How body torque and Strouhal number change with swimming speed and developmental stage in larval zebrafish

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Small undulatory swimmers such as larval zebrafish experience both inertial and viscous forces, the relative importance of which is indicated by the Reynolds number (Re). Re is proportional to swimming speed (v_swim) and body length; faster swimming reduces the relative effect of viscous forces. Compared with adults, larval fish experience relatively high (mainly viscous) drag during cyclic swimming. To enhance thrust to an equally high level, they must employ a high product of tail-beat frequency and (peak-to-peak) amplitude f_A_tail resulting in a relatively high f_A_tail/v_swim ratio (Strouhal number, St), and implying relatively high lateral momentum shedding and low propulsive efficiency. Using kinematic and inverse-dynamics analyses, we studied cyclic swimming of larval zebrafish aged 2–5 days post-fertilization (dpf). Larvae at 4–5 dpf reach higher f (95 Hz) and A_tail (2.4 mm) than at 2 dpf (80 Hz, 1.8 mm), increasing swimming speed and Re, indicating increasing muscle powers. As Re increases (60 → 1400), St (2.5 → 0.72) decreases nonlinearly towards values of large swimmers (0.2–0.6), indicating increased propulsive efficiency with v_swim and age. Swimming at high St is associated with high-amplitude body torques and rotations. Low propulsive efficiencies and large yawing amplitudes are unavoidable physical constraints for small undulatory swimmers.

1. Introduction

Being small has costs and benefits for swimmers and flyers. On the one hand, small swimmers and flyers experience relatively strong viscous forces resulting in high drag, reduced stride length (distance travelled per cycle) and propulsive efficiency [1–5]. On the other hand, they have relatively high muscle strength and low body inertia, affording small flyers and swimmers excellent manoeuvrability—they achieve high rotational accelerations [6–8]. Small swimmers often move in the intermediate flow regime, where both viscous and inertial forces play an important role. The ratio of inertial to viscous forces is expressed by the Reynolds number:

$$Re = \frac{\rho \ell_{body} v_{swim}}{\mu},$$  

with \(\rho\) the density of water, \(\ell_{body}\) the body length of the fish, \(v_{swim}\) the swimming speed (defined here as the speed of the centre of mass (CoM)) and \(\mu\) the dynamic viscosity of water. Symbols and definitions are listed in the electronic supplementary material, table S1.

Fish larvae, compelled to generate high thrust with their posterior body to overcome the high drag on the anterior body [9], must use high tail-beat frequencies and amplitudes to generate the required high rate of change of momentum of the fluid. Fast, large-amplitude tail beats can cause large lateral forces on the body and large torques around the CoM, in turn causing large yaw accelerations. Large yaw can increase drag, which then requires more thrust to overcome. The large body deformations should also cause significant fluctuations in the fish’s moment of inertia. Furthermore, we expect fluctuations in swimming speed and kinetic energy due to the time-varying nature of thrust.
production with a flapping propeller that causes large fluctuations in instantaneous force, both in direction and in amplitude. So far, these consequences have not been explored systematically and their relation with swimming speed and $Re$ is unclear. Here, we quantify these aspects in zebrafish larvae using a combined kinematic and inverse-dynamics approach and show how body kinematics and dynamics vary with $Re$.

Large body undulations affect also the fluid-dynamic efficiency of swimming and cost of transport. Computational studies of larval swimmers have shown that increasing body-wave amplitude steadily increases energy cost per unit distance while propulsive efficiency plateaus at a value just above 0.3 at tail-beat frequency $f = 57$ Hz [9], suggesting that fish larvae use body-wave amplitudes that maximize fluid-dynamic efficiency at acceptable costs of transport. Nevertheless, swimmers in the viscous and intermediate flow regime ($Re < 300$) often achieve only low propulsive efficiency [3,2]. Propulsive efficiency in fluids strongly depends on vortex shedding dynamics, which correlates with the Strouhal number:

$$St = \frac{f A_{\text{tail}}}{\bar{\nu}_{\text{swim}}}$$

where $\bar{\nu}_{\text{swim}}$ is the mean swimming speed during cyclic swimming, $A_{\text{tail}}$ is the peak-to-peak amplitude of the tail tip. Several studies suggest [10–13] that swimmers in the inertial flow regime swim close to the St that maximizes efficiency ($St = 0.25–0.35$ for carangiform swimmers and 0.4–0.5 for anguilliform swimmers [2,14–16]). By contrast, small organisms swimming in the viscous and intermediate flow regimes experience relatively higher drag forces, which reduces relative stride length ($l_{\text{stride}}/l_{\text{body}}$) and increases St, indicating a high-energy wake with a relatively large component of lateral momentum and thus low efficiency [2,7,17]. Adult fish increase $\bar{\nu}_{\text{swim}}$ in proportion to $f$ while keeping $A_{\text{tail}}$ nearly constant, implying that St and propulsive efficiency remain nearly constant [17–19]. In cyclic swimming, St must increase with decreasing $Re$ if a swimmer is to balance thrust and drag over the tail-beat cycle [2]. Fish larvae are particularly interesting because they swim in the critical $Re$ range that corresponds to the transition from high to low St [2,20]. As body size and swimming speed increase, $Re$ increases, and so should efficiency.

