

Modelling of Swimming Ability Limits for Marine Fish

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The total energy of fish movement and the maximum burst swimming speed were estimated and formulated in accordance with body length and water temperature for several species in fisheries by empirical methods and also by using published results. Under the assumption of swimming energy reserve of a fish at the initial rest state, the swimming endurance of fish with different body lengths, swimming speeds and angular velocity was calculated using the relevant equations under similar conditions in tank experiments as well as natural conditions in field. Relative swimming energy efficiency or the transition swimming speed between red and white muscle for energy consumption was represented as a trigonometric function of swimming speed ratio. Therefore, this model does closely approach the actual swimming abilities and their limits especially in relation to the fishing gear operation and allow for the greater vitality of the wild fish in the fields.

Key words : modelling fish swimming ability, speed limits, endurance, energy efficiency

Introduction

The swimming performance of fish is very important manoeuvre in natural ecosystem, feeding, migration or especially in fish capture process of the active fishing gear (Wardle, 1993). The swimming ability of fish, expressed as swimming speed or endurance, is affected by many factors such as species, body length, water temperature, muscle composition as well as individual differences (Wardle, 1975, 1979; Webb, 1975; Videler and Wardle, 1991; Videler, 1993). The experimental results showed a wide range of variation even for fish of a similar size within the same species and can depend on fish condition and the measurement method. In relation to the towing speed of the fishing gear, normally at 2~4 knots (1~2 m/s), fish can always swim faster using white muscle anaerobically unless the stored glycogen has been exhausted. However response behaviour of fish as swimming performance showed much variation of swimming speed and angular velocity (Kim, 1996).

The total energy used for anaerobic swimming by white muscle can be estimated using either the amount of glycogen in white muscle transferred to biological energy or the power output integrated with endurance time (Webb, 1971, He, 1986). The amount of glycogen in a rested fish varied according to the ratio of white muscle to total body weight and the ratio of glycogen per unit

weight of white muscle. Furthermore, the endurance and the energy efficiency of fish swimming showed much variation with swimming conditions (Videler and Wardle, 1991). Therefore simple mathematical model for swimming ability limit is necessary to predict swimming endurance for relatively high speed including changeable swimming behaviour (He, 1993).

The purpose of the present model of swimming ability is to allow estimation of the available quantity of swimming energy in order to predict the relationship between swimming speed and endurance and as it moves within the fishing gear. The total energy of fish movement and the maximum burst swimming speed were estimated and formulated for several species in fisheries by empirical methods and also by using published results.

Methods and Modelling

1. Assumptions

The main factors limiting the swimming ability of fish are water temperature, and total body length both of which modify the muscle contraction time and stride length. The total swimming energy is considered to be at a maximum value when the fish is in a rested state. The swimming ability in this model is treated as the mean values of individual fish. The other assumptions are explained in the relevant part of the modelling.

2. Modelling of swimming energy and burst swimming speed

Swimming speed of fish can be classified as three steps by muscle reaction (Videler and Wardle, 1991). Those are first slow speed as aerobic swimming using red muscle solely, second medium speed as aerobic swimming using both red and white muscle and third high speed as anaerobic swimming using white muscle only. The critical swimming speeds of fish are called as the maximum sustained swimming speed (V_s , m/s) at the first step, the maximum cruising swimming speed (V_m , m/s) at the second step and the maximum burst swimming speed (V_b , m/s) at the last step. It was assumed simply that swimming ability of fish is varied by these swimming steps as represented as swimming speed.

The rate of energy consumption (dQ_s) for swimming speed by red and white muscle during fish swimming (Webb, 1971, He, 1986) can be expressed as integration over time t in terms of the current swimming speed V_t (m/s) and the transition swimming speed V_r between red and white muscle as follows:

$$dQ_s = \eta \int (V_t^\beta - V_r^\beta) dt \quad (V_t \geq V_s) \quad (1)$$

where η is the relative energy efficiency and β is a coefficient. The above equation should be used only for faster swimming when $V_t \geq V_s$. If the swimming speed (V_t) is maintained solely by anaerobic swimming using white muscle, $V_t > V_m$, then V_r is nil. The transition swimming speed V_r between red and white muscle is varied from V_s to zero as described later. Otherwise if swimming speed V_t is smaller than V_s , there is no swimming energy consumed maintaining permanent swimming endurance more than 2 hours generally (He and Wardle, 1988).

