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# Energetic Advantages of Pause-Travel At Low Speeds

Saminu Iliyasu Bala

Department of Mathematical Sciences, Bayero University Kano, Nigeria  
[saminub@yahoo.com](mailto:saminub@yahoo.com), +2348035338768

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**ABSTRACT:** Some larval fish species do not swim continuously but forage using intermittent locomotion pattern which consist of relatively high speed swimming interspersed by pauses. This type of locomotion is known as pause-travel. In this paper, a mathematical model that examines the advantages of pause-travel over continuous swimming is developed. The results of the present calculations show that pause-travel is an efficient strategy to adopt over certain range of travel speeds. The results also show that the advantage of using this mode of swimming will increases as the size of the larva increases.

Key words and phrases. Pause-travel, Drag, Larva, Inertia, Viscosity.

## 1 Introduction

Many species of fish such as Atlantic cod *Gadus morhua* do not swim continuously but forage following an intermittent locomotion pattern, consisting of bursts of relatively high speed swimming movements, interspersed with pauses when they scan the water column for prey (see [6, 13, 14]). Thus, the dynamics of intermittent locomotion consist of movement in discrete units of time along with pauses, by means of which they adjust their behaviour to changing circumstances. This type of movement is known as pause-travel or burst-and-coast swimming pattern.

Numerous theoretical studies have shown that pause-travel swimming pattern is more efficient for fish than continuous swimming (see [23, 21, 19]). The analysis presented by these authors revealed that this strategy is associated with large energy savings of over 50% as compared to continuous movement and that the advantage increases with size. According to these reports, fish larvae do not share the advantage of pause-travel swimming, due to the dominant influence of water viscosity at small Reynolds numbers. However, this conclusion fundamentally deviates from experimental studies which show that pause-travel is commonly observed in numerous species of larval fish. Example of larval species following the pause-travel strategy include the white crappie (*pomoxis annularis*), the Golden shiner (*Notemigonous Crysolecus*), the Atlantic cod larvae (*Gadus morhua*), see [4, 10, 6, 12, 15] for details. The

fundamental assumption made by these authors in their formulations is that the Reynolds numbers base on the animals scale is above 1000. With this assumption, their models were formulated for the energy expenditure needed to overcome drag at high Reynolds number which is independent of viscosity. Reports by [20, 17] have shown that the dynamics of pause-travel involves both inertial and viscous components. Other factors affecting pause-travel are temperature of the flow regime and the age of the larva (see [11]).

This paper examines the possible advantages of pause-travel motion by fish larvae over continuous swimming at constant speed. Specifically, a new energy saving function (ratio of the energy required to cover a given distance using pause-travel to the energy required to cover the same distance by swimming continuously) that is valid over a wide range of Reynolds number will be derived analytically. Since temperature is inversely proportional to viscosity, the influence of the former on the saving function will be investigated indirectly through changes in the former. Consequently, the model that will be developed here will be dependent on body size of the larva and the water viscosity. Through the consideration of the energy saving function it is possible to determine theoretically the range of travel speeds over which pause-travel is more advantageous over swimming at constant speed.

## 2 Model formulation

The equation of motion for a swimming larvae producing thrust  $T_m$  is (see [19])

$$T_m = M \frac{dv_p}{dt} + \text{drag force}, \quad (1)$$

where  $M$  is the mass of the larvae. Equation (1) was used by [23, 19] using drag force that is independent of viscosity. In this paper, we wish to derive an equation that is made up of both the inertial and the viscous forcing.

Consider a fish larva moving at constant direction and depth. The larva must overcome resistance due to drag force which can be written (see [23]) as

$$D_F = \frac{1}{2} \rho A_w C_D v_p^2, \quad (2)$$

where  $A_w$  is the frontal area,  $\rho$  is the density of the fluid,  $C_D$  is the drag coefficient and  $v_p = v_p(t)$  is swimming speed. This force actually depend upon the Reynolds number regime. Weihs 1986 classify the Reynolds number base on body length ( $Re_L$ ) into three regimes

- $1 \leq Re_L \leq 30$  is called the viscous region, where viscosity dominate the inertial forcing.
- The inertial regime is defined as the regime where  $Re_L > 200$ .
- In between the viscous and the inertial regime is refer to as the intermediate regime.

