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Swimming of Fish

Seminar

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Abstract

This paper presents general considerations of swimming at large Reynolds numbers and outlines some of the theories involved in its description. Great majority of fishes use their tail fin as the main means of propulsion; this mode of swimming is explained in Lighthill's theory of slender fish. Recent experimental research and numerical simulations have provided vorticity models, which can help explain their observed efficiency and maneuvering capabilities. Finally, drag reduction mechanisms of dolphins are considered, especially the reported beneficial effect of flaking of the upper layers of their skin.

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1 Introduction

Scientists and engineers have long been impressed with the swimming speed and agility of fish and aquatic mammals. These animals' locomotion offers a different paradigm of propulsion than utilized in human-engineered vehicles, employing a rhythmic unsteady motion of the body and fins. Research suggests that this kind of motion may be utilized to achieve high propulsive efficiency and even to reduce hydrodynamic drag.

Natural selection has ensured that the mechanical systems evolved in fish, although not necessarily optimal, are highly efficient with regard to the habitat and mode of life for each species. Their often remarkable abilities could inspire innovative designs to improve the ways that man-made systems operate and interact with the aquatic environment. An example application that could substantially benefit are autonomous underwater vehicles (AUV's) [1]. As research and use of AUV's are expanding, there is increased demand for improved efficiency to allow for longer missions to be undertaken. The highly efficient swimming mechanisms of some fish can potentially provide inspiration for a design of propulsors that will outperform the thrusters currently in use. Existing systems are also insufficient when it comes to maneuvering and dextrous manipulation, and coarse compared to the abilities of fish. The advantages of noiseless propulsion and a less conspicuous wake could be of additional significance, particularly for military applications.

High-efficiency and high-performance aquatic locomotion depends highly on the external morphology and the propulsive movement pattern adopted by swimming animals. It is, therefore, not unexpected that analysis of natural swimming is, from the standpoint of classical fluid mechanics, a difficult subject. Typically the geometry is complicated, the flow field highly nonstationary, the Reynolds numbers range awkward.

Analytical theories and calculations have provided some insight into the subject and give us an estimation of hydrodynamic characteristics of swimming fish. A more complete description (and sometimes understanding) can be obtained by experimental observations of live fishes and models (especially by means of particle image velocimetry – PIV), and by detailed, computationally intensive numerical simulations.

1.1 Fish Anatomy

To aid in the description of the fish swimming mechanisms, Figure 1 illustrates the terminology used to identify morphological features of fish, as it is most commonly found in literature and used throughout this text. The fin dimensions normal and parallel to the water flow are called span and chord, respectively.

1.2 Forces Acting on a Swimming Fish

Swimming involves the transfer of momentum from the fish to the surrounding water (and vice versa) [2]. The main momentum transfer mechanisms are via drag, lift, and acceleration reaction forces. Swimming drag consists of the following components:

- skin friction between the fish and the boundary layer of water (viscous or friction drag): Friction drag arises as a result of the viscosity of water in areas of flow with large velocity gradients. Friction drag depends on the wetted area and swimming speed of the fish, as well as the nature of the boundary layer flow.
- pressures formed in pushing water aside for the fish to pass (form drag). Form drag is caused by the distortion of flow around solid bodies and depends on their shape. Most of the fast-cruising fish have well streamlined bodies to significantly reduce form drag.

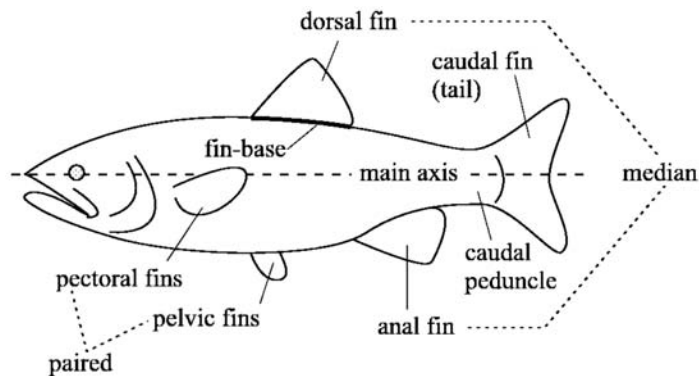


Figure 1: Terminology used in the literature to identify fins and other features of fish [2].

- energy lost in the vortices formed by the caudal and pectoral fins as they generate lift or thrust (vortex or induced drag): Induced drag depends largely on the shape of these fins.

