Mechanical efficiency of fish thrust induced by tail beating: comparison between kinetic energy and metabolic energy

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Abstract—There are few studies that compare thrust power $P_T$ induced by tail beating with net metabolic power $P_{net}$ obtained from oxygen consumption and mechanical efficiency $\eta$ ($= P_T / P_{net}$) of fish thrust. In this study, $P_T$ and $P_{net}$ were obtained using two species of chub mackerel and Japanese dace, and $\eta$ was calculated by comparing kinetic energy and metabolic energy. $P_T$ was calculated by multiplying swimming speed $V_{swim}$ and thrust force $T$ obtained using two calculation methods, the Milne–Thomson principle and Kutta–Joukowski theorem. Comparing each value, $\eta$ showed a certain ratio irrespective of fish species and swimming speed. Linear approximation resulted in $P_T = 0.21 P_{net}$ for Milne–Thomson and $P_T = 0.44 P_{net}$ for Kutta–Joukowski.

Index Terms—chub mackerel, Japanese dace, particle image velocimetry, thrust, Milne–Thomson principle, Kutta–Joukowski theorem, oxygen consumption, mechanical efficiency

I. INTRODUCTION

Most fish that perform lateral movement of the caudal fin push fluid backward and acquire thrust via the reaction force. [1] Fish locomotion varies, depending on the fish species, because of the different bases of producing thrust. In previous studies, the wake flow induced by tail beating has been visualized using particle image velocimetry (PIV) in swimming experiments of such fish species as mackerel, eel, and sharks, and the thrust power has been analyzed. [2, 3, 4]

Regarding the metabolic rate of swimming, measurement experiments on oxygen consumption have been conducted for various fish species, such as mackerel and tuna. [5, 6, 7, 8] Regarding the mechanical efficiency of fish thrust, comparison of resistance and propulsion using a fish swimming model by two-dimensional viscous numerical simulations or by using PIV analysis and a fish-type robot with three-force-component meter has been conducted. [9, 10] Webb calculated the mechanical efficiency of fish thrust by comparing the net metabolic energy due to oxygen consumption and the resistance measured by towing dead fish. [11] However, there are few studies comparing the net metabolic rate $P_{net}$ obtained from oxygen consumption and the thrust power $P_T$ obtained from the transition of wake flow induced by tail beating of a living body.

In this study, the wake flow induced by the swimming of two fish species, chub mackerel (Scomber japonicus) and Japanese dace (Tribolodon hakonensis), was visualized using PIV in a flume tank. The thrust force of fish can be calculated from the circulation of the vortex, because reverse Karman vortex streets, which are generated by tail beating, can be observed using PIV. The thrust forces were estimated using two different methods: calculating the momentum of the vortex ring in the wake flow based on the Milne–Thomson principle, and calculating the lift force of the caudal fin from the Kutta–Joukowski theorem. [2, 12] From these values, $P_T$ per unit mass of the individual at swimming was obtained and compared with the $P_{net}$ obtained from oxygen consumption, and the mechanical efficiency of individual swimming in each fish species was examined.

II. MATERIALS AND METHODS

Experimental fish and PIV

Experimental fish were captured using a hook-and-line method in the wild. These fish were adapted in a fish tank. In the PIV experiment, tracer particles with an average particle diameter of 120 μm were suspended in a flume tank. The flow field visualized by irradiating laser light from both sides was photographed using a high-speed camera (k8-USB, KOKEN CO., LTD, 300 fps, 1280 × 768 px) equipped with a CCTV lens (Fig. 1). After image processing of the obtained image, the flow velocity and vorticity distribution of the flow field were analyzed using the PIV analysis software FtrPIV (Flowtech Research CO., LTD). The velocity vector obtained using PIV analysis adopted a direct correlation method that calculates the amount of movement from the transition in the minute time of the luminance distribution. Experiments were conducted in an environment suitable for each fish species, because the ecology greatly differs between Japanese dace and mackerel.
The forces in the left–right direction (y-axis direction) cancel each other, because the tail beating is repeated. Therefore, the thrust force $T$ is a force acting in the forward direction (x-axis direction) (Fig. 2). The angle $\alpha$ of the flow was obtained from the angle formed by the vortex ring and was calculated using the following equation. [2,10,13,14]

$$T_{Milne} = F \cos \alpha = \frac{\rho \Gamma A}{t} \cos \alpha$$  \hspace{1cm} (3)

