

# Morphology and Experimental Hydrodynamics of Fish Fin Control Surfaces

George V. Lauder and Eliot G. Drucker

**Abstract**—Over the past 520 million years, the process of evolution has produced a diversity of nearly 25 000 species of fish. This diversity includes thousands of different fin designs which are largely the product of natural selection for locomotor performance. Fish fins can be grouped into two major categories: median and paired fins. Fins are typically supported at their base by a series of segmentally arranged bony or cartilaginous elements, and fish have extensive muscular control over fin conformation.

Recent experimental hydrodynamic investigation of fish fin function in a diversity of freely swimming fish (including sharks, sturgeon, trout, sunfish, and surfperch) has demonstrated the role of fins in propulsion and maneuvering. Fish pectoral fins generate either separate or linked vortex rings during propulsion, and the lateral forces generated by pectoral fins are of similar magnitudes to thrust force during slow swimming. Yawing maneuvers involve differentiation of hydrodynamic function between left and right fins via vortex ring reorientation. Low-aspect ratio pectoral fins in sharks function to alter body pitch and induce vertical maneuvers through conformational changes of the fin trailing edge.

The dorsal fin of fish displays a diversity of hydrodynamic function, from a discrete thrust-generating propulsor acting independently from the body, to a stabilizer generating only side forces. Dorsal fins play an active role in generating off-axis forces during maneuvering. Locomotor efficiency may be enhanced when the caudal fin intercepts the dorsal fin wake. The caudal fin of fish moves in a complex three-dimensional manner and evidence for thrust vectoring of caudal fin forces is presented for sturgeon which appear to have active control of the angle of vortices shed from the tail. Fish are designed to be unstable and are constantly using their control surfaces to generate opposing and balancing forces in addition to thrust.

Lessons from fish for autonomous underwater vehicle (AUV) design include 1) location of multiple control surfaces distributed widely about the center of mass, 2) design of control surfaces that have a high degree of three-dimensional motion through a flexible articulation with the body, 3) the ability to modulate fin surface conformation, and 4) the simultaneous use of numerous control surfaces including locating some fin elements in the downstream wake generated by other fins.

The ability to manufacture an AUV that takes advantage of these design features is currently limited by the nature of available materials and mechanical drive trains. But future developments in polymer artificial muscle technology will provide a new approach to propulsor design that will permit construction of biomimetic propulsors with conformational and articulation flexibility similar to that of fish fins.

**Index Terms**—Fin, fish, hydrodynamics, locomotion, particle image velocimetry.

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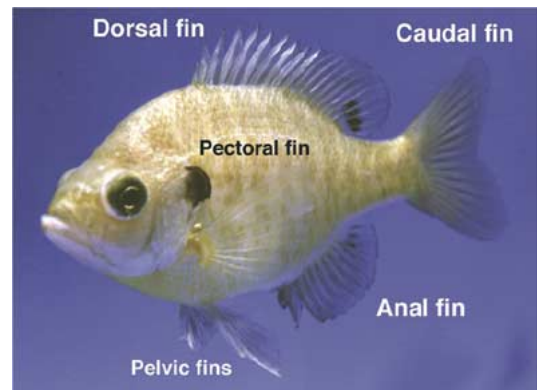


Fig. 1. Photograph of bluegill sunfish (*Lepomis macrochirus*) showing the configuration of median and paired fins in a representative spiny-finned fish.

## I. INTRODUCTION

**D**URING the last 520 million years, the process of evolution has produced a diversity of nearly 25 000 species of fish [1]. This diversity includes thousands of different fin designs that are largely the product of natural selection for locomotor performance. Many species of fish possess fins that display remarkable locomotor properties. For example, the tail of scombrid fish (tuna and relatives) is a high-performance hydrofoil allowing rapid propulsion [2]–[6]. Dorsal and caudal fins of fish may interact hydrodynamically to enhance thrust production, and dorsal fins are used by fish to generate off-axis forces during turning maneuvers [7]. The paired pectoral fins of teleost fish function as flexible foils under complex motor control that permit high performance swimming and maneuvering [8]–[14], while pectoral fins of other species such as sharks and sturgeon function to enhance maneuverability and induce low speed maneuvers [15]–[17]. And the elongate ribbon-like fins of knifefish and triggerfish function as undulatory propulsors distinct from the body [18]–[21]. It is thus natural to consider the fins of fish generally, and pectoral fins in particular, as a model system for one design component of a biorobotic autonomous undersea vehicle.

