

Review of Fish Swimming Modes for Aquatic Locomotion

Michael Sfakiotakis, David M. Lane, and J. Bruce C. Davies

Abstract—Several physico-mechanical designs evolved in fish are currently inspiring robotic devices for propulsion and maneuvering purposes in underwater vehicles. Considering the potential benefits involved, this paper presents an overview of the swimming mechanisms employed by fish. The motivation is to provide a relevant and useful introduction to the existing literature for engineers with an interest in the emerging area of aquatic biomechanisms. The fish swimming types are presented, following the well-established classification scheme and nomenclature originally proposed by Breder. Fish swim either by body and/or caudal fin (BCF) movements or using median and/or paired fin (MPF) propulsion. The latter is generally employed at slow speeds, offering greater maneuverability and better propulsive efficiency, while BCF movements can achieve greater thrust and accelerations. For both BCF and MPF locomotion, specific swimming modes are identified, based on the propulsor and the type of movements (oscillatory or undulatory) employed for thrust generation. Along with general descriptions and kinematic data, the analytical approaches developed to study each swimming mode are also introduced. Particular reference is made to lunate tail propulsion, undulating fins, and labriform (oscillatory pectoral fin) swimming mechanisms, identified as having the greatest potential for exploitation in artificial systems.

Index Terms—Hydrodynamics, kinematics, marine animals, mobile robots, underwater vehicle propulsion.

I. INTRODUCTION

THIS PAPER presents an overview of fish swimming and the analytical methods that have been applied to some of their propulsive mechanisms. The motivation is to provide a relevant and useful introduction to the existing literature on the subject for engineers involved in underwater vehicle design and control and for those with an interest in the fast-growing area of biomimetic swimming robots.

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 in and interact with the aquatic environment. An example application that could substantially benefit are

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autonomous underwater vehicles (AUV's). 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 pelagic fish can potentially provide inspiration for a design of propulsors that will outperform the thrusters currently in use. For maneuvering or hovering purposes, the existing systems are insufficient when it comes to demanding applications, such as 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. Robotic devices are currently being developed to assess the benefits and study the ways of "porting" mechanisms utilized by fish and other aquatic animals to artificial systems (for examples, see [1]–[9]). Under this perspective, engineers working in this area should have a background knowledge of the swimming abilities and performance of fish that provide benchmarks for evaluating our own designs and drive further theoretical developments. Biologists have shown a much renewed interest in the area over the last five years, owing largely to the advent of improved experimental techniques that have shed new light on a number of the fish swimming mechanisms.

After an introduction to the classification of the various fish swimming types (Section II), the latter are presented in more detail covering general characteristics as well as kinematic data and mathematical models (Sections III–V). Section VI concludes with some discussion on the relevance to underwater vehicle design.

II. FISH SWIMMING MODES

A. Forces Acting on a Swimming Fish

The main properties of water as a locomotion medium that have played an important role in the evolution of fish are its incompressibility and its high density. Since water is an incompressible fluid, any movement executed by an aquatic animal will set the water surrounding it in motion and vice versa. Its density (about 800 times that of air) is sufficiently close to that of the body of marine animals to nearly counterbalance the force of gravity. This has allowed the development of a great variety of swimming propulsors, as weight support is not of primary importance [10].

To aid in the description of the fish swimming mechanisms, Fig. 1 illustrates the terminology used to identify morphological features of fish, as it is most commonly found in literature and used throughout this text. Median and paired

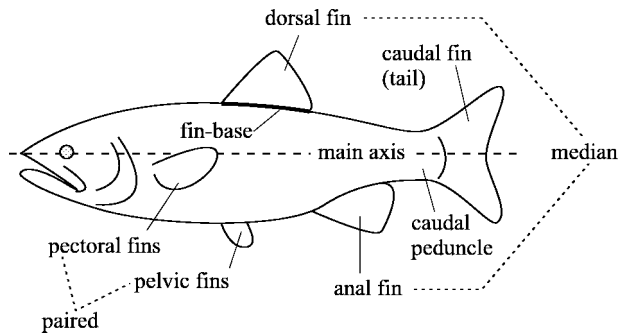


Fig. 1. Terminology used in the text to identify the fins and other features of fish.

fins can also be characterized as either *short-based* or *long-based*, depending on the length of their fin base relative to the overall fish length. The fin dimensions normal and parallel to the water flow are called span and chord, respectively.

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

- 1) 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.
- 2) 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.
- 3) 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*. Comprehensive overviews of swimming drag (including calculations for the relative importance of individual drag components) and the adaptations that fish have developed to minimize it can be found in [11] and [12].

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. Different formulas are used to estimate acceleration reaction depending on whether the water is accelerating and the object is stationary, or whether the reverse is true [13]. 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 [14], [15].

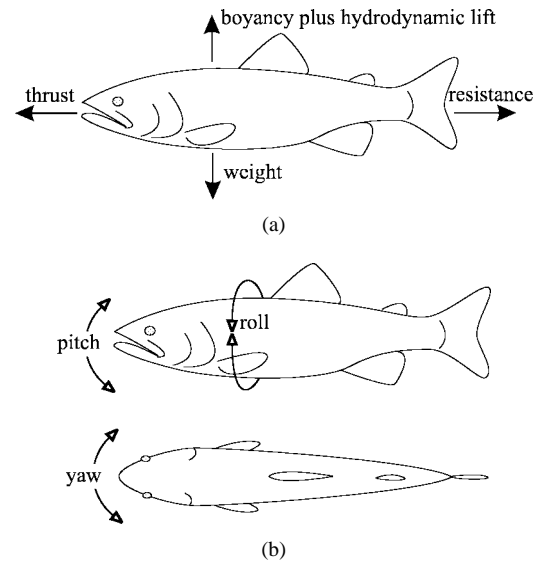


Fig. 2. (a) The forces acting on a swimming fish. (b) Pitch, yaw, and roll definitions. (Adapted from Magnuson [11].)

The forces acting on a swimming fish are weight, buoyancy, and hydrodynamic lift in the vertical direction, along with thrust and resistance in the horizontal direction [Fig. 2(a)].

For negatively buoyant fish, hydrodynamic lift must be generated to supplement buoyancy and balance the vertical forces, ensuring that they do not sink. Many fish achieve this by continually swimming with their pectoral fins extended. However, since induced drag is generated as a side effect of this technique, the balance between horizontal forces will be disturbed, calling for further adjustments for the fish to maintain a steady swimming speed. For a discussion on this coupling of the forces acting on a swimming fish, see [11]. The hydrodynamic stability and direction of movement are often considered in terms of pitch, roll, and yaw [Fig. 2(b)]. The swimming speed of fish is often measured in body lengths per second (BL/s).

For a fish propelling itself at a constant speed, the momentum conservation principle requires that the forces and moments acting on it are balanced. Therefore, the total thrust it exerts against the water has to equal the total resistance it encounters moving forward. Pressure drag, lift, and acceleration reaction can all contribute to both thrust and resistance. However, since lift generation is associated with the intentional movement of propulsors by fish, it only contributes to resistance for actions such as braking and stabilization rather than for steady swimming. Additionally, viscous drag always contributes to resistance forces. Finally, body inertia, although not a momentum transfer mechanism, contributes to the water resistance as it opposes acceleration from rest and tends to maintain motion once begun. The main factors determining the relative contributions of the momentum transfer mechanisms to thrust and resistance are: 1) Reynolds number; 2) reduced frequency; and 3) shape [15].

The Reynolds number (Re) is the ratio of inertial over viscous forces, defined as

$$Re = \frac{LU}{\nu}$$

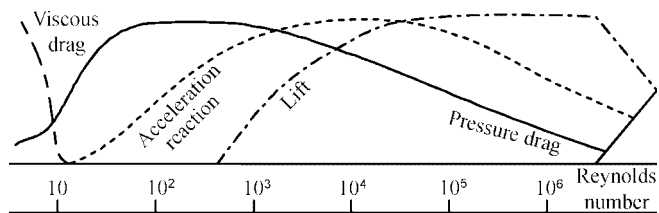


Fig. 3. Diagram showing the relative contribution of the momentum transfer mechanisms for swimming vertebrates, as a function of Re . The shaded area corresponds to the range of adult fish swimming. (Adapted from Webb [15].)

where L is a characteristic length (of either the fish body or the propulsor), U is the swimming velocity, and ν is the kinematic viscosity of water. In the realm of Re typical of adult fish swimming (i.e., $10^3 < Re < 5 \cdot 10^6$), inertial forces are dominant and viscous forces are usually neglected. At those Re , acceleration reaction, pressure drag, and lift mechanisms can all generate effective forces (Fig. 3).

