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Group Effect on Oxygen Consumption of the Ayu (*Plecoglossus altivelis*) in Relation to Growth Stage

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Abstract Group effects on oxygen consumption of the ayu, *Plecoglossus altivelis*, in relation to growth stage were investigated by a polarographic oxygen electrode, using continuous flow respirometry. The oxygen consumption of an isolated fish in the respirometer tube, which either had shown signs of aggressive behavior in the aquarium when kept together with a number of fish, or had grown to 9 cm in standard length in the aquarium when kept solitarily, increased markedly when the fish was placed in visual contact with conspecific fish. However, when an isolated fish, which had neither shown signs of aggressive behavior nor grown to 9 cm in standard length, was placed in the same visual condition, its oxygen consumption decreased or did not change. Such an excitatory group effect on oxygen consumption seems to be established depending on the habit of solitary living and aggressive behavior, while a soothing group effect seems to be caused by the habit of schooling, according to growth stage.

Research on fish aggregation has shown that oxygen consumption of fishes is controlled or modified by the number of fishes mutually participating in fish respiration. "Group effects" may be displayed in one or both of the ways, a soothing and an excitatory effect. A soothing effect is shown by the fact that aggregating fish have a lower rate of oxygen consumption per fish than those in isolation (Shlaifer, 1938 on the goldfish; Geyer and Mann, 1939 on *Perca*; Job, 1955 on *Salvelinus*; Stefan, 1958 on the stickleback and minnow; Delco, 1963 on the cyprinid fishes; Ryzhkov, 1970* on the bream; Uematsu, 1971 on the guppy; Parker, 1973 on the gizzard shad etc.; Itazawa et al., 1978 on the rainbow trout and the medaka; Smatresk and Herreid, 1980 on the swordtails; Kanda and Itazawa, 1981 on the catfish eel). The so-called soothing effect is also present when the rate of oxygen consumption of the fish does not change according to group composition (Bowen, 1932 on the catfish; Schuett, 1934 on the goldfish; Umezawa and Watanabe, 1979 on the medaka). The excitatory effect is shown when aggressive behavior occurs among, for example, the pumpkinseed, elevating its oxygen consumption rate by nearly one-half the active level (Brett and Sutherland, 1965). The sight of its mirrored image increases the oxygen consumption of blennies (Wirtz and Davenport, 1976), or the oxygen consumption of an isolated goby in the respirometer tube increases markedly not only when the fish is placed in visual contact with conspecific fish, but also with heterospecific species having similar feeding habits as the test goby (Umezawa and Kanikawa, 1980; Umezawa et al., 1981).

The purpose of the present study is to repeat the analysis of the group effect on the oxygen consumption of the ayu, because this species exhibits changes of behavioral patterns according to growth stages, i.e., schooling behavior in the anadromous period in the juvenile stage, aggressive behavior in the segregative habitat period in the young stage, and schooling behavior in the catadromous breeding migration period in the adult stage.

* His data, however, show that the rate of oxygen consumption of the isolated fish in the respirometer placed in aquarium with 10 fishes either increased or decreased.

Materials and methods

Secondary freshwater ayu, *Plecoglossus altivelis*, between 3 and 13 cm standard length (SL) were used. The juvenile fish had been acclimatized in freshwater after artificial fertilization and breeding in large brackish water tanks at the Kochi Prefecture Freshwater Fisheries Laboratory. Test fish had been collected from the

