Spacing and Jumping Behaviour of the Ayu Plecoglossus altivelis

Katsumi Tsukamoto*1 and Kazuo Uchida*1
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Interstock differences in spacing pattern and jumping activity were compared for 5 groups (stocks) of juvenile ayu: landlocked lake stock (Wild-L), amphidromous river stock (Wild-R), and reared fish from 3 hatcheries (Reared-A, -B, -C).

Reared-A and -B formed a tight aggregation (Ø 15–30 cm; diameter) in the daytime, while Wild-L dispersed throughout an experimental tank (Ø 108 cm), and Wild-R exhibited behaviour intermediate between Wild-L and hatchery fishes, forming a loose aggregation and/or schooling in a circle (Ø 70–80 cm). At night, however, there was no difference between the 4 groups; i.e. all fish moved randomly and were inactive. If assuming that a spacing pattern was maintained by an interindividual distance (Optimum Distance to the Nearest Neighbour: ODNN) peculiar to a fish group, Wild-L appeared to have a large ODNN, while Reared-A and -B, a small ODNN, and Wild-R, intermediate value.

Jumping activity was highest in Wild-L (77.9: percentage of the first-time jumpers), followed by Wild-R (60.4), Reared-B (56.3), Reared-C (56.0) and Reared-A (33.6). Diel variations in jumping behaviour of the 5 fish groups were synchronized with each another, showing remarkable peaks from 14:00 till 20:00 hours, corresponding to a rise in temperature of river water.

In conclusion, spacing and jumping behaviour were closely related to each other: i.e. fish with the larger ODNN in spacing presented the more active jumping behaviour.

Juveniles of the ayu, Plecoglossus altivelis, an amphidromous species of salmonid fish, exhibit vigorous jumping activity when confronted with waterfalls during upstream migration from the sea in spring.1,2 Jumping behaviour of the ayu3 is known to have a close relationship with a tendency to migrate upstream.4,5 Furthermore, the jumping activity was revealed to be available as a predictive index for the stocking effectiveness of the ayu in a river, since the strength of this behaviour is positively related with the recapture rate of stocked fish.6 A jumping test had been carried out to estimate fish quality prior to stocking.7,8 After upstream migration, the ayu settle at a part of river and exhibit territorial behaviour to keep a certain area.6,9 An individual feeds on algae on the rocks in the territory, and attacks invaders to drive them out. This suggests that the ayu is sensitive to an area or a space, and that spacing behaviour would have an essential key to understanding the behavioural characteristics of this species. However, little is known on the spacing behaviour of the ayu.4,5

In the present study, the spacing pattern and jumping activity are investigated for different fish stocks (groups) of juvenile ayu, and their diel changes are observed. Furthermore, the interrelationship between these two behaviours is discussed in order to accumulate knowledge on the behavioural aspect of upstream migration of the ayu.

Materials and Methods

Materials
Five fish groups from 2 wild stocks and 3 reared fish from different hatcheries were used (Table 1). Wild-L were landlocked stock in the Lake Biwa. They were caught in May at a weir 1 km upstream from the mouth of an inlet stream, the River Ado. Wild-R were collected from the

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amphidromous stock in the River Yabe in May during upstream migration from the sea by draining the fishway at a small dam 5 km upstream from the mouth of river. Before transportation, collected fish were kept for a few days in ponds near each sampling location to remove injured fish.

Reared-A, -B and -C fish were fish groups from three different hatcheries, Oita, Fukuoka and Hiroshima hatcheries, respectively.*1,2 Hatchery procedure for the ayu was roughly the same at each hatchery: i.e. eggs were kept in freshwater till hatching, hatched larvae were reared in sea water and fed with rotifer, artemia, yolk of domestic fowl and the artificial diet for ayu.*1,2 The rearing temperature ranged from 10-20°C in the hatcheries.

All fish groups were transported to the Oita Prefectural Freshwater Fisheries Experimental Station (OFFES). Healthy fish of about 7 cm in body length were selected from each fish group and were reared separately in indoor tanks which were supplied with running river water. Fish were fed with artificial diet. All fish groups were marked by fin clipping after being well acclimated to the rearing condition (Table 1). The effect of fin clipping on the swimming ability of the ayu has been estimated as negligible.8) After acclimation of 1 week, when fish recovered well from the operation of fin clipping, healthy individuals were used for the experiments on spacing and jumping behaviour in May-June.

