ENERGETIC ADVANTAGES OF BURST-AND-COAST SWIMMING OF FISH AT HIGH SPEEDS

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SUMMARY

A theoretical model describes how an intermittent swimming style can be energetically advantageous over continuous swimming at high average velocities. Kinematic data are collected from high-speed ciné pictures of free swimming cod and saithe at high velocities in a burst-and-coast style. These data suggest that fish make use of the advantages shown by choosing initial and final burst velocities close to predicted optimal values. The limiting role of rapid glycogen depletion in fast white anaerobic muscle fibres is discussed.

INTRODUCTION

Burst-and-coast swimming behaviour in fish consists of cyclic bursts of swimming movements followed by a coast phase in which the body is kept motionless and straight. The burst phase starts off at an initial velocity (U_i), lower than the average velocity (U_c). During a burst the fish accelerates to a final velocity (U_f), higher than U_c. The cycle is completed when velocity U_i is reached at the end of deceleration during the coast phase.

Swimming in bursts as well as steady swimming is observed at low cruising speeds where fish use red aerobic muscles, and at high velocities (Hemmings, 1973) where propulsive power is provided by the bulk of white anaerobic muscles.

Weihs (1974) developed a theoretical model showing the energetic advantages of burst-and-coast swimming at velocities lower than maximum aerobic cruising speed. At these speeds considerable energy savings are possible if fish choose the right initial and final velocities, especially at average velocities lower than half the maximum cruising speed.

Small aquatic creatures such as small fish larvae just after hatching do not share the advantages of intermittent swimming. Here water viscosity is the dominant factor (the Reynolds number is small) and continuous swimming is the efficient form of locomotion. For growing fish larvae this gradually changes, the Reynolds number increases and burst-and-coast swimming becomes the more economical mode (Weihs, 1980).

Videler (1981) studied high-speed ciné films of swimming behaviour of cod (*Gadus morhua*) and calculated the work per meter distance covered for intermittent and steady swimming at fast anaerobic speeds. Intermittent swimming appeared to be cheaper than steady swimming at average velocities well above maximum cruising speed.

In the present paper the mathematical model of Weihs (1974) is adapted to anaerobic swimming velocities. The new model shows how fish can choose the cheapest burst-and-coast cycle for a given average speed. Kinematic data from high-speed ciné recordings of fast cod (*Gadus morhua*) and saithe (*Gadus virens*), swimming in the intermittent mode, show that these fish tend to choose the cheapest solution.

SYMBOLS

U	velocity	T_c	constant swimming thrust
U_i	initial velocity burst phase	T_e	maximum anaerobic thrust
U_f	final velocity burst phase	D	drag on a rigid body
U_c	average velocity of burst-and-coast	D_s	drag on a swimming body
	= constant swimming velocity	C_d	drag coefficient
U_e	maximum anaerobic velocity	m	mass of fish plus added mass of
$\bar{U}_c$	U_c/U_e		water
$\bar{U}_i$	U_i/U_e	ρ	density of medium
$\bar{U}_f$	U_f/U_e	A	frontal area
l_0	distance covered during burst-and-	η	efficiency factor
	coast	α	D_s/D
l_1	distance covered during burst phase	E_i	energy spent during burst phase
l_2	distance covered during coast phase	E_c	energy spent during constant swim-
t_1	duration of burst phase		ming
t_2	duration of coast phase	R	E_i/E_c
T	thrust	L	body length

THE THEORETICAL MODEL

We start by arguing, after Weihs (1974), that the resistance of a rigid streamlined body for Reynolds numbers greater than 1000, can be expressed as:

$$D = \tfrac{1}{2}\rho A C_d U^2 = cU^2, \tag{1}$$

where D is the resistance, ρ the density of the medium, A the frontal area, C_d a non-dimensional drag coefficient and U the velocity of the streamlined body (Hoerner, 1965).