Thrust power lost of fish swimming in curved a track from argument by Weihs (1981) could be considered as deduction of swimming endurance or swimming speed redefined by He and Wardle (1988). Let change of swimming direction as swimming curved track be dA which is difference of swimming direction over time difference $dt \geq 1s$ as definition of angular velocity in fish movements by Kim (1996). Then, the rate of energy consumption for angular velocity dQA can be simply represented by 5% of linear increment of swimming energy when angu-

lar velocity 0.2π (rad/s) which is one circle turn during 10 s as follows:

$$dQ_A = \omega dA/dt \quad (2)$$

where ω is a coefficient. Resultant rate of energy consumption dQ by both swimming speed and angular velocity can be combined with equation (1) and (2) as follows:

$$dQ = \eta (1 + \omega dA/dt) \int (V_t^\beta - V_r^\beta) dt \quad (V_t \geq V_s) \quad (3)$$

The initial swimming energy reserve for anaerobic swimming was estimated using equation (3) with measured data from tank experiments (Videler and Wardle, 1991) and some data from field observations (Main and Sangster, 1981, 1983). With energy efficiency as a mean relative value ($\eta=1$) and coefficients $\omega=0.25/\pi$ and $\beta=3$, the estimated energy represented as the actual consumable swimming energy using above empirical data, is plotted against body length for 5 species of round fish and a flatfish in Fig. 1. Then initial swimming energy (Q_0 , J) is defined as the total available swimming energy for white muscle and can be represented with total body length (L_t , m/s) as follows:

$$Q_0 = B_q L_t^n \quad (4)$$

where B_q is an intercept and n is a coefficient.

The temperature effects on swimming ability for cod (*G. morhua*) were estimated using muscle contraction time, tail beat frequency and stride length (Wardle, 1979). These data are adapted to an approximation of the temperature effects as a linear relationship between B_q and current water temperature (T_w , °C) proportional to the swimming energy (Q_s) at $T_w=8^\circ\text{C}$ by conversion from swimming endurance and swimming speed as follows:

$$B_q = a Q_s + b Q_s T_w \quad (5)$$

where a and b are coefficients. By combining the equation (4) and (5) using a conversion of each data

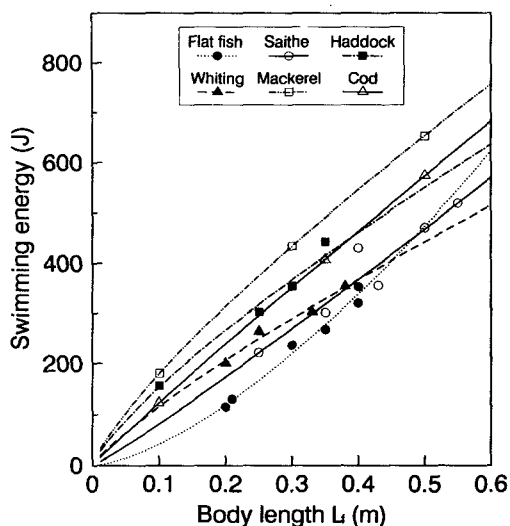


Fig. 1. The relationship between initial swimming energy reserve and total body length, adapted to water temperature of 10°C for 5 species of round fish such as haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), whiting (*Merlangius merlangus*), Atlantic mackerel (*Scomber scombrus*), Atlantic cod (*Gadus morhua*) and flatfish such as dace (*Leuciscus leuciscus*), plaice (*Pleuronectes platessa*), lemon sole (*Microstomus kitt*), dabs (*Limanda limanda*).

set with water temperature, species and body length, the total swimming energy (Q_0) can be transformed with two variables such as body length (L_f) and temperature (T_w) as follows:

$$Q_0 = (E_0 + E_1 T_w) L_f^n \quad (6)$$

where E_0 and E_1 are coefficients. Actual output swimming energy could be decreased with higher temperature over optimum temperature T_o (°C) as decreased in swimming speed (Brett, 1967). Therefore, if current water temperature is over than optimum temperature, T_w of equation (6) should be substituted as $2T_o - T_w$. The power n in equation (4) is calculated as a slope in Fig. 1 and coefficients E_0 and E_1 are estimated using equation (5) of cod for other species.