In this region there is a gradual transition from viscous to inertial regime as  $Re_L$  increases. In the inertial regime,  $C_D$  is approximately constant (see [19]). However, in the viscous and the intermediate regimes  $C_D$  depends upon the Reynolds number (see [5]). For a 5 mm larva swimming with speed up to 10 mm/s in the viscosity regime of  $\nu = 1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ , we have  $Re_L \leq 50$  which places it into the intermediate Reynolds number regime. During the pausing

phase, the combination of the low swimming speed and small size might mean that the larva is within the viscous hydrodynamic regime. It is therefore reasonable to think that its environment is composed of both the viscous and the intermediate regimes. Vehagen [20] estimated the drag coefficient on a larval fish by representing the head as a sphere with diameter  $D$  and the remainder of the body by splitter plate of height  $D$ . He arrived at the following result which is valid for  $0 < Re_D < 200$

$$C_D = \frac{4}{5} + 24 \frac{\nu}{v_p D}, \quad (3)$$

where  $Re_D$  is the Reynolds number base on diameter. This result can be viewed as an estimate of passive drag. Experimental data have shown that the drag on a swimming body is greater than drag on a rigid body by a factor  $\alpha_s > 1$ . For example, experimental measurement of drag on pause-travel fish larvae by [25] have shown that the drag coefficient is 0.242 during the travel phase and 0.06 during the pausing phase. Using equations (3) and (2) and the definition of  $\rho = M/L^3$ ,  $A_w = \pi L^2$  for a sphere ( $L$  is length scale of the larva) we can write the drag force on a swimming larva as

$$F = M(\lambda_l v_p^2 + v_p \delta_l), \quad (4)$$

where  $\lambda_l = \frac{2\pi\alpha_s}{5L}$  and  $\delta_l = \frac{6\pi\nu\alpha_s}{L^2}$ . Equation (4) is a hybrid formula comprising of both the viscous and the inertial regimes. If  $v_p$  is small the viscous term will dominate. Similarly if  $v_p$  is large the inertial term dominate.

Swimming performance is widely accepted as a main character determining survival in many species of fish larvae and other aquatic animals (see [18]). It is also assumed that efficient swimming performance is closely related to larval ability to escape predators, find food or mate. The effects of different environmental conditions or pollutants on fish fitness or survival in an ecological system is usually evaluated by its critical (maximum sustained) swimming speed ( $U_{crit}$ ). Measurements of  $U_{crit}$  at different temperatures are available in literature (see [24, 8, 7]). For example [24] reported  $U_{crit}$  values for three different sizes of fish larvae (9, 13 and 17 mm) at 15 and 20° C.

The results from Table 1 of that paper are summarised in Table 1 of this paper. The equation of motion of a fish larvae (see equation (1) ) is usually solved during the travel phase with the right hand side replaced by the maximum sustained thrust (see [19, 21]). For mathematical simplicity, the maximum sustained thrust during the travel phase of pause-travel behaviour is usually written in terms of  $U_{crit}$ .

Table 1. Summary of experimental data for three size classes of larval fish at two temperatures. The table shows the critical swimming speeds at some temperatures. The data are extracted from Table 1 of [24].

