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Modeling Rheotaxis based on Preference to Predict Fish Migration Behavior in A River

Rina Febrina
Division of Civil Engineering, Malahayati University
Jl. Pramuka No.27 Kemiling, Bandar Lampung 35153, Indonesia
E-mail: febrinacivil@yahoo.com

Abstract

In this research, we attempt to determine preference of rheotaxis and estimated weight values in laboratory experiments using adult and juvenile ayu (Plecoglossus altivelis altivelis). We conducted paired comparisons of ayu distribution between the upper and lower sections of a test watercourse using several velocity conditions (10, 30, and 40 cm/s for juveniles; 20, 30, 50, 70, and 90 cm/s for adults). In upper watercourse sections, juvenile ayu preferred velocities of 30 cm/s and 40 cm/s, and adults preferred a velocity of 50 cm/s. Even when a highly preferred illumination condition of 4000 lux was present in the lower section, fish maintained a higher distribution in the upper section. We design a procedure to calculate rheotaxis preference and built it into our fish behavior simulation model on geographic information system (GIS) software. The model successfully predicted natural migration behavior of fish.

Keywords: *Rheotaxis, Fish preference model, Fish migration simulation in rivers, Illumination, Ayu.*

Abstrak

Penelitian ini mencoba untuk menentukan preference dan weight value dari rheotaxis melalui percobaan di laboratorium dengan menggunakan ikan dewasa dan anak ikan ayu (Plecoglossus altivelis altivelis). Penelitian ini membandingkan penyebaran ikan ayu dibagian atas dan bagian bawah dari daerah percobaan dengan menggunakan beberapa kondisi kecepatan aliran (10, 30, dan 40 cm/s untuk anak ikan; 20, 30, 50, 70, dan 90 cm/s untuk ikan dewasa). Pada bagian atas daerah percobaan, anak ikan lebih menyukai kecepatan aliran dari 30 dan 40 cm/s, sedangkan ikan dewasa lebih menyukai kecepatan aliran 50 cm/s. Meskipun pada saat itu kondisi penerangan yang sangat nyaman untuk ikan yaitu 4000 lux terpasang di bagian bawah daerah percobaan tetapi distribusi ikan menunjukkan lebih banyak di area atas. Kami susun prosedur untuk memperoleh rheotaxis preference, memasukkannya untuk perilaku simulasi ikan dengan menggunakan software Geographic System (GIS). Model yang diperoleh dari software itu sukses meramalkan gaya hidup alami dari ikan ketika bermigrasi.

Kata-kata Kunci: *Rheotaxis, Preference model ikan, Simulasi migrasi ikan di sungai, Illuminasi, Ayu.*

Introduction

Fish exhibit rheotropic behavior in response to water currents. They respond directly, to water flowing over the body surface, or indirectly, as a response to the visual, tactile, or inertial stimuli that result from displacement in space (Harden and Jones, 1968; Arnold, 1974). The rheotropic response consists of an orientational and a kinetic component. For example, fish generally turn to head into a current and adjust their swimming speeds in response to flow rate. Environmental factors that affect the orientational and kinetic components of rheotropism have an important role in migration (Arnold, 1974; Dodson and Young, 1977).

A core problem for the study of rheotaxis is the effect of current orientation on fish behavior patterns. Modeling behavior to determine if virtual fish can swim up a virtual river is a promising technique for determining the barriers to fish migration. However, rheotaxis has been treated as an a priori driving force in most fish migration modeling research. Because rheotaxis is one of the most important factors that determine swimming direction, it should be expressed from the view point of preference. In laboratory studies, we determined preferences for rheotaxis and estimated values for weights in adult and juvenile ayu (*Plecoglossus altivelis altivelis*). We then confirmed the formula through field experiments. We choose ayu as a model because it is a migratory species and is the most important commercial amphidromous fish in Japan (Ishida, 1976). This research consisted of three experiments. First, we performed paired comparisons with varying illumination levels. Second, we observed ayu distribution under a uniform illumination of 11000 lux and variable velocity conditions (10, 30, and 40 cm/s for juvenile fish; 20, 30, 50, 70, and 90 cm/s for adult fish). Last, to estimate the values for the weights, we observed ayu distribution in the upper section at 11000 lux and in the lower section at 4000 lux, with the same velocity conditions used in the second experiment.

