Effects of Environmental Factors on Jumping Behaviour of the
Juvenile Ayu Plecoglossus altivelis with Special Reference to
Their Upstream Migration

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The jumping behaviour against a waterfall, of ayu is known to be closely related with the
tendency to migrate upstream in a river. In order to determine the triggering mechanism for
upstream migration in the ayu, the effects of environmental factors on jumping activity were ob-
served.

Jumping behaviour was active in the time corresponding to daytime even under constant
light conditions, LL and DD photoperiods, as well as 16L8D. The jumping activity was facilitated
by changes in light intensity, a raise in the water temperature, shallow water depth, and deprivation
of food. Accordingly, these changes in environmental factors appeared to have the potential to
act as a trigger of the migration.

The ayu Plecoglossus altivelis is an amphidromous salmonoid fish of the family Plecoglossidae
with a life span of only 1 year. In autumn, newly
hatched larvae, 6 mm long, drift downstream to
the sea and spend the winter months there.1) The juveniles (about 60 mm long) begin upstream
migration in spring and grow to a length of 150–300 mm by the end of summer when mature fish
spawn and then die.

Field observations have shown that the up-
stream migration of the juvenile ayu mainly
occurs during the daytime.2-4) However, the
timing of the peak of migration varied between
rivers as well as between dates in the same river.5-4) These lines of facts indicate that environmental
factors such as a rise in water temperature may
trigger the migration.6)

Our approach adopted here was a laboratory
experiment to test this assumption. Migrating
ayu juveniles fling themselves against waterfalls at
dams of rivers8,7) in the same way as salmon.8-10) This “jumping behaviour” was defined here as
the jumping response to stimuli of a waterfall.11) Tsukamoto et al.11) has shown in the laboratory
that the tendency of jumping behaviour against a
waterfall is positively related to the tendency to
migrate upstream in both artificial and natural
rivers; i.e., the more active the jumping, the
stronger the tendency to go upstream. Thus, jumping behaviour in the laboratory was con-
sidered to be available as an index to estimate a
tendency of upstream migration by the ayu in
natural rivers.13)

To test the role of environmental factors as a
final trigger for the upstream migration of ayu,
the present study was carried out to observe
the effects of environmental factors on their
jumping behaviour.

Material and Methods

Fish

The fish used in this study were the juveniles
(70 mm SL) of landlocked ayu caught at Lake
Biwa in June (Table 1). Lake Biwa fish of this
size are known to show a strong tendency to
migrate upstream when released in a river.11-13)
Fish were usually acclimated to outdoor ponds
for a week after having been transported to the
laboratories prior to the experiments.

Diel Rhythm

Diel variations in jumping activity were
observed in the three sets of type-A apparatus
shaded with black covers (Fig. 1A) under a con-
stant water temperature (19.3°C) and controlled

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light conditions. Two hundred fish were placed in each tank and given photoperiods of 16L8D (lightness from 4:00 to 20:00, darkness from 20:00 to 4:00), LL (constant lightness), and DD (constant darkness), respectively. Light intensity at the water surface in the tank was 60 lx when a fluorescent light was on and was less than 0.02 lx during the dark period.

The number of jumping fish was continuously counted with a photoelectric sensing system for 5-9 days. The jumping rate was calculated as follows:

\[
\text{Jumping rate (\%) = 100 \times \frac{\Sigma J}{N}}
\]

where \( \Sigma J \) is the accumulated number of jumping fish per hour, \( N \) is the number of fish placed in the test tank.

**Light**

Effect of sudden change in light intensity was tested with the same fish and apparatus used for the diel rhythm test. The fish acclimated to LL for 9 days in the test of diel rhythm were subjected to L (60 lx)-D (<0.02 lx) alternations at intervals of 0.5-2 h from 9:00 to 22:00 hours. The fish acclimated to DD for 5 days were subjected to L (1500 lx)-D (<0.02 lx) alternations at random during a 32 hours period. The jumping rate was determined in the same manner as for the test of diel rhythm.

**Water Temperature**

Three sets of the type-A apparatus (Fig. 1) were placed indoors, each of which contained a group of 150 fish. The effects of temperature on the jumping rate were examined for the following three categories. (1) temperature level: three groups of 150 fish had been acclimated to 10, 15, and 20°C for 24 h, following which jumping rates were measured for 2 h at each temperature. (2) acclimation temperature: three groups of 150 fish had been acclimated to 10, 15, and 20°C for 27 hours, following which they were subjected to 15°C. Measurements were made at 15°C for 2 h. (3) temperature fluctuations: two groups of 150 fish were subjected to 5°C rises and 5°C falls at 7°C/h from the acclimation temperature of 15°C. The light intensity was kept less than 50 lx during the experiments. The jumping rate was estimated as those in the test of
Diurnal rhythm.