One hallmark of fish propulsive systems is the use of multiple control surfaces, and the diversity of fish fins can be divided into two major groups: paired and median fins (Fig. 1). Most fish have a total of at least seven separate fins, although this number can be considerably more in fish with multiple dorsal fins or finlets located in front of the tail. There are commonly four paired fins, consisting of the pectoral and pelvic fins with one fin of each type located on each side of the body. There are typically three median fins: a dorsal, anal, and caudal (tail) fin. Steady rectilinear propulsion may be achieved through the

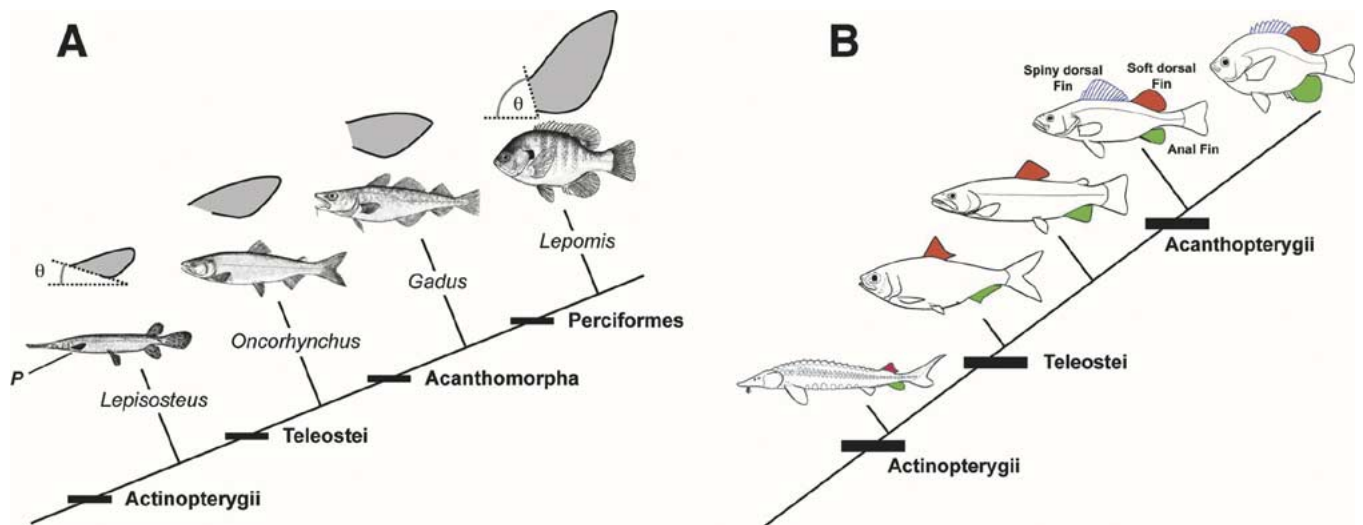


Fig. 2. Major phylogenetic patterns to paired and median fin structure in ray-finned fish (Actinopterygii). (A) Evolution of pectoral fin orientation on the body. *P*, pectoral fin;  $\theta$ , angle of pectoral fin base. (B) Evolution of median fin design. The soft dorsal fin is shown in the anal fin in red and green. [(A) after [34]; images in (B) modified from [99].]

use of just the pectoral fins [9], [10], [22], [23], via the dorsal and anal fins alone [18], [21], [24], or through primary use of the body and caudal fin [25]–[28]. In addition, propulsion can involve use of multiple fins simultaneously [7], [13], [29], [30].