The latter two components are jointly described as pressure drag.

Like pressure drag, lift forces originate from water viscosity and are caused by asymmetries in the flow. As fluid moves past an object, the pattern of flow may be such that the pressure on one lateral side is greater than that on the opposite. Lift is then exerted on the object in a direction perpendicular to the flow direction.

Acceleration reaction is an inertial force, generated by the resistance of the water surrounding a body or an appendage when the velocity of the latter relative to the water is changing. Acceleration reaction is more sensitive to size than is lift or drag velocity and is especially important during periods of unsteady flow and for time-dependent movements.

1.3 Main Classifications

Swimming locomotion has been classified into two generic categories on the basis of the movements' temporal features:

- 1 *Periodic swimming*, characterized by a cyclic repetition of the propulsive movements. Periodic swimming is employed by fish to cover relatively large distances at a more or less constant speed.
- 2 *Transient* movements that include rapid starts, escape maneuvers, and turns. Transient movements last milliseconds and are typically used for catching prey or avoiding predators.

Periodic swimming has traditionally been the center of scientific attention among biologists and physicists. This has mainly been because, compared to sustained swimming, experimental measurements of transient movements are difficult to set up, repeat, and verify. However, aspects of locomotion associated with transient movements are significant, as they provide fish with unique abilities in the aquatic environment.

Most fish generate thrust by bending their bodies into a backward-moving propulsive wave that extends to its caudal fin, a type of swimming classified under body and/or caudal fin (BCF) locomotion. Other fish have developed alternative swimming mechanisms that involve the use of their median and pectoral fins, termed median and/or paired fin (MPF) locomotion. Although the term paired refers to both the pectoral and

the pelvic fins (Fig. 1), the latter (despite providing versatility for stabilization and steering purposes) rarely contribute to forward propulsion and no particular locomotion mode is associated with them in the classifications found in literature. An estimated 15% of the fish families use non-BCF modes as their routine propulsive means, while a much greater number that typically rely on BCF modes for propulsion employ MPF modes for maneuvering and stabilization.

In BCF swimming modes, a propulsive wave traverses the fish body in a direction opposite to the overall movement and at a speed greater than the overall swimming speed. The four undulatory BCF locomotion modes identified in Fig. 2 reflect changes mainly in the wavelength and the amplitude envelope of the propulsive wave.

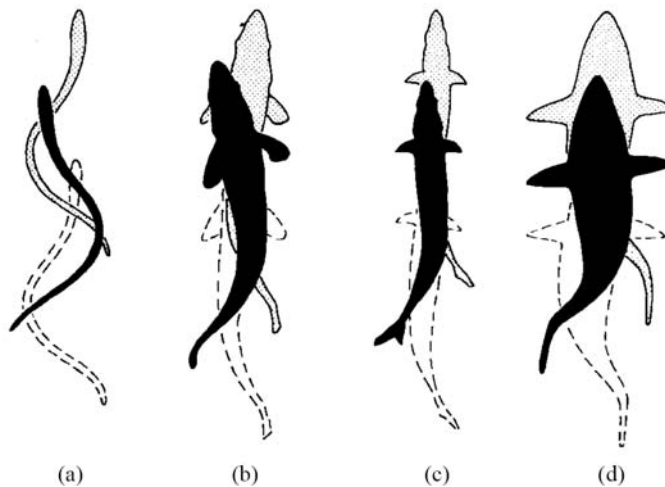


Figure 2: Gradation of BCF swimming movements from (a) anguilliform, through (b) subcarangiform and (c) carangiform to (d) thunniform mode [2].

2 Eulerian Swimming of Slender Fish

The Navier-Stokes equations present us with a rather simple dynamical balance in which pressure and viscous forces are balanced by the inertial forces associated with the acceleration of the fluid. With the typical velocity of the fluid U , length scale associated with fluid motions L and kinematic viscosity ν , we can define the *Reynolds number*

$$Re = UL/\nu, \quad (1)$$

which gives us an estimate of the ratio of inertial to viscous forces. The range of Reynolds number applicable to animal movements is enormous, ranging from $\sim 10^{-5}$ for bacteria to $\sim 10^5$ for some large fish.

It is important to distinguish the two extremes of small and large Reynolds number. Flows at small Reynolds numbers, also known as *Stokes flows*, are dominated by viscous forces and the inertia of the fluid is negligible. Motion at high Reynolds numbers dominated by inertial forces is known as *Eulerian* realm of locomotion.