Larval size (mm)	Temperature (°C)	$U_{crit}$ (m s <sup>-1</sup> )
9	15	63
9	20	78
13	15	73
13	20	100
17	15	87
17	20	116

In our formulation, the maximum sustained thrust can be written as

$$T_{crit} = M(\lambda_1 U_{crit}^2 + U_{crit} \delta_t) \tag{5}$$

Thus, in our formulation we can write equation (1) in terms of  $T_{crit}$  as

$$M \frac{dv_p}{dt} + M(\lambda_1 v_p^2 + \delta_t v_p) = T_{crit} \tag{6}$$

## 2.1 Formulation of the energy saving function

The energy saving function can be described as the ratio of the energies require to cover a given distance using pause-travel ( $E_{sal}$ ), to the energy require to cover the same distance by continuous swimming using the same average swimming speed ( $E_{cru}$ ). More succinctly, the saving function can be defined as

$$E_{ratio} = \frac{E_{sal}}{E_{cru}} \tag{7}$$

For pause-travel to be energetically more viable  $E_{ratio} < 1$ . If this turn out to be greater than one, then continuous swimming is more benefitting. The ratio is equal to one when the energy expenditure from both modes of swimming are the same. In order to formulate the energy saving function, the energy expenditures during the pause-travel and continuous swimming need to be defined.

### 2.1.1 Formulation of ( $E_{sal}$ )

Suppose a larva is required to cover a distance  $d$  in time  $\tau_c = t_1 + t_2$  by alternating a period of active swimming with powerless glide. In doing so, the distance  $l_1$  is desired to be crossed within a time  $t_1$  which will be assumed to be the travel phase. During the pause phase,

the larva is required to cover a distance  $l_2$  in time  $t_2$ . In fulfilling this requirement no energy is expended during the pause phase because no thrust is produced (see [19]). Thus energy is expended during the travel phase only. The net energy expenditure during pause-travel can be defined as

$$E_{sal} = \frac{1}{\beta_c \tau_c} \int_0^{t_1} T_{crit} v_p dt. \quad (8)$$

Here  $\beta_c$  is the swimming efficiency which will be assumed constant (see [22]). Defining the energy in terms of  $T_{crit}$  will impose higher energy demand on a larva than defining it in terms of its travel speed. The reason for writing the thrust in terms of the maximum sustained thrust is to reflect the cost of acceleration as a larva moves out of the low Reynolds number pause phase to the higher Reynolds number travel phase. Equation (8) can be written as

$$E_{sal} = \frac{T_{crit}}{\beta_c \tau_c} \int_0^{t_1} v_p dt. \quad (9)$$

Note that the integral term in equation (9) is just the distance ( $l_1$ ) covered during the travel phase. So  $E_{sal}$  becomes

$$E_{sal} = \frac{T_{crit} l_1}{\beta_c \tau_c}. \quad (10)$$

### 2.1.2 Formulation of ( $E_{cru}$ )

Suppose now the larva is allowed to take a different course of action to cross the same distance  $d$  with a certain constant speed  $v_p^c = \frac{l_1 + l_2}{t_1 + t_2}$ . The thrust ( $T_c$ ) applied can be defined by

$$T_c = M \left( \lambda_l v_p^c{}^2 + v_p^c \delta_t \right), \quad (11)$$

we can then write the corresponding energy expenditure as

$$E_{cru} = \frac{M}{\beta_c} \left( \left( \frac{l_1 + l_2}{t_1 + t_2} \right)^3 \lambda_l + \left( \frac{l_1 + l_2}{t_1 + t_2} \right)^2 \delta_t \right). \quad (12)$$

Therefore  $E_{ratio}$  can be written as

$$E_{ratio} = \frac{A l_1 (t_1 + t_2)^2}{(l_1 + l_2)^3 \lambda_l + (l_1 + l_2)^2 (t_1 + t_2) \delta_t}, \quad (13)$$

where  $A = T_{crit}/M$ . To calculate  $E_{ratio}$  numerically, we need the expressions for  $t_1, t_2, l_1$  and  $l_2$  that appear in equation (13).

## 2.2 Determination of $t_1, t_2, l_1$ and $l_2$

To obtain explicit formulae for  $t_1, t_2, l_1$  and  $l_2$  in terms of the other parameters, we shall use equation (6) for the travel phase. During the pause phase the thrust applied is zero and the equation can be solved by setting the right hand side equal to zero (see [23]). It will be assumed

that  $v_p = v_1$  during travels and  $v_p = v_2$  during the pause phase,  $v_1$  and  $v_2$  are constants and that  $v_1 \neq v_2$ .