By changing $\bar{\nu}_{\text{swim}}$, larvae change $Re$ and thus the relative influence of inertial and viscous forces. Using $\bar{\nu}_{\text{swim}}$ to compute $Re$ (electronic supplementary material, equation (S3.3)), it follows that St relates to $Re$ as

$$St = \frac{\rho_{\text{water}} f A_{\text{tail}} l_{\text{body}}}{\mu Re} = \frac{Sw}{Re}$$

where $Sw = \rho_{\text{water}} f A_{\text{tail}} l_{\text{body}} / \mu$ is the dimensionless swimming number (introduced by Gazolla et al. [21]). To explore how St varies with $Re$, and hence what larval fish can do to increase hydrodynamic efficiency, we determined $f$ and $A_{\text{tail}}$ for a range of (nearly) cyclic swimming speeds spanning more than one order of magnitude.

Changes in $Re$ and St are confounded by larval development. We expect developmental stage to profoundly affect swimming performance, because body shape and size as well as sensory, neural and muscular properties change rapidly in the first days of larval development. The changes in muscle size, structure and physiology are expected to provide a higher power output, enabling an increase in $f$ or $A_{\text{tail}}$ or a combination of both.

We aim to quantify the body kinematics and dynamics of larval zebrafish aged 2–5 dpf (days post-fertilization), including body torques and Strouhal number, and their relation with developmental age and swimming speed, which indirectly yields performance requirements for swimming muscles. Our data also provide validation criteria for computational swimming models.

### 2. Material and methods

#### 2.1. Animals

Zebrafish larvae (Danio rerio Hamilton 1822) were reared in the laboratory from wild-type stock at a water temperature of 28°C and a 12:12 L:12 D cycle. We used larvae at age 2, 3, 4 and 5 dpf. Larvae were fed Paramecium twice a day at age 5 dpf.

#### 2.2. Kinematic analysis and force on centre of mass

We used custom software developed in Matlab R2013a (Mathworks, MA, USA) for our analysis. To collect kinematic data of cyclically swimming larvae, we used three video set-ups recording at 1000–2000 frames s$^{-1}$ (see the electronic supplementary material, §2 for details). We recorded spontaneous and elicited swimming sequences (by approaching individual larvae with a horse hair) and selected 8–11 sequences per age group. We manually digitized 18–25 points on the fish’s midline of every video frame, then smoothed and interpolated the midlines to obtain 51 equidistant points (see the electronic supplementary material, §3.1 for details). We defined two Cartesian coordinate systems, an earth-bound frame of reference, XYZ, and a ‘fish-bound frame’ $X_{\text{fish}}, Y_{\text{fish}}, Z_{\text{fish}}$ with the origin located at the fish’s CoM and axes parallel to XYZ. We selected sequences with a small Z-component, and assumed that fish moved parallel to the XY-plane. To ensure that we include only (near-)cyclic swimming events (a prerequisite for computing Strouhal numbers), we identified 38 close-to-cyclic swimming events by calculating auto-correlation functions of the body wave (expressed as 51 segment angles) for all tail beats of a given event and selected video sequences comprising at least three consecutive tail beats above the normalized auto-correlation threshold of 0.975 and at least two extrema in the body angle ($\omega_{\text{body}}$).

To determine the body shape of larvae (details in the electronic supplementary material, §3.1), we digitized the outline of the fin fold, body, eye and yolksac in dorsal and lateral views of larvae aged 2–5 dpf (five per age group) at 51 equidistant points from snout to tail tip. We selected the larva whose values were closest to the per age average, to represent the body shape of its age group.

We estimated body volume by modelling the fish as a series of 51 segments by fitting ellipses to the head, eyes, fin fold, trunk (excluding fins) and yolksac (for details, see the electronic supplementary material, §3.1 and figure S1). We assumed a uniform mass density ($\rho_{\text{fish}} = 1000$ kg m$^{-3}$) over the entire body. For each segment, we computed volume $V_i$, mass $m_i$, and position vector $r_i$ of the local CoM by numerical integration. The average $l_{\text{body}}$ for stages 2–5 dpf were 3.39, 3.81, 4.37 and 4.36 mm ($N = 5$ larvae per age group). Body mass $m_{\text{body}}$ was computed as the sum of the segmental masses, resulting in 239, 289, 414 and 373 $\mu$g for stages 2–5 dpf. These values for $l_{\text{body}}$ and $m_{\text{body}}$ were used for all subsequent computations.

We then calculated the instantaneous position, velocity, acceleration and force acting on the CoM from the instantaneous positions of the body segments (see electronic supplementary material, §3.1 for details).
2.3. Instantaneous moment of inertia, body angle, angular velocity and torque

For each body segment \( i \), we computed the moment of inertia \( I_i \) about the segmental vertical centre line and the moment of inertia with respect to the CoM \( I_{i,\text{CoM}} \), about the vertical axis \( z_{\text{mov-axis}} \). Equation (S3.6) and (S3.7) (see figure 6–9) using an optimization procedure with Matlab’s findpeaks function. Fitted variables were scaled by their mean value, then we computed for each set of optimized coefficients the perpendicular distance from each data point to the curve (i.e. total least-squares approach for either a line, a parabola, a power curve or a power curve plus a constant). We used the sum of squared distances as the objective function for the optimization and estimated 95% confidence intervals for the coefficients of each curve fit with a Monte Carlo approach (see the electronic supplementary material, §3.5 for details). We computed the ratio of the root of the sum of squared distances for each nonlinear curve fit and the corresponding linear curve fit. Standard linear regression curve fits were applied for the log transformed data of \( S_w \) and \( Re \) for a comparison with previous work [21].