Fig. 2. Milne–Thomson principle

The Kutta–Joukowski theorem calculates the lift acting on a wing from the circulation of the vortex around the wing. In this study, the lift force $L$ was calculated assuming that the caudal fin was a single airfoil shape. [13]

$$L = \rho \Gamma V_{\text{inlet}} b$$  \hspace{1cm} (4)

$\rho$ is the fluid density (kg m$^{-3}$), $\Gamma$ is the circulation (m$^2$ s$^{-1}$), $V_{\text{inlet}}$ is the inlet flow velocity to the caudal fin (m s$^{-1}$), and $b$ is the span of caudal fin (m). The inflow velocity $V_{\text{inlet}}$ and the angle $\theta$ of the flow relative to the caudal fin were determined from the swimming speed $V_{\text{swim}}$ and the tail beating speed $V_{\text{tail}}$. 

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**Measurement of thrust force**

Fish push fluid backward by tail beating, and they acquire thrust via its reaction force. At that time, torus vortex rings are induced. They appear as two pairs of vortices on the cross section of the vortex ring when observed in a two-dimensional section using PIV. The thrust can be calculated using the circulation of the vortex and the distance and angle between the two vortex centers. In this research, the thrust was calculated using the following two kinds of calculation method.

The Milne–Thomson principle calculates the impulse given by the disk accelerating in fluid from the circulation of the vortex around the disk. In this study, it was calculated from the circulation of the vortex around the caudal fin. Depending on how much fluid is pushed out during the movement of the caudal fin for one stroke, the impulse $I$, which is a change in momentum, can be obtained using the following formula.

$$I = \rho \Gamma \frac{\pi R b}{2} = \rho \Gamma A$$  \hspace{1cm} (1)

$\rho$ is the fluid density (kg m$^{-3}$), $\Gamma$ is the circulation (m$^2$ s$^{-1}$), and $A$ is the vertical projected area of the vortex ring (m$^2$). [13] In this study, the projected area $A$ is the area of the ellipse with the span of the caudal fin ($b$) on the short axis and the diameter of the vortex ring ($2R$) on the long axis. The diameter of the vortex ring, $2R$, is the distance of a pair of positive and negative vortices visualized on a two-dimensional section by connecting the coordinates of the lattice points where the absolute value of the vorticity becomes maximum with a straight line. The force $F$ of the tail beating per unit time was calculated from dividing the impulse by the time $t$ required for one stroke of the tail beating.

$$F = \frac{\rho \Gamma A}{t}$$  \hspace{1cm} (2)

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![Diagrammatic representation of PIV experiment](image)
The lift force $L$ and the thrust $T$ as the forward-direction (x-axis direction) component were calculated (Fig. 3).

$$T_{Kutta} = L \sin \theta = \rho \frac{b}{\Gamma} V_{swim} \sin \theta = \frac{\rho V_{swim}}{\sin \theta}$$

(7)

Fig. 3. Kutta–Joukowski theorem

The circulation $\Gamma$ was obtained by integrating the vorticity $\omega$ (1 s$^{-1}$) within the region that is the cross-sectional area $\delta$ (m$^2$) of the vortex ring.

$$\Gamma = \omega \delta$$

(8)

In this study, the calculated lattice point where the vorticity is the maximum value was taken as the vortex center. The circulation was obtained using the average value of vorticity from each calculated lattice point that was $5\%$ or more of the maximum vorticity and multiplying it by the cross-sectional area of the vortex ring.