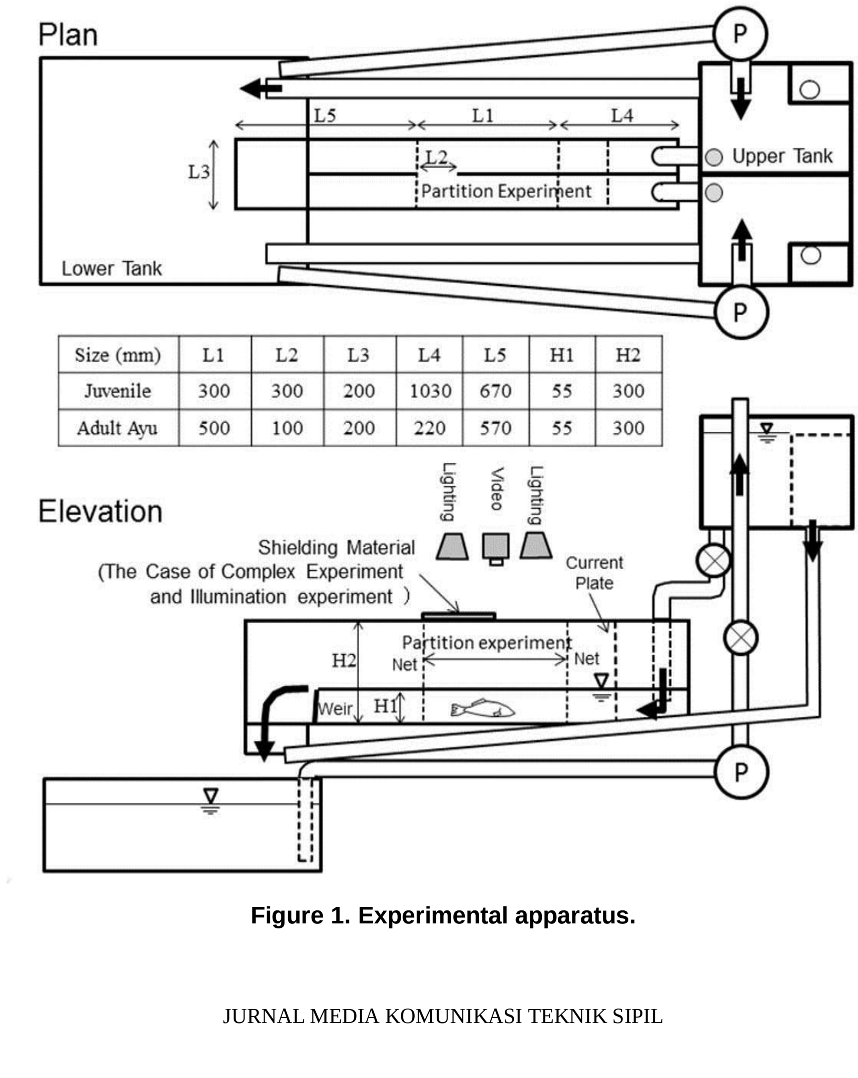
Materials and Methods

Experimental animals

Juvenile (7±1cm) and adult ayu (16±1cm) were purchased from the Fushinogawa River Fishing Cooperative. We maintained the fish in a large tank (150 cm long ×60 cm width ×80 cm height) under recirculated, temperature-controlled conditions (21±1°C) with supplemental aeration. We fed them once per day, after experiments were completed, or at 1500 h on the days they were not included in an experiment (0.5g/fish, *Kawazakana no esa*, Kyorin Co., Japan)

Experimental set-up

To determine rheotactic responses, juvenile and adult ayu were placed in similar experimental apparatus and water flow set-ups (Fig. 1). The watercourse for juvenile fish was 30 cm long × 20 cm wide × 30 cm high and was 50 cm long × 20 cm wide × 30 cm high for the adults. It was made of transparent acrylic and was surrounded by gray curtains to minimize the effect of visual stimuli. Two halogen lights were installed above the watercourse to maintain light conditions at approximately 11000 lux. In the downstream section, the illumination intensity was varied by changing the shielding material, which consisted of a transparent plastic wrap, cheesecloth, and a black plastic sheet. By varying and overlaying these materials, eight levels of illumination intensity (500–11000 lux) were created (Table 1).



Size (mm)	L1	L2	L3	L4	L5	H1	H2
Juvenile	300	300	200	1030	670	55	300
Adult Ayu	500	100	200	220	570	55	300

Figure 1. Experimental apparatus.

Table 1. Shielding materials and surface illumination conditions in the rheotaxis experiments

Shielding material	Illumination (lx)	Example
Without shielding	11000	Full daylight (not direct sun)
A transparent wrap	9500	
One white cheesecloth	8000	
One black cheesecloth	6000	Cloudy
Two black cheesecloth	4000	Boxing ring
Two black cheesecloth + one white cheesecloth	3000	Baseball infield of night game
Three black cheesecloth	2000	Convenience store
A black plastic sheet	500	Office lighting

Experimental method

Experiments were performed between 0900 h and 1900 h to control for the effects of diurnal variability in behavior (Jidong et al., 2001). For each test, three fish at a time (i.e., three replicates) were randomly selected from the stock tank and placed in the watercourse to acclimate for 10 min (water temperature = 21±1°C). After testing was completed, fish were moved to a different tank to avoid using them in multiple experiments in1 day. Fish distribution in the tank was recorded every 10 s with a video camera (SONY SR-60) placed above the watercourse.

For the illumination experiments, the velocity was kept at 10 cm/s without shielding material during the initial 10-min acclimation period. After acclimation, the shielding material was placed in the lower section, the velocity set to 0 cm/s, and the light was turned on for a second (5 min) acclimation period. After the 5-min acclimation to light conditions, fish distribution was recorded for 10 min.

Rheotaxis experiments and combined condition experiments were performed together. We exposed juvenile ayu to three velocity conditions (10, 30, and 40 cm/s) and exposed adult ayu to five velocity conditions (20, 30, 50, 70, and 90 cm/s). Illumination was a constant 11000 lux. During the first 10-minacclimation period, the velocity was maintained at the intended value. After the 10-min period, fish distribution was recorded for 10 min. At the end of the 10-min observation period, the shielding material was placed around the lower section to create 4000 lux illumination, fish were acclimated for 5 min, and then the distribution was recorded for 10 min.

Theory

The formulation method of preference

Fish orientation preference in a specific environment has been previously described by an equation (Tanaka and Shoten, 2006) and using laboratory experiments with a u-shaped experimental watercourse (Sekine et al., 2004).

$$P^* = \prod_{j=1}^{J} \left(P_j\right)^{\frac{W_j}{W_{max}}} \quad (1)$$

$$W_{max} = \begin{cases} \max_{J\in V}\left(W_j\right) & V \neq \phi \\ \infty & V = \phi \end{cases} \quad (2)$$

$$V = \left\{ j \middle| \left(\exists i, i`\right)\left(P_{j,i} \neq P_{j,i`}\right) \right\} \quad (3)$$

Where P^* is an overall preference, P_j is a preference for an environmental condition,j, W_j is a weight for the environmental condition,j, $W_{max}$is the maximum weight among the weight sets,V,with different levels of preference in the surrounding water body, ϕ represents the null set, $\exists$ is an existential quantifier, and i represents a segmented location of an water body.