### Table 1. Materials used in the study

<table>
<thead>
<tr>
<th>Fish group</th>
<th>No. fish examined</th>
<th>SL (mm)</th>
<th>BW (g)</th>
<th>Locality</th>
<th>Parental origin</th>
<th>Fin clipping</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spacing Experiment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild-L</td>
<td>100</td>
<td>80±2*2</td>
<td>3.5±0.3*2</td>
<td>Lake Biwa</td>
<td>Wild-L</td>
<td>Left pectoral fin</td>
</tr>
<tr>
<td>Wild-R</td>
<td>100</td>
<td>78±9</td>
<td>3.1±1.3</td>
<td>River Yabe</td>
<td>Wild-R</td>
<td>Right pectoral fin</td>
</tr>
<tr>
<td>Reared-A</td>
<td>100</td>
<td>72±5</td>
<td>4.9±1.1</td>
<td>Oita Hat.</td>
<td>Wild-R</td>
<td>Adipose fin</td>
</tr>
<tr>
<td>Reared-B</td>
<td>100</td>
<td>81±6</td>
<td>8.1±2.0</td>
<td>Fukuoka Hat.</td>
<td>Wild-R</td>
<td>Right ventral fin</td>
</tr>
<tr>
<td><strong>Jumping Experiment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild-L</td>
<td>200, 173*2</td>
<td>78±4</td>
<td>4.7±0.7</td>
<td>Lake Biwa</td>
<td>Wild-L</td>
<td>Left pectoral fin</td>
</tr>
<tr>
<td>Wild-R</td>
<td>50, 24</td>
<td>62±5</td>
<td>2.2±0.7</td>
<td>River Yabe</td>
<td>Wild-R</td>
<td>Right pectoral fin</td>
</tr>
<tr>
<td>Reared-A</td>
<td>200, 168</td>
<td>62±5</td>
<td>2.7±0.8</td>
<td>Oita Hat.</td>
<td>Wild-R</td>
<td>Adipose fin</td>
</tr>
<tr>
<td>Reared-B</td>
<td>199, 171</td>
<td>76±7</td>
<td>5.0±1.5</td>
<td>Fukuoka Hat.</td>
<td>Wild-R</td>
<td>Right ventral fin</td>
</tr>
<tr>
<td>Reared-C</td>
<td>195, 161</td>
<td>65±3</td>
<td>2.9±0.5</td>
<td>Hiroshima Hat.</td>
<td>Wild-L</td>
<td>Left ventral fin</td>
</tr>
</tbody>
</table>

*1 Standard length (SL) and body weight (BW) are shown in the mean±SD.

*2 Number of fish examined in Jumping Experiment shows the numbers used in Experiment-1 and -2, respectively.

Water temperature during acclimation at OFFES ranged from 14 to 24°C.

### Spacing

Four opaque plastic tanks (φ108 cm, 800 liter), each of which contained 200 liter of river water (about 22 cm: water depth) and one air stone for aeration, were placed outdoor. One hundred fish from each stock, Wild-L, -R, Reared-A and -B, were kept separately in the tanks. About half the volume of water in the tank was exchanged for “fresh” water every other day. Observations were conducted 2-4 times a day around 06:00, 12:00, 18:00 and 24:00 hours, in principle, and continued for 5 days. Each observation period was 5-10 minutes. The pattern of spacing was recorded according to the following definition (Table 2): “aggregation” was a mass of fish aggregating one another without parallel orientation; “pod”9) was an advanced state of aggregation with a diameter less than 30 cm, where the bottom of the tank was invisible through the mass of fish because of the high fish density; “schooling” was maneuverous swimming with parallel orientation of neighbours; “dispersion” was a distribution of fish fully spread throughout the tank; “wriggling” was characterized by a random movement at much lower swimming speed (less than 10 cm/s) without any typical distribution. Since the outline of every spacing pattern observed was roughly circular, the diameter of spacing was regarded as an index to

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Table 2. Terminology on the spacing patterns of juvenile ayu contained in a circular plastic tank

