Influences of microhabitat use and foraging mode similarities on intra- and interspecific aggressive interactions in a size-structured stream fish assemblage

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Abstract Aggressive interactions, foraging behaviour and microhabitat use were observed among four sympatric stream fishes inhabiting the water column: ayu (*Plecoglossus altivelis*), white-spotted charr (*Salvelinus leucomaenis*), masu salmon (*Oncorhynchus masou*) and Japanese dace (*Tribolodon hakonensis*), each species being categorised into five body-size classes (species-size groups; SSG's). Aggressive interactions were observed between most pairs of SSG's, an almost linear dominance order being apparent throughout the three-month study period. Ayu were relatively subordinate in June, but became the second most dominant in July and the most dominant in August, as a consequence of a reversal in dominance order with salmon. In contrast, smaller-sized dace, which continually suffered from intra- and interspecific aggression, occupied the most subordinate ranks throughout the study period. Intensive aggression was observed among various SSG's, exhibiting same microhabitat propensity throughout the three months. The direction and frequency of aggressive interactions varied month by month due to a reversal in dominance order between ayu and masu salmon, and/or changes in density, body size and resource use of the component members. Opponent selectivity was higher within SSG's, where resource use was assumed to be highly overlapping, rather than among SSG's throughout the study period. Correlation analysis indicated that opponent selectivity in aggressive interactions among SSG's was positively correlated with similarity in microhabitat selectivity in June, but not in other months or with that in foraging habits, suggesting that intensive aggressive behaviour reflected overlapping habitat use among assemblage members during a certain period.

Key words. — Interference; dominance hierarchy; body size; intra- and interspecific interactions.

Most interspecific aggression involves competition for some overlapping limited resource, such as food or space (Drickamer and Vessey, 1992). Although many studies to date have reported interspecific aggressive interactions in stream-dwelling fishes, most of these have dealt only with morphologically and ecologically similar, closely-related species, wherein competition for both space and food is expected to be intense (e.g. Newman, 1956; Fausch and White, 1986; Hearn, 1987; Katano, 1994; Nakano and Furukawa-Tanaka, 1994; Nakano, 1995a). However, aggressive interactions have also been observed among taxonomically distant species in both marine and lentic environments, if resource demands are largely overlapping (Low, 1971; Ebersole, 1977; Williams, 1979; Hori, 1987; Kohda, 1991). In reality, many distantly-related species also coexist in streams, attempting simultaneously to exploit the same resource or to partition alternative ones. Nevertheless, few studies have addressed interspecific aggression with reference to resource use patterns in lotic environments (but see Symons, 1976; Reeves et al., 1987).

Resource use by fishes varies according to their ontogenetic stage (Werner and Gilliam, 1984). In a structured population (sensu Mittelbach and Osenberg, 1993), in which individuals are separated into ecologically distinct life history stages, the intensity of interspecific interference may change due to differences in resource demands, and therefore, the degree of overlap between species at each growth stage. Moreover, the direction and influence of such interference are likely to shift between species, according to the stage, since superiority in aggressive interactions between fishes is often associated with relative body size (Fausch, 1984; Grant, 1990; Huntingford et al., 1990; Nakano, 1995a). Thus, body size structure must be taken into consideration in order to understand the precise relationship between aggressive interactions and resource use. To date, no such studies have been published.

For this report, field observations were conducted on several size-classes of four fish species inhabiting the water column in a coastal stream in southern Hokkaido, Japan, to examine variability in interspecific aggression according to monthly changes in the assemblage members and to describe the relationship between aggressive interactions and microhabitat use, and foraging behaviour.

Materials and Methods

Study area

The study was conducted from June to August 1994, in an 80 m stretch of the Kokamotu Stream (41°32′N, 140°00′E), which discharges into the Sea of Japan on the north coast of Osima Peninsula, southern Hokkaido, Japan. The study reach, located approximately 300 m upstream from the river mouth, was 5–15 m wide and included three pools and two low-gradient riffles. The streambed was composed mainly of cobbles and pebbles, with small areas of exposed bedrock. The riparian vegetation was grass (*Miscanthus sinensis* and *Zizania latifolia*). Stream discharge was measured in the study reach three to five times monthly using the U.S. Geological Survey midsection method (Orth, 1983). The average water discharge was 3.8 m^3/sec in June, 2.9 m^3/sec in July and 3.7 m^3/sec in August. Stream discharge often exceeded 45 m^3/sec, some 16 times the summer base flow, during heavy precipitation (>20 mm/day). Water temperature, recorded four or five times monthly with a maximum-minimum mercury thermometer, also varied; 12.0–18.3°C in June, 16.0–23.7°C in July and 18.8–24.0°C in August.

