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On the Significance of the Social Structure for the Mode of Density Effect in a Salmon-like Fish, "*Ayu*", *Plecoglossus altivelis* TEMMINCK et SCHLEGEL[1]

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Introduction

Since the publication of their excellent studies by PEARL and PARKER (1922) on the density effects upon the growth of *Drosophila*, many authors have devoted their efforts to the same problem, using not only the fly but also other animals. Various species of fishes have also been studied by many investigators in this respect, and they have come to the same conclusion that the bigger is the population density of fish the less becomes their growth (WILLER & SCHNIGENBERG, 1927; KAWAZIRI, 1928; KAWAZIRI *et al.*, 1930; MATSUI, 1940, 1952; LECREN, 1949; SWINGLE, 1950; SWINGLE & SMITH, 1950; BARDACH, 1951; YOSHIHARA, 1952; NAKAMURA *et al.*, 1954, 1958; KOYAMA, 1956; KAWAMOTO *et al.*, 1957; etc.).

Using a salmon-like fish, *Plecoglossus altivelis*, called "*Ayu*" in Japanese, our research group has started socio-ecological investigation since 1951. During the course of our study, we found out that the situation mentioned above was not always the case. The present paper deals in some detail with this subject, the data of which were obtained from 1955 to 1957.

Material

Plecoglossus altivelis is one of the most dominant fishes in the rivers of Japan, both numerously and sociologically. It is an anadromous and annual fish, and its life-cycle is summarized as follows: In autumn, the fries hatch out on the lower course of a river and in an instant they are carried down into the sea. The fingerlings spend the winter in the sea and feed on animal plankters. In spring, they ascend a river in schools, and settle down gradually in the stream to graze on diatoms and blue-green algae growing on stones. The adult attains about 15–30 cm in size within the summer season. In autumn, the fish descend to the lower course of the river, spawn on pebble bottoms and die there.

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As we have already reported in the other papers, the fish in the settling season shows various social behaviours (MIYADI *et al.*, 1952, 1953; MIZUHARA *et al.*, 1955; KAWANABE *et al.*, 1956, 1957a; KAWANABE, 1957). These behaviour types may be classified as follows: schooling, solitary wandering, non-territorial solitary residential, solitary territorial and aggregation. The schooling is a social type in which all of its members show common behaviours, e.g., swimming in the same direction or grazing in the similar manner. Solitary wanderers behave independently from one another and have no definite home, but they sometimes come together to form a school or join the school passing nearby. The non-territorial solitary resident is a solitary dweller having a certain range but it does not show the territorial or attacking behaviour to the nearby individuals. In the territorial solitary type each fish has its own defended territory, the area of which being about one square metre. The aggregation is the gathering of the fish in the sleeping and resting time, in which the fishes come together within a certain area but do not show the common active behaviour.

It is also important to remember that a certain individual does not always adhere to a definite social behaviour type, but changes the behavioural type even within a short range of time.

Methods

The social behaviour of the fish was observed either by diving with "Schnaufer-glas", or from bridges or banks using a pair of spectacles with polarlized glass.

The body length of the fish was estimated chiefly from the observation mentioned above but was occasionally checked by the measurement on the caught samples. The error of observation checked in this way was within about five percent.

Table 1. Population in the River Ukawa (between the river-mouth and the upper end of the distribution) of *Ayu* in the years of 1955–1957.

	1955	1956	1957
Number of individuals in ascending season, estimated by direct observation* and recovery of tagged fish	1,000,000	250,000	20,000
Ratios	50	12	1
Number of individuals in settled season, estimated by direct observation and catching record	500,000	80,000	10,000
Ratios	50	8	1
Densities in settled season per 1 m^2 of water-surface (the average value in the whole investigated area)	5.4	0.9	0.1

* The number was counted at the dam near the river-mouth, i.e., between the spawning region and the station of Ukawa-basi. This place is indicated by the symbol of *water-fall* (⩪) in Fig. 1.