Any neglect of viscous stresses implicitly assumes that the second derivatives of the velocity of the fluid \mathbf{u} are not so large as to prevent this neglect. If they are unbounded at some point, this may not be the appropriate limit, because $\nu \nabla^2 \mathbf{u}$ need not be small

locally irrespective of ν . Such singular behavior necessarily occurs near the boundary of a swimmer, where the *no-slip condition* applies even when viscosity is extremely small. We must therefore admit a boundary layer theory that complements the inviscid or perfect fluid limit $\nu = 0$.

2.1 Small-Perturbation Theory

Although there are certainly exceptions, many fish change shape rather gradually along the anterior-posterior axis. It is therefore natural to begin a study of fish swimming by considering a slender, neutrally buoyant organism [3]. The “slender” body, which will be described by this theory, should have the following properties:

- When “stretched straight” it is laterally symmetric. This is a property of most fish.
- With the exception of the vicinity of the nose and the downstream vertical edge of the caudal fin, the body is smooth and surface slopes are small.
- The cross-sectional area is zero at both ends, the downstream section being the edge of the caudal fin, hence a line segment, and the upstream section reducing to a point.

A fish is described by a function $h(x, t)$, which specifies the lateral distance of the fish’s outline from the symmetry plane along the main axis x . The small-amplitude approximation requires that

$$\left| \frac{\partial h}{\partial x} \right| \ll 1, \quad \left| \frac{\partial h}{\partial t} \right| \ll U \quad (2)$$

where U is the swimming speed (in the direction of negative x). In this regime the material derivative is simplified to

$$\frac{d}{dt} \simeq \frac{\partial}{\partial t} + U \frac{\partial}{\partial x} = D. \quad (3)$$

Using these assumptions *Lighthill* derived his small-amplitude theory. The derivation is based upon an insightful division of the calculation into two different evaluations of the same quantity, namely the rate of working of the fish’s body on the fluid \mathcal{W}_L . First, this quantity is calculated directly, utilizing only the definitions of apparent mass and rate of working. Then, the law of energy conservation is used to relate this rate of working to the whatever work is done by thrust and the creation of kinetic energy in the fluid. This brings the thrust T into the picture, all other quantities being directly computable from the motion of the body.

The resulting mean rate of working, expressed with $m(x)$, the apparent mass of a slice of the fish’s body and $w(x, t) = Dh(x, t)$, the material derivative of the lateral displacement, is

$$\langle \mathcal{W}_L \rangle = U \left\langle mw \frac{\partial h}{\partial t} \right\rangle_{x=L}. \quad (4)$$

and depends only on the conditions at the downstream edge of the moving body. The thrust is obtained from the mean rate of working in the form

$$\langle T \rangle = m(L) \left\langle w \frac{\partial h}{\partial t} - \frac{1}{2} w^2 \right\rangle_{x=L}. \quad (5)$$

This is an interesting result, because it implies that mean thrust, although it may be realized by adding pressure forces over the entire body, is fully determined by conditions

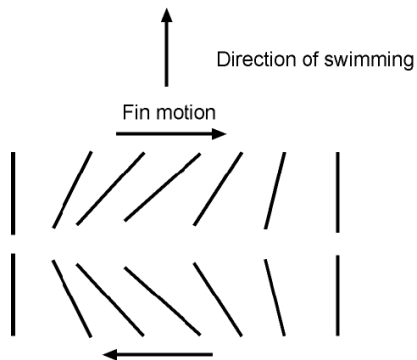


Figure 3: Efficient propulsion with a positive thrust requires that fin slope and speed reach a maximum simultaneously [3].

at the edge of the caudal fin. It is also intriguing biologically – the almost universal occurrence among fish of a well-developed caudal fin can be taken as evidence of its importance to propulsion.

Efficiency of propulsion is usually expressed as *Froude efficiency*

$$\eta = \frac{U \langle T \rangle}{\langle \mathcal{W}_L \rangle}, \quad (6)$$

which measures the rate at which mechanical power is transformed into thrust. In the finite-amplitude theory, using $W = \partial h / \partial t|_{x=L}$, this can be written as

$$\eta = 1 - \frac{1}{2} \frac{\langle w^2 \rangle}{\langle wW \rangle}. \quad (7)$$

An example of a waving plate, where $h(x, t) = h_0 \sin(kx - \omega t)$ gives the following expressions for thrust and efficiency:

$$\langle T \rangle = \frac{m(L)h_0^2 k^2}{4} (V^2 - U^2), \quad \eta = \frac{U + V}{2V}, \quad (8)$$

where $V = \omega/k$ is the wave speed. It can be seen that in order to achieve thrust the wave speed V must exceed swimming speed U , and that efficiency is a maximum at just that point $U = V$, where thrust vanishes.