**2.2.1 Determination of  $t_1$  and  $l_1$**

More compactly, equation (6) which can be written as

$$\frac{dv_p}{dt} + (\lambda_1 v_p^2 + \delta_1 v_p) - A = 0. \tag{14}$$

This equation has the general form

$$\frac{dy(t)}{dt} = f_0(t) + f_1(t)y(t) + f_2(t)(y(t))^2. \tag{15}$$

Equations having this general form are called Ricatti equations. The time and distance  $t_1$  and  $l_1$  can then be obtained by solving this equation subject to the condition that at  $t = 0, v_p = v_2$ . There are many procedures for solving this type of equations. Perhaps the easiest in this case is to use the substitution  $y(t) = \frac{du(t)}{dt} / (-u(t)f_2)$  (see [2]) which reduces the equation into second order linear

$$\frac{d^2}{dt^2} u(t) + \delta_1 \frac{d}{dt} u(t) - \lambda_1 A u(t) = 0. \tag{16}$$

The solution of equation (16) is

$$u(t) = C1e^{(-1/2\delta_1+p)t} + C2e^{(-1/2\delta_1-p)t}, \tag{17}$$

where  $C1$  and  $C2$  are arbitrary constants and  $p = 1/2\sqrt{\delta_1^2 + 4\lambda_1 A}$ . The solution of equation (14) can now be written as

$$v_p = \frac{(-1/2\delta_1 + p)e^{pt} + C3(-1/2\delta_1 - p)e^{-pt}}{(e^{pt} + C3e^{-pt})\lambda_1}, \tag{18}$$

where  $C3 = C2/C1$ . Now at  $t = 0, v_p = v_2$ . This condition lead to

$$C3 = \frac{-\delta_1 + 2p - 2v_2\lambda_1}{\delta_1 + 2p + 2v_2\lambda_1}. \tag{19}$$

Substituting the expression for  $C3$  into equation (18) and simplifying we obtained

$$v_p = \frac{\cosh(pt)}{b_1 \sinh(pt) + a_1 \cosh(pt)} + \frac{\sinh(pt)}{b_2 \sinh(pt) + a_2 \cosh(pt)}, \tag{20}$$

where  $a_1 = 1/v_2, b_1 = \frac{(2v_2\lambda_t + \delta_t)}{2pv_2}, a_2 = \frac{2p}{(2A - \delta_tv_2)}, b_2 = \frac{(2v_2\lambda_t + \delta_t)}{(2A - \delta_tv_2)}$ . Applying the condition that at  $t = t_1, v_p = v_1$  in equation (20) we obtained the time required to cover the distance  $l_1$  as

$$t_1 = 1/2 \ln \left( \frac{(2v_2\lambda_t + \delta_t - 2p)v_1 + (\delta_t + 2p)v_2 - 2A}{(2v_2\lambda_t + \delta_t + 2p)v_1 + (\delta_t - 2p)v_2 - 2A} \right) p^{-1}. \quad (21)$$

If equation (20) is integrated with respect to time, the distance travelled  $l_1$  can be obtained. Now (see [1])

$$\int \frac{\cosh(x)}{b \sinh(x) + a \cosh(x)} dx = \begin{cases} \frac{ax - b \ln \cosh(x + \tanh^{-1}(b/a))}{a^2 - b^2}, & a > b, \\ \frac{-ax + b \ln \sinh(x + \tanh^{-1}(a/b))}{b^2 - a^2}, & b > a \end{cases} \quad (22)$$

and

$$\int \frac{\sinh(x)}{b \sinh(x) + a \cosh(x)} dx = \begin{cases} \frac{a \ln \cosh(x + \tanh^{-1}(b/a)) bx}{a^2 - b^2}, & a > b, \\ \frac{bx - a \ln \sinh(x + \tanh^{-1}(a/b))}{b^2 - a^2}, & b > a. \end{cases} \quad (23)$$