Maneuvering by fish usually involves coordinated use of both median and paired fins (as well as body bending), and the complexity of interactions among fins and the hydrodynamic roles of different fins in generating propulsive movements has only recently been studied [7], [12], [31], [32].

In this paper we provide an overview of the anatomy of both median and paired fins in fish and review recent progress in understanding the hydrodynamic function of fish fins with a focus on fin function during both horizontal and vertical maneuvering. Lessons learned from studies of fish hydrodynamics relevant to autonomous underwater vehicle (AUV) design are summarized in the last section.

## II. MORPHOLOGY OF FISH FIN CONTROL SURFACES

### A. Overview of Fish Control Surface Design

Major patterns to the diversity of median and paired fins in fish have been documented in the literature for nearly 100 years, and seven key trends stand out as relevant to this overview of fish fin structure and function (Fig. 2). The first three trends relate to paired fin function, while the last four focus on median fins.

- 1) Pectoral fins are positioned at the ventrolateral margins of the body in basal ray-finned fish (and in sharks), while in more derived species the pectoral fins are located laterally on the side of the body [Fig. 2(A)] [33]. This lateral positioning may enhance yaw maneuvering relative to fish with ventrolateral fins, but this hypothesis has yet to be quantitatively tested [34].
- 2) The orientation of the pectoral fin base is more horizontal in fish with ventrolateral fin positions (such as sharks and sturgeon) and becomes more vertically oriented in the spiny-finned fish [Fig. 2(A)]. This change in fin base orientation may be correlated with the ability to direct pectoral fin forces in both horizontal and vertical planes and

hence contribute to enhanced maneuverability, but again this hypothesis has only been tested in a preliminary way [34].

- 3) In basal ray-finned fish and sharks the pelvic fins are located at an approximately mid-body position, posterior to the center of mass [Fig. 2(A)], while in more derived ray-finned fish the pelvic fins have moved anteriorly and are located beneath the center of mass (e.g., [33], [35], [36]). This transformation repositions the pelvic fins so that they have little effect on body yaw when used simultaneously but are capable of inducing roll movements. The hydrodynamic function of pelvic fins in fish remains virtually unstudied with the sole exception of the excellent early work of Harris [37], [38].
- 4) The tail of sharks and sturgeon is heterocercal in shape, with an asymmetrical morphology around the horizontal body axis. The vertebral column bends into the upper tail lobe which is larger and extends further posteriorly than the ventral lobe [Fig. 2(B)]. The trailing edge of the heterocercal tail is inclined to the horizontal and this has a significant impact on the orientation of vortex rings shed into the wake [39]. This contrasts with the evolutionarily derived condition of a homocercal tail, seen in teleost fish, in which the tail is externally symmetrical about the horizontal axis with a vertical trailing edge [30], [40].
- 5) Within most species of more derived teleost fish, the trailing edge of the dorsal fin is located posteriorly compared to its midbody location in more basal species. For example, in trout the dorsal fin is located just posterior to the center of mass in a midbody position, while in sunfish or perch the dorsal fin trailing edge is just anterior to the tail and located above the caudal peduncle region [Fig. 2(B)].
- 6) In teleost species such as shad or trout, the dorsal fin is supported by soft fin rays similar in character to those supporting the tail. However, in a large group of spiny-finned teleost fish (the Acanthopterygii), the dorsal fin

retains the soft portion but a new spiny dorsal fin occurs in which the fin membrane is supported by multiple rigid spines [41]. The spiny and soft dorsal fins may be attached by a thin connective tissue membrane or they may be separate [Fig. 2(B)]. During steady swimming, the spiny dorsal fin is generally folded down and is non-propulsive, but the soft dorsal fin generates both thrust and lateral forces during steady swimming, and is also important during maneuvering [7]. The function of the spiny dorsal fin has yet to be studied experimentally.

