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Aggressive Interactions between the Dark Chub, *Zacco temmincki*, and the Pale Chub, *Z. platypus*, in Relation to Their Feeding Behaviour

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Abstract Dark chub, *Zacco temmincki*, and pale chub, *Z. platypus*, coexisting in two rivers near Kyoto City, exhibited both intra- and interspecific aggressive behaviour. Larger individuals more frequently utilized the region near the water surface and were more dominant in both intra- and interspecific aggressive encounters than smaller ones. Both were omnivorous, although *Z. platypus* fed upon algae more frequently. The two species used similar feeding areas wherein frequent aggressive interactions occurred. The frequency of intraspecific aggressive interactions was correlated with that of algae feeding by both species. Individuals of the two species commonly occupied overlapping home ranges, but on one occasion defended a territory against all other individuals.

Several species of cyprinid fish frequently coexist in rivers and lakes of Asia (Nakamura, 1969; Miyadi et al., 1976; Winfield and Nelson, 1991). Investigations of cyprinid diets have shown most species to be omnivorous, feeding upon both algae and invertebrates (Mizuno et al., 1958; Kawanabe, 1959; Maki, 1964; Nakamura, 1969; Miyadi et al., 1976; Winfield and Nelson, 1991). However, few studies have been conducted on interspecific interactions between coexisting Asian cyprinids. Consequently, the existence or otherwise of aggressive interactions between these species are unknown, as are the mechanisms of their habitat and food utilization. Furthermore, interspecific interactions between omnivorous fishes have been poorly studied compared to those between carnivorous and/or herbivorous fishes (Wootton, 1990). However, since omnivorous fishes are common in freshwater habitats, their utilization of different food resources distributed in different parts of the habitat, as well as their interspecific relationships and microhabitat use, may be important in understanding the general structure of such fish communities.

Two congeneric species, the dark chub, *Zacco temmincki*, and the pale chub, *Z. platypus*, are distributed in eastern Asia (Nakamura, 1969; Miyadi et al., 1976). Although there is a slight difference in habitat use between the species (Mizuno et al., 1958; Nagoshi et al., 1962; Mizuno et al., 1964; Nakamura, 1969) and diet (Mizuno et al., 1958; Kawanabe, 1959; Nagoshi et al., 1962), both are known to coexist in the same reaches of streams (Mizuno and Gose, 1972). However, to date their competitive relationships have not been investigated.

Both species exhibit aggressive behaviour towards conspecifics (*Z. temmincki*: Katano, 1983, 1985, 1990; *Z. platypus*: Nakamura, 1952; Nagoshi et al., 1962), but interspecific aggressive behaviour has not been reported. Since both *Z. temmincki* and *Z. platypus* are omnivorous, competitions for food may occur when they coexist under conditions of food shortage and/or high population densities. Consequently, interspecific aggressions between the species might be expected to occur.

In this study *Z. temmincki* and *Z. platypus* were observed in two rivers near Kyoto City, in order to describe patterns of intra- and interspecific aggressive interactions and feeding behaviour, and discuss the mechanisms of habitat utilization by each species.

Materials and Methods

Diurnal observations on *Zacco temmincki* and *Z. platypus* were made along a 5.4 m length (16.2 m^2) of the Kamo River near Ichihara, Kyoto City, Japan, on June 9, 1981, and a 3.3 m length (4.6 m^2) of the Takano River, a tributary of the Kamo River, near Yase, on June 6, 8, 10, 11 and 17, 1981. Supplementary observations of aggressive behaviour of the two species were made in a natural riverside pond (26.6