Comparing equations (5) and (7) we see that in order to maintain positive thrust and reach high efficiency simultaneously, w and W should be positively correlated while w should be kept as small as possible. This correlation implies that fin slope $h_x(L, t)$ and $-h_t$ reach maxima and minima simultaneously (see Figure 3).

2.2 Finite-Amplitude Theory

Although the assumption of the slenderness is a natural one for the analysis of fish locomotion, the assumption of small perturbations is an ad hoc simplification which makes the problem linear [3]. It is possible to exploit the slenderness of the body in a nonlinear theory, where the geometry is allowed to depart substantially from the stretch-straight position. The results of the finite-amplitude theory allow us to study lateral forces as well as thrust and can be applied to such large-amplitude swimming

maneuvers as turning and starting, where the lateral velocity of the fin is comparable to the swimming velocity.

However, these results do not differ significantly from the small-amplitude approximation in their implications – mean thrust is still produced only by the downstream edge of the caudal fin, and in order to achieve maximum efficiency at high speeds, the fish should minimize lateral excursions, reducing the problem to small-amplitude swimming.

2.3 Thunniform swimming

The thunniform mode being a highly efficient method of swimming has attracted much recent interest, due to its potential for providing artificial systems with advanced propulsor designs. The benefits have already been demonstrated in the form of the RoboTuna robotic fish that was shaped after an actual tuna, for which mean propulsive efficiencies as high as 91% have been reported [2]. Its success spawned further work in the area of swimming robots. Work has also been directed at the prospect of applying oscillating foil propulsion to traditional sea-surface vessels.

Fish swimming in the thunniform mode are characterized by a stiff caudal fin, shaped like a tapered hydrofoil of a moderate sweepback angle with a curved leading edge and a sharp trailing edge (Fig. 4a). The caudal fin performs a combination of pitching and heaving motions, tracing an oscillating path as the fish moves forward. There are very small lateral movements of the body, mainly concentrated near the tail. Thrust is obtained by the lift force acting on the oscillating fin surface and by leading-edge suction, i.e. the action of the reduced pressure in the water moving around the rounded leading edge of the caudal fin. The developed thrust and the propulsive efficiency generally depend on the following parameters:

- 1 the aspect ratio (AR) of the caudal fin $AR = b^2/S_c$. High aspect ratio fins lead to improved efficiency, because they induce less drag per unit of lift or thrust produced. In thunniform swimmers, AR values range from 4.5 to about 7.2.
- 2 the shape of the caudal fin, as it is defined by the sweepback angle Λ and the curvature of its leading edge. A curved leading edge is beneficial, because it reduces the relative contribution of leadingedge suction to the total thrust, avoiding boundary layer separation for high thrust values.
- 3 the fin stiffness. The benefit of a higher degree of stiffness is increased thrust generation capability, with only a relatively small drop in efficiency.
- 4 the oscillatory motions of the fin. The optimal Strouhal number is in the range of $0.25 < St < 0.4$.

3 Vortex Manipulation

The wake left behind the tail of undulatory BCF swimmers is an array of trailing discrete vortices of alternating sign, generated as the caudal fin moves back and forth (Fig. 5b). Vortices in the wake have a reversed rotational direction compared to the well-documented *von Kármán vortex street*, which is observed in the wake of stationary objects such as cylinders or aerofoils (see Fig. 5a) [4]. A more detailed three-dimensional analysis reveals that the vorticity in the wake is actually concentrated in a series of strong counter-rotating elliptical vortices, linked together as vortex loops [5]. A schematic example is shown in Figure 6.