Stations

The River Ukawa, in which most of our studies were carried on, is a small river (ca. 22 km in length), emptying into the Japan Sea on the north coast of Kyoto Prefecture.

The fish population of this river is relatively dense as compared with that of many other rivers, though the annual fluctuation is very large. The population counts in both ascending and settling seasons from 1955 to 1957 are shown in Table 1.

The investigations were made chiefly on three stations in the middle course of this river (Fig. 1). The station "Miyanosita" is chosen as a representative of "Hayase-rapids" one of the river-bed types in which water seeths white on loosely packed boulders. The station "Ukawa-basi" is a representative of "Hirase-rapids", in which the bottom consists mainly of gravels half buried in sand and the water surface is smooth. The station "Maekake" is an example of "Huti-pools", or a slowly flowing deep with rock walls on one side of the banks. Beside these three types, there is a type called "Toro-pool" of shallow sandy bottom, but is not utilized by *Ayu* in its settling season. The details as to the mode of utilizing these various river-beds by *Ayu* have already been reported in the other papers (KAWANABE *et al.*, 1957b, c).

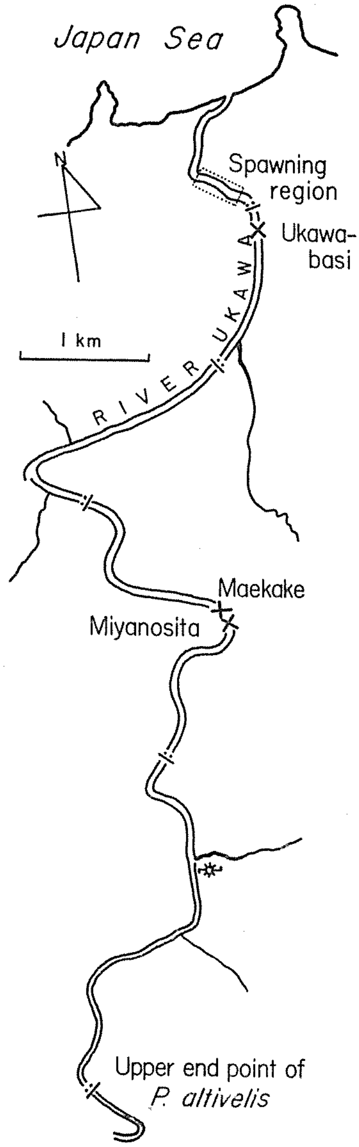

Fig. 1. Map of the River Ukawa. Cross marks indicate three main stations.

Results

A) *Social behaviour in different population density*

The social behaviours of *Ayu* as mentioned above, except the aggregation which is a resting form, may be divided roughly into two major groups, namely wandering and staying types. The former includes schooling and solitary wandering, and the latter involves non-territorial solitary residential and solitary territorial.

