different days, during which the habitat variables of 83 focal points on average were recorded for each species (496 total).

Sample analyses

Terrestrial and aquatic invertebrates in both stomach contents and stream drift samples were identified to order and family, respectively, using a binocular microscope, with aquatic insect adults being categorized as terrestrial invertebrates. The biomass of each of 32 invertebrate categories was measured as wet mass (nearest 0.01 mg) after blotting for 10 s. Larvae and adults of terrestrial insects were considered separately. The dry mass (after drying at 60°C for 24 h) of random subsamples was measured (nearest 0.01 mg) for each category, and the wet mass thereafter was converted to dry mass for both stomach contents and stream drift samples (see Nakano et al. 1999c).

The biomass of drifting invertebrates ($\mathrm{mg\,m^{-3}}$) was calculated for each category by dividing the total estimated dry mass of invertebrates retained in each net by the water volume sieved. The percentage of dry mass contributed by each prey category was determined for each drift net and averaged for each layer for each sampling site, with data from the five pools being combined. The percentage of dry mass contributed by each prey category was determined for each individual fish and averaged for each species for each sampling site. For all of the analyses, all terrestrial orders were combined, and minor aquatic invertebrate families were grouped into orders.

Overlap between allopatric or sympatric charr and salmon in diet composition (by dry mass) was quantified by using a proportional similarity index (Feinsinger et al. 1981):

$$\mathrm{PS} = 1 - 0.5\sum_{i=1}^{m}\left|p_i - q_i\right|$$

where p_i and q_i are the proportions (dry mass) of prey category i in groups p and q, respectively. The index ranged from 0 (no overlap) to 1 (complete overlap).

The important contribution of terrestrial invertebrates to the diet of salmonids has been well documented in many forested headwater streams, where this prey category often comprises more than 50% of such diets during the summer (Furukawa-Tanaka 1985; Wipfli 1997; Nakano et al. 1999a,b,c). Moreover, the use of terrestrial prey has often been considered as a critical element of food resource partitioning in stream salmonid guilds in summer (Nakano et al. 1992, 1999a; Nakano and Kaeriyama 1995; Nakano 1999). Thus, the overall selectivity of terrestrial invertebrates was calculated for individual fish captured in the Atotsu Stream and averaged for each species at each sampling site. Manly's index (Chesson 1978) was used as a measure of prey selectivity:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j},\ i = 1,\ldots,m$$

where r_i and n_i are the proportions by dry mass of prey category i occurring in stomach contents and stream drift, respectively. The index, which ranges from 0 (prey never eaten) to 1 (only one prey category eaten), removes bias resulting from the different availability of prey categories.

All statistical tests were two-tailed. Log_{10} transformations for exact values and arcsine-square-root transformations for percentages were conducted in order to standardize variances and improve normality, to satisfy the assumption of ANOVAs. For any ANOVA models, multiple comparisons using Scheffé tests were conducted after one-way ANOVAs when necessary. For all these tests, the alpha level was set at 0.05, although reduced alpha levels ($P = 0.05/n$, where n is the number of pairwise comparisons) were employed to correct for experimental error.