Although the generation mechanism of the vortices is still unclear, the observed phenomenon, named *reverse von Kármán street*, appears to be tightly associated with thrust generation. Research shows that a variety of fish and cetaceans swim with a

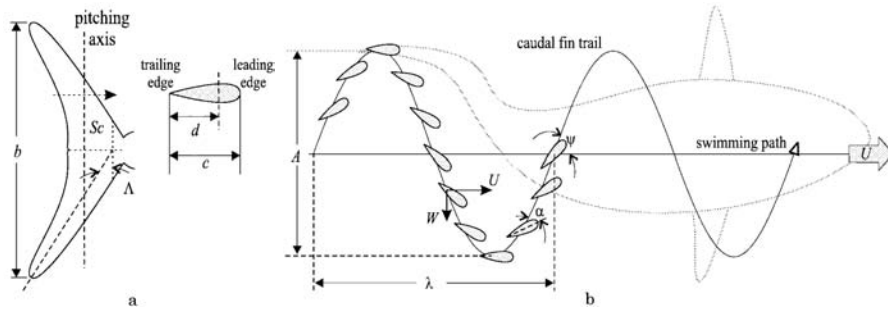


Figure 4: (a) Lateral view of caudal fin shape for thunniform swimmers, showing span b , chord c , pitching axis position d , sweepback angle Δ and surface area S_c . (b) Trail of an oscillating caudal fin showing amplitude A , wavelength λ , feather angle ψ , and attack angle α of the fin. [2]

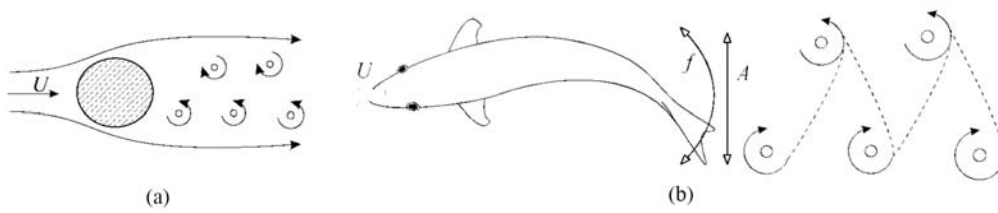


Figure 5: (a) The von Kármán street generates a drag force for bluff bodies, placed in a free stream. (b) The wake of a swimming fish has reverse rotational direction, associated with thrust generation. [2]

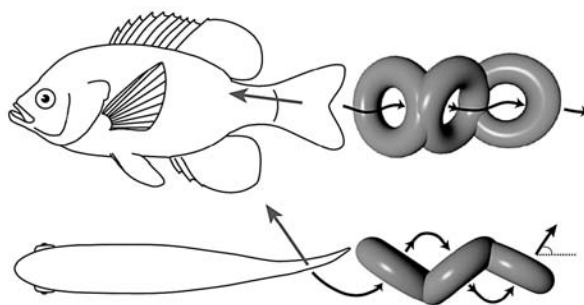


Figure 6: Lateral and dorsal views of sunfish swimming with the caudal fin, which generates a chain of linked vortex rings in the wake [6].

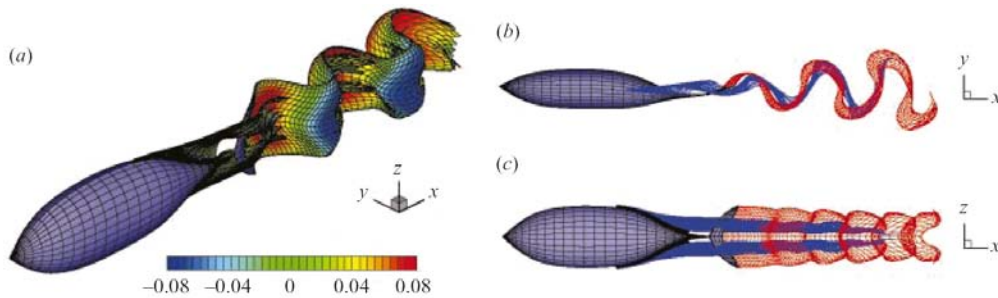


Figure 7: Formation of the wake sheets of a simulated straight-swimming tuna – (a) the wake sheets contoured by the distribution of dipole strength, (b) the top and (c) side views of the position of the wake sheets shed from the tail (red) and the dorsal/ventral median fins (blue) [8].

frequency and amplitude of tail motion that are within a narrow range of Strouhal numbers, minimizing energy lost in the wake for a given momentum and increasing efficiency. This Strouhal number range corresponds to the regime of maximum stability of the vortex wake [7].

Experimental studies and numerical simulations suggest that fish can actively manipulate vortices encountered in their environment or produced by themselves, to reduce energy losses in steady swimming, increase thrust when accelerating, and achieve high agility in maneuvering.

3.1 Steady Swimming

In steady swimming of real fish, flow around the body is not entirely laminar and vortices are not produced only at the edge of the caudal fin. Upstream vortices are created in front of the tail either from separation of the boundary layer (due to large variations of the body shape) or the sharp edges of secondary fins or finlets.