- 7) Within teleost fish, the anal fin expands in area and in many species is located posteriorly on the body ventral to the soft dorsal fin [Fig. 2(B)]. In many spiny-finned fish, the anal fin and soft dorsal are nearly equal in area and in longitudinal position along the body. In basal teleost fish such as trout, the soft dorsal fin and anal fin are offset along the length of the body and hence are likely to make unequal contributions to yaw torques during propulsion and maneuvering.

Fish pectoral fins typically range in aspect ratio (AR) from 1.5 to about 5, where aspect ratio is defined as  $\text{span}^2/\text{area}$ . Leopard shark pectoral fins, for example, have aspect ratios of approximately 1.5 [17]. Labrid fish have pectoral fins that vary in AR from 1.5 to 3.5 [14], [42], while the caudal fins of scombrid fish have ARs that range from 4 to nearly 10 [4].

### B. General Fin Morphology

Both median and paired fins of fish possess a similar structure: the fin itself is supported by elongated, segmented, thickened rods (fin rays) that articulate with basal cartilaginous elements. In sharks, these fin rays are called ceratotrichia and are composed of collagen arranged into keratinized rods. In ray-finned fish, the fin rays contain a central bundle of collagen surrounded by small segmented bony elements and are called lepidotrichia [43]. The bony segmented elements are paired, and hence each fin ray has a design similar to a bimetallic strip with two elongate bony elements separated by the central collagen core [44]. Each individual element is called a hemitrich. At the distal tip of lepidotrichia two small keratinous actinotrichia are located.

We will now separately consider the structure of paired and median fins, especially as it relates to the control of movement relevant to AUV design. Comprehensive studies of fish fin anatomy are presented in a number of previously published monographs [45]–[47].

### C. Paired Fin Anatomy: Osteology and Musculature

The pectoral and pelvic fins of fish contain muscles that control both fin position relative to the body as well as surface conformation, allowing fish to alter fin shape during locomotion. The pectoral and pelvic girdles are composed of bony or cartilaginous elements that support the fin on the body and provide a locus of fin muscle origin. In sharks, the pectoral fins are supported internally by the scapulocoracoid cartilage which in turn supports three large cartilages located inside the body

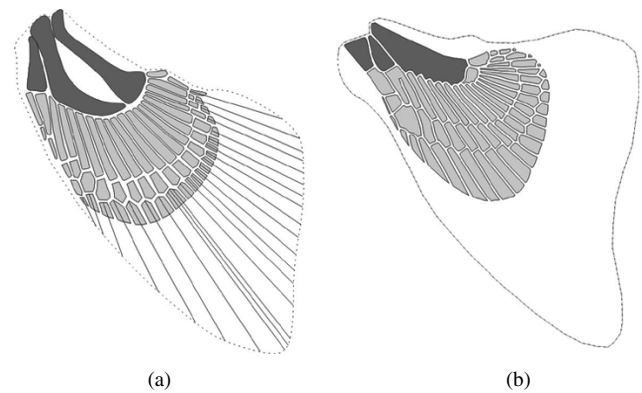


Fig. 3. Skeletal structures in the pectoral fins of (a) spotted bamboo sharks *Cephaloscyllium plagiosum* and (b) leopard sharks *Triakis semifasciata*. Note the three enlarged basal cartilages (shaded dark gray) that articulate with the pectoral girdle and the large number of small rectangular radial elements (light gray) supporting the fin rays (shown on left as thin lines). (From [15], modified from [100].)

