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Food Competition among Fishes in Some Rivers of Kyoto Prefecture, Japan[1]

By

Hiroya KAWANABE

Zoological Institute, College of Science, University of Kyoto

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Introduction

The interspecific competition is one of the most important as well as famous problems in ecology. Since DARWIN (1859), many naturalists, ecologists as well as agri- and aqui-culturists devoted their efforts to this problem, by viewing from various stand points such as the field observation, experimental culture and mathematical treatment, and by using various species of plants or animals. But, on fish populations, there are relatively few papers which deal directly with the subject of competition for food (FROST, 1946; HARTLEY, 1948; LARKIN, 1956; LAGLER, 1944; NIKOLSKII, 1945, 1954; and STARRETT, 1950); and several papers which refer to this problem stand on such a very simple assumption as two or more species which eat the same food item at the same time compete strongly with each other.

Since 1955, we have carried on some investigations about the food habits of fishes in several rivers of Kyoto Prefecture. During the course of this study, it was found out that both the amount of food consumed and the feeding habit of a certain species were different according to their habitats, and that these differences seemed to be due not only to the discrepancy in the relative quantity of available food organisms but also to that in the faunal composition and the population of fishes. These observations have led me to settle up an opinion on the concept of food competition, which will be dealt with in some detail in the present paper.

General View of Research Areas

The research area for our study was chosen out of the middle courses of four rivers in Kyoto Prefecture, i.e., the Rivers Ukawa, Yuragawa, Katuragawa and Inukaigawa (Fig. 1).

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1) The expenses of the present work have been defrayed in part by the Grant in Aid for Fundamental Scientific Research of the Ministry of Education.