Research shows free vortices forming well ahead the tail and travelling along the body to reach the caudal fin, which manipulates them and re-positions them in the wake [8]. It has been demonstrated, that fish use two different modes of vorticity control in straight-line swimming to optimize performance by utilizing body-generated vortices.

The constructive mode employs a vortex reinforcement scheme, whereby the oncoming body-generated vortices are repositioned and then paired with tail-generated same-sign vortices, resulting in a strong reverse Kármán street, and hence increased thrust force (see Fig. 7).

The destructive mode, in contrast, employs a destructive interference scheme, whereby the body-generated vortices are repositioned and then paired with tail-generated opposite-sign vortices, resulting in a weakened reverse Kármán street, thus extracting energy from the oncoming body-shed vorticity and increasing swimming efficiency.

3.2 Turning and Fast Start

Fish are known to have outstanding capabilities for fast-starting and maneuvering. They can turn through 180° on a radius considerably less than their body length, whereas man-made underwater vehicles require several body lengths to execute a similar turn. Fast-starts – sudden accelerations from rest – are tightly associated with prey capture and escaping from predators. Some species of fish have been observed to reach accelerations as high as $25g$ [9].

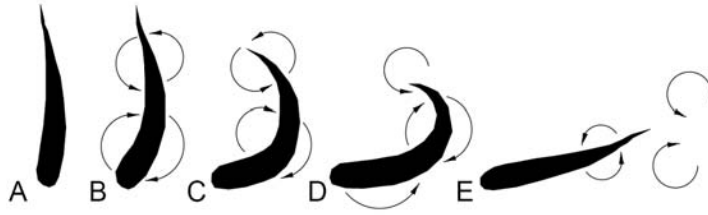


Figure 8: A model summarizing vorticity control mechanisms in a fish executing a 60° turn to its right [7].

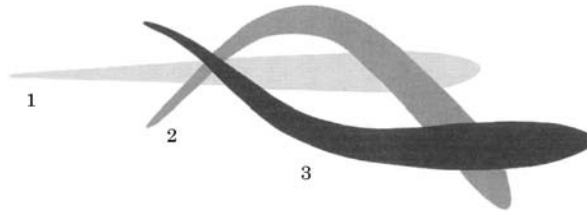


Figure 9: The stages of a fast-start acceleration: (1) a straight-stretched fish, (2) preparatory stage, the fish is bent into a C-shape and (3) propulsive stage with a powerful reverse stroke.

By examining the near-body flow and the wake produced by the turning motions of the fish, the concepts of vorticity shedding and manipulation by the tail can be extended to explain fish maneuvering performance [7]. The phases of turning are shown in Fig. 8, which also depicts vortices generated and manipulated in the process. The fish starts the turning by bending its backbone (Fig. 8B), which causes a pair of oppositely signed bound vortices to develop. They move closer to the tail as the fish bends into a tight 'C' shape (Fig. 8C). Straightening of the body starts as the counterclockwise vortex is released into the wake through manipulation of the caudal fin (Fig. 8D). Initiation of straight-line swimming completes the release of clockwise vorticity into the wake, as shown in Fig. 8E.

Fast-start acceleration of fish can be described using similar mechanisms. It consists of three phases (see Fig. 9): a *preparatory stage* in which the straight-stretched fish bends into a C or S shape, a *propulsive stage* in which the fish executes a reverse bend, and a variable stage, which may be a subsequent power stroke, steady swimming or unpowered coasting. Experimental simulations [9] also show that optimal acceleration depends on the resting time between the preparatory and propulsive stage (for the simulated tail, the delay was 0.9s) as well as on the flexibility of the caudal fin (fins with intermediate flexibility produce larger impulses than either stiff or very flexible tails). The vortices produced in the fast-start maneuver are similar to those seen in turning.

3.3 Swimming Upstream

Many fish exhibit distinct behavior in response to flow conditions generated by stationary objects in their environment. It has been shown that most fish, in the presence of objects that shed a drag wake consisting of alternating counter-rotating vortices (Kármán vortex street), synchronize their tail beat frequency and body kinematics to that of the vortices. They “slalom” between the vortices, exploiting their energy and thus minimizing their energy loss compared to swimming in steady flow [1].

