The fish tail motion forms an attached leading edge vortex

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The tail (caudal fin) is one of the most prominent characteristics of fishes, and the analysis of the flow pattern it creates is fundamental to understanding how its motion generates locomotor forces. A mechanism that is known to greatly enhance locomotor forces in insect and bird flight is the leading edge vortex (LEV) reattachment, i.e. a vortex (separation bubble) that stays attached at the leading edge of a wing. However, this mechanism has not been reported in fish-like swimming probably owing to the overemphasis on the trailing wake, and the fact that the flow does not separate along the body of undulating swimmers. We provide, to our knowledge, the first evidence of the vortex reattachment at the leading edge of the fish tail using three-dimensional high-resolution numerical simulations of self-propelled virtual swimmers with different tail shapes. We show that at Strouhal numbers (a measure of lateral velocity to the axial velocity) at which most fish swim in nature (approx. 0.25) an attached LEV is formed, whereas at a higher Strouhal number of approximately 0.6 the LEV does not reattach. We show that the evolution of the LEV drastically alters the pressure distribution on the tail and the force it generates. We also show that the tail’s delta shape is not necessary for the LEV reattachment and fish-like kinematics is capable of stabilising the LEV. Our results suggest the need for a paradigm shift in fish-like swimming research to turn the focus from the trailing edge to the leading edge of the tail.

1. Introduction

The analysis of the flow patterns that are generated by the movement of the body and appendages of organisms is the prerequisite for gaining insights on how locomotor forces are generated in different organisms. Previous works have suggested that the reattachment of the leading edge vortex (LEV) is the most important mechanism for enhancing locomotor force in insect, bird and bat flight [1–10]. The LEV is formed when the angle of attack of the wing/aerofoil is increased such that it creates a separation bubble at the leading edge that reattaches before reaching the trailing edge to maintain the Kutta condition [3,5]. The separation bubble creates a lower pressure region on the suction region of the aerofoil, which greatly increases the force production. This is the single most important feature of flows during insect and bird flight [5], which has not been observed in aquatic swimming probably owing to the following reasons: first, many fishes swim by undulating their bodies with a wave speed higher than the swimming speed, which is known to prohibit separation along the body of the fish [11–14]; second, it is quite challenging to measure the flow, especially along the leading edge of the tail owing to the resolution and optical access requirements. Therefore, the majority of previous works have focused on the trailing wake [15–17] among others. Even in the most recent three-dimensional flow measurements using volumetric imaging on the shark tail, the emphasis has been on the trailing edge [18].

The two non-dimensional parameters that characterize the wake of a swimmer are the Reynolds number, \( Re = U/L \nu \), of the flow and the Strouhal number, \( St = fA/U \), of the undulatory body motion [16,19]. In the \( Re \) and \( St \) definitions, \( L \) is the fish length, \( U \) is the steady inline swimming speed, \( \nu \) is the kinematic viscosity of the water, \( A \) is the maximum lateral excursion of the tail over a cycle and \( f \) is the tail-beat frequency. Most fishes in nature swim at Strouhal numbers in the range of 0.2–0.3 [20,21], whereas fish larvae [22] or fishes swimming at low speed, e.g. pacific salmon, [23] have been observed to swim at higher \( St \) numbers.
simulations are continued until quasi-steady state is reached, regime) and at the infinite viscosity limit (inertial regime). The experiments with flapping foils also have revealed the maximum efficiency in the range of 0.2–0.3 [19,20].

The efficiency of carangiform swimmers in the inertial regime ($St \approx 0.25$) is approximately 40 per cent for all our swimmers, and in the transitional regime ($St \approx 0.6$) is approximately 20 per cent similar to our previous works [11,24]. The force generation and efficiency are directly related to the flow; therefore, we visualize the flow and relate the time history to the force/efficiency.

To see whether the flow forms a vortex at the leading edge, we visualize the flow in the near-tail region using streamlines similar to previous insect flight simulations [9]. Figures 2 and 3 visualize the streamlines for the inertial ($St \approx 0.25$) and transitional ($St \approx 0.6$) regimes, respectively, for different tail shapes at an instant with the phase angle $\varphi = 2\pi f t = \pi/3$ of the fish body’s backwards travelling wave (instant C marked in the electronic supplementary material, figure S8)—see also electronic supplementary material, appendix. Comparing figures 2 and 3, significant differences are observed in streamlines near the tail. The efficiency of carangiform swimmers in the inertial regime ($St \approx 0.25$), a LEV is clearly visible, spiralling from the root to the tail tip for all tested tail shapes. The LEV connects with the tip vortex forming vortex loops as they advect downstream. On the other hand, in figure 3 ($St \approx 0.6$), the LEV is completely separated behind the tail for all of the tested tail shapes. The streamlines in figures 2 and 3 are coloured by vorticity magnitude. It can be observed in figure 2 that the vorticity in the middle of the LEV is much larger than the vorticity elsewhere.