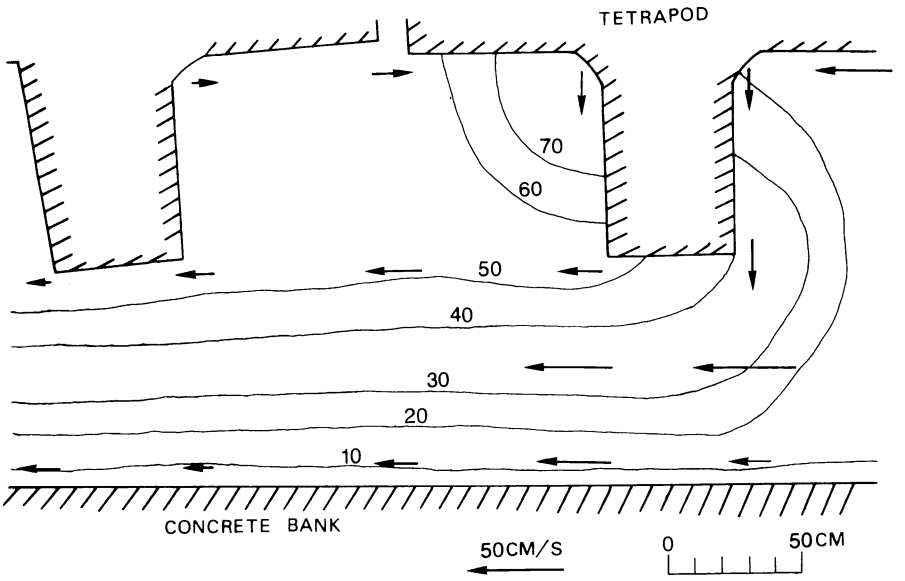

Fig. 1. Map, water depth and current velocity in the Takano River study area. Water depth and current velocity were measured at intervals of about 70 cm. Numerals near contour lines indicate water depths (cm). Current velocities are indicated by arrow lengths.

m^2) near Yase from August 7 to 23, 1980.

In the Takano River study site, water depth reached a maximum of 72 cm, the river bed comprising mud and pebbles (Fig. 1). Surface current velocities ranged from 9.6 to 52.1 cm per second. The Kamo River was about 4 m in width, the river bed comprising mud, pebbles, boulders and rocks. Water depth reached a maximum of about 1 m in the study area, but current velocity was not measured. A map and details of the riverside pond are given by Katano (1983, 1987).

The swimming course of an individual was traced and aggressive interactions and feeding behaviour during a one-minute period recorded on a map from the river bank. Whether or not the fish used the region near the water surface (10 cm or less from the water surface) was also recorded. The vertical habitat use of each species was categorized as U, fish using only a region near the water surface during the observation period, B, fish using only a region far from the water surface, or M, fish using both regions. Twenty-eight *Z. temmincki* and one *Z. platypus* in the riverside pond were identified individually by the method described by Katano (1983). Individual identifications over a long period were not made in either river, but several fish were identified individually throughout a single day by noting body colour patterns and markings. A ruler (30 cm) was placed in the study area for estimating the approximate standard length (SL) of fish to the nearest 0.5 cm. While following individuals in the Takano River, others that were within 10 cm of the former were also recorded. However, it was not possible to determine which individual, if either, actively approached which. In the Takano River the positions of all *Z. temmincki* and *Z. platypus* larger than 5 cm SL were recorded on a map four times on June 11 and 17. A similar mapping census was conducted once in the Kamo River, at 18 : 00 on June 9. In each census fish were roughly classified into larger ($SL \geqq 8$ cm) or smaller ($SL < 8$ cm) individuals. For convenience in investigating the distribution patterns of individuals and the locations at which feeding and aggressive behaviour were observed in the Takano River, each side of the river in the study area was divided into two, equally-sized (2.3 m^2) parts, near ($\leqq 23$ cm) and far (> 23 cm) from the bank.