2.4. Kinetic energy and power

We computed the total kinetic energy of the body \( E_{\text{kin,\text{body}}} \) as well as the kinetic energy associated with translation of the CoM, \( E_{\text{trans,\text{CoM}}} \), and the kinetic energy due to rotation of the body segments about the CoM, \( E_{\text{rot,\text{body}}} \). The latter is a close approximation of the internal kinetic energy of the body. We computed also the total power due to kinetic energy changes of the body, \( P_{\text{kin,\text{body}}} \), the power associated with translation of the CoM, \( P_{\text{trans,\text{CoM}}} \) and the power associated with rotation of the body about the CoM, \( P_{\text{rot,\text{body}}} \). Specific energies and powers were computed by dividing the respective values by body mass (designated as \( E^* \) and \( P^* \)). Details on energy computations are provided in the electronic supplementary material, §3.4.

2.5. Dimensionless quantities and trend analyses

We defined dimensionless swimming speed along the path of the CoM as

\[ \bar{v}_{\text{swim}} = \frac{v_{\text{swim}}}{\ell_{\text{body}}} \]

To compute \( f \) for (near-)cyclic swimming events, we first determined a series of positive and negative extremes in \( \theta_{\text{body}} \) with the ‘findpeaks’ function of Matlab’s Signal Processing toolbox (v. 2013a). Frequency was computed as

\[ f = \frac{n - 1}{2(t_n - t_1)} \]

where \( n \) is the number of extrema in \( \theta_{\text{body}} \), and \( t_1 \) and \( t_n \) the time, respectively, at the first and last extreme in \( \theta_{\text{body}} \). Dimensionless tail amplitude was computed as

\[ \hat{A}_{\text{tail}} = \frac{A_{\text{tail}}}{\ell_{\text{fish}}} \]

Dimensionless body torque was defined as

\[ \hat{\tau}_{\text{body}} = \frac{\tau_{\text{body}}}{I_{\text{body}}} \]

where \( \tau_{\text{body}} \) is the value of \( \tau_{\text{body}} \) for the straight fish. Details about the computation of \( Re \) and \( S_t \) are provided in the electronic supplementary material, §3.2.

We fitted curves to the datasets used for trend analyses (figures 6–9) using an optimization procedure with Matlab’s fminsearch function. Fitted variables were scaled by their mean value, then we computed for each set of optimized coefficients the perpendicular distance from each data point to the curve (i.e. total least-squares approach for either a line, a parabola, a power curve or a power curve plus a constant). We used the sum of squared distances as the objective function for the optimization and estimated 95% confidence intervals for the coefficients of each curve fit with a Monte Carlo approach (see the electronic supplementary material, §3.5 for details). We computed the ratio of the root of the sum of squared distances for each nonlinear curve fit and the corresponding linear curve fit. Standard linear regression curve fits were applied for the log transformed data of \( S_w \) and \( Re \) for a comparison with previous work [21].

3. Results and discussion

3.1. Body morphology

During larval development, mass is redistributed within the body as the yolk sac is absorbed and the body grows allometrically (e.g. [22,23]; electronic supplementary material, figure S3). Yet, the shift in mass distribution does not affect the location of the CoM along the straight fish (expressed as fraction of total length). At 2 dpf, the CoM is at 0.287 \( \ell_{\text{body}} \) from the snout tip, at age 5 dpf at 0.286 \( \ell_{\text{body}} \).

3.2. Larval fish swim with small centre of mass sideslip and large body angle fluctuations

Fish larvae typically swim with wide body undulations [7] (see figure 1a,b for an example with \( v_{\text{swim}} \approx 50 \ell_{\text{body}} \, \text{s}^{-1}, \, f \approx 83 \text{ Hz} \)). Snout tip (figure 1a: green curve) and tail tip (figure 1a: red curve) oscillate substantially. While the large-amplitude body undulations do not result in large sideslip (lateral movements of the CoM, figure 1a: black curve; lateral component of net force with respect to \( r_{\text{CoM}} \), figure 1d: dotted curve), they do cause the CoM to move outside the body (twice per cycle) (figure 1b). CoM speed (\( \bar{v}_{\text{swim}} \)) fluctuates strongly (figure 1c), a result of the oscillating net force on the body (figure 1d). The forward speed of the fish fluctuates over the tail-beat cycle in tune to the fore–aft force component (figure 1c,d).

Body yaw is smaller than head yaw—the peak-to-peak amplitude of the body angle \( \theta_{\text{body}} \) is half that of the head angle \( \alpha_{\text{head}} \) (figure 2f, for event in figure 1). Changes in \( \theta_{\text{body}} \) are also delayed with respect to \( \theta_{\text{head}} \). Thus, \( \alpha_{\text{head}} \) is not a valid approximation for \( \theta_{\text{body}} \) in undulatory swimming fish larvae. Both \( \theta_{\text{body}} \) and \( \hat{\theta}_{\text{body}} \) reach high amplitudes, up to 10 \( \text{ms}^{-1} \) and up to 5 \( \text{ms}^{-2} \) for the example event (figure 2bc); \( \hat{\theta}_{\text{body}} \) generally shows a double peak per tail beat.