The burst swimming speed which is defined as the maximum swimming speed for a period of 2~6 s is one of the most difficult values to estimate in swimming experiments, due to the doubt that the fish are swimming their best either voluntarily or when forced. When fish escape from fish-

ing gear the fish might be using its maximum speed as the burst swimming speed. The burst swimming speed from published swimming data (Wardle and He, 1988) or the estimated burst swimming speed derived from equation (3) considering the natural vitality of fish in the sea, are plotted against body length in Fig. 2.

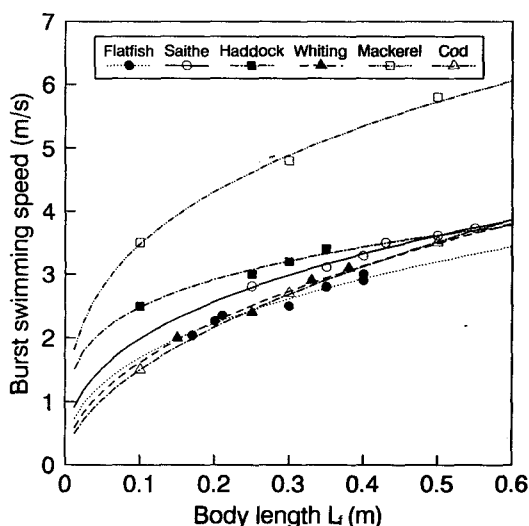


Fig. 2. The relationship between burst swimming speed and body length for fish adapted to a water temperature 10°C for 5 species of round fish and a flatfish (Refer to species in Fig. 1).

The burst swimming speed can also be expressed as a function of body length and water temperature in a similar way to the swimming energy equation (6). In addition, the burst swimming speed could be decreased with decreasing swimming energy reserved and can be expressed by the swimming energy reserve ratio (R_Q) which is the ratio of the current swimming energy (Q_c) to the initial total energy (Q_0). Let critical energy reserve ratio representing fatigue point be R_c which can affect the maximum burst swimming speed. The resultant burst swimming speed (V_B) is calculated from the 3 variables L_f , T_w and R_Q as follows:

$$V_B = (H_0 + H_1 T_w) (1 - G + GR_Q/R_c) L_f^m \quad (7)$$

where H_0 , H_1 , G and m are coefficients and $R_c = 1$ when $R_Q > R_c$. If current water temperature is over than optimum temperature, T_w of equation (7) should be substituted as $2T_o - T_w$ according to the measurements for sa-

Table 1. The estimated values of coefficients in equation (6) and (7) for swimming limit of fish

Species	Swimming energy					Swimming speed				
	E ₀	E ₁	n	N	r	H ₀	H ₁	m	N	r
Haddock	123.39	61.69	0.747	4	0.997	1.514	0.279	0.345	4	0.999
Whiting	112.72	56.36	0.834	4	0.985	1.776	0.257	0.477	4	0.989
Saithe	145.49	72.74	0.793	6	0.960	1.877	0.259	0.321	6	0.990
Cod	222.63	111.32	0.958	3	0.999	2.095	0.288	0.528	3	0.999
Mackerel	162.44	81.22	0.801	3	0.999	2.077	0.404	0.310	3	0.999
Anchovy	4.56	10.72	0.801*	6	0.999	3.063	0.281	0.859	6	0.999
Herring	113.84	56.92	0.801*	2	-	1.537	0.296	0.310*	2	-
Skipjack	1556.38	171.22	0.801*	1	-	2.478	0.248	0.310*	1	-
Flatfish	123.39	61.69	0.995	7	0.999	1.457	0.232	0.396	7	0.981

N : Number of data r : Correlation coefficient

* : Estimated using same coefficients as mackerel

Species are anchovy (*Engraulis japonica*), herring (*Clupea harengus*) and skipjack (*Katsuwonus pelamis*) in addition to Fig. 1.

lmon (*Oncorhynchus nerka*) by Brett (1967). The power m is calculated as a slope in Fig. 2 and coefficient H₀ and H₁ are estimated as linear relationship between swimming speed and water temperature from the estimation results of Wardle (1979).