Drag on an actively swimming body (D_s) is α times greater than the drag on a rigid body, so:

$$D_s = \alpha cU^2, \tag{2}$$

where α is always greater than 1. The equation of motion of a fish producing thrust T is
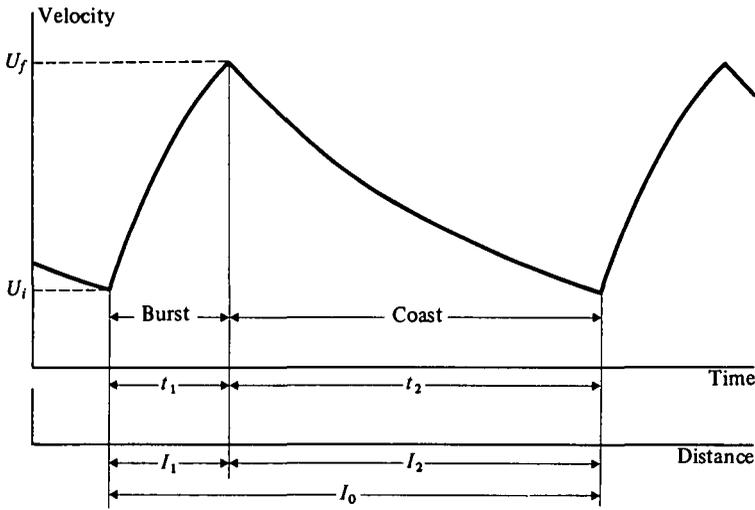
$$T = m(dU/dt) + \alpha cU^2, \tag{3}$$

Fig. 1. Velocity against time and distance during a burst-and-coast swimming cycle (schematic description, not to scale).

where m is the mass of the fish plus some added mass of water. At high velocities the efficiency (η) will probably be approximately constant (Videler & Wardle, 1978) and so:

$$\eta = k. \tag{4}$$

Fig. 1 shows that in one burst-and-coast cycle, distance l_0 is covered in time $t_1 + t_2$ (the duration of the burst plus the duration of the coast). In the intermittent swimming mode, energy is expended during the burst phase only and the energy required to cover distance l_0 equals

$$E_i = \frac{1}{\eta} \int_0^{t_1} TU\,dt. \tag{5}$$

When the same distance l_0 is crossed at a constant speed U_c (the average speed of the burst-and-coast mode), the energy required is

$$E_c = \frac{1}{\eta} T_c U_c (t_1 + t_2). \tag{6}$$

The energy expenditure of burst-and-coast swimming and steady swimming can thus be compared by using the ratio

$$R = \frac{E_i}{E_c} = \frac{\displaystyle\int_0^{t_1} TU\,dt}{T_c U_c (t_1 + t_2)}. \tag{7}$$

We assume that the thrust during the burst is the maximum anaerobic thrust T_e (Weihs, 1974), which is constant for a given species and so

$$R = \frac{T_e \displaystyle\int_0^{t_1} U\,dt}{T_c U_c (t_1 + t_2)}. \tag{8}$$

The integral term is equal to the distance l_1, covered during the burst phase. This reduces (8) to

$$R = \frac{T_e l_1}{T_c U_c (t_1 + t_2)}.$$ (9)

U_c was chosen as the average velocity during the whole cycle so that

$$U_c = \frac{l_0}{t_1 + t_2} = \frac{l_1 + l_2}{t_1 + t_2},$$ (10)

and so

$$R = \frac{T_e l_1}{T_c (l_1 + l_2)} = \frac{T_e}{T_c} \frac{l_1}{l_1 + l_2}.$$ (11)

During swimming at a constant velocity, thrust equals drag and equals the average thrust for intermittent swimming over a number of cycles at the same average velocity. The equation of motion (3) reduces to

$$T = \alpha c U^2$$ (12)

and

$$R = \frac{\alpha c U_e^2}{\alpha c U_c^2} \frac{l_1}{l_1 + l_2},$$ (13)

where U_e is the maximum anaerobic velocity.