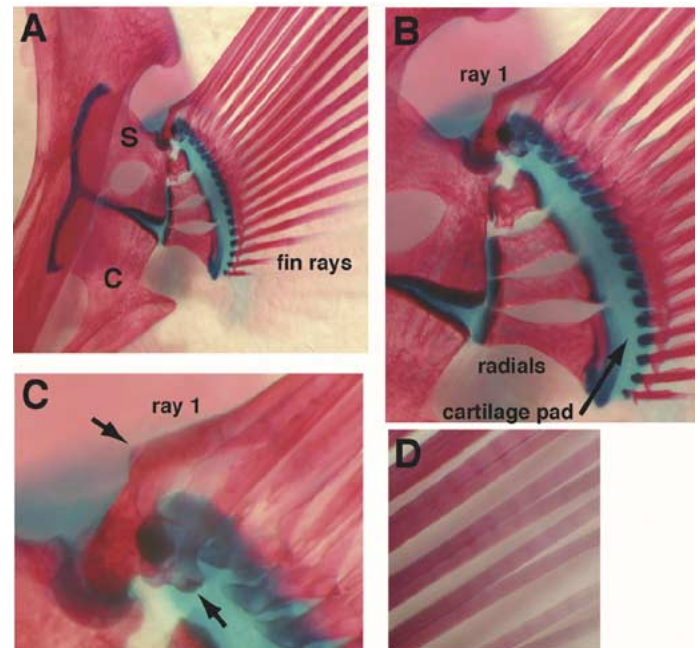


Fig. 4. Pectoral fin anatomy in fish. (A) The pectoral girdle supporting the fin rays. (B) Small hourglass-shaped bones termed radials articulate with the pectoral girdle and with a large cartilage pad that supports the heads of the fin rays. (C) All fin rays have distinct heads for muscle tendon attachment, but ray 1 is unique in having a prominent process for the arrector muscle (upper arrow) as well as a second process for adductor and abductor muscles (lower arrow). (D) Each fin ray is composed of paired segmented bony elements that are branched distally. S: scapula; C: coracoid.

wall (Fig. 3). Three rows of numerous small cartilaginous radial bones articulate with these three cartilages, the most distal row of which supports the fin rays (Fig. 3). The pelvic girdle in sharks consists of elongate cartilaginous elements oriented roughly parallel to the body axis, embedded in the body wall, which support the pelvic fin rays [48].

In ray-finned fish, the pectoral girdle is composed of large scapula and coracoid bones [Fig. 4(A)] which are anchored to the pectoral girdle medially and support the small hourglass-shaped radial elements distally. These bony radials support an elongate cartilage pad that in turn supports the proximal heads of the bony fin rays [Fig. 4(B)]. Each hemitrich has an expanded