The undulatory body movements cause the body moment of inertia \( I_{\text{body}} \) and its rate \( \dot{I}_{\text{body}} \) to fluctuate (figure 2d,e). They also cause \( \dot{I}_{\text{body}} \) to be smaller than \( I_{\text{f}} \) of the straight fish. Furthermore, specific power (\( P_{\text{kin,\text{body}}} \)) fluctuates due to changes in kinetic energy (up to 20 \( \text{W kg}^{-1} \) in figure 2f).
3.3. Body dynamics during cyclic swimming: insights from torque

Body torque around the CoM ($\tau_{\text{body}}$) fluctuates strongly (figure 3a), causing large changes in $\dot{\alpha}_{\text{body}}$, $\omega_{\text{body}}$ and $\dot{\omega}_{\text{body}}$ (figure 2a–c). Torque $\tau_{\text{body}}$ oscillates in a non-sinusoidal manner with usually a double peak per tail beat (four peaks per tail-beat cycle; figure 3a), consistent with the double peak in $\dot{\omega}_{\text{body}}$. Body torque is just ahead of the fluctuations in angle-of-attack of the tail with respect to the local velocity vector ($\nu_{\text{local}}$), which is also double peaked and deviates considerably from a sine wave (figure 3b) due to the large-amplitude motion. These observations indicate that the force associated with tail velocity may contribute significantly to $\tau_{\text{body}}$.

We will now consider how the segmental contribution to the inertial torque about the CoM varies in time and along the body (derived by an inverse-dynamics analysis; electronic supplementary material, §3.3; note that this is not a distribution of the segmental inertial torque with respect to the segmental CoM). The amplitude of the inertial torque about the CoM per unit length $\tau^i_{\text{body},c}$ is largest at the head and tail, as indicated by the amplitude envelope over a tail-beat cycle (figure 3c). Although the tail has less mass per unit length than the head, it contributes similar to inertial torque of the body, because the tail is further away from the CoM and moves at higher accelerations. The location of the ‘neck’ at about 0.28 $\ell_{\text{body}}$ of the envelope corresponds to the caudo-rostral location of the CoM in the straight fish. Inertial torque behaves as a travelling wave along the flexible posterior two-thirds of the body and as a standing wave along the stiff head (figure 4a).

To explore how external forces on the body contribute to the external torque on the body, we estimated $\tau_{\text{dyne},i}$ (figure 4c), $\tau_{\text{fric},i}$ (figure 4d) and $\tau_{\text{acc},i}$ (figure 4f) for the swimming event of figure 1. Our simplified approach to calculate external torque contributions is useful for our analysis but causes the sum of $\tau_{\text{dyne}}$, $\tau_{\text{fric}}$ and $\tau_{\text{acc}}$ to not equal the inertial body torque $\tau_{\text{body}}$. Torque $\tau_{\text{dyne}}$ (figure 4e; green curve) is of similar magnitude and phase as $\tau_{\text{body}}$ (figure 4c; black curve). By far the highest $\tau_{\text{dyne}}$ amplitudes are found in the tail region (figure 4c). By contrast, $\tau_{\text{fric}}$ contributes little and is shifted forward in phase with respect to $\tau_{\text{body}}$ (figure 4e: blue and black curve, respectively), indicating that skin friction has a relatively small effect on body torque. Peak values of $\tau_{\text{fric},c}$ are found in the tail region where high velocities occur (figure 4d). Finally, the estimated contribution to the external torque due to the force on the body in the direction of (continuous curve) and perpendicular to (dotted curve) the instantaneous velocity vector. The blue and red '+' signs in panel (c) and (d) correspond to the minima and maxima in $\alpha_{\text{body}}$ (figure 2a). The time between two '+' signs of the same colour represents a full tail-beat cycle.

Figure 1. A 5 dpf fish larva swimming at approximately 50 $\ell_{\text{body}}$ s$^{-1}$. (a) Sequence of body midlines at 0.5 ms intervals (blue); path of snout tip (green), tail tip (red) and CoM (black). (b) Body shape at 3 ms intervals. CoM (red sphere) periodically falls outside the body. (c) Translational speed of body and tail, as indicated by the amplitude envelope over a tail-beat cycle (figure 3c). Significant magnitude of the 'neck' at about 0.28 $\ell_{\text{body}}$ of the envelope corresponds to the caudo-rostral location of the CoM in the straight fish. Inertial torque behaves as a travelling wave along the flexible posterior two-thirds of the body and as a standing wave along the stiff head (figure 4a).
shows that instantaneous and mean $E_{rot,CoM}$ are higher than the corresponding values for $E_{rot,CoM}$ at a relatively high swimming speed (figure 5a), whereas the low-speed example (figure 5b) shows the reverse, which suggests a lower efficiency at the lower speed. Most of the in-phase reductions of both kinetic energy components over the swimming cycle will be dissipative (without useful conversion into elastic energy). Both translational kinetic energy and rotational kinetic energy fluctuate in phase (figure 5), mainly due to the varying amplitude and direction of the fluid force on the posterior body that causes oscillations in both $F_{CoM}$ and $\tau_{body}$.