Results

Number and distribution of individuals

The mean number of individuals did not differ significantly between species (*Zacco temmincki*: $n = 4$, 17.5 ± 3.5 SD; *Z. platypus*: $n = 4$, 8.0 ± 3.9 SD) in

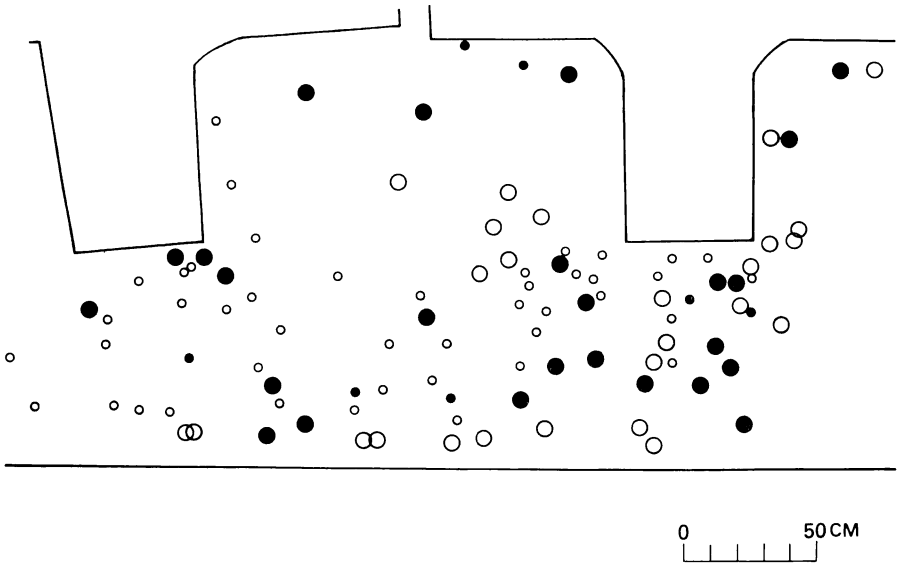

Fig. 2. Distribution of *Zacco temmincki* (○) and *Z. platypus* (●) in the Takano River study area, according to four mapping censuses conducted at 14:00 on June 11 and at 11:45, 12:30 and 15:30 on June 17. Large and small circles indicate fish larger and smaller than 8 cm, respectively.

the Takano River study area (Fig. 2, ANOVA, $p > 0.05$). Individuals larger than 8 cm SL numbered 6.5 ±2.1 for *Z. temmincki* and 6.3±2.5 for *Z. platypus* (no significant difference between the two species, ANOVA, $p > 0.05$). In the Kamo River study area, all five *Z. temmincki* seen and 11 out of 17 *Z. platypus* exceeded 8 cm SL.

In the Takano River, the numbers of larger individuals of both species and smaller *Z. temmincki* did not differ significantly between the areas near and far from the banks (Fig. 2, chi-squared test, $p > 0.05$). Differences were not testable for smaller *Z. platypus* because of the small sample sizes. There was no significant difference in horizontal habitat use between the two species (chi-squared test, $p > 0.05$).

The body lengths of *Z. temmincki* and *Z. platypus*, whose movements were traced, ranged from 6.5 to 11.0 cm ($n = 44$, mean±SD = 8.6±1.3) and 6.0 to 12.0 cm ($n = 32$, mean±SD = 9.7±1.6), respectively, in the Takano River, and from 8.5 to 12.0 cm ($n = 11$, mean±SD = 11.1±1.1) and 7.0 to 12.0 cm ($n = 14$, mean±SD = 11.4±1.3), respectively, in the Kamo River. The body lengths of *Z. temmincki* were larger than those of *Z. platypus* in the Takano River (ANOVA, $F_{1,74} = 11.1$, $p < 0.01$), but there was no significant difference in the Kamo River ($p > 0.05$).