The velocities in (13) are divided by the theoretical maximum velocity U_e to make them non-dimensional:

$$R = \frac{1}{(U_c / U_e)^2} \frac{l_1}{l_1 + l_2}.$$ (14)

We define $\bar{U}_c = U_c / U_e$ and rearrange (14) as:

$$R = \frac{1}{\bar{U}_c^2} \frac{1}{1 + (l_2 / l_1)}.$$ (15)

We use the technique described by Weihs (1974, pp. 219–220) to calculate R. His equation (21) describes l_1:

$$l_1 = \frac{m}{\alpha c} \ln (\cosh B + (U_i / U_e) \sinh B),$$ (16)

where

$$B = \tanh^{-1} \frac{(U_f / U_e) - (U_i / U_e)}{1 - (U_f U_i / U_e^2)} = \tanh^{-1} \frac{\bar{U}_f - \bar{U}_i}{1 - \bar{U}_f \bar{U}_i}$$ (17)

and equation (24a) shows that

$$l_2 = \frac{m}{c} \ln (U_f / U_i).$$ (18)

The ratio l_2 / l_1 from equation (15) can now be expressed as

$$\frac{l_2}{l_1} = \frac{(m/c) \ln (U_f / U_i)}{(m/c\alpha) \ln (\cosh B + U_i / U_e \sinh B)} = \frac{\alpha \ln (U_f / U_i)}{\ln (\cosh B + \bar{U}_i \sinh B)}.$$ (19)

$\bar{U}_c$ is described by Weihs (1974) equation (25):

$$\bar{U}_c = \frac{\alpha \ln\left(U_f/U_i\right) + \ln\left(\cosh B + U_i \sinh B\right)}{B + \alpha(1/\bar{U}_i - 1/\bar{U}_f)} \qquad (20)$$

Equations (15, 17, 19 and 20) show that for different values of α and a certain maximum anaerobic velocity U_e, R depends on U_f and U_i. For a given α we now choose a final velocity $\bar{U}_f$ and calculate R and $\bar{U}_c$ for different $\bar{U}_i$ values from the equations above.

Burst-and-coast swimming is more efficient ·than steady swimming when R is smaller than unity.

A dubious factor in these calculations is α. The model shows that values of R are approximately inversely proportional to α.

KINEMATIC DATA

Fish are trained to swim up and down a tank 14 m long, passing through the field of view of a high-speed camera, looking downward, in a fixed position over the middle of the tank. Fish are triggered to do so by association of underwater flashing lights with the appearance of food. A background illumination technique is used to make frame rates up to 200 frames s^{-1} possible without exposing the fish to high light levels (Videler, 1981). Burst-and-coast swimming at velocities above the maximum cruising speed of 2 ls^{-1} is frequently observed during training sessions with cod and saithe. These species start to use this swimming mode after a few runs up and down the tank. Smaller fish seem to use it more readily than bigger fish. The films show that movements during the burst phase are standard: a fish moves the tail slowly to one side, followed by two fast flicks of the tail, whereupon the fish restores its straight posture and coasts. This is reminiscent of the three phases of rapid starting (Weihs, 1973). Shots of ciné film on which the whole fish is in the field of view of the camera during the burst phase are selected for analysis. These shots typically show how the head of the coasting fish enters the field of view and how after the burst the tailtip of the straight body leaves the frames of film during the next coast-phase.

From these top views the displacement of the head and the tip of the tail in a horizontal plane is traced by digitizing the position every 0·01 s, using an HP 9874A digitizer on line with an HP 9834A desk-top computer. The mean path of motion is defined to be the X-axis in a frame of reference where Z is the perpendicular axis in the horizontal plane. The instantaneous velocity, the time derivative (dx/dt) of the displacements in the X-direction, is calculated using the five points differentiation formula of Lagrange (Abramowitz & Stegun, 1970).

The velocity of the tip of the head is considered to represent the velocity of the centre of mass of the fish. After the head has left the field of view, the tailtip velocity is used instead.

Fig. 2 shows a typical example of results obtained by this method. Initial velocity U_i and final velocity U_f, as well as the duration of the burst t_1, can be determined from this graph. An average burst acceleration rate is estimated as the velocity increase over t_1.