The entire study reach was divided into 1 m×1 m grids by placing painted cobbles at the grid intersections on the streambed. The grid squares were re-established every month due to substrate movement caused by flood, so the total water surface area covered by the grid differed from month to month due to changes in the water surface area and shape of the stream; 145 m^2 in June, 215 m^2 in July and 230 m^2 in August.

Fish assemblage

The four fish species studied included: ayu (*Plecoglossus altivelis*), white-spotted charr (*Salvelinus leucomaenis*), masu salmon (*Oncorhynchus masou*) and Japanese dace (*Tribolodon hakonensis*). The ayu is amphidromous, with a 1-year life cycle (Kawanabe and Mizuno, 1989). The remaining species have anadromous life cycles, and include both stream residual and sea-run types in their populations (Kawanabe and Mizuno, 1989). Ayu are herbivorous, grazing on stones (Kawanabe and Mizuno, 1989), charr and salmon intercept drifting organisms or take benthic invertebrates (Nakano, 1995a), and dace exhibit omnivorous feeding habits, consuming a wide range of both plant and animal material (Mizuno et al., 1958; Nakamura, 1969).

Movements of various size classes of each fish species (species-size group: see below) and growth of the assemblage members were examined in the same reach during the same study period (Usio and Nakano, in press). Growth, immigration, emigration and/or mortality were evident in all the species, such factors shaping the body size structure of the fish assemblage.

In addition to the four species inhabiting the water column, the stream also included five benthic fishes; floating goby (*Chaenogobius urotaenia*), striped-floating goby (*Chaenogobius* sp.), common freshwater goby (*Rhinogobius* sp.), flathead goby (*Luciogobius guttatus*) and river sculpin (*Cottus hangiongensis*), which were excluded from the present study because of the difficulty of direct observations due to their cryptic habits. Sea-run salmon and charr, seen only rarely in the study reach, were also omitted from the study.

Observations of fish behaviour

Underwater observations of fish behaviour were carried out from 7:00–19:00 h for a four- or five-day period every month. The standard length of each fish was estimated to the nearest 10 mm underwater by reference to a nearby ruler. Errors in the length estimates were within 5% in the pilot trials (N=50: maximum error estimates were±10 mm of SL). Each species was subsequently classified into five size classes (hereafter termed species-size group; SSG): 1, standard length≤40 mm (SS); 2, 50–90 mm (S); 3, 100–140 mm (M); 4, 150–190 mm (L); 5, ≥200 mm (LL). Each SSG was treated separately for each month when analyzed. During the course of the study, 26 SSG's, 13 in June, 7 in July and 6 in August, were recognised in the study reach.

The observers lay motionless in an upstream direction at the downstream end of each pool or riffle, and waited for at least 5 min until fish had resumed normal activities. The focal animal observation method (Altmann, 1974) was adopted; a focal individual was randomly chosen and observed for 3 min, during which all foraging and aggressive acts were recorded. In each month, 150 to 200 individuals were observed, a total of 507 observations being made during the study. Since we were not able to trace all individuals for 3 min, individuals observed for at least 1 min (112 [22%]) were also included in the analysis. Prior to and after the behavioural observations, the position of the focal individual was recorded to assess microhabitat use of each SSG. Foraging behaviour was classified into four categories (see Usio and Nakano, in press): 1, nipping filamentous algae; 2, grazing unicellular algae; 3, intercepting drifting invertebrates in the water column; and 4, picking or sucking benthic invertebrates. Since fish were rarely observed to jump out of the water to catch flying insects, instances of such behaviour were included in drift foraging. After several observations had been made at one location, the observers moved slowly upstream to repeat the procedure.