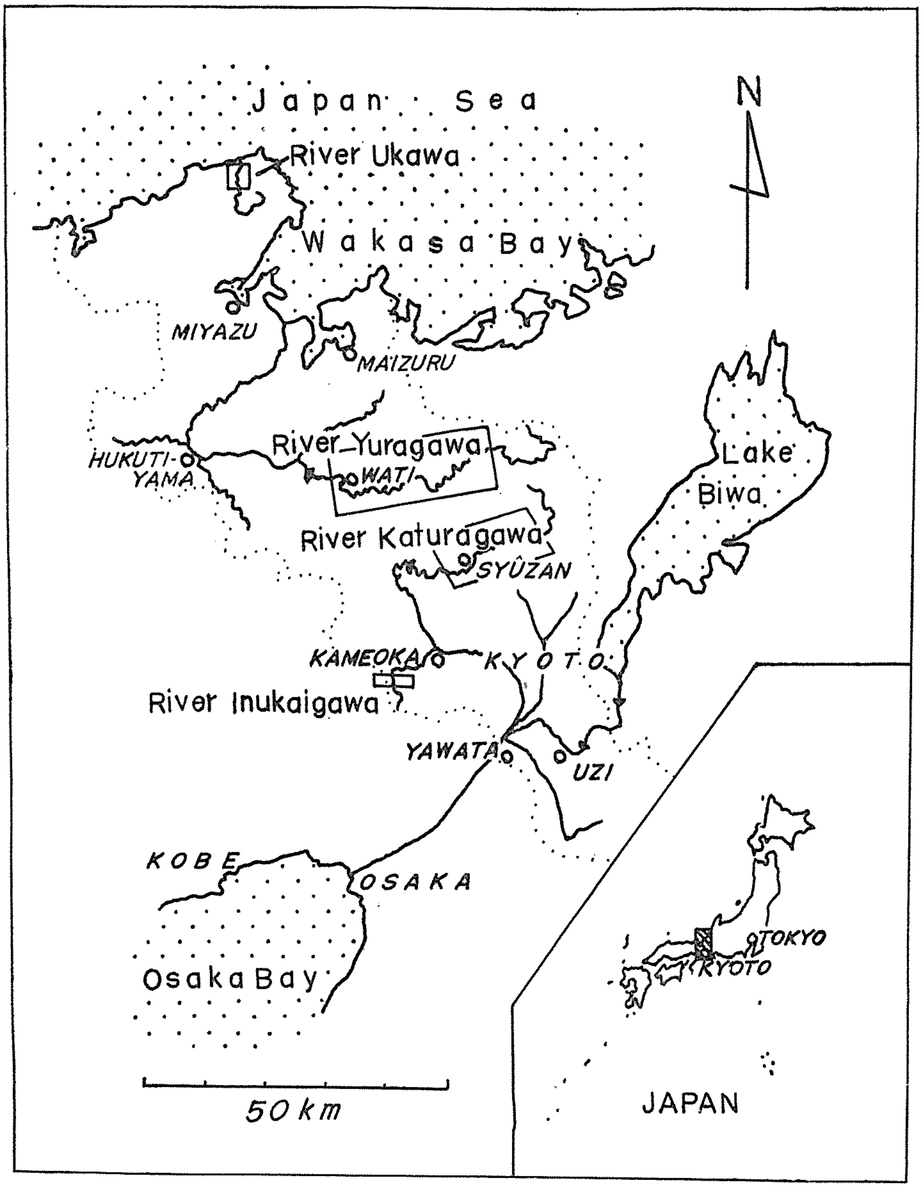

Fig. 1. Map of the Rivers Ukawa, Katuragawa, Inukaigawa and Yuragawa. Research areas in 1955–1959 are surrounded by unbroken lines. Thin dotted line presents the boundary of Kyoto Prefecture.

A) *Physical Conditions.*

Both the River Ukawa and the River Yuragawa empty into the Japan Sea on the north coast of Kyoto Prefecture. The former is a small river (ca. 25 km in length), while the latter is large (ca. 150 km in length). On the other hand, the River Katúragawa (ca. 125 km in length) runs southward, joining the River Yodogawa which flows from Lake Biwa to the Bay of Osaka. The River Inukaigawa (ca. 20 km in length) is a tributary of the River Katuragawa.

The middle courses of rivers have some common characteristics. From the topographical point of view, a river consists of units each of which is composed of two parts, i.e., the river-rapid in which water seethes white on loosely packed boulders and the river-pool or the slowly flowing deep with rock walls on one side of the banks. In the middle course, these two parts are distinguished clearly, and one meander consists only of one rapid and one pool (KANI, 1944). Except the Ayu-fish, *Plecoglossus altivelis*, which is an anadromous fish, the dace (*Tribolodon hakonensis*) or the chubs (*Zacco* spp.) are the dominants of the middle course, and our research areas may belong to the "dace or chub region" (TSUDA and GOSE, 1954).

Some physical conditions are shown in Table 1. The investigation was carried on in all seasons since 1955, but in the present paper, I discuss on the data of summer seasons only.

Table 1. The research areas with some physical conditions.

River	Ukawa	Katuragawa	Inukaigawa	Yuragawa
River system	Ukawa	Yodogawa	Yodogawa	Yuragawa
Length (km)	25	123	20	147
Research area				
from	Kawakubo	Kuroda		Tauta
to	Maruyama	Uogahuti		Nakamura
length (km)	8	23	4	25
average breadth (m)	10	20	6	25
average discharge in summer (m^3/sec.)	1.5	18	0.3	22
water temperature in summer (°C)	27–31	21–26	25	21–27
Season of investigation	summer, 1955 summer, 1958	summer, 1957 summer, 1959	summer, 1958	summer, 1958

B) *Bottom algae and benthic invertebrates.*

The quantitative survey of bottom algae and benthic invertebrates of these rivers were carried out by NEGORO, TSUDA and his students, and the members of our research group, in the same occasion as the fishes were caught and their behaviours were described by us. The major parts of the results of these investigations have been reported by KAMEGAI (1959), KAWANABE *et al.* (1956, 1959), MIZUNO *et al.* (1958), MORITA (1959), OHGUSHI *et al.* (1956, 1957), TEZUKA (1959) and TEZUKA and KAMEGAI (in press). These results, with some additions from the unpublished data by NEGORO, TEZUKA and TSUDA, are summarized in Tables 2–5. The flora and fauna of all research areas belonged to "oligosaprobionts" characteristic of the middle course.

The standing crops of the bottom algae were within the limits of 18 milligrams and 23 milligrams (wet weight) per one square centimetre as average values, the River Inukaigawa being an exception with about 10 milligrams. Thus, it may be admitted, so far as this paper is concerned, that the gravimetric algal production was nearly equal, with an exception of the River Inukaigawa.

In the same manner, the standing crop of the benthic insects may be assumed as nearly equal in any year and place (7.3–9.5 g/m^2), with an exception (4.0 g/m^2) of the River Ukawa in 1958.