To clearly demonstrate the difference between the attached and the separated LEV in these two flow regimes, we carried out high-resolution simulations for just the tail under similar conditions as the complete fish, i.e. inertial regime ($Re = 25 000/50 000$, $St = 0.25$) and transitional regime ($Re = 4000$, $St = 0.6$). The higher resolution of these simulations near the tail allows us to closely examine the flow and LEV in the vicinity of the tail. These simulations demonstrate: (i) the existence of an attached and a detached LEV at low and high $St$, respectively (see the electronic supplementary material, figures S4–S7); (ii) the relationship between the time-varying LEV and the time course of force and power coefficients (see the electronic supplementary material, figure S8); and (iii) the role of the LEV and its evolution in completely altering the pressure distribution on the tail (see the electronic supplementary material, figures S9 and S10), which plays an important role in generating forces. The details of the earlier-mentioned discussions and figures S4–S10 can be found in the electronic supplementary material.

Considering most fish tails resemble delta wings, on which the first leading edge vortices were observed [3], along with their large oscillations and angles of attack, it is reasonable to believe that the flow at the leading edge might separate. To test this hypothesis, we have carried out high-resolution numerical simulations around virtual swimmers with different tail shapes under different flow conditions.

2. Material and methods

We carried out self-propelled simulations of the virtual swimmers with different tails using the exact same method as in our previous work [24]. The details of our method can be found in previous publications [11,12,24–26], and only a brief description of the technique is given here. The equations governing the fluid motion are solved in the non-inertial reference frame attached to the fish centre of mass (COM) [24]. The motion of the fish body is prescribed based on carangiform kinematics [27], whereas the motion of the COM is calculated based on the fluid forces on the fish body through our fluid–structure interaction algorithm [25]. The method has been validated extensively for flows with moving boundaries [25,28] and has also been applied to simulate steady swimming of tethered [11,12] and self-propelled [24] carangiform and anguilliform swimmers.

We construct different virtual swimmers from our mackerel body, which is closely modelled after the actual anatomy of a mackerel, by modifying their tail geometry (figure 1). We use three different tail geometries: a homocercal forked tail, e.g. mackerel; a heterocercal with larger top lobe, e.g. shark tail; and a homocercal unforked tail, e.g. bull trout.

Different virtual swimmers tested in this study are built by attaching different tail geometries to a mackerel body and meshed with triangular elements required by the curvilinear, immersed boundary method [25,26]. We test three different tail geometries: a homocercal forked tail, e.g. mackerel; a heterocercal with larger top lobe, e.g. shark tail; and a homocercal unforked tail, e.g. bull trout.

Figure 1. Different virtual swimmers tested in this study are built by attaching different tail geometries to a mackerel body and meshed with triangular elements required by the curvilinear, immersed boundary method [25,26]. We test three different tail geometries: a homocercal forked tail, e.g. mackerel; a heterocercal with larger top lobe, e.g. shark tail; and a homocercal unforked tail, e.g. bull trout.

3. Results

To test our hypothesis about the LEV on fish tails, we carried out simulations in two different flow regimes similar to our previous work [24] for all of our virtual swimmers: a moderately viscous fluid with $Re$ approximately 4000 (transitional regime) and at the infinite $Re$ limit (inertial regime). The simulations are continued until quasi-steady state is reached, i.e. average swimming velocity remains constant. Different swimmers with different tail shapes reach a slightly different swimming velocity in quasi-steady state, i.e. $Re$ and $St$ of different swimmers are slightly different, but still close. In fact, for all swimmers, $St$ is around 0.6 in the transitional regime, whereas in the inertial regime, $St$ is approximately 0.25. The $St$ of approximately 0.25 in the inertial regime is within the typical $St$ range (0.2–0.3) observed in nature for fishes [20]. However, the $St$ in the transitional regime (low $Re$) of approximately 0.6 is not typical for most fishes, but has been observed for fish larvae [22] or fish swimming at a low speed, e.g. pacific salmon [23].

The efficiency of carangiform swimmers in the inertial regime ($St \approx 0.25$) is approximately 40 per cent for all our swimmers, and in the transitional regime ($St \approx 0.6$) is approximately 20 per cent similar to our previous works [11,24]. The WK method has been validated extensively for flows with moving boundaries [25,28] and has also been applied to simulate steady swimming of tethered [11,12] and self-propelled [24] carangiform and anguilliform swimmers.

