

Video Analysis of the Schooling Behavior of Juvenile Chum Salmon under Light and Dark Conditions Using a Mathematical Model

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Many fish form schools, which provide several advantages such as protection from predators and improving prey search efficiency (Pitcher and Parrish 1993). Chum salmon (*Oncorhynchus keta*) form small schools when they enter saltwater (Salo 1991). In most cases, the predominant sensory systems used for forming and maintaining schools are vision and the lateral line (Partridge and Pitcher 1980). The object of this study was to investigate the role of vision and the lateral line in the schooling behavior of juvenile chum salmon under different light conditions.

Juvenile chum salmon were collected by a set net in Hakodate Bay (southern Hokkaido, Japan) during June 2005 and held in a circular tank (12,000 liter, diameter 4 m, water depth 1 m) for 3–7 days. Fish of similar size (72.2 ± 6.1 mm body length) were selected for the experiments. An experimental group of fish was placed in seawater containing 0.5 g l^{-1} streptomycin sulphate for 3 hours to deactivate the lateral line system (Blaxter and Fuiman 1989). Experiments were carried out under uniform light intensity. A cylindrical tank (diameter 1.8 m) was used for the experiments. The water column was shallow (10 cm deep) to minimize the vertical movement of fish. The water temperature in the experimental tank was 10°C . The swimming behaviors of the experimental group and a control group (not exposed to streptomycin sulphate) were observed under both light (80 lx) and dark (< 0.01 lx) conditions. The school size examined for each group was 15 individuals randomly sampled from the stock tank.

The two-dimensional motion of individuals during three minute observation periods was digitized and processed, and a fish behavior model (Sannomiya and Matuda 1987; Sannomiya et al. 1993) based on Newton's second law of motion was used to quantify the forces dominating the swimming behavior. In this model, the motions of N_f fish in a school are described by

$$\dot{\mathbf{x}}_i = \mathbf{v}_i \quad (1)$$

$$\begin{aligned} m\dot{\mathbf{v}}_i &= \mathbf{F}_{i1} + \mathbf{F}_{i2} + \mathbf{F}_{i3} + \mathbf{F}_{i4} \\ &= a_i \mathbf{f}_{i1} + k_{wi} \mathbf{f}_{i2} + k_{bi} \mathbf{f}_{i3} + k_{ci} \mathbf{f}_{i4} \end{aligned} \quad (2)$$

where $\dot{\mathbf{x}}_i$ and $\dot{\mathbf{v}}_i$ are the velocity and acceleration vectors, respectively, of individual i ($i = 1, 2, \dots, N_f$), m is the mean mass of individuals, and \mathbf{F}_i is the resultant of four forces that cause the motion of individual i (\mathbf{F}_{i1} , a propulsive force; \mathbf{F}_{i2} , a resultant force of repulsion and attraction from tank wall; \mathbf{F}_{i3} , an interactive force to keep a proper distance between neighbor fishes; and \mathbf{F}_{i4} , a schooling force to make the velocity of each fish uniform).

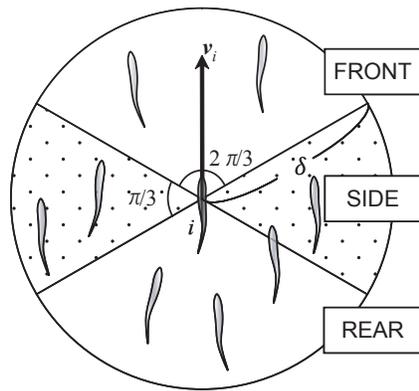
To evaluate the magnitude of each schooling force that is affected by neighbors in three separated areas (Fig. 1), partial schooling forces in front, side, and rear areas, \mathbf{F}_{i4}^F , \mathbf{F}_{i4}^S , and \mathbf{F}_{i4}^R were defined as

$$\begin{aligned} \mathbf{F}_{i4} &= \mathbf{F}_{i4}^F + \mathbf{F}_{i4}^S + \mathbf{F}_{i4}^R \\ &= k_{ci}^F \mathbf{f}_{i4}^F + k_{ci}^S \mathbf{f}_{i4}^S + k_{ci}^R \mathbf{f}_{i4}^R \end{aligned} \quad (3)$$

The magnitude of each force can be compared by estimating the coefficients a_i , k_{wi} , k_{bi} , and k_{ci} from Equation (2). The least squares method was then applied to the linear equations derived from observed data in each time step, and the unknown parameters were estimated for an individual in each experimental condition. The parameters in each case were calculated by substituting time-series coordinates for an individual as described in a previous paper (Suzuki et al. 2003).