Results

Prey availability

The taxonomic composition of drift prey varied between the surface and bottom layers in the water column, with the percentage of terrestrial invertebrates at the surface being much higher than at the bottom (Fig. 2). We excluded two prey categories, heptageniid nymphs and lepidostomatid larvae, from statistical analyses, because the categories were hardly found in the bottom layers of the allopatric reach. Two-way multivariate analysis of variance (MANOVA) (factor = layer; bottom vs surface, reach; allopatry vs sympatry) on six testable prey categories revealed significant layer ($F_{6,\ 116} = 11.51$, $P < 0.001$) and reach ($F_{6,\ 116} = 11.13$, $P < 0.001$) effects, but no interaction effects ($F_{6,\ 116} = 0.69$, $P = 0.660$). Separate one-way ANOVAs on each prey category, after a significant difference was found by one-way MANOVA ($F_{8,\ 118} = 11.82$, $P < 0.001$), showed that the percentage of terrestrial invertebrates ($F_{1,\ 123} = 59.68$, $P < 0.001$; reduced alpha level [0.008 = 0.050/6] was used here) in the surface drifts was significantly higher than in the bottom layers. In contrast, the percentage of baetid nymphs ($F_{2,\ 123} = 7.74$, $P = 0.006$) in the bottom layer was significantly higher than in the surface layer, with no significant difference in any other prey categories ($F_{1,\ 123} < 4.41$, $P > 0.038$ for all of the remaining four). However, no significant differences between the sympatric and allopatric reaches were encountered in the percentages of terrestrial invertebrates ($F_{1,\ 123} = 0.30$, $P = 0.586$) by separate ANOVAs after a significant MANOVA result ($F_{8,\ 118} = 12.07$, $P < 0.001$), although the percentages of two other prey categories in the allopatric reaches were significantly higher than those in the sympatric reaches (dipteran larvae, $F_{2,\ 123} = 31.48$, $P < 0.001$; plecopteran larvae, $F_{2,\ 123} = 14.06$, $P < 0.001$).

Diet variation

The composition of the diet differed considerably between white-spotted charr and masu salmon in sympatric reaches, whereas the dietary difference between sympatric salmon and allopatric charr was rather minor. In particular, the utilization of terrestrial invertebrates in the diets of both allopatric charr and sympatric salmon was approximately twice as great as that in the diet of sympatric charr (Fig. 3). The overall diet composition differed significantly by dry mass, both between streams (Atotsu vs. Sugoroku vs. Shimosa streams; two-way MANOVA on eight testable prey categories: $F_{16,\ 590} = 4.82$, $P < 0.001$) and fish categories (allopatric charr vs. sympatric charr vs. sympatric salmon; $F_{16,\ 590} = 8.66$, $P < 0.001$), with a significant interaction effect ($F_{32,\ 1178} = 3.47$, $P < 0.001$). The results of subsequent one-way MANOVA for each stream showed that the dietary composition differed significantly among fish categories in the Atotsu ($F_{16,\ 176} = 3.04$, $P < 0.001$), Sugoroku ($F_{16,\ 176} = 9.50$, $P < 0.001$), and Shimosa streams ($F_{16,\ 176} = 5.61$, $P < 0.001$). However, the similarities in dietary composition between sympatric salmon and charr (PS = 0.60 in Atotsu, 0.67 in Sugoroku, and 0.64 in Shimosa streams) were significantly lower than those between the salmon and allopatric charr (0.85 in Atotsu, 0.77 in Sugoroku, and 0.87 in Shimosa streams; $z = 1.96$, $P < 0.05$ by Mann-Whitney U-test).

A large portion (52%–65%) of the diets of both sympatric salmon and allopatric charr was composed of terrestrial invertebrates, whereas this prey category generally made up only an intermediate portion (11%–29%) of the sympatric charr diets in any of the three streams (Fig. 3).

