Hydrodynamics of burst swimming fish larvae; a conceptual model approach

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Received 24 March 2003; received in revised form 4 March 2004; accepted 26 March 2004

Abstract

Burst swimming of fish larvae is analysed from a hydrodynamic point of view. A picture of the expected flow pattern is presented based on information in literature on unsteady-flow patterns around obstacles in the intermediate Reynolds number region. It is shown that the acceleration stage of burst swimming under restricted conditions can be treated as a frictionless impulsive motion. The stream pattern resulting from this motion is presented and the efficiency of locomotion during the acceleration stage is calculated. The flow pattern in the post-acceleration stage is sketched and the origin of an interaction between the viscous and the reactive force contribution to the propulsive force in this stage is discussed. It is explained how this interaction can lead to an increase in propulsive efficiency. A conceptual model is developed describing the three stages in burst swimming locomotion: the acceleration stage, the post-acceleration stage and the gliding stage. Data from literature of the travel distance versus time relation of the common carp larva (Cyprinus carpio) of 5.5-mm length has been used to test the model results. The test appeared remarkably successful, and the model results for larger larvae up to 22mm length are presented. The gliding distance as a function of larval length resulting from the model has been compared with experimental data from literature.

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Keywords: Carp larva (Cyprinus carpio); Burst swimming; C-start; Impulsive motion; Acceleration

1. Introduction

Fish larvae can perform two modes of swimming, cruising and burst swimming. The latter mode of locomotion is the subject of this paper.

The propulsive force generated by swimming fish larvae is the net result of pressure and viscous force-components in swimming direction integrated over the body surface. In order to get an impression of the relative importance of inertial and viscous contribution to the propulsive force, Webb and Weihs (1986) distinguished three ranges of Reynolds numbers (ReL) based on body length L. ReL between 1 and 30 is called the viscous region where the viscous forces dominate, inertial forces dominate when ReL is greater than 200. In the intermediate region there is a gradually shift from viscous to inertial regime with increasing Re number.

Because the energetic costs of swimming in small organisms are substantial it has great advantages from an evolutionary point of view to develop a mode of swimming which limits the energetic costs as much as possible (Weihs, 1980). The question can be raised; is the hydrodynamics during the initial stage of the burst type of locomotion sufficiently well understood?

Based on hydrodynamic arguments it will be shown that the fish larva of about 5–15mm length can accelerate from rest to an escape velocity in such a short time interval that viscous forces are negligible in comparison with inertial forces during the initial acceleration stage in locomotion. The result of this observation is that, despite the smallness of the Reynolds number, the energy loss in viscous resistance could be neglected which is very beneficial from an energetic point of view. A simple conceptual model based on these and other hydrodynamic arguments will
be presented. The model results will be compared to data from Osse and Drost (1989) on burst swimming carp larvae of 5.45 mm filmed at 200 frames/s. The model results appeared in excellent agreement with the data. Extrapolation of model results to larger fish larvae will be shown.

2. The stream pattern created during the initial stage of burst swimming fish larvae

Consider the S-shaped fast-start swimming of a fish larva. Detailed kinematic studies of this type of larval movements are presented by Spierts and van Leeuwen (1999) and recently by Müller and van Leeuwen (2004). They measured tail beat frequencies up to 100 Hz during cyclic swimming. Fish larval body movements during the initial stage of burst swimming are of large magnitude and short duration and may be usefully considered as an impulsive motion.

2.1. Theory of impulsive motion of a fluid

In the equation of motion of the fluid all terms involving only velocities or their spatial derivatives are negligible by comparison with the acceleration term.

The approximate form of the equation of motion during the sudden change reduces to

\[ \frac{\partial \mathbf{u}}{\partial t} = -\frac{1}{\rho} \nabla p, \quad (1) \]

where \( \mathbf{u} \) is the fluid velocity vector, \( t \) the time, \( \rho \) the water density, and \( \nabla p \) the pressure gradient in \( \mathbf{u} \) direction. The velocity just before the change begins is zero, so the velocity \( \mathbf{u}_j \) after the change is

\[ \mathbf{u}_j = -\frac{1}{\rho} \int_0^{\delta t} p \, dt, \quad (2) \]
where
\[
\int_0^{\delta t} \rho \, dt = \Pi
\]
(3)
is termed the pressure impulse.

Note that effects of viscosity of the fluid are also neglected in Eq. (1) compared to the acceleration term. This is justified only if the range of integration \(\delta t\) is small compared to the ratio between the length scale of the larval tail divided by the fluid velocity \(u\). A more precise formulation of the last criterium will be specified in Section 4.

An important feature of Eq. (2) is that, if the velocity before the impulse is zero and thus irrotational, that after the impulse is likewise irrotational with velocity potential
\[
\phi_j = -\frac{1}{\rho} \Pi.
\]
(4)
The physical interpretation of Eq. (4) is that the velocity potential of a given irrotational flow may be interpreted as \(-1/\rho\) times the pressure impulse required to set up the given motion from rest.

Turning our attention again to the initial stage of burst swimming. The advance ratio, defined as the ratio between swimming velocity and mean lateral velocity of the tail tip, must be small compared to one especially at the initial stage of burst swimming where the swimming velocity is nearly zero. The extremely fast oscillating tail seems to act as a propulsive device comparable with a two-dimensional version of a helicopter rotor in vertical climbing/descent translation, or comparable with the transient hovering performance of hummingbirds (Chai et al., 1997). In modelling these problems the fast variation in the propulsive force related to the rotor- or the wingbeat-frequency is usually neglected and the equation of mean motion of the body is solved. The mentioned physical examples have been studied in literature using the classical actuator disk theory. The accuracy of the actuator disk theory applied to a helicopter rotor has been analysed recently by Spalart (2003). He found that the simple textbook actuator disk model gives a correct description of the time-averaged effect of helical vortex sheets shed by the helicopter blades on thrust and induced power. Classical results for induced power is unchanged and the approximation appeared exact within the steady inviscid problem statement.

The problem of burst swimming fish larvae with their extremely high-tail beat frequencies will be treated as an actuator two-dimensional “disk” or plate starting from rest and suddenly set in translation broadside on. The corresponding force impulse generated by this impulsive motion can be found.