Fig. 2 gives the ratios in different river-bed

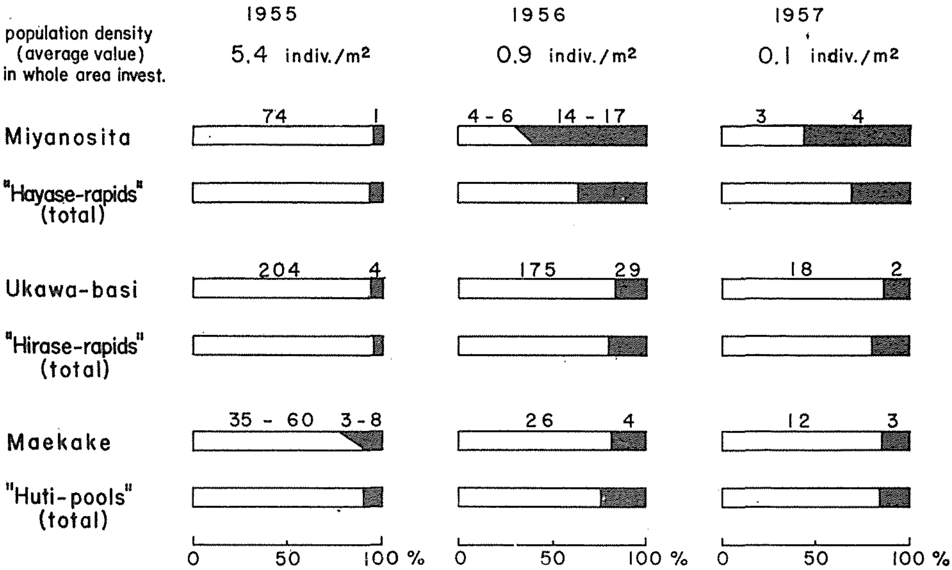

Fig. 2. Diagram showing the numerical ratio of *Ayu* belonging to the wandering and staying behaviour groups observed at three river-bed types in the settled season (July) of the years 1955–1957. Two figures on the upper row show the results obtained at the river-bed type of Hayase-rapid, of which the former is the result at the station Miyanosita which is chosen as a typical example of the river-bed type, and the latter is the total of the counts at all river-beds belonging to this type. The figures of the middle and lower rows indicate the results obtained at the types of Hirase-rapid and Huti-pool. The wandering fish are indicated by white and the staying ones by black columns. The number on the first figure of each row indicates the estimated number of the fish.

types of the fish adhering to either of the two behaviour groups. In 1955, when the density of *Ayu* was high, most fish showed the wandering behaviour, and only a few fish were staying. In both years of 1956 and 1957, on the contrary, the density was lower and the staying behaviour was shown by more fish than in 1955. These findings seem to suggest that the pattern of social behaviour changes in different population densities. Moreover, by examining their behaviour more

Table 2. Average value and its confidence interval (reliability: 90 percent) of the body length of *Ayu* living in three river-bed types in the settled season of each year.

	1955	1956	1957
Hayase-rapids	16.2±0.9*	13.0±0.7*	15.5±0.7*
Hirase-rapids	15.5±1.1	10.1±2.0	14.2±0.6
Huti-pools	17.0±0.8	12.4±0.6	14.9±0.7