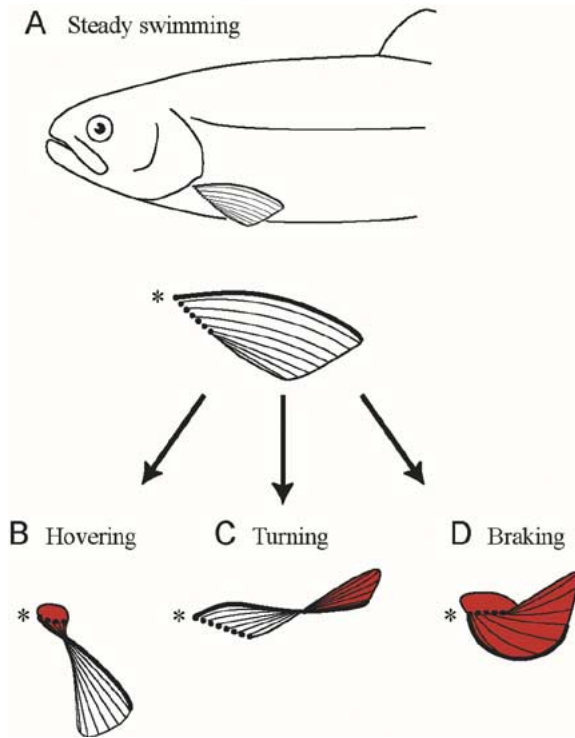


Fig. 5. Kinematic repertoire of the pectoral fin of rainbow trout. (A) During steady swimming, the fin remains adducted against the body. The enlarged image of the fin below the body illustrates the angle of inclination of the fin base (dotted line) and the first fin ray (thick line) whose proximal end is indicated by an asterisk. During maneuvering, pronounced rotation and flexion of the pectoral fin occurs. In (B)–(D), white and red areas indicate fin surfaces that face laterally and medially, respectively, when the fin is at rest in an adducted position [as in (A)]. (B) While hovering, trout twist the fin along its spanwise axis to enable fore-and-aft sculling beneath the body. (C) Turning is characterized by rotation of the fin in the opposite direction above the ventral body margin. (D) Braking involves fin rotation in the same direction as during turning, but to a greater degree such that the fin surface which faces medially at rest becomes dorsolaterally oriented. Note that the pectoral fin base rotates to a nearly horizontal orientation during maneuvering locomotion. The trout pectoral fin has considerable kinematic versatility. (From [31].)

base that serves as the site of muscle attachment. Since each fin ray is composed of two hemitrichs, there are two distinct sites at which muscles can attach, and hence rotate the fin rays around the cartilage pad supported by the radials.

An important, and generally unrecognized, element of fish pectoral fin function is the extent to which the fin base itself can be reoriented during execution of the variety of maneuvering behaviors that make up the diverse locomotor repertoire of fish. In most papers, the orientation of the pectoral fin base is taken as a general reflection of the major axis of fin rotation and is accepted as a relatively fixed parameter for each species. However, a recent study of trout pectoral fins [31] has shown that both the pectoral fin base and surface can be dramatically reconfigured during maneuvering compared to their positions during rectilinear locomotion. This surface reorientation is illustrated in Fig. 5, which shows that the trout pectoral fin can undergo extensive spanwise rotation and that the medial fin surface can be reoriented into an anterodorsal configuration during behaviors such as braking. This demonstrates that pectoral fins can be actively reoriented to execute maneuvers and that mobility of the radial elements of the fin needs to be studied if we are to fully understand the function of fish fins during maneuvering.

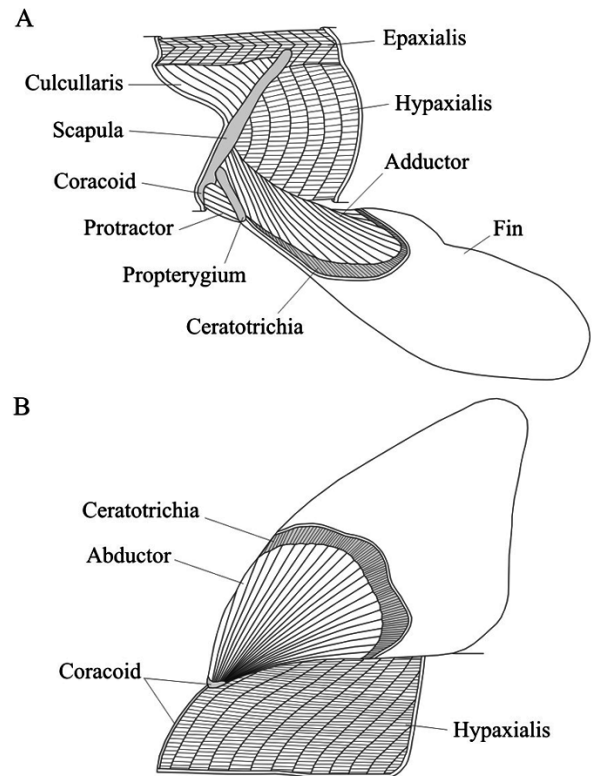


Fig. 6. (A) Side and (B) ventral views of the musculature of the pectoral fin in the spotted bamboo shark (*Cephaloscyllium plagiosum*). (From [15].)

Pectoral fin musculature allows active control of fin position. In sharks and sturgeon that have relatively low aspect ratio pectoral fins, dorsal and ventral adductor and abductor muscles control elevation and depression of the whole fin as well as allow the trailing edge to be moved in a vertical plane [16], [17]. In sharks, the adductor muscle originates from the scapula and fans out into the fin's dorsal surface to insert onto the heads of the ceratotrichia. The fin abductor originates on the coracoid and fans out posterolaterally to insert on the ventral heads of the ceratotrichia. In addition, a protractor muscle originates from the coracoid and inserts on the first (proximal) basal support (Fig. 6). This muscle allows protraction (anterior rotation) of the entire fin, extending it from the body.