The reduced frequency σ indicates the importance of unsteady (time-dependent) effects in the flow and is defined as

$$\sigma = 2\pi \frac{fL}{U}$$

where f is the oscillation frequency, L is the characteristic length, and U is the swimming velocity. The reduced frequency essentially compares the time taken for a particle of water to traverse the length of an object with the time taken to complete one movement cycle. It is used as a measure of the relative importance of acceleration reaction to pressure drag and lift forces. For $\sigma < 0.1$, the movements considered are reasonably steady and acceleration reaction forces have little effect. For $0.1 < \sigma < 0.4$, all three mechanisms of force generation are important, while for larger values of σ acceleration reaction dominates. In practice, for the great majority of swimming propulsors, the reduced frequency rarely falls below the 0.1 threshold [15].

Finally, the shape of the swimming fish and the specific propulsor utilized largely affect the magnitude of the force components. The relationship is well documented for steady-state lift and drag forces, but relatively little work has been done on the connection between shape and acceleration reaction.

A common measure of swimming efficiency is Froude efficiency η , defined as

$$\eta = \frac{\langle T \rangle U}{\langle P \rangle}$$

where U is the mean forward velocity of the fish, $\langle T \rangle$ is the time-averaged thrust produced, and $\langle P \rangle$ is the time-averaged power required.

B. Main Classifications

Fish exhibit a large variety of movements that can be characterized as swimming or nonswimming. The latter include specialized actions such as jumping, burrowing, flying, and gliding, as well as jet propulsion, the description of which is beyond the scope of this paper. Swimming locomotion has

been classified into two generic categories on the basis of the movements' temporal features [16]:

- 1) *Periodic (or steady or sustained) 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 (or unsteady) 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 mathematicians. This has mainly been because, compared to sustained swimming, experimental measurements of transient movements are difficult to set up, repeat, and verify. Therefore, periodic swimming will inevitably be the main focus of this paper. However, given the significant aspects of locomotion associated with transient movements, which provide fish with unique abilities in the aquatic environment and the more recent interest among scientists in describing them, reference will also be made to transient propulsion where possible.

The classification of swimming movements presented here adopts the (expanded) nomenclature originally put forth by Breder in [17]. Breder's nomenclature has recently been criticized as oversimplified and ill-defined (see, for example, [18] and [19]) in describing fish swimming. Nevertheless, since we are mainly concerned with descriptions of the fish propulsors, on which Breder's classification is based, it serves as a convenient reference frame, provided its limitations are held in mind. The interested reader is referred to [19], where a more holistic classification scheme of swimming is proposed, relating the swimming propulsors, kinematics, locomotor behavior, and muscle fiber used to the notion of *swimming gaits*.

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 [18].

A further distinction, and one that is common in literature, made for both BCF and MPF propulsion is on the basis of the movement characteristics: *undulatory* motions involve the passage of a wave along the propulsive structure, while in *oscillatory* motions the propulsive structure swivels on its base without exhibiting a wave formation. The two types of motion should be considered a continuum, since oscillatory movements can eventually be derived from the gradual increase of the undulation wavelength. Furthermore, both types of motion

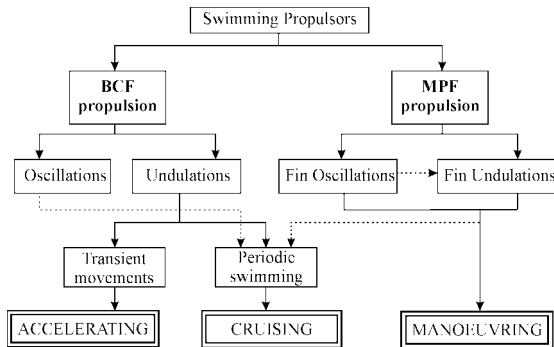


Fig. 4. Diagram showing the relation between swimming propulsors and swimming functions. (Adapted from Webb [20].)

result from the coupled oscillations of smaller elements that constitute the propulsor (i.e., muscle segments and fin rays for BCF and MPF propulsion, respectively).

Generally, fish that routinely use the same propulsion method display similar morphology. However, form differences do exist and these relate to the specific mode of life of each species. Webb [20] identified three basic optimum designs for fish morphology, derived from specializations for accelerating, cruising, and maneuvering. Although describing these designs is beyond the scope of this paper, it should be pointed out that they are closely linked to the locomotion method employed (Fig. 4). Also, since they are largely mutually exclusive, no single fish exhibits an optimal performance in all three functions. But neither are all fish specialists in a single activity; they are rather locomotor generalists combining design elements from all three specialists in a varying degree. Further details on the relation between function and morphology in fish swimming can be found in [19] and [20].

Within the basic grouping into MPF and BCF propulsion, further types of swimming (often referred to as *modes*) can be identified for each group, based on Breder's [17] original classification and using his nomenclature (Fig. 5). These modes should be thought of as pronounced points within a continuum, rather than discrete sets. Fish may exhibit more than one swimming mode, either at the same time or at different speeds. Median and paired fins are routinely used in conjunction to provide thrust with varying contributions from each, achieving smooth trajectories. Also, many fish typically utilize MPF modes for foraging, as these offer greater maneuverability, the ability to switch to BCF modes at higher speeds, and high acceleration rates.

The following sections present the modes of Fig. 5 in more detail, along with some of the mathematical models developed to describe them. Additional biological characteristics and literature references can be found in [10].

III. BCF PROPULSION

A. General

In undulatory BCF modes, the 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. 5(a) reflect changes mainly in the wavelength and the amplitude envelope of the propulsive wave, but also in the way thrust is generated. Two main methods have been identified: an added-mass method and a lift-based (*vorticity*) method. The latter is primarily used in *thunniform* swimming, while *anguilliform*, *subcarangiform*, and *carangiform* modes have long been associated with the added-mass method. However, recent studies suggest that vorticity mechanisms are also important for subcarangiform and carangiform swimming (see text below).

A qualitative description of the added-mass method is given by Webb in [20] (see also [21] for a more mathematical description) and is summarized here. As the propulsive wave passes backward along the fish, each small body segment (called *propulsion element*) generates a force that increases the momentum of the water passing backward. An equal opposing force (the reaction force F_R) is subsequently exerted by the water on the propulsive element. For most fish, the magnitude of F_R can be approximated (neglecting viscous effects) as the product of the water mass accelerated and its acceleration (see Section III-D). F_R is normal to the propulsion element and is analyzed into a lateral F_L and a thrust F_T component (Fig. 6). The thrust component contributes to forward propulsion, while F_L sheds water laterally and can lead to significant energy losses. Furthermore, the lateral component induces tendencies for the anterior part of the body to sideslip and yaw (*recoil* tendencies). F_T is larger for the propulsive elements near the tail, since the rear elements traverse greater distances and have larger speeds, hence accelerating the water more. Furthermore, since the amplitude of the propulsive wave increases toward the caudal fin, the propulsion elements there are oriented more toward the overall direction of movement, ensuring that the reaction force F'_R has a larger thrust component F'_T (Fig. 6).

The ratio U/V (where U is the overall fish swimming speed and V is the wave propagation speed) has long been used as an indication of swimming efficiency.

Body movements are particularly significant during unsteady swimming actions, like fast starts and rapid turns, that are characterized by high accelerations. Relatively few kinematic data have been available for these, due to the difficulties in setting up repeatable experiments and the complexity and speed of the movements involved. However, recent advances in measurement and filming techniques have shed new light on the high acceleration values obtainable (up to 25 g for the pike reported in the comprehensive summary of relevant kinematic data found in [18]).