<table>
<thead>
<tr>
<th>Spacing pattern</th>
<th>diameter (cm)</th>
<th>orientation</th>
<th>description</th>
</tr>
</thead>
<tbody>
<tr>
<td>pod</td>
<td>&lt;30</td>
<td>nonparallel</td>
<td>an advanced state of &quot;aggregation&quot;</td>
</tr>
<tr>
<td>aggregation</td>
<td>30 ~ 100</td>
<td>nonparallel</td>
<td>a mass of fish gathering in a circle</td>
</tr>
<tr>
<td>schooling</td>
<td>30 ~ 100</td>
<td>parallel</td>
<td>a maneuverous swimming</td>
</tr>
<tr>
<td>dispersion</td>
<td>108</td>
<td>nonparallel</td>
<td>scattering throughout a tank</td>
</tr>
<tr>
<td>wriggling</td>
<td>108</td>
<td>random</td>
<td>inactive random movement at night</td>
</tr>
</tbody>
</table>

estimate the tightness of spacing of a fish group. Comparing fish groups, the diameter of spacing in each tank was determined by naked eye, for which the value was calibrated by photographs taken 1-3 times a day. Fish were fed with commercial diet every other day just before the exchange of water in a tank, and spacing patterns and diameters were observed before and after feeding. Water temperature in each tank was measured by thermistor thermometer at every observation. The water temperature ranged from 14-23°C during the experiment.

Jumping

Experiment-1: an experimental tank was set indoors near a window and supplied with a waterfall of river water as a stimulus (Fig. 1). About 200 fish of each group except Wild-R of 50 fish (a total of 844 individuals) were contained in the tank. The number of fish which jumped towards the waterfall and were trapped in the basket of wire-netting was counted for each stock twice a day, at 10:00 and 22:00 hours, for 4 days, where fish group was identified by a mark of fin clipping (Table 1). After counting, fish were given a further mark by clipping a bit of either lobe of the caudal, anal or dorsal fin as an indicator of jumping career. In order to keep fish density as close to constant as possible, trapped jumpers were put back in the tank and the experiment was continued. Dead fish were picked out and the number was counted for each stock.

Two parameters were used to estimate the jumping activity of a fish group: (1) the number of 'first-time jumpers' which jumped for the first time during the experimental period, and (2) the number of total jumpers at an observation time, including multiple-jumpers regardless of jumping career. The rate of first-time jumpers and that of total jumpers to the population of each stock were calculated at each observation time. The water temperature in the experimental tank was monitored by thermistor thermometer at every observation, and ranged between 16-23°C during the experiment.

Experiment-2: diel variation in jumping behavior was examined in an outdoor tank with a waterfall of river water as a stimulus (Fig. 1). A total of 697 fish were contained in the tank (Table 1). Total jumpers of a group was counted 4 times a day, at 02:00, 08:00, 14:00 and 20:00 for 2 days. Unlike Experiment-1, no additional fin clipping which showed a jumping career was given to jumpers. The percentage of total jumpers for each stock was calculated at each observation time. Other experimental procedures were the same as those in Experiment 1. Water temperature in the experimental tank was measured by thermistor thermometer, which ranged between 15-23°C during the experiment.

Data Analysis

Difference in spacing diameter during daytime was compared between 2 groups by Wilcoxon's signed-ranks test. The jumping activity represented by the rate of pooled first-time jumpers was compared between 5 fish groups by G-test. Similarly, the rate of total jumpers, including multiple-jumpers, was also examined among fish groups by G-test. In Experiment-1, first-time jumpers at day and night were pooled separately, and the incidence of first-time jumping was compared by G-test.
Results

Spacing

A remarkable difference in spacing was observed between Wild-L and Reared-A and -B during the daytime (Fig. 2, Table 3): Wild-L were completely scattered throughout the tank ("dispersion", see Wild-L in Fig. 2), whereas reared fish congregated together forming a "pod" (Reared-A in Fig. 2) or a tight "schooling" (Reared-B in Fig. 2). At night, however, there was no difference between the 4 fish groups (Table 3): fish in every group were scattered randomly and moved about slowly, which was categorized in "wriggling". The spacing diameter during daytime was largest in Wild-L (mean, 96 cm), followed by Wild-R (79 cm), Reared-A (47 cm) and -B (35 cm) in order (Table 3). The difference in diameter was highly significant (p<0.01) in every pair for the 4 fish groups except between Reared-A and Reared-B (p>0.05). A precise description on the diel variations in spacing was as follows (Fig. 3):