### 3.5. Changes in swimming speed and tail-beat amplitude with frequency

To reach higher speeds, fish tend to increase tail-beat frequency $f$ rather than body-wave amplitude [7,20]. However, the relationship between $f$ and mean swimming speed $v_{swim}$ is not a simple proportionality in larval zebrafish (figure 6a) during (near-)cyclic swimming. We previously found a decreasing slope with speed [7], based on a small dataset biased towards younger stages. Based on a much larger dataset, this study found that younger larvae swim slower than older larvae at $f > 50$ Hz (figure 6a). Stage 2 dpf reached frequencies of close to 80 Hz with $v_{swim} \approx 40$ s$^{-1}$ (figure 6b). Stages 3–5 dpf top off at about 95 Hz and 60 s$^{-1}$. The largest improvement in maximum swimming speed occurs between stage 2 and 3 dpf.

Swimming speed depends also on tail-beat amplitude. When looking at the trend of $A_{tail}$ with $f$ within age groups, there is only a weak trend in early larvae (figure 6c,d blue line: data for 2 and 3 dpf combined). By contrast, $A_{tail}$ increases markedly with frequency in older larvae (figure 6c,d red-green line: data for 4 and 5 dpf combined). Older larvae use higher amplitudes as $f > 50$ Hz. Correspondingly, for $f > 50$ Hz swimming speed tends to be higher in older larvae for the same tail-beat frequency (figure 6a). While younger larvae mainly increase frequency, older larvae increase both frequency and amplitude to swim faster. Increasing both frequency and amplitude requires more muscle power, suggesting that 4–5 dpf larvae have more powerful muscles than younger larvae. Non-dimensionalizing $A_{tail}$ reduces the differences in how much amplitude changes with frequency (figure 6d), showing the importance of size in between-stage differences.

Plots of $v_{swim}$ against $f_{A_{tail}}$ and $\tau_{swim}$ against $f_{A_{tail}}$ show the expected upward trend (electronic supplementary material, figure S4), yet the scatter is largest at the highest swimming velocities (caused by a relatively large range of tail-beat amplitudes of the 4–5 dpf larvae and small deviations from an ideal cyclic swimming pattern).

### 3.6. Body torque and yawing angle

Higher swimming speeds imply higher drag and require more thrust, resulting in higher amplitudes of body torques and yaw, because local forces on the body are generally not in line with the CoM (figure 7a). This trend remains even after removing size effects (figure 7b). With swimming speed proportional to $Re$, torque increases with increasing $Re$ (figure 7c,d). Higher torques at higher speeds result in higher body yaw (despite the decreasing cycle time with
increasing $\bar{v}_{\text{swim}}$)—the peak-to-peak amplitude of $\alpha_{\text{body}}$ increases with swimming speed (figure 7c,f), reaching almost $40^\circ$. Head yaw (fluctuation in $\alpha_{\text{head}}$) is twice as large as body yaw (fluctuation in $\alpha_{\text{body}}$; mean ± s.d. of peak-to-peak ratio of $\alpha_{\text{head}}$ over $\alpha_{\text{body}}$ is $2.11 \pm 0.49$), indicating that head yaw is not a valid proxy of body yaw. Maximum $\tau_{\text{body}}$ increases fivefold from stage 2 to 4 dpf (figure 7a,c). Maximum torque more than doubles from stage 2 to 3 dpf. Non-dimensionalizing torque reduces these increases (although it increases scatter), showing the important effect of size on torque (figure 7b,d).

### 3.7. Effects of Reynolds number on Strouhal number and swimming number

The same increase in the product of tail-beat frequency and amplitude causes a larger increase in swimming speed at high than at low swimming speeds (electronic supplementary material, figure S4a). This larger increase in speed for a given increase in $f_{\text{tail}}$ causes St to drop with increasing $Re$, which is proportional to $\bar{v}_{\text{swim}}$. The lowest swimming speeds result in Strouhal numbers of up to 2.5; St drops to 0.72 as larvae reach top swimming speeds of nearly 0.30 m s$^{-1}$ or 60 $v_{\text{body}}$ s$^{-1}$ (figure 7g). The decrease in St is largely explained by the increase in $Re$: St decreases from 2.5 to 0.72 (with $\approx 0.72/2.5 = 0.29$) at a similar rate as the ratio of the product of tail-beat frequency and amplitude to $Re$—the product $f_{\text{tail}}$ increases by a factor of $\approx 8$ as $Re$ increases by a factor of $\approx 23$ ($8/23 \approx 0.30$). More precisely, the St relates to $Re$ as $St = f_{\text{tail}}/Re_{\text{cub}}/\mu Re = Sw/Re$. The $St=Re$ data of larval fish are described well by a (negative) power function plus a constant ($St = c_1 Re^{c_2} + c_3 = 41.29 Re^{-0.741} + 0.525$; figure 7g, black curve). The youngest larvae of 2 dpf do not reach the high $Re$—low St combinations exploited by the older larvae. With $St=Sw/Re$, our curve fit can be rewritten as $Sw = c_1 Re^{1-c_2} + c_3 Re$, which deviates from a simple power function. When plotted on a double logarithmic scale (figure 7h) this fit is still curved, the slope decreases with increasing $Re$.