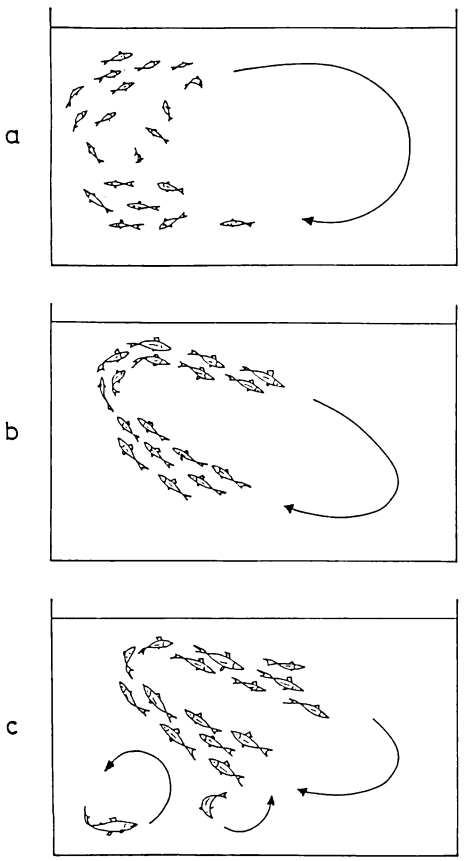

Fig. 1. Behavior pattern of fish when kept together with about one hundred and fifty fish in an aquarium (50×100×40 cm deep). a, aggregation of fish in the range of 4～6 cm SL; b, schooling of fish in the range of 6～9 cm SL; and c, aggressive behavior of fish longer than 9 cm SL. For full description, see text.

tank and about one hundred and fifty fish were transferred into each of two aquaria (50×100×40 cm deep) with well-aerated tap water.

When these juvenile fish grew to about 5 cm SL, three fish were kept together and one fish was kept solitarily in each aquarium (30×60×35 cm deep) in which a relatively larger stone (12×10×7 cm in height) was placed on the pebbles spread on the bottom of the central region. The ayu accepted food at a temperature of about 20°C throughout the experiment.

The experimental set-up used to determine group effect on oxygen consumption is similar to that used in a previous report (Umezawa et al., 1981). Determination of oxygen consumption was made on a fish kept in a respirometer tube ranging from 1.1 to 5.0 cm in diameter according to the body size, which was immersed in an open container filled with water at 20°C. The fish was alternately placed in visual contact with no surrounding fish (isolated) and with two conspecific fish, one on each side (grouped), separated by side septa, which were placed over the entire length of both sides of the respirometer tube and kept horizontally. The septa were raised and lowered with a miniature motor. No marked signs of respiratory responses of the fish were found after rising and lowering of the septa, independent of the presence of the surrounding fish.

Determinations of group effect on oxygen consumption were made on the same fish in isolated or grouped state. The oxygen consumption rates averaged the values from successive measurements of at least 30 min duration, excluding the initial 15 min after the fish was placed in visual contact with other specimens.

The experiments were carried out from May to October in 1981 and 1982. About 20 to 100 test fish were used in each experiment. Experimental fish were removed at least 7 days before the next experiment. The same surrounding fish were used two or three times in each experiment, then allowed to rest for several days.

Results

Some observations on habits. Attempts to observe the appearance of aggressive behavior of the ayu were made on about one hundred and fifty juvenile fish which were kept together in an aquarium (50×100×40 cm deep). In the beginning they continued to swim separately in all directions (Fig. 1a), and then tended to form a school in a corner of the aquarium (Fig. 1b). The school continued to move a particular direction until it was altered by some influence, which could be either extrinsic or intrinsic. When the fish grew up and began to swim actively, it was found that one larger fish (about 9 cm SL) attacked other smaller fish and kept a territory (Fig. 1c). When such an aggressive fish was removed, another larger fish would similarly showed signs of aggressive behavior after about one day.

Similar experiments were performed on three

fish kept together in an aquarium (30×60×35 cm deep). In this case three fish of about 5 cm SL were simultaneously placed together in the aquarium. From the beginning the fish swam together in the same direction (Fig. 2a). When they grew to about 9 cm SL, one of them showed signs of aggressive behavior and occupied a territory, which was formed sometimes around the stone set at the bottom of the central region of the aquarium, as an immovable center (Fig. 2b, c).

Group effect on oxygen consumption.

Responses of test fish showed signs of aggressive behavior. Measurements were made of oxygen consumption of the isolated fish, which had been either kept together with a number of fish or with three of fish, in relation to change in visual conditions. The results expressed in percentage of oxygen consumption rate of the fish in isolated state* (Fig. 3) indicated that fish occurring in groups consumed more oxygen than solitary individuals. There were statistically significant differences in comparison of the means in oxygen consumption of grouped fish and isolated ones ($P<0.001$), using a t-test.

Responses of test fish showing no signs of aggressive behavior. Measurements were performed on oxygen consumption of the isolated fish, which had been either kept together with a number of fish or with three fish, in relation to change in visual conditions. The results obtained in percentage of oxygen consumption rate of the fish in an isolated state showed a lower rate of oxygen consumption than those in groups (Figs. 4, 5). Comparisons between the means in oxygen consumption of the fish in grouped states and isolated individuals resulted in a statistically significant difference ($P<0.001$ in Fig. 4) and no statistically significant difference ($P>0.1$ in Fig. 5), using a t-test.