The mean values a^* , k_w^* , k_b^* , and k_c^* of the normalized parameters of a_i , k_{wi} , k_{bi} , and k_{ci} were calculated to compare the predominance of each force on the swimming behavior under each experimental condition (Fig. 2). The propulsive force magnitude a^* in all experimental conditions, and the schooling force magnitude k_c^* in both

Fig. 1. The three separated areas for evaluating directivity of the schooling force. δ : an influence range for the schooling force.



stronger directivity when using the lateral line than when using vision.

Juvenile chum salmon probably form schools using both vision and lateral line under light condition, and yet they may be more dependent on vision for schooling. Low light condition influences the synchronization of individuals in the school, thus it may reduce their ability to avoid predators, and fishing and sampling gears.

Fig. 2. Normalized values of each force in the model.

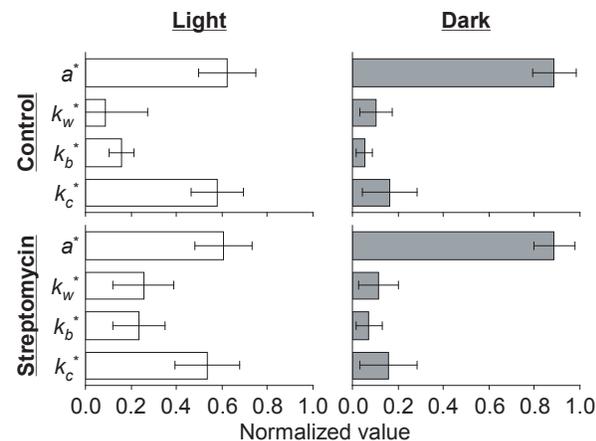
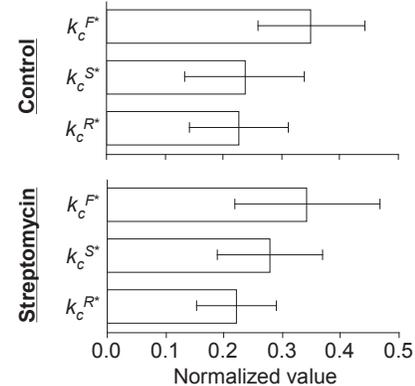


Fig. 3. Normalized values of partial schooling forces in three separate areas.



groups under light condition were large. Thus, both F_{i1} and F_{i4} dominated the swimming behaviors under light condition, and only F_{i1} dominated the swimming behavior under dark condition. In all experimental conditions k_w^* and k_b^* were relatively small, thus F_{i2} and F_{i3} did not strongly affect the swimming behavior. These results suggest that the crucial function for schooling of juvenile chum salmon is not so much the interactive force as the schooling force, and that they depend on vision to form schools.

The mean values $k_c^{F^*}$, $k_c^{S^*}$, and $k_c^{R^*}$ of the normalized parameters of k_{ci}^F , k_{ci}^S , and k_{ci}^R were calculated to compare the predominance to the fish behavior under each experimental condition. Figure 3 shows the results from only the light condition because the schooling force did not strongly affect the swimming behavior in the dark condition. For the control group, $k_c^{F^*}$ was significantly larger than $k_c^{S^*}$ and $k_c^{R^*}$ ($P < 0.05$, Scheffe's test). For the experimental group, $k_c^{F^*}$ and $k_c^{S^*}$ did not significantly differ. These results suggest that there is

REFERENCES

Blaxter, J.H.S., and L.A. Fuiman. 1989. Function of the free neuromasts of marine teleost larvae. *In* Mechanosensory lateral line: neurobiology and evolution. Edited by S. Coombs, G. Gerner, H. Münz. Springer, Berlin. pp. 481–500.

Partridge, B.L., and T.J. Pitcher. 1980. The sensory basis of fish schools: Relative roles of lateral line and vision. *J. Comp. Physiol.* 135: 315–325.

Pitcher, T.J., and J.K. Parrish. 1993. Functions of shoaling behaviour in teleosts. *In* Behaviour of teleost fishes, second edition. Edited by T.J. Pitcher. Chapman & Hall, London. pp. 363–439.

Salo, E.O. 1991. Life history of chum salmon, *Oncorhynchus keta*. *In* Pacific salmon life histories. Edited by C. Groot and L. Margolis. Univ. B.C. Press, Vancouver. pp. 231–309.

Sannomiya, N., and K. Matuda. 1987. Least squares parameter estimation in fish behavior model. *Nippon Suisan Gakkaishi* 53: 1951–1957.

Sannomiya, N., A. Shimada, and H. Nakamine. 1993. Modeling of autonomous decentralized mechanism in fish behavior. *Trans. Soc. Instrument and Control Engineers* 29: 211–219. (In Japanese).

Suzuki, K., T. Takagi, and T. Hiraishi. 2003. Video analysis of fish schooling behavior in finite space using a mathematical model. *Fish. Res.* 60: 3–10.