To determine fish preference for flow rate, we set up two parallel flows with two different flow rates (Fig. 2a). These flows were partly connected so that fish could choose a side to swim in. We then observed the distribution ratio of the fish in the left and right side ($D_{right} + D_{left} = 1$), and

$$\frac{D_{left}}{D_{right}} = \frac{P_{v,left}}{P_{v,right}} \quad (4)$$

where D_{left} is the fish distribution ratio at the left side of the watercourse, D_{right} is the distribution ratio of fish at the right side of the watercourse,$P_{v,left}$ is the flow rate preference on the left side, and $P_{v,right}$ is the flow rate preference on the right side.

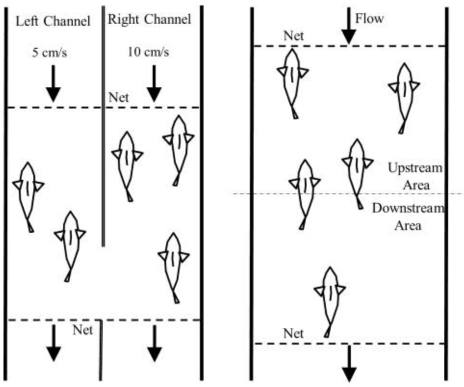
By observation, we can know the relative relationship between P_v and the flow rates at the left and right sides of the channel (Fig. 2a). For example, if there is a fixed constant flow rate value at the right channel, and the experiment is repeated by changing only the flow rate at the left channel, a functional form of P_v can be determined. However, it cannot be calculated when D is zero. When D was zero, we used 0.01 and 0.99. In addition, P has only a relative meaning in Eqs. (1) – (3), but was normalized so that the maximum value of P was 1. P is used as an expression of preference for many environments, and is used in habitat evaluation procedures (Tanaka and Shoten, 2006).

When W_j for a single factor is considered, it does not matter when W_j/W_{max} = 1, and the result can be ignored. However, when multiple factors are involved, it is necessary to set a value for P_j. After setting P_j using a single factor experiment, an experiment was carried out using two factors(j, j`) to obtain $W_j$ and $W_j$` . Likewise, the values for P_j , W_j , and W_j` are relative. Normalization was performed when the maximum value = 1. Furthermore, W_j is not independent from P_j . Therefore, we cannot discuss the importance of a factor by comparing only the values of W_j.

Formulation of the concept of rheotaxis

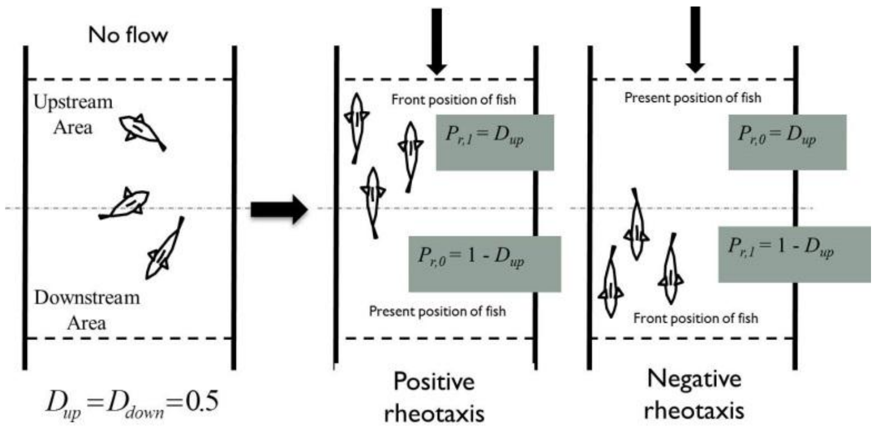
We developed rheotaxis preference values from paired comparisons of the upstream and downstream fish distribution ratios. We did not compare between the left and right sides of the watercourse (Fig.2b). We added multiple fish at a flow rate of 0 cm/s (when the other conditions are uniform, then $D_{up} = D_{down} = 0.5$) (Fig.3a). We then increased the current speed. Fish position was noted as follows: if fish swam against the current (positive rheotaxis), then D > 0.5. If fish swam following the current or oriented downstream (negative rheotaxis), then D < 0.5.

To convert the distribution ratio into rheotaxis preference (P_r) , we did the following: when positive rheotactic behavior was displayed and the present position of the fish was in the downstream area (D_{down}) and the front of the fish was facing the upstream area (D_{up}), we used (D_{up}) for the preference value (Fig. 3b). For negative rheotaxis, we assumed that even though the position of the fish was in the upstream area (D_{up}), the fish would be facing downstream (D_{down}), so (D_{down}) was used for the rheotaxis preference value (Fig. 3c).