Table 2. Standing crops and abundant species of bottom algae and benthic invertebrates in the middle course of the River Ukawa during the summer season of 1955 and of 1958 (data from KAWANABE *et al.*, 1956, 1959; OHGUSHI *et al.*, 1956, 1957; TEZUKA and KAMEGAI, in press; and NEGORO, unpublished).

	river-rapid	river-pool	average
1955			
Algae			
standing crop (wet weight per 1 cm^2)	25 mg	6 mg	18 mg
abundant species	*Cymbella tumida* *C. turgidula* *Synedra ulna* *Symploca* sp.	*Cymbella sinuata* *C. turgidula* *Cocconeis placentula*	
Benthic invertebrates			
standing crop (wet weight per 1 m^2)	5–18 g	0.03–3 g	8.5 g
abundant species	*Parastenopsyche sauteri* *Hydropsyche ulmeri* *Epeorus latifolium* *Antocha* spp.	*Potamanthus kamonis* *Choroterpes trifurcata* *Phaenopsectra* sp.	
1958			
Algae			
standing crop (wet weight per 1 cm^2)	32 mg	10 mg	20 mg
abundant species	*Symploca* sp. *Oscillatoria* spp. *Navicula cari* *N. cryptocephala*	*Symploca* sp. *Oscillatoria* spp. *Navicula cari* *Achnanthes lanceolata*	
Benthic invertebrates			
standing crop (wet weight per 1 m^2)	0.6–8.4 g	0.4–4.0 g	4.0 g
abundant species	*Metaeopsephenus japonicus* *Macromia* sp. *Stenopsyche griseipennis*	*Metaeopsephenus japonicus* *Atherix* sp. *Potamanthus kamonis* *Choroterpes trifurcata*	

Table 3. Standing crop and abundant species of bottom algae and benthic invertebrates in the middle course of the River Katuragawa during the summer season of 1957 and of 1959 (data from MIZUNO *et al.*, 1958; and TEZUKA, unpublished).

	river-rapid	river-pool	average
1957			
Algae			
standing crop* (wet weight per 1 cm^2)			20 mg
Benthic invertebrates			
standing crop (wet weight per 1 m^2)	12 g	4 g	9.3 g
abundant species	*Stenopsyche griseipennis* *Hydropsyche ulmeri* *H. nakaharai* *Epeorus latifolium*	*Psychomyia* spp. *Ephemera* spp. *Aphelocheirus vittatus* Chironomidae	
1959			
Algae			
standing crop (wet weight per 1 cm^2)	27 mg	19 mg	23 mg
Benthic invertebrates			
standing crop (wet weight per 1 m^2)	8.3–10.7 g	0.4–1.0 g	7.6 g
abundant species	*Parastenopsyche sauteri* *Epeorus latifolium* *Hydropsyche ulmeri* *Stenopsyche griseipennis*	*Potamanthus kamonis* *Isoperla nipponensis* *Psychomyia* spp. Chironomidae	

* Unfortunately, the quantitative study on algae was not carried out in this year. The data was presumed by actual eye-observation.

Table 4. Standing crop and abundant species of bottom algae and benthic invertebrates in the middle course of the River Inukaigawa during the summer season of 1958 (data from KAMEGAI, 1959; and TEZUKA, 1959).

	river-rapid	river-pool	average
Algae			
standing crop (wet weight per 1 cm^2)	6–35 mg	7 mg	10 mg
abundant species	*Symploca thermalis* *Cymbella turgidula* *Navicula cari*	*Symploca thermalis* *Achnanthes lanceolata*	
Benthic invertebrates			
standing crop (wet weight per 1 m^2)	8 g	4 g	7.2 g
abundant species	*Hydropsyche ulmeri* *H. nakaharai* *Parastenopsyche sauteri* *Epeorus latifolium*	*Kiotina* sp. *Sieboldius japonicus* *Atherix* sp.	

Table 5. Standing crop and abundant species of bottom algae and benthic invertebrates in the middle course of the River Yuragawa during the summer season of 1958 (data from MORITA, 1959; NEGORO, unpublished; and TSUDA, unpublished).

	river-rapid	river-pool	average
Algae			
standing crop (wet weight per 1 cm^2)	17–36 mg		19 mg
abundant species	*Cymbella tumida* *C. turgidula* *Synedra ulna* *Achnanthes minutissima*		
Benthic invertebrates			
standing crop (wet weight per 1 m^2)	3–42 g		8 g
abundant species	*Parastenopsyche sauteri* *Kamimuria quadrata* *Epeorus latifolium* *Metaeopsephenus japonicus*		

C) *Fish fauna and the population.*

The fishes of the four rivers and their population densities in the research areas are shown in Table 6.

Table 6. Fish fauna of the Rivers Ukawa, Katuragawa, Inukaigawa and Yuragawa, and the population density of fishes in the research area of the four rivers. The figures indicate the number of individuals per one square metre.

