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Energy-saving Effect of Fish Schooling in the Japanese Mackerel, *Scomber japonicus*

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Abstract

Schooling and shoaling pertain to a spatial organization of fish that increases the chances of escaping predators or encountering prey. Weih's theoretically demonstrated that fish schooling also provides the advantage of minimizing the use of kinetic energy during movement. The present study evaluated the swimming properties of fish using constrained swimming and three-dimensional free-ranging swimming experiments, as well as examined the schooling effect from the point of view of kinetics. This study also presumed that members of the school have the advantage of conserving energy during rapid swimming or by adapting a planar school configuration.

1 Introduction

Fish schooling is considered as a form of organization that increases the chances of escape from predators, as well as enhancing predation efficiency [1-3]. As school or shoal has its own spatial configuration, this may increase the chance of experiencing predation. Fukuda [4-6] investigated the response behavior of an individual to a stimulus and the propagation of information to its neighbors using a two-dimensional experiment involving juvenile Pacific Bluefin Tuna. The results of the study showed that schooling increased the individual's potential to avert or attract an object through the use of a chain of responses. Functionality, however, does not only enhance that particular response behavior. Belyayev[7] reported that the swimming endurance in a school was two to six times greater than that observed in solitary fish. Weih's [8] theoretically showed that schools that used a diamond-shaped configuration were associated with a reduction in the tracking capacity of the follower. On the bases of these results, we thus predict that fish schooling not only facilitates the rapid expression of behavior, but also improves the fluid dynamics of kinetic energy of their movement. Kikken et al. [9] reported that the metabolic energy of followers in mullet schools were significantly less than that of the leading fish. However, most studies have focused on the effects of ranking in schools on metabolic energy expenditure, and the relative effect of a specific positions in a school on the kinetic energy requirements during swimming remain elusive. Furthermore, the effects of the school on free-ranging individuals in a three-dimensional (3-D) space have not been evaluated due to the difficulties in performing 3-D measurements.

This study evaluated the effect of rank order in a fish school by examining the position of individuals and the associated kinetic differences during swimming by conducting a flume tank test using Japanese mackerels. In addition, the paths of the free-ranging swimming fishes in a school were measured using a stereo-video camera system, and these were used to evaluate the 3-D effects of the school on the kinetic properties of its members during movement.

2 Materials and Methods

Fifty 39-day-old Japanese mackerels were obtained from the Shirahama Station of Fisheries Laboratory of Kinki University. The mackerels were bred in a large tank with a constant temperature of 18.9–19.9ºC. The flume tank and 3-D free-swimming tests were carried out in August 2012. The average body length (BL) of the mackerels was 8.48 cm ± 0.42 cm and their average body weight was 1.94 ± 0.72 g.

Constrained swimming test

Four fishes were randomly selected from the breeding tank and were transferred to a flume tank for the constrained swimming in various uniform current flows. The observation section of the tank was 100 cm in length, 30 cm in width, and 20 cm in height, and covered with a watertight acrylic roof to allow observation of their swimming motion from the top. The water current speed was changed to three different speeds, 15 cms^{-1} (1.8 BLs^{-1}), 23 cms^{-1} (2.7 BLs^{-1}), and 31 cms^{-1} (3.6 BLs^{-1}). Upon fish transfer into the flume tank, these were allowed to acclimatize for approximately 24 h by supplying sufficient air and allowing them to swim for 3 min at each current speed. The swimming motions were observed and captured using a video camera (Panasonic, HDC-TM750, Japan). Each video file covered fish motion for approximately 5 sec, operating at a speed of 60 fps, and was used to analyze fish kinetic motion. The two-dimensional coordinates of the rostrum- and tail-end of each fish were measured on the horizontal plane of the video images, and the neighbor distances (ND) between two individuals were estimated by measuring the position of each rostrum. Additionally, α, which was defined as the angle between the line connecting the rostrums of two individuals and the current vector, was measured, as shown in Fig. 1.