Table 1 summarizes the collected data. U_i and U_f are divided by a theoretical maximum anaerobic velocity to make them suitable for use in the model as the normal-
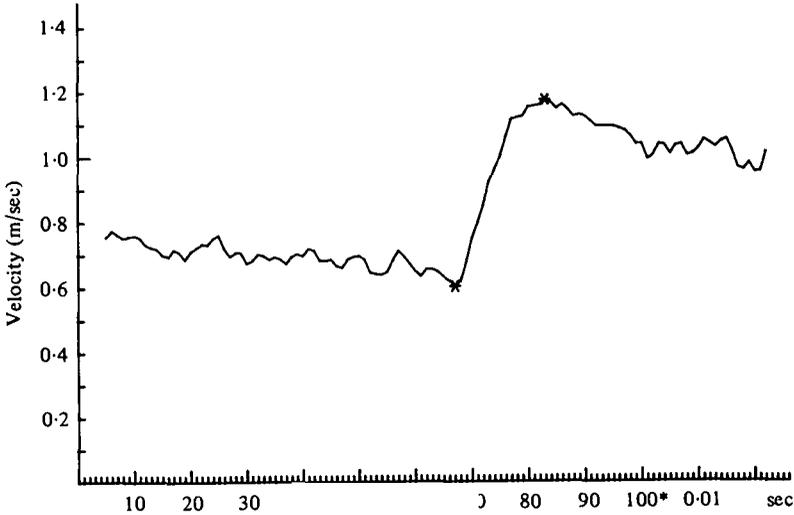
Gadus morhua, length: 0·26 m

Fig. 2. Part of the v   g burst-and-coast swimming
at an aver   ut 3·2 l s⁻¹ of cod.

Table 1. *Data from burst-and-coast swimming bouts of cod and saithe*

($U_i = U_i/10\,l\,\text{s}^{-1}$; $U_f = U_f/10\,l\,\text{s}^{-1}$; U_c and R are calculated using equations (20) and (15). The absolute minimum values of R (R_{min}) are obtained from Fig. 3. The data with an asterisk are used as examples in Fig. 3.)

Species/length	Average acceleration (m s⁻²)	U_i (m s⁻¹)	U_f (m s⁻¹)	$\bar{U}_i$	$\bar{U}_f$	$\bar{U}_c$	R	R_{min}
Cod: 0·26 m	1·0	0·65	0·90	0·25	0·35	0·29	0·36	0·35
	1·8	1·30	1·60	0·50	0·61	0·55	0·42	0·41*
	2·5	0·88	1·40	0·34	0·52	0·42	0·40	0·37*
	3·3	0·60	1·20	0·23	0·46	0·32	0·41	0·36
	3·5	0·60	1·16	0·23	0·45	0·32	0·41	0·36
Cod: 0·30 m	1·0	0·64	0·90	0·21	0·30	0·25	0·36	0·35
	1·9	0·60	0·90	0·20	0·30	0·24	0·36	0·34*
	2·1	0·90	1·30	0·30	0·43	0·36	0·38	0·36
	4·5	0·70	1·24	0·23	0·41	0·30	0·39	0·35*
Saithe: 0·35 m	1·3	0·53	0·90	0·15	0·26	0·19	0·37	0·34
	3·3	1·20	1·90	0·34	0·54	0·43	0·41	0·38
	3·7	1·40	2·00	0·40	0·57	0·48	0·41	0·39

ized velocities $\bar{U}_i$ and $\bar{U}_f$. An estimate of the maximum anaerobic velocity of $10\,l\,\text{s}^{-1}$ for cod and saithe of the present size range is based on Wardle (1977, fig. 5). There is no obvious relation between the velocities and the rates of acceleration in Table 1. It looks as if these fish have a free choice. The highest average acceleration rate is 4·5 m s⁻² for a 0·3 m cod. The acceleration rate during the first part of the burst of this shot is as high as 6·2 m s⁻² (Videler, 1981).

The present values of $\bar{U}_i$ and $\bar{U}_f$ are used to calculate R from $\bar{U}_c$, l_2 and l_1 using equation (15), disregarding the fact that the model demands maximum thrust during the burst phase, which would give the highest possible acceleration rates.