The approximated coefficients from equation (6) and (7) for the 8 species of round fish and a flatfish (Blaxter and Dickson, 1959; Yuen, 1966; Lee, 1975; Wardle, 1979; Main and Sangster, 1981, 1983; He, 1986, 1991; He and Wardle, 1988; Videler and Wardle, 1991) are shown in Table 1.

The transition swimming speed (V_t) between red and white muscle in equation (3) is assumed to be proportional to the current swimming speed (V_t) with linear change. When V_t is between V_s and V_B, and using possibly both red and white muscle for swimming, the anaerobic swimming energy reserves are conserved giving longer endurance. The transition swimming speed V_t is observed to be linearly changed by He (1986) although this transition point was not clear in the estimation of swimming speed and endurance. It was assumed in this study as a cosine function of the swimming speed ratio between V_s and V_B as follows:

$$V_t = R_v V_B \cos\{k (V_t/V_B - R_v)\} \quad (V_t/V_B \geq R_v) \quad (8)$$

where R_v is the maximum ratio of V_s to V_B at the optimum water temperature and rest state as R₀=1 and k is a coefficient. If calculated V_t is appeared as negative value, then V_t is zero. For example R_v was estimated as 0.27 and k=1.85π for Atlantic mackerel (*S. scombrus*)

from Videler and Wardle (1991).

It also assumed that the relative value of energy efficiency (η) in equation (1) varies with swimming speed. The relative efficiency of swimming energy is increased with current swimming speed V_t from the maximum sustained swimming speed to the optimum cruising speed V_m and then decreased from V_m to the maximum burst swimming speed V_B when using white muscle solely as represented in Fig. 3. Therefore, this relative swimming efficiency can be expressed as sine function of swimming speed as follows:

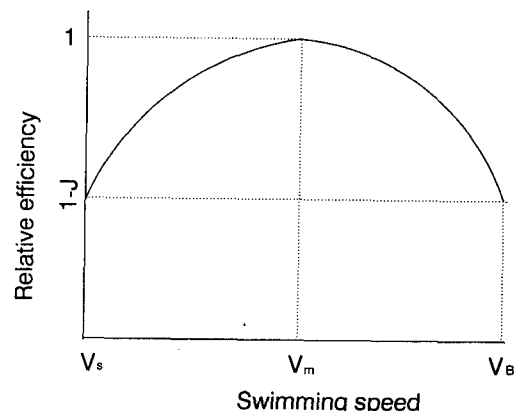


Fig. 3. Schematic diagram of the relative swimming energy efficiency in relation to swimming speed as represented in equation (9).

V_s : maximum sustained swimming speed

V_m : optimum cruising speed assumed at relative swimming efficiency 1

V_B : maximum burst swimming speed

J : Variation range of the relative swimming efficiency

$$\eta = 1 - J + J \sin\{\pi (V_f - V_s) / (V_B - V_s)\} \quad (V_f \geq V_s) \quad (9)$$

where J is a coefficient as the variation range of the relative swimming efficiency. As a result, current swimming energy reserve (Q_t) at any elapsed time can be represented as a deduction of the consumed energy in equation (3) from the initial total energy in equation (6).

Results and Discussion

The swimming endurance of fish with different body lengths and swimming speeds was calculated using the previous equations of the relevant coefficients in Table 1 and others as $\omega = 0.25/\pi$, $\beta = 3$, $G = 0.2$, $R_c = 0.3$, $R_v = 0.27$, $k = 1.85\pi$ and $J = 0.2$ under similar conditions in tank experiments. The simulation results are shown in Fig. 4 for saithe in order to compare with the measurements from Videler and Wardle (1991) and in Fig. 5 for the Atlantic cod based on measurements by He (1991).