ND and α can be defined using the following equations:

$$\mathrm{ND} = \sqrt{\left(x_i - x_j\right)^2 + \left(y_i - y_j\right)^2} \qquad (\mathrm{i} \neq j;\ i\ or\ j = 1,2,3,4) \qquad (1);\ \text{and}$$

$$\cos\alpha = \frac{\vec{u}\cdot\overrightarrow{p_{ij}}}{|\overrightarrow{p_{ij}}|} \quad (2),$$

in which (x_i, yi) is the x-y coordinate of the focal individual on the two dimensional horizontal plane; $\overrightarrow{\mathrm{p}_{ij}}$ is the vector defined from the rostrums of the individual *i* and *j*; and $\vec{\mathrm{u}}$ is the current flow unit vector.

The tail beat frequencies and amplitude were estimated from the time series data of the coordinates of the fish tail ends, and then Strouhal numbers (St) were estimated using the following equation:

$$\mathrm{St}=fAU^{1} \qquad (3)$$

in which f (s^{-1}) is the tail beat frequency; and A (m) is the tail beat width, which is generally twice the tail beat amplitude; and U is the current flow speed (ms^{-1}). St is known to govern a well-defined series of vortex growth and shedding regimes for airfoils undergoing pitching and heaving motions, and usually peaks within the range of $0.2<\mathrm{St}<0.4$ [10, 11]. In the present study, the St of each individual in a school was estimated and the differences depending on the rank order and the various current speeds were examined. The experiments were carried out in five replicates.

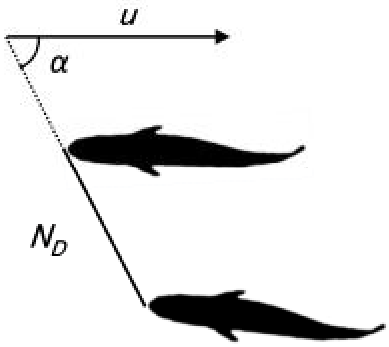

Fig. 1. ND and α are defined. U is the current flow vector.

Free-ranging swimming test

Four mackerels were selected from the breeding tank and transferred to an acrylic tank that was 2 m in length, 1 m in width, and 0.9 m in height. After acclimatization for 24h, the 3-D swimming paths of the fishes were measured by detecting the rostrums using the Direct Linear Transformation (DLT) method and capturing the motion using a stereo video camera (Panasonic HDC-TM750, Japan); tail beat frequency was also measured. Free-ranging fish school swimming was video-imaged for 3 min, at 60 fps, and 600 flames were used for analysis. The experiments were carried out in triplicate. The swimming speed (V_i) of each individual (i), the nearest-neighbor distance (NND), and the separation swimming index (SSI), were estimated from the video images[12] as follows:

$$|V_i| = \sqrt{\left(x_{i,n+1} - x_{i,n}\right)^2 + \left(y_{i,n+1} - y_{i,n}\right)^2 + \left(z_{i,n+1} - z_{i,n}\right)^2} / \Delta t \quad (4);$$

$$\text{NND} \ = \sqrt{(x_i - x_{ni})^2 + (y_i - y_{ni})^2 + (z_i - z_{ni})^2} \quad (\text{i} \neq ni; i\ or\ j = 1,2,3,4) \quad (5); \text{ and}$$

$$\text{SSI} = 2\sqrt{|V_i|^2 + \left|V_j\right|^2 - 2|V_i|\left|V_j\right| \cos\theta} / \left(|V_i| + \left|V_j\right|\right) \quad (\text{i} \neq j;\ i\ or\ j = 1,2,3,4\ ) \quad (6);$$

in which ($x_{i,n}$, $y_{i,n}$, $z_{i,n}$) are the 3-D coordinates of the individual i at the time n; θ is defined as the angle between vectors, V_i and V_j; Δt is the time step between two successive positions. A lower SSI generally equates with a greater schooling polarity. Additionally, if the behavior of the individuals is completely random, SSI has to be converged to 1.5. To evaluate the geometry of the school, the volume V (m^3) and the surface area S (m^2) of the tetrahedral, which had corners that corresponded to the four individual's rostrums, were estimated.