* unit : cm

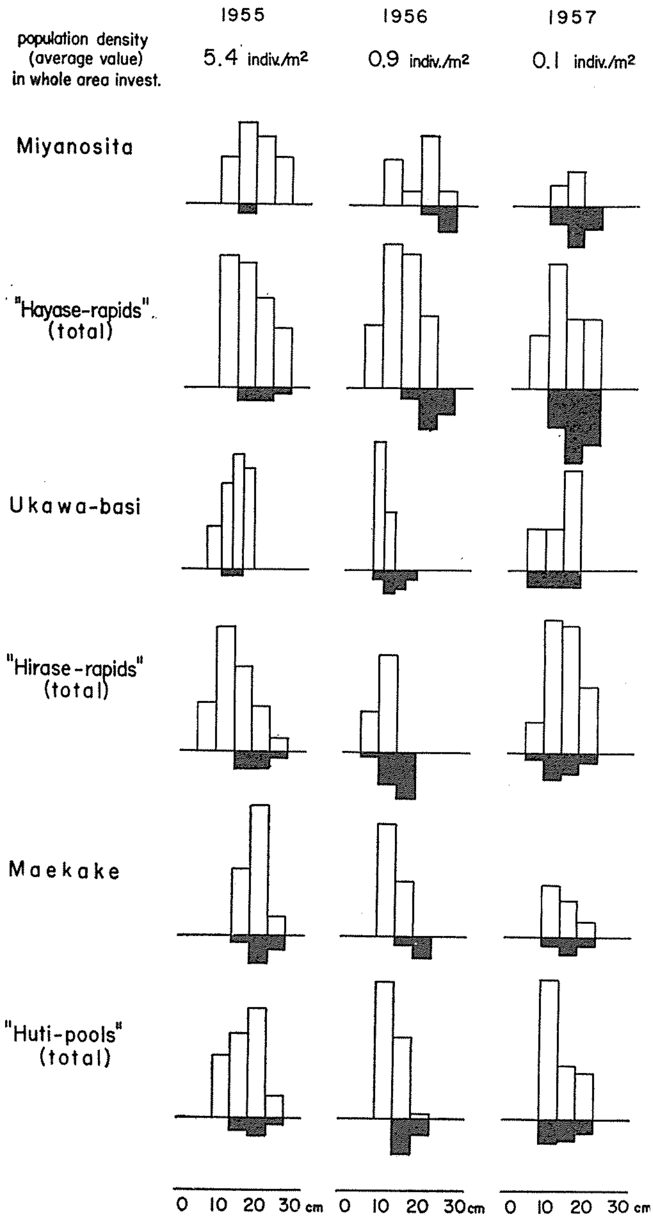

Fig. 3. Diagrams of the body length distribution of *Ayu* to show the two behaviour groups in the settled season of the years 1955–1957. Observed stations are referred to Fig. 2. The wandering fish are indicated by white histograms, and the staying ones by black.

precisely, it was revealed that the behaviour type of *Ayu* was influenced by other individuals behaving in the same ways as well as in different ones.

In 1955, when the fish population was very high, the wandering group was very common, and most of them were of the schooling type. Among the rest of fishes which belonged to the staying group, though they were few, non-territorial dwellers were more numerous than the territorial ones. Under these social conditions, it was frequently met with that the schooling group often drove into the territories of other fishes. In such an occasion, a territorial fish tries to defend against the invaders for a while, but usually fails to drive them away, and finally gives up the chase to become a member of the school, because the invaders are too numerous and come too often. In this way, it is apparent that the life of territorial type is less stable than that of the schooling type under the condition of very high density as occurred in 1955.

On the contrary, in 1956, the territorial behaviour was the common and stable type, and was found in almost whole area of the "first class" river bottom. The wandering fish, which were less numerous, tried to invade a certain territory, but they were usually driven away and forced by territorial fishes to become solitary and live in worse places such as the pebble or sand bottoms placed near the bank. In other words, it was difficult for the wandering fish to change their behaviour type and to become the territorial fish. This is a marked social difference between 1955 and 1956.

In 1957, when the density was very low, the life of both the territorial and schooling types seemed equally stable both in social and food conditions.

B) *Body length distribution and feeding in different density*

The distribution of body length of *Ayu* is shown in Fig. 3 and Table 2.

In 1955, no marked difference was seen in the body length between the fish of wandering and staying types. The frequency of the feeding behaviour on the algae, too, did not differ so markedly between the two behaviour groups (KAWANABE *et al.*, 1956).

In 1956, however, a difference in the body length was notable between the fish of the two behaviour groups, i.e., staying fish were much larger than wandering ones; and the staying fish grazed more frequently on better algae than the wandering ones.

In the case of much lower density as was found in 1957, the difference in the body length was not seen between two behaviour groups.

Discussion and Conclusion

In the earlier paper of our research group, it was revealed that different social behaviours were shown by *Ayu* in accordance with the different population densities. That is, the territorial behaviour is stable only when the population density is low, and when the density is high the territory is broken down by the frequent invasions of the schooling fish. In a very high density, if a certain territorial fish should succeed in keeping its own range against the invasion of the schooling fish, it would become too busy to have the time for grazing, since the fish had to spend all the time in driving away the invaders from its territory. Thus, it may be concluded that only the low density will permit the establishment of the territoriality.

Next, we can supply some new data on the relation between the body length and the social structure. In 1957, no marked difference was found in the body length among the fish showing different social behaviours. This may be due to the very low population density, which enabled the fish to choose whichever type of life they lived with no social interference.

In 1956, the territorial fish were abundant and their territories were stable, but both the schooling and the wandering fishes were less frequent. Under this social structure, the difference in body length was recognized between the fish showing the different behaviours. How the difference in body length was brought about? As one of the chief reasons, it may be taken into account that wandering fish can not invade the "first class" grazing ground which is preoccupied by territorial one.