Scientific name	Japanese name	River Ukawa 1955	River Ukawa 1958	River Katuragawa 1957	River Katuragawa 1959	River Inukai-gawa 1958	River Yura-gawa 1958
Petromyzonidae							
Entosphenus japonicus	kawayatume	+	+	:	:	—	:
E. reissneri	sunayatume	+	+	+	+	+	+
Salmonidae							
Onchorhynchus keta	sake	+	+	—	—	—	:
O. masou, f. *masou*	sakuramasu	+	+	—	—	—	:
O. masou, f. *ishikawae*	yamame	:	:	—	—	—	:
O. rhodurus, f. *macrostomus*	amago	—	—	:	:	+	—
Salmo gairdnerii irideus	nizimasu	—	—	:	:	—	:
Plecoglossidae							
Plecoglossus altivelis	ayu	5.4	0.3	0.06	0.3	2.2	0.03
Cyprinidae							
Acheilognathinae							
Acheilognathus lanceolata	yaritanago	—	—	+	+	+	+
A. limbata	aburabote	—	—	+	+	+	+
Paracheilognathus cyanostigma	itimonzitanago	—	—	+	+	+	+

Scientific name	Japanese name	River Ukawa 1955	River Ukawa 1958	River Katuragawa 1957	River Katuragawa 1959	River Inukai-gawa 1958	River Yura-gawa 1958
Gobioninae							
Pungtungia herzi	mugituku	—	—	+	+	+	+
Sarcocheilichthys variegatus	higai	—	—	+	+	+	+
Gnatopogon gracilis	itomoroko	—	—	+	+	+	+
G. elongatus	tamoroko	—	—	+	+	+	+
Pseudogobio esocinus	kamatuka	—	—	0.1	0.07	0.1	0.01
Hemibarbus barbus	nigoi	—	—	—	—	—	0.01
H. longirostris	zunaganigoi	—	—	0.01	0.01	0.09	0.02
Pseudorasbora parva	motugo	—	—	+	+	—	+
Leuciscinae							
Tribolodon hakonensis	ugui	0.1	0.1	0.1	0.07	—	0.05
Moroko steindachneri	aburahaya	:	:	+	+	+	+
Zacco platypus	oikawa	0.3	0.6	0.2	0.1	0.05	0.03
Z. temminckii	kawamutu	1.0	0.3	0.1	0.05	0.4	0.01
Cyprininae							
Carassius auratus	huna	0.2	0.05	0.01	0.01	0.01	+
Cyprinus carpio	koi	+	+	+	+	—	+
Cobitidae							
Misgurnus anguillicaudatus	dozyo	+	+	+	+	+	+
Cobitis biwae	simadozyo	0.2	0.1	0.01	0.01	0.01	+
C. delicata	azimedozyo	—	—	0.02	0.01	—	—
Siluridae							
Parasilurus asotus	namazu	—	—	+	+	—	+
Bagridae							
Pelteobagrus nudiceps	gigi	—	—	+	+	+	+
Liobagrus reinii	akaza	+	+	+	+	+	+
Anguillidae							
Anguilla japonica	unagi	++	++	++	++	++	++
Cyprinodontidae							
Oryzias latipes	medaka	+	+	+	+	+	+
Serranidae							
Coreoperca kawamebari	oyanirami	—	—	—	—	—	+
Eleotridae							
Mogrunda obscura	donko	—	—	+	+	+	+
Gobiidae							
Tridentiger obscurus	titibu	+	+	—	—	—	:
Rhinogobius similis	yosinobori						
sea-run form		0.9	0.6	:	:	—	:
land-locked form		—	—	0.2	0.3	0.6	0.04
Chaenogobius urotaenia	ukigori	0.5	0.2	:	:	—	:
Luciogobius guttatus	mimizuhaze	+	+	—	—	—	:
Cottidae							
Cottus pollux	kazika	:	:	+	+	+	+
C. kazika	kamakiri	+	+	—	—	—	:

+ : The population density of less than 0.01 individuals per one square metre.
++ : Unknown population density, presumedly larger than 0.01 individuals per one square metre.
: : The fish which lives in the river, but is absent in the research area.
— : The fish which does not live in the river.

It must be pointed out that there are remarkable differences between the fish fauna of the River Ukawa and that of other three rivers. In the River Ukawa, the bitterlings (Acheilognatinae), large piscivorous catfishes (*Parasilurus* and *Pelteobagrus*), and especially the bottom-dwelling cyprinids (Gobioninae) were lacking, though they were quite abundant in other rivers. The population of Ayu-fish, which is the most dominant fish sociologically in the warmer months in most of the Japanese rivers, was different in different years. While its density reached 5.4 and 2.0 individuals per one square metre respectively in the River Ukawa (1955) and in the River Inukaigawa, less than 0.3 individuals per one square metre was the average value in other places and years.

Food of Fishes

The food items are arranged according to the "points method" (SWYNNERTON and WORTHINGTON, 1940; FROST, 1943; and HYNES, 1950), and shown in the form of food-chain (Figs. 2–7). For further details, the readers are referred to other papers (KAWANABE *et al.*, 1956; KODAMA, in press; and MIZUNO *et al.*, 1958).