In handbooks, see for instance Batchelor (1967), the impact of a flat plate slamming on the water surface is usually treated as an example of impulsive motion. Although the phenomena involved in this physical problem are more complicated than put forward in handbooks, the treatment of this classical case is very valuable\(^1\) and will be reproduced for the present application in Section 2.3.

2.2. Kinematics of the tail motion

Consider an elongated body of length \(L\) that is displaced laterally by
\[
h(x, t) = h_m(t)\xi(x)\cos(\omega t + k(x)x),
\]
(5)
where \(x\) is the position along the length measured from the tail tip, \(t\) the time, \(\omega\) the angular frequency, \(\xi(x)\) the amplitude envelope along the length, \(h_m(t)\) the maximum amplitude of the tail tip, \(k(x)\) the wave number which could also be a function of \(x\). Note that the formulation does not include any variation in lateral movement over time apart from the pure periodic oscillation. At the tail tip \(x = 0\) the amplitude envelope \(\xi(0) = 1\) and the derivative is taken zero \(d\xi/dx|_{x=0} = 0\). The amplitude \(h_m(t)\) is expected to be a decreasing function of time with a time-scale small compared to \(1/\omega\), so the derivative is taken about zero \(dh_m/dt|_{t=0} \approx 0\).

Eq. (5) can be seen as a description of the tail movement of the larva, especially for values of \(x\) small compared to \(L\). Fig. 1 shows the shape of a larva with body length \(L = 5.5\ mm\), for the following values of parameters: \(h_m(0)/L = 0.25\), \(k(0) = (2\pi/\xi(0))\), where \(\xi(0)/L = 0.8\) is the length of the wave along the body near the tail tip. If the slip in velocity between the tail tip and the water near the tail is neglected and the water is assumed to leave the tail smoothly the resulting propulsive jet velocity in negative \(x\)-direction at \(x = 0\) in a coordinate system moving with the fish body would be
\[
U_j = \frac{\partial h}{\partial t} \bigg|_{x=0} = \frac{\omega \lambda(0)}{2\pi} = \lambda(0) f,
\]
(6)
where \(f\) is the tail beat frequency.

Note that \(U_j\) is independent of time \(t\).

2.3. Stream pattern created during the start of burst swimming

The mathematical treatment of the flow generated by the impact of a flat-bottomed body on the water surface is a.o.—described by Tietjens (1960) and the results will be applied to the acceleration stage of burst swimming larvae.

\(^1\)Slamming is an important issue in naval-hydrodynamics; the author investigated that problem several decades ago experimentally and theoretically and found that the air caught between impacting plate and water surface substantially reduced the pressure forces during impact, see Verhagen (1967).
Consider in Fig. 1 the line-segment \(-h_m(0) \leq y \leq h_m(0)\) connecting the points of the maximum tail-tip amplitude. The problem is treated as two dimensional i.e. changes in flow perpendicular to the plane of drawing are not considered. The line segment is build up of water particles initially at rest and suddenly set in motion at \(t = 0\) in such a way that the velocity component \(U_w\) is equal to \(U_w = \frac{1}{2}\rho a^2 U\). The result obtained from this two-dimensional theory do not substantially differ from the result of a three-dimensional analysis. Batchelor (1967) found that the force impulse on a circular disk of radius \(a\) suddenly set in motion broadside on, is equal to \(\frac{1}{2}\rho a^2 U\), a result which is numerically comparable to \(m_{tail}\) because the height of a larva \(s\) is usually of the same order of magnitude as \(h_m\).

The added mass of an accelerating sphere with diameter \(D\) is

\[
m_{add} = \frac{1}{4\pi} \rho \pi D^3
\]

the latter relation is needed later on in the paper.

3. The escape velocity of the larva

The water velocity \(U_j\) leaving the fish tail at time \(\delta t\) in a coordinate system moving with the escape velocity of the larva \(U_f\) is given by Eq. (6). So, in an earth-bound coordinate system the water velocity \(U_w\) at \(x = 0\) at time \(\delta t\) must be

\[
U_w = U_j - U_f.
\]

The ratio \(U_w/U_f\) follows from applying the conservation of momentum to the total system. On the one hand, the momentum of the added mass of the fluid pushed backwards due to the tail motion, on the other hand, to the momentum of the mass of the larva including the added mass of the larval head accelerated in forward direction. The action = reaction law of momentum gives

\[
m_{tail}U_w = (M + m_{add})U_f,
\]

where \(m_{tail}\) and \(m_{add}\) are given in the preceding section.

Now the value of the various parameters in the above equations will be estimated as a function of the size of the larva valid for a specific reference larva of a given size. The common carp larva (Cyprinus carpio) of 5.5-mm body length is chosen as the reference larva. The data are obtained from Osse and van den Boogaart (1995).

The relation between the mass \(M\) and the body length of the common carp is according to these authors:
Fig. 2. Streamlines in the horizontal plane set up by the impulsive start of a burst swimming larva. Streamlines are shown for $\Psi/\mu h_m = 0, -0.1, -0.2, ..., -0.8$.

Fig. 3. Right-hand side: Distribution of velocity vector $u/U$ over $y/h_m$ at $x = 0^+$ at time $t = \delta t$. Left-hand side: A sketch of the path of the tailtip and of the water velocity (vectors $a$, $b$, $c$, $d$) leaving the tailtip at the high pressure side of the tail at four moments during the first tail cycle. In the impulsive motion theory the distance travelled by the larva (stride length) as well as the distances travelled by the water particles during the first tail cycle are assumed small compared to $2h_m$. This assumption justifies the vectorial summation of water velocities $a$ and $b$ as well as $c$ and $d$ as shown on the left-hand side of the figure.
valid for the smallest larvae up to a body length of about 20 mm. The relation between body depth \( D \) and body length \( L \) in \( C. \) carpio in the same length class is according to Hoda and Tsukahara (1971) \( D \propto L^{1.632} \).

The above allometric relations are for the sake of simplicity modified into \( M \propto L^{4.48} \), \( D \propto L^{1.5} \), so \( M \propto D^3 \).