Our experimental data do not conform with the theoretical prediction of Gazolla et al. [21], which states that $St \propto Re^{0.25}$ and $Re \propto Sw^{1/3}$ (giving a straight line in a double log $Re$–Sw plot) based on small-amplitude body undulations and Blasius resistive theory for the laminar swimming regime. The predicted exponent of $-0.25$ lies outside the 95% confidence interval $[-1.250, -0.389]$ of
the experimentally obtained exponent of $-0.741$. A large deviation is to be expected because neither assumption is substantiated by the actual swimming motions of larval fish. To further compare the predicted exponent with our data, we also made linear regressions for log $Re = c_2 \log Sw + c_1$. For the full $Sw - Re$ range in the dataset, we obtained values for $c_2$ of 1.464 and 1.572 for, respectively, $Re$ and $Sw$ as the dependent variable. Both values are well above 4/3. Restricting the maximum in $Re$ to 800 (used as upper limit for numerical simulations of the laminar regime in Gazella), we found corresponding values of 1.614 and 1.710, deviating even more from 4/3. The higher value of the exponent for the lower $Re$ range is in agreement with the curved shape of the double log $Sw - Re$ fit (figure 7b).

3.8. Kinetic energy and power

Translational and rotational kinetic energy increase nonlinearly with swimming speed (figure 8a,b). The contribution of translational versus rotational kinetic energy changes with age and swimming speed (figures 5 and 8a,b). Maximum mass-specific $E_{kin,CoM}$ and $E_{rot, body}$ more than triple between age 2 and 4 dpf. Translational energy outweighs rotational energy in most recorded swimming events (figure 8c,d) except a few young larvae (age 2 dpf) at low $\nu_{swim} (<15 \ell_{body} s^{-1})$ and high $St$, when the tail produces a relatively high lateral force component. In general, rotational kinetic energy is a substantial component of the total kinetic energy of the body in larval swimmers.

Maximum specific power due to fluctuations in kinetic energy of the body increases nonlinearly with $\nu_{swim}$ (figure 9a). The two main contributors to power are translational and rotational power (figure 9b). Rotational power exceeds translational power rarely and only at low $\nu_{swim}$ (figure 9b). Specific power triples within 3 days of development—peak $P_{kin, body}$ at the highest observed $\nu_{swim}$, in 5 versus 2 dpf larva is 22 versus 7 W kg$^{-1}$. These values are much lower than the total power required for swimming, neglecting energy dissipated in the body and power spent on external fluid flow. Assuming that this body kinematics-based motion power is 25% of muscle power, and that 50% of the body is locomotion musculature, and 50% of these contribute at any one time, zebrafish larvae require muscle peak power outputs of 112–352 W kg$^{-1}$ muscle at the respective maximum performance at 2 and 4–5 dpf with contraction frequencies of 80–95 Hz. Given the high maximum tail-beat frequencies,

![Figure 5. Specific kinetic energy for (a) a near-cyclic swimming event at approximately 50 $\ell_{body} s^{-1}$ (age 5 dpf) (same as figure 1) and (b) approximately 8 $\ell_{body} s^{-1}$ (age 3 dpf). Total kinetic energy of the body ($E_{kin, body}$, black), kinetic energy due to speed of the CoM ($E_{kin,CoM}$, red), and sum of specific kinetic energy due to rotation of the segmental masses around CoM and rotation of the segments about their central vertical axis ($E_{rot, body}$, blue). $E_{kin, body} \approx E_{kin,CoM} + E_{rot, body}$.

![Figure 6. Swimming kinematics during (near-)cyclic swimming for 9–11 swimming events per age group (2–5 dpf). (a) Mean swimming speed $\nu_{swim}$ along the path of the CoM (O) and along a straight line approximation of the path of motion (†) against cycle frequency $f$. Both speeds differ little, indicating small sideslip. 2, 3 dpf larvae reach lower speeds for a given $f$ than 4, 5 dpf larvae. (b) Specific swimming speed ($\nu_{swim} = \nu_{swim}/\ell_{body}$) against $f$ (same dataset as (a)). (c) Peak-to-peak tail-beat amplitude $A_{tail}$ against $f$. Data in (c) and (d) were fitted by total least squares. In (c), the black curve shows the fit for the total dataset. The combined datasets for 2 and 3 dpf (blue-cyan line) and 4 and 5 dpf (red-green line) were fitted also separately. The 4–5 dpf age group tended to use higher $A_{tail}$ than the 2–3 dpf group for $f > 50$ Hz, and they vary $A_{tail}$ more over the frequency range. Panel (d) shows same data as (c) for dimensionless tail-beat amplitude ($\tilde{A}_{tail} = A_{tail}/\ell_{body}$). Parameter values for each curve fit are given in electronic supplementary material, table S2.


these projected muscle powers match or exceed the currently known maxima for aerobic fast, super-fast and asynchronous muscles (tree frog: 200 W kg\(^{-1}\) (peak), 54 W kg\(^{-1}\) (average in work loop) at 44 Hz at 25°C [24]; toadfish: 14 W kg\(^{-1}\) (average in workloop) at 22 Hz at 15°C [25]; beetle: 200 W kg\(^{-1}\) (peak), 127 W kg\(^{-1}\) (average in workloop) at 94 Hz at 35°C [26]), but are less than maximum power in anaerobic quail muscles (1121 W kg\(^{-1}\) (peak), 390 W kg\(^{-1}\) (average during shortening phase in workloop) at 23 Hz at 40°C [27]).