3 Results and Discussion

Constrained swimming test

The tail beat frequency showed a remarkable correlation with swimming speed [13]. Fig. 2 shows the tail beat frequencies at each current flow speed. The frequencies of the leading individual and followers were plotted and the frequencies values were expressed as the average of measurements collected from the five experiments. The mean tail beat frequency of the followers was 3.1%, 4.2%, and 18% less than that of the leading individual at a current speed of 1.8, 2.7, and 3.6 BLs^{-1}, respectively. At fastest current speed, the followers' frequencies were significantly less than that of the leading fish; thus, it presumed that there was a significant conservation of metabolic energy among followers, which may then be used during events that require rapid movement.

Fig. 3 shows the relationship between the St of the leading fish and its nearest neighboring individual in each experiment. St varied widely at a current speed of 1.8 BLs^{-1}, whereas the St of the leading fish was greater than that of the followers when the current speed was at 3.6 BLs^{-1}. Taylor *et al.* [10] examined the St of nine aquatic animal species, including sharks and dolphins, during swimming, and showed that all St were within the range $0.2<St<0.4$. The report also showed that the St of the mackerel reached almost 0.3. During cruising at a lateral oscillating motion, the animal can most efficiently move when $0.2<St<0.4$ [11]. In the present study, this St of the leading fish <0.3 was only observed at a current speed of 1.8 BLs^{-1}. The St at the faster current speeds were greater, and the St in all experiments using a current speed of 3.6 BLs^{-1} were greater than 0.4; however, in this case, the St of the followers were remarkably smaller than that of the leading fish. This result implies that the followers can efficiently move regardless of the behavior of rapid swimming. Sepulveda *et al.* [14] reported that the optimum swimming speed of Bonito was 1.4 FLs^{-1}; this is similar to the current speed in which the St were in the range of $0.2<St<0.4$ in most cases. Therefore, in such optimal swimming speed range, fish may find it difficult to conserve energy during swimming in a school configuration.

Fig. 4 shows the decreasing rate, Rst, using various follower positions. The origin of the graph indicates the rostrum of the leading fish. The decreasing rate can be expressed as follows:

$Rst=1-Stf/Stl$ (7),

in which Stf is the mean St of the followers in the school; and Stl is the St of the leading individual. Therefore, when Rst is high, the St of the followers is lower than that of the leading fish. Fig. 4 shows that no decrease in St was detected among the followers positioned in the vicinity of the lateral sides of the leading fish, whereas a greater St was observed among the rest of the followers. No followers within the vicinity of the leading fish were observed during swimming at a current speed of 3.6 BLs^{-1}. When the Rst was high, the positions of the followers were located near the diagonal line in the aft part of the leading fish. This observation may potentially support the theory of Weih [15], in which the induced velocity was generated by the leading fish by producing a vortex through tail beating, which in turn affects followers that are located at a diagonal orientation to the leading fish; the followers then utilize this velocity as thrust force.

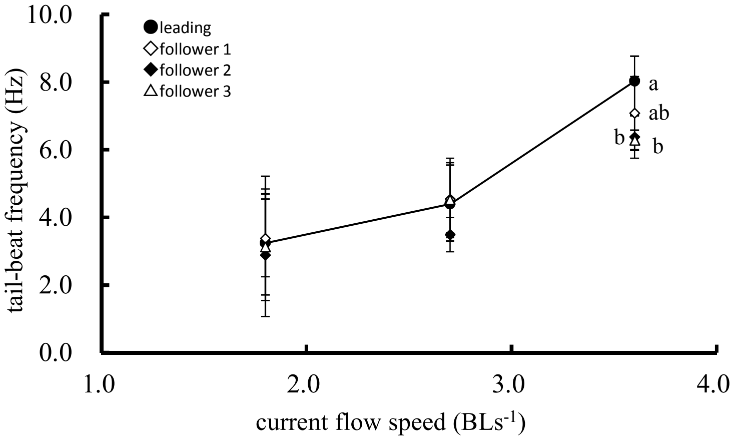

Fig. 2. The tail beat frequency vs. the swimming speed. In the case of the fastest current speeds, the tail best frequency of the leading individual was significantly different from that of followers 2 and 3 (P < 0.01 using Bonferroni's method)