In anguilliform mode, the whole body participates in large-amplitude undulations [Fig. 7(a)]. Since at least one complete wavelength of the propulsive wave is present along the body, lateral forces are adequately cancelled out, minimizing any tendencies for the body to recoil. Many anguilliform swimmers are capable of backward as well as forward swimming by altering the propagation direction of the propulsive wave. Backward swimming requires increased lateral displacements and body flexibility [22]. Typical examples of this common locomotion mode are the eel and the lamprey. See [23] for a summary of existing kinematic data on anguilliform

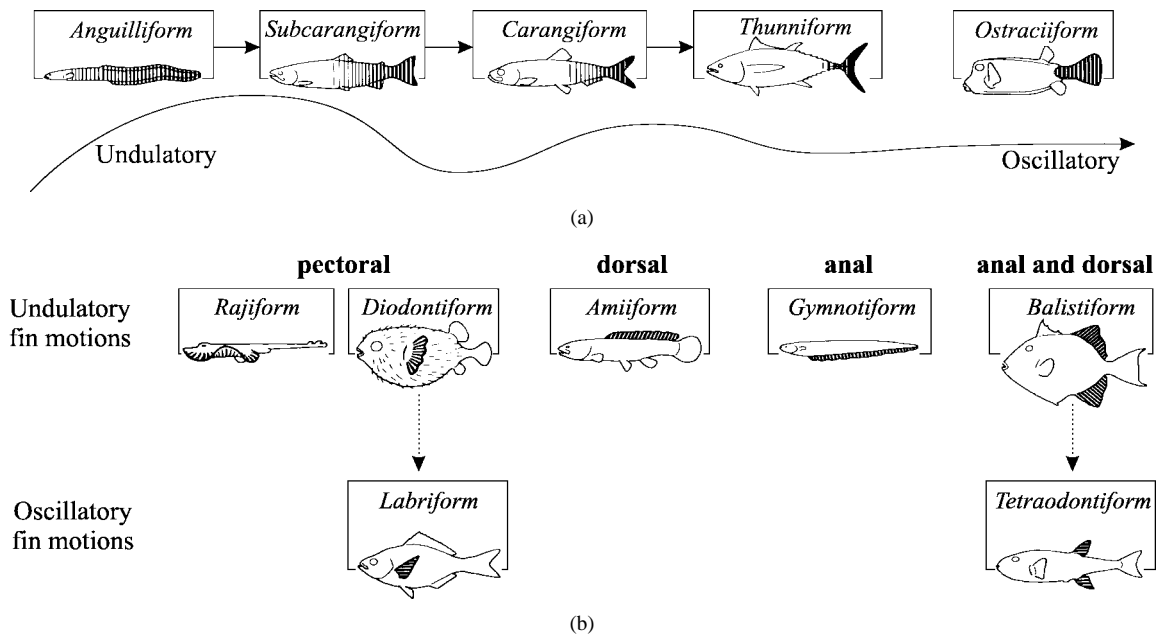


Fig. 5. Swimming modes associated with (a) BCF propulsion and (b) MPF propulsion. Shaded areas contribute to thrust generation. (Adapted from Lindsey [10].)

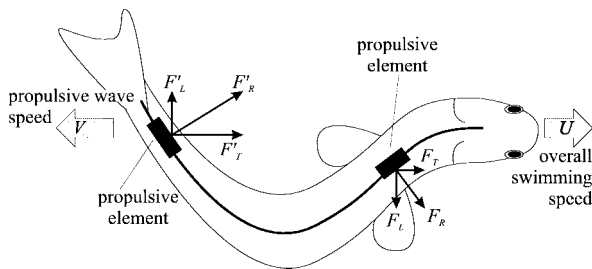


Fig. 6. Thrust generation by the added-mass method in BCF propulsion. (Adapted from Webb [20].)

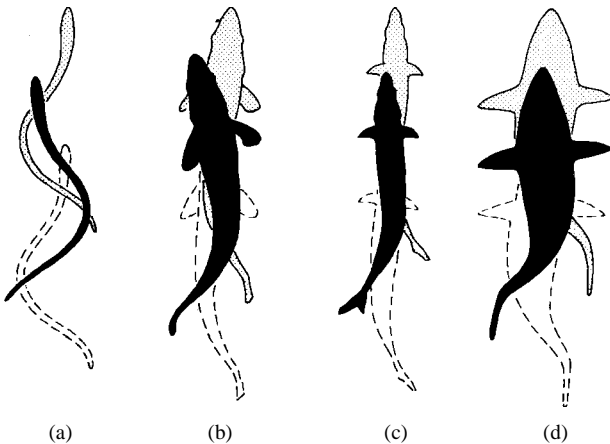


Fig. 7. Gradation of BCF swimming movements from (a) anguilliform, through (b) subcarangiform and (c) carangiform to (d) thunniform mode. (Taken from Lindsey [10].)

locomotion. Similar movements are observed in the subcarangiform mode (e.g., trout), but the amplitude of the undulations is limited anteriorly, and increases only in the posterior half of the body [Fig. 7(b)]. For carangiform swimming, this is even more pronounced, as the body undulations

are further confined to the last third of the body length [Fig. 7(c)], and thrust is provided by a rather stiff caudal fin. Carangiform swimmers are generally faster than anguilliform or subcarangiform swimmers. However, their turning and accelerating abilities are compromised, due to the relative rigidity of their bodies. Furthermore, there is an increased tendency for the body to recoil, because the lateral forces are concentrated at the posterior. Lighthill [24] identified two main morphological adaptations that increase anterior resistance in order to minimize the recoil forces: 1) a reduced depth of the fish body at the point where the caudal fin attaches to the trunk (referred to as the *peduncle*, see Fig. 1) and 2) the concentration of the body depth and mass toward the anterior part of the fish.

Thunniform mode is the most efficient locomotion mode evolved in the aquatic environment, where thrust is generated by the lift-based method, allowing high cruising speeds to be maintained for long periods. It is considered a culminating point in the evolution of swimming designs, as it is found among varied groups of vertebrates (teleost fish, sharks, and marine mammals) that have each evolved under different circumstances. In teleost fish, thunniform mode is encountered in scombrids, such as the tuna and the mackerel. Significant lateral movements occur only at the caudal fin (that produces more than 90% of the thrust) and at the area near the narrow peduncle. The body is well streamlined to significantly reduce pressure drag, while the caudal fin is stiff and high, with a crescent-moon shape often referred to as *lunate* [Fig. 7(d)]. Despite the power of the caudal thrusts, the body shape and mass distribution ensure that the recoil forces are effectively minimized and very little sideslipping is induced. The design of thunniform swimmers is optimized for high-speed swimming in calm waters and is not well-suited to other actions such as slow swimming, turning maneuvers, and rapid acceleration from stationary and turbulent water (streams, tidal rips, etc.).

Ostraciiform locomotion is the only purely oscillatory BCF mode. It is characterized by the pendulum-like oscillation of the (rather stiff) caudal fin, while the body remains essentially rigid. Fish utilizing ostraciiform mode are usually encased in inflexible bodies and forage their (usually complex) habitat using MPF propulsion [25]. Caudal oscillations are employed as auxiliary locomotion means to aid in thrust production at higher speeds, to ensure that the body remains adequately rigid, or to aid prey stalking [10]. Despite some superficial similarities with thunniform swimmers, the hydrodynamic adaptations and refinements found in the latter are missing in ostraciiform locomotion, which is characterized by low hydrodynamic efficiency.

B. Body Undulations and Friction Drag

Swimming viscous drag is calculated using the standard Newtonian equation

$$D_v = \frac{1}{2} C_f S U^2 \rho$$

where C_f is the drag coefficient (which depends on the Reynolds number and the nature of the flow), S is the wetted surface area, and ρ is the water density. Flexing the body to achieve propulsion is expected to increase viscous drag by a factor of q compared to that for an equivalent rigid body, since the motion of the propulsive elements increases their velocity with respect to the surrounding fluid. This is known as the “boundary layer thinning” effect, as lateral body movements reduce the boundary layer, resulting in increased velocity gradients and, hence, shear stress. Exactly how extensive the increase in viscous drag is has long troubled scientists. Originally, indirect estimations suggested (see, for example [26] and [24]) that q lies between 4 and 9. Webb in [27] indicates that this must be a significant overestimation, placing a greater importance on the energy losses arising from recoil forces. A value of $q = 1.8$ for a swimming tadpole has been calculated in [28] using three-dimensional (3-D) numerical simulation, at $Re = 7200$. The rather low Re prohibits safe application of this value of q to adult fish swimming. In the same study, it is shown that the relative amplitude of body undulations in tadpoles is significantly larger than those observed in fish. When the model was adapted to swim using the kinematics of a saithe, q was reduced to 1.12, stressing the connection between large lateral motions and increased friction drag [28].

C. Wake Structure and Generation

The wake left behind the tail of undulatory BCF swimmers is a staggered array of trailing discrete vortices of alternating sign, generated as the caudal fin moves back and forth. A jet flow with alternating direction between the vortices is also visible [Fig. 8(c)]. The structure of the wake is of a thrust-type, i.e., has a reversed rotational direction compared to the well-documented drag-producing Karman vortex street. The latter is typically observed in the wake of bluff (nonstreamlined) objects [Fig. 8(a)] for a specific range of Reynolds numbers (roughly $40 < Re < 2 \cdot 10^3$), but also in the wake of stationary [Fig. 8(b)] or low-frequency-heaving aerofoils (see [29]).