Comparing  $a_1$  and  $b_1, a_2$  and  $b_2$  it can be seen that  $a_1 > b_1$  and  $a_2 > b_2$ . Integrating equation (20) from  $t = 0$  to  $t = t_1$  by means of equations (22) and (23) the distance covered ( $l_1$ ) during the travel phase is

$$\begin{aligned} l_1 = & \left( a_1 p t_1 - b_1 \ln \left( \cosh \left( p t_1 + \tanh^{-1} \left( \frac{b_1}{a_1} \right) \right) \right) \right) p^{-1} (a_1^2 - b_1^2)^{-1} \\ & + a_2 \ln \left( \cosh \left( p t_1 + \tanh^{-1} \left( \frac{b_2}{a_2} \right) \right) \right) b_2 t_1 (a_2^2 - b_2^2)^{-1} \\ & - 1/2 b_1 \ln \left( 1 - \frac{b_1^2}{a_1^2} \right) p^{-1} (a_1^2 - b_1^2)^{-1}. \end{aligned} \quad (24)$$

### 2.2.2 Determination of $t_2$ and $l_2$

During the pausing, the thrust is zero and the drag coefficient is simply the passive drag. The equation of motion (6) becomes

$$\frac{dv_p}{dt} + \frac{1}{\alpha_s} (\lambda_l v_p^2 + \delta_t v_p) = 0. \tag{25}$$

This is the Bernoulli equation. It is assumed that at the beginning of the pause phase,  $v_p = v_1$ . The solution of the equation subject to this condition is then

$$v_p = \delta_t v_1 \left( -\lambda_l v_1 + e^{\frac{\delta_t t}{\alpha_s}} \lambda_l v_1 + e^{\frac{\delta_t t}{\alpha_s}} \delta_t \right)^{-1}. \tag{26}$$

At the end of the pausing,  $t = t_2, v = v_2$ . This conditions enable us find the analytic derivation of  $t_2$  as,

$$t_2 = \ln \left( \frac{v_1 (\delta_t + v_2 \lambda_l)}{v_2 (\lambda_l v_1 + \delta_t)} \right) \alpha_s \delta_t^{-1}. \tag{27}$$

The distance travelled ( $l_2$ ) during the pausing phase can be obtained by integrating equation (26) with respect to time, that is

$$l_2 = \int_0^{t_2} \delta_t v_1 \left( -\lambda_l v_1 + e^{\frac{\delta_t t}{\alpha_s}} \lambda_l v_1 + e^{\frac{\delta_t t}{\alpha_s}} \delta_t \right)^{-1} dt,$$

which is simplified to give

$$l_2 = \alpha_s \left( \ln \left( \frac{\delta_t v_1}{v_2} \right) - \ln \left( \frac{v_1 (\delta_t + v_2 \lambda_l)}{v_2 (\lambda_l v_1 + \delta_t)} \right) - \ln(\delta_t) \right) \lambda_l^{-1}. \tag{28}$$

Inserting the expressions for  $t_1, t_2, l_1$  and  $l_2$  into equation (13)  $E_{ratio}$  can be written in terms of speeds, larva size and viscosity.

### 3 Results

As stated earlier the numerical value of  $E_{ratio}$  indicates the relative efficiency of pause-travel and continuous swimming motions. If  $E_{ratio} > 1$  continuous swimming is more efficient. Equation (13) will now be studied for various parameters involved. One contentious parameter in the equation is the ratio of swimming to pausing drag  $\alpha_s$ . Weihs [23] used  $\alpha_s = 2$  in his study of larval anchovy. However [21] believed that this parameter is greater than 2 and that the average value is around 3.3. Report by [25] for pause-travel koi larva show that  $\alpha_s = 4.3$ .