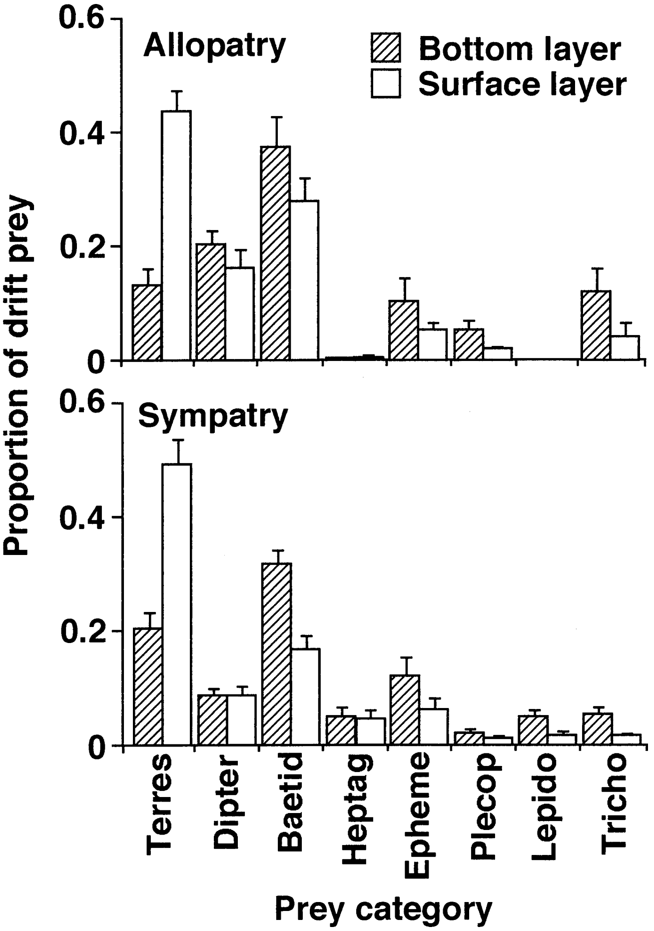

Fig. 2. Differences in drift composition according to dry mass (mean ± 1SE) between bottom and surface layers of the water column in allopatric and sympatric reaches of the Atotsu Stream. *Terres*, terrestrial invertebrates; *Dipter*, Dipteran larvae; *Baetid*, baetid nymphs; *Heptag*, heptageniid nymphs; *Epheme*, other ephemeropteran nymphs; *Plecop*, plecopteran larvae; *Lepido*, lepidostomatid larvae; *Tricho*, other trichopteran larvae