The social structure found in 1955 was notable in that most fish showed the schooling behaviour, and only a few fish could take unstable territorial behaviour. Under such conditions, there occurred no marked difference in the body length, regardless of the social behaviours. Here, it is worthy of notice that any fish may choose either of the schooling and territorial types of life, but the territory is repeatedly broken down by the schooling fishes in the high population density. By this reason, the fishes of different behaviour types may be said to be placed under similar condition in regard to the grazing chance. It is, therefore, natural that there occurs no difference in the body length.

If the body length is to become smaller under the high density than under the low density, smaller average length should be expected in 1955 than in 1956. But in fact, the average body length of *Ayu* in 1955 was rather larger than that in 1956, being inconsistent with the results obtained by previous authors. The concept of suboptimum density will not be applied in this case, because the density in 1956 is nearly the average density of *Ayu* of this river.

There is no doubt that the growth of the fish is related intimately to the amount of the food substance. We do not, however, consider that the difference of body length in our case is attributable *solely* to the difference in the production of food algae in both the years. Although the population density in 1955 was, as mentioned above, very high as 5.4 individuals per square metre, almost all fish grew into good size. This fact seems to indicate that even in such a high population, the quantity of food algae was not insufficient for the growth of fish. It was true that the quantity of algae in 1956 was a little less than that in 1955, but the difference seemed very slight as compared with the difference of the fish density in the two years. Under these circumstances, it seems unprobable in this case that the amount of algae was directly responsible for the difference of the body length.

It is indeed surprising that the average body length is rather larger in 1955 when the density was much higher than in 1956 (Fig. 3 and Table 2), but the difference becomes more evident in the comparison of the size of the fish which have different social behaviours. While no marked difference was recognized in the average body length between all fishes of 1955 and the territorial ones in 1956, the wandering fish without territory in 1956 was much smaller than either of the former two groups. Here the question might be raised whether the social behaviour of *Ayu* and its body length would differ from those found in our actual observation, if the quantity of food algae in 1956 was more abundant or nearly equal to that in 1955. So far as the results obtained by preceding investigators and our collaborators concern, the possibility is negative, i. e., the break down of the territoriality is not probable in such a low density as was found in 1956; and the social form has not been recorded in such a dense population of *Ayu* as 5.4 individuals per square metre, except in our investigation. Furthermore, our observation has revealed that the territory is about one square metre in size, which does not change *directly* with the difference in the quantity of algae itself.

Thus we are led to the conclusion that the growth of non-territorial fish is controlled not only by the production of the food algae, but also by the presence of territoriality. In other words, the social structure changes in accordance with the difference in the population density, and the social structure interfers with growth of those placed in worse habitat.

As was mentioned in the introduction, previous authors have usually emphasized that the greater is the population density the less is the growth size. In contrast to this thesis, however, our investigation seems to present a case in which the growth in the dense population is larger than that in the thin one. As a cause of such an odd situation the mediation of the social structure may be considered. Our opinion is that the population density influences the growth of the fish, but it does so through the definite social structure peculiar to a species. The growth, of course, may be influenced, besides food substances, by some internal or external factors such as the condition of earlier life in the sea, water temperature, discharge of river, etc. Our present knowledges about these factors are insufficient, so that the thorough solution of the above phenomenon must be expected in future.

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Summary

The population density, the social structure and the growth of a salmon-like fish *Plecoglossus altivelis*, or *Ayu* in Japanese, were studied in the River Ukawa from 1955 to 1957, with the following results.

1) The social structure of *Ayu* differs according to the difference in the population density.

2) Although the body length distribution of *Ayu* is influenced by its population density, the effects of the latter on the growth size are not direct but are mediated by the social structure, i. e., the difference in size within a population is brought about between the fishes in different social situations by the differentiation of the social structure.

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