NOTES

EFFECTS OF SWIMMING PATH CURVATURE ON THE ENERGETICS OF FISH MOTION

Many respiration and other behavioral and physiological studies of larger pelagic fish species are carried out in round tanks (Fry 1957; Bainbridge 1958; Magnuson 1970; Neill et al. 1976). These tanks have structural and space advantages, since round tanks have the largest volume to surface area of any flat-sided enclosure.

However, circular tanks introduce an additional stress factor not usually encountered by wild fish. This is the centripetal force required for continued motion in a curved path. This force is proportional to the fish mass, and inversely proportional to the path radius. The tank radii are limited by the fact that respiration and heat transfer data are obtained from the medium, resulting in a requirement of relatively small volumes so that changes in the measured parameters (oxygen concentration, temperature, etc.) are enhanced.

As will be shown here, this constraint on tank size causes the centripetal contribution to the force balance to become dominant in certain experimental situations. I therefore developed a correction factor to be applied to data collected in round or annular tanks so as to make the data representative of fish swimming freely in a straight line, in open waters.

Analysis

For a neutrally buoyant fish swimming horizontally in a straight line at a constant speed the force balance in that plane (excluding forces due to buoyancy and its compensation) is, in absolute values,

$$T = D \qquad (1)$$

where T is the thrust and D is the total hydrodynamic drag. Equation (1) also describes the force balance in the tangential direction for curvilinear motion. However, an additional balance must be made between the natural centrifugal force F_c driving the fish to stay in a straight line and the countering centripetal force F causing it to remain on a curved path (see Figure 1A). This force

(A) FORCES IN THE HORIZONTAL PLANE
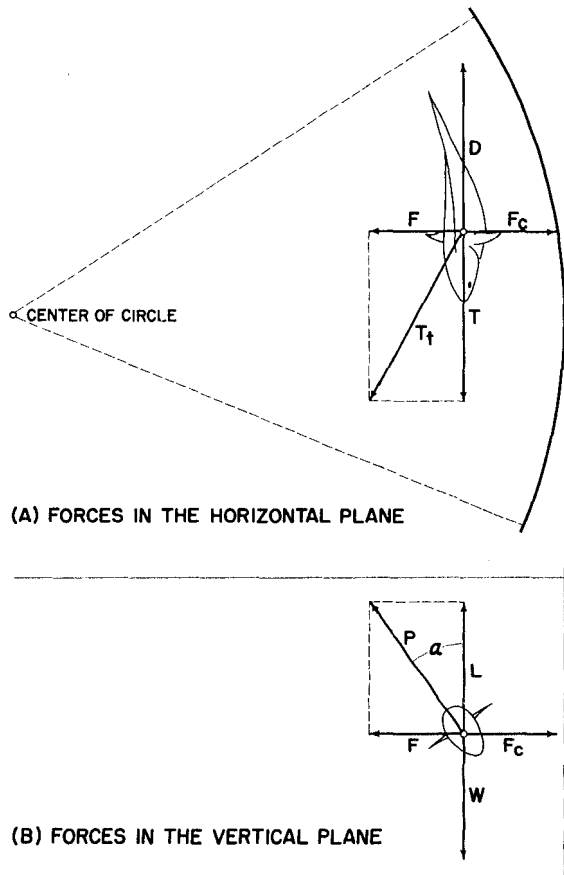
(B) FORCES IN THE VERTICAL PLANE

FIGURE 1.—Schematic description of forces acting on a fish when swimming in a curved path. A. Forces in the horizontal plane. B. Forces in the vertical plane.

F, which is equal in magnitude and opposite in sign to F_c, is of magnitude

$$F = \frac{m^1 U^2}{R} = \frac{VU^2}{R} (\rho_f + \rho_w \lambda) \qquad (2)$$

where m^1 is the virtual mass of the fish, ρ_f is the density (averaged) of the fish, V is its volume, U is the forward speed of the fish, λ is the longitudinal added mass coefficient, and R is the instantaneous radius of the curved path. The added mass coefficient λ is multiplied by the density of water ρ_w as the added mass is the volume of water dragged

along with the fish. The hydrodynamic drag can be written as (Hoerner 1965)

$$D = \frac{1}{2}\rho_w V^{2/3} U^2 C_{Dt} \qquad (3)$$

where C_{Dt} is the total drag coefficient based on the two-thirds power of the volume, as reference area. Here drag includes gill drag, induced drag due to pectoral fin extension and lift, etc. (see Magnuson 1978 for an excellent description of the various components of drag).