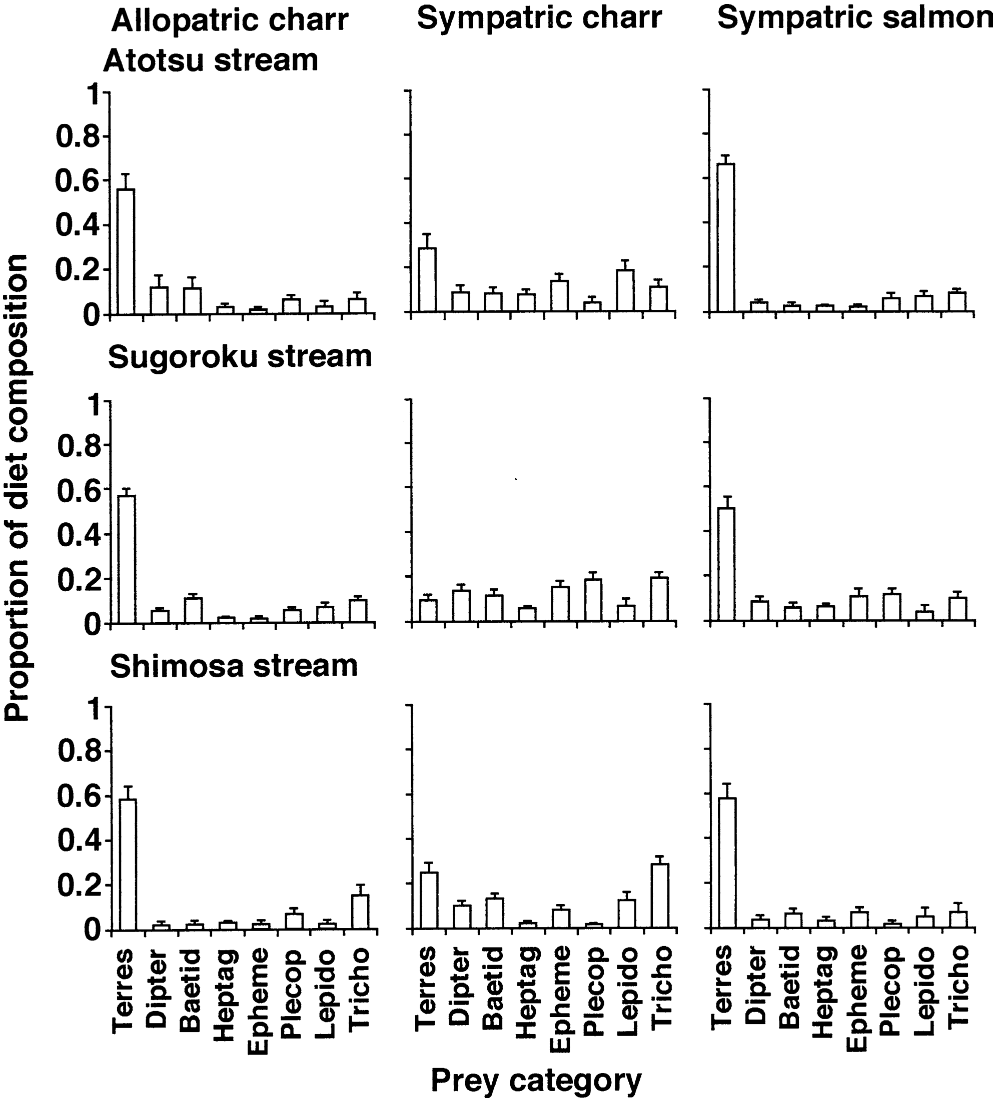

Fig. 3. Differences in diet composition by dry mass (mean ± 1SE) among allopatric and sympatric charr and sympatric salmon sampled in the Atotsu, Sugoroku, and Shimosa streams. See Fig. 2 for abbreviations of invertebrate taxon names

One-way ANOVAs, carried out separately for each prey category, showed significant differences between the fish categories in the percentage of terrestrial invertebrates in the Atotsu ($F_{2, 96}$ = 13.48, $P < 0.001$; a reduced alpha level [0.006 = 0.050/8] was used here), Sugoroku ($F_{2, 180}$ = 10.06, $P < 0.001$), and Shimosa streams ($F_{2, 96}$ = 13.76, $P < 0.001$). Both sympatric salmon and allopatric charr consumed more terrestrial invertebrates than did sympatric charr in any of the streams ($P < 0.008$ for all by Scheffé tests), with no significant difference between the sympatric salmon and the allopatric charr ($P > 0.125$ for all). In addition to terrestrial invertebrates, significant differences in the percentages of aquatic prey categories were also evident among the fish categories in the Atotsu (other ephemeropteran nymphs, $F_{2, 96}$ = 9.09, $P < 0.001$; lepidostomatid larvae, $F_{2, 96}$ = 6.21, P = 0.003), Sugoroku (other ephemeropteran nymphs, $F_{2, 180}$ = 8.19, $P < 0.001$; dipteran larvae, $F_{2, 180}$ = 6.78, P = 0.001), and Shimosa streams (baetid nymph, $F_{2, 96}$ = 7.05, P = 0.001; plecopteran larvae, $F_{2, 96}$ = 14.01, $P < 0.001$).

Selectivity for terrestrial invertebrates significantly differed among the fish categories in the Atotsu stream ($F_{2, 95}$ = 16.40, $P < 0.001$). Those for allopatric charr (0.67 ± 0.07 [1SE]) and sympatric salmon (0.77 ± 0.04) were both significantly greater than for sympatric charr (0.35 ± 0.07; P = 0.001 and $P < 0.001$, respectively, by Scheffé tests), with no significant difference between the allopatric charr and the sympatric salmon (P = 0.443). No significant differences in selectivities for eight aquatic prey categories were found among the fish categories in each of the streams ($P > 0.326$ for all).