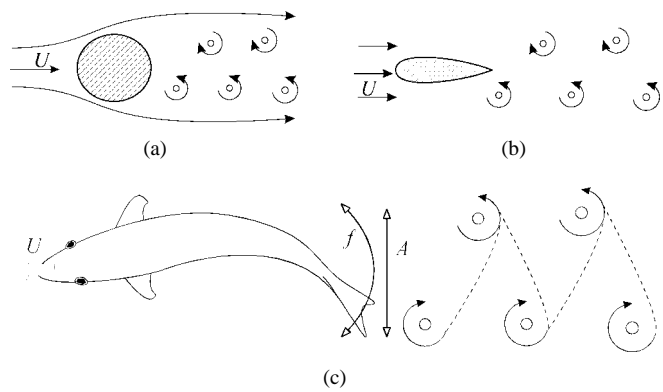


Fig. 8. The Karman street generates a drag force for either (a) bluff or (b) streamlined bodies, placed in a free stream. (c) The wake of a swimming fish has reverse rotational direction, associated with thrust generation.

The main parameter characterizing the structure of such wakes is the *Strouhal number*, defined, for a fish swimming by BCF movements, as

$$St = \frac{fA}{U}$$

where f is the tail-beat frequency in hertz, A is the wake width (usually approximated as the tail-beat peak-to-peak amplitude), and U is the average forward velocity. The Strouhal number is essentially the ratio of unsteady to inertial forces. Triantafyllou *et al.* [29] concluded that, in oscillating foils, thrust development is optimal for a specific range of St (namely $0.25 < St < 0.40$). Existing data on a number of fish species revealed that, for high-speed swimming, their calculated St values lie within this predicted range. Interestingly, this was valid for species representing not just thunniform (traditionally associated with oscillating foils) but also subcarangiform and carangiform modes, at a range of $10^4 < Re < 10^6$. These results have placed increased significance to vorticity effects and established the Strouhal number as a prominent factor when analyzing BCF modes. Detailed data on the morphology of the wave shed behind a mullet (swimming at $Re = 22 \cdot 10^3$) can be found in [30].

The generation mechanism of this wake structure is still unclear, as a number of contradicting hypotheses have been put forth. Lighthill [24] and Videler [18] support that the reversed Karman street results exclusively from the tail movements. This wake structure has indeed been observed behind oscillating foils that were not attached to a body (see, for example, [31]). Rosen [32] was among the first to conduct flow visualization experiments of carangiform fish and observed attached vortices being generated by the anterior half of the fish body. He proposed a “vortex peg” mechanism, whereby fish thrust their body against these vortices, extracting their rotational energy to move forward. Fully formed attached vortices have not been observed in the more recent visualization experiments. Rather, suction and pressure zones appear in the flow pattern (Fig. 9).

Müller *et al.* supported an “undulating pump” mechanism whereby these zones create a circulating flow around the inflection points of the body. The circulating flow propagates along the body, and upon reaching the caudal fin, it interacts

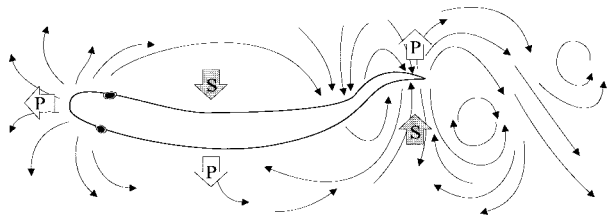


Fig. 9. The flow field around the body of a carangiform swimmer, as obtained from PIV data. The symbols *P* and *S* correspond to pressure and suction zones that form the basis of the “undulating pump” mechanism. (Adapted from Müller *et al.* [30].)

with the bound vortices created by the tail movements, forming the discrete vortices shed in the wake. Based on their particle image velocimetry (PIV) data, the authors concluded that about a third of the total energy shed to the water is provided by the anterior body.

A similar mechanism is proposed by Triantafyllou and Triantafyllou [33] as a means of recapturing energy and reducing the apparent drag of swimming, by at least 50% [5]. This could provide an explanation to “Gray’s Paradox” that has long troubled scientists. Gray [34] estimated the power requirements for a cruising dolphin, assuming that its drag can be approximated by that of a rigid model and considering turbulent flow. The calculations indicated that the power required exceeded the estimates of muscle power output by a factor of seven, thus the paradox. Despite the numerous adjustments and corrections of Gray’s original estimations and the varied explanations suggested (see [11]–[13], [21]), no definite conclusions have been drawn on the matter. The new hypothesis is supported by efficiency measurements of an articulated robot swimming by body undulations (the “Robo-Tuna”—see [5] and [6]), flow visualizations of swimming fish [35], as well as experiments and simulations with oscillating foils extracting energy from incoming vortices [35]–[37]. The implication of this theory is that the apparent swimming drag is actually lower for an undulating body than that of the rigid equivalent. This is in complete contrast to the traditional assumptions that estimate the apparent swimming drag to be three to five times that of the rigid-body equivalent, due to the increased friction drag and inertial recoil energy losses associated with BCF undulatory motions. There is a need to reexamine existing data, assumptions, and trends observed in nature and assess them in the context of these new theoretical developments.

Vorticity control mechanisms were originally proposed in the early 1970’s in the context of fish schooling behavior often observed in scombrids. As each vortex is shed by individual swimming fish, it induces a water motion that is opposite to the swimming direction immediately behind the fish, but in the swimming direction at the sides [Fig. 8(c)]. Therefore, a fish situated laterally midway between the two fish of the preceding column (Fig. 10), rather than directly behind one of them, avoids having to overcome increased incoming flow. A “channeling effect” has also been suggested, provided the fish stay close together, to utilize the favorable flow at the sides of the vortex-street. The advantage is greater when fish in the same column swim in antiphase with the neighbors. These

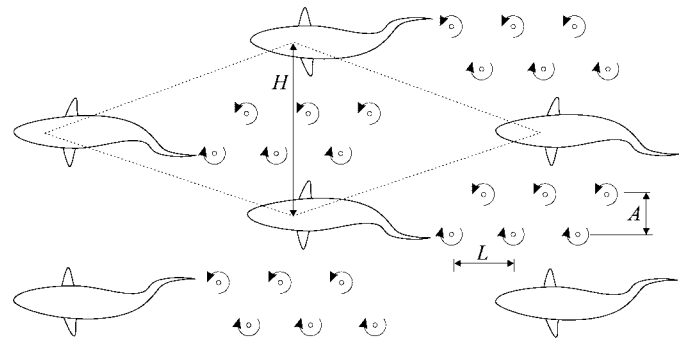


Fig. 10. Plan view of a horizontal layer of a fish school, showing its diamond-shaped building block structure. The configuration is described by the wake width *A*, the vortex spacing *L*, and the lateral distance *H* amongst fish of the same column. (Adapted from Weihs and Webb [16].)

requirements point to an elongated diamond-shape pattern as the basic optimum structure in fish schools (Fig. 10). Evidence from aerial photographs of schooling scombrids support this prediction. The hydrodynamic benefits of schooling seem to vary for each column, as partial or complete cancellation of vortices can occur. Magnuson [11] estimates average energy savings of 10%–20% from schooling. Details can be found in [11], [16], and [38].

D. Mathematical Analysis

Scientists from varying backgrounds have attempted to formulate mathematical models to describe the observed kinematics of fish. Work has been hindered by the inherent variability and complexity encountered in natural processes, limiting the accuracy and repeatability of experiments and measurements compared to other areas of engineering.

Early “resistive” hydrodynamic models (see, for example, [39]) were based on a quasi-static approach that uses steady-state flow theory to calculate the fluid forces for sequential “frames” of the fish’s motion. Their applicability is restricted to low Reynolds numbers, due to neglecting inertial forces and the oversimplified assumptions concerning fish motions and body shapes. Later models dealt with more realistic fish-type motions, assuming an inviscid (frictionless) fluid. Wu [40] originally developed a two-dimensional (2-D) waving plate theory, treating the fish as an elastic plate. Along with the “slender body theory” that stems from aerodynamics, it formed the basis for Lighthill’s *elongated-body theory* [41], [42], which is well suited to subcarangiform and carangiform modes. The flows induced by the undulating body are assumed to cancel out over a tailbeat cycle and the mean thrust is estimated from the trailing edge kinematics. The original theory was extended by Lighthill in [43] to cater for fish motions of arbitrary amplitude, leading to the *large-amplitude elongated-body theory* that is better suited to carangiform swimming, where the lateral motions of the caudal fin are large. Mechanical thrust power for a fish swimming at an average speed *U* is calculated [27] as

$$P_T = mWwU - \frac{mw^2U}{2\cos\theta}$$

where

$$m = \left(\frac{B}{2}\right)^2 \pi \rho$$

is the added mass per unit length (B is the trailing edge span and ρ the density of the water), while

$$W = \frac{fA\pi}{1.414}$$

is the rms value of the lateral speed of the trailing edge (f is the frequency of the caudal fin oscillations and A is their amplitude). The velocity w given to the water at the trailing edge is obtained as

$$w = W \left(1 - \frac{U}{V}\right)$$

where V is the velocity of the propulsive wave. Finally, θ is the angle of the trailing edge to the lateral plane of motion. Filmed sequences of the swimming fish are used to determine these parameters. The hydromechanical efficiency is calculated as

$$\eta = 1 - \frac{1}{2} \left(1 - \frac{U}{V}\right).$$

As the above equation shows, η is never less than 0.5 (as $U \rightarrow V$, $\eta \rightarrow 1$, while for $U \gg V$ $\eta \rightarrow 0.5$).