The discussion in this paper mainly concern small fish larvae and so we are interested in obtaining values of  $U_{crit}$  for fish larvae smaller than those listed on Table 1 Assuming that the  $U_{crit}$  values listed on the Table are linearly related to larval size at a given temperature, we can estimate the critical swimming speeds of fish larva of length 5 mm at 15 and 20° C as 50 and 60 mm/s respectively. It now makes sense to set a lower limits for both pause and travel speeds. Newly hatched fish larvae are small in size, about 3.2 mm and swim with an average speed of 0.25 mm/s (see [9, 8]). This value will be assumed to be the minimum value of the travel speed throughout. During the pausing phase, the larva will be assumed to have a swimming speed of 0.001 mm/s. Variations of  $E_{ratio}$  with travel speeds,  $\alpha_s$  viscosity and the size of the larva will be



discussed below.

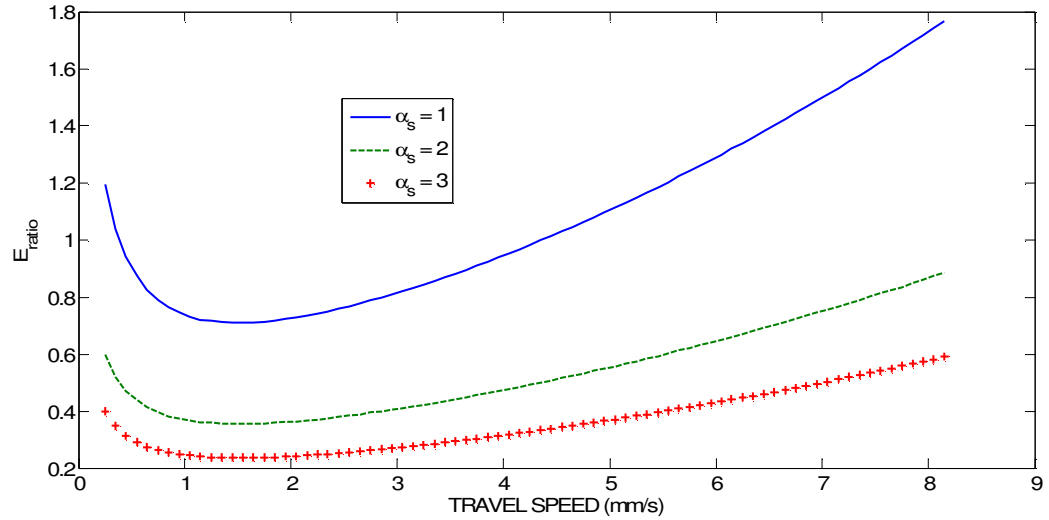


Figure 1. Variation of  $E_{ratio}$  as a function of travel speed for a fish larva with size  $L = 5$  mm, assuming  $U_{crit} = 60$  mm/s,  $v_2 = 0.001$  mm/s, with the viscosity value  $\nu = 1 \times 10^{-6}$  m<sup>2</sup> s<sup>-1</sup> and drag ratios as shown. This corresponds to sea surface temperature of 20°C. These results are obtained by using equations (21), (24), (27) and (28) in equation (13). The Figure depicts the results for three different drag ratios:  $\alpha_s = 1$  (— solid curve),  $\alpha_s = 2$  (- - dash curve), and  $\alpha_s = 3$  (+ line).

Figure 1 shows the variation in  $E_{ratio}$  (energy required per unit distance in pause-travel motion to that required in steady speed swimming at the same average velocity) as a function of the travel speed. The calculations were made for three different drag ratio and viscosity regimes shown. In all the calculations the speed  $v_2 = 0.001$  mm/s is assumed during the pausing phase. The viscosity value used is  $\nu = 1 \times 10^{-6}$  m<sup>2</sup> s<sup>-1</sup>. This corresponds to sea surface temperature of 20°C (see [3]). The critical swimming speed used is  $U_{crit} = 60$  mm/s, this corresponds to a larva with size  $L = 5$  mm. General observation of the Figure reveal that when the value of  $\alpha_s$  is small, the gains are smaller and the region of travel speed for which pause-travel technique is useful becomes more limited. The result for drag ratio  $\alpha_s = 1$  is represented with solid line,  $\alpha_s = 2$  is represented with dashed (- -) line and  $\alpha_s = 3$  is shown with + line. It can be seen that even when  $\alpha_s = 1$ , there is a range of possible travel speeds (about 0.7 to 4 mm/s) that will save energy ( $E_{ratio} < 1$ ). Outside this range, continuous swimming become more efficient strategy. As for the other values of  $\alpha_s$ , pause-travel is most efficient over all range of swimming speeds considered here. However, the trend show a monotonic decrease in energy saving as the travel speed increases. The conclusion that can be drawn from this is that, for any value of  $\alpha_s > 1$  pause-travel is more efficient at certain range of low travel speeds. The range of these speed will increase with increasing  $\alpha_s$ . The instinctive question arising here is which travel speed should a larva use, so as to minimize the energy expenditure during each cycle. Looking at the result it