Foraging microhabitat

Focal point velocities differed considerably between salmon and charr, irrespective of the stream or the presence of a potential competitor (Fig. 4). Two-way ANOVA (factor = stream; Atotsu vs Sugoroku vs Shimosa streams, fish category; allopatric charr vs sympatric charr vs sympatric

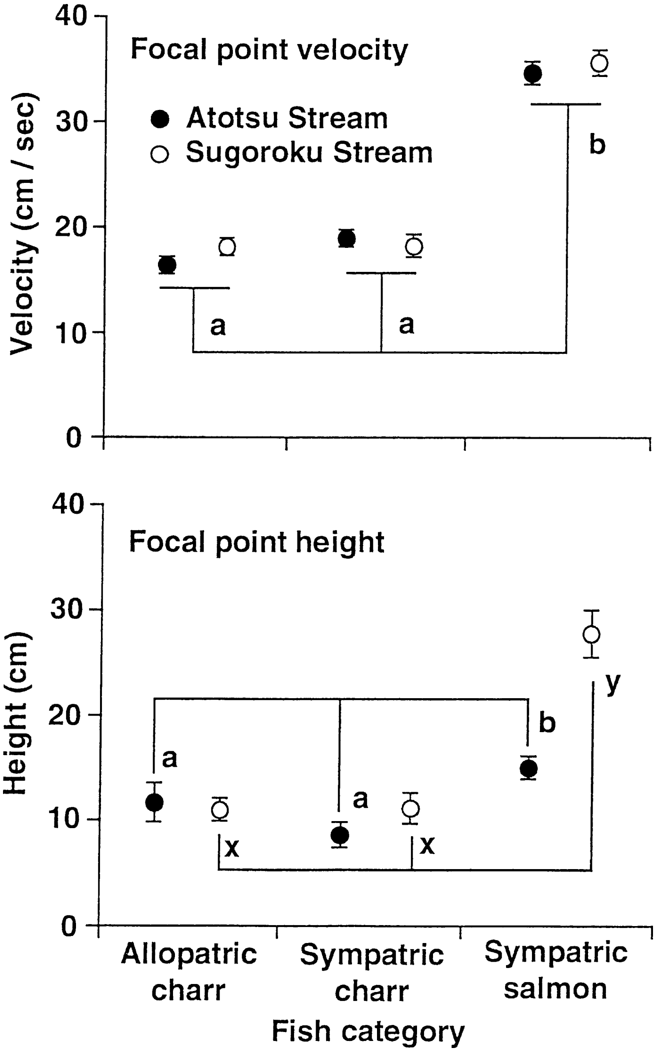

Fig. 4. Differences in focal point velocity and height (mean ± 1SE) among allopatric and sympatric charr and sympatric salmon observed in the Atotsu and Sugoroku streams. Differences in letters denote statistically significant differences (alpha level of 0.05) based on the Scheffé test

salmon) revealed a significant effect of fish category ($F_{2,490} = 212.76$, $P < 0.001$), but no significant stream effect ($F_{1,490} = 1.11$, $P = 0.292$) or interaction effect ($F_{2,490} = 2.38$, $P = 0.094$) on focal point velocity. Subsequent one-way ANOVA on the combined streams again found a significant effect of fish category on focal point velocity ($F_{2,\ 493} = 224.14$, $P < 0.001$). The focal point velocity of salmon (30–40 cm s^{-1}) was approximately twice that of charr (15–20 cm s^{-1}) in both allopatric and sympatric reaches ($P < 0.001$ for both by Scheffé tests; Fig. 4), although there was no significant difference between allopatric and sympatric charr ($P = 0.249$).