The number of individuals in each SSG was counted from the downstream to the upstream end of the study reach once or twice daily, usually before and/or after daily behavioural observations (see census data in Usio and Nakano, in press). Sixteen surveys were made during the overall study period. SSG's of monthly mean densities less than $0.005/m^2$ were omitted from the present analysis.

Microhabitats

Water depth and current velocity, measured with a portable current meter (cf. Tanida et al., 1985) at 0.6 of the depth below the water surface, were measured at each corner of the quadrat. Substrate types were classified by eyes as follows by a modified Wentworth scale after Power and Stewart (1987): sand (mineral particles<2 mm in diameter), pebbles (2–64 mm), cobbles (65–256 mm), boulders (>256 mm) and bedrock (fixed rock formations). Mud was not seen in the study site. The contribution of each substrate category in each quadrat was visually estimated to the nearest 10%. Values of 1 to 5 were allocated to the five substrate types, as in Bain et al. (1985): sand=1, pebbles=2, cobbles=3, boulders=4 and bedrock=5. The substrate score, as an index of substrate coarseness, was calculated for each quadrat by the following formula:

$$S=\sum_{i=1}^{5} n_i \cdot P_i \qquad (1)$$

where n_i and P_i are the allocated point and proportion of the substrate type i in the quadrat, respectively.

The mean water depth and current velocity at the four corners of the quadrat, and the substrate score, were used to represent the microhabitat characteristics of each quadrat.

Aggressive interactions and dominance hierarchy

If a fish exhibited aggression towards another individual, forcing the latter to flee or stop foraging, it was regarded as an effective attack. Such attacks included charge, chase and lateral displays (see Noakes, 1980). All other contacts were recorded as ineffective aggression. A dominance hierarchy among SSG's was constructed from the record of effective aggressive attacks, after Katano (1990). Although each SSG did not interact with all others, the dominance order could be determined in sequence using this method, unless a SSG neither attacked nor was attacked by others.

Data analysis

Similarity of foraging habits was evaluated between each pair of SSG's by a niche overlap index (Colwell and Futuyma, 1971):

$$C_{ih}=1-1/2\sum_{j}\left|P_{ij}-P_{hj}\right| \qquad (2)$$

where P_{ij} and P_{hj} are proportions of foraging mode j exhibited by SSG i and h, respectively.

The composition of microhabitats characterised by the three variables, mean depth, mean current velocity and substrate score varied significantly during the study period (MANOVA: Hotelling-Lawley Trace= 0.348, $F_{6,1168}=33.892$, $p=0.0001$). Therefore, the three variables were subjected to k-means cluster analysis (PROC FASTCLUS: SAS Institute, 1989) with the data for different months being separately treated. The FASTCLUS procedure performs a disjoint cluster analysis on the basis of Euclidean distances computed from one or more quantitative variables (SAS Institute, 1989). A set of points, called 'cluster seeds,' is selected as a first guess of the cluster means. Each observation is assigned to the nearest seed to form temporary clusters and the process repeated until no further changes occur in the latter (SAS Institute, 1989). Since PROC FASTCLUS is sensitive to outliers, care was taken to prevent outliers from being included in the seeds; 20 clusters were specified as initial seeds without iteration (max iteration=0), in which clusters with five or fewer observations were deleted as being regarded as outliers, and the remaining cluster means used as the seeds for the subsequent FASTCLUS analysis designating four clusters. Finally, the deleted outliers were assigned to the clusters. In the present study, the cells (145 in June, 215 in July and 230 in August) were classified into four microhabitat types separately for each month (Table 1). Microhabitats were characterised by the combination of three variable states: water depth (Shallow, Moderate or Deep), current velocity (Calm, Moderate or Rapid) and substrate coarseness (Fine, Moderate or Coarse). For example, microhabitats with shallow, calm and fine substrate attributes were named SCF, after the initials.

Preference for each microhabitat type was evaluated by Manly's index (Chesson, 1983) for each SSG:

$$\alpha_i = (r_i/n_i)/\left(\sum_{j=1}^{m} r_j/n_j\right), \quad i=1, \cdots, m \qquad (3)$$

where r_i and n_i are the proportions of microhabitat i used by the SSG and present in the study site, respectively. This index removes bias introduced by differences in availability of microhabitats (Chesson, 1983). Preference for a microhabitat ranges from 0 (no aggression) to +1 (complete concentration on that microhabitat). Random use $= 1/m$, where m is the number of microhabitats; in this case, $\alpha_i=0.25$ indicates random use. Similarity of microhabitat preference between each pair of SSG's was evaluated by the niche overlap index (Formula 2) using Manly's index values.