Fishes are classified into four groups in accordance with their food habits. Three free-swimming cyprinids belonging to Leuciscinae fed mainly on terrestrial insects and/or bottom algae. There were, however, some differences between the food of these fishes, i.e., while the dark chub (A) depended rather chiefly on terrestrial insects, the pale chub (B) fed more algae, and the dace (C) was frequent to feed also on benthic insects. It is noteworthy that these three species displayed a similar tendency to depend mainly on terrestrial insects in the River Ukawa in 1955 and in the River Inukaigawa, but mainly on algae in the River Katuragawa in 1957 and 1959, and in the River Yuragawa. In the River Ukawa, the food quality of these fishes in 1958 was between the above two tendencies. The Ayu-fish (Plecoglossidae, D) was the algal feeder in all cases. Three fishes, which belonged to bottom dwelling Gobioninae, fed only on benthic insects, i.e., the striped shiner (E) was the caddis-worm feeder but sometimes fed also on midges, and both the long-nosed barbel (F) and the gudgeon (G) fed on any benthic insects, although the latter had a tendency to feed mainly on midges or other dipterous larvae. The crussian carp (*Carassius*), gobies (Gobiidae) and loaches (Cobitidae) fed on algae and/or benthic insects. Every species showed the similar tendency of feeding mainly on benthic insects for food in the River Ukawa in 1955, but mainly on algae in the River Katuragawa in both 1957 and 1959 and in the River Yuragawa. In both the River Ukawa (1958) and the River Inukaigawa, the kinds of food of these species were between the two tendencies.

Food Competition

It is a common knowledge that the food of fish differs according to such factors as the size of the fish, difference in seasons and the population of available food organisms. In the present paper, I wish to deal with the food of adult fishes in the middle course of four rivers during the summer season. As was mentioned above, the standing crops of the algae and benthic invertebrates were nearly equal in all observations with two exceptions. Notwithstanding these facts, the food of fishes differed greatly among our researches. What factors should have brought about such differences in the food of the fishes?

Here, the readers are referred once more to the comparison of the food-chains in relation with the populations of several fishes living together. The free-swimming cyprinids depended chiefly on terrestrial insects when the population of the Ayu-fish was dense, while they tended to feed mainly on bottom algae when the Ayu-fish was not densely populated. It seems to indicate that the food of free-swimming fishes changes under the influence of the population of the Ayu-fish.

It was already reported (MIYADI *et al.*, 1952) that the pale chub lived in the central part of a river-rapid when the Ayu-fish were absent in a river; but, as the Ayu-fish ascended the river and settled down gradually in the stream, the pale chub was thrust away to such worse places as the river-periphery or the boundaries between a rapid and a pool; and when the Ayu-fish descended the river, it returned to former places. I observed in the River Ukawa in 1955 that the Ayu-fish, whose population was very dense, lived in every place so far as the bottom algae was growing on gravels or stones; and the pale chub was driven away to extremely worse places for its life such as the quiet places under willow trees and a stoneless bottom. In such places, there grow a very few algae, but the quantity of terrestial insects which fall into the river is rather large, exceptionally so in the peripheral places. It is natural that the pale chub depended more strongly on terrestrial insects in the River Inukaigawa where the standing crop of algae was poorer than in other rivers.

I want to add the following observation. In general, a dark chub lives in slow-flowing areas, especially under the hanging branches of willow trees (MIZUNO *et al.*, 1958). In the River Ukawa in 1955, however, it invaded even to the central part of the river-rapid where the Ayu-fish were grazing. My interpretation of this phenomenon is that the pale chub, which was forced by the Ayu-fish, lived in the peripheral parts of a river and drove out the dark chub to the central part. The dark chub and the Ayu-fish are different in their requirement of food and both of them can live in the same habitat. But this latter observation was not sufficiently supported by the change in the food of the dark chub.

Next, the food items of gobies, loaches and the crussian carp differed in different rivers, and these differences seemed to be due to the presence or the absence of the bottom-dwelling gobionids in the research area. These phenomena led me to suppose that the bottom-dwelling cyprinids pressed the gobies and some other fish to change their food items from benthic insects to algae, and the following observations on the behaviour of the gudgeon and the stone loach seems to intensify the possibility of this supposition.