It is clear, therefore, that the increased oxygen consumption of ayu in groups is not independent of aggressive behavior.

Responses of test fish which had been reared solitarily. Similar measurements were made of oxygen consumption in relation to the size of the test fish. The results obtained from various sized test fish placed in visual contact with surrounding fish are shown in Fig. 6. Fig. 6 indicates that the rate of oxygen consumption in smaller test fish (less than about 9 cm SL) showed no differences between grouped and isolated fish, giving no statistically significant difference between the means ($P>0.1$) using a t-test. The rate of oxygen consumption in larger test fish (more than about 9 cm SL) was higher when grouped than when isolated, giving statistically a significant difference between the means ($P<0.001$) using a t-test. Thus, it is surmised that larger fish differ essentially from smaller ones in response to surrounding fish and that about 9 cm SL seems to be critical for the group effect on oxygen consumption.

Moreover, it may be an important fact that the ayus had potential aggressive abilities even when they had been reared solitarily in the aquarium. Unfortunately, no measurements

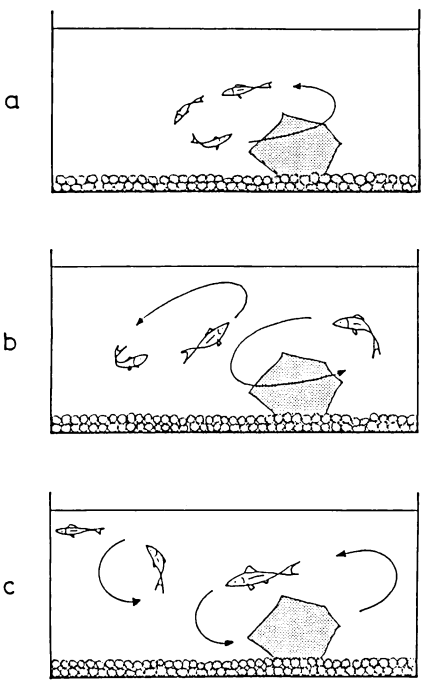

Fig. 2. Behavior pattern of fish when kept with two other fish in an aquarium (30×60×35 cm deep). a, schooling of fish in the range of 6～8 cm SL; b, aggressive behavior of fish in the range of 8～9 cm SL; c, territory and aggressive behavior of fish longer than 9 cm SL. For full description, see text.

* The standard oxygen consumption is in the range 250～400 ml/kg/h at 20°C with average flow rates (about 125 cm/h).

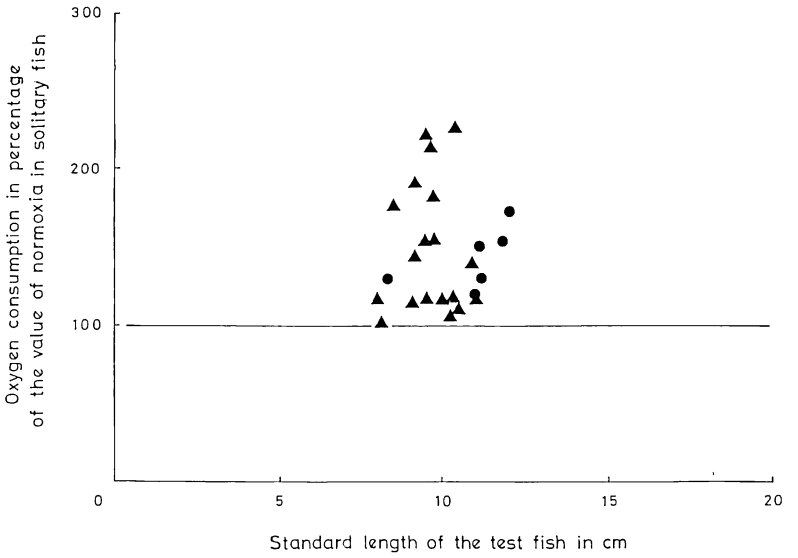

Fig. 3. Changes in oxygen consumption of various sizes of test fish which showed signs of aggressive behavior when kept together with a number of fish (●) and with two other fish (▲). Each fish was placed in visual contact with two conspecifics. Temp., 20°C.