Wild-L: spacing of this stock was characterized by dispersion from dawn till dusk. Schooling was never observed (Table 3). Sometimes, however, a loose aggregation with a diameter of 45~55 cm was observed at dawn (04:55~05:05 hours; light intensity, 15~65 lux; water temperature, below 17°C, showing a minimum of the day). Regardless of the weather being fine or cloudy, jumping was observed at the rate of 6~15 times/min from noon till dusk when water temperature rose above 20°C. Furthermore, at 23°C in the afternoon (21, 22 May), fish gathered at the periphery of the tank forming a ring distribution ("doughnut" shaped dispersion, see Wild-L in Fig. 3) and exhibited active jumping along the wall of the tank. A doughnut dispersion was essentially different from schooling because the orientations of fish movement were not parallel (Table 2). At night, they showed a random movement near the surface of the water and were inactive (wriggling).

Wild-R: typical spacing of this stock in the daytime was a loose "aggregation" or "schooling" in a circle with a diameter of 70~80 cm (Wild-R in Fig. 2, Fig. 3). The diameter of spacing of this stock always lay between those of Wild-L and the Reared fish except one observation (18:50, 19 May, in Table 3). At dawn, the fish usually formed a more compact aggregation or schooling (30~50 cm) than in the afternoon (Table 3, Fig. 3). Even at dawn, however, when the water temperature was as high as 20°C (06:00, 23 May), they showed a wide dispersion. Weak jumping activity

Fig. 2. Typical spacing of the juvenile ayu of 4 different stocks (groups) in the daytime: landlocked stock from the Lake Biwa (Wild-L) in 'dispersion', amphidromous stock from the River Yabe (Wild-R) in loose 'schooling', and 2 groups of reared fish from Hatchery A and B (Reared-A and Reared-B) in 'pod' and tight 'schooling', respectively.
Table 3. Patterns (P) and sizes (D: diameter in cm) of spacing in the 4 different fish groups (stocks) of 100 juvenile ayu contained in a circular plastic tank (800 l, 108 cm; diameter) with 200 l freshwater in 22 cm depth

<table>
<thead>
<tr>
<th>Observation day</th>
<th>W/T (°C)</th>
<th>Light intensity (lux)</th>
<th>Wild-L</th>
<th>Wild-R</th>
<th>Reared-A</th>
<th>Reared-B</th>
</tr>
</thead>
<tbody>
<tr>
<td>18 May 24:00</td>
<td></td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td></td>
<td>(wri 108)</td>
<td>(wri 108)</td>
</tr>
<tr>
<td>19 May 06:00</td>
<td>13.3</td>
<td>agg 45</td>
<td>agg 40</td>
<td>pod 15</td>
<td>pod 20</td>
<td></td>
</tr>
<tr>
<td>12:00</td>
<td>19.2</td>
<td>40000</td>
<td>sch 70</td>
<td>pod 12</td>
<td>pod 15</td>
<td></td>
</tr>
<tr>
<td>18:50</td>
<td>18.5</td>
<td>350</td>
<td>dis 108</td>
<td>sch 100</td>
<td>dis 108</td>
<td>pod 20</td>
</tr>
<tr>
<td>24:00</td>
<td>17.0</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
</tr>
<tr>
<td>20 May 07:00</td>
<td>16.6</td>
<td>3000</td>
<td>agg 55</td>
<td>agg 50</td>
<td>pod 25</td>
<td>pod 25</td>
</tr>
<tr>
<td>12:00</td>
<td>20.5</td>
<td>50000</td>
<td>dis 108</td>
<td>sch 70</td>
<td>agg 30</td>
<td>sch 60</td>
</tr>
<tr>
<td>18:40</td>
<td>20.4</td>
<td>500</td>
<td>dis 108</td>
<td>sch 70</td>
<td>agg 50</td>
<td>agg 40</td>
</tr>
<tr>
<td>24:00</td>
<td>19.6</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
</tr>
<tr>
<td>21 May 08:40</td>
<td>18.4</td>
<td>50000</td>
<td>dis 108</td>
<td>dis 108</td>
<td>sch 80</td>
<td>sch 35</td>
</tr>
<tr>
<td>23:00</td>
<td>20.1</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
</tr>
<tr>
<td>22 May 12:00</td>
<td>20.8</td>
<td>50000</td>
<td>dis 108</td>
<td>dis 108</td>
<td>sch 55</td>
<td>agg 55</td>
</tr>
<tr>
<td>24:00</td>
<td>19.8</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
<td>(wri 108)</td>
</tr>
<tr>
<td>23 May 06:00</td>
<td>20.3</td>
<td>10000</td>
<td>dis 108</td>
<td>dis 108</td>
<td>agg 30</td>
<td>agg 40</td>
</tr>
<tr>
<td>10:00</td>
<td>20.8</td>
<td>50000</td>
<td>dis 108</td>
<td>agg 70</td>
<td>agg 65</td>
<td>sch 40</td>
</tr>
</tbody>
</table>