To clearly demonstrate the difference between the attached and the separated LEV in these two flow regimes, we carried out high-resolution simulations for just the tail under similar conditions as the complete fish, i.e. inertial regime ($Re = 25 000/50 000$, $St = 0.25$) and transitional regime ($Re = 4000$, $St = 0.6$). The higher resolution of these simulations near the tail allows us to closely examine the flow and LEV in the vicinity of the tail. These simulations demonstrate: (i) the existence of an attached and a detached LEV at low and high $St$, respectively (see the electronic supplementary material, figures S4–S7); (ii) the relationship between the time-varying LEV and the time course of force and power coefficients (see the electronic supplementary material, figure S8); and (iii) the role of the LEV and its evolution in completely altering the pressure distribution on the tail (see the electronic supplementary material, figures S9 and S10), which plays an important role in generating forces. The details of the earlier-mentioned discussions and figures S4–S10 can be found in the electronic supplementary material.
4. Discussion

(a) Leading edge vortex: a common feature in lift-based propulsion

The simulations here show that LEV reattachment can be a common feature of swimming with lift-based propulsion on different tail geometries. In lift-based propulsion, the tail acts as a foil whose motion creates an angle of attack relative to the incoming flow (see the electronic supplementary material). This angle of attack induces a leading edge vortex, which is visible in the flow visualizations.

Figure 2. The flow near the tail in the inertial regime ($St \sim 0.25$) visualized by streamlines coloured by the vorticity magnitude at phase angle $\varphi = 2\pi ft = \pi/3$ ($f$ is frequency and $t$ is time). A stable, leading edge vortex with spiralling flow around it is visible. See the electronic supplementary material, movie S1 for the evolution of the streamline during one cycle. (Online version in colour.)

Figure 3. The flow near the tail in the transitional regime ($St \sim 0.6$) visualized by streamlines coloured by the vorticity magnitude at phase angle $\varphi = 2\pi ft = \pi/3$ ($f$ is frequency and $t$ is time). Owing to a high lateral velocity of the tail relative to the axial velocity, the vortex at the leading edge grows and becomes unstable. See the electronic supplementary material, movie S2 for the evolution of the streamline during one cycle. (Online version in colour.)
material, figure A2). The foil with an angle of attack creates a lift force such that it has a component that propels the fish forward. The lift-based mechanism is used by carangiform/thunniform swimmers, e.g. mackerel and tuna, which typically swim at Strouhal numbers in the range of 0.2–0.3 [20,21]. These types of swimmers typically have thick bodies, whose width decreases at the peduncle where the body attaches to a V-shaped, sweptback tail [29]. By contrast, anguilliform swimmers, such as eel, mostly use a reactive acceleration (drag-based) mechanism to propel themselves, i.e. accelerating the adjacent fluid similar to a paddle. They have long, narrow bodies, and the width of the body remains almost constant from head to tail [29]. Furthermore, the amplitude of body undulations in anguilliform swimmers is large over the whole body length [29]. The LEV might not occur in anguilliform swimming (owing to different body motions and lack of relatively high aspect-ratio tails) or the fishes that use their pectoral fins for propulsion.

(b) Leading edge vortex: tail kinematics or the delta shape?

Delta wings are known to create leading edge vortices whose pattern is well-established experimentally and theoretically [3,30]. The shear layer separates at the leading edge of the delta wing and curves upward and inboard and eventually rolls up, forming a core in which the velocity and pressure fields are roughly axially symmetric [30]. The LEV not only increases the lift but also changes the distribution of the lift rather drastically [31], as shown by comparing the spanwise pressure distribution calculated based on potential theory with the measured ones [32], as well as our results discussed previously (see the electronic supplementary material, figures S9 and S10). Nevertheless, a stable LEV has also been observed in wings that are not swept back [1,2,4,7]. Here, we have sweptback tails similar to the delta wings. This raises the question of whether this LEV is due to the kinematics of the tail, or as a result of the highly sweptback tail geometry similar to delta wings. To answer this question, we construct another virtual swimmer with a rectangular tail (figure 4) that moves exactly the same as our previous swimmers. Because the delta shape in the rectangular tail cannot be the reason for the formation of the LEV, if the LEV is observed, then we can conclude that the fish-like kinematics creates a stable LEV similar to insect flight. We can observe from figure 4 that even in the rectangular tail the LEV is present. Therefore, the kinematics of the tail is such that it creates a stable LEV, i.e. the delta shape is not necessary for the stable LEV. Nevertheless, the delta shape probably enhances the stability of the LEV on the fish tail similar to sweptback bird wings [6,33].

