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In the wake of the fish

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CHAPTER 7

Conclusions and summary

Ulrike K. Müller

The objective of this thesis was to examine the interaction between fish and water. Fish respond to the physical constraints imposed by the water onto their swimming performance. The physical constraints are not uniform throughout the life history of fish, but change from predominantly viscous effects in the larval stage to constraints imposed by inertial forces as the fish grows into an adult. Larvae of several fish species exhibit an allometric growth pattern in response to the changing flow regime. They enhance their length growth to escape the viscous drag and reach high Reynolds numbers (**Chapter 2, table 1**). The more immediate effects of the fish-water interaction become obvious in the wake shed by a swimming fish. Fish larva swimming in the low and intermediate flow regime produce typical viscous flow patterns similar to the wake of a bluff body at low Reynolds numbers (**Chapter 3, figures 2 and 4**). This flow pattern never occurs in adult fish performing an identical swimming manoeuvre (**Chapter 3, figures 3 and 5**). Adult fish exhibit different swimming styles, all generating a characteristic wake. Burst and glide swimming generates a start and a stop vortex system during the one tail flick of the burst phase (**Chapter 3, figures 2 and 3**). The wake during steady swimming depends on the shape of the body wave amplitude. Mullet with its curvilinearly increasing amplitude envelope sheds a double row of single vortices

with a undulating backward jet in-between (Chapter 4, figure 5). Eel with its almost linearly increasing body wave amplitude shed a double row of vortex pairs with no discernible backward flow in the wake (Chapter 6, figure 8). The wake shape is also influenced by the ratio of swimming speed U to wave speed V . For U/V ratio below 1, mullet sheds a double row of alternating vortices with an undulating, backward jet. At a U/V of 1, it sheds a single row of vortices with jets perpendicular to the mean path of motion (Chapter 5, figure 6).

Influence of viscous flow regime

Effects on the ontogeny of fish. Some fish larvae respond to the intermediate Reynolds number regime not simply by trying to optimally adapt their swimming behaviour to suit the viscous effects. 12 species from three families enhance their length growth, thereby increasing the Reynolds number to values where inertial effects are dominant. All four Clupeiformes species examined conform to this safe harbour hypothesis. For the four species studied of the Gadiformes and seven further Pleuronectiformes and Perciformes species, no conclusive evidence for such an adaptive growth pattern could be found.

Effects on the swimming of fish larvae. Zebra danio larvae swim in a burst and glide style. During the burst as well as the gliding phase, the flow field generated by a 4 mm larva shows clear viscous effects. In the burst and well as in the gliding phase flow field, the high viscosity of the water causes rotational flows adjacent to the larva's body. These rotational flows represent the huge body of water dragged along by the larva and stop the larva almost immediately after the thrust generation ceases. Those rotational flows are absent in adult zebra danios performing a comparable swimming manoeuvre. A second effect of the high viscosity concerns the shape of the start and the stop vortex shed by a tail flick during the burst phase. Larval vortices have a much larger core relative to the size of the vortex structure: the ratio of core radius to ring radius is 0.5 or higher in larvae, in adult fish it is between 0.14 and 0.19. The angular velocity of the core is also lower in larvae than in adults resulting in a lower circulation of the vortex. The relatively large vortex cores together with low circulation reduce the hydrodynamic efficiency of a larval tail flick (30%) considerably compared to the adult fish (above 90%).

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Hydrodynamics of unsteady undulatory swimming

Fish swimming in a burst and glide mode initiate a swimming bout with a single tail flick followed by a gliding period. During the gliding period, the body is usually kept straight to fully exploit the lower drag value of a straight as opposed to an undulating body. The tail flick generates a start and a stop vortex. The two vortices are separated by a jet with a flow direction away from the fish. This wake pattern can be observed in fish larvae at Reynolds numbers below 100 as well as in adult fish at Reynolds numbers above 1000. The wake of larval and adult zebra danios differs not so much in the positioning of the vortices and the jet as in the structure of the vortex itself. Adapting a method developed for bird flow fields (Spedding *et al.* 1984), I obtained estimates for the thrust and the hydrodynamic efficiency from the circulation and the geometry of the vortex structure. The thrust values are in the order of magnitude of 0.1 mW for adult fish of 35 mm body length. In larval fish of 3 to 4 mm body length, the thrust is 3 orders of magnitude smaller.

Hydrodynamics of steady undulatory swimming

Flow generation and body wave geometry

The swimming fish generates water flows adjacent to its body. The lateral movements of the undulating body create a succession of suction and pressure flows in the concave and convex bends of the body. The flow velocities in those suction and pressure zones increase posteriorly with the increasing amplitude of the lateral undulations (Chapter 4, figure 4 and chapter 6, figure 3).

In a mullet with its curvilinearly increasing body wave amplitude, the flow velocities increase curvilinearly with the steepest increase at the tail where the body wave amplitude increases significantly. Due to the considerable width of the mullet's body relative to the body wave amplitude, particularly in the first body half, there is much less lateral movement on the pressure side, the body contour does not significantly exceed the head contour (Chapter 4, figure 7). As a consequence, the pressure flows on the convex body side are much weaker than the suction flows on the concave body side (Chapter 5, figure 8). In eel with its almost linear amplitude increase and much larger body wave amplitude relative to the width of its body, the flow velocities in the pressure and suction zones increase linearly and are not very different (Chapter 6, figure 4).