Both *Z. temmincki* and *Z. platypus* used the region near the water surface more frequently in the Kamo River than in the Takano River (Table 1, Fisher's exact probability test, categories M and B were combined, *Z. temmincki*: $p < 0.01$, *Z. platypus*: $p <$

Table 1. Vertical habitat use by *Zacco temmincki* and *Z. platypus* in the Takano and Kamo Rivers. Figures in parentheses indicate percentages

River	Species	No. of observations (min.)	Vertical movement*		
			U	M	B
Takano	*Z. temmincki*	44	22 (50.0)	21 (47.7)	1 (2.3)
	Z. platypus	32	5 (15.6)	20 (62.5)	7 (21.9)
Kamo	*Z. temmincki*	11	11 (100.0)	0 (0.0)	0 (0.0)
	Z. platypus	14	13 (92.9)	0 (0.0)	1 (7.1)

* See text for explanation of U, M and B.

0.001). In the latter more *Z. temmincki* used the region near the water surface than *Z. platypus* (categories M and B were combined, $\chi^2=9.6$, $df=1$, $p<0.01$), but there was no significant difference between the two species in the Kamo River (Fisher's exact probability test, $p>0.05$).

The body length of Takano River individuals that used only the region near the water surface (*Z. temmincki*: $n=22$, 9.1 cm$\pm$1.0 SD; *Z. platypus*: $n=5$, 11.4$\pm$0.5 SD) was significantly larger than in other individuals (*Z. temmincki*: $n=22$, 8.1$\pm$1.5 SD; *Z. platypus*: $n=27$, 9.4$\pm$1.6 SD, ANOVA, *Z. temmincki*: $F_{1,42}=6.9$, $p<0.05$; *Z. platypus*: $F_{1,30}=7.3$, $p<0.05$).

Aggressive interactions

Both *Zacco temmincki* and *Z. platypus* exhibited aggressive behaviour towards each other as well as towards conspecifics at each study site (Table 2). In most aggressive interactions, one individual attacked and chased the other, which fled. However, one example of *Z. temmincki* observed in the Kamo River, when chased by a smaller conspecific individual, exhibited lateral display (presentation of the side of the body to the opponent, with all fins extended [Katano, 1985]). None of the aggressive displays described by Katano (1985) for *Z. temmincki* were observed between *Z. platypus* individuals. However, on two occasions a Takano River *Z. platypus*, when chased by *Z. temmincki*, performed an aggressive lateral display to the latter. In the riverside pond, a male *Z. platypus* that was attacked and butted by a *Z. temmincki* individual, was noted on one occasion to stay in the same position in the current, rather than flee.

Table 2. Aggressive interactions of *Zacco temmincki* and *Z. platypus*. Figures in parentheses indicate frequency (per minute)

River	Species	No. of observations (min.)	Opponent		χ^2 ($df=1$)
			Z. temmincki	*Z. platypus*	
Takano	*Z. temmincki*	44	23 (0.52)	9 (0.20)	2.4 NS
	Z. platypus	32	9 (0.28)	9 (0.28)	
Kamo	*Z. temmincki*	11	11 (1.00)	10 (0.91)	0.0 NS
	Z. platypus	14	17 (1.21)	16 (1.14)	
Total	*Z. temmincki*	55	34 (0.62)	19 (0.35)	1.8 NS
	Z. platypus	46	26 (0.57)	25 (0.96)	

NS: not significant at the 5% level; the opponent in aggressive interactions did not differ significantly between the Takano and Kamo Rivers for either species ($p>0.05$).

Table 3. Relative body sizes of fish that won or were defeated in aggressive encounters. The total number of encounters are shown, but those in which the body lengths of both individuals were identical or not recorded, are not indicated. Figures in parentheses show percentages