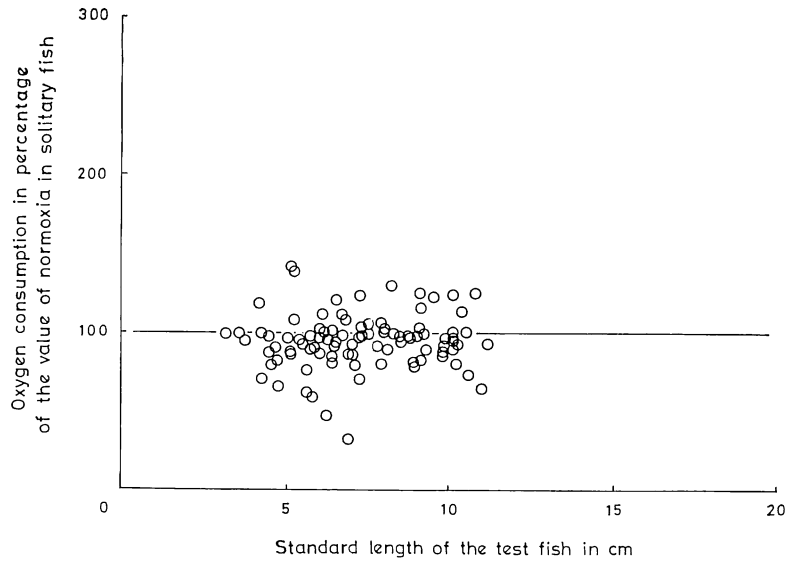

Fig. 4. Changes in oxygen consumption of various sizes of test fish which did not show signs of aggressive behavior when kept together with a number of fish. Each fish was placed in visual contact with two conspecifics. Temp., 20°C.

were performed on sexually mature fish in the aquaria, because of markedly weakened viability.

Discussion

According to some authors (Shlaifer, 1938; Geyer and Mann, 1939; Job, 1955; Stefan,

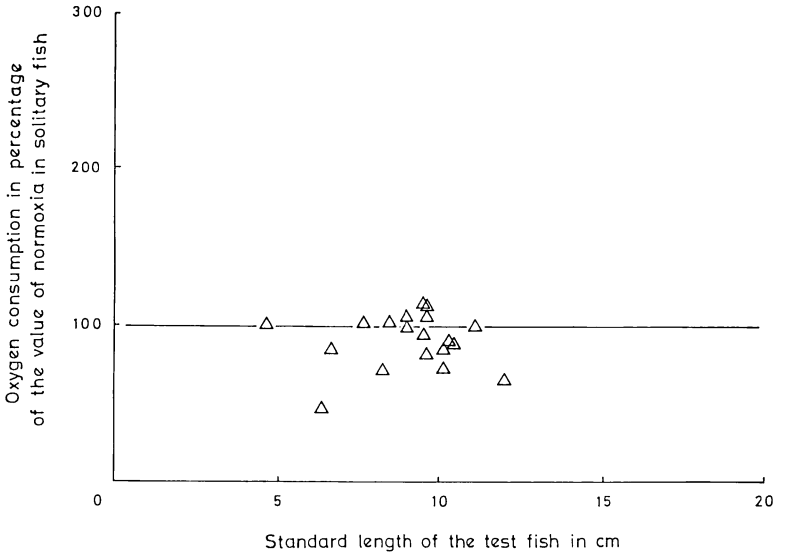

Fig. 5. Changes in oxygen consumption of various sizes of test fish which did not show signs of an aggressive behavior when kept with two other fish. Each fish was placed in visual contact with two conspecifics. Temp., 20°C.