(a) (b)

Figure 2. The channel concept. (a) u-shaped watercoures; (b) rheotaxis experiment



(a) (b) (c)

Figure 3. Determination of rheotaxis preference. (a) no flow; (b) positive rheotaxis; (c) negative rheotaxis

RESULTS

llumination experiment

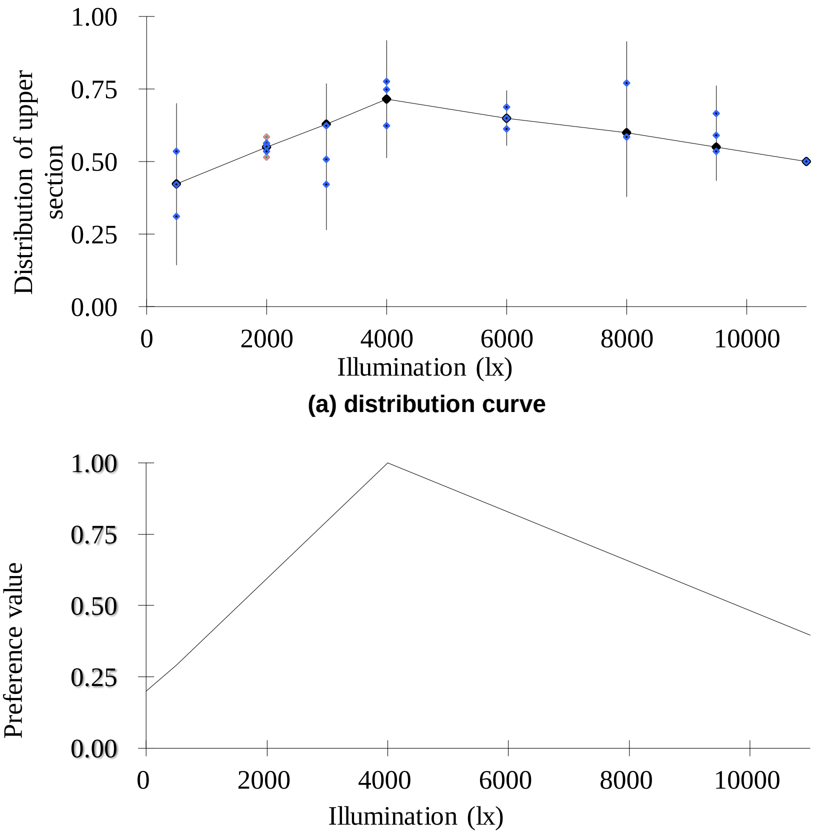
The results of the experiment shown in Table 2 were estimated from the data presented in Figs.4 and 5. On the upstream side, the maximum distribution ratio for juvenile (0.72) and adult (0.72) ayu occurred at 4000 lux. The distribution ratios at 11000 lux = 0.5 and at 4000 lux = 0.72. Based on these results, we decided to use the following ratio of illumination conditions for the composite experiments: illumination upstream: illumination downstream = 11000 lux: 4000 lux.

Rheotaxis experiment

The distribution data for the upstream side of the experimental watercourse are presented in Figs. 6 and 7. Table 3 presents a summary of the results and includes the calculated preference weights based on Eqs.(1)–(3).Juveniles in all flow rate conditions exhibited positive rheotaxis behavior that was particularly strong at 30–40cm/s. Adult fish exhibited slightly negative rheotaxis behavior at flow rates <30cm/s and positive rheotaxis at 50 and 70cm/s.

Table 2. Experiment results for illumination preferences.

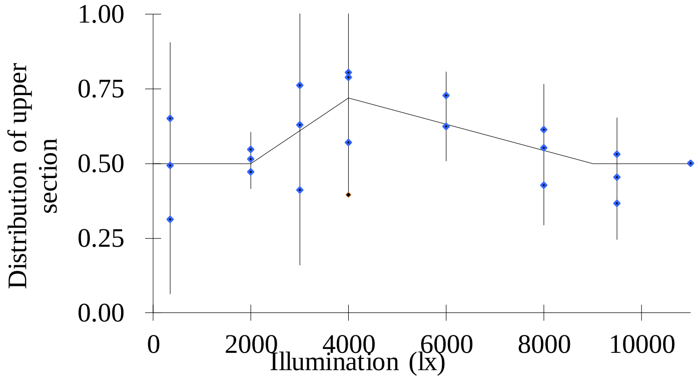
Illumination (lx)	Distribution ratio of juvenile Ayu at upstream area	Distribution ratio of adult Ayu at upstream area
11000	0.5	0.5
9500	0.45	0.6
8000	0.53	0.65
6000	0.66	0.65
4000	0.72	0.72
3000	0.6	0.52
2000	0.51	0.55
500	0.48	0.42



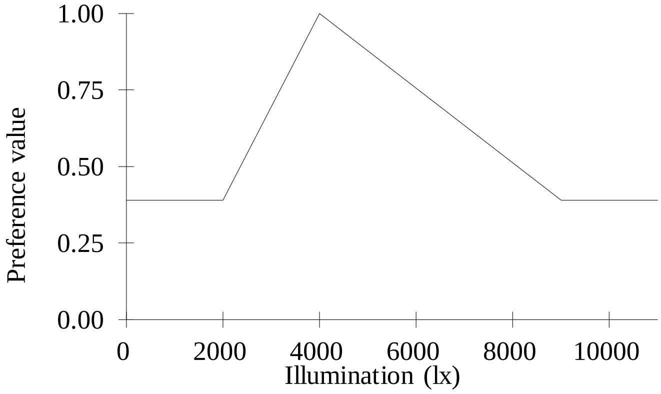
(a) distribution curve

(b) preference curve

Figure 4. Results for the various illumination conditions for the adult ayu.