Thrust power

The thrust power $P_T$ (J kg$^{-1}$ s$^{-1}$) per unit mass is calculated by multiplying the thrust force $T$ (N) by the swimming speed $V_{swim}$ (m s$^{-1}$) and dividing by the mass $M$ (kg) of the experimental fish.

$$P_T = \frac{T V_{swim}}{M}$$

(9)

Measurement of oxygen consumption

The rate of oxygen uptake per hour in unit mass of experimental fish $V_{O_2}$ (mgO$_2$ kg$^{-1}$ h$^{-1}$) was calculated by dividing the oxygen consumption $V'_{O_2}$ (mgO$_2$ h$^{-1}$) by the experimental fish mass $M$ (kg). $V'_{O_2}$ was calculated by multiplying the volume of the flume tank $C$ (L) and the decreased tendency of dissolved oxygen in a flume tank $V_{DO}$ (mgO$_2$ L$^{-1}$ h$^{-1}$), which was measured using a dissolved-oxygen meter (JFE Advantech Co., Ltd., RINKO).

$$V_{O_2} = \frac{C V_{DO}}{M} = \frac{V'_{O_2}}{M}$$

(10)

The number of individual mackerel used for the measurement of oxygen consumption was 3, FL was 16.9 ± 0.3 cm, and the body mass was 47.0 ± 4.1 g. The experiment was conducted on September 10 and 14, 2017, and July 26, 2018. In the experiments on September 14 and July 26, because the measurement was repeated twice, the total number of experiments was 5. The flow velocity in a flume tank with a capacity of 396 L was set at 4–5 values of velocity for each individual within the range of 12.8–68.3 cm s$^{-1}$, and oxygen consumption for 1200 s, when the fish was stably swimming, at each velocity, was measured for each individual.

The number of individual dace used for the measurement of oxygen consumption was 5, FL was 20.1 ± 0.7 cm, and body mass was 75.0 ± 6.4 g. The experiment was conducted on July 10–13 and 17, 2018. Because the experiment was conducted once for each experimental fish, the number of experiments was 5. The flow velocity in a flume tank with a capacity of 810 L was set at 5 velocities: 6.3, 22.0, 37.0, 51.7, and 65.8 cm s$^{-1}$, and oxygen consumption for 2000 s, when the fish was stably swimming, at each velocity, was measured for each individual.

In consideration of the effect on oxygen consumption due to digestion of food, an experimental fish that had fasted for more than one day was used.

Net metabolic rate

The obtained $V_{O_2}$ was converted from a metabolic formula (14.1 J mgO$_2$ s$^{-1}$) and 1 h (3600 s) to total metabolic rate per unit time $P_{total}$ (J kg$^{-1}$ s$^{-1}$).

$$P_{total} = \frac{14.1 \ V_{O_2}}{3600}$$

(11)

The net metabolic rate required for swimming $P_{net}$ was the difference of total metabolic rate $P_{total}$ and standard metabolic rate (SMR).

$$P_{total} = P_{net} + SMR$$

(12)

The SMRs of the experimental fish were obtained from oxygen consumption at a swimming speed of 0 cm s$^{-1}$ calculated using the approximate expression obtained from the oxygen consumption of swimming at each velocity. From the measurement result of $V_{O_2}$ at each swimming speed of the experimental fish, exponential approximation with $V_{O_2}$ as $y$ and $V_{swim}$ as $x$ was performed under the condition that the residual sum of squares was at minimum (Fig. 4). [15] The approximation formulae of $V_{O_2}$ to the swimming speed, the fork length, and the body mass of each experimental fish are summarized in Table 1 for chub mackerel and Japanese dace.
Mechanical efficiency of fish thrust

The mechanical efficiency of fish locomotion $\eta$ was calculated using the comparison of metabolic power $P_{\text{net}}$ obtained from the oxygen consumption and kinetic power $P_T$ obtained from the thrust force caused by tail beating. \[ \eta = \frac{P_T}{P_{\text{net}}} \] (13)

III. RESULTS

Wake-field of scombrid and cyprinid

In this study, the wake area was visualized during the swimming of chub mackerel and Japanese dace. The instantaneous velocity fluctuation vector of the flow field was calculated by subtracting the average flow velocity at each calculation lattice. The vortex that had been already generated behind the fish body was vortex 0, and the vortex that was generated by the first stroke near the rear end of the caudal fin was vortex 1 (Fig. 5). In the same order, vortices 1–6 generated from 6 continuous strokes of 3 tail beatings are visualized. For color scale, a warm color indicates positive vorticity and cold color as negative one.