Mean diameter ± SD (cm) 96 ± 23 79 ± 24 47 ± 29 35 ± 14

Patterns were classified into 4 types: pod (pod), aggregation (agg), schooling (sch), dispersion (dis) and wriggling (wri). Mean diameter ± SD was calculated for the data in the daytime.

Fig. 3. Diel changes in the spacing behaviour of the juvenile ayu of 4 different stocks (groups): landlocked stock from the Lake Biwa (Wild-L), amphidromous stock from the River Yabe (Wild-R), and 2 groups of reared fish from Hatchery A and B (Reared-A and Reared-B). Reared-A and -B showed roughly the same change. Every stock exhibited ‘wriggling’ at night (left). Wild-L sometimes showed ‘doughnut’ dispersion (top, right).
at a rate of about 2 times/min was observed along
the wall or from the position of aeration at 23°C
in the afternoon of 21 and 22 May, when Wild-L
formed a doughnut dispersion with active jumping.
Wild-R also showed wriggling at night.

Reared-A and -B: spacing patterns of reared
fish were characterized by a pod of 15~30 cm in
diameter, a tight aggregation and schooling of
30~50 cm diameter (see Reared-A, -B in Fig. 2,
Fig. 3). Aggregation switched to schooling in a
circle with a slightly larger diameter of 30~70 cm,
and vice versa. A pod consisted of 4~6 circular
horizontal layers in which fish came and went
across the diameter. A pod was sometimes
observed even after dusk until 19:35 at less than
10 lux.

Diel variations in spacing pattern of Reared-A
and -B were essentially the same each other (Fig.
3). The diameter of spacing showed a tendency
to increase from dawn till dusk (15~40 to 20~
108 cm in diameter), with a rise in temperature
of 4~5°C. However, the spacing diameter of
reared fish never exceeded that of Wild-R and
Wild-L at any time except for one inversion be-
tween Reared-A and Wild-R (18:50, 19 May,
Table 3). Jumping was never observed in Reared-
A and Reared-B. The swimming speed of reared
fish was a little faster (ca. 15~20 cm/s) than that
of Wild-L and Wild-R (ca. 10~15 cm/s). At
night, reared fish were also in wriggling.

Diameters of spacing of Wild-L (40~60 cm)
and Wild-R (40 cm) diminished after feeding to
40 and 30 cm, respectively. In Reared-A and
-B, however, no change occurred before and
after feeding.

Jumping

Experiment-1: total rate of the first-time jum-
ners was highest in Wild-L (75.2 %), and followed
by Wild-R (60.4 %), Reared-C (55.4 %), Reared-B
(55.2 %) and Reared-A (32.5 %) in order (Table
4). Differences in the total rate of first-time
jumpers were significant between Wild-L and
every other group (p<0.01) and between Reared-
A and every other group (p<0.01 or 0.05), where-
as there was no significant difference between
Wild-R, Reared-B and Reared-C (p>0.05).
The rate of total jumpers was highest in Wild-L
(145.5 %), with Reared-C (123.2 %), Reared-B
(85.3 %), Wild-R (83.3 %) and Reared-A (51.3 %)
following in order. The rate of first-time jum-
ners indicated that Wild-L included more jumpers
with a high activity, while Reared-C also had some
individuals as active as Wild-L, but the number
of jumpers was not so many, and was similar to
Reared-B.