Species	River	Larger fish won	Smaller fish won	χ^2 ($df=1$)
Z. temmincki vs. *Z. temmincki*	Takano	19 (100)	0 (0)	19.0***
	Kamo	6 (75)	2 (25)	——
	Total	25 (93)	2 (7)	19.6***
Z. platypus vs. *Z. platypus*	Takano	6 (100)	0 (0)	——
	Kamo	10 (100)	0 (0)	10.0**
	Total	16 (100)	0 (0)	16.0***
Smaller *Z. temmincki* vs. larger *Z. platypus*	Takano	1 (17)	5 (83)	——
	Kamo	15 (94)	1 (6)	12.3***
	Total	16 (73)	6 (27)	4.5*
Larger *Z. temmincki* vs. smaller *Z. platypus*	Takano	7 (100)	0 (0)	——
	Kamo	5 (100)	0 (0)	——
	Total	12 (100)	0 (0)	12.0***

*$p<0.05$; **$p<0.01$; ***$p<0.001$; NS: $p>0.05$; ——: sample sizes too small to test statistically.

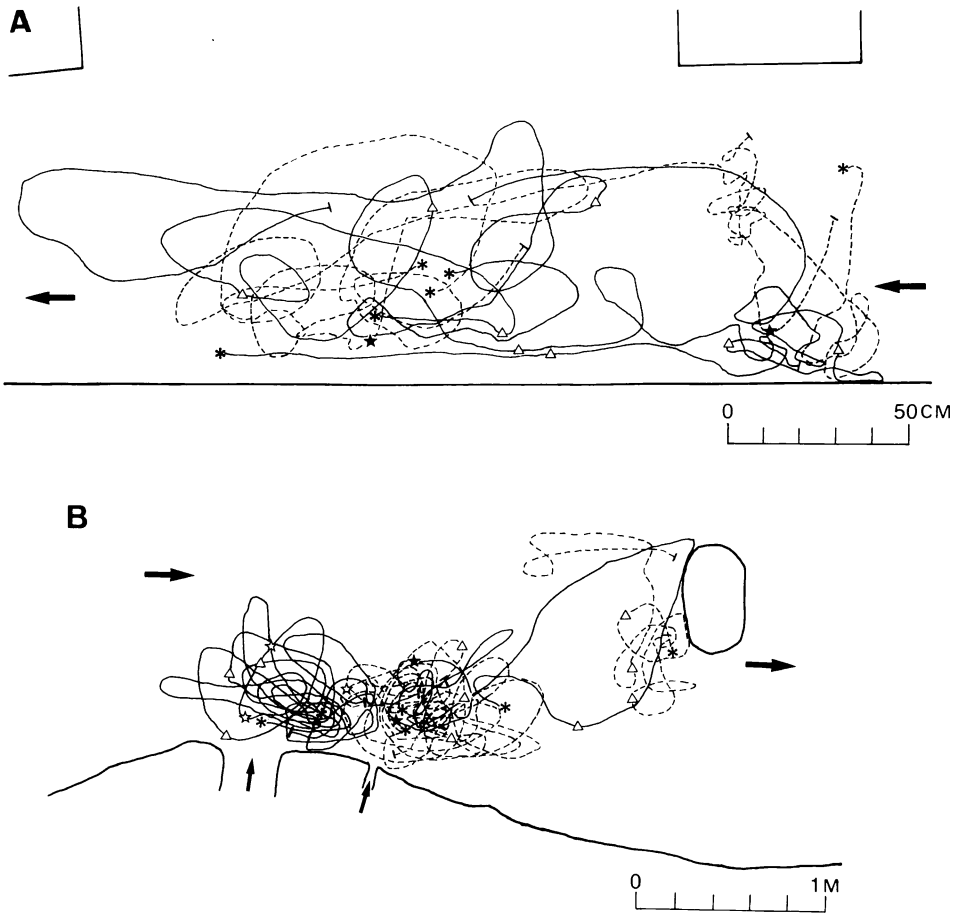

Fig. 3. Examples of movements and aggressive interactions of *Zacco temmincki* and *Z. platypus*. A) Takano River, three minute traces of *Z. temmincki* and *Z. platypus*, respectively, from 13:35 to 14:19 on June 11; B) Kamo River, three minute traces of *Z. temmincki* and *Z. platypus*, respectively, from 17:39 to 18:10 on June 9. Two minute traces of *Z. temmincki* and *Z. platypus* near the bank in example B indicate the movement of single individuals of each species. Solid and broken lines indicate the traces of *Z. temmincki* and *Z. platypus*, respectively. Feeding behaviour is not shown. Arrows show the direction of water flow. Start of observations (*); intraspecific aggressive interactions (win: △; defeat: ▲); interspecific aggressive interactions (win: ☆; defeat: ★).