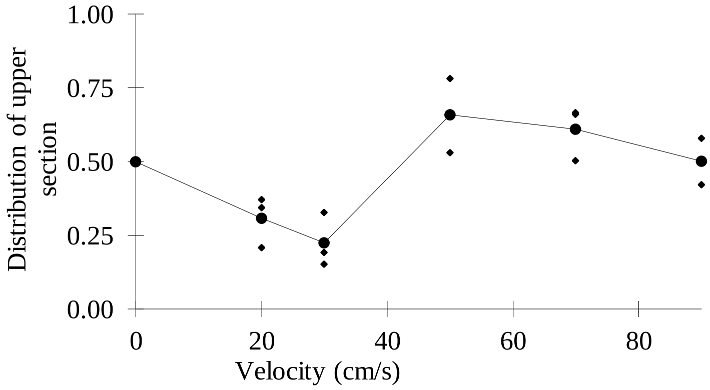


(a) distribution curve

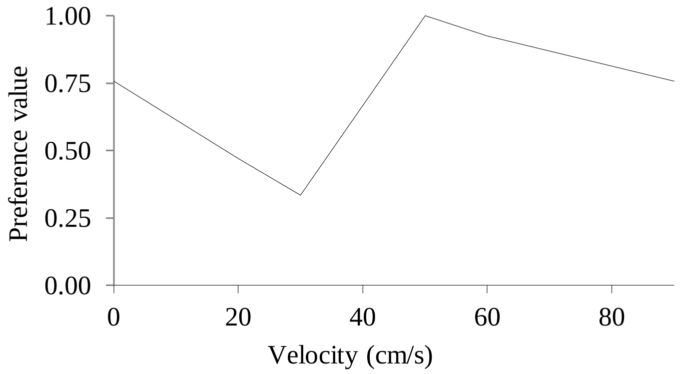


(b) preference curve

Figure 5. Results for the various illumination conditions for the adult ayu.

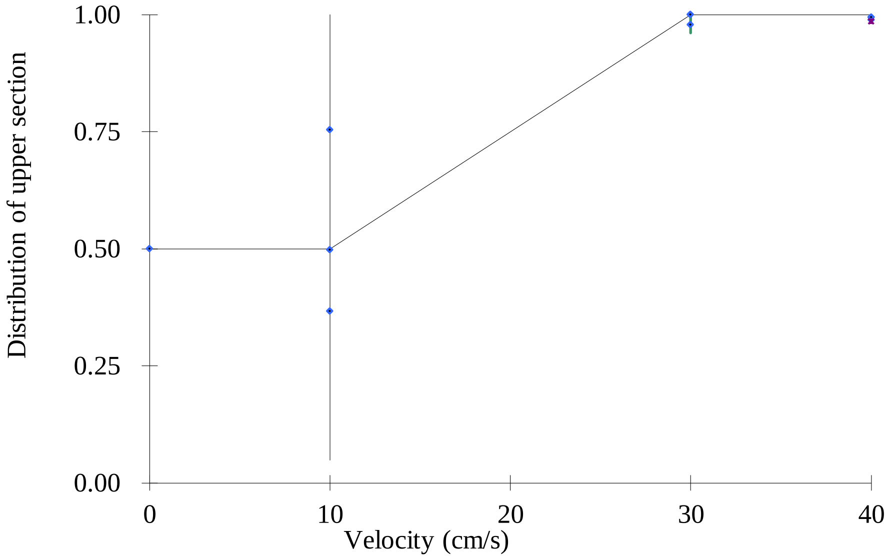


(a) distribution curve

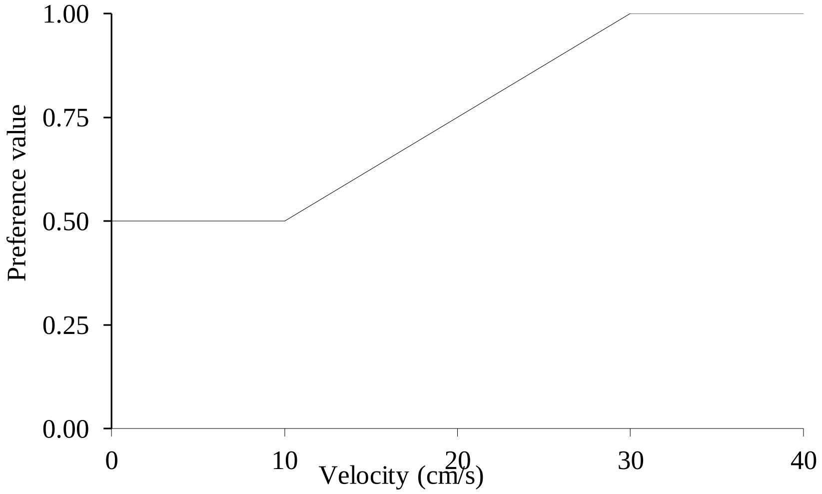


(b) preference curve

Figure 6. Rheotaxis experiment result for adult ayu



(a) distribution curve



(b) preference curve

Figure 7. Rheotaxis experiment result for adult ayu

Weight experiment

Under composite conditions, the peak distribution ratios were at flow rates of 30 and 40 cm/s for juveniles and at 50 cm/s for adults. Two environmental factors, j (j = {rheotaxis, illumination}), were included in the calculation of the values for the weights. The ratio of fish distribution between the upper and lower sections, R, was:

$$R = \frac{D_{Up}}{D_{Low}} = \frac{P_{r(Up)}^{\frac{W_r}{W_{max}}} \, P_{ill(Up)}^{\frac{W_{ill}}{W_{max}}}}{P_{r(Low)}^{\frac{W_r}{W_{max}}} \, P_{ill\,(Low)}^{\frac{W_{ill}}{W_{max}}}} \quad \text{...........} \quad (5)$$

Where D_{Up} was the upstream distribution, D_{Down} was the downstream distribution, P_r was the rheotaxis preference, P_{ill} was the illumination preference, W_r was the rheotaxis weight, W_{ill} was the illumination weight, and $W_{\max}$ was the maximum weight value used for each environmental factor.