The allometric relations used in this paper are summarized in Table 6.

The dimensions of the reference larva are about \( L_0 = 5.5 \text{ mm}, \ D_0 = L_0/6.5 \), and \( M_0 = 0.9 \text{ mg} \), Osse and van den Boogaart (1995). So the foregoing allometric relations can be specified as

\[
M = M_0 \left( \frac{D}{D_0} \right)^3, \quad D = D_0 \left( \frac{L}{L_0} \right)^{1.5} \quad \text{(see, Table 6)}
\]

valid for body length between 5.5 and about 20 mm. Substituting Eq. (11) in Eq. (10) gives

\[
\frac{U_v}{U_f} = \frac{M_0 (D/D_0)^3 + \frac{1}{12} \pi \rho D^3}{\pi \rho h_m^2 s} = 0.5562 \left( \frac{D}{h_m} \right)^2 \frac{D}{s}.
\]

The body depth—tail fin width ratio \( D/s \) seems to be equal to 1. The maximum tail-amplitude/body length ratio seems to be a decreasing function of \( L \). Osse and van den Boogaart (1995) presented curvature profiles over the body length of burst swimming carp larvae during the acceleration phase at four length classes from 5.5 to 20.3 mm. They found that curvature profiles changed from more are less uniform over the body length for the smallest larva to a steeply rising profile from head to tail for the largest size classes. From their Fig. 13A it can be derived that the maximum angle between the tail and the swimming direction is large, about 90°, and nearly independent of body size, and that the maximum tail amplitude/body length ratio is approximately

\[
h_m(0) = 0.25 \left( \frac{L}{L_0} \right)^{-0.5}.
\]

Substituting the last relations into Eq. (12) yields

\[
\frac{U_v}{U_f} = 0.5562 \left\{ \frac{1}{6.5} \left( \frac{L}{L_0} \right)^{0.5} \right\} \left( \frac{L}{h_m} \right)^2 = 0.2106 \left( \frac{L}{L_0} \right)^2.
\]

Observe that the escape velocity of the larva \( U_f \) in this example is nearly a factor 5 larger than the water velocity in an earth-bound coordinate system pushed backwards by the moving tail. Taking in mind that the function of the larval burst swimming locomotion is often to escape from a predator this result is of great advantage. The advantage results from the fact that the added mass of the water pushed backwards is large compared to the mass of the larva. So the larva is pushed forward by the impulsive motion (the action) with a much larger speed than the speed of the water moving backwards (the reaction). The added mass of the water pushed backwards is large because the tail tip amplitude—body length ratio \( h_m/L \) is large.

The escape velocity can be written as

\[
U_f = \frac{U_f}{1 + 0.2106 (L/L_0)^2}.
\]

With \( U_f = \lambda(0)^f \) and \( \lambda(0) = 4.4 \text{ mm}, \ f = 50 \text{ Hz} \), approximately valid for our reference larva (Osse et al., 1995) we get \( U_f = 220 \text{ mm/s}, \ U_w = 38 \text{ mm/s}, \ U_f = 182 \text{ mm/s}. \) An escape velocity of about 182 mm/s is indeed considerable for a larva of about 5.5 mm, amounting 33 BL/s. An estimate of the value of the Froude efficiency of propulsion for this important stage can be obtained as follows:

### 3.1. The propulsive efficiency of the impulsive motion

The energy required to reach the escape velocity \( U_f(\delta t) \) at the end of the impulsive motion period \( \delta t \) is

\[
E_v = \frac{1}{2} (M + m_{add}) U_f^2(\delta t).
\]

The energy expended by the larval fish in pushing the water mass \( m_{tail} \) backward during the time period \( \delta t \) is

\[
E_w = \frac{1}{2} m_{tail} U_w^2(\delta t).
\]

The total actual energy expended by the larval fish during the impulsive motion is

\[
E_{tot} = E_v + E_w,
\]

which can be written as

\[
E_{tot} = \frac{1}{2} (M + m_{add}) U_f(U_f + U_w) = \frac{1}{2} (M + m_{add}) U_f U_f.
\]

The hydrodynamic Froude efficiency of propulsion of the impulsive motion is therefore

\[
\eta = \frac{E_v}{E_{tot}} = \frac{U_f}{U_f} = \frac{1}{1 + 0.2106 (L/L_0)^2}, \quad \text{see Table 1.} \]

Observe that the Froude efficiency is moderate to high for the smallest two larval sizes. The high efficiency results from the fact that the added mass of the water pushed backwards is large compared to the mass of the larva, or explained in dimensionless terms; a small value
of the radius of an equivalent sphere with the same mass as the larva divided by the tail amplitude. The efficiency reduces strongly with increasing size. The efficiency seems poor for the larger larvae and juvenile fishes, which asks for another way of propulsion. Osse et al. (1995) observe that transition from anguilliform to carangiform swimming seems to coincide with the ossification of the caudal fin rays when larval size increases. These authors hint to the possibility of a transition to more lift-generated propulsion for larvae in the larger size classes. Also Wakeling et al. (1999) mention that efficient swimming can be achieved by modifications in a “carangiform” swimming style, an increase in body depth and by caudal and median fins stiffened with fin rays (see Table 1).

The above propulsive efficiency consideration is based on the assumption that at the end of the impulsive motion a steady-state situation in the final escape velocity is reached. Of course this is not the case, friction effects become more and more important as \( t \) becomes larger than \( \delta t \).

4. How small should the time duration \( \delta t \) be to justify the impulsive pressure approach?

As stated in Section 2.1, \( \delta t \) must be small enough to justify the neglect of the quadratic terms and viscous term in the equation of motion. On the other hand, \( \delta t \) should be at least of the same order of magnitude as the period of the tail movements because only in that case the lateral forces during the initial start of burst swimming cancel to some extent. In this section an estimate of the magnitude of \( \delta t \) and so of the tail beat frequency \( f \), which is needed to justify the impulsive pressure approach, will be given.