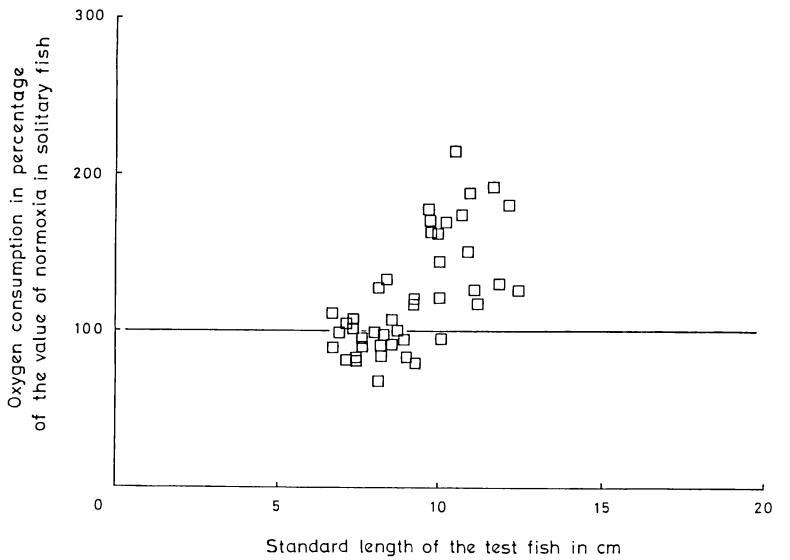

Fig. 6. Changes in oxygen consumption of various sizes of test fish which had been reared solitarily. Each fish was placed in visual contact with two conspecifics. Temp., 20°C.

1958; Delco, 1963; Ryzhkov, 1970; Uematsu, 1971; Parker, 1973; Itazawa et al., 1978; Smatresk and Herreid, 1980; Kanda and Itazawa, 1981), an isolated fish consumes more oxygen than do fish with contact with other conspecifics. Other authors (Bowen, 1932; Schuett, 1934; Umezawa and Watanabe, 1979) indicated that group fish show no significant difference from isolated fish in the amount of oxygen consumption. Therefore, it is suggested

that the effect of grouping on oxygen consumption of fishes, which have been thought of as schooling or non-schooling fish, is a kind of "soothing group effect" as described by Parker (1973) as a "calming effect".

On the other hand, several authors reported that species with a tendency for aggressive behavior consumed a higher rate of oxygen when grouped than when isolated (Brett and Sutherland, 1965 on the pumpkinseed; Wirtz and Davenport, 1976 on the blennies; Umezawa and Kanikawa, 1980 and Umezawa et al., 1981 on the goby). Thus it is necessary to establish another effect, i.e., "excitatory group effect" on oxygen consumption of fishes.

As mentioned previously, the ayu exhibits changes in behavioral patterns with growth stages in natural environments: i.e., anadromous migration, habitat segregation and catadromous migration. Correspondingly, they show signs of schooling, solitary and schooling-like habits, respectively, and exhibit a tendency to be aggressive in the stage of habitat segregation.

In the present experiments an isolated ayu was kept in the respirometer tube and placed in visual contact with surrounding conspecifics. The results obtained indicated that oxygen consumption of the fish was affected or not affected by changes in visual conditions to growth stages. The fish which showed signs of aggressive behavior consumed more oxygen when placed in visual contact with surrounding conspecifics. It was also found that the oxygen consumption of ayu of about 9 cm SL, increased markedly when placed in the visual condition even when the fish had been reared solitarily in the aquaium. However, when fish less than 9 cm SL, which had not shown signs of aggressive behavior, were placed in visual contact, their oxygen consumption decreased or did not change.

These results give evidence that ayu show substantial differences in oxygen consumption according to growth stages when they are placed in visual contact with surrounding conspecifics.

Thus, it is surmised that a soothing group effect shown by a decrease or no change in oxygen consumption of the ayu in younger stages is caused from its habit of schooling, and that an excitatory group effect indicated by an increase in the oxygen consumption during the period of habitat segregation results from its habit of solitary living and aggressive behavior at that stage.

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アユの酸素消費量に及ぼす群効果

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アユの酸素消費量に及ぼす群効果をアユの成長段階との関係から調べた．アユは稚魚から成長するにつれて遡河，すみわけ，降河と行動習性がかわり，すみわけの時期では攻撃行動を示す．酸素消費量はポーラログフ酸素電極を用い，流水式の呼吸室により，アユの呼吸前後の水の溶存酸素量の差から求めた．呼吸室に入れた単独のアユが両側に1個体ずつ配した同種の魚に視覚的に接した場合，単独アユが群れ飼育及び3個体飼育で攻撃行動を示した個体あるいは単独飼育で標準体長およそ 9 cm に成長した個体のときは酸素消費量が増加したが，これらの飼育で攻撃行動を示さなかった個体あるいは標準体長がおよそ 9 cm に達しない個体のときは酸素消費量が減少したか，もしくは変化を示さなかった．アユの酸素消費量に及ぼす群効果には成長段階による相違があり，酸素消費量の増加の興奮効果はアユのすみわけと攻撃行動習性に由来し，酸素消費量の減少の安静効果は群行動習性に起因すると云えよう．

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