Manly's index (Formula 3) was used as a measure of opponent selectivity, where r_i is the proportion of aggression exhibited against SSG i and n_i is the proportion of SSG i in the assemblage. Random attacks (α_i) were 0.08 in June, 0.14 in July and 0.17 in August.

The relationship between opponent selectivity and similarity in foraging habits, and microhabitat use between SSG's were examined with correlation analysis. Of the two possible directions between every pair of SSG's, the higher opponent selectivity values were used for the correlation analysis, the lower values being discarded. Aggressive interactions within each SSG were excluded in the present analysis.

Data were checked for normality and homogeneity of variances when performing parametric tests. To meet these criteria, absolute numbers were $\log_{10}(x+1)$ or square-root transformed and relative frequencies were arcsin-square-root transformed (Sokal and

Table 1. Stream habitat variables of four microhabitats classified by k-means cluster analysis (PROC FASTCLUS; SAS Institute, 1989) (see text) from June to August 1994 in the Kokamotu Stream

	Microhabitats	n	Water depth (cm)	Current velocity (cm/s)	Substrate (score)
June	SCM	63	26.76±0.79	19.51±1.96	2.24±0.05
	MCF	30	46.94±1.54	18.45±2.15	1.64±0.07
	MRC	31	40.41±2.32	38.77±4.82	3.76±0.13
	DMM	21	78.66±1.27	21.96±2.30	2.24±0.12
July	SCM	75	26.59±1.04	13.17±0.70	2.36±0.03
	MMM	65	52.73±0.98	29.30±1.05	2.28±0.03
	MRC	15	47.69±1.47	31.02±1.12	3.78±0.07
	DMM	60	61.83±1.18	28.36±1.14	2.71±0.03
August	SMM	74	25.97±0.62	33.96±0.70	2.50±0.02
	MCM	69	38.50±1.06	26.44±0.61	2.66±0.02
	MMM	67	38.27±1.07	33.59±0.55	2.15±0.02
	MRM	20	37.23±2.60	48.10±1.53	2.76±0.06

Microhabitats were characterised by the combination of three variable states: water depth (Shallow, Moderate or Deep), current velocity (Calm, Moderate or Rapid) and substrate coarseness (Fine, Moderate or Coarse); for example, SCM=Shallow-Calm-Moderate. Note that microhabitats characterised by the same abbreviations in different months are treated separately. Data are mean±1 SE. n=sample size.

Rohlf, 1981). When normality and homoscedasticity could not be obtained by such data transformations, nonparametric tests were used. All statistical tests were two-tailed. In all cases, statistical significance was evaluated at $p<0.05$.

Results

A concurrent study documented the movement, mortality and/or growth of the assemblage members during the same period (see fig. 1; Usio and Nakano, in press). All sized groups of charr, SS-salmon and SS-, L- and LL-dace disappeared, while L-ayu appeared from June to July. Subsequently S-ayu disappeared from July to August. Moreover, the monthly mean density of M-ayu increased from June to July and decreased in August, whereas S-salmon increased continually from June to August. On the other hand, M-dace decreased as the months proceeded. As a result of the movement and/or mortality, the total fish density decreased significantly from June to August (Kruskal-Wallis ANOVA: $H=11.765$, $p=0.0028$; see Fig. 1).

Among SSG's, which were observed throughout the three months, foraging habits of S- and M-dace

Table 2. Microhabitat selectivity (Manly's α) of each species-size group (SSG) from June to August 1994 in the Kokamotu Stream