The increasing body wave amplitude creates a rotational movement of the body around its inflexion points that entrains the adjacent fluid (**Chapter 4, figure 4 and chapter 6, figure 3**). The inflexion point forms the centre of a bound vortex formed of the suction and of the pressure flow in front and behind the inflexion point. When the inflexion point reaches the tail, this bound vortex is shed.

Vortex position and body wave geometry

The wake behind a steady undulatory swimmer is the product of the circulatory flows generated by the body and by the tail. The body creates a circulating flow around the inflexion point of the midline. The tail acts as a hydrofoil creating a circulatory flow around the tail blade. These two circulatory flows can add up to form a single vortex or they can be shed as separate vortices depending on the relationship between the tail beat cycle and the inflexion point position. The whereabouts of the inflexion point itself depend on the geometry of the body wave, in particular on the amplitude envelope.

The most simple body wave would be a pure sine wave with a constant amplitude from head to tail. For this case, the wave of lateral displacement and its second derivative are in phase. This means that the point where the midline crosses the mean path of motion coincides with the inflexion point of the midline along the whole body. The inflexion point would travel down the body along the mean path of motion. Any circulation building up around it would be shed as a vortex with its centre at the mean path of motion. The same applies to a pure sine body wave with an exponentially increasing amplitude envelope. Crossing point and inflexion point are in phase, the flow around the inflexion point is shed on the mean path of motion. Any other amplitude envelope causes a phase shift between the crossing point and the inflexion point. This phase shift can be constant along the whole body like in eel (**chapter 6**), large mouth bass *Micropterus salmoides* (Jayne and Lauder, 1995), and the salamander *Siren intermedia* (Gillis, 1997). The phase shift can increase from head to tail like in mullet (**Chapter 5, figure 9**) and mackerel (Katz and Shadwick, submitted).

In this study, mullet and eel were chosen as exemplary species of two rather different wave geometries. Mullet with its curvilinearly increasing amplitude exhibits a phase shift between crossing point and inflexion point that increases from head to tail (**Chapter 5, figure 9**). As a result, the inflexion point moves further and further

away from the mean path of motion as it travels down the body (Chapter 5, figure 5). It reaches the tail when the tail is in its most extreme lateral position. The rotational sense of the flow around the inflexion point and the flow around the tail blade have the same sense; they combine into a single vortex shed at a lateral position equivalent to the tail beat amplitude. After they have been shed, the vortices remain stationary in an earth-bound frame of reference. In-between the shed vortices forms an undulating jet with a flow direction opposite to the fish's swimming direction.

The almost linearly increasing amplitude envelope of the eel generates a different phase relationship between the crossing point and the inflexion point. The phase shift is constant and causes the inflexion point to travel down the body laterally offset from the mean path of motion (Chapter 6, figure 5). The posteriorly decreasing wave length of the body wave causes the inflexion point to cross the path of motion as it reaches the last third of the body. The inflexion point reaches the tail at a point when the tail has crossed the path of motion and moves towards its extreme lateral position. There, the rotating flow building up around the inflexion point is shed as a vortex. Shortly after the inflexion point vortex has been shed, the tail reaches its maximum lateral excursion and a start-stop vortex is shed. The two vortices are of opposite rotational sense and together form a vortex pair with a jet flow in-between. This jet flow is perpendicular to the path of motion. The vortex pairs move away from the path of motion as they die off.

Wake and thrust

The shape of the wake not only depends on the amplitude envelope, but also on the relationship between the swimming speed U of the fish and the wave speed V with which the body wave travels down the body. The ratio U/V is inversely proportional to the slip between the fish and the water, which itself is proportional to the thrust production of a fish. According to Newton's second law of motion, the fish must create backward momentum to gain equal forward momentum. As the slip and the thrust decrease, so should the backward momentum shed in the wake. This should affect the structure of the wake.

In mullet, U/V ratios between 0.7 and 1.0 are observed. The wake structure changes accordingly (Chapter 5, figure 6). At a U/V ratio of less than 1, the wake consists of a double row of vortices. In-between the vortices runs a backward, undulating jet representing the

backward momentum shed by the fish. The fish itself gains an equivalent forward momentum, it is producing thrust. At a U/V ratio of 1, the wake consists of a single row of vortices. The jet in-between the vortices is perpendicular to the mean path of motion, it has no backward momentum. The fish is neither gaining nor losing any momentum, it is free-wheeling.

In eel, only sequences with U/V ratios below 1 were recorded. Due to the linearly increasing amplitude envelope, eel is generating a very different wake from mullet (**Chapter 6, figure 8**). In all recorded sequences, the wake consisted of a double row of vortex pairs. The jet in-between the two vortices of a pair is perpendicular to the path of motion. No backward jet is visible in the wake. Even at U/V ratios of 0.7, the wake behind an eel does not contain any discernible backward momentum. Only the change in the mean velocity vector of the total visible flow field shows that the fish is indeed producing a backward momentum in the flow. In the wake of an eel, there is no feature representing the backward momentum like the undulating jet in the wake of a mullet.

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