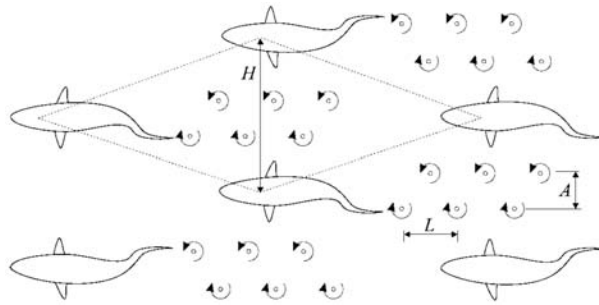


Figure 10: Plan view of a horizontal layer of a fish school, showing its diamond-shaped building block structure. The configuration is described by the wake width A , the vortex spacing L , and the lateral distance H amongst fish of the same column.

Similar effects can be observed in schools, where fish organize themselves in an elongated diamond-shaped pattern (Figure 10) to exploit each-other’s vortex wake. The advantage is greater when the fish in the same column swim in antiphase with the neighbors. Estimates show that schooling can save up to 20% of energy [2].

4 Drag Reduction

Studies of drag-reducing mechanisms were triggered by an influential analysis of swimming dolphins by Gray in 1936. Using reported speeds of dolphins and then-known estimates of muscle power, he estimated that the drag on a swimming dolphin must be several times lower than that on a towed rigid model of the dolphin body [10]. This finding, dubbed “Gray’s Paradox,” triggered numerous studies to determine swimming drag and a search for drag-reducing mechanisms. Although apparent inequalities between drag and muscle power were largely resolved by better data on speeds and muscle performance, Gray’s Paradox continues to be influential, stimulating searches for ways that fish might perform better than human vehicles.

4.1 Compliant Skin and Strata-Corneas Desquamation

Recent research in marine biology, naval engineering and fluid engineering has investigated the connection between drag reduction and the properties of dolphin’s skin. The soft skin on the ventral side of dolphins is compliant (elastic) and interacts with the surrounding turbulent flow, descending or ascending in response to the shear stress of the fluid. It is known that the upper layer of skin on a swimming dolphin produces new cells approximately every 2 h. During swimming, small pieces of skin peel off from the surface; the process is known as *strata-corneas desquamation*.

To investigate the effects of these properties, computer models were built that simulate how a dolphins skin interacts with turbulent water flow and how it flakes off [11]. The simulation was carried out for pulsating turbulent flow near the compliant wall with many models of beads and springs to represent the strata corneas separating from the dolphin surface. The results show that the undulating shape of the skin slightly reduces the drag. The flakes of skin shed by the dolphin increase the wall shear stress, because the flow is accelerated between the small separated pieces of skin and the wall. When the flakes move further away from the wall, they lower the drag significantly by reducing the number of vortices that form in the turbulent flow.

