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Modelling the hydrodynamics of swimming fish, from individuals to infinite schools

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INTRODUCTION

The swimming of fish has fascinated humans for ages. The underwater environment, a dense, viscous liquid, is almost entirely alien to ours. Fish propel themselves through it, almost weightless due to their buoyancy. The seemingly effortless ease with which they do so has inspired scientists and engineers, who have spent much time attempting to understand the mechanics of fish propulsion (Gray, 1933; Lighthill, 1960, 1971; Triantafyllou et al., 1993; Barrett and Triantafyllou, 1995). Vertebrate life originated in the ocean, with the first undulatory swimmers such as jawless fish similar to lampreys. Given the long evolutionary history of undulatory swimming, it is reasonable to expect it to be an optimal mode of propulsion. However, which aspect of swimming is optimised, be it speed, manoeuvrability, efficiency, stealth to predators or cost of “construction,” remains to be determined.

The majority of species of fish spend some stage of their development in a group of some kind, ranging from drifting clouds of larvae to travelling schools of millions of adults. Living in groups is theorised to have all sorts of advantages, including protection from predators, increased access to mates and greater foraging efficiency (Krause and Ruxton, 2002). A further supposed benefit (and the focus of this thesis) is increased hydrodynamical efficiency.

1.1 EMPIRICAL STUDY OF FISH SWIMMING

Here is presented a brief overview of the history of the empirical study of fish swimming - (for a more thorough overview, see Videler (1993) and Drucker and Summers (2007)).

The earliest scientific discussion of fish swimming comes from Aristotle, who noted the morphological variety across species in number of fins, and argued that many-finned fish (i.e.. possessing paired pectoral and pelvic fins) should propel themselves by flapping their fins, while those with fewer fins should do so through undulating their body. As was the case for many other subjects, Aristotle’s ideas on fish swimming remained unquestioned through the middle ages, until Giovanni Borelli in 1680 published *On the Movement of Animals*, a groundbreaking work on biomechanics. He noted that, since the majority of the muscles of fish are found aligned with the spine in the body rather than attached to the fins, it is much more likely that it is the undulating body that does the work when fish swim. These matters rested until the invention of the ciné camera.

The modern study of the swimming of fish through the use of films was spearheaded by the work of Gray (1933). Especially important were his attempts to calculate the forces of swimming such as forwards thrust and rearwards drag from the movements of the fish. These calculations and experiments underlie much of the theory of fish hydrodynamics

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of the twentieth century (Lighthill, 1960; Wu, 1961). The most well-known outcome of his work is ‘Gray’s paradox,’ which states that (according to his calculations) dolphins can not produce enough thrust to reach the high speeds at which they swim. This led to the idea that something about undulatory swimming made it extremely efficient, greatly increasing the research on it (Fish, 2006). The paradox was only solved recently, by using the modern Digital Particle Image Velocimetry technique to map the flow around the tail of the dolphin, demonstrating that the force it generates is well in excess of that predicted by Gray (Wei et al., 2008).

The Digital Particle Image Velocimetry technique came into use in 1993, and has greatly improved our understanding of biohydrodynamics. It involves seeding the water with neutrally buoyant particles, and shining a flat sheet of laser light through the area where the flow is of interest. Subsequently, digitised high-speed video of the movement of the particles is analysed, resulting in a two-dimensional vector flow field that is a cross-section of the three-dimensional flow. The technique has been applied over a wide range of scales, from tiny (for example copepods (van Duren et al., 2003)) to large (for example eels (Tytell, 2007)). From these flow fields, inferences can be made about the power and efficiency of swimming (Müller et al., 1997; Tytell and Lauder, 2004). It should be noted however that, as pointed out by Dabiri (2005), for accurate estimations of the forces of swimming and thus the efficiency, the pressure field should also be measured, which is currently not possible.