Fig. 5 shows the expected stream pattern around a burst swimming fish larva of 5.5 mm length somewhere in the beginning of the post-acceleration stage. Viscosity effects in propulsion can no longer be neglected as soon as the wake formation in the hollow of the curved beating tail becomes substantial. It is postulated here that the effect of viscosity on propulsion will be limited if the thickness of the vorticity region \( d_v(t) \) developed at the rear-side of the sweeping tail at the end of one bout is small compared to \( 2h_m \), say \( d_v(t) < h_m/2 \).

Batchelor (1967) treated the problem of wake formation behind a bluff body suddenly made to move from a speed zero to a steady speed \( U_0 \). He derived the following expression for the thickness of the vorticity region (the length of the wake) behind a circular cylinder of radius \( a \) as a function of time during this unsteady motion

\[
d_v(t) = \text{const} \times \sqrt{\frac{va}{2U_0}} \exp \left( \frac{2U_0 t}{a} \right),
\]

where the constant is order unity.

Translating this result to the problem of the wake formation in the hollow of the beating tail directly after the start of the impulsive motion we substitute \( U_f \) for \( U_0 \), and \( h_m \) for \( a \). At the end of the first swimming bout \( t = 1/(2f) \), and the effect of viscosity on propulsion will be limited as \( d_v(t)_{t=1/(2f)} < h_m/2 \). Thus

\[
\sqrt{\frac{h_m v}{2U_f}} \exp \left( \frac{U_f}{h_m f} \right) < \frac{h_m}{2}
\]

or if the tail frequency \( f \) is larger than

\[
f_m = \frac{2U_f}{h_m \ln(h_m U_f/2v)}.
\]

For our reference larva \( h_m = L_0/4 = 1.375 \) mm, \( U_f = 150 \) mm/s. Substituting in the last expression gives \( f_m \approx 47 \) Hz. According to Osse et al. (1995) \( f = 50 \) Hz for the 5.5 mm larva. So the conclusion is that the impulsive pressure approach...

Table 1

<table>
<thead>
<tr>
<th>Total body length (mm)</th>
<th>Froude efficiency ( \eta ) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.5</td>
<td>82.6</td>
</tr>
<tr>
<td>11</td>
<td>54.3</td>
</tr>
<tr>
<td>16.5</td>
<td>34.4</td>
</tr>
<tr>
<td>22</td>
<td>22.9</td>
</tr>
</tbody>
</table>

![Fig. 5. Expected viscous stream pattern in the boundary layer created by a burst swimming fish larva of 5.5-mm length at time ~25 ms somewhere in the beginning of the post-acceleration stage. The streamline pattern at the impulsive start is an approximation of the real flow pattern. The distance travelled during the first full tail cycle (the stride length) is assumed negligible small in the impulsive motion approach.](image_url)
pressure approach is justified for the 5.5-mm larva during the first full tail cycle.

5. The stream pattern in the post-acceleration stage. Some hydrodynamical considerations

The conclusion so far is that the hydrodynamic Froude-efficiency of propulsion in the burst swimming mode during the first full tail cycle, the acceleration stage, is high especially for the smaller larvae. Now, the number of swimming bouts in burst swimming is usually larger than one, in case of the 5.5 mm reference larva 5–7 cycles. The question is what is the contribution to the propulsion and what is the hydrodynamic efficiency of the remaining part of the swimming movements?

In this paper a possible answer is given to the above question.

Attention is again drawn to Fig. 5.

The stream pattern is sketched on the basis of extensive information found in literature on flow patterns around obstacles in steady and unsteady flow in the “Reynolds number” region 1–150 and not on the basis of experimental visualization of the flow created by real burst-swimming fish larva. Literature on flow generated by 5–15 mm burst-swimming fish larvae is scarce.

Why this stream patterns?

Looking to the shape of a fish larva it seems remarkable to observe that the tail region is marvellous streamlined shaped while the head is like an irregular-shaped blunt body.

This observation leads to the impression that viscous resistance of the swimming larva is largely based on the resistance of the head. Therefore, the relevant Re number must be based on the diameter of the head and on the escape velocity of the larva, and not on the body length L. So \( Re_D = U/\nu \). For our reference larva \( D = 0.85 \text{ mm} \) and \( U = 150 \text{ mm/s} \), so \( Re_D \approx 130 \).

Past a sphere in a uniform steady stream at about \( Re = 24 \) a standing ring-eddy is formed (Batchelor, 1967). The length of the region of closed streamlines (a so-called vorticity region) behind the sphere grows with increasing Re-number up to about 1.2 times the sphere-diameter at \( Re_D = 150 \). At \( Re_D > 130 \) the flow pattern in the wake becomes more and more unstable. Above \( Re_D \approx 2500 \) the wake behind the sphere becomes fully turbulent.

Applying the above information to the swimming fish larva reveals that instability in the wake behind the head could be expected. Moreover, the head of the burst swimming fish larva oscillates laterally with the tail beat frequency, due to the forces and moments acting on the swimming larva. The result will be that instead of the mentioned ring eddies a regular array of eddies, known as the von Kármán vortex street start to develop, just as in the wake of a circular cylinder. The streamlined fish body including the fins behind the head act as a kind of “splitter” plate strengthening the two-dimensional character of the eddies formed behind the oscillating larval head, in the Re-number region considered. The frequency of lateral oscillation of the larval head appears approximately equal to the frequency at which eddies separate behind a non-oscillating cylinder with diameter \( D \). The latter frequency \( f \) is equal to about \( \text{Str}^* U/D \), where Str is the so-called Strouhal number being about 0.2 in case of a circular cylinder and 0.3 in case of a sphere, so \( f = 0.3 U/D \approx 50 \text{ Hz} \). Therefore the conclusion seems reasonable that the periodically moving head of the swimming fish larva generates a kind of vortex street behind the head as sketched in Fig. 6.

Fig. 6 shows the expected viscous stream pattern in the post-acceleration stage. Say at \( t \approx 50 \text{ ms} \), where \( U = 120 \text{ mm/s} \), and \( f \approx 42 \text{ Hz} \).

The distance between successive opposite rotating eddies on both sides of the larva is \( U/f = 120/42 \approx 3 \text{ mm} \).