When $P_{r(Up)}$ does not equal $P_{r(Low)}$ and $P_{ill(Up)}$ does not equal $P_{ill(Low)}$, then V becomes {rheotaxis, illumination}(from Eq. (4)) and $W_{\max}$ is W_r or W_{ill} (from Eq. (2)). Although, we cannot know explicitly whether $W_{\max}$ is W_r or W_{ill}, we can obtain these values recursively. If we assume that $W_{\max}$ is W_r, Eq. (5) becomes:

$$R = \frac{D_{Up}}{D_{Down}} = \frac{P_{r(Up)}^{\frac{W_r}{W_r}} P_{ill(Up)}^{\frac{W_{ill}}{W_r}}}{P_{r(Down)}^{\frac{W_r}{W_r}} P_{ill\,(Down)}^{\frac{W_{ill}}{W_r}}} \text{ .... } (6)$$

$$\frac{W_{ill}}{W_r} = In\left(R\frac{P_{r(Up)}}{P_{r(Low)}}\right) \div In\left(\frac{P_{ill(Up)}}{P_{ill(Low)}}\right) \text{ .... } (7)$$

The various values for $P_{j,i}$ were defined from the single environmental factor experiment, and R was obtained from the composite experiment, so the value of $\frac{W_{ill}}{W_r}$ could be estimated. When the value of $\frac{W_{ill}}{W_r}$is between 0 and 1, the values of W_{ill} and W_r are determined because there is no meaning in the absolute value of W_j, but the relative relationship among W_j `s is essential (Eq. (1)). When $\frac{W_{ill}}{W_r}$>1, then $W_{ill} > W_r$, which contradicts the assumption that $W_{\max}$ is W_r. In this case, we can accept the assumption that $W_{\max}$ is W_{ill}, and Eq. (1) becomes:

$$R = \frac{D_{Up}}{D_{Low}} = \frac{P_{r(Up)}^{\frac{W_r}{W_{ill}}} P_{ill(Up)}^{\frac{W_{ill}}{W_{ill}}}}{P_{r(Down)}^{\frac{W_r}{W_{ill}}} P_{ill\,(Down)}^{\frac{W_{ill}}{W_{ill}}}} \text{ .... } (8)$$

$$\frac{W_r}{W_{ill}} = In\left(R\frac{P_{ill(Up)}}{P_{ill(Low)}}\right) \div In\left(\frac{P_{r(Up)}}{P_{r(Low)}}\right) \text{ .... } (9)$$

A comprehensive summary of the results of the experiments is presented in Table 3.

Discussion

The capacity of juvenile and adult fish to swim against (positive rheotaxis) or with (negative rheotaxis) a current will affect migration. The results of these experiments indicate that rheotaxis depends on current velocity. As the velocity increased, a greater number of fish turned against the current. However, this progression was not always linear. Although pushed back by strong currents, most fish continued to be oriented against the flow, and active downstream swimming was rarely observed. Some fish on the bottom did face downstream or lay crosswise. Sometimes fish facing upstream turned around and faced downstream. Only adult ayu (i.e., no juveniles) displayed a slightly negative rheotaxis at flow rates of 20 cm/s and 30 cm/s.

Several environmental factors affect the orientational and kinetic components of rheotropism (Arnold, 1974). We used illumination as an additional environmental factor because it affects fish movement. The ability of fish to swim against a current and to modify rheotactic behavior in response to changing light conditions suggests that these environmental factors might influence horizontal migration. Our results indicate that juvenile and adult ayu tend to remain in 4000lux illumination conditions. We used this result for the composite experiment to obtain the weight values, illumination upstream area: illumination downstream area = 11000 lux : 4000 lux.

Table 3. Distribution ratios for the upstream rheotaxis experiment and the composite experiment. Estimated ratio values for the composite experiment using the intensity distribution preference values.

	Juvenile Ayu				Adult Ayu					
Flow rate	0	10	30	40	0	20	30	50	70	90
Observed upstream distribution for rheotaxis experiment	0.5	0.54	0.99	0.99	0.5	0.31	0.22	0.66	0.61	0.5
Rhotaxis (+: positive, -: negative)	±	+	+	+	±	-	-	+	+	±
Observed upstream distribution for composite experiment	0.28	0.18	0.91	0.98	0.28	0.04	0.11	0.58	0.34	0.11
Weight of rheotaxis	-	-	0.71	1	-	-	-	1	0.63	-
Weight of illumination	-	-	1	0.74	-	-	-	0.36	1	-
Calculated upstream distribution for composite experiment with weight	0.28	0.31	0.91	0.98	0.28	0.15	0.1	0.58	0.34	0.28
Calculated upstream distribution for composite experiment without weight	0.28	0.31	0.97	0.97	0.28	0.15	0.1	0.43	0.38	0.28

In the composite experiment, the distribution ratio for the upstream area decreased in all conditions because of the high preference for 4000 lux illumination. However, the rate of decline was smaller at 30–40cm/s for the juveniles and at 50cm/s for the adult ayu. This result indicates that ayu have a higher weight for rheotaxis at these flow rates. The upstream distribution of10cm/s for juveniles and 90cm/s for adults were lower than expected based on the preference for illumination. This kind of disagreement is often observed for conditions that are not as important for, or severely affect, the fish. For adult fish, weights for the 20 and 30cm/s velocities could not be calculated because in these cases the rheotactic and illumination preferences were higher for the lower watercourse.

Figure 8 presents the calculated and the observed distribution ratios. A weight value=1 was used for the conditions for which weights were not obtained. High reproducibility results when weights are used, but the direction of movement can be correctly determined without weights. Non-weighted calculations are useful for behavioral simulations (e.g., for studying the direction of movement of fish).