To find the relative importance of the centripetal force, we divide Equation (2) by Equation (3), obtaining

$$\frac{F}{D} = 2\frac{V^{1/3}}{RC_{Dt}}\left(\frac{\rho_f}{\rho_w} + \lambda\right) \qquad (4)$$

showing that the fish's velocity does not influence the ratio of centrifugal to drag forces in this case. Equation (4) can now be used to obtain the correction to the force produced by the fish, since the total force T_t that the fish requires for swimming in a circular path in the horizontal plane is, by vectorial addition,

$$T_t = \sqrt{D^2 + F^2} . \qquad (5)$$

Dividing by D^2 and applying Equation (1), we obtain the required thrust increase for neutrally buoyant fish, as a function of what will now be called the correction factor F/D,

$$\frac{T_t}{T} = \sqrt{1 + \left(\frac{F}{D}\right)^2} . \qquad (6)$$

Most studies of respiration and energetics in fish measure the aerobic oxygen consumption of the test animals as an indication of energy consumption. To obtain the correction required when the test data are obtained in a round tank, we recall that, for constant speed swimming

$$\dot{E} = TU \qquad (7)$$

where $\dot{E}$ is the rate of working. Thus the ratio of work (per unit time) for a continually turning fish, compared with that of fish swimming in a straight line at the same speed, is

$$\frac{\dot{E_t}}{\dot{E}} = \frac{T_t U}{TU} = \frac{T_t}{T} . \qquad (8)$$

The basic assumption of such respiration studies is that the oxygen uptake rate $\dot{V}_{O_2}$ is directly proportional to $\dot{E}$, so that

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = \frac{T_t}{T} \qquad (9)$$

and with Equation (4) we can write this ratio in terms of experimentally measurable quantities:

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = \sqrt{1 + 2\frac{V^{1/3}}{RC_{Dt}}\left(\frac{\rho_f}{\rho_w} + \lambda\right)^2} \qquad (10)$$

i.e., the equivalent oxygen uptake for a free-swimming fish moving in a straight line is always lower than that measured in a round tank. Also, for a given turning radius, the larger the fish, the greater the increase in oxygen uptake, or conversely, for a given fish, the oxygen uptake increases with decreasing turning radius. The increase is almost independent of swimming speed except for a possible weak Reynolds number dependence of C_{Dt}, neglected here.

The method shown above for obtaining the centripetal force by increasing the thrust is one possibility. A different way of getting the required forces is by means of hydrodynamic lift.

Negatively buoyant fish, such as most of the scombrids, produce lift by swimming continuously in order to maintain a horizontal course. This defines a hydrodynamical minimum swimming speed for horizontal motion (Magnuson 1970) and causes an additional effect due to swimming in a curved path.

The lift required is usually produced by the pectoral fins being placed at a small angle of incidence to the direction of motion. This force is at right angles to the longitudinal axis of the fish. It can therefore be applied to the production of the centrifugal force, by banking towards the center of curvature (see Figure 1B). Such behavior is an alternative to the added asymmetric thrust calculated above [Equations (4)-(6)], as no direct extra thrust is needed. However, the total lift force on the fins is now larger (Figure 1B), resulting in higher induced drag (Webb 1975; Magnuson 1978), which increases the thrust required.

For motion at a given speed we assume that the only component of drag that varies between straight-line and circular swimming is the induced drag. This is probably an underestimate, because the friction and form may also increase slightly, as mentioned in the previous section. Neglecting these, however, we find that the drag when turning D_t (the drag D, appearing in Equations (1)-(9), is D_t) is greater than the straight-line drag at the same speed D_s by

$$D_t - D_s = D_{it} - D_{is} \qquad (11)$$

where D_{it} and D_{is} are the induced drag in turning and in straight-line swimming, respectively. The drag is usually (Hoerner 1965) written as a function of the fin lift force G

$$D_i = \frac{2G^2}{\epsilon \pi \rho b^2 U^2} \qquad (12)$$

where b is the fin span and ϵ a fin shape factor. For our purposes, D_i can be written as

$$D_i = K \frac{G^2}{b^2 U^2} \qquad (13)$$

as the quantities collected in K are invariant for a given fish.

The fin span is variable, as many species of interest can adjust the sweepback angle, changing the span.