The question is could these generated eddies be important in drag reduction or in an increase in propulsive force? Recently this question attracts much attention, see Taylor et al. (2003) and Liao et al. (2003). The first authors discussed the exploitation of vortexes by an animal in a flock created by the preceding animal.

![Fig. 6. Expected viscous stream pattern around a burst swimming fish larva of 5.5-mm length in the post-acceleration stage at time t≈50 ms, U≈120 mm/s and f≈42 Hz.](image-url)
in the flock. In the present paper, the same physical phenomenon is discussed but now for an individual larva creating and exploiting its own vorticity regions.

The stream pattern as suggested here in the post-acceleration phase of the motion shows that the vorticity regions created by boundary layer separation at the fish head can be used in propulsion in two ways. First, it can be observed that the velocity of the vorticity region near the body surface points in swimming direction, so part of the rotation energy in the eddy is used as a contribution in viscous thrust, secondly there is a contribution to the inertial thrust force. The latter argument needs further explanation.

Fig. 6 shows that the vorticity region is caught at some point in time in the hollow formed by the curved rear end of the body and the tail. The catch of that eddy by the sweeping tail is facilitated by three mechanisms. The first one is the convergence of streamlines in the vicinity of the tail, due to the non-viscous flow away from the body surface resulting from the acceleration of the added mass belonging to the tail movement. The second mechanism is the attraction of the fluid lump containing the vorticity region exerted by the low pressure in the hollow of the curved fast-sweeping tail. The last mechanism is due to the boundary layer separation at the sharp edges of the tail fin. The resulting dividing streamline (also called a “vortex sheet”) leaves the tail tip smoothly and creates a clear distinction between the vorticity region and the surrounding nearly rotationless fluid. The vorticity region receives an amount of momentum during the tail sweep. This amount of momentum is already partially accounted for by the inertial propulsive force contribution, which is a component in swimming direction of the product of the added mass of the tail and the acceleration of the tail. The difference, however, is that added mass is a virtual mass; the mass of the eddy is a real mass because the eddy can be considered as a fluid lump with a so-called coherent structure, (i.e. the fluid velocities in the fluid lump differ substantially in magnitude and/or direction compared to its surroundings). Momentum applied to a coherent structure has an analogy to rigid body dynamics. The velocity of the centre of mass of the eddy in the hollow of the tail follows more or less the lateral movement of the tail (which is near the tail tip of the same order of magnitude as the swimming velocity) and the lateral component of the momentum of that specific eddy is compensated by the impact between eddy and tail when the tail-beat is reversing direction. So, only the axial component of the momentum of the eddy leaving the tail is left, which means a recovery of energy otherwise lost by unprofitable water motions, making benefit of the physical properties of eddies. The conclusion is that the large lateral component of the momentum exerted by the swimming larva on this coherent structure is cancelled by the reversed lateral component half a period later which is acting on the same fluid entity. The propulsive device in this special Reynolds-number region is therefore avoiding unprofitable generation of kinetic energy in the water perpendicular to the swimming direction.

The increase in propulsion efficiency due to the acceleration of tail-connected eddies is therefore a combined effect of viscosity (during the creation of these eddies) and of an effect of inertia. Webb and Weihs (1986) introduced two contributions in fish larva propulsion, namely a resistive and a reactive contribution. The contribution discussed above, is in fact an interactive contribution, which could be important in the Re-number region in which small fish larvae usually operate. See Discussion.

6. Calculation of the swimming velocity during burst swimming. A conceptual model

During the initial period of burst swimming $0 < t < \delta t$ the swimming speed of the reference larva increases more or less linear from zero at $t = 0$ to about 165 mm/s at $t = \delta t = 20$ ms. For $t \geq \delta t$ viscosity effects can no longer be neglected. A rough calculation of the swimming speed can be obtained by applying the momentum equation in $x$-direction to the swimming larva as follows:

$$\frac{dU_f}{dt} = F + \frac{1}{2} \rho C_D A U^2,$$  \hspace{1cm} (19)

where $F$ is the propulsive force, and $C_D$ the drag coefficient of the swimming fish larva based on its frontal surface area $A$. The initial condition is $U_f = 0$ for $t = 0$.

The frontal area of a sphere with diameter $D$ is $A = (\pi/4)D^2$. $M + m_{add}$ has been specified earlier as 1.7474 $\rho D^3$.

The impulsive pressure–force is

$$F = (M + m_{add}) \frac{(U_f)_{escape}}{\delta t}, \hspace{1cm} (20a)$$

where $(U_f)_{escape} = 182$ mm/s in our example larva.

The magnitude of the propulsive force for $t \geq \delta t$ must be related to the magnitude of the impulsive pressure–force. It seems reasonable to assume that $F$ decreases exponentially with time for $t > \delta t$. The time-scale of decrease is chosen equal to $\delta$ based on oral information from Osse that the number of beats in burst swimming seems rather constant (about 5–7). So for $t \geq \delta t$ it is assumed that

$$F = (M + m_{add}) \frac{(U_f)_{escape}}{\delta t} e^{(-\delta t)/\delta t}. \hspace{1cm} (20b)$$

The fast decrease in propulsive force with time for $t > \delta t$ can be explained as follows: The propulsive force is

$$F = (M + m_{add}) \frac{(U_f)_{escape}}{\delta t} e^{(-\delta t)/\delta t}.$$  \hspace{1cm} (20b)
more or less proportional to
\[
\left( \frac{h_m}{L} \right)^2 \left( f^2 - \left( \frac{U_f}{\lambda(0)} \right)^2 \right),
\]

(Lighthill, 1971), so the reduction in propulsive force is the result of the fast decrease in the slipstream \( f(0) - U_f \) at the tail tip in the post-acceleration stage and of the gradual decrease of \( h_m(0)/L \) during that stage.