In this thesis we study fish kinematics only in terms of the undulatory wave that passes rearwards through their body. Of this wave the characteristic length, frequency and amplitude (measured at the tail tip) are most frequently reported. Especially the tailbeat frequency is seen as important, and has been shown to be a major factor in what causes the swimming speed of fish (Bainbridge, 1958; Webb et al., 1984). Rarer are reports of how the amplitude of undulation varies along the body. Using Fourier analysis of digitised films of fish, Videler and Hess showed that the undulation can be described by a multiplication of a sine function that varies with time, and an “envelope” function that varies with the position along the body (Videler and Hess, 1984). This envelope function differs greatly among species. For example, for saithe it is quadratic, with the point on the body of lowest lateral movement behind the head, at approximately 25% of the body length. In contrast, for eels the envelope function is exponential, with a minimum at the head (Gillis, 1998; Tytell and Lauder, 2004) (Fig. 1.1).

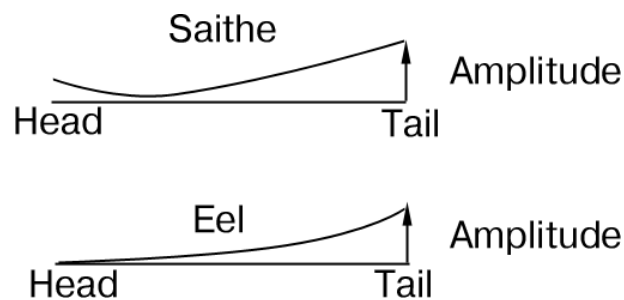


Figure 1.1.: Amplitude envelope functions of saithe and eel.

An important number when discussing hydrodynamical systems is the Reynolds number, which describes the relative importance of inertial and viscous forces, with higher Re indicating higher inertia. It is given by $Re = UL/\nu$, where U is the speed, L is the characteristic size (usually length when discussing fish) and ν is the kinematic viscosity of the fluid.

The most recent thorough overview of how the kinematics of fish swimming are interrelated, as well as their effect on swimming speed, is in John Videler's *Fish Swimming* (Videler, 1993). Since then, much experimental work has been done, but an integration of these results is lacking. We attempt to do so in the final chapter of this thesis.

1.2 THEORETICAL STUDY OF FISH SWIMMING

The swimming of fishes has been studied in models in many different ways, from single fish to groups, from detailed kinematics of individual fish to groups of travelling point particles. However, there is very little work that combines group dynamics with a somewhat realistic embodiment or 'situatedness' of the individuals, for example as regards their mass, size, shape or hydro/aerodynamics. This is unfortunate, because such embodiment strongly affects the mechanics of a system (Pfeifer and Scheier, 1999). For example, realistic flocking behaviour of starlings in a model was only achieved once the individuals were made to follow simple rules of aerodynamics (Hildenbrandt et al., 2010). In this thesis, rather than attempting to add hydrodynamics to already-existing models of flocking, we start with the modelling of hydrodynamics.

Modelling the hydrodynamics of swimming fish greatly improved in the last half century or so, most notably by Sir James Lighthill's Elongated Body Theory (Lighthill, 1960, 1971). This influential theory formed the basis for many experiments as well as calculations based on those experiments, for example to estimate the efficiency. The theory does not take viscosity into account however, and its predictions are largely qualitative.

Since the middle of the 1990s, computational power has advanced sufficiently to allow computer simulations of hydrodynamics on a scale that is sufficient to model fish swimming in detail as regards their complex shape and undulation. The first work of interest was that by Liu et al., who studied the swimming of a tadpole and fish in a computational fluid dynamics model (Liu et al., 1996, 1997). Their work shows the power of simulations to not only allow the study the flow and forces on the swimmers, but also to test several unrealistic situations, for example to make a fish undulate like a tadpole and vice versa. Liu et al. indicated that the swimming mode of the tadpole was uniquely suited to its shape and developmental history: its efficiency and flow field were unaffected by the addition of leg-like stumps, whereas a regular fish suffered greatly reduced efficiency and speed when leg-like stumps were added to it, or when it was made to undulate like the tadpole. Further interesting computational work on the hydrodynamics of swimming is that of Kern & Koumoutsakos who investigated the differences between 2- and 3-dimensional simulations of swimming fish (Kern and Koumoutsakos, 2006). Their results show that simulations in 2 dimensions, while differing in several aspects from the 3-dimensional ones, greatly resemble the experimental results of real fish. Also of great importance is the recent work by Borazjani and Sotiropoulos, whose simulations of swimming lampreys and mackerels

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clearly demonstrate the importance of both kinematics and body shape to the efficiency of swimming fish (Borazjani and Sotiropoulos, 2008, 2009, 2010).