For examples of practical application of the large-amplitude elongated body, see [44] and [45]. Lighthill's work has been further refined to include the effects of body elasticity [46], recoil movements [47], centerline curvature, and the interaction of the caudal fin with the vortex sheets shed from dorsal fins [48]. The importance of body thickness effects in relation to thrust and drag have been studied in [49] and [50]. All these analytical approaches have shed significant light on the morphology and swimming mode of fish. Large-amplitude elongated-body theory has also been used by Weihs to study the hydrodynamics of BCF turning maneuvers [51] and fast starts [52]. The outlines of large-amplitude elongated-body theory found in [44] and [18] are recommended as introductory texts on the subject. Linear and nonlinear extensions of the waving plate theory have also appeared in Tong *et al.* [53] and Root and Long [54]. The latter allows the analysis of fast starts as well as steady swimming.

Elongated-body theory cannot be applied to thunniform mode, because the shape of the caudal and pectoral fins violates the fundamental assumption of slenderness. The theories that have been developed stem from work on oscillating aerofoils and consider the caudal fin independent from the rest of the fish body. These are presented separately in Section III-E. Models that integrate viscous and pressure drag with acceleration reaction should provide further insights, particularly for anguilliform locomotion, where viscous forces seem to play a significant role. This need has been set forth early [24] and, in principle, viscous and inertial forces can be calculated separately, the latter estimated using inviscid theory. Characterizing the flow around the fish body is very complicated, rendering the formulation of such a model problematical and possibly impractical for application to and validation by actual data [21].

In another hydrodynamic approach, the energy costs of swimming are estimated indirectly by calculating the energy shed into the wake, based on the size and circulation of the discrete vortices [30]. Application of this method to PIV data obtained for a swimming mullet yielded a propulsive efficiency greater than 90%.

Concerning ostraciiform locomotion, Blake in [55] considered the thrust force generated by a rigid tail oscillating, while the fish body is held straight. He applied both elongated-body theory and a reactive model of a finite circular oscillating disc moving in its own plane and in a perfect fluid, found in [56]. Propulsive efficiencies were calculated to be around 0.5, considerably lower than those obtained for undulatory BCF modes.

As a final remark, numerical studies involving computational fluid dynamics (CFD) techniques have lately appeared in literature, exploiting the increased power of computers. The objective is to calculate the flow patterns and pressure field around the undulating fish body and/or caudal fin by solving the Navier–Stokes equations in order to determine the forces generated as a result of the momentum changes. The potential benefits in understanding the way the swimming body interacts with water are immense, as many of the assumptions found in analytical methods can, in theory at least, be dispensed with. The increased computational task for such simulations meant that initial attempts assumed 2-D flows or simplified movements [57]. Recently, 3-D CFD models have emerged, utilizing advanced computational techniques and the power of supercomputers [28], [58], [59].

E. Elements of Lunate Tail Propulsion

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 [5] that was shaped after an actual tuna and combined oscillating foil tail movements with carangiform body kinematics (i.e., presenting more extensive undulations than those encountered among actual scombrids). Mean propulsive efficiencies as high as 91% have been reported for the RoboTuna. Its success spawned further work in the area of swimming robots [1]. In [4], the use of a dual flapping foil device for propulsion and/or maneuvering of a rigid cylinder-shaped body is demonstrated, investigating both a “clapping” and a “waving” mode of operation. Work has also been directed at the prospect of applying oscillating foil propulsion to traditional sea-surface vessels (see [2] for a list of references).

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. 11(a)]. The caudal fin performs a combination of pitching and heaving motions, tracing an oscillating path as the fish moves forward, characterized by a peak-to-peak amplitude A , a tail-beat frequency f , and a wavelength λ [Fig. 11(b)]. There are very small lateral movements of the body, mainly concentrated near the penduncle

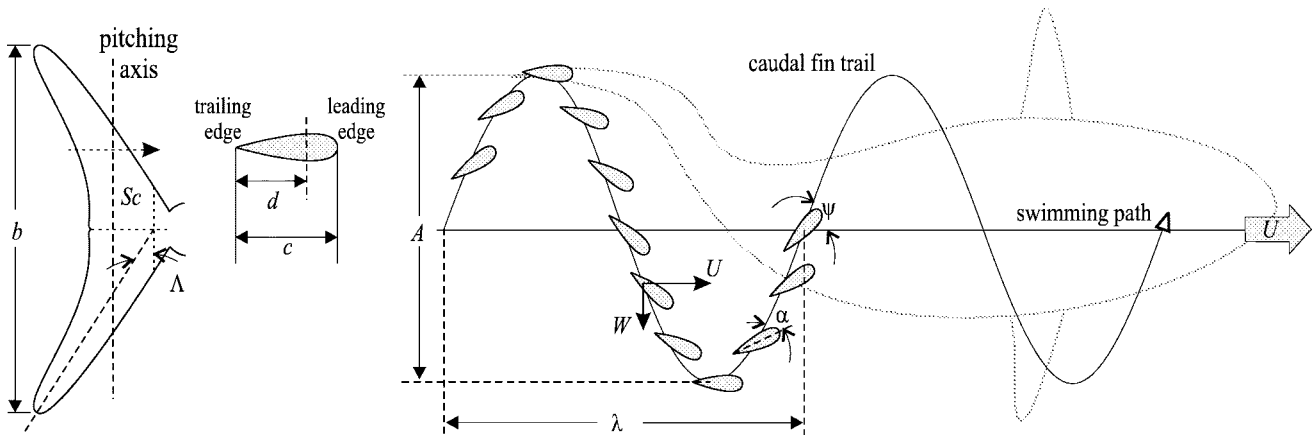


Fig. 11. (a) Lateral view of caudal fin shape for thunniform swimmers, showing span b , chord c , pitching axis position d , sweepback angle Λ and surface area S_c . (b) Trail of an oscillating caudal fin showing amplitude A , wavelength λ , feather angle ψ , and attack angle α of the fin. (Adapted from Magnuson [11].)

area. As the fin moves along this trail, its forward velocity U is the same as that of the fish, while its lateral velocity W changes in time. Other important parameters of its motion include the angle of attack α (with respect to its trail) and the feathering angle ψ [Fig. 11(b)]. Feathering is the angle between the fin trail and the overall path of the fish. Both α and ψ change as the caudal fin sweeps laterally in order to obtain maximal thrust during the whole of the fin-beat cycle. Detailed data from several references on all these variables for the scombrids fish family have been gathered in [11], where tail-beat frequencies as high as 14.5 Hz are documented for a 40-cm-long Kawakawa (swimming at a speed of 8.2 BL/s, $Re = 1.3 \cdot 10^6$). 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. This is defined as the fin span b squared, divided by the projected fin area S_c [Fig. 11(a)]

$$AR = b^2/S_c.$$

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 [Fig. 11(a)]. A curved leading edge is beneficial, because it reduces the relative contribution of leading-edge suction to the total thrust, avoiding boundary layer separation for high thrust values [11].
- 3) the fin stiffness. The benefit of a higher degree of stiffness (achieved by fusing the many fin-rays consisting the caudal fin) is increased thrust generation capability, with only a relatively small drop in efficiency [11].
- 4) the oscillatory motions of the fin.