To get an estimate of the drag coefficient \( C_D \) of the swimming larva, the larva is schematized to a sphere of diameter \( D \) representing the head and a splitter plate height \( D \) and length \( L - D/2 \) representing the remainder of the fish body including the nodal fin. The head diameter is usually somewhat smaller than the body depth of the larva. To avoid too much detail in the conceptual model both dimensions are taken equal. The physical argument behind this assumption is that, due to the lateral movements of the head, the frontal area in the expression of the viscous resistance depends not only on the diameter of the head but also on the depth of the body. The drag coefficient for a sphere with diameter \( D \) for \( Re_D < 1 \) is \( 24/Re_D \). For \( 0 < Re_D < 200 \) curve-fitting of the \( C_D \)-data given by Hoerner (1965) yields
\[
C_D \approx 0.8 + 24 \frac{V}{U_f D}.
\]  

The drag coefficient of a sphere with a splitter plate is usually substantially less than of a sphere alone. The few experimental data given by Hoerner (1965) show that the reduction in the drag coefficient could be 10 up to 40%. The reduction in drag can also be considered as a contribution in the propulsive force for \( t > 0 \) and is already accounted for.

Substituting the above expressions in the equation of motion of the swimming larva and dividing the equation by \( M + m_{add} \) gives
\[
\frac{dU_f}{dt} = \left( \frac{U_f}{\lambda(t)} \right)_{\text{escape}} - \frac{U_f^2}{4.45D} \left( 0.8 + 24 \frac{V}{U_f D} \right),
\]
where \( f(t) = 1 \), for \( 0 \leq t \leq \delta t \), and \( f(t) = e^{-(t-\delta t)/\delta t} \), for \( t > \delta t \). Using Eq. (14) the initial acceleration for our reference larva becomes 9086.4 mm/s². With the initial condition \( U_f = 0 \) at \( t = 0 \) the equation of motion for our reference larva of 5.5 mm can be solved.

The solution is presented in Fig. 7A.

As time proceeds the exponential decreasing propulsive force becomes smaller and smaller compared to the

Fig. 7. (A) Velocity and distance travelled by the 5.5-mm burst swimming carp larva as a function of time. The conceptual model results are compared with the experimental data from Osse and Drost (1989). (B) The model results for a carp larva of 11-mm total body length. (C) The model results for a carp of 16.5-mm total body length. (D) The model results for a carp of 22-mm total body length.
drag force. At time \( t = t_g \) the value of the propulsive force is only a small fraction, say 5% of the drag force. This means that after \( t = t_g \) the swimming movements of the larva do not really contribute to propulsion anymore and the body movements of the larva may as well cease. The time \( t = t_g \) marks the start of the gliding stage of the larval motion. After \( t = t_g \) the resistance of the streamlined body behind the head comes into play. An estimate of the resistance can be obtained as follows: The resistance of a double sided flat plate with length \( L \) and width \( D \) in laminar flow is according to Blasius

\[
W_{\text{plate}} = 1.328 \rho U_f^2 LD \sqrt{\frac{v}{U_f L}}. \tag{23}
\]

This is the resistance of a flat plate moving stationary with velocity \( U_f \). The resistance of a flat plate starting from rest to the stationary velocity \( U_f \) can be obtained by multiplying the last expression by \( e^{-s t} \), where \( s \) is the distance travelled by the plate after \( t = t_g \).

So the right-hand side of the equation of motion has to be completed with the term

\[
- \frac{W_{\text{plate}}}{M + m_{\text{add}}} \tag{24}
\]

which is equal to

\[
-0.760 U_f^2 \frac{L}{D} \sqrt{\frac{v}{U_f L}} e^{-(S(t) - S(t_g))/L},
\]

valid for \( S(t) > S(t_g) \),

where \( S(t_g) \) is the distance travelled at \( t = t_g \). The flat plate resistance does not contribute much to the decay in swimming velocity in the 5.5-mm larva. The influence increases with the larger larvae, and is therefore taken into account. The distance travelled by the larva as a function of time is

\[
S(t) = \int_0^t U_f(t') \, dt'
\]

is also presented in Fig. 7A.

The distance travelled by the larva after the tail-movements ceased is called the gliding distance, and is specified as

\[
S_{\text{gliding}} = S(t_{\text{glid}}) - S(t_g). \tag{25}
\]

For our reference larva this leads to a gliding distance of \( S_{\text{glid}}/L = 0.402 \).

7. Extrapolation of model results to larvae larger than 5.5 mm up to say 22 mm

The explanation of the physical mechanisms behind burst swimming has been translated into a model from which the swimming velocity has been calculated as a function of time, for the larva of 5.5 mm.

The excellent agreement found between the model results and the experimental data of Osse and Drost (1989), see Fig. 7A, justify an extrapolation of the model results to larger larvae.

First an assumption has to be made about the relation between the magnitude of the impulsive pressure force and the length \( L \) of the larva. Based on mechanical considerations it is postulated here that the peak in pressure difference between front and backside of the sweeping tail is independent of the size of the larva. According to Eq. (2) the pressure difference impulse \( \nabla \Pi \) is in that case proportional to \( \delta t \) or inverse proportional to \( f \). So \( U_f f \) is size independent. The water velocity leaving the fish tail resulting from the impulsive pressure is \( U_j = \dot{\lambda}(0) f \). The ratio \( \dot{\lambda}(0)/L \) is in fact a measure of the gradient of the tail tip (see Fig. 1) during the initial stage of burst swimming, and is assumed independent of \( L \). The conclusion is that \( \dot{\lambda}(0)/L^2 \) is size independent, so the tail frequency \( f \) must be proportional to \( L^{-1/2} \), and \( U_j \) must be proportional to \( L^{1/2} \).

Table 6 summarizes the applied allometric scaling parameters made throughout the paper.

The alternate vortices shed behind the head of the burst swimming larva bear a close relationship with the Kármán vortex street behind a cylinder. As suggested in this paper the existence of these vortices play an important role in the efficiency of the propulsion in the post-acceleration stage defined as the time interval \( \delta t < t < t_g \). An efficient propulsion could be expected if the distance between two vortices on one side of the vortex street is about equal to the body length, so if \( U_j f \approx L \), where \( U \) is the water velocity in the boundary layer near the fish body. Because \( U \) is somewhere in between \( U_f \) and \( U_j \) it may be concluded that the conditions for efficient propulsion for this thrust component are fulfilled. Note that also \( \delta t \) must be proportional to \( \sqrt{L} \).