Regarding interspecific aggressive encounters, *Z. temmincki* chased *Z. platypus* in 16 out of 18 cases (88.9%) in the Takano River, but in only 8 out of 27 cases (29.6%) in the Kamo River, the differences between the rivers being significant ($\chi^2=15.2$, $df=1$, $p<0.001$).

A comparison of relative body size of individuals that exhibited aggressive behaviour showed that larger individuals won more frequently than smaller ones in both intra- and interspecific encounters, irrespective of species (Table. 3).

The frequency of intra- and interspecific aggressive interactions was not correlated with body length in either species in the two rivers (simple r, $p>0.05$). Nor was there any significant difference in the frequency of intra- or interspecific aggressive interactions between Takano River individuals that used only the region near the water surface and other individuals (ANOVA, $p>0.05$).

When the distance between individuals was less than 10cm, *Z. temmincki* attacked conspecifics (in 21 of 40 cases, 52.5%) more frequently than did *Z. platypus* (in 9 of 35 cases, 25.7%, $\chi^2=6.6$, $df=1$, $p<0.05$). When the distance between heterospecifics

was less than 10 cm, aggressive behaviour occurred in 14 of 63 cases (22.2%). The interspecific aggression rate was significantly less than that between *Z. temmincki* individuals ($\chi^2=9.5, df=1, p<0.01$), but did not differ from that between individuals of *Z. platypus* ($p>0.05$).

There were several aggressive interactions between individually identified *Z. temmincki* and *Z. platypus*. In the Kamo River, a male *Z. platypus*, 12 cm SL, was chased by a similarly sized *Z. temmincki* on four occasions, but was seen to chase other *Z. temmincki* (10 cm SL and 8.5 cm SL) once, respectively. In the riverside pond in 1980, *Z. temmincki* were classified into 12 dominance ranks (Katano, 1987). One individually identified male *Z. platypus* chased *Z. temmincki* in the 6th, 9th and 11th ranks, but was itself chased by those in the 2nd and 4th ranks. Although data did not include all of the individuals in the Kamo River and pond, the results indicated that individuals of the two species are organized in a mixed-species dominance hierarchy.

The movements of several individuals suggested that different patterns of social organization of *Z. temmincki* and *Z. platypus* occurred in different sites (Fig. 3). Example A indicates that both *Z. temmincki* and *Z. platypus* had markedly overlapping home ranges, with no sign of territory formation. On the other hand, example B shows that single individuals of *Z. temmincki* and *Z. platypus* occupied a small home range near a small stream inlet. These individuals chased away all other individuals from their respective home ranges, indicating that the latter constituted territories against both con- and heterospecifics.

Feeding behaviour

Six kinds of feeding behaviour for *Zacco temmi-*

Table 4. Feeding behaviour of *Zacco temmincki* and *Z. platypus*, including total number of cases. Figures in parentheses indicate frequency per minute. Feeding behaviour T was not observed

River	Species	No. of observations (min.)	Feeding behaviour*				
			S	F	D	B	P
Takano	*Z. temmincki*	44	42 (0.95)	0 (0.00)	4 (0.09)	0 (0.00)	106 (2.41)
	Z. platypus	32	5 (0.16)	0 (0.00)	1 (0.03)	0 (0.00)	191 (5.97)
Kamo	*Z. temmincki*	11	15 (1.36)	1 (0.09)	0 (0.00)	1 (0.09)	5 (0.45)
	Z. platypus	14	12 (0.86)	1 (0.07)	0 (0.00)	0 (0.00)	69 (4.93)

* See text for explanation of S, F, D, B, P and T.