Substituting Equation (13) in Equation (11) and applying the geometrical relations of Figure 1B

$$D_t - D_s = \frac{K_1}{U^2} \left(\frac{P^2}{b_t^2} - \frac{L^2}{b_s^2} \right), \qquad (14)$$

where b_t and b_s are the pectoral fin span in turning and in straight-line swimming, respectively. Dividing by D_s,

$$\frac{D_t}{D_s} = 1 + \frac{K_1}{U^2 D_s} \left[\frac{P^2}{b_s^2} \left(\frac{b_s}{b_t} \right)^2 - \frac{L^2}{b_s^2} \right]. \qquad (15)$$

However, $D_{is} = K_1 L^2 / U^2 b_s$, so that

$$\frac{D_t}{D_s} = 1 + \frac{D_{is}}{D_s} \left[\left(\frac{P}{L} \right)^2 \left(\frac{b_s}{b_t} \right)^2 - 1 \right]$$

$$= 1 + \frac{D_{is}}{D_s} \left[\left(\left(\frac{F}{L} \right)^2 + 1 \right) \left(\frac{b_s}{b_t} \right)^2 - 1 \right]. \qquad (16)$$

In horizontal swimming $L = W$, so that

$$\frac{D_t}{D_s} = \frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}}$$

$$= 1 + \frac{D_{is}}{D_s} \left[\left(\left(\frac{F}{W} \right)^2 + 1 \right) \left(\frac{b_s}{b_t} \right)^2 - 1 \right], \qquad (17)$$

and as $W = (\rho_f - \rho_w) g V$, by substituting Equation (2)

$$\frac{\dot{V}_{O_2 t}}{\dot{V}_{O_2 s}} = 1$$

$$+ \frac{D_{is}}{D_s} \left[\left(\left(\frac{\rho_f + \lambda \rho_w}{\rho_f - \rho_w} \frac{U^2}{gR} \right)^2 + 1 \right) \left(\frac{b_s}{b_t} \right)^2 - 1 \right], \qquad (18)$$

and again, as in Equation (10), the oxygen consumption is higher when the fish is swimming in a circular path. The two techniques, analyzed above are available to negatively buoyant fish, which can choose between producing the centripetal force by asymmetric thrust or by banking. Neutrally buoyant fish would have a more difficult time using the banking method [Equation (18)], as the vertical component L would cause upward motion, or complicated and strenuous compensatory motions.

Returning to the negatively buoyant species, such as skipjack tuna, *Katsuwonus pelamis*, it is reasonable to assume that they will choose the less costly method, or a combination of the two techniques. This will be studied quantitatively in the next section, but one can see immediately that the banking method is highly dependent on swimming speed. This indicates that there may be a threshold speed for each species above which the banking method is more costly.

Next, we estimate the influence of swimming in a curved path on the hydrodynamic minimum swimming speed (Magnuson 1970). At the minimum swimming speed, the pectorals are already producing the highest possible lift coefficient C_L (which will be designated as $C_{L\max}$). Banking the fins reduces the vertical component of the force (Figure 1B), since part of the hydrodynamic force is used to turn the fish. But the vertical force is prescribed by the weight, so that the swimming speed must be increased to obtain the required

forces. Thus, the minimum swimming speed for moving in a curved path is always higher than that for swimming along a straight line. This further increases the effort required to swim in circular tanks above and beyond the thrust corrections found before, when the fish wants or has to move at minimum speed.

At the minimum speed U_m

$$W = \tfrac{1}{2} \rho_w A_f C_{L\,max} U_m^{\,2} \qquad (19)$$

where W is the submerged weight of the fish and A_f is the fin lifting area. If the fish turns (when it is confined to a round tank) and still remains at minimum speed, the pectoral fins are banked. The force produced on the fins is then (see Figure 1B)

$$P = \sqrt{W^2 + F^2} \qquad (20)$$

or $$\frac{P}{W} = \sqrt{1 + \left(\frac{F}{W}\right)^2}. \qquad (21)$$

P is produced while the fins are at C_{Lmax} so that

$$P = \tfrac{1}{2} \rho_w A_f C_{Lmax} U_t^{\,2} \qquad (22)$$

where U_t is the minimum speed for a horizontal turn. This is a function of the turning radius, through F [see Equation (2)].