The initial acceleration of the fish larva \( (U_j)_{\text{escape}}/\delta t \) in Eq. (22) for the various sizes is calculated using Eq. (14) and \( \dot{\lambda} = 1/\left[ \omega_0 (L/L_0)^{1/2} \right] \). Table 2 shows the result.

Now the equation of motion Eqs. (22) and (24) can be solved also for various values of \( L \).

This has been done for a larva of 2, 3 and 4 times the length of the reference larva, so for 11, 16.5 and 22 mm total body length.

Figs. 7B–D show the results. Also the distance travelled by the larvae as calculated with Eq. (25) is shown.

<table>
<thead>
<tr>
<th>( L/L_0 )</th>
<th>Initial acceleration (\text{mm}/s\textsuperscript{2})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9086.4</td>
</tr>
<tr>
<td>2</td>
<td>5970.5</td>
</tr>
<tr>
<td>3</td>
<td>3799.1</td>
</tr>
<tr>
<td>4</td>
<td>2517.4</td>
</tr>
</tbody>
</table>
Table 3: Calculated gliding distance as function of body length using Eqs. (25) and (26)

<table>
<thead>
<tr>
<th>Total body length $L$ (mm)</th>
<th>Duration pressure imp. $\delta t$ (ms)</th>
<th>Start gliding stage $t_g$ (ms)</th>
<th>End of gliding stage $t_{x_e}$ (ms)</th>
<th>$S(t_g)$ (mm)</th>
<th>$S(t_{x_e})$ (mm)</th>
<th>Gliding distance body length ratio $S_{d/L}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.5</td>
<td>20.0</td>
<td>144.0</td>
<td>456.0</td>
<td>11.81</td>
<td>14.02</td>
<td>0.40</td>
</tr>
<tr>
<td>11</td>
<td>28.28</td>
<td>181.0</td>
<td>1940.3</td>
<td>23.44</td>
<td>41.40</td>
<td>1.63</td>
</tr>
<tr>
<td>16.5</td>
<td>34.64</td>
<td>214.8</td>
<td>4503.3</td>
<td>28.49</td>
<td>72.49</td>
<td>2.67</td>
</tr>
<tr>
<td>22</td>
<td>40.0</td>
<td>248.0</td>
<td>9000</td>
<td>29.73</td>
<td>109.84</td>
<td>3.64</td>
</tr>
</tbody>
</table>

Table 4: Measured gliding distance of burst swimming larval and juvenile carp by Osse and van den Boogaart (1995)

<table>
<thead>
<tr>
<th>Total body length $L$ (mm)</th>
<th>Gliding distance body length ratio of burst swimming carp larvae as measured by Osse et al. (1995)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.5</td>
<td>0.7</td>
</tr>
<tr>
<td>10.4</td>
<td>1.4</td>
</tr>
<tr>
<td>23.6</td>
<td>3.4</td>
</tr>
</tbody>
</table>

Table 3 summarizes the calculated results of gliding distance as a function of body length using Eqs. (25) and (26).

Observe that the total number of swimming bouts in burst swimming is according to the model equal to $t_g/\delta t$ and appears nearly independent of the size of the larva decreasing a bit from about 7 for $L = 5.5$ mm to about 6 for $L = 22$ mm. The velocity of the larva at the end of the gliding motion decreases exponential to zero, making the value of $t_{x_e}$ numerically not well defined. The end of the gliding stage is specified at that point in time where $U_f$ is reduced to 1 mm/s.

Osse and van den Boogaart (1995) measured the gliding distance of burst swimming larval and juvenile carp. Table 4 shows their experimental results.

The agreement between results of the conceptual model and these experimental data is not bad.

For the sake of completeness a check has been carried out to see whether the tail frequency $f$ is indeed high enough to justify the impulsive pressure approach also for the larvae larger than 5.5-mm. The condition was $f > f_{min}$, where

$$f_{min} = \frac{2U_f}{h_m \ln(h_m U_f/2\nu)}$$

Table 5 shows the result.

The conclusion is that the impulsive pressure approach applied for the first full swimming bout of the burst-swimming larvae is consistent for the larvae in the size class 5.5–22 mm. Table 6 summarizes the allometric relations used in this paper.

8. Discussion and conclusions

The initial start in burst swimming mode of a small fish larva seems from an energetic point of view the most efficient way of propulsion. The main part of the acceleration stage in this swimming mode is due to an impulsive motion during which viscosity does not play a substantial role.

The distinction in an inertia and viscous component in fish-larva propulsion made by Webb and Weihls (1986) has appeared very valuable in analysing the fish-larva propulsion problem. The approach is especially valuable in analysing the continuous swimming mode, and in fact also in the post-acceleration phase of the burst swimming mode. The approach needs further elaboration in the initial stage of burst swimming where in the limiting case of $t \ll \delta t$ the velocity of the larva and thus $Re_D$ is small but viscosity does not play a role. In fact Jordan (1992) did so by quantifying the inertia and viscous contribution in the rapid start mode swimming. Indeed he found that the inertial forces in the initial start of the motion were extremely high. Jordan (1992) simply added the inertia and viscous contribution to propulsion. Although this is a valuable first approach the question can be raised; is a simple summation of effects always appropriate? Lateral viscous forces are not always in phase with the lateral velocity of the fish body section. This is especially the case if a cross-section of a fish larva is considered where boundary layer separation occurs at the sharp edges of the nodal fins when it is oscillating broadside on, as discussed in relation to Fig. 6. If the shift between lateral viscous force and velocity is taken into account it can be shown that a third contribution to the thrust comes into play, which I called the interactive force contribution. The physical background...
Table 6
Summary of the allometric relations used in this paper

<table>
<thead>
<tr>
<th>$M_0$</th>
<th>$D_0 = L_0/6.5$</th>
<th>$(h_m(0)/L)_o = 0.25$</th>
<th>$s = D_0$</th>
<th>$f_0 = 50 \text{ Hz}$</th>
<th>$(U_j)_{h_1} = 220 \text{ mm/s}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M = M_0 (D/D_0)^{3}$</td>
<td>$D = D_0 \left( \frac{L}{L_0} \right)^{3/2}$</td>
<td>$h_m(0)/L = 0.25 \left( \frac{L}{L_0} \right)^{-1/2}$</td>
<td>$s/D = 1$</td>
<td>$f = f_0 \left( \frac{L}{L_0} \right)^{-1/2}$</td>
<td>$U_j = (U_j)_{h_1} \left( \frac{L}{L_0} \right)^{1/2}$</td>
</tr>
</tbody>
</table>

of this interactive force, being an interaction between viscous and reactive force, is described in this paper. An extended version of Jordan’s model including the interactive force and the effect of this force on the propulsive efficiency for a continuous swimming larva is in preparation.