Those results of swimming ability model are fit very well to the relevant results of the measurements. Validation of this model for several marine fishes in Fig. 1 or Fig. 2 which are derived from empirical data is not needed another test between the model and measurements. However further measurements of swimming performance for the other species are needed to check up this

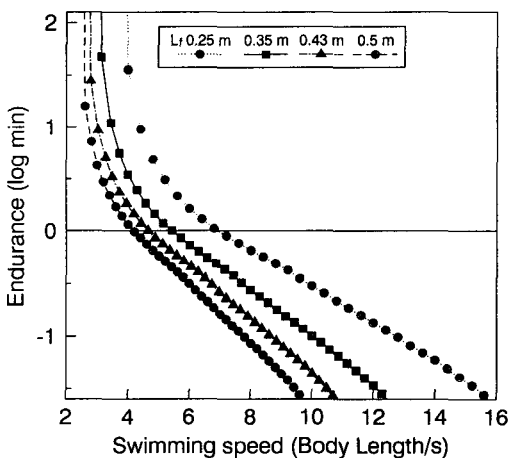


Fig. 4. The calculated swimming endurance against swimming speed at a water temperature of 10°C for saithe, *P. virens* (Refer to measured values by Videler and Wardle, 1991).

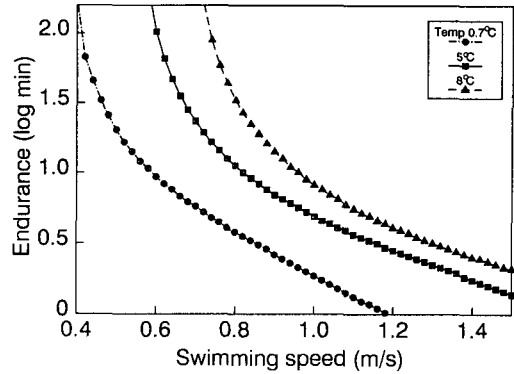


Fig. 5. The calculated swimming endurance against swimming speed under 3 different water temperatures for cod, *G. morhua* with body length L_f of 0.3m (Refer to measured values by He, 1991).

swimming limit model.

As a whole, the calculated values from this model of swimming speed limits, are slightly higher endurance and swimming speeds than the measured values in the tank experiments, since this model was also adapted with the data of endurance time in trawl operations observed by Korotkov (1970) and, Main and Sangster (1981, 1983). Therefore, this model can represent natural swimming abilities as the maximum burst swimming speed and endurance in relation to the fishing operation and predict for the greater ability limits of the marine fish in the sea. That vitality can be adjusted by coefficient E_0 for swimming energy and H_0 for burst swimming speed.

The swimming ability of fish is varied by so many biological and environmental conditions such as species, physiological and ecological state of fish, water temperature, body size, individual differences etc. In this model for mean maximum swimming energy reserve and mean maximum swimming speed, main factors are only treated as body length, water temperature and ratio of swimming speed or ratio of energy reserve. The other factors can be modified by coefficients of the relevant equations for specific conditions of fish or sea.

Swimming speed of fish is closely related with contraction time of swimming muscle for tail beat frequency, stride length and water temperature limit in relation to living conditions. Furthermore, measurement of swimming speed could be varied by pickup time and individual difference of voluntary swimming between fishes. The hi-

ghest swimming speed for adult teleost fish is about 20 body length per second as examples for yellowfin tuna (*Thunnus albacares*) by Walters and Fierstine (1964) and for mullet (*Mugil saliens*) by Komarov (1971).

Initial swimming energy reserve at resting state can be calculated for conversion energy from the amount of glycogen in white muscle of fish and compared with the swimming endurance time as an example using the Atlantic mackerel in the gantry tank experiments (He, 1986). However, problem of energy estimation by glycogen conversion method is that overall efficiency of swimming energy is very complicated in fish body as related so many factors.

Aerobic swimming energy efficiency was slightly increased with sustained swimming speed for horse mackerel (*Trachurus trachurus*) after Wardle *et al.*, (1996). Therefore energy efficiency for overall swimming speed in this model is formulated as sine function of ratio of swimming speed. Swimming endurance as followed energy consumption over time difference including ambient swimming speed should be considered for change of swimming direction as observed in a curved path of the gantry tank experiments (Weihs, 1981; Wardle *et al.*, 1996).

There was an interesting suggestion on energetic advantage of burst swimming of fish as kicking and gliding performance (Weihs, 1974, Videler and Weihs, 1982). In this model swimming energy and endurance were not considered such as kick and glide effects because deduction of energy consumption during intermediate swimming speed using both red and white muscle was already involved in relevant equation. However kick and glide performance of fish in relation to swimming energy consumption which is one of the most difficult items should be examined and provided precisely near future.