Focal point height differed according to both fish category and stream (Fig. 4). Two-way ANOVA (factor = stream, fish category) revealed that fish category ($F_{2,490} = 63.33$, $P < 0.001$), stream ($F_{1,490} = 26.06$, $P < 0.001$) and their interaction effect ($F_{2,490} = 6.86$, $P = 0.001$) were both significant, with the focal point height of fish in the Atotsu Stream being significantly lower than that in the Sugoroku Stream. Subsequent one-way ANOVA, considering the streams separately, found a significant effect of fish category in both the Atotsu ($F_{2,\ 307} = 22.54$, $P < 0.001$) and the Sugoroku streams ($F_{2,\ 183} = 46.00$, $P < 0.001$); in both of these streams, the focal point height of salmon was significantly greater than that of both allopatric (Atotsu, $P < 0.001$; Sugoroku, $P < 0.001$ by Scheffé tests) and sympatric charr (Atotsu, $P < 0.001$; Sugoroku, $P < 0.001$; Fig. 4). However, the focal point height of allopatric and sympatric charr did not differ significantly in either the Atotsu ($P = 0.265$) or the Sugoroku stream ($P = 0.988$).

Discussion

In all three tributaries examined, the dietary similarity of allopatric white-spotted charr to masu salmon was greater than that of sympatric charr. The major difference in diet between allopatric and sympatric populations of charr was due to shifts in terrestrial invertebrate use across the tributaries, although the contribution of some aquatic insect taxa also varied between the two populations in each tributary. Both sympatric salmon and allopatric charr exploited terrestrial stream drift invertebrates most intensively among the eight prey categories, whereas that the contribution of terrestrial invertebrates to the diet of sympatric charr was less than that of two other fish populations in all tributaries. Such food-resource divergence between sympatric species has been found in several stream salmonid systems and is considered circumstantial evidence for the operation of interspecific competition (Nakano et al. 1992, 1999a; Nakano and Furukawa-Tanaka 1994; Nakano and Kaeriyama 1995; see review by Nakano and Taniguchi 1996). However, in order to satisfy the conditions necessary for acceptance of a competition explanation, it is still necessary to show that the sympatry-allopatry variation in the charr diets indeed reflected the presence of salmon, but neither resource nor habitat bases. We here attempt to delineate environmental conditions that alternatively explain the dietary variation between allopatric and sympatric charr.

One potential null hypothesis is that the relative availability of terrestrial invertebrates varied between the allopatric and sympatric reaches, and that the observed differences in the charr diets simply reflected sampling from different resource bases in each of the tributaries. However, no difference was found in terrestrial invertebrate availability between the areas of charr sympatry and allopatry in the Atotsu Stream, where the available prey composition in the stream drifts was examined simultaneously. In addition, a significant difference, which remained after the variation due to dissimilar resource bases was removed, existed in the diets of sympatric and allopatric charr. The selectivity of allopatric charr for terrestrial invertebrates was much greater than that of sympatric charr, being closer to that of masu salmon located separately downstream. The potential effects of varying availability of prey could be ameliorated by using the selectivity index, which does not change with prey availability unless accompanied by changes in foraging behavior or microhabitat changes (Chesson 1978; Schmitt and Coyer 1983). Therefore, the difference in selectivity for terrestrial invertebrates is consistent with the predictions of competition.