The reverse Karman vortex induced by tail beating was confirmed from the visualized wake flow area, and the circulation $\Gamma$ of each vortex was calculated in the calculation area ($48 \times 48$ px) centered on the computed lattice point where the absolute value of the vorticity became the maximum value. From the analysis results obtained from 6 reverse Karman vortices (vortex 1 through vortex 6) at each swimming speed $V_{\text{swim}}$, the average value of each parameter, the circulation $\Gamma$ for each fish species, the vertical projected area $A$ of the vortex ring, the time per stroke of the caudal fin $t$, tail-beating frequency $f$, Strouhal number $St$, jet angle $\alpha$ of outflow induced by tail beating, inlet angle $\theta$ of inflow to caudal fin, velocity of tail beating $V_{\text{tail}}$, and velocity of inlet flow $V_{\text{inlet}}$ were measured (Table 2). The Reynolds number Re was calculated assuming that the fork length FL of the experimental fish was the characteristic length, and the kinematic viscosity coefficient $\nu$ was $1.0 \times 10^{-6}$. The Strouhal number $St$ was calculated with the range of oscillation $V_{\text{tail}}$ and the time per stroke of the caudal fin $t$ as the characteristic length of the flow.

\[
Re = \frac{FL}{\nu} \frac{V_{\text{swim}}}{V}
\]
\[
St = \frac{fv_{\text{tail}}t}{V_{\text{swim}} = \frac{fD}{V_{\text{swim}}}}
\]

As seen in Table 2, both circulation $\Gamma$ and tail-beating frequency $f$ increased with increasing swimming speed $V_{\text{swim}}$ in both fish species. The projected area $A$ of the vortex ring showed similar values regardless of swimming speed in mackerel and dace but increased in dace except for results at 50.0 cm s$^{-1}$. In addition, the value of circulation $\Gamma$ of dace at 57.2 cm s$^{-1}$ was approximately twice the swimming speed just before. This may be because the swimming dace at 57.2 cm s$^{-1}$ slightly accelerated against the flow in the flume tank.

Measurement of thrust power

The thrust force and thrust power were calculated from each parameter obtained via PIV analysis (Table 3). The values of the thrust force differed greatly depending on the difference in calculation method, despite using the circulation of the same vortex. In particular, the value of thrust force $T$ of dace significantly differed with calculation method, occurring more than three times at swimming speeds of 34.8, 42.3, and 50.0 (cm s$^{-1}$). Therefore, the thrust power $P_T$ tended to be higher for the Kutta–Joukowski theorem than for the Milne–Thomson principle.

Measurement of net metabolic rate

$V_{O_2}$ at each swimming speed was obtained for each mackerel and dace using a dissolved-oxygen meter (Fig. 6). $V_{O_2}$ tended to be higher as the swimming speed was higher, in both fish species of chub mackerel and Japanese dace.

Using the metabolic formula converted from the obtained value, the total metabolic rate $P_{\text{total}}$ and net metabolic rate $P_{\text{net}}$ excluding standard metabolic rate SMR of each individual were calculated from $P_{\text{total}}$ (Fig. 7).
Fig. 5. Visualization of the wake area at 6 strokes of tail beating in chub mackerel (55.8 cm s$^{-1}$) and Japanese dace (57.2 cm s$^{-1}$)
Table 1. Experimental fish data for measurement of oxygen consumption

| Parameter                  | Chub mackerel, Scomber japonicus | Japanese dace, Tribolodon hakonensis |
|----------------------------|----------------------------------|--------------------------------------|
| Experimental No.           | 1                                | 2                                    |
| Experimental date          | 2017.09.10                       | 2017.09.14                           |
| Water temperature (°C)     | 19.5                             | 19.3                                 |
| Fork length (cm)           | 17.2                             | 16.6                                 |
| Body mass (g)              | 50.3                             | 42.9                                 |
| Range of V_{swim} (cm s\(^{-1}\)) | 12.8 - 68.3                       | 64.4 - 65.8                           |
| Approximation of V_{swim}  | y = 205.2x^{0.305}, y = 186.4x^{0.365}, y = 258.2x^{0.405}, y = 296.2x^{0.405} | 64.4 - 65.8                           |
| Correlation coefficient r | 0.01                             | 0.96                                 |