Substituting Equations (22), (19), and (2) in Equation (21) we have

$$\left(\frac{U_t}{U_m}\right)^2 = \sqrt{1 + \frac{m^1 U_t^{\,2}}{RW}} \qquad (23)$$

$$\left(\frac{U_t}{U_m}\right)^4 = 1 + \frac{2m(1 + \lambda \rho_w/\rho_f)}{\rho_w R A_f C_{Lmax}} \left(\frac{U_t}{U_m}\right)^2 \qquad (24)$$

from which $$\frac{U_t}{U_m} = \left[B\left(1 + \sqrt{1 + \frac{1}{B^2}}\right)\right]^{1/2} \qquad (25)$$

where $$B = \frac{m(1 + \lambda \rho_w/\rho_f)}{\rho_w C_{Lmax} A_f} \frac{1}{R}.$$

From Equation (25) we see that $U_t > U_m$ for all

finite values of R and that the minimum swimming speed grows as the radius decreases. The increase in minimum speed also is reflected in the total effort required for swimming in the round tank, as the rate of working goes up as the cube of the velocity. The induced drag changes [Equation (11)] are included since the fins are producing maximum lift coefficients both in straight-line swimming and in turning

$$\left(\frac{\dot{V}_{O_2t}}{\dot{V}_{O_2s}}\right) \text{minimum speed} = \left(\frac{U_t}{U_m}\right)^3. \qquad (26)$$

Results and Discussion

To estimate the actual significance of the various corrections developed in the previous section, numerical values of the parameters are now substituted for a negatively buoyant species, the skipjack tuna.

Most of the quantities appearing in the oxygen consumption ratios [Equations (10), (18), and (26)] are easily measurable. The added mass and drag coefficients (λ and C_{Dt}) are more difficult to obtain, as both may also be dependent on the turning radius (due to higher drag when turning and additional added mass effects due to the fish body curvature). However, no such information is presently available, so both these quantities have to be estimated from data on rigid engineering structures.

The most complete set of data for estimation of D appears in Magnuson (1978, table 6) for skipjack tuna. These data will now be used to obtain a typical value of the correction factor Equation (4). The total drag for a 44 cm skipjack tuna swimming at 66 cm/s was estimated to be 19,780 dyn. The mass of the fish is approximately 1.67 kg (Nakamura and Uchiyama 1966), and with an average density of 1.09 (Magnuson 1978, table 3) the volume of the fish is 1,530 cm^3. The drag coefficient C_{Dt} (which is different from Magnuson's drag coefficient because of the different reference area) is found, from Equation (3), to be

$$C_{Dt} = \frac{2 \cdot 19,780}{1.025 \cdot (1,530)^{2/3} \cdot 66^2} = 0.067 . \qquad (27)$$

Magnuson's (1978) data are partially based on the study of ram ventilation by Brown and Muir (1970) which was carried out in the holding tanks of the National Marine Fisheries Service Kewalo Research Facility in Honolulu, which are of 7.3 m in

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diameter. These allow a maximum path radius of about 300 cm. Recalling that the longitudinal added mass for a streamlined fish shape is $\lambda \approx 0.2$ (Webb 1975) and substituting the above values first into Equation (4), we obtain

$$\frac{F}{D} = 2\frac{(1{,}530)^{1/3}\,(1.06 + 0.2)}{300 \cdot 0.067} = 1.44 . \quad (28)$$

This means that the centripetal force is actually larger than the total drag force under these circumstances. The total force exerted by the fish swimming in a circular path of 300 cm radius is thus, from Equation (6), $T_t/T = 1.76$, i.e., 76% greater than that required for straight swimming at the same speed. This is also, from Equation (9), the ratio of oxygen consumption. The ratio F/D grows essentially proportionally to fish length, so that larger fish expend an even greater proportion of energy in swimming in a curvilinear path.

We now look at the ratio of oxygen consumption obtained for fish swimming under the same circumstances while banking their fins. This is calculated from Equation (18), assuming that at this low (close to minimum) speed the pectoral fins are fully stretched so that $b_s/b_t = 1$. The ratio D_{is}/D_s is found from Magnuson's (1978) table 6, to be approximately 0.3;

$$\frac{D_t}{D_s} = \frac{\dot{V}_{O_2t}}{\dot{V}_{O_2s}} = 1 + 0.3\left[\left(\left(\frac{1.09 + 0.2 \cdot 1.025}{1.09 - 1.025}\ \frac{66^2}{981 \cdot 300}\right)^2 + 1\right) \cdot (1) - 1\right] = 1.026 , \quad (29)$$

i.e., the increase in energy requirements is only 2.6%, much less than for the asymmetric thrust, nonbanked type of swimming. We can conclude therefore that skipjack tuna moving at low speeds in circular paths will use the banked swimming technique once they are adjusted. The banking angle can be obtained by banking the body and keeping symmetrical fin angles (as in Figure 1B), or by asymmetric deployment of the pectorals. An experimental program to study these angles by photography is underway at present, as this is the most obvious and easily measured prediction of the present theory. The predicted value of the banking angle (from the vertical) is obtained from Equation (20) as

$$\tan \alpha = \frac{F}{W} \qquad \alpha = \tan^{-1} \frac{m\left(1 + \dfrac{\lambda\rho_w}{\rho_f}\right) U^2}{RW} , \quad (30)$$

which for the skipjack tuna example above is 12.0°.