RESULTS AND DISCUSSION

The $\bar{U}_f$ values of the four shots marked with an asterisk in Table 1 are used to visualize the results of the model in Fig. 3. Three hypothetical $\bar{U}_f$ values (0·75, 0·85 and 0·95) are added. The ratio between swimming drag and coasting drag (α) is estimated to be 3. Each curved line is a collection of $\bar{U}_c$ values for different U_i's, starting from one given $\bar{U}_f$. These $\bar{U}_c$ values correspond with values of the ratio R. R will be bigger than 1 if burst-and-coast swimming is energetically more expensive than steady swimming at the same average velocity $\bar{U}_c$. Fish can choose many combinations of initial and final velocities which will result in average velocities with R values lower than 1. In these cases burst-and-coast swimming costs less energy than constant swimming. The model predicts a lower limit of R as a function of $\bar{U}_c$, indicated by the dotted line in Fig. 3. This minimum value changes hypothetically from 1, when the average velocity equals the maximum velocity, to $1/\alpha$ when the average velocity is zero. The circles on the curved lines indicate the calculated $\bar{U}_c$ values for the four examples. The corresponding R values are close to the theoretical minimum (see the actual values in Table 1).

Fig. 4 illustrates the relation between α and R using the fastest example of Fig. 3. The energetic advantage of interrupted swimming increases with an increase of α. For $\alpha = 1$, continuous swimming is the cheapest method. Burst-and-coast swimming with $\alpha = 2$, 3, 4 and 5 is respectively 1·6, 2·4, 2·9 and 3·6 times cheaper than uninterrupted swimming. Alpha is certainly bigger than 2 but there is hardly any evidence for a more precise estimate. Videler (1981) found an average value of 3·3 for the difference between the drag during steady swimming and coasting of cod. This indicates that the value, $\alpha = 3$, used in this paper is an underestimate.

For average velocities below the maximum aerobic cruising speed (0·2 in Fig. 3) the model of Weihs (1974) has to be used because the efficiency η is no longer constant but has a linear relation with velocity. The U_f values used in the anaerobic case are normalized with respect to the maximum aerobic velocity and used to calculate $\bar{U}_c$ values for swimming at cruising speeds. The lines showing these $\bar{U}_c$ values in Fig. 3 make comparison between the advantages of burst-and-coast swimming at low and high speeds possible.

Videler (1981) observed how cod frequently use constant swimming at velocities between 1·4 $l\mathrm{s}^{-1}$ and 2 $l\mathrm{s}^{-1}$ ($\bar{U}_c$ between 0·14 and 0·2) and an intermittent swimming style below 1·4 $l\mathrm{s}^{-1}$.

At average velocities higher than 2·5 $l\mathrm{s}^{-1}$ ($\bar{U}_c = 0·25$), intermittent swimming is again the usual mode and constant swimming is occasionally observed during short single bouts.

Saithe behave similarly under the same circumstances. Both species use two muscle systems for locomotion. A thin outer layer of red muscle fibres is used for swimming ⬤w maximum cruising speed. These fibres use an oxidative metabolism and are
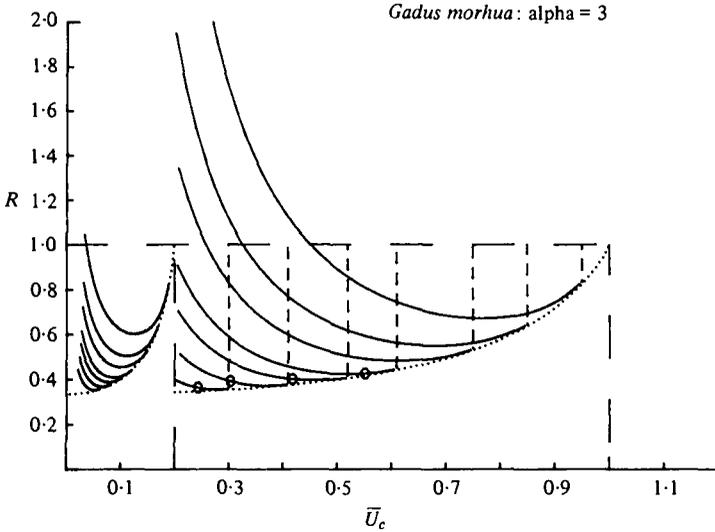
Fig. 3. The ratio of energy per unit distance required for continuous swimming over interrupted swimming, R, versus the normalized average velocity $\bar{U}_c$. See text for further explanation.

virtually unexhaustible. The speed of contraction is slow and determines the upper limit of aerobic swimming speed (general reference: Goldspink, 1980). Fig. 3 shows that Weihs's (1974) model predicts that no significant energetic gain can be expected from burst-and-coast swimming at this highest cruising speed ($\bar{U}_c = 0.2$).