**Water Depth**

The effect of water depth was tested using the type B apparatus of 3 cages with a flat bottom (Fig. 1) set in an outdoor pond. Three water depths, i.e., 5, 19, 50 cm, were chosen for the cages. To exclude the density effect on the jumping rate, the number of fish placed in each cage was equalized per area of the bottom of cage (experiment 1) or per volume of water in the cage (experiment 2). In the experiment 1, 56 individuals were placed per cage (352 individuals/m²). In the experiment 2, fifteen, 56, and 149 individuals (1978 individuals/m³) were used respectively for 5, 19, and 50 cm deep cages. Twenty four hours later, the number of fish remaining in the cages were counted and the jumping rates (percentage of the number of fish jumping out of the cage to the number of fish placed in the cage) were compared between the cages and between the experiments 1 and 2. The water temperature was varied between 16 and 23°C.

**Starvation**

A total of 1209 fish were divided into two groups and each group was marked by fin clipping. One group was fed with commercially prepared dry diets to near satiation several times a day for 4-5 days. During that period, the other group was starved. About 300 fed fish and 300 starved fish were placed together in the type-C apparatus (Fig. 1) in the morning. Six hours later, the jumping rate (percentage of the number of fish jumping out of the cage to the number of fish placed in the cage) was determined for each group (Trial 1). A similar experiment was carried out on the remaining 300 fed fish and 300 starved fish (Trial 2). Temperature ranged from 19 to 20°C during the experiments under natural light conditions.

**Data Analyses**

G-test was used for statistical analysis of the data obtained.

**Results**

**Diurnal Rhythm**

In 16L8D, the mean jumping rates by day and by night during the experimental period were 12.7 and 1.1%/h respectively. Those in LL were 9.8 by day and 2.1%/h by night, and 6.6 and 1.4%/h in DD, respectively. Thus, the jumping rates by day were 5–12 times as high as those at night under every light condition examined here (P<0.001; Fig. 2), presenting a clear diurnal rhythm. This rhythm might be under control of the endogenous circadian rhythm of the ayu, since jumping behaviour was active in the time corresponding to the daytime even under constant environmental conditions (LL, DD).

The jumping activity under every light condition were decreasing after the start of the experiment. This phenomenon may be attributed to the fish's internal conditions, since it was usually observed that jumping activity was high when fish were at first transferred to the apparatus and then decreased with acclimation to its conditions. However, it should be noted that, in DD and LL, the activity rapidly decreased and was poor when compared to that in 16L8D. The rapid decrease and/or poor activity in LL and DD was caused by constant light intensity; i.e., fluctuations in light intensity seemed to be necessary to maintain jumping activity. The evidence is shown in Fig 3.

**Light**

The mean jumping rate during the experimental period, of LL-acclimated fish was 76.1%/h in darkness, 42 times as high as 1.8%/h in lightness (p<0.001; Fig. 3A). Conversely, DD-acclimated fish showed the jumping rate of 13.6%/h in lightness, 9 times as high as 1.5%/h in darkness (p<0.001; Fig. 3B). Thus, sudden changes in light intensity, both rise and fall, facilitated jumping.

**Water Temperature**

Temperature level: the jumping rate at acclimation temperature of 20°C was the highest, 149%/h, and those at 15°C and 10°C were 52%/h and 3%/h in order (P<0.001; Fig. 4). Thus, high temperature level stimulate jumping behaviour.

Acclimation temperature: the jumping rates of fish acclimated to 10, 15, and 20°C prior to the experiment were 73, 45, and 12%/h when tested at 15°C, respectively (Fig. 5). These values were significantly different to one another (P<0.001) and even at the same temperature level, fish previously acclimated to lower temperatures were facilitated in jumping, while those acclimated to higher temperature were depressed.

Temperature fluctuations: a rise in water temperature facilitated jumping behaviour of the juvenile ayu, while a fall inhibited it (Fig. 6), which changes in the activity should be noted to...
be reversible according to temperature fluctuations.

**Water Depth**

The jumping rate of fish contained in shallower water depth was higher than that of fish in deeper water (Fig. 7): jumping rates of fish in 5 cm deep significantly differed from those at 50 cm in both experiments 1 and 2 (P < 0.05). Since the values at each depth did not differ between the experiments 1 and 2 (P > 0.05), the difference in jumping rates among different depths were caused by the depth itself, not by density effects.

**Starvation**

Starvation increased the jumping rate (Table 2): starved groups showed a higher jumping rate than fed groups in both trials 1 (P < 0.01) and 2 (P < 0.001).