Table 2. Values of parameters of chub mackerel and Japanese dace obtained via PIV analysis

| Parameter                  | Chub mackerel, Scomber japonicus | Japanese dace, Tribolodon hakonensis |
|----------------------------|----------------------------------|--------------------------------------|
| FL = 19.7 (cm), Mass = 96.2 (g), b = 5.1 (cm) | Fluid density \(\rho = 1023.3 \text{ (kg m}^{-3}\) | Fluid density \(\rho = 999.1 \text{ (kg m}^{-3}\) |
| Velocity of swim \(V_{\text{swim}}\) (cm s\(^{-1}\)) | 28.3                             | 34.8                                 |
| Velocity of swim \(V_{\text{swim}}\) (FL s\(^{-1}\)) | 1.4                              | 1.7                                 |
| Reynolds number Re \(\times 10^5\) | 0.56                             | 0.73                                 |
| Circulation \(I'\) (cm\(^{2}\)) | 87.0 ± 17.4                      | 44.9 ± 6.6                           |
| Projected area of vortex ring \(A\) (cm\(^{2}\)) | 19.8 ± 6.1                       | 59.9 ± 8.4                           |
| Stroke duration \(s\) | 0.12 ± 0.01                      | 0.16 ± 0.02                          |
| Tail-beating frequency \(f\) (Hz) | 4.2 ± 0.6                        | 3.5 ± 0.6                            |
| Strouhal number \(St\) | 0.54 ± 0.04                      | 0.41 ± 0.07                          |
| Jet angle \(a\) (deg) | 49.4 ± 17.1                      | 80.4 ± 4.4                           |
| Inlet angle \(\theta\) | 47.3 ± 2.1                       | 22.9 ± 6.1                           |
| Velocity of tail beating \(V_{\text{tail}}\) (cm s\(^{-1}\)) | 30.9 ± 4.3                       | 14.9 ± 4.4                           |
| Velocity of inlet flow \(V_{\text{inlet}}\) (cm s\(^{-1}\)) | 41.9 ± 1.7                       | 38.1 ± 1.7                           |

Table 3. Thrust power of chub mackerel and Japanese dace obtained via PIV analysis

| Parameter                  | Chub mackerel, Scomber japonicus | Japanese dace, Tribolodon hakonensis |
|----------------------------|----------------------------------|--------------------------------------|
| FL = 19.7 (cm), Mass = 96.2 (g), b = 5.1 (cm) | Fluid density \(\rho = 1023.3 \text{ (kg m}^{-3}\) | Fluid density \(\rho = 999.1 \text{ (kg m}^{-3}\) |
| Velocity of swim \(V_{\text{swim}}\) (cm s\(^{-1}\)) | 28.3                             | 34.8                                 |
| Velocity of swim \(V_{\text{swim}}\) (FL s\(^{-1}\)) | 1.4                              | 1.7                                 |
| Reynolds number Re \(\times 10^5\) | 0.56                             | 0.73                                 |
| Milne- Thomson principle   |                                  |                                      |
| Total force \(F\) (mN) | 139.4 ± 34.3                     | 76.1 ± 24.1                          |
| Lateral force (Thrust force) \(T\) (mN) | 87.0 ± 34.7                      | 12.2 ± 4.7                           |
| Thrust Power \(P_T\) (J kg\(^{-1}\) s\(^{-1}\)) | 0.26 ± 0.10                      | 0.04 ± 0.02                          |
| Kutta-Joukowski theorem    |                                  |                                      |
| Lift force \(L\) (mN) | 100.9 ± 42.4                     | 112.7 ± 18.6                         |
| Lateral force (Thrust force) \(T\) (mN) | 140.8 ± 34.5                     | 44.6 ± 16.1                          |
| Thrust Power \(P_T\) (J kg\(^{-1}\) s\(^{-1}\)) | 0.41 ± 0.10                      | 0.16 ± 0.06                          |