1.3 EMPIRICAL STUDY OF FLOW EXPLOITATION

The previous sections addressed the study of single fish in uniform flows. Here we discuss the available empirical evidence that indicates whether and how fish in schools might exploit the wakes of others. There are several indications that they do so. In short, first, fish can sense flows in great detail, second, fish can exploit flows to reduce swimming effort, and third, schools of fish as a whole are more efficient than single fish.

Just as we can feel the strength and direction of a breeze, fish can sense the flows of water. They can do so with great sensitivity and precision, due to a specialised system of sensors, much of which is concentrated (in most fish) in a thin groove along the length of the body, commonly called the lateral line. Through the lateral line fish can sense not only the direction of flows, but also (within a certain distance) their precise point of origin in space (Engelmann et al., 2000). This sensitivity is applied to several purposes. For instance, catfish can track their prey by following their wake (Pohlmann et al., 2001). The lateral line also plays an important part in schooling, as was elegantly shown in a series of experiments by Partridge and Pitcher (1980), who found that blindfolded fish with an intact lateral line could still school, and that fish with intact vision but disabled lateral lines took up different positions relative to their neighbours than entirely intact fish. The lateral line also plays a role in the exploitation of wakes. Rainbow trout whose lateral line was disabled spent much less time in the wake of a cylinder than intact ones did, and were much less likely to display the characteristic wake-exploiting gait reported by Liao et al. (2003b); Liao (2006).

This brings us to the point that fish have clearly been shown to exploit wakes, specifically those of cylinders. The downstream wake of a cylinder in flow at medium to high Reynolds number consists of a series of vortices that are shed alternately from the sides of the cylinder, with an area of low velocity zig-zagging between them. This is known as a von Kármán vortex street. Rainbow trout in a flow tank exploited the vortex wake of a cylinder by adopting a unique gait, slaloming between the vortices and moving from side to side much more than they did when swimming outside of the wake. From measurements of the muscle activity of the fish it became clear that this gait in the wake greatly reduced the effort the fish expended to stay in place (Liao et al., 2003b,a). Interestingly, later experiments showed that this reduction in effort may arise passively. When tethered behind the cylinder, a dead (but still flexible) fish would undulate and move upstream due to the buffeting of the vortex wake (Beal et al., 2006).

Fish also exploit the wakes of others when travelling in schools, as shown by experimental evidence dating back to as far as the 1960s (Belyayev and Zuyev, 1969). Fish were shown to decrease their oxygen consumption when swimming in schools, and fish at the rear of the school appeared to have lower tailbeat frequency, which may indicate that they spend less effort (Herskin and Steffensen, 1998). Further, it was demonstrated that fish preferred specific distances to one another, indicating that some positions are better than others (Svendsen et al., 2003). None of these experiments has shown exactly *how* the fish are improving their efficiency, however. For example, no experimental evidence has supported the rigid spatial

structure which is theoretically optimal (Partridge and Pitcher, 1979; Abrahams and Colgan, 1985). The theory of wake exploitation is further outlined below.

1.4 THEORY OF FLOW EXPLOITATION

Regarding the hydrodynamical efficiency of schooling, Weihs has made several predictions, however this theory of hydrodynamics ignores viscosity and the shape of the body of the fish (Weihs, 1973). His first prediction was that for optimal efficiency groups of fish should adopt regular, fixed positions relative to one another, in horizontal, two-dimensional layers. Within these layers, individuals should swim in staggered rows, resulting in diamond-like lattices (Fig. 1.2). The lateral distance between neighbours should be approximately two times the width of their wake, and the longitudinal distance between rows (measured from tail to nose) should be at least 0.7 fish lengths. The second prediction was that lateral neighbours increase an individual's efficiency, and the third that in the diamond lattice structure, lateral neighbours should beat their tails in antiphase to one another (Weihs, 1973, 1975).