4. General discussion

4.1. Body dynamics of undulatory swimming in larval fish: improving swimming skills within a narrow time window

Using a distributed-mass inverse-dynamics approach, we shed new light on the swimming mechanics of larval fish. Across the observed range of swimming speeds, large body undulations do not cause large sideslip of the CoM, but considerable body yaw. We expect that adult fish, which use narrower, lower frequency body waves, will show considerably lower relative fluctuations in body yaw, torque and moment of inertia.

Comparing within larval stages, swimming performance greatly improves between 2 and 5 dpf. Over this age range, larval fish increasingly favour intermittent over cyclic swimming [7]. Yet burst periods are sufficiently long and cyclic to analyse trends that elucidate the physics of swimming in the intermediate Reynolds regime and the development of swimming in larval fish. From 2 to 3 dpf, the larvae increase maximum tail-beat frequency \(f_{\text{max}}\) from 80 to 95 Hz. The 4 dpf larvae used similar \(f_{\text{max}}\) as 3 dpf larvae, but generated higher maximum tail-beat amplitudes for frequencies above 50 Hz. The higher tail-beat frequencies and amplitudes lead to higher swimming speeds and indicate that maximum power output of the swimming musculature increases rapidly after hatching. Improving swimming speed reduces the predation risk of larval fish [28] and enhances their ability to catch prey when they start feeding at 5 dpf. Several other performance criteria require future attention, such as fast-start performance and manoeuvres in three-dimensional space.

4.2. Coping with high-friction forces: trading efficiency for thrust

Vortex shedding mechanics (as expressed by \(St\)) changes with flow regime (as expressed by \(Re\)) in a nonlinear way [16,19,29]. The inverse relationship between \(St\) and \(Re\) is mapped out by larval fish (figure 7g). Slow larvae swim at higher \(St\) (\(St \approx 2.5\) at \(Re \approx 60\)) than fast larvae (\(St \approx 0.72\) at \(Re \approx 1400\)). Thus, across the examined larval size range (body length 3–4.5 mm), increasing swimming speed by one order of magnitude from 25 to 250 mm s\(^{-1}\) causes a drastic, nonlinear drop in \(St\). The Strouhal number remains roughly constant across the typical speed range of adult fish and cetaceans (\(St = 0.2–0.4\) for \(Re = 10^{5}–10^{6}\) [13,16,19,30]). When adult fish increase tail-beat frequency, their swimming speed increases proportionally without increasing tail-beat amplitude, so \(St\) drops little with increasing speed [31]. The Strouhal number reflects differences in vortex shedding mechanics caused by body shape. Swimmers with high aspect-ratio tail fins use lower \(St\) values [16,30] than anguilliform swimmers [16,31]. Overall, undulatory swimmers operate close to optimal \(St\) values, yet optimal Strouhal numbers vary with body shape and swimming speed.

Undulatory swimmers use high Strouhal numbers in high-friction environments. High Strouhal numbers occur not just at small body sizes, but generally in systems with high body drag, such as adult lungfish moving through...
highly viscous watery solutions \cite{32}; sandfish and nematodes moving through granular media \cite{33–36}; and alligators (data in \cite{21}). When facing higher frictional forces, undulatory swimmers swim at lower stride lengths—tail-beat frequency $f$ and amplitude $A_{\text{tail}}$ must increase to achieve the same displacement (computational: \cite{2,14,15,37}, experimental: \cite{19,32,38,39}). Theoretical studies \cite{10,16} show that maximal efficiency decreases and St increases with decreasing Re. When viscous or other frictional forces become large relative to inertial forces, undulatory swimmers must sacrifice efficiency for higher thrust.

The Strouhal number decreases steeply as undulatory swimmers transition from the viscous to the inertial flow regime (figure 7g,h), consistent with the inverse relationship between St and Re. As seen in larval fish, swimming at lower Re requires generating relatively higher propulsive forces by increasing $f$ and $A_{\text{tail}}$ (figure 7h). Both increase the torque around the CoM and hence decrease the ratio of translational to rotational kinetic energy. Undulatory swimmers have no known mechanisms to store rotational kinetic energy. Hence, a lower ratio of translational to rotational kinetic energy implies a lower propulsive efficiency, as indicated

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**Figure 8.** Specific kinetic energy due to translation $E_{\text{tr,CoM}}^*$ and rotation $E_{\text{rot, body}}^*$ during (near-)cyclic swimming for the same dataset as figure 6. (a,b) Maximum (○) and mean (+) values against mean swimming speed $v_{\text{swim}}$. Second-order polynomial curve fits for maxima (continuous curve) and mean (dashed curve) are shown in (a,b). (c,d) Ratio of the maxima (c) and the means (d) of $E_{\text{tr,CoM}}$ and $E_{\text{rot, body}}$ over $v_{\text{swim}}$. The horizontal dashed line indicates a ratio of 1. Parameter values for each curve fit in (a) and (b) are given in electronic supplementary material, table S4.