Table 5. Sites of aggressive and feeding behaviour exhibited by *Zacco temmincki* and *Z. platypus* in the Takano River. Figures in parentheses indicate percentages

Behavioural type	No. of observations		χ^2 ($df=1$)
	Near banks	Far from banks	
Aggressive behaviour			
Z. temmincki chased *Z. temmincki*	15 (65.2)	8 (34.8)	2.1 NS
Z. platypus chased *Z. platypus*	5 (55.6)	4 (44.4)	——
Total	20 (62.5)	12 (37.5)	2.0 NS
Z. temmincki chased *Z. platypus*	16 (100.0)	0 (0.0)	16.0*
Z. platypus chased *Z. temmincki*	2 (100.0)	0 (0.0)	——
Total	18 (100.0)	0 (0.0)	18.0*
Feeding behaviour			
S or D feeding of *Z. temmincki*	38 (82.6)	8 (17.4)	19.6*
S or D feeding of *Z. platypus*	4 (66.7)	2 (33.3)	——
Total	42 (80.8)	10 (19.2)	19.7*
P feeding of *Z. temmincki*	105 (99.1)	1 (0.9)	102.0*
P feeding of *Z. platypus*	173 (90.6)	18 (9.4)	125.8*
Total	278 (93.6)	19 (6.4)	225.9*

*$p<0.001$; NS: not significant at the 5% level; ——: sample sizes too small to test significantly.

ncki (S, snapping at an object which had fallen onto the water surface; F, jumping out of the water towards an object in the air; D, dashing towards an object carried by the current; B, sucking up a bottom object; P, picking off a quantity of algae or moss with accompanying head shaking; T, picking at and occasionally tearing off some part of terrestrial plants overhanging or floating on the water surface) were classified by Katano (1987). Most of these behavioural types, except B (for *Z. platypus*) and T (for both species), were also noted in the Takano and Kamo Rivers (Table 4). *Z. platypus* principally employed P-type feeding at both river study sites. Although *Z. temmincki* did likewise in the Takano River, that species undertook S-type feeding in the Kamo River. Chi-squared tests showed that feeding behaviour differed significantly between *Z. temmincki* and *Z. platypus* in the two rivers (feeding type S, F, D and B were combined, $df=1$, Takano: $\chi^2=50.1$, $p<0.001$; Kamo: $\chi^2=31.9$, $p<0.001$).

In neither *Z. temmincki* nor *Z. platypus* in the Takano River, was there a significant difference in the frequency of S or P-type feeding between individuals that used only the region near the water surface and other individuals (ANOVA, $p>0.05$). Nor was there any correlation of body length with either feeding behaviour in either species in either river (simple r, $p>0.05$).

In the Takano River, the frequency of intraspecific aggressive interactions was positively correlated with that of P-type feeding in *Z. temmincki* ($r=0.334$, $p<0.05$), but was negatively correlated with that feeding in *Z. platypus* ($r=-0.469$, $p<0.01$).

Intraspecific aggressive interactions of *Z. temmincki* occurred both near and far from the banks in the Takano River (Table 5), but could not be tested in *Z. platypus* because of the small sample sizes. On the other hand, interspecific aggressive interactions occurred solely near the banks. Feeding behaviour was also frequently observed near the banks in both species.

Discussion

This study showed that coexisting *Zacco temmincki* and *Z. platypus* exhibited both intra- and interspecific aggressive behaviour. Although many ecological studies on these species have been conducted in other rivers (Mizuno et al., 1958; Kawanabe, 1959; Nagoshi et al., 1962; Maki and Kakiuchi, 1971; Maki, 1972, 1976), interspecific aggressive interactions have not been reported presumably because these studies did not focus on social relationships between the species. Both *Z. temmincki* and *Z. platypus* used areas adjacent to and more distant from the banks, with interspecific aggressive interactions occurring solely at the former in the Takano River. Since most feeding activities took place near the banks, aggressive behaviour might function to prevent individuals of other species from utilizing the same food resources.