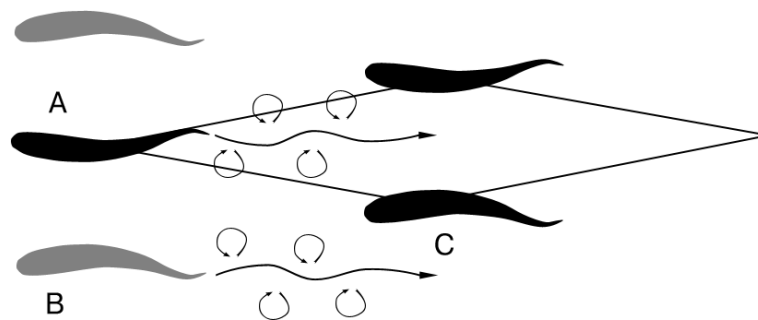


Figure 1.2.: Diamond-shaped spatial structure as predicted to be optimal by Weihs. Lateral neighbours A and C are undulating in antiphase, and trailing fish B is profiting from the area of low velocity between their wakes.

Only very recently have computers become powerful enough to model the hydrodynamics of multiple, undulating fish. To date only a few theoretical studies have investigated hydrodynamical interactions between swimming fish. The two most relevant ones to this thesis were first, a single fish swimming between the wakes of two predecessors (Deng and Shao, 2006) and second, an infinitely wide phalanx of side-by-side fish (Dong and Lu, 2007). Unfortunately, both studies were unbiological as regards either their parametrisation (Deng and Shao, 2006) or the constant, fixed speed of the individuals (Dong and Lu, 2007), making the value of their results unclear. That said, an increase in efficiency was found in both studies: in the case of three fish the third, trailing fish was more efficient and needed to beat its tail less widely, and the fish in an infinite phalanx saved power if they were swimming in phase (Dong and Lu, 2007). Of course, neither a phalanx nor a group of three fish are a test of the predictions of a diamond structure. This thesis aims to be the first true test.

1.5 COMPUTER SIMULATIONS OF HYDRODYNAMICS

Hydrodynamics is described by the Navier-Stokes equations. However, no general solution to these equations exists, and therefore all methods simulating hydrodynamics involve discretisation of time and space in some way. Computer models of hydrodynamics can be roughly divided into two categories based on their methods of discretisation, namely numerical and particle-based simulations. Below they are both briefly described, followed by a description of the method used for our simulations (Multiparticle Collision Dynamics), as well as the reasons why we chose this particular method.

The numerical models solve the Navier-Stokes equations by discretising them onto a spatial grid. It is necessary for such methods to adapt the grid to the shape of whatever object or organism is being simulated (Fig. 1.3). If the object is moving or deforming (as in the case of an undulating fish) the grid needs to be re-adapted frequently, which is a process that is both complex and computationally demanding.

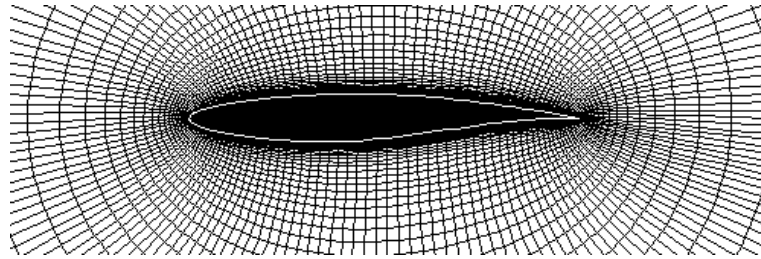


Figure 1.3.: Example of a grid around an airfoil shape, to be used in a numerical simulation of hydrodynamics around it. Note that the grid would need to be entirely recalculated if the airfoil changed shape or position.