	SSG	n	Microhabitat selectivity			
			SCM	MCF	MRC	DMM
June	S-Ayu	37	0.074	0.346	0.284	0.296
	M-Ayu	11	0.512	0.063	0.245	0.181
	S-Charr	12	0.073	0.153	0.665	0.109
	M-Charr	33	0.244	0.027	0.575	0.154
	L-Charr	7	0.633	—	0.367	—
	SS-Salmon	10	0.272	—	0.184	0.544
	S-Salmon	34	0.072	0.275	0.582	0.072
	M-Salmon	12	0.126	0.332	0.257	0.285
	SS-Dace	9	0.375	0.473	0.152	—
	S-Dace	46	0.262	0.147	0.408	0.183
	M-Dace	19	0.437	0.344	—	0.219
	L-Dace	6	0.659	0.173	0.168	—
	LL-Dace	4	1.000	—	—	—
			SCM	MMM	MRC	DMM
July	S-Ayu	20	0.095	0.361	0.136	0.408
	M-Ayu	41	0.072	0.321	0.258	0.348
	L-Ayu	6	—	0.735	—	0.265
	S-Salmon	35	0.254	0.188	0.254	0.305
	M-Salmon	5	—	0.356	0.515	0.129
	S-Dace	40	0.107	0.221	0.384	0.288
	M-Dace	18	0.050	0.546	—	0.404
			SMM	MCM	MMM	MRM
August	M-Ayu	27	0.142	0.278	0.143	0.437
	L-Ayu	12	0.605	0.216	0.178	—
	S-Salmon	42	0.210	0.398	0.244	0.148
	M-Salmon	12	0.197	—	0.073	0.730
	S-Dace	65	0.383	0.164	0.169	0.283
	M-Dace	6	0.514	0.138	0.189	0.159

n=sample size. See Table 1 for abbreviations of microhabitats.

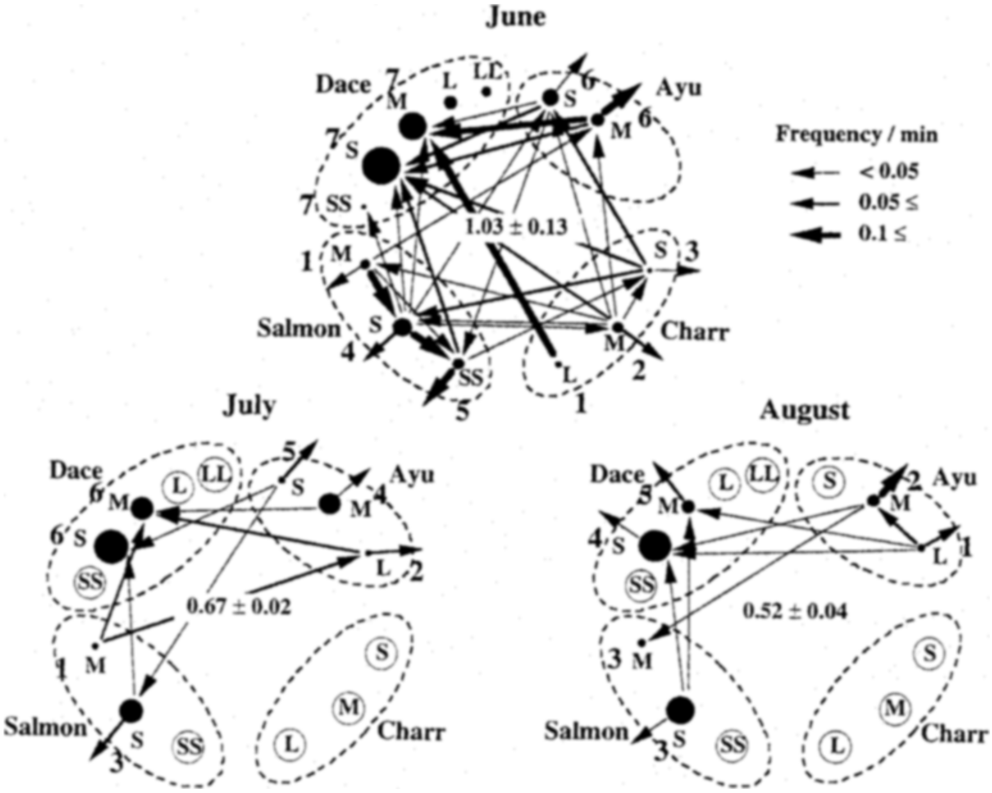

Fig. 1. Monthly mean frequencies (per min) of aggressive interactions among and within (indicated by arrows pointed outwards) species-size groups. Relative monthly mean densities of species-size groups were calculated from Usio and Nakano (in press), shown by solid circles with each species delimited by dotted ellipses. Species-size groups, which were observed in previous month(s) but not the month figured, are indicated by open circles. The total fish density (mean±SE) for each month is shown at the centre of each diagram. The dominance hierarchy among species-size groups are indicated by numbers from 1 (most dominant) to 7. Species-size groups of unknown dominance rank have no numbers.