Since larger individuals were at an advantage in both intra- and interspecific aggressive encounters, there being a dominance-subordination relationship between some *Z. temmincki* and *Z. platypus*, a size-dependent dominance hierarchy might exist involving both species. A size-dependent dominance hierarchy is common intraspecifically (Braddock 1945; Greenberg, 1947; Frey and Miller, 1972; Colgan, 1983; Katano, 1987, 1990), but has been reported in interspecific relationships only in salmonids (Newman, 1956; Nakano and Furukawa-Tanaka, in press) and cichlids (Kohda 1991).

The frequency of aggressive interactions was correlated with that of feeding behaviour. Although not investigated in the present study, the distribution of food resources is thought to differ between shallow and deeper waters in streams. For instance invertebrates that fall onto the water surface or are drifting in the current are generally abundant near the water surface (Furukawa-Tanaka, 1985, 1992; Katano, 1987). Therefore, large dominant individuals in both species might use the region near the water surface for feeding upon invertebrates, smaller individuals occasionally leaving that region in order to avoid attacks by dominants. The occurrence of aggressive interactions might markedly affect feeding tactics and success in *Z. temmincki* and *Z. platypus*, and their microhabitat utilization.

The home ranges of *Z. temmincki* commonly overlapped with each other, although some individuals formed a territory in a site to which food resources were carried by the water current (Katano, 1987). The territory owner was determined by a dominance hierarchy, but since the active times within a day differed between individuals, with dominant individuals occasionally disappearing from the territory into holes or recesses, the territory ownership changed frequently (Katano, 1987). Although the observation times were short in the present study, single individuals of *Z. temmincki* and *Z. platypus* defend-

ed territories for feeding both intra- and interspecifically in the Kamo River, although there was no sign of territory formation in the Takano River. This suggests that, as reported for *Z. temmincki*, relationships between *Z. temmincki* and *Z. platypus* individuals change markedly between different habitats because of the different distribution patterns of food resources.

There were several different behavioural patterns between *Z. temmincki* and *Z. platypus*. The probability of aggressive interactions per approach was clearly greater in encounters between *Z. temmincki* individuals than between *Z. temmincki* and *Z. platypus*, or between *Z. platypus* individuals, indicating that the former was more aggressive. Both species were omnivorous, but *Z. platypus* fed upon algae more frequently than *Z. temmincki*, as previously reported (Mizuno et al., 1958; Miyadi et al., 1976). Deeper regions were also more frequently used by *Z. platypus* than by *Z. temmincki*. However, since both species lived sympatrically interacting with each other, it was not evident whether the interspecific differences observed in fact represented real specific characteristics, or were behavioural modifications brought about by the presence of other species. To understand the influences of other species on *Z. temmincki*–*Z. platypus* relationships, further experiments with controlled food resources and individual numbers of both species may be necessary.

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カワムツとオイカワの摂餌に関連した攻撃的干渉

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京都市の二河川でカワムツとオイカワが同所的に生息し，同種内と同様に二種間でも攻撃行動を行った．両種において大型個体は小型個体より頻繁に表層部を利用し，種内及び種間の干渉において優位であった．カワムツとオイカワの両種とも雑食性であったが，オイカワの方がカワムツよりも付着藻類を摂食する頻度が高かった．両種の摂餌場所には大きな違いはなく，その周辺で多くの種間攻撃が起こった．両種とも攻撃的干渉と付着藻類摂餌行動の頻度との間に有意な相関関係がみとめられた．両種の個体の行動圏は多くの場合互いに重複していたが，同種及び他種に対して縄ばりが形成されることも観察された．

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