An experimental model was built to check the computer simulations. They used

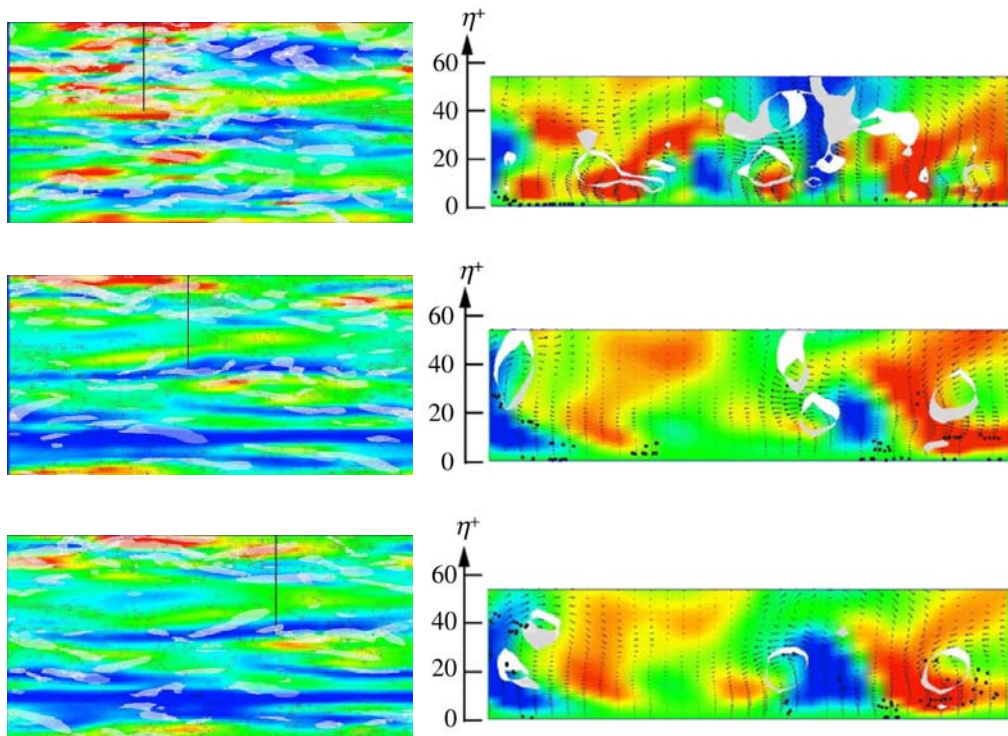


Figure 11: Snapshots of coherent structure of pulsating flow with models of separated pieces for different times ($t^+ = 1275, 1800$ and 1815 from top to bottom). (*left*) Snapshots of the top view of hairpin vortices in white and the colour contour map of wall shear stress in the entire region. (*right*) Low-speed streaks, high-speed streaks and the cross-section of the vortices on the (η, z) plane at the vertical lines in figures on the left.

waterproof glue to attach small squares of plastic film, measuring 1.5 by 0.8 millimetres, onto a wavy metal plate that represented the skin of the dolphin. The plastic squares gradually detached from the plate as the glue dissolved in the flow of water in a tank.

5 Conclusions

Having looked at some of the biomechanical aspects of certain swimming modes employed by fish, one can only marvel at the developed mechanisms and their significance in relation to the aquatic environment. It seems highly desirable to successfully replicate them in artificial devices.

However, although the evolved designs are highly effective for the fish adapting to their habitat, it should be kept in mind that the locomotor methods employed cannot necessarily be considered optimal *per se*. This is because their development has always been in the context of compromises for various activities (feeding, predator avoidance, energy conservation, etc.). Further research and understanding of fluid dynamics, physiology, and biological factors involved in swimming is therefore necessary to determine the value of individual techniques for engineering applications and to understand their significance in natural environments.

References

- [1] BLAKE R. W., *Fish Functional Design and Swimming Performance*, J. Fish Biol. **65**, 1193 (2004).
- [2] SFAKIOTAKIS M., LANE D. M., BRUCE J. and DAVIES C., *Review of Fish Swimming Modes for Aquatic Locomotion*, J. of Oceanic Eng. **24**, 237 (1999).
- [3] CHILDRESS S., *Mechanics of Swimming and Flying*, Cambridge University Press (1981).
- [4] CHENG J.-Y. and CHAHINE G. L., *Computational Hydrodynamics of Animal Swimming: Boundary Element Method and Three-Dimensional Vortex Wake Structure*, Comp. Biochem. and Physiol. A **131**, 51 (2001).
- [5] NAUEN J. C. and LAUEN G. V., *Hydrodynamics of Caudal Fin Locomotion by Chub Mackerel, Scomber japonicus (Scombridae)*, J. Exp. Biol. **205**, 1709 (2002).
- [6] LINDEN P. F. and TURNER J. S., *'Optimal' Vortex Rings and Aquatic Propulsion Mechanisms*, Proc. R. Soc. Lond. B **271**, 647 (2004).
- [7] WOLFGANG M. J., ANDERSON J. M., GROSENBAUGH M. A., YUE D. K. P. and TRIANTAFYLLOU M. S., *Near-Body Flow Dynamics in Swimming Fish*, J. Exp. Biol. **202**, 2303 (1999).
- [8] ZHU Q., WOLFGANG M. J., YUE D.K.P. and TRIANTAFYLLOU M. S., *Three-Dimensional Flow Structures and Vorticity Control in Fish-Like Swimming*, J. Fluid Mech. **468**, 1 (2002).
- [9] AHLBORN B., CHAPMAN S., STAFFORD R., BLAKE R. W. and HARPER D. G., *Experimental Simulation of the Thrust Phases of Fast-Start Swimming of Fish*, J. Exp. Biol. **200**, 2301 (1997).
- [10] SCHULTZ W. W. and WEBB P. W., *Power Requirements of Swimming: Do New Methods Resolve Old Questions?*, Integr. Comp. Biol. **42**, 1018 (2002).
- [11] NAGAMINE H., YAMAHATA K., HAGIWARA Y. and MATSUBARA R., *Turbulence Modification by Compliant Skin and Strata-Corneas Desquamation of a Swimming Dolphin*, J. Turbulence **5**, 18 (2004).