Observations of cod and saithe in large tanks in the Marine laboratory in Aberdeen and under-water observations of saithe in the field show that intermittent swimming at very low speeds is used for feeding purposes. This is very advantageous since foraging takes a large part of the daily time budget of these fish.

The second muscle system is represented by the bulk of white fibres in each myotome. White fibres are fast and use glycogen anaerobically as an energy source. They fatigue rapidly and constant swimming at velocities above $2\,l\mathrm{s}^{-1}$ ($\bar{U}_c = 0.2$) can only last for a few minutes, after which glycogen is depleted and muscles are full of lactic acid. These short high-speed swimming bouts have a high survival value because they can be used to escape from predators. White muscle fibres can more efficiently be used in a burst-and-coast swimming mode, as shown by the present model. This model, however, requires maximum thrust during the burst period which would give maximum acceleration rates. The examples in Table 1 show a variety of acceleration rates, indicating that thrust has not always been at a maximum. Thrust depends on the speed of contraction and on the propulsive force generated. The speed of contraction is an intrinsic property of the fibres and depends on temperature (Wardle, 1975). The propulsive force is a function of the number of fibres involved. The different acceleration rates reflect the number of white fibres recruited for contraction. This probably indicates that fish can choose to use certain numbers of white fibres in turn, which would avoid rapid depletion. The data in Table 1 suggest that R is closer to $R_{\min}$ when the average acceleration is slow.

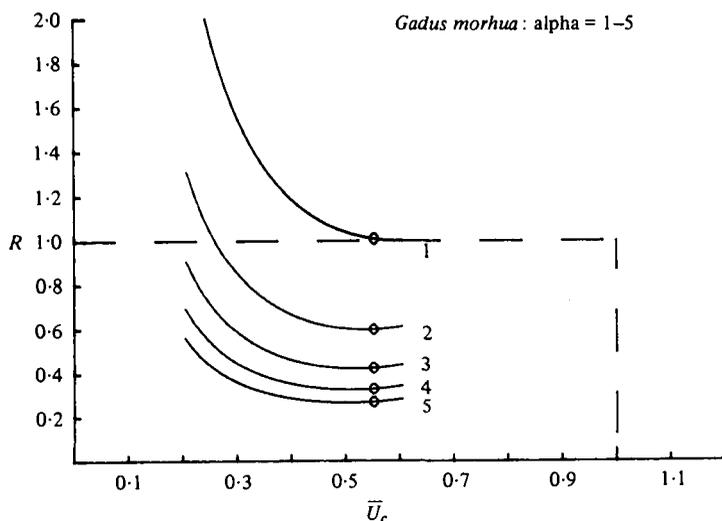Moderate acceleration makes precise determination of optimal final and initial

Fig. 4. The energy ratio R against the normalized average velocity $\bar{U}_c$ of one example of intermittent swimming of cod for 5 different values of the ratio swimming drag over gliding drag, Alpha.

velocities easier. This improves efficiency, but on the other hand the burst phase will last longer and this reduces efficiency.

Fish will have to search for an optimal solution. An example is probably represented in Table 1 by the fastest burst-and-coast swimming bout of saithe. This fish is swimming at an average velocity of almost $5\,l\mathrm{s}^{-1}$ with an average acceleration during the burst phase of more than $10\,l\mathrm{s}^{-2}$. Optimal initial and final velocities make the intermittent swimming mode in this case 2·5 times cheaper than constant swimming, and the burst-and-coast swimming fish will have more stamina as an extra bonus.

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