can be seen that this minimum exist. Finding the minimum value analytically from equation (13) will be extremely difficult.

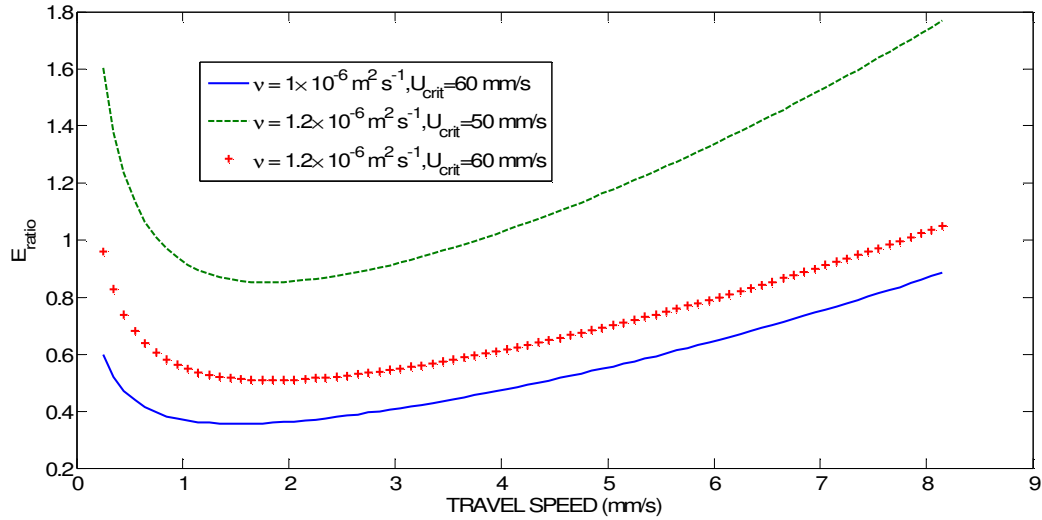


Figure 2. Variation of  $E_{ratio}$  as a function travel speed for a fish larva with size  $L = 5$  mm, assuming a drag ratio  $\alpha_s = 2$  at two different viscosity regimes shown. These results are obtained by using equations (21), (24), (27) and (28) in equation (13). The results for  $U_{crit} = 60$  mm/s in the viscosity regime  $\nu = 1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  is the lower curve represented with solid (—) line. The middle and upper curves are the results for the same viscosity regimes  $\nu = 1.2 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  and  $U_{crit} = 60$  mm/s (- - line), and  $U_{crit} = 50$  mm/s (+ line).

Figure 2 shows the result of similar calculations of  $E_{ratio}$  at two different viscosity and critical swimming speed values for a 5 mm long fish larva. The results for the viscosity regime  $\nu = 1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ ,  $U_{crit} = 60$  mm/s is the lower curve depicted with solid curve. The result from this shows that within two decimal places, the minimum value of  $E_{ratio}$  is 0.35 with travel speeds in the range [1.45 1.55] mm/s. Also shown are the results for the viscosity regime  $\nu = 1.2 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at two different  $U_{crit} = 50, 60$  mm/s. These are represented with dash (- -) and + curves respectively. Comparing the upper (dash - -) and the lower (solid) curves we can see that viscosity does make a difference in optimal energy saving. Looking at the upper curve we can see to the left of the minimum point the low travel speeds ensure that viscous effects dominates. Hence continuous swimming is more efficient in this region. Gradually, as the travel speed increases up to about 3.5 mm/s pause-travel becomes more effective. The result on the lower curve show that pause-travel is more effective over all range of speeds shown. To the left of the minimum the low travel speed brings about relatively smaller gain in energy savings.