**Discussion**

In order to migrate upstream, it is necessary for the ayu to fill the endogenous conditions such as age and size peculiar to the migration time and endocrinological development to an appropriate state. Environmental cues are well known to play an important role as a final trigger of fish migration. Field observations suggested that environmental factors such as a rise in water temperature is a factor determining seasonal or diel timing for upstream migration by the ayu. The juvenile ayu crowd into river mouths in the early spring but they do not migrate upstream when the river temperature is low or lower than that of the sea (or lake). The juveniles start their upstream migration at a river temperature of above 10°C, following which they increased their upstream migration with the spring rise in temperature. The upstream migration mainly occurs during the daytime. However, the diel peak of migration varied between rivers as well as between dates in the same river. The number of migratory fish increased with a diel rise in the river temperature. Sudden changes in light intensity also facilitated the upstream migration at fishways of dams. The present study found that jumping behav-
Our data supported the above observations in the field. Shallow water also facilitates swimming upstream in an...

Fig. 3. The effects of sudden changes in light intensity on jumping rate of juvenile ayu at 19.3°C. Prior to the experiment, fish were acclimated to constant light intensity of LL (60 lx) for 9 days (A) and DD (<0.02 lx) for 5 days (B). L-D alternations are shown in light regimes represented on abscissa.

Fig. 4. Jumping rate of juvenile ayu at three different temperature levels. Measurements were made for 2 h. Fish were acclimated to each temperature for 24 h prior to the experiments. Asterisks indicate significant differences (P < 0.001; G-test).

Fig. 5. The effects of the acclimation temperature on jumping rate of juvenile ayu at 15°C. Prior to the experiments fish were acclimated to 20°C (A), 15°C (B), and 10°C (C) for 27 hours, respectively. Asterisks indicate significant differences (P < 0.001; G-test).

Fig. 6. The effect of temperature fluctuations on the jumping rate of juvenile ayu. Two experimental groups A and B were simultaneously exposed to the symmetrical changes in water temperature. Fish were acclimated to 15°C prior to the experiments.
artificial river.\footnote{M. Ujiie, S. Fushiki, and Y. Ohno: Sci. Rep. Shiga Pref. Fish. Exp. Stn., 36, 21-35 (1983).} This depth effect on the jumping behaviour may be caused by increase in stimulation intensity of a waterfall with decreases in water depth, since the increase in the sound pressure level (as an element of stimuli of a waterfall) facilitated jumping.\footnote{Uchida and Tsukamoto, unpublished data} Current velocity (stimuli) may also affect the upstream migration of the ayu.\footnote{T. Kobayashi: Aquabiology, 17, 440-444 (1981).} However, a similar depth effect was observed in jumping behaviour without the stimuli of a waterfall.\footnote{K. Naka, S. Tazawa, E. Mizutani, and H. Yagi: Sci. Rep. Shiga Pref. Fish. Exp. Stn., 25, 63-68 (1974).} Another cause may lie in "space sense" in the ayu, which directly related to the water depth. This may be supported by the fact that juvenile ayu appear to be very sensitive to space and/or distance to nearby individuals: ayu juvenile shows a strong territorial response; and furthermore, high fish density, which makes the interindividual distance short, also facilitates jumping and swimming upstream.\footnote{1) T. Iwai: Bull. Misaki Mar. Biol. Inst. Kyoto Univ., 2, 1-101 (1962). 2) H. Hotta: Japan. J. Ichthyol., 2, 113-116 (1952). 3) R. Kusuda: Nippon Suisan Gakkaishi, 29, 817-821 (1963). 4) R. Kusuda: Nippon Suisan Gakkaishi, 29, 822-827 (1963). 5) K. Tsukamoto, R. Ishida, K. Naka, and T. Kajihara: in "Common Strategies of Anadromous and Catadromous Fishes", American Fisheries Society Symposium 1, (eds. by M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper), American Fishery Society, Bethesda, Maryland, USA, 1987, pp. 492-506.} Food deprivation facilitated jumping, indicating that the internal state of "hunger" influenced upstream migration. Hungry chum salmon \textit{Oncorhynchus keta} increased their downstream movements.\footnote{Uchida and Tsukamoto, unpublished data} Hungry fish make a loose school, while well-fed fish make a tight one in the ayu.\footnote{Uchida and Tsukamoto, unpublished data}

**Table 2.** Comparison of jumping rate (\%) between fed and starved groups of the juvenile ayu \textit{Plecoglossus altivelis}

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<tr>
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<th>Starved</th>
<th>Fed</th>
<th>Probability</th>
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<tbody>
<tr>
<td>Trial 1</td>
<td>35 (103/295)</td>
<td>25 (75/301)</td>
<td>P&lt;0.01</td>
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<tr>
<td>Trial 2</td>
<td>65 (200/306)</td>
<td>44 (135/307)</td>
<td>P&lt;0.001</td>
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Parenthesis shows actual number of jumping fish per the number of fish used in the experiments.

**Fig. 7.** The effect of water depth on jumping rate of juvenile ayu at the density of 352 individuals/m$^2$ (solid circles, experiment 1) and at 1978 individuals/m$^3$ (open circles, experiment 2). Asterisks indicate significant differences (P<0.001; G-test).


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**References**

Environmental Triggers for Ayu Upstream Migration