Weihs (1980) developed a theoretical model showing that intermittent swimming is more efficient than continuous swimming for larval fishes and adults larger than 5 mm. The advantage increases with larval size up to a length of 15 mm. According to Weihs the smallest fish larvae do not share the advantage of intermittent swimming, due to the dominant influence of water viscosity at small Reynolds numbers. Weihs found that the gain in energy increases the smaller the ratio between burst and glide period. These conclusions seem partly in agreement and partly in contradiction with the ideas presented in this paper. The agreement is that indeed the ratio of burst to glide period, in the present notation $\delta t/(t_{\infty} - t_g)$ decreases strongly with size from 0.064 to 0.0046 for 5.5 to 22 mm length as can be verified from the data given in Table 3. The disagreement is that the ideas presented in this paper lead to the conclusion that especially for the smaller larvae of 5–10 mm burst swimming is an efficient way of locomotion, and the efficiency decreases strongly with size, see Table 1. This disagreement is a consequence of the fact that Weihs (1980) based his energy considerations only on the energy required for the fish to travel a certain distance assuming that the ratio between energy required to energy actually expended by the fish larva i.e. the hydrodynamic Froude efficiency during the burst swimming period is independent of size. The last assumption seems less justified for larvae in the size range 5–15 mm according to Eq. (17) of this paper.

The ideas presented lead to the following conclusions:

- Validity of the impulsive pressure approach needs that the time duration of the initial start of the motion should be as short as possible, but equal or higher than one tail period. Say $\delta t = 1/f$.
- Viscosity effects in propulsion during the first tail period could be neglected if the tail beat frequency is equal or larger than $2(U_j/h_m)\ln(h_m U_j/2\nu)$.
- The tail beat frequency in the post-acceleration stage should be $f \approx 0.3 \frac{U_j}{D}$ where $D$ is the diameter of the head of the larva. This frequency is approxi-

mately equal to the frequency of eddy formation behind a sphere of diameter $D$ in a steady stream with velocity $U_j$.
- The tail of the smallest larva in this study should be relatively long and thin in order to make large tail amplitude possible with a minimum amount of body weight. The viscous flat-plate resistance of this long tail does not really contribute to the total viscous resistance of the larva.
- The number of swimming bouts in burst swimming is rather insensitive to the size of the larva and amounts to about 6 till 7. In fact this is not a result of the model but a result of the assumption on the decay in propulsive force with time after the first tail beat cycle as given by Eq. 20b.
- The Reynolds number based on the head diameter $D$, $Re_D$ must be larger than 100–150 and smaller than 2500. In that Reynolds number region a Kármán vortex street behind a cylinder in a stream is developed. Above $Re_D = 2500$ the Kármán-eddies are no longer distinguishable, the flow is fully turbulent and chaotic and the beneficial effect of the proposed physical mechanism in propulsion in the post-acceleration stage is lost.

Finally, the author wishes to stress the point that the ideas presented in this paper are based on professional knowledge of fluid mechanics and not on real pictures of the flow generated by a burst swimming fish larva. The conceptual model contains several assumptions for which insufficient proof is furnished. A proper survey of biological literature to look for evidence of assumptions has not been made. Therefore the author kept the model as simple as possible to make it easy for others to improve the model-assumptions wherever necessary.

Acknowledgements

I thank Dr Mees Muller for urging the necessity to publish my ideas. I also thank Prof Dr Jan Osse from whom I have learned so much and Dr Peter Aerts for inspiration emerging from our cooperation on a related problem. Prof Dr Peter Troch critically read the manuscript.
Appendix

Streamlines set up by the impulsive motion.

The x, y values defining the lines \( \psi/(Uhm) = \psi_n \) is constant in the upper right quadrant of Fig. 2 are given by

\[
\begin{align*}
x_{hm} &= \frac{1}{2} \left( \sin \theta - \frac{\psi_n}{\sin \theta} \right) \cos \theta, \\
y_{hm} &= \frac{1}{2} \left( \sin \theta + \frac{\psi_n}{\sin \theta} \right) \sin \theta,
\end{align*}
\]

where the dummy variable \( \theta \) is in the interval \( \theta_m \leq \theta \leq \pi/2 \); the lower bound is \( \theta_m = \arcsin \psi_n \).

The streamlines are further symmetrical around \( x = 0 \) and \( y = 0 \).

The distribution of the velocity vector \( \mathbf{u}/U \) for \( x \) is approaching zero from the negative side and for \( y/h_m = 0 \) as shown in Fig. 3 is: For \( |y/h_m| < 1 \) the component of \( \mathbf{u}/U \) in \( x \)-direction is 1, and the component in \( y \)-direction is

\[
y/U = \text{sign}(x) \frac{y/h_m}{\sqrt{1 - (y/h_m)^2}}.
\]

The mathematical specification of the impulsive pressure distribution as a function of \( x \) and \( y \) as shown in Fig. 4 is

\[
\frac{\Pi(x, y)}{\rho U hm} = \text{REAL} \left[ z - \text{sign}(x) \sqrt{z^2 + 1} \right],
\]

where \( z = (x + iy)/h_m \).

This reduces for \( x = 0^+ \) to:

\[
\frac{\Pi(x, y)}{\rho U hm} = -\sqrt{1 - \left( \frac{y}{h_m} \right)^2},
\]

and for \( x = 0^- \) to

\[
\frac{\Pi(x, y)}{\rho U hm} = +\sqrt{1 - \left( \frac{y}{h_m} \right)^2}.
\]

References