In modeling fish preference, the proposed equations have important characteristics in that the parameter values for the environmental preference equations and the weight values among the environmental factors can be determined separately. Consequently, the values for the preference parameters and the weights can be kept constant when a new factor that affects fish distribution is introduced. These features are essential when working with living organisms or when researchers exchange quantitative information (Sekine et al., 1991, 1997).

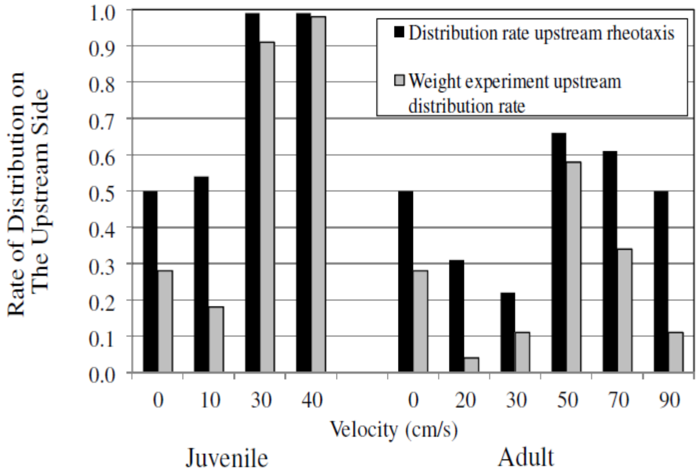


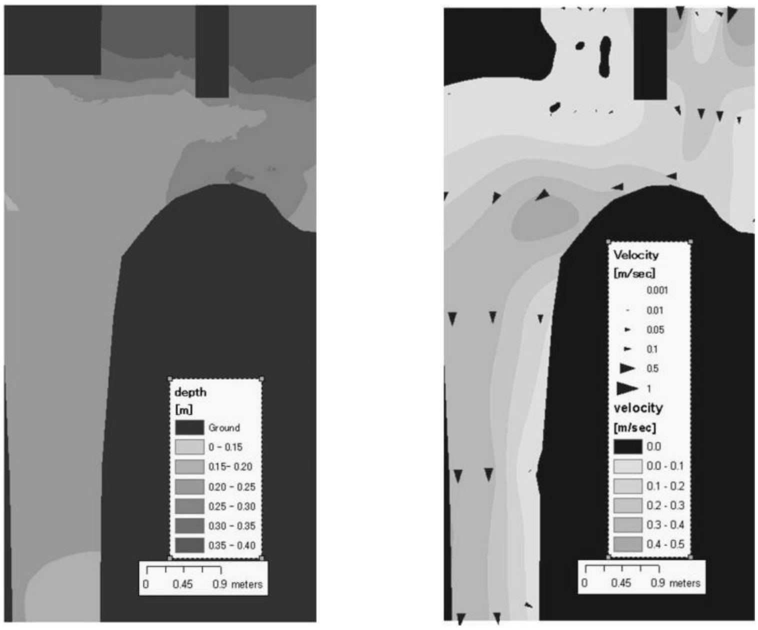
Figure 8. Distribution rate of rheotaxis experiment and weight experiment

Figure 9. The observation area.

We presented a modeling framework for the simulation of fish behavior. The model was validated using fish movement data. We also performed a field experiment in the Sawanami River near our university campus. The experiment was conducted on 20 April 2007. The water temperature was approximately 15°C. The experimental section was set downstream of the entrance of a fishway, and we tracked the behavior of fish released at the lowest point in the section. We released 20 juvenile ayu (10 cm body length) into the river and videotaped their behavior. Figure 9 presents the experimental river section, surrounded by a net. Figure 10 presents the velocity and depth conditions.

In this outdoor research, we used only velocity preference in addition to rheotaxis preference because the depth of the raceway section was deep enough for juvenile ayu to maintain a constant preference. Except for a rock and concrete substrate at the upstream entrance, the substrate was a uniform mixture of gravel and sand. The velocity preference curve is presented in Fig.11.

In this simulation, nine surrounding locations, including the current location of a virtual fish, were compared. The virtual fish moved to the most preferred location, based on Eq. (1). When there was more than one high preference location, fish chosee randomly. As discussed in the previous section, preference weight was not used in this calculation. Figure 12 presents the surrounding locations and the rheotaxis calculation method.



(a) depth **(b) velocity magnitude and flow direction.**

Figure 10. Environmental conditions.

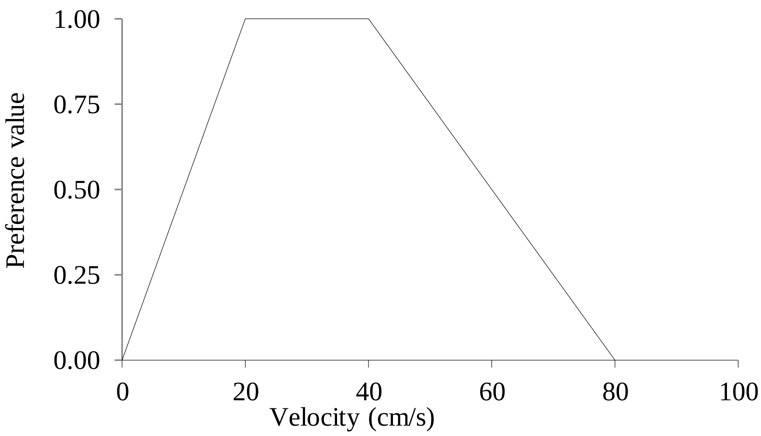


Figure 11. Velocity preference curve.

The simulation was performed using Visual Basic for Applications (Microsoft Corporation, Redmond, WA USA) and ArcGIS 8.3 (ESRI, Redlands, CA USA). In this simulation, we supply the velocity preference raster layer (CSI), the horizontal velocity raster layer (Vx), and the vertical velocity raster layer (Vy). The initial location of a virtual fish is supplied as a point layer (Track). When the program runs, the virtual fish movement at each time step is tracked as a point on the "Track" layer.