Variation in habitat properties of stream channels between allopatric and sympatric charr populations, but not the presence of masu salmon, may simply alter the availability of terrestrial invertebrates for charr. The focal point height and velocity of both allopatric and sympatric charr were much lower than those of salmon, although the microhabitat variables were not altered by the presence of sympatric salmon (see also Nakano 1995a). Current velocity, in particular, is regarded as one of the most important components of microhabitat variables for drift-foraging fishes in the water column, because the drift foragers face a tradeoff between an increasing energy cost of swimming and increasing drift prey supply with velocity (Fausch 1984; Hill and Grossman 1993). The difference in foraging microhabitat, therefore, could be largely a species-specific feature, being determined primarily by physiology rather than by the effects of competition (Nakano 1995a, Nakano et al. 1998). In some stream-dwelling salmonids, the target species occupied similar microhabitats both when alone and when the other species was present (e.g., Baltz and Moyle 1984, *Salmo gairdneri* and *Catostomus occidentalis*; Dolloff and Reeves 1990, *O. Kisutch* and *S. malma*; Nakano et al. 1992, *S. confluentus* and *O. clarki lewisi*). In addition, terrestrial invertebrates supplied from riparian canopies occurred primarily in the surface layer of the stream flow in both allopatric and sympatric reaches of the Atotsu Stream (see also Furukawa-Tanaka 1992). Since the downstream sympatric reaches were generally deeper than the headwater allopatric reaches in each tributary, the lower focal point height of charr might simply have led to less efficiency compared with salmon in foraging on such surface drift prey. However, despite the fact that the sympatric reaches of both the Atotsu (64 cm in mean maximum pool depth, Table 1) and Shimosa streams (67 cm) were shallower than the allopatric reaches of the Sugoroku Stream (72 cm), the proportion of terrestrial invertebrates in the charr diets in the sympatric reaches (29% in the Atotsu and 24% in the Shimosa stream, Fig. 3) were much lower than in the allopatric reaches (58% in the Sugoroku Stream). Although we did not examine stream drifts in the Sugoroku and Shimosa streams, a difference in stream depth by itself could not explain such allopatric–sympatric variations in the charr diet. Thus, we contend that the circumstantial evidence supports the presence of a potential sympatric competitor (salmon) altering the food resource use of charr.

Nakano (1995a), who studied aggressive interactions and foraging behavior of sympatric white-spotted charr and masu salmon in the Atotsu Stream, reported that fishes within a single pool formed an interspecific, size-structured dominance hierarchy. In the hierarchy, dominance depends almost entirely on body size, although salmon achieved relative superiority over similarly sized charr. The study also found that dominant individuals of both species held focal points at the location that ensured priority of access to drift prey, the foraging territories being maintained against both subordinate conspecifics and heterospecifics. Thus, superiority in interference interactions is an important factor in achieving higher foraging return, by selective exploitation of profitable prey in the stream drifts (see Nakano 1995b). The average body size of salmon, however, was rather smaller than that of sympatric charr in both the Atotsu and the Shimosa streams, and nearly equal to that of the sympatric charr in the Sugoroku Stream. Considering the results of the comparison of body size between the two species, the clear dietary niche shift of sympatric charr, which resulted in food resource divergence between the species, cannot be explained clearly by interference competition. We will try to explain this niche shift of sympatric charr by another competition theory, scramble competition over drift prey in the surface layer, i.e., terrestrial invertebrates. To describe both the behavioral process and the ecological outcome of intraspecific competition, Nicolson (1954) interestingly defined a scramble as the kind of competition exhibited by a crowd of boys striving to secure broadcast sweets. In this study, terrestrial invertebrates, corresponding to broadcast sweets defined by Nicolson, are often preferred over aquatic prey by drift-foraging fishes, because terrestrial prey generally have greater individual body size than aquatic prey and thus provide greater energy intake efficiency for the consumer (Nakano et al. 1999b). Taking the explanation of the scramble competition, the different focal points of the two salmonids operate the efficiency in the acquisition of the drift prey in the surface layer. Within sympatric reaches, salmon, which held focal points higher from the bottom than those of charr, would have an advantage in the acquisition of terrestrial invertebrates, irrespective of the consequences in body size of the two species. Even if the salmon is not regarded as being competitively superior in interference interactions, we could understand the mechanisms responsible for the charr niche shift according to the outcomes in scramble interactions. Because salmonids in a temperate forested stream have been estimated to consume >50% of the terrestrial invertebrate input (Kawaguchi and Nakano 2001), scramble competition over these prey items would be operative in resource partitioning among sympatric stream salmonids. We argue, therefore, that spatial heterogeneity in food-resource distribution in the water column alters the apparent outcome of competition between salmonid species varying in preferred foraging microhabitat, even within small-scale habitats such as streams.

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