varied month by month (MANOVA: S-dace, Hotelling-Lawley Trace=0.235, $F_{8,264}=3.879$, $p=0.0002$; M-dace, Hotelling-Lawley Trace=0.601, $F_{8,72}=2.702$, $p=0.012$; see table 2 in Usio and Nakano [in press] for original data). In both SSG's, propensities to drift foraging were relatively high in July, whereas those to benthos foraging declined as the month proceeded. Both SSG's exhibited much algae nipping behaviour in August compared to the former two months. In contrast, M-ayu and S- and M-salmon maintained unchanging foraging habits throughout the overall study period (MANOVA: M-ayu, Hotelling-Lawley Trace=0.043, $F_{4,148}=0.800$, $p=0.527$; S-salmon, Hotelling-Lawley Trace=0.020, $F_{4,190}=0.473$, $p=0.756$; M-salmon, Hotelling-Lawley Trace=0.244, $F_{4,42}=1.279$, $p=0.294$), the former exclusively grazing algae while S- and M-salmon spent most time on drift foraging. Excepting the above five SSG's, others appeared to only temporarily exhibit either specialized (e.g. S-ayu) or generalized (e.g. L-dace) foraging habits.

In contrast to foraging behaviour, most SSG's were microhabitat generalists in June and July, exhibiting selectivity towards more than one microhabitat, whereas four out of six SSG's were microhabitat specialists in August, exhibiting high selectivity towards only one microhabitat (Table 2). The most popular and unpopular microhabitats among SSG's in June were shallow (SCM) and deep (DMM) microhabitats, respectively, whereas the order was reversed in July, most SSG's preferring deep (DMM) microhabitats. In August, shallow (SMM) microhabitats were again highly selected for by SSG's.

Aggressive interactions were observed both among and within SSG's. A dominance hierarchy was constructed for each month based on the results of effective attacks (Fig. 1). The most dominant SSG's changed during the three-month period. L-charr and M-salmon were the two most dominant SSG's in June. In July, M-salmon remained in the most domi-