The total of first-time jumpers at night was
1.4~11.1 times more than that in the morning
(Table 4). Differences were significant between
day and night observation (p<0.05 in Reared-C
and p<0.01 in other groups), suggesting that
fish jumped more actively during daytime than
night, since night observation at 22:00 represent
jumping activity from 10:00 till 22:00, and day

Table 4. Jumping activity of 5 stocks (groups) of juvenile ayu. Number of the first-time jumpers
(A), which were trapped in the basket for the first time during the experiment, and the number
of fish of a group (stock) in the apparatus at that time (B) are expressed as A/B together with
the jumping rate (%) in parentheses

<table>
<thead>
<tr>
<th>Fish group</th>
<th>Observation time*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>27 May</td>
</tr>
<tr>
<td></td>
<td>10:00</td>
</tr>
<tr>
<td>Wild-L</td>
<td>8/200</td>
</tr>
<tr>
<td></td>
<td>(4.0)</td>
</tr>
<tr>
<td>Wild-R</td>
<td>4/50</td>
</tr>
<tr>
<td></td>
<td>(8.0)</td>
</tr>
<tr>
<td>Reared-A</td>
<td>14/200</td>
</tr>
<tr>
<td></td>
<td>(7.0)</td>
</tr>
<tr>
<td></td>
<td>(14.6)</td>
</tr>
<tr>
<td>Reared-B</td>
<td>29/199</td>
</tr>
<tr>
<td></td>
<td>(15.4)</td>
</tr>
<tr>
<td>Reared-C</td>
<td>30/195</td>
</tr>
<tr>
<td></td>
<td>(15.4)</td>
</tr>
<tr>
<td>Total (%)</td>
<td>49.0</td>
</tr>
</tbody>
</table>

* Observation was made 8 times in the morning (10:00) and night (22:00) for 4 days from 27 May to 30 May.
Observation at 10:00, that from 22:00 till 10:00. On 27 May, the number of jumpers at the first observation in the morning exceeded the jumpers at night in every group except Wild-L, which could be due to the excitement of fish as a result of being transferred to an unfamiliar environment (Table 4).

Experiment-2: fish jumped most actively from 14:00 to 20:00 for every group except for the second peak (14:00) in jumping activity of Wild-R (Fig. 4). Diel variations in jumping activity and water temperature coincided well each other. The rate of total jumpers for 2 days was highest in Wild-L (100%), and followed by Wild-R (34%), Reared-A (8%), Reared-C (7%) and Reared-B (5%) in order. Differences in the jumping rate was highly significant (p<0.01) between Wild-L and Wild-R and between Wild-R and other reared fish.

Discussion

Factors Affecting Behaviours of the Ayu

Environmental conditions were not manipulated in the present study. However, diel changes in spacing and jumping activity observed here strongly suggest the involvement of the environmental factors to the control mechanism of these behaviours in the ayu.

The water temperature has a potential to control both spacing and jumping behaviour in the ayu: a rise in temperature facilitated jumping activity,\textsuperscript{10} and expanded the spacing,\textsuperscript{91} and \textit{vice versa}. Starvation also increased the jumping rate,\textsuperscript{16} and induced an enlargement of spacing,\textsuperscript{91,2} while feeding suppressed jumping\textsuperscript{10} and dimin-

\textsuperscript{91} Uchida and Tsukamoto, unpublished.
ished spacing.*1,2 A reduction of spacing was also observed in juvenile jack mackerel after feeding.11) Several other factors are known to facilitate jumping activity and/or expand spacing: e. g. a rise in fish density,4) a change in light intensity,10> a decrease in water depth10) and a circadian rhythm.10) All results obtained in the present study are not contradictory to the above considerations.