Table 4. Mechanical efficiency of chub mackerel and Japanese dace

| Parameter                  | Chub mackerel, Scomber japonicus | Japanese dace, Tribolodon hakonensis |
|----------------------------|----------------------------------|--------------------------------------|
| FL = 19.7 (cm), Mass = 96.2 (g), b = 5.1 (cm) | Fluid density \(\rho = 1023.3 \text{ (kg m}^{-3}\) | Fluid density \(\rho = 999.1 \text{ (kg m}^{-3}\) |
| Velocity of swim \(V_{\text{swim}}\) (cm s\(^{-1}\)) | 28.3                             | 34.8                                 |
| Velocity of swim \(V_{\text{swim}}\) (FL s\(^{-1}\)) | 1.4                              | 1.7                                 |
| Total metabolic rate \(P_{\text{total}}\) (J kg\(^{-1}\) s\(^{-1}\)) | 5.57                             | 1.35                                 |
| Net metabolic rate \(P_{\text{net}}\) (J kg\(^{-1}\) s\(^{-1}\)) | 1.76                             | 0.69                                 |
| Milne—Thomson principle   |                                  |                                      |
| Thrust Power \(P_T\) (J kg\(^{-1}\) s\(^{-1}\)) | 0.26 ± 0.10                      | 0.04 ± 0.02                          |
| Mechanical efficiency \(\eta\) | 0.15 ± 0.06                      | 0.06 ± 0.02                          |
| Kutta—Joukowski theorem    |                                  |                                      |
| Thrust Power \(P_T\) (J kg\(^{-1}\) s\(^{-1}\)) | 0.41 ± 0.10                      | 0.16 ± 0.06                          |
| Mechanical efficiency \(\eta\) | 0.23 ± 0.06                      | 0.22 ± 0.08                          |
**Mechanical efficiency of fish thrust**

Thrust power $P_T$ per unit body mass, total metabolic rate $P_{\text{total}}$, and net metabolic rate $P_{\text{net}}$ for swimming are shown in a semi-log graph with y-axis as logarithm for mackerel (Fig. 8) and dace (Fig. 9). The mechanical efficiency $\eta$ is a ratio showing how much thrust power contributed to the power consumption of muscles used for propulsion. In Table 4, $\eta$ is shown at each swimming speed.

The value of $\eta$ greatly varied depending on the calculation method. In addition, the $\eta$ of dace at 57.2 cm s$^{-1}$ was 0.92, which was close to 1. This seems to be caused by slight acceleration against the flow velocity, because the tail-beating frequency $f$ during swimming is not stable compared with other velocities from Table 2, and the position of the snout tip of dace is moving forward from Fig. 5. The following is thought to have influenced $\eta$ that the value of $P_T$ became larger than $P_{\text{total}}$ obtained from the approximate expression because of accelerating fish swimming.
IV. DISCUSSION

Mechanical efficiency of fish thrust

To swim more efficiently, fish have to push fluid in the opposite direction to the swim direction along the x-axis, because fish push fluid backward and acquire thrust via the reaction force. Because real fish swim by pushing fluid obliquely rearward of the body, this principle works not only in the x-axis direction but also in the y-axis direction. Fish can swim straight, because the forces in the y-axis direction cancel each other from repeated and continuous motion, and the resistance of the lateral side is greater. In other words, it is unlikely that tail beating includes the force of the y-axis component, which does not contribute to thrust.

As shown in Table 4, the thrust power \( P_t \) never exceeded the net metabolic power \( P_{net} \). The relationship of \( P_t \) to \( P_{net} \) when fish swim with the same speed is shown in Fig. 10. In the figure, \( \eta = P_t / P_{net} \) is also indicated by a broken line. Looking at the relationship of \( P_t \) to \( P_{net} \), it can be seen that the mechanical efficiency \( \eta \) is lower than 1 in both fish species. Interestingly, the relationship of \( P_t \) to \( P_{net} \) shows a certain ratio regardless of fish species and swimming speed, except for the result for dace at 57.2 cm s\(^{-1}\). Although there is a difference in metabolic energy consumption depending on swimming speed, this result suggests that the mechanical efficiency \( \eta \) may be almost constant in fish propelled via the same swimming mode.

The report by Schmidt-Nielsen indicates that energy consumption varies depending on body mass, even for fish species with markedly different forms. [17] Therefore, the relationships of \( P_t \) to \( P_{net} \) of mackerel and dace can be divided by using only the calculation method without considering the influence of fish species. Linear approximation was also performed to obtain the mechanical efficiency of fish thrust (Fig. 10). When linear approximation was made with intercept 0, \( P_t = 0.21 \ P_{net} \) for Milne–Thomson and \( P_t = 0.44 \ P_{net} \) for Kutta–Joukowski. These approximations indicate that \( \eta \) in fish swimming is 21% for Milne–Thomson and 44% for Kutta–Joukowski, when kinetic power and metabolic power are compared.