To study the effects of 4) on thrust production, three factors have traditionally been considered in the models developed

for lunate tail propulsion: the reduced frequency and the *proportional feathering* parameters, along with the position of the pitching axis [defined by d in Fig. 11(a)]. For a thunniform swimmer, the reduced frequency σ represents the ratio of the time to swim a distance equal to the caudal fin chord (usually calculated as $c = b/S_c$) to the tailbeat period

$$\sigma = 2\pi \frac{fc}{U}$$

The proportional feathering parameter θ , originally proposed by Lighthill in [24], is defined as the ratio of slopes between α and ψ and can be computed [12] as

$$\theta = \alpha_{\max} U/W_{\max}$$

where α_{\max} is the angle of attack in radians (the slope of α), W_{\max} the maximum lateral velocity of the fin, and U is the swimming speed. Values of θ between 0.6 and 0.8 have been calculated by Lighthill [60] to yield optimal combinations of leading-edge suction and hydromechanical efficiency.

Lighthill [42] was the first to apply a simple linear 2-D (i.e., for $AR = \infty$) wing theory on lunate tail propulsion. The fluid is assumed inviscid and irrotational, and potential theory is used to calculate the thrust for small-amplitude oscillations. In his optimization analysis, Wu [61] calculated that efficiencies close to unity are attainable in such a 2-D model. A large-amplitude 2-D theory based on the impulse approach was developed by Chopra [62]. Extension to three dimensions (confined to rectangular wings and small-amplitude oscillations) based on the vorticity distribution was made by Chopra in [63]. Chopra and Kambe used a 3-D unsteady lifting-surface theory in [64] to study thrust production from a variety of different wing shapes. Lan also considered a 3-D problem in [65], where an unsteady quasi-vortex lattice method is used. All these models assume rigid tails. The effects of passive chordwise flexibility of the caudal fin performing large-amplitude motions for the 2-D case were studied by Katz and Weihs in [66]. A linearized low-frequency unsteady lifting-line theory was applied by Ahmadi and Widnall in [67]. A strip theory considering small-amplitude pitching motions was developed by Bose and Lien in [68] to calculate the hydrodynamic performance of a fin

whale's flukes that operate on a similar principle. Cheng and Murillo developed a 3-D theory considering a curved centerline for the caudal fin (relating to the term "lunate") in [69] that was subsequently applied in [70] to determine the influence of the sweepback angle and the centerline curvature. Three-dimensional triangular hydrofoils were analyzed by Cheng *et al.* using the unsteady vortex ring method in [71]. A summary of the developed hydromechanical theories can be found in [72]. Recently, a time-domain panel method was used by Liu and Bose [73] to study the effects on propulsive efficiency of 3-D foils with spanwise flexibility. Most of the above theories assume a planar vortex wake without considering the rotational vortical patterns developed, as shown in Fig. 8.

The wake theories of oscillating foil propulsion developed by Triantafyllou *et al.* [29], [31] consider the Strouhal number St and the maximum angle of attack α_{\max} , based on their direct relevance to the thrust coefficient and the wake dynamics. The conditions for optimal thrust production are summarized in [31] as follows.

- 1) The Strouhal number is in the range of $0.25 < St < 40$.
- 2) The maximum angle of attack is between $15^\circ < \alpha_{\max} < 25^\circ$.
- 3) The ratio of the heave amplitude over the chord length ($\frac{1}{2}A/c$) should be of order one.
- 4) For $d = \frac{2}{3}c$, the pitching movement should lead the heaving motion by about 75° .

Research has also been performed on the elastic properties of the caudal fins of cetaceans [74] and the advantages involved in reducing the energy requirements of swimming robots [75]. The development of artificial propulsion systems based on oscillating foils requires reformulating the above theories to derive dynamic models of the foil, needed for the control system design (for examples, see [75] and [76]).

IV. MEDIAN/PAIRED FIN UNDULATIONS

A. General

Undulating fins are routinely used by many fish as auxiliary propulsors, as well as for maneuvering and stabilization. They can also provide adequate thrust to be used as the sole means of locomotion, at generally low speeds (below 3 BL/s). The fins of teleost fish consist of the fin-rays that have varying span and stiffness and a flexible membrane connecting them together. In median fins, a set of muscles (usually six) for each fin-ray provide the latter with two degrees-of-freedom movement capability, while it has been suggested that certain fish can actively bend the rays of their median fins. Paired fins have an even more complex muscular system, enabling movements such as rotations of individual finrays. The literature on the structure and properties of teleost fins is reviewed in [10] and [18]. Their versatility has played a key role in the development of the undulatory MPF modes [Fig. 5(b)], presented next.

Rajiform mode is found in fish such as rays, skates, and mantas, whose swimming has been likened to the flight of birds. Thrust generation involves the passing of vertical

undulations along the pectorals that are very large, triangular-shaped, and flexible. The amplitude of the undulations increases from the anterior part to the fin apex and then tapers again toward the posterior. The fins may also be flapped up and down.

Similarly, in *diodontiform* mode, propulsion is achieved by passing undulations down broad pectoral fins. Up to two full wavelengths may be visible across the fins, while undulations are often combined with flapping movements of the fin as a whole.

In *amiiform* mode, swimming is by undulations of a (usually long-based) dorsal fin, while the body axis is in many cases held straight when swimming. The best examples of this characteristic are found among the African freshwater electric eels. The anal and caudal fins are missing, while the dorsal fin extends along most of the body length, tapering to a posterior point, and exhibits a large number of fin-rays (up to 200).

Gymnotiform mode can be considered as the upside-down equivalent of amiiform mode, since propulsion is obtained by undulations of a long-based anal fin. The dorsal fin is usually absent and the body is again held straight during swimming. This tendency found among electric eels (using either amiiform or gymnotiform mode) for a rigid body during swimming has long been considered a necessity, due to the electrosensory system they possess. However, it may also be connected to the absence of friction drag increase associated with undulatory movements (see Section IV-C).

Finally, in *balistiform* locomotion, both the anal and dorsal fins undulate to generate the propulsion forces. This is seen mainly in the family *Balistidae* (e.g., the trigger fish). A typical characteristic is that their median fins are usually inclined relative to each other, while the body is usually flat and compressed laterally. These design features have been associated with enhanced propulsion efficiency.

B. Kinematics and Vector Analysis

According to the qualitative description of Breder and Edgerton in [77], the thrust produced by an undulating fin can be analyzed using two components: a force F_N (normal to the fin base due to the simple oscillation of the fin-rays, and a force F_P (parallel to the fin base, resulting from the passage of the wave along the fin) (Fig. 12).

This vector analysis has been verified experimentally (see, for example, [78]) and can be applied to most undulatory MPF modes, providing insights to the locomotory habits of the fish utilizing them. F_N does not contribute to thrust when the fin base is parallel to the body axis. Therefore, unless it serves for buoyancy compensation, it will induce pitching couples for median fin undulations and lead to increased energy losses. Observation reveals that, for most of the electric eels (that swim in either the amiiform or the gymnotiform mode), the fin base is inclined to the horizontal body axis to ensure that the resultant vector is (or can be) parallel to the body axis to avoid these energy losses [Fig. 13(a) and (b)]. This is even more pronounced in the balistiform swimmers of the *Balistidae* family, in which the anal and dorsal fins are characteristically inclined to each other, so that all force components of the

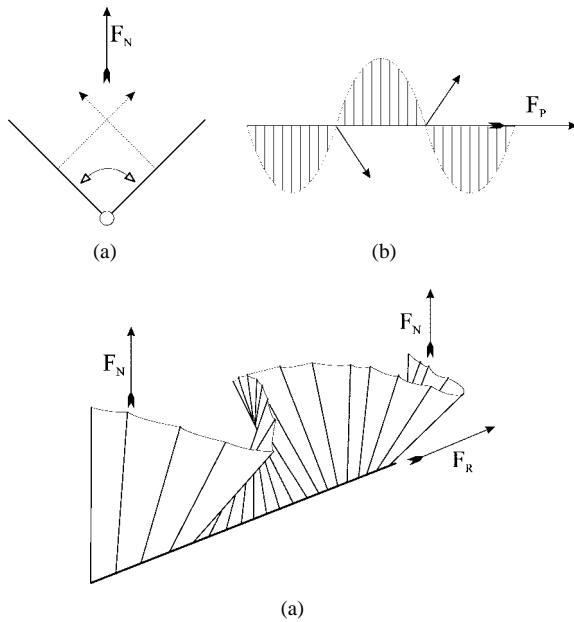


Fig. 12. Vector analysis of an undulating fin. (a) A single fin-ray oscillating exerts an upward thrust. (b) When many fin-rays are connected via a flexible membrane (plan view), additional forces are exerted as indicated by the black arrows. Their resultant is parallel to the fin base. (c) Perspective view of an undulating fin, showing both force vectors. (Adapted from Breder and Edgerton [77].)