We see above that the banking technique is much more efficient at a relatively low swimming speed. However, the ratio of energy consumption [Equation (18)] is proportional to the speed to the fourth power, so it is important to check on its values at higher swimming speeds. There is no complete set of data available for such speeds, so we have to make some assumptions about the behavior of the various parameters. The ratio D_{is}/D_s is most probably not speed-dependent, as the total and induced drag are both proportional to the speed squared. Thus, we can use the value 0.3 found above. Next, we assume that fin extension is the same (at each speed) for straight-line swimming and turning (the extension can change as a function of speed, but the ratio remains constant). This assumption will also be checked in the experimental program mentioned before, as it is easily corrected in Equation (18).

Skipjack tuna can move at up to 10 body lengths/s, i.e., over 400 cm/s in the present case. Applying Equation (18) at different speeds (still for a turning radius of 300 cm), we obtain

U cm/s	66	100	120	150	175	200	300	400
$\dfrac{\dot{V}_{O_2t}}{\dot{V}_{O_2s}}$	1.026	1.137	1.285	1.696	2.289	3.199	12.13	36.18

i.e., at speeds of about 160 cm/s ($\approx$ 4 body lengths/s) the asymmetric thrust method, which is independent of speed, becomes the better way of compensating for circular swimming. One can therefore establish a general upper limit for the centrifugal increase in oxygen consumption from Equation (10), with the proviso that at lower speeds the banking method is more efficient.

Next, we calculate the increase in the minimum swimming speed of the tuna mentioned above, for which $m = 1{,}670$ g, $C_{Lmax} = 1.0$, $A_f = 36$ cm^2 (Magnuson 1973), $\rho_w = 1.025$, $\lambda = 0.2$, and $R = 300$ cm. From Equation (25) we obtain $U_t/U_m = 1.093$. The measured minimum speed in the round tank is thus 10% higher than for the same fish moving in a straight line.

Using the allometric data of Magnuson (1973), we can obtain U_t/U_m as a function of fish size for various species. This appears in Figure 2 for the
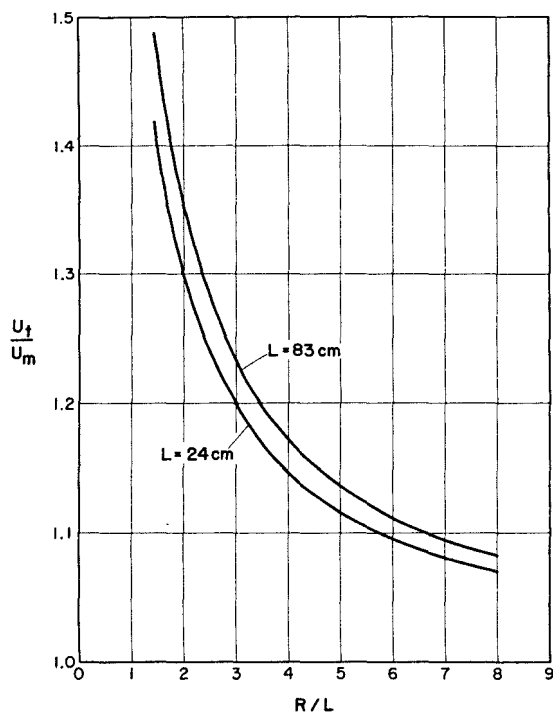
FIGURE 2.— Ratio of minimum speed when moving in a circular path, to the minimum speed in straight-line swimming versus the ratio of turning radius to fish length, for skipjack tuna, *Katsuwonus pelamis*.

skipjack tuna, for which $m = 0.00490L^{3.36}$ and $A_f = 0.00749L^{2.24}$, so that a slight dependence on fish length is retained, even after normalizing by the length. These curves can now be used to establish the increase in minimum energy consumption, with the aid of Equation (26).

In conclusion, it is seen that running fish in circular tanks can cause very significant additional stresses. These have to be taken into account when applying data collected under such circumstances to naturally occurring situations.

Acknowledgments

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