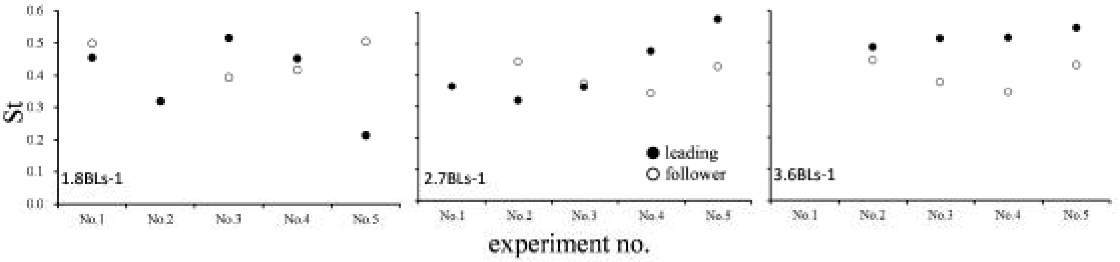

Fig. 3. St of the leading individual (filled circle) and the follower individual (open circle) at various current speeds.

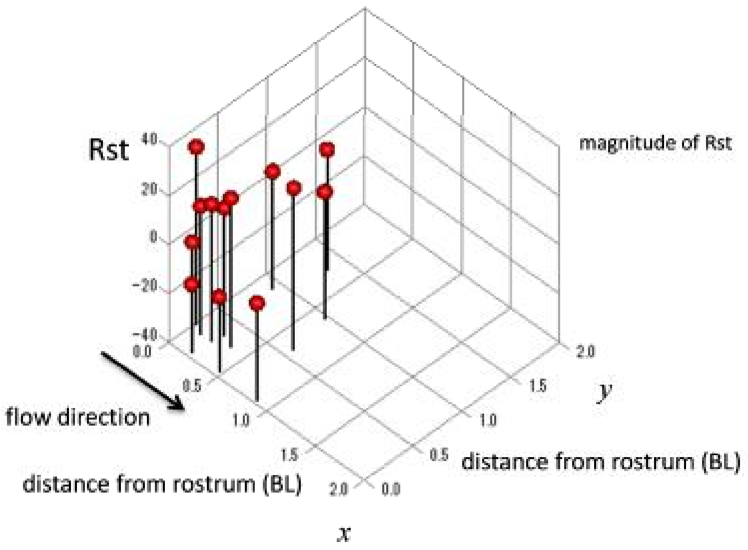

Fig. 4. The position of the follower and the decreasing rate of St. A higher rate the greater difference between St of the leading fish and the follower.

Free-ranging swimming test

Fig. 5 shows the relationship between NND and swimming speed in free-ranging fish belonging to a school. NNDs were almost within the range of 1–1.5 BL at each swimming speed. Fig. 6 shows the relationship between ND and SSI; the NDs showed a strong correlation with SSI. Thus, the closer the distance between individuals, the more likely that polar schooling would be observed. The tetrahedral volumes, V (cm^3), and its surface area, S (cm^2), were estimated from three experiments, and the following index, SB (cm), was calculated to represent the steric-bulkiness of the fish school configuration.

$SB = VS^{-1}$ (8)

If SB was smaller, then the school followed a planar configuration. SB in Experiment Nos. 1 and 2 was 2.8 (BL) and 2.8 (BL), respectively; however, the SB in Experiment No. 3 was 7.7 (BL). The result in No. 3 indicates that the school configuration was sterically bulky in the vertical direction.

The St of the leading fish and followers were estimated in each experiment and compared to that of the fish schooling configuration. However, it was difficult to measure the amplitude of free-ranging fish because the image videos were taken from the lateral sides of fish school. Therefore, the values of the tail beat amplitude in the flume tank experiments were used to estimate the St. Although the St of the followers were smaller than that of the leading fish in all experiments, the differences between the leading fish and follower were greater in the planar configurations in Experiment Nos. 1 and 2, as shown in Fig. 7. This observation implies that planar schooling provides the advantages of conserving energy; however, statistical significance using the t-test was only observed in Experiment No. 1.