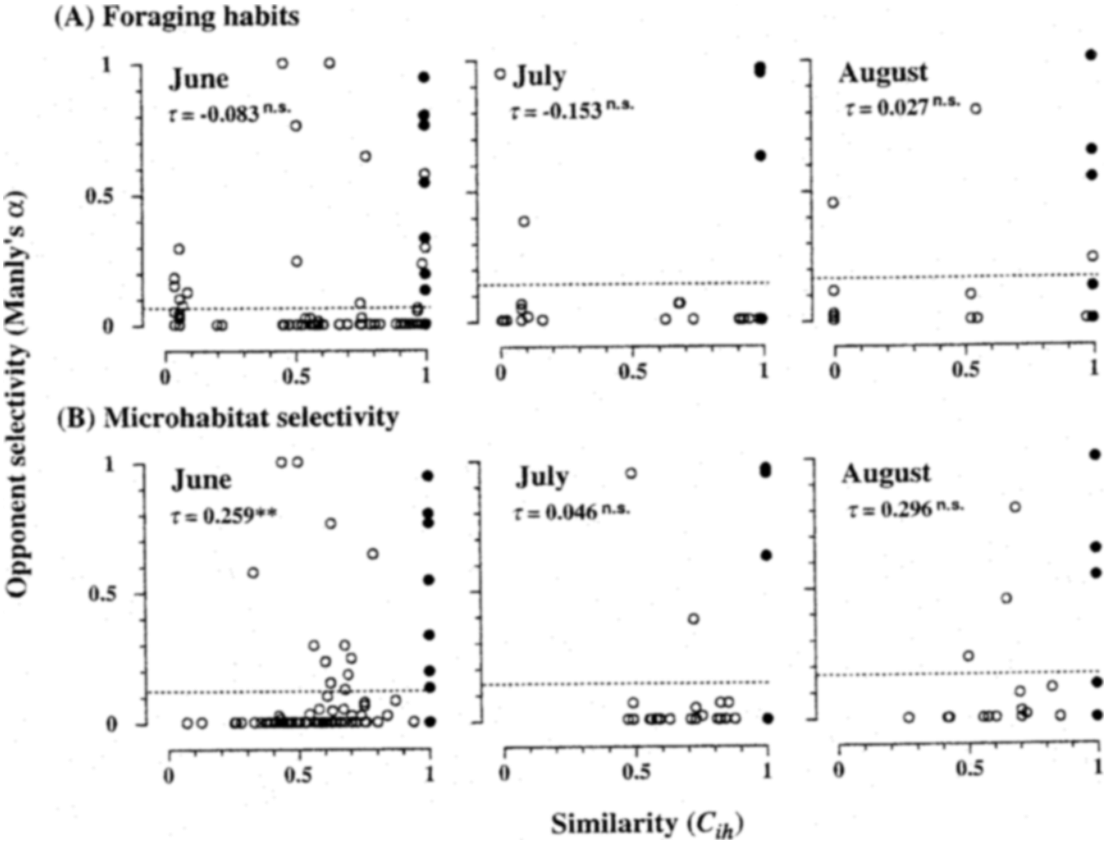

Fig. 2. Relationship between opponent selectivity in aggressive interactions (Manly's α; Chesson, 1983) and similarity (C_{ih}; Colwell and Futuyma, 1971) of (A) foraging habits and (B) microhabitat selectivity (Manly's α), between and within species-size groups, shown by open circles and solid circles, respectively. C_{ih} within SSG's was assumed as 1. Dotted lines indicate random attacks. $^{**}p<0.01$; n.s.=not significant.

nant position, whereas L-charr disappeared due to emigration or mortality (Usio and Nakano, in press). Finally, in August, L-ayu occupied the most dominant rank. The most subordinate rank was usually occupied by smaller-sized (SS, S and/or M) dace. On the other hand, the ranks of larger-sized (L and LL) dace could not be assessed, since they rarely initiated or received attacks. Next to smaller-sized dace, S- and M-ayu were ranked the second lowest in June. However, as ayu reached L-size, in July, that group became the second most dominant, finally becoming the most dominant in August. As a consequence of the monthly changes in rank of ayu, a reversal in dominance order occurred between salmon and ayu. In June, S- and M-ayu were subordinate to SS-salmon. In July, however, only L-ayu were attacked by M-salmon. Finally in August, M-salmon, which was the most dominant group in June and July became subordinate to M- and L-ayu. As a result, no ayu size groups were recipients of aggression from any other SSG's of different species. In contrast, S- and M-dace continually suffered aggression from other groups during the three-month period.

The direction and frequency of aggressive interactions varied markedly among the three months (Fig. 1). In particular, aggressive interactions were frequently initiated from L-charr to M-dace, M-ayu to M-dace, M-salmon to S-salmon and S-salmon to SS-salmon in June; from L-ayu to M-dace, and M-salmon to M-dace and L-ayu in July; and from L-ayu to M-ayu in August. Most of these SSG's exhibited either high selectivity towards same microhabitats and foraging habits or solely the former (Table 2). For example, L-charr and M-dace both preferred microhabitat SCM in June, and M-salmon and M-dace showed a high preference for microhabitat MMM in July.

To examine the relationship between opponent selectivity and foraging similarity, and microhabitat preference, correlation analyses were made for each month (Fig. 2). Significant relationship was detected against microhabitat selectivity in June but not in the later two months (Kendall's rank correlation; June: $\tau=0.259$, $p=0.003$; July: $\tau=0.046$, $p=0.799$; August: $\tau=0.296$, $p=0.285$). On the other hand, there was no correlation between opponent selectivity and foraging similarity in any month (June: $\tau=-0.083$, $p=0.347$; July: $\tau=-0.156$, $p=0.382$; August: $\tau=0.027$, $p=0.906$). The mean opponent selectivity within and among SSG's differed significantly in each month with higher values being evident in the former (Wilcoxon rank-sum test; June: $Z=2.141$, $p=0.032$; July: $Z=2.043$, $p=0.041$; August: $Z=2.311$, $p=0.021$).