When we calculated \( \eta \) via the same procedure considering the difference between fish species, \( \eta \) of mackerel is 19% for Milne–Thomson and 39% for Kutta–Joukowski, while the \( \eta \) of dace is 28% for Milne–Thomson and 64% for Kutta–Joukowski. These results show that Japanese dace has higher mechanical efficiency than chub mackerel. However, excluding the outlier value for Japanese dace at 57.2 cm s\(^{-1}\), the \( \eta \) is 9% for Milne–Thomson and 37% for Kutta–Joukowski. In this case, the value for mackerel was slightly higher than the corresponding value for dace. The possible reason why there was not much difference between the values of \( \eta \) in this experiment is Japanese dace is an anadromous fish and, compared to goldfish and carp, can migrate for a long time.

\[
\eta = \frac{P_t}{P_{net}} = 0.21 \quad \text{for Milne–Thomson} \\
\eta = 0.44 \quad \text{for Kutta–Joukowski}
\]

Fig. 10. The relationship of \( P_t \) to \( P_{net} \) of chub mackerel and Japanese dace

\[
\eta = \begin{cases} 
0.21 & \text{for Milne–Thomson} \\
0.44 & \text{for Kutta–Joukowski}
\end{cases}
\]

\( P_{net} \) of chub mackerel was greater than that of Japanese dace. There may be a possibility that the chub mackerel was smaller in size than the Japanese dace during the measurements of oxygen consumption.

Measurement of thrust power

The value of \( \eta \) should theoretically be equivalent regardless of the cross section position of vortex ring. In this study, the thrust power values determined from different calculation methods are significantly different from each other. In order to investigate the cause of the difference, the following equation by \( T_{Kutta} / T_{Milne} \) can be derived.

\[
\frac{T_{Kutta}}{T_{Milne}} = \frac{\eta \ I \ V_{tail} b}{\pi \ R \ \cos \alpha} = \frac{V_{tail} b \ t}{\pi \ R \ \cos \alpha} = \frac{2D}{\pi \ R \ \cos \alpha}
\]

(16)

\( D \) is the range of oscillation (m), \( R \) is the radius of the vortex ring (m), and \( \alpha \) is the jet angle formed by the vortex ring. Because there is only one true value of thrust power, these calculated values of thrust power should converge to the same value regardless of the calculation method used. However, the values calculated from different methods were significantly different from each other.

Possible errors for each calculation method are as follows. First, in the case of Kutta–Joukowski, \( D \) in equation (16) is obtained directly from the position of the tip of the caudal fin, the accuracy of which depends on...
the frame rate of the high-speed camera. Because the high-speed camera used in this experiment acquired images at intervals of 1/300 s, the error range is $V_{\text{rel}}$ (m s$^{-1}$) $\times$ 1/300 (s). $V_{\text{rel}}$ does not change greatly depending on the position of caudal fin in the same phase; therefore, possible error in Kutta–Joukowski is considered to be due to the above-mentioned frame rate.

In Milne–Thomson, on the other hand, the irradiation position had an influence on the caudal fin via laser sheet. The distance between the pair of positive and negative vortexes ($2R$) changes depending on the visualized position because the vortex ring is doughnut-shaped. In this experiment, it was difficult to capture the moment when the fish swam stably on the laser sheet, and the position of the laser sheet irradiated on the fish body was different depending on the analysis image. Therefore, the value of $R$ is thought to be underestimated compared to the actual value, which became the factor in the difference from the calculation method.

**Conclusion**

In this experiment, the data obtained using PIV refer to six pairs of reverse Karman vortexes, but the number of individuals referring to both mackerel and dace is only one individual. Metabolic data, such as oxygen consumption, were obtained from multiple individuals; however, mackerel data were fewer than those for dace, and the experiment time for mackerel was as short as 1200 s, compared with 2000 s for dace. In addition, the values of thrust power differed depending on the calculation method used. Considering the above, mechanical efficiency cannot necessarily be asserted to be 21% or 44%. However, the aforementioned values can be thought of as one of the possible results for mechanical efficiency considered from both the kinetic aspect, evaluated via PIV analysis, and metabolic aspect, analyzed via oxygen consumption measurement.

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