Interstock Differences
Different fish groups presented different spacing and jumping activities in the present study. It seems improbable that the behavioral differences among fish groups observed here depend mainly on differences in swimming ability, fish size or development of locomotor muscles and visual sense,5) although these factors surely influence the behavior in long-term. In the present study, fish size was roughly the same (Table 1). Swimming abilities of Reared-A, -B and -C were estimated to be 1.9~2.6 times higher than those of Wild-L and Wild-R.5) As regards optokinetic response, no significant difference was detected between wild and reared fish.5) Thus, the differences observed here can not be explained by the lack of ability or by the presence of undeveloped organs in reared fish. Different groups of ayu exhibited different values of plasma thyroxine concentration.12) Furthermore, a significant positive correlation was observed between the plasma thyroxine level and the upstream migratory behaviour.12) Accordingly, interstock differences in jumping behaviour may be derived from the different level of plasma thyroxine in each stock, since a tendency to migrate upstream was positively correlated to jumping activity.5) Parental origin has some effect on the spacing and jumping behaviour of the offspring.10) Both Reared-A, -B and Wild-R fish have parents derived from natural stock in a river (Table 1), but they showed different behaviours in spacing and jumping (Figs. 2~4, Tables 3 and 4). Wild-L and Reared-C fish, in which jumping rates differed, were derived from the same stock, Wild-L. Therefore, both genetic factors and rearing conditions appear to have the potential to influence the behaviours of ayu. Especially, it is probable that hatchery-reared fish may obtain a tolerance to "crowding" through a long acclimation period under rearing conditions at high fish density (relative to wild

Optimum Distance between Individuals
At night, every fish group showed wriggling with a distribution of 108 cm in diameter (Table 3). At first sight, this type of spacing at night resembles the uniform dispersion in the daytime. However, these are different ones, since swimming speed was faster in the daytime than at night. Furthermore, in the daytime dispersion, fish appear to maintain their mutual distances, i. e. there exists a "repulsive force" acting between the fish. Thus, the fish would disperse more widely when placed in a larger tank. However, night distribution does not exhibit any biological "forces" between individuals, either repulsive or attractive.

In the analysis of the structure of fish schools, the concept of the distance between individuals is usually introduced.11,14~16) Therefore, as an element of spacing, we assume the existence of the "Optimum Distance to the Nearest Neighbour" (ODNN) between individuals. ODNN is an equilibrium point of attractive and repulsive tendencies in a sufficiently wide space,17) and is a value peculiar to a given species at a given developmental stage under fixed physiological conditions. Since fish form a school or aggregation so that they may keep their own ODNN value constant, a 'repulsive force' occurs between individuals when they come close enough to enter the range of their ODNN, and then, they go away from each other.17) Contrarily, when they are far apart beyond the ODNN, 'attractive force' acts between neighbours, and they approach each other to the ODNN distance. The value of ODNN can be given as the mean of the distances between nearest neighbours in a school or an aggregation.

Different fish stocks had different values of ODNN in spacing: i. e. Wild-L would have much larger ODNN than Reared-A and -B, and Wild-R was an intermediate value. During most of the observation time in the spacing experiment, Wild-L showed full dispersion (108 cm) throughout the tank and sometimes exhibited jumping against the wall (Table 3). Fish with a larger ODNN would be stressed when contained in a narrow space at high fish density, since wild fish have less tolerance to "crowding". As a result, they would have a larger repulsive force, and jump to "escape"

*1 Uchida and Tsukamoto, unpublished.
from an unfavourable situation.

Interrelationship among Behaviours

Wild-L with a larger ODNN showed a strong tendency to jump, while Reared-A and -B stocks with small ODNN showed a far weaker tendency. For Wild-R with intermediate ODNN, the jumping rate was also intermediated in value. That is, the larger the ODNN, the stronger the tendency to jump. This suggests the possibility that these two behaviours are controlled by a common behavioural mechanism. Based on a series of studies on the behavioural aspects of stocking effectiveness of the ayu, several behaviours of the juvenile ayu are linked one another: fish with a larger ODNN show a wider spacing, a more active jumping (the present study) and a stronger tendency to swim upstream in an artificial stream and exhibit more active migratory behaviour in a natural river and thus result in a higher recapture rate during fishing season. Consequently, the spacing pattern of the juvenile ayu as well as the jumping behaviour can be used as a predictive index for the stocking effectiveness of the ayu.

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