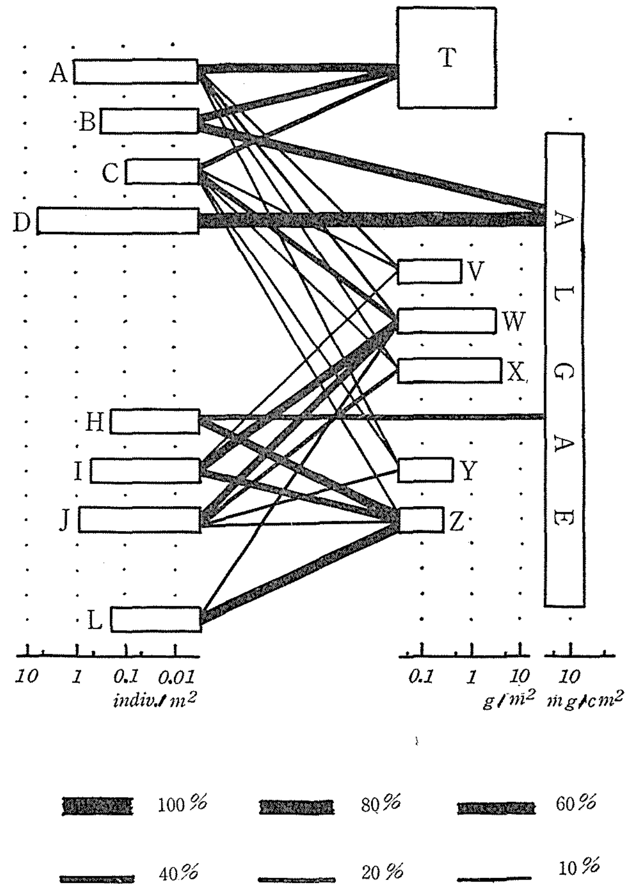

Fig. 2. Food-chain relationships for the main fishes in the research area of the River Ukawa during the summer of 1955. The alphabetical letters symbolize the names of fishes and insects as follows.

Free-swimming cyprinids (Leuciscinae)

A : dark chub, *Zacco temminckii*
B : pale chub, *Z. platypus*
C : dace, *Tribolodon hakonensis*

Salmon-like fish (Plecoglossidae)

D : Ayu-fish, *Plecoglossus altivelis*

Bottom-dwelling gobionids (Gobioninae)

E : striped shiner, *Pungtungia herzi*
F : long-nosed barbel, *Hemibarbus longirostris*
G : gudgeon, *Pseudogobio esocinus*

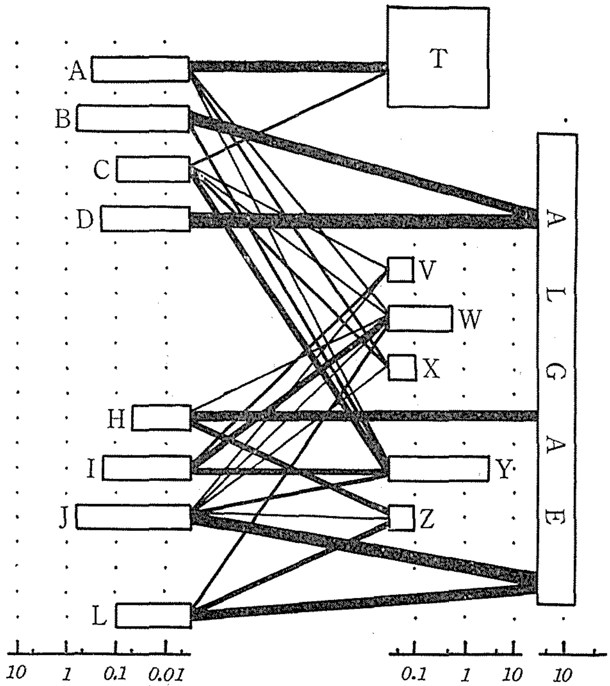

Fig. 3. The same of 1958.

Other bottom dwelling fishes
(Cyprininae, Gobiidae and Cobitidae)

H : crussian carp, *Carassius auratus*
I : tongue-divided goby, *Chaenogobius urotaenia*
J : common goby, *Rhinogobius similis*
K : delicate loach, *Cobitis delicata*
L : stone loach, *C. biwae*

Terrestrial insects

T : terrestrial insects such as Coleoptera, Lepidoptera, Hemiptera, Hymenoptera, etc.