The particle-based methods on the other hand discretise hydrodynamics into particles that move and collide. These particles represent small quantities of fluid. This coarse-graining leads to the common term of 'meso-scale' modelling, with its scale lying between the micro-scale of molecules and the macro-scale of hydrodynamical phenomena such as vortices. From the interactions between particles at the meso-scale, hydrodynamics according to the Navier-Stokes equations emerge at the macro-scale. The particles may be restricted to a grid, such as in the commonly-used Lattice Boltzmann method (Sui et al., 2007), or move freely as in several other methods (Monaghan, 1992; Kajtar and Monaghan, 2008; Malevanets and Kapral, 1998). In case they move freely, the interactions among particles may be smoothed over longer ranges, such as in the Smoothed Particle Hydrodynamics method (Monaghan, 1992; Kajtar and Monaghan, 2008), or be more local, as in the Multiparticle Collision Dynamics method (Malevanets and Kapral, 1998).

For our simulations of swimming fish we chose to use the Multiparticle Collision Dynamics method. It is a relatively new method, being introduced in the late 1990s. It has been shown to produce hydrodynamics consistent with the Navier-Stokes equations, and numerical expressions for several of its properties such as viscosity and transport coefficients have been

found (Malevanets and Kapral, 1999; Kikuchi et al., 2003; Padding and Louis, 2006). We thus regard the method as reliable and well-understood.

We chose to use the Multiparticle Collision Dynamics method because it has several advantages. Most importantly, the representation of space is continuous, meaning that there is no grid. Therefore smooth, organic shapes (such as of a fish) can be represented in the model. Further, the interaction of the fluid with the fish can be modelled relatively simply through collisions between the fluid particles and the body, in contrast with numerical simulations where special border conditions are required for example at the sharp trailing edges of a fish tail. Another advantage is that the method is computationally very efficient. This efficiency is further increased because the short range of interactions between particles makes the method ideally suited for parallelisation. Therefore we could use the graphics processor of modern graphics cards for much of the fluid-dynamical calculations, which increased the simulation speed by a factor of 10.

1.6 WORK PRESENTED IN THIS THESIS

The aim of this thesis is to increase the understanding the swimming of fish, both singly and in groups. We do so through computer modelling and a meta-analysis of experimental literature.

Our modelling work is presented in chapters 2-4. They proceed in logical order from least to most complex, each representing a step in the implementation process and its careful testing. In chapter 2, we validate our implementation of the Multiparticle Collision Dynamics model for the classic cases of flow past a static square and circular cylinder. Further, we study more complex, biological shapes, including a fish and tadpole (both with and without leg-like growths) and several cylinder shapes with trailing thin plates. We show that the trailing plates increase drag at low Reynolds numbers but decrease drag at higher ones by increasing the suppressing vortex shedding. In chapter 3, we extend the model with moving shapes that change their orientation, position and shape. We validate the model as regards changing orientation and position by comparing the forces of a flapping cross-section of an insect wing in our model against those of both an empirical and a numerically-simulated one. We subsequently simulate undulating fish, measuring their speed, efficiency and forces of thrust and drag for several Reynolds numbers. Our results show that the common practise in simulations to constrain the fish to not accelerate laterally skews the results to resemble those of free fish with a higher tail beat frequency. Finally, in chapter 4, we simulate infinitely-large schools of undulating fish (similar to those of chapter 3) in several different spatial configurations. The spatial configurations we study are the diamond-shaped lattice that Weihs predicted to be optimal (Weihs, 1973) and a rectangular lattice. Further, in order to investigate the effects of longitudinal and lateral neighbours separately we simulate an infinitely long progression, or 'line' and an infinitely wide 'phalanx'. Our results show that swimming directly behind a fish in its undisturbed wake is beneficial as regards speed and efficiency in most cases. Besides, we confirm Weihs' predictions that having lateral neighbours is beneficial for efficiency, and that a closely-spaced diamond lattice causes individuals to encounter a low-velocity area ahead of them. However, his prediction that this would increase efficiency is not borne out by our results.

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We expand on the insights gained from our simulation studies by means of a meta-analysis of the scientific literature on steady swimming. The size of our data set results in several new significant insights. Most importantly, we show that the strongest predictor of swimming speed is the speed of the body wave. Further insights include the fact that the slip ratio U/V is a function of the Reynolds number (which is also the case in our model).