Figure 13 presents results using four initial locations. Using rheotaxis preference values, the calculated results show good agreement with observed fish behavior. Without rheotaxis values, virtual fish tend to stay at a local peak of velocity preference. Our modeling is in the initial stages of the quantitative evaluation of rheotaxis. However, our simulation model successfully reproduced an observed juvenile ayu migration behavior in a river.

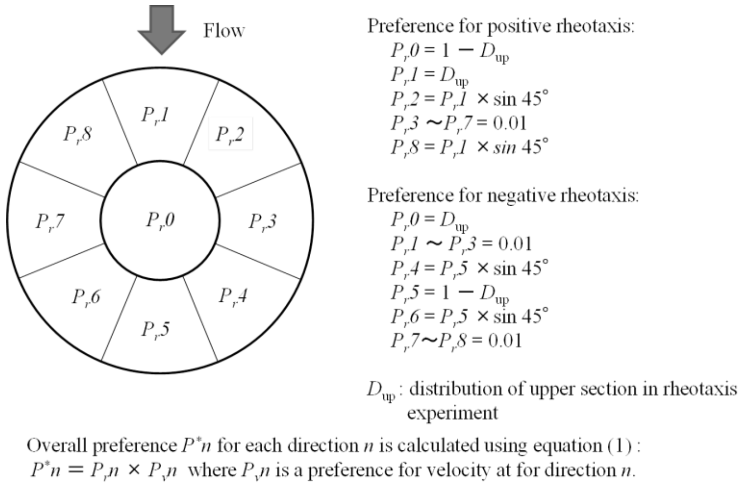
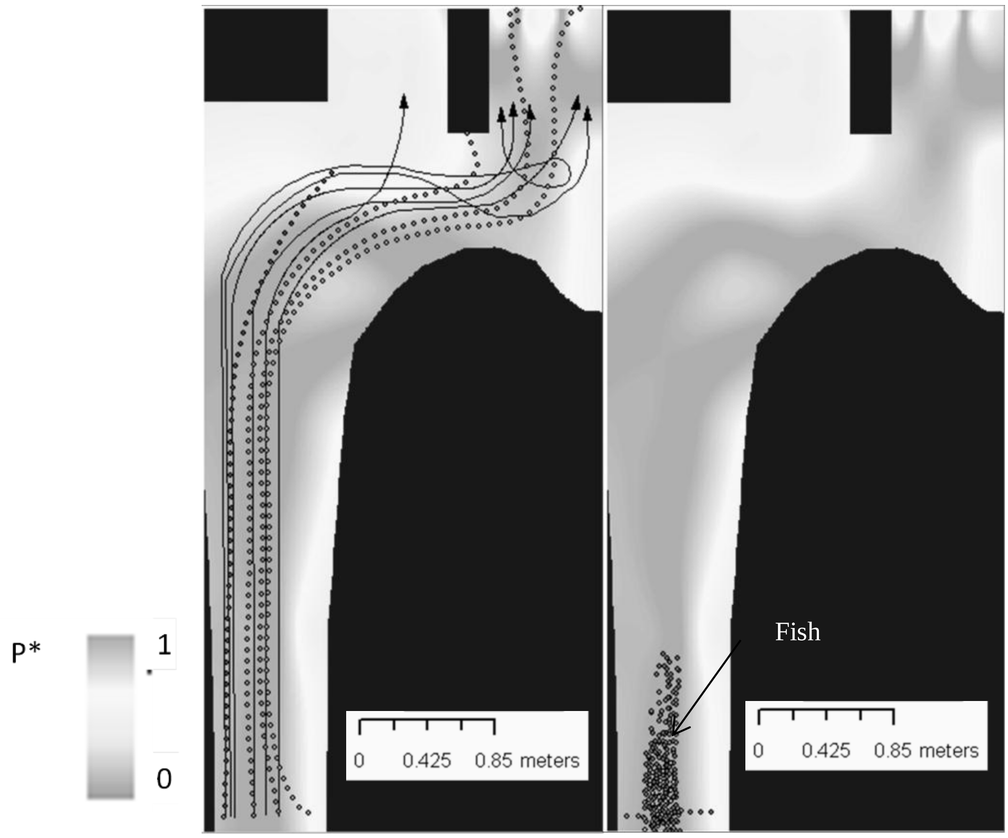


Figure 12. Estimation of overall preference in the simulation study.



(a) with rheotaxis (b) without rheotaxis

Figure 13. Simulation results for juvenile ayu

Conclusion

We modeled rheotaxis preferences in juvenile and adult ayu. Juvenile ayu displayed a strong positive rheotactic response at flow rates of30–40cm/s. Adult ayu displayed a positive response at flow rates of 50–70cm/s, but it was a weaker response than for the juvenile fish. We also estimated weight values for rheotaxis and illumination. For the rheotaxis response, estimated weight values=1 (for 40 cm/s) and 0.71 (for 30 cm/s). For the response to illumination, weight values=0.74 (for 40 cm/s) and 1 (for 30 cm/s).At a flow rate of 50 cm/s, weight values for rheotaxis and illumination responses in adult ayu were 1 and 0.36, respectively. At a flow rate of 70 cm/s, rheotaxis and illumination weight values were 0.63 and 1, respectively. We also proposed a framework for the incorporation of rheotaxis into fish behavior simulations. Our simulation model successfully reproduced natural juvenile ayu migration behavior. We have demonstrated that the rheotaxis response can be accurately modeled and quantified.

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