(c) Comparison with previous work

Experiments with two-dimensional flapping foils have shown that they are more efficient when alternating sides of the foil form a moderately strong LEV per half cycle, which is convected downstream and interacts with trailing edge vorticity, eventually resulting in the formation of a reverse Karman street [34]. This is similar to the delayed stall observed by Maxworthy [7], who visualized the LEV for the two-dimensional motion of the wing. Furthermore, Dickinson & Gotz [35] showed that in the two-dimensional wing a new LEV is created when the trailing edge vortex is shed into the wake. The LEV sheds into the wake after the trailing edge vortex to create a Karman street behind the wing. In contrast to two-dimensional models, the three-dimensional models did not shed vortices and the LEV stayed attached even after many chord lengths of travel [2,36]. This was shown for the first time by Ellington et al. [2] by smoke visualization of the three-dimensional hawkmoth model Manduca sexta.

The mechanism for prolonged attachment of the LEV at high and low Reynolds numbers is different and is subject to active research [1,36]. At high Re, the reason behind the prolonged attachment of the LEV in the three-dimensional wing versus the two-dimensional wing has been related to the spanwise flow from the wing base to the wing tip that stabilizes the vortex similar to the delta wings [2,5,8]. Such spanwise flow was not observed at low Re of approximately 120 [1], but was observed at higher Re of 1400 [36] similar to the hawkmoth model [2,4]. Lentink & Dickinson [37] have argued that centrifugal acceleration is the probable mechanism to stabilize the LEV at low Re. They also state that at high Re, the pressure gradient can explain the spanwise flow in the core of the vortex, whereas the centrifugal pumping can explain the spanwise flow behind the LEV [37].

The Reynolds numbers relevant to fish swimming and the simulations performed in this work are much higher than 120, i.e. the spanwise flow is probably the cause of the prolonged attachment here [36]. The spanwise flow interacts with the LEV, causing the spanwise flow to spiral towards the wing tip [4]. By connecting the vorticity out of the vortex, the spanwise flow prevents it from accumulating into a large vortex that becomes unstable in two-dimensional [2,8,37]. The spanwise pressure gradient necessary to drive the spanwise flow is, by definition, absent in two-dimensional flapping foil studies [2]. Our results clearly show the existence of the spanwise flow near the LEV at both low and high St (see the electronic supplementary material, figure S12) similar to those observed in three-dimensional insect flows. The magnitude of the spanwise flow has the same order as the swimming velocity (see the electronic supplementary material, figure S12). However, the simulations presented here cannot

![Figure 4. The leading edge vortex on the rectangular tail in the inertial regime (St ~ 0.25) is visualized using streamlines coloured by vorticity magnitude, which demonstrates that the fish-like kinematics without the delta shape is capable of stabilizing the LEV. (Online version in colour.)](http://rspb.royalsocietypublishing.org/)
fully demonstrate the mechanisms for the stability of the LEV and the creation of the spanwise flow, because pressure gradients, rotational acceleration and centrifugalumping forces are all present [2,4,37].

We believe the difference between the stable and detached LEV in the inertial and transitional regime is owing to the Strouhal number difference in these two regimes. Based on definition, Str is a measure of lateral velocity to the axial (swimming) velocity $U_l$. In fact, at $St = 0.25$, the maximum lateral velocity is $0.5826U_l$, whereas at $St = 0.6$, it is $1.3982U_l$. The higher lateral velocity increases the angle of attack of the tail as well (see the electronic supplementary material, figure A2). The higher angle of attack and lateral velocity creates a stronger LEV, which needs to be stabilized by the spanwise flow (root to tip) convecting vorticity out of the LEV [4,8]. As can be observed in the electronic supplementary material, figure S12, both low and high Str cases have a similar spanwise flow (same order of magnitude as swimming (axial) velocity), i.e. at low $St$, the spanwise flow magnitude is enough to stabilize the LEV (see the electronic supplementary material, figures S4 and S6), but at high $St$, the vortex grows and moves away from the leading edge (see the electronic supplementary material, figure S5 and S7).

The plunging motion (without rotational acceleration) [38] for low sweepback tails was found to be insufficient to stabilize the LEV, but the plunging motion for the high sweepback tail stabilized the LEV. Nevertheless, we showed that the delta shape is not the driving force behind the LEV generation here because it was present in the rectangular tail flow field as well (figure 4), i.e. the tail kinematics can produce a stable leading edge without the delta shape. This is, to our knowledge, the first time that the LEV has been observed in fish-like swimming. Considering the significance of the LEV in force production, our results suggest a paradigm shift in flow visualization near fish tails to focus the attention from the trailing edge to the leading edge.

Finally, we have to mention that in this work we have not considered the dorsoventral (top-bottom) asymmetry in the motion of the tail, which has been observed in fishes [39,40]. The dorsoventral asymmetry in the fish tail is active because it bends against the tail motion, i.e. it is not just bending out of the way [39]. We hypothesize that such dorsoventral asymmetry might be related to the formation of the LEV on the tail, which will be investigated further in future work.

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References

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