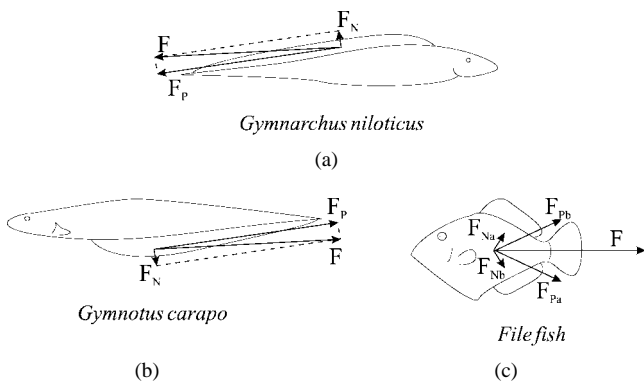


Fig. 13. Diagrams relating morphology to how the vector components of undulating fins could be combined to yield a net forward thrust for (a) an amiiform, (b) a gymnotiform, and (c) a balistiform swimmer.

propulsive waves combine to produce a net forward thrust [Fig. 13(c)]. A significant advantage of this arrangement is that elaborate maneuvering can be achieved by varying the individual force components of the median fins and direct the resulting force vector with precision. Breder and Edgerton observed this high degree of maneuverability for the seahorse [77] which swims exclusively by undulations of its dorsal and anal fins. They identified a number of physical and behavioral factors that can alter the relative magnitude of the parallel and normal force components. Physical factors include variations in the interdistance, length, and flexibility of the individual fin-rays. Behavioral factors affect the amplitude, wavelength, and phase differences along the fin and in time. The fin-rays also perform small longitudinal as well as lateral movements, and they tend to be held like an open fan. The musculature supporting the seahorse fins is flexible and strong enough to

provide additional functionality; Blake [78] observed that the fins can change their long axes relative to the body axis, as well as move parts of the fin relative to others. These abilities are utilized during turn maneuvers to compensate for the inflexible body of the seahorse. Also, the entire fin may be held at various angles to the body, allowing it to be deflected far to one side and undulated in that position. Finally, most undulatory median fin swimmers are able to swim backward just as effectively as forward by simply reversing the direction of propagation of the propulsive wave [79], [80].

In undulating pectoral fins, the vertical force components are lateral to the fish body and create yawing couples that are generally cancelled out for symmetrical movements of the fins. Powered maneuvers can be obtained by asymmetric movements and different phase relationships in the undulating paired fins [81].

Apart from swimming, fish utilize fin undulations extensively for hovering in mid-water. Small corrective forces are generated by the fins to compensate for disturbances due to pressure variations, minor sudden currents, or even the jet-effect of the respiratory flow [26].

C. Mathematical Analysis

A simple method used to calculate the hydromechanical efficiencies for undulatory fin swimmers is the *actuator-disc theory*, a special application of the momentum principle in fluid dynamics. The mechanism operating on the fluid (in this case, an undulating fin) is reduced to an idealized device (actuator disc) that generates a pressure rise in the fluid passing through it. The thrust force can be calculated by integrating the pressure rise over the whole disc. The main advantage of this approach is that the fin is regarded as a “black box,” requiring no detailed knowledge of its kinematics. However, the assumptions involved can be quite restrictive. For applications of the actuator-disc theory to fish propulsion and hovering, along with discussions on its limitations, see [82]–[84].

The similarity of the waveforms observed in median fins and those found in the undulating bodies of BCF swimmers has encouraged the application of large-amplitude elongated-body theory to the undulatory median fin propulsion modes. The initial work reported in [80], [84], and [85] was extended in a series of papers [86]–[89] by Lighthill and Blake. It is there shown that, for rigid deep-bodied fish, the momentum shed into the water can be increased by a factor of about three, compared to the momentum expected by the movement of the fins “on their own.” This increment does not apply to the shedding of “unproductive” energy into the wake. Furthermore, the minimization of lateral forces, due to the fact that they largely cancel out over the fin length, means that the fish body can remain rigid, avoiding increases in viscous drag. These factors all combine to significantly increase the overall efficiency of undulating median fin propulsion. For a speed range from 0.2 to 5 BL/s (corresponding to a *Re* from 10^3 to 10^5), Blake [80] calculated a propulsive efficiency between 0.7 and 0.9 for electric eels and knifefishes. The application of the latest wake theories developed for undulatory

BCF propulsion to gymnotiform and amiiform locomotion presents an interesting field of research that, along with flow visualization experiments, could determine whether vorticity control mechanisms are employed by fish swimming in these modes.

Finally, rajiform locomotion has been analyzed by Daniel using a combination of unsteady aerofoil theory and blade-element theory in [90], where the significance of unsteady effects and wing shape in thrust generation is demonstrated.

V. MPF OSCILLATIONS

A. General

Fin oscillations usually involve short-based median or paired fins. In *tetraodontiform* mode, the dorsal and anal fins are flapped as a unit, either in phase or alternating to achieve propulsion. The ocean sunfish is an extreme example of tetraodontiform swimmer: it has virtually no caudal fin or body musculature and propels itself by synchronized oscillations of its very high dorsal and anal fins. Tetraodontiform mode can be viewed as a continuation of balistiform mode, where the wavelength of the propulsive wave is very large, and, consequently, the individual fin-rays oscillate more or less in phase.

In *labriform* mode, propulsion is achieved by oscillatory movements of the pectoral fins. Due to the large variability of these movements, as well as the significance of pectoral fin swimming amongst fish and the potential for building stabilization/maneuvering devices based on them (see, for example, [7] and [91]), the following section is dedicated to a more detailed discussion of labriform locomotion.

B. Labriform Swimming

Swimming using the pectoral fins is widespread among teleost fish, but only recently has it received scientific attention. This is largely because of the difficulty in observing and analyzing the fin kinematics due to the speed, variability, and complexity of the movements performed (flapping, rotations and undulations), as well as the transparent nature of the fin membrane. Recently, a number of sophisticated filming techniques have evolved, enabling the acquisition of detailed kinematic data, that can help us gain a better understanding of the hydrodynamic forces involved.

Blake [82] identified two main oscillatory movement types for the pectoral fins: 1) a “rowing” action (*drag-based* labriform mode) and 2) a “flapping” action, similar to that of bird wings (*lift-based* labriform mode). According to Vogel [13], drag-based methods are more efficient at slow speeds, when the chordwise flow over the fin is small, while lift-based methods are more efficient at higher speeds. Later observations (see [91] and [92]) emphasized the importance of acceleration reaction in thrust generation. They also indicate that pectoral fin movements are usually very complicated owing to the highly flexible character of the membrane and the fin-rays, as well as to the hydrodynamic interactions of the fins with the moving water and the fish body. Thus, fish rarely exhibit a clearly rowing or flapping movement. Instead, they use a

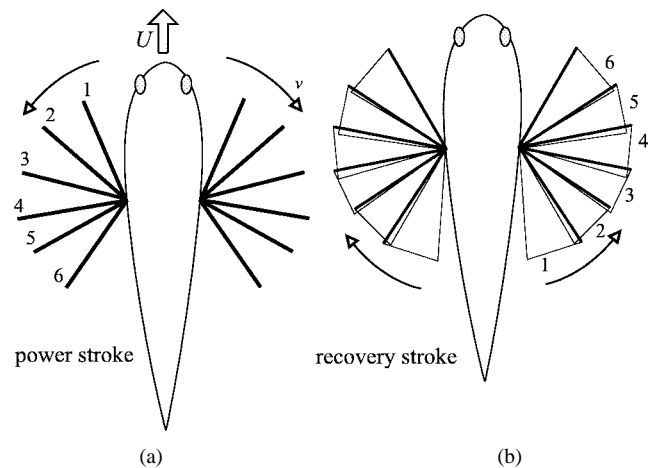


Fig. 14. Diagram showing the fin positions and attack angles during (a) the power stroke and (b) the recovery stroke for a fish swimming in drag-based labriform mode. (Adapted from Blake [84].)

combination of them that generally varies with speed. Undulations are also often passed along the fins (*diodontiform* mode), and the great diversity of movements attainable can generate thrust in almost any direction, achieving high maneuverability. The complexity of the pectoral fin motions is illustrated in the detailed 3-D kinematic data recently available [91], [92], [93]. Comprehensive reviews of pectoral fin swimming can be found in [18] and [91]; the latter discusses a number of issues pertinent to the design of artificial fins for use in underwater vehicles. To understand the basics of thrust generation in pectoral fin movements, it is helpful to go back into the original studies of the purely drag- and lift-based labriform locomotion, for which mathematical models have been easier to develop.