Benthic insects

V : stone-fly nymphs (Plecoptera)
W : may-fly nymphs (Ephemeroptera)
X : caddis-fly larvae or pupae (Trichoptera)
Y : lympet-like larvae or nymphs (Hemiptera or Coleoptera)
Z : midges, etc. (Diptera)

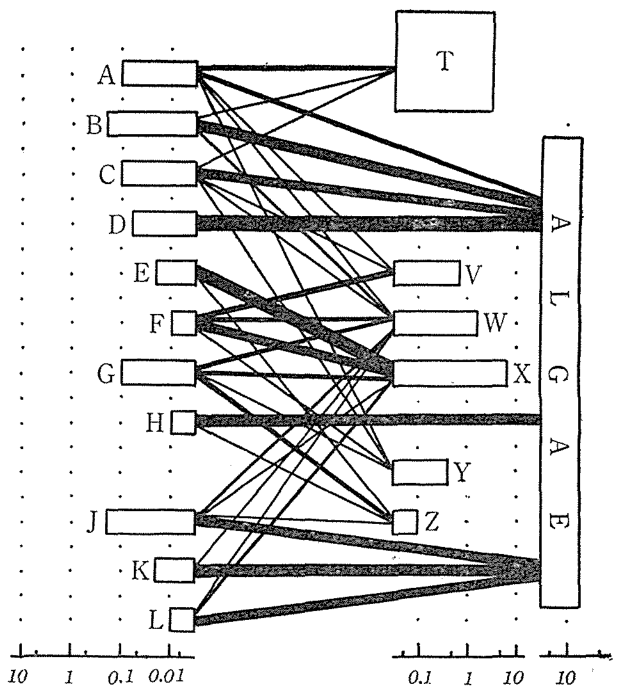

Fig. 4. Food-chain relationships for the main fishes in the research area of the River Katuragawa during the summer of 1957.

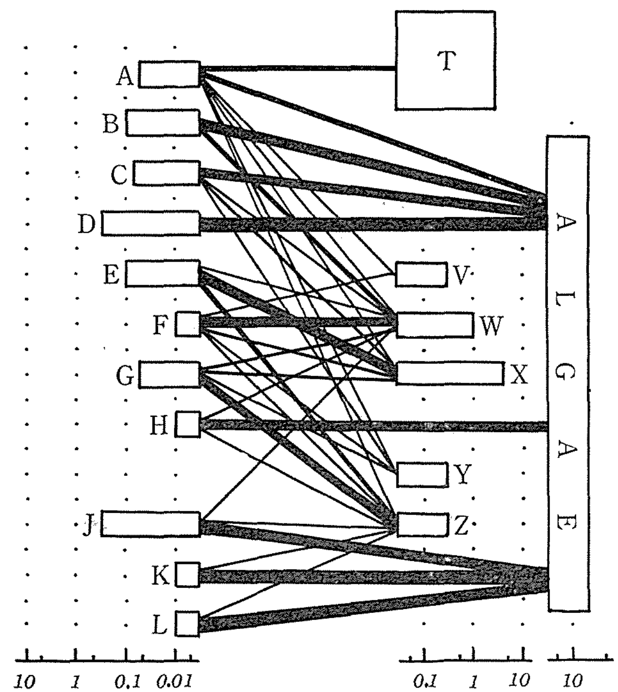

Fig. 5. The same of 1959.

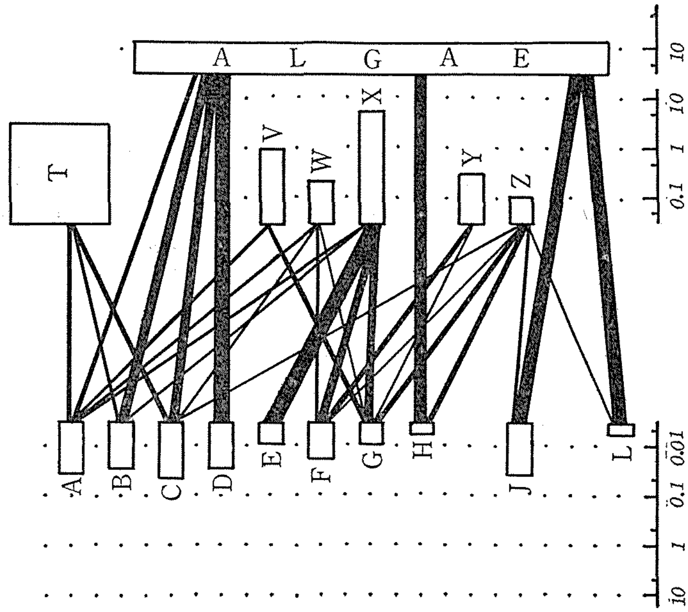

Fig. 7. The same of the River Yuragawa during the summer of 1958.