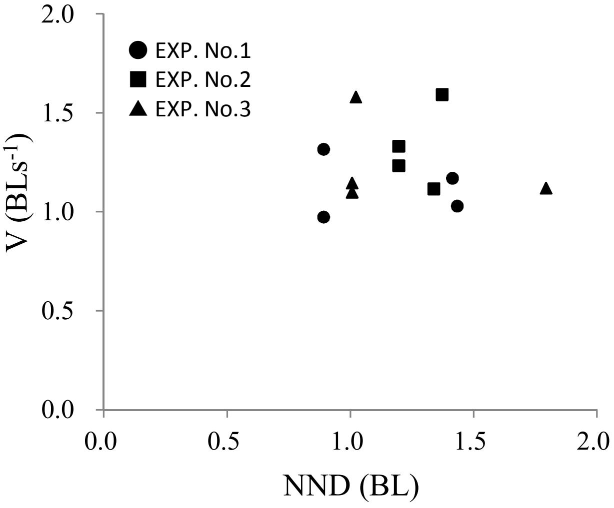

Fig. 5. NND vs. the swimming velocity of each individual in the free-ranging fish school

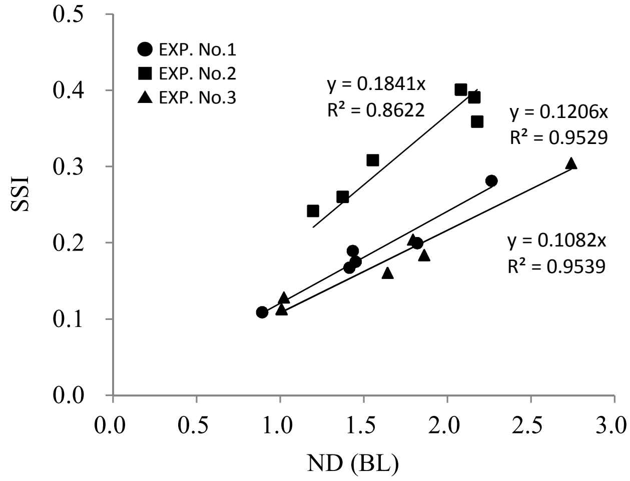

Fig. 6 SSI vs. ND of each individual in a free-ranging fish school.

This study has shown that faster and planar schools were associated with lower St among the followers, as compared to that in the leading fish. To produce the thrust force for scombrid fishes, the swimming mode was defined as “tuniform” or “carangiform” by Lindsey [16]. The vortex rings produced by this swimming mode produce jets behind the tail and generate reaction forces that thrust the body toward a particular direction. The vortices generates a counter-flow, which supports the propulsion of the followers. We therefore presumed that the induced flow by vortices provides an effective advantage to followers positioned along the same horizontal plane, including the leading fish. Thus, the large differences in St between the leading fish and the followers during lower SB, as shown in Fig. 7, may be caused by this particular mechanism. In addition, faster swimming enhances the induced vortices that were produced by the leading fish, allowing the followers to conserve their kinetic energy during rapid migration. It is also possible that fish schools utilize this mechanism of movement and conservation of kinetic energy for long-distance migration.

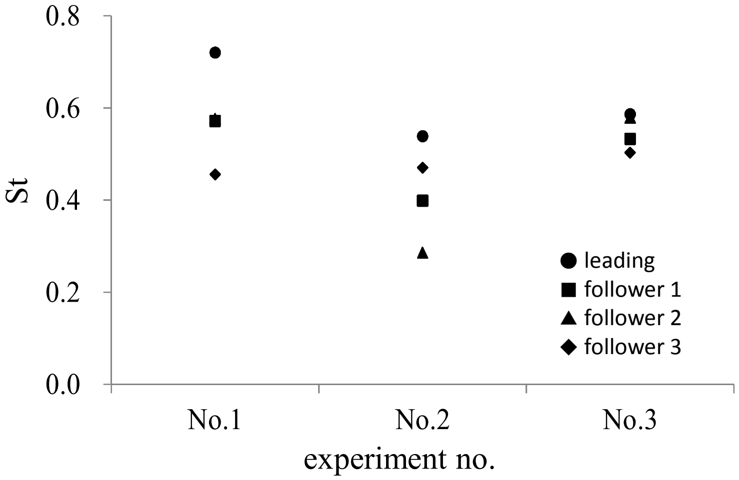

Fig. 7. St of each individual in a free-ranging fish school. The St of the leading fish was significantly different from that of the followers in Experiment No. 1 (*t*-test, $P < 0.05$).

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