1) *Drag-Based Mode*: Blake presents kinematic data and a mechanical analysis of drag-based labriform locomotion in [94] and [95], as it is utilized by angelfish for an extensive range of swimming speeds. The fins usually have a short base that forms a high angle with the main axis. Rowing action consists of two phases [94]: the *power stroke*, when the fins move posteriorly perpendicular to the body at a high attack angle and with a velocity v greater than the overall swimming speed U [Fig. 14(a)], and a *recovery stroke*, when the fins are “feathered” to reduce resistance and brought forward [Fig. 14(b)].

Thrust is generated due to the drag encountered as the fin is moved posteriorly, as well as due to the acceleration reaction of the water being rapidly hauled at the initial part of the power stroke. Since thrust is only produced during the power stroke, it is discontinuous. This is in contrast to BCF propulsion, where a usefully directed thrust force is generated over most of the tail-beat cycle.

Blade-element theory has been applied to drag-based labriform propulsion, whereby the pectoral fins are divided into a number of rigid sections, each inclined at an angle to the incident flow. According to the results obtained for an 8-cm-long angelfish specimen swimming at about 0.5 BL/s, the outermost 40% of the fin area produces over 80% of the total hydrodynamic force. A propulsive efficiency of 16% for the complete rowing stroke is derived using the same calculations [95]. A simple hydromechanical model developed in [96] predicts

that, for a given planform area, triangular fins will create less interference drag over the fish body than square or rectangular ones. This is in accordance with the actual fin shape observed in drag-based labriform swimmers. More recently, Kato and Inaba used the unsteady vortex lattice method to calculate the hydrodynamic forces on a rigid pectoral fin model [3] in drag-based labriform mode. The propulsive efficiencies calculated do not exceed 10%, a result in accordance with their experimental measurements and the predictions of blade-element theory. Despite these low values, Blake suggested [94] that rowing propulsion is more efficient for slow swimming than BCF modes, the efficiency of which falls off rapidly for decreasing speed. There is evidence for that in nature, as many fish use labriform locomotion for slow-speed swimming, switching to BCF propulsion at higher speeds. In [97], the velocity at which this transition occurs for a certain species (*Notothenia Neglecta*, average adult length 28 cm) is quoted as 0.8 BL/s. However, the use of labriform locomotion at low speed could be attributed to nonenergetic factors, such as higher maneuverability or being less conspicuous to predators.

2) *Lift-Based Mode*: Lift forces are generated in the plane perpendicular to the direction of the fin motion, whereas drag forces appear in the plane of the fin motion. As a result, in lift-based labriform mode, for the pectoral fins to propel the fish forward, they have to move up and down in a plane that is roughly perpendicular to the main axis of the fish's body. This implies that no recovery stroke is necessary and lift can be generated during both the upstroke and the downstroke. Additionally, lift forces can be an order of magnitude greater than the drag forces generated by a fin of the same area. Thus, lift-based fins can generate larger, more continuous, and more efficient thrust than fins performing rowing motions (see [91] for relevant data). The fin shapes for lift-based labriform swimmers tend to differ from those using drag-based mechanics. One reason is the need to minimize the crossflow around the fin tip that decreases lift and increases drag. As a result, lifting fins tend to be diamond-shaped, with a high aspect ratio and tapered at both ends, while their base usually forms a small angle relative to the main axis [20].

Kinematics obtained by Webb [98] for the pectoral fin propulsion of the seaperch have since been used to outline lift-based labriform mode, although the movements performed cannot be considered a pure flapping; they are, however, simpler and more tractable than those found in more recent data (see [99] and [97]). Along with oscillating in a dorso-ventral motion, the pectoral fins of the seaperch pass a wave back over their length as a result of phase lags in the movement of the individual fin rays. The wavelength of this wave varies with swimming speed, resulting in phase lags from about π (for velocities below 2 BL/s) to about 0.2π (at higher velocities) between the leading and trailing edges of the fin.

Webb divided the fin-beat cycle in the seaperch into *abduction* [Fig. 15(a)], *adduction* [Fig. 15(b)], and *refractory* [Fig. 15(c)] phases. The terminology has been since adopted, although inconsistencies concerning the movements characterizing each phase do appear in the literature. Generally, during abduction, the fin is moved away from the body and downwards. It is then brought back to the body surface

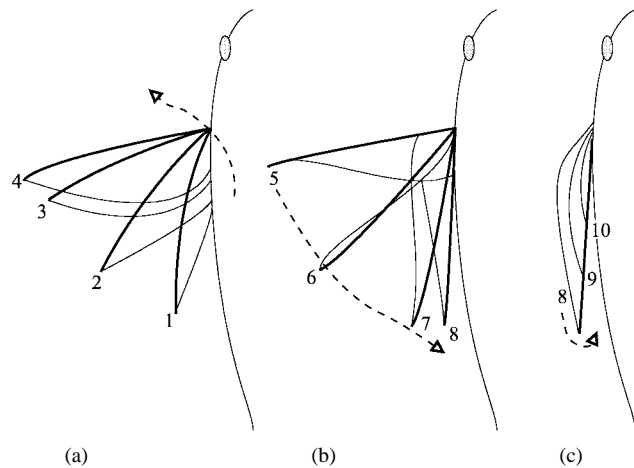


Fig. 15. Dorsal view of the fin movements in the lift-based labriform mode for the seaperch. The diagrams show how the fin trailing edge (thin line) lags behind during (a) the abduction, (b) the adduction, and (c) the refraction of the leading edge (thick line). The fish used had an average length of 14.3 cm and swam at 1.2 BL/s. (Adapted from Webb [98].)

(adduction phase) and, during refraction, the fin is orientated to its original position by rotation of the leading edge. Due to the subtlety of these movements, the angle of attack for the fin changes during each phase. As a result, the lift forces generated have an elevation as well as a thrust component that causes the body to move up and down during normal forward swimming. Additionally, thrust forces will be generated discontinuously because of the pattern of fin-beat and refractory phases. Between abduction and adduction, and during the refractory phase, no lift-based thrust is generated. Webb estimated a propulsive efficiency between 0.6 and 0.65, for it has been suggested in [99] that some small thrust could result from a jet propulsion effect during refraction as water is being displaced out of the decreasing space between the fins and the body. If present, its effect should be minimal, and the fish generally tends to accelerate during abduction and adduction and to decelerate in between. The net result of these motions is that the fish body moves relative to the flow in a figure-eight motion, whose parameters change with speed, reflecting variations in the elevation and thrust components [98]. Recent observations show that fish can smooth out their movements by complimentary actions of the other fins.

A blade-element analysis of flapping pectoral fins is given by Blake in [84]. Again, a purely lift-based labriform mode is considered and the fin is assumed to consist of a series of straight elements. The generalized applicability of blade-element theory to labriform locomotion is questioned (see [92] for a discussion), due to the curvatures and shape changes observed for the pectoral fins when a combination of lift- and drag-based methods is used, as is generally the case.

VI. SUMMARY

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.). An illustrative example can be found in the seahorse, as it is presented in [78]. The dorsal fin rays oscillate at very high frequencies (up to about 40 Hz), compared to most other species utilizing fin undulations for propulsion (rarely exceeding 10 Hz). The high fin-beat frequency is related to the short wavelength of the wave propagating along the dorsal fin of the seahorse and is associated with reduced swimming efficiency [83], [86]. To account for this, it has been suggested that it actually helps the seahorse avoid potential predators because the fin beat frequency lies beyond the fusion frequency of the predators' eyes, rendering the seahorse indistinguishable from surrounding vegetation. Therefore, when considering designs and kinematics for porting from nature to artificial systems, the significance of these nonlocomotor factors and the extent to which they have compromised performance need to be assessed. Some of these issues are addressed in Webb's recent comparative review of fish versus man-made designs [100]. Clearly, there is much to be learned from the examples that have evolved in fish. However, our capacity to utilize these evolutions is very much dependent on our ability to construct actuators and control systems that possess suitable material and motion properties. Current efforts rely on tendon- [5] or hydraulic-driven [1] mechanical links, shape memory alloys [101], ionic conducting polymer film [102], and polymer-metal composites [103], [104] as artificial muscles to implement BCF undulations. To our knowledge, no attempt has been made to mimic the structure of teleost fins (membrane and rays), and existing fin-like structures are rigid approximations [3], [105].

From our perspective, we are interested in the application of flexible actuators to the synthesis of fish propulsion mechanisms. In particular, the "elephant's trunk" actuator [106], currently under development as a finger for the AMADEUS subsea dextrous hand [107], offers potential for simple and robust implementation of devices based on either the thunniform mode or on undulating fins, for propulsive or stabilizing action, respectively. Details of design and practical results from the testbed under development will be the subject of future publications.

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