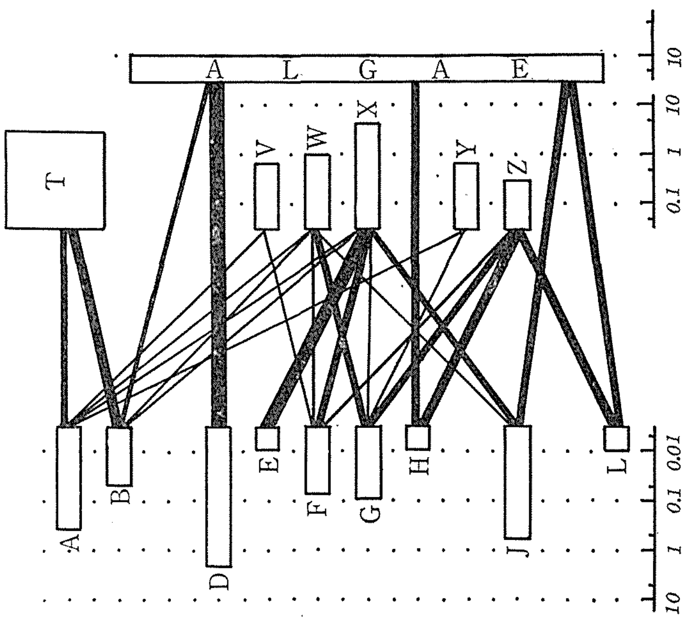

Fig. 6. Food-chain relationships for the main fishes in the research area of the River Inukaigawa during the summer of 1958.

The gudgeon, living on the gravel or sand bottom, usually sucks small animals with sand, which dwell under or among the sand or stones, by pushing small gravels or sand aside with the pectral fins. The stone loach in the River Ukawa, where the gudgeon was absent, was seen to take small animals in the same way as the gudgeon, i.e., it sucked small animals with sand. The stomach contents of the stone loach in the River Ukawa were similar to those of the gudgeon in other rivers, though the former were limited to such smaller animals as midges. On the contrary, in the River Katuragawa and the River Yuragawa, the stone loach lived in more peripheral parts of the river, where the bottom consisted not of sand but of large stones half buried in mud or fine sand. Here, the feeding behaviour of the loach was not the same as in the River Ukawa. It seemed to nip off or pick up the food substances attached to gravels or growing on the surface of mud bottom.

In the River Ukawa of 1958 as well as in the River Inukaigawa, the stomach contents of gobies, loaches and the crussian carp were unusual, and these facts were related respectively with the poor standing crop of aquatic invertebrates in the former and bottom algae in the latter.

The above-mentioned observations concern chiefly with the relations between the free-swimming cyprinids and the Ayu-fish, or between bottom dwelling gobionids and gobies, loaches or the crussian carp, namely the inside relations among free-swimming or bottom-dwelling fishes. Then was there no conflicting relation between free-swimming and bottom-dwelling fishes? It was observed that the common goby, which happened to present just at the same moment and in the same place when/where the Ayu-fish was grazing algae attached on stones, was driven away by the Ayu-fish irrespective of the territorial or schooling behaviour of the latter (KAWANABE, 1958). Being repeatedly interfered by the Ayu-fish, the common goby tended to crawl under or among stones. But the influence of this conflicting relation was not manifested clearly in the difference of the food of the common goby, perhaps because the relation between the goby and the Ayu-fish was weaker than that between the goby and the gudgeon.

The above considerations led us to a presumptive thesis that the food consumption by a fish is influenced not only by the amount of available food organisms, but also by the composition and population of the fish society to which it belongs.

*

As was mentioned in the introduction, most previous authors stood on such an assumption as two or more species eating the same food item at the same time compete strongly with each other. It may be right in cases of monophagous animals, but doubtful in cases of heterophagous or omnivorous animals to which most fresh-water fishes belong. Both STARRETT (1950) and NIKOLSKII (1953) suggested that some fishes tended to change their diet to other more abundant food when available rather than enter into severe competition. And the present paper seems to support their suggestion.

It may be correct to recognize the interspecific competition for food when two or more species *demand* a certain common food substance. However, I can not decide whether the interspecific competition for food is severe or not from such a fact only that two or more species *feed actually on* a certain common food substance. For example, in an impoundment Sagamiko, cyprinid fishes were found to feed on *Cyclops*, chydorids, midges and some other animals in spring, but almost all fishes depended on bosminids only in summer when the population of the latter increased excessively (Sagamiko Branch, 1957). Is it right to say that the food competition was very severe when fishes of many kinds fed on bosminids only? The competition is not severe in such a case, but the very contrary was the case. I recognize the exsistence of a severe competition when a fish changes its food habit, i.e., in the forced food segregation which is brought about by the interspecific relation among fishes.

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Summary

The standing crops of bottom algae and benthic invertebrates as well as the population and the food of fishes were studied in the middle course of four rivers in Kyoto Prefecture, with the following results.

1) The stomach contents of freshwater fishes change in accordance not only with the composition and amount of their food substances but also with the composition and population of the fish society itself.

2) The food segregation, which is forced by the social relation among fishes, indicates the existence of severe interspecific competition.

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