**Figure 9.** Maximum specific power computed as rate of change of kinetic energy of the body per body mass during (near-)cyclic swimming for same dataset as figure 6. (a) Total (○), translational (×) and rotational (+) power over mean swimming speed. Second-order polynomial curve fits for maximum total (continuous curve), and translational, and rotational (dashed curves) powers are shown. (b) Ratio of maximum translational to rotational power. The horizontal dashed line indicates a ratio of 1. Parameter values of the curve fits in (a) are given in electronic supplementary material, table S4.
by a high St value. As Re drops, a given increase in f or $A_{tail}$ causes less of an increase in swimming speed and St increases. By swimming faster, larval fish crank up their Re, which might enable them to increase propulsive efficiency at the expense of higher power expenditure. High swimming speeds require very high tail-beat frequencies, which demand super-fast muscles, which are known to have low efficiencies [40], which counteracts the gain in fluid-dynamic efficiency. In larval zebrafish of 4–5 dpf, this limitation tops off $f_{max}$ at about 100 Hz and Re at about 1400. The general trend of a decreasing St with Re in the intermediate regime has been predicted by CFD studies (e.g. [2,20,21]).

4.3. Scaling of the swimming number Sw

We obtained a more complex relationship between Re and the swimming number Sw than suggested by Gazolla et al. [21]. They explored the relation between Re (range 200–20 000) and Sw with CFD simulations. They suggested that the nonlinear Sw–Re relationship can be described by first approximation by two power functions. While the theoretical prediction matches both the CFD and the experimental data on large swimmers, the match is less convincing in the laminar flow regime, where the power exponents predicted using Blasius theory ($Re \propto Sw^{1.33}$) and CFD ($Re \propto Sw^{1.31}$) are considerably lower than the experimentally observed exponent ($Re \propto Sw^{1.52}$, power function fit to zebrafish data over $10 \leq Re \leq 1000$) and depend critically on the exact value of transitional Re—Gazolla et al. obtain a good fit between Blasius prediction (exponent 1.33), CFD data (exponent 1.31) and experimental data (exponent 1.33) partly by placing the transition from the laminar to the turbulent flow regime at different Re and Sw (CFD: Re 800, Sw 2000; experimental data: Re 3000, Sw 10 000).

The large discrepancy between experimental data on the one hand and theoretical Blasius prediction on the other hand stem from the complex fluid-dynamic effects caused by large-amplitude tail motion. Any high anterior drag must be balanced by high thrust, which the swimmer generates by increasing tail-beat amplitude and frequency, which in turn increase anterior drag by positive feedback on $\theta_{body}$ and hence amplitudes of $\theta_{head}$ and $\theta_{body}$. The nature of this feedback depends on Re and body shape. The Blasius prediction of Gazolla et al. is not able to capture this complex feedback, leading them to underestimate drag and hence St.

4.4. Swimming performance varies with size and speed

Small organisms ($\ell_{\text{body}} < 10$ mm) operating in the intermediate flow regime ($10^3 < Re < 10^5$) reach not only much higher tail-beat frequencies, but also higher $\ell_{\text{body}}$-specific swimming speeds than large undulatory swimmers ($\ell_{\text{body}} > 10$ mm). Despite experiencing relatively higher viscous fluid forces and despite a lower swimming efficiency, zebrafish larvae can reach extreme forward speeds of up to 60 $\ell_{\text{body}}$ s$^{-1}$, because they can generate relatively high propulsive forces at tail-beat frequencies of up to 95 Hz. By contrast, large undulatory swimmers have considerably lower tail-beat frequencies and $\ell_{\text{body}}$-specific swimming speeds. And adult fish retain those low values when placed in more viscous flow regimes. Lungfish maintain swimming speeds of 0.15–0.25 $\ell_{\text{body}}$ s$^{-1}$ and tail-beat frequencies of 1–2 Hz over a 1000-fold increase in viscosity [32]. Sandfish ‘swimming’ in sand use similar tail-beat frequencies (1–4 Hz) [33]. Compared with small undulatory swimmers, which are adapted to the intermediate flow regime, large undulatory swimmers have muscles optimized to operate at low cycle frequencies in order to swim at low Strouhal numbers. Large swimmers cannot adjust to increased friction forces by increasing tail-beat frequency by orders of magnitude, because their axial muscles have a low maximum cycling frequency.

Across body sizes, distance/$\ell_{\text{body}}$ covered per tail beat in the viscous flow regime is low compared with undulatory swimmers in the inertial flow regime: lungfish and sandfish reach 0.1–0.2 $\ell_{\text{body}}$/tail-beat cycle [32,33], zebrafish larvae 0.2–0.6 [4,7], tadpoles 0.3–0.6 [41], insect larvae 0.3 [42]. By contrast, adult fish in the inertial flow regime swim at 0.4 (anguilliform swimmers; [43,44]) to 0.9 $\ell_{\text{body}}$/tail-beat cycle (carangiform swimmers; [45–47]) during routine swimming. In summary, during undulatory swimming in systems with high viscous or friction forces, St is high and efficiency is low.

## References


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