Discussion

Aggressive interactions were observed between every pair of species in the present study, with almost all the SSG's being ranked in sequence. Previous studies have documented that salmonid size-structured dominance order is often established among con- and/or hetero-specific individuals (Newman, 1956; Elliott, 1990; Grant, 1990; Nakano, 1994, 1995a, b). All size classes in the two salmonids observed in the present study were ranked according to their body size, regardless of the species identity, thereby supporting the previous findings.

In cyprinids, aggressive behaviour has been reported in chubs (Katano, 1985, 1990, 1994), in which dominance order is established in sequence with body size (Katano, 1985, 1990), as found in salmonids. However, no studies have reported aggressive interactions in dace. Despite the perspective that aggression does not occur in this species because of its shoaling habit, some degrees of aggression were observed within smaller-sized (S and M) dace in August, but were never initiated towards other SSG's (Fig. 1). In contrast, dace frequently received aggression from other species. This finding was partly consistent with that of Magnan and Fitzgerald (1984), whose study of interactions between a salmonid (brook charr: *Salvelinus fontinalis*) and cyprinid (creek chub: *Semotilus atromaculatus*) showed one-sided aggression directed from the former to the latter.

Territorial ayu individuals in streams on Honsyû Island, Japan, often exhibit strong aggression towards non-territorial individuals, but only very occasionally towards other territorial conspecifics (Mizuno and Kawanabe, 1957) or other species (Iguchi, 1991). Another study reported that ayu also attack heterospecifics intensively (Miyadi, 1960). Ayu observed in the Kokamotu Stream were similar to that observed in the latter study; larger-sized (M and L) ayu intensively attacked not only smaller- and larger-sized conspecifics, but also smaller-sized (S and M) dace and M-salmon (Fig. 1).

Changes in abundance of SSG's resulted from growth, immigration, emigration and/or mortality during the study period (fig. 1; Usio and Nakano, in press). Such numerical changes in the assemblage structure consisted one of the factors that altered the direction and frequency of aggressive interactions among assemblage members in the three-month period. Another factor that changed the direction of aggressive interactions was the reversal in the dominance order between ayu and salmon. Despite occupying the same size groups, the superiority of M- and L-ayu and M-salmon was reversed between July and August. Although the reason(s) were unclear, the reversal in the dominance order was probably due to increased water temperature. Several experimental studies have addressed the reversal of superiority in interference competition between species under different water temperatures (Cunjak and Green, 1986; Glova, 1986; Reeves et al., 1987; De Staso and Rahel, 1994). Furthermore, Uchida et al. (1995) reported that within the temperature range of 10–25°C, ayu exhibit more aggressive behaviour (peaked at 23°C) as the temperature increase. In the present study, the water temperature in August (18.8–24.0°C) was probably too high for the salmon, of which the upper thermal tolerance for active feeding is approximately 18°C (Mayama, 1992). Consequently, ayu would have been advantaged.

In the present study, the opponent selectivity in aggressive interactions was significantly higher towards the same SSG's than other SSG's, possibly due to highly overlapping foraging habits and microhabitat preferences. Likewise, intense aggression towards heterospecifics is often attributed to a broad niche overlap (e.g. Low, 1971; Ebersole, 1977). Opponent selectivity, however, was not correlated with similarity of foraging habits in any months. In reality, frequent aggressive interactions were observed between herbivorous ayu and insectivorous salmon or charr. In the Kokamotu Stream, fish diets expected from observed foraging behaviour were closely consistent with digestive tract contents (Usio and Nakano, in press), suggesting that aggressive behaviour has less function in the utilization of food resource. In contrast, opponent selectivity was positively correlated with similarity of microhabitat selectivity in June, when the total fish density was the highest and intensive aggression was observed between most SSG pairs as well as within SSG's (Fig. 1). When resources are limited, fish are known to present strong competitive relationships (see reviews by Ross, 1986). Thus, microhabitat was expected to be limited among assemblage members in June, whereas in accordance with the decrease in the total fish density from June to July, intense aggression among SSG's would have been reduced in the later two months. Further experimental studies are needed to clarify the factors and mechanisms between aggressive interactions and resource use by the assemblage members.

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