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References

- Blaxter, J.H.S. and Dickson, W. 1959. Observations of the swimming speeds of fish. *J. Cons. perm. int. Explor. Mer* 24, 472~479.
- Brett, J.R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Bd., Canada* 24 (8), 1731~1741.
- He, P. 1986. Swimming performance of three species of marine fish and some aspects of swimming in fishing gears. PhD Thesis, University of Aberdeen, UK. pp. 171~185.
- He, P. 1991. Swimming endurance of the Atlantic cod, *Gadus morhua* L., at low temperatures. *Fish. Res.*, 12, 65~73.
- He, P. 1993. Swimming performance of marine fish in relation to fishing gears. In: C.S. Wardle and C.E. Hollingworth, (Eds.). *Fish behaviour in relation to fishing operations*. ICES Marine Symposia 196, 183~189.
- He, P. and Wardle, C.S. 1988. Endurance at intermediate swimming speeds of Atlantic mackerel *Scomber scombrus* L., herring, *Clupea harengus* L., and saithe, *Pollachius virens* L. *J. Fish Biol.* 33, 255~266.
- Kim, Y-H. 1996. Developing a model of fish behaviour to towed fishing gear. PhD Thesis. University of Aberdeen, UK. pp.93~158.
- Komarov, V.T. 1971. Speed of fish movement. *Zool. Herald* 4, 67~71 (Translation from Russian, *Fish. Res. Bd. Canada. Transl. Ser. No. 2030*, 1972).
- Korotkov, V.P. 1970. The speed and endurance of fishes escaping from a trawl. *J. Ichthyol.* 10 (6), 832~836.
- Lee, B-G. 1975. The swimming ability of anchovy. *Publ. Inst. Mar. Sci. Nat. Fish. Univ. Busan* 8, 1~13 (In Korean with English abstract).
- Main, J. and Sangster, G.I. 1981. A study of the fish capture process in a bottom trawl by direct observations from a towed underwater vehicle. *Scot. Fish. Res. Rep.* 23, 1~8.
- Main, J. and Sangster, G.I. 1983. Fish reactions to trawl gear-A study comparing light and heavy ground gear. *Scot. Fish. Res. Rep.* 27, 1~19.
- Videler, J.J. 1993. *Fish swimming*. Chapman & Hall. pp. 113~206.
- Videler, J.J. and Wardle, C.S. 1991. Fish swimming stride by stride: speed limits and endurance. *Rev. Fish Biol. & Fish.* 1, 23~40.
- Videler, J.J. and Weihs, D. 1982. Energetic advantages of burst-and-coast swimming of fish at high speeds. *J. exp. Biol.* 97, 169~178.
- Wardle, C.S. 1975. Limit of fish swimming speed. *Nature (London)* 255, 725~727.
- Wardle, C.S. 1979. Effect of temperature on the maximum swimming speed of fish. In: M.A. Ali (ed), *Environmental physiology of fish*. Plenum. pp.519~531.
- Wardle, C.S. 1993. Fish behaviour and fishing gear. In: T.J.

- Pitcher (Ed). Behaviour of teleost fishes (2nd Edition). Chapman & Hall. pp.609~644.
- Wardle, C.S. and He, P. 1988. Burst swimming speeds of mackerel, *Scomber scombrus* L. J. Fish Biol. 32, 471~478.
- Wardle, C.S., Soofiani, N.M., O'Neill, F.G., Glass, C.W. and Johnstone, A.D.F. 1996. Measurements of aerobic metabolism of a school of horse mackerel at different swimming speeds. J. Fish Biol. 49, 854~862.
- Walters, V. and Fierstine, H.L. 1964. Measurements of swimming speeds of yellowfin tuna and wahoo. Nature (London) 202, 208~209.
- Webb, P.W. 1971. Swimming energetics of trout. I. Thrust and power output at cruising speeds. J. exp. Biol. 55, 489~520.
- Webb, P.W. 1975 Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd. Canada 190, 1~158.
- Weihs, D. 1974. Energetic advantage of burst swimming of fish. J. theor. Biol. 48, 215~229.
- Weihs, D. 1981. Effects of swimming path curvature on the energetics of fish motion. US. Fishery Bulletin 79, 171~176.
- Yuen, H.S.H. 1966. Swimming speed of yellowfin and skipjack tuna. Trans. Am. Fish. Soc. 95, 203~209.

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