General observations of the results show that pause-travel is more effective at intermediate travel speeds and that more energy is expended in a more viscous regime. We may argue that this conclusion does not hold because of the difference in critical swimming speeds in addition to viscosity. Critical swimming speed is widely recognized as a measure of fitness in both larva and adult fish and its value increases with larval size and decreases with viscosity (see [8, 24]). Assuming that the  $U_{crit}$  is independent of viscosity, more calculations of  $E_{ratio}$  were done at  $\nu = 1.2 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  and  $U_{crit} = 60$  mm/s, the results are presented as the middle (red +)

curve. However, even under this unrealistic assumption the conclusion remain the same as can be seen by looking at the lower (solid) and the middle (+) curves. This change in critical swimming speed reduces the difference between the upper and the lower curves by more than 50%, thus influencing the energy saving. For example, the maximum energy saving from the dash (- -) curve is 15% (corresponding to the minimum value of 0.85) at  $v_1 = 1.85$  mm/s. From the + curve the maximum saving is 49% at the same speed. This implies that changing  $U_{crit}$  has the effect of increasing the amount of energy savings. At the same temperature (viscosity) larger values of  $U_{crit}$  corresponds to increase in larval size. This might be interpreted to mean that larger larvae will be expected to be more efficient in pause-travel motion. In fact this supports the results of Hunter 1976, that at 18° C three days old larval anchovy with size 4 mm are observed to spend only 20% of their time in pause-travel mode. When they do so, they do it with an average speed of 3.2 mm/s. As they grow older by two days, they are observed to spend 90% of their time in pause-travel mode. These findings support the 'safe harbour hypothesis' (see [16]) that fish larvae, instead of devising an optimal strategy for adapting to the viscous flow regime, increases their swimming speeds or sizes to escape into the inertia regime considered as a safe harbour.

## 4 Conclusion

In this paper a new model of energy saving function was formulated. This function is basically the ratio of energies required to cover a given distance by pause-travel to the energy required to cover the same distance by continuous swimming. The function is denoted by  $E_{ratio}$  and it serves as a quantitative criterion indicating which mode of motions is more efficient. For values of  $E_{ratio} < 1$  pause-travel is more effective than continuous swimming. The expression for  $E_{ratio}$  was formulated in terms of times spent in travel and pause modes and the distances covered during these periods. To calculate the numerical values of  $E_{ratio}$  explicit formulae for the times and distances are required. To obtain these formulae, modified equation of motion was used. The modified equation was obtained by using drag coefficient that is made up of both the viscous and the inertial terms. This differs from other formulae in the literature which consist of either the inertial term or the viscous term only. Subsequently, the model was used to study the variation of  $E_{ratio}$  with respect to travel speed, ratio of travel to pausing drag coefficient ( $\alpha_s$ ) and changes in the viscosity of the flow regime. The main conclusions are as follows:

1. Investigations with three different values of  $\alpha_s$  show that the higher the value of this parameter, the larger the energy that will be saved by swimming using the pause-travel. The exact value of the parameter appear to be contentious in literature and so more experimental investigations are required to resolve this.
2. The present study indicates that there exist a range of travel speeds over which continuous swimming is less effective than pause-travel. The range of these speed will be affected by viscosity.
3. The range of travel speeds over which continuous swimming is less effective decreases with viscosity.
4. The combination of size and enhanced swimming speed means that pause-travel is more

effective in larger larvae than smaller ones.

In summary, we can say that it is the complex interactions of size, temperature, that will determine to a large extent the survival and growth of small fish larvae. The combination of small size and low temperature will imply a reduce activity which limits the ability of a larva to find food.

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