Experimental studies of fin position and conformation in three dimensions as well as analysis of muscle activity patterns has shown that activation of these muscle groups allows repositioning of the fin and trailing edge and that these movements are related to control of body position during maneuvering locomotion [16], [17]. Shark fins are often held at a negative dihedral angle to the body and this angle changes as a result of adductor and abductor muscle activity during maneuvering [17]. Rays, with their expanded wing-like fins, have a complex musculature that has yet to be completely studied, but preliminary descriptions are provided by Bone [49] and Rosenberger [50], [51].

In ray-finned fish, the muscles that control the paired fins are complex [22], [45], [46], [52]. A schematic view of pectoral fin musculature is illustrated in Fig. 7 to show the major muscle groups and their lines of action. Laterally located abductor muscles originate from the surface of the cleithrum and coracoid

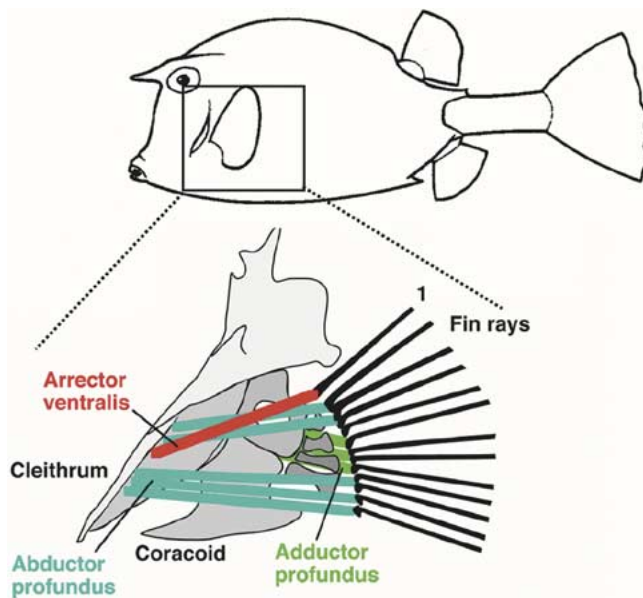


Fig. 7. Schematic illustration of major pectoral fin muscle groups. The arrector dorsalis muscle and the superficial divisions of the abductor and adductor muscles are not shown. Fish figure modified from [99].

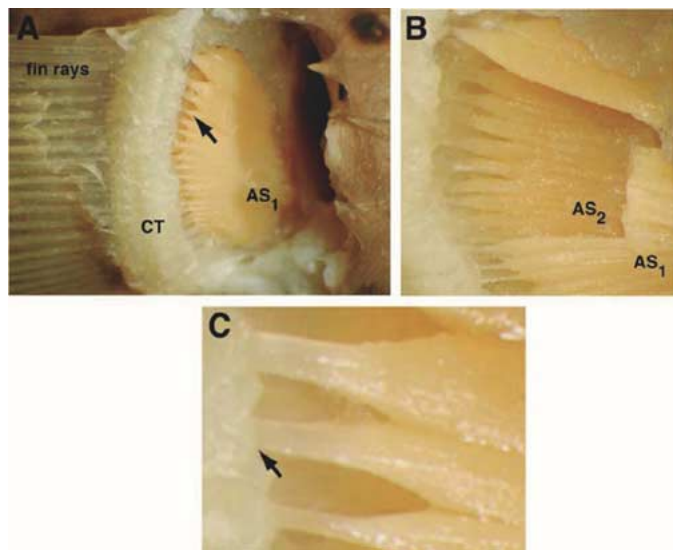


Fig. 8. Pectoral fin muscles in boxfish. (A) Just posterior to the gill opening the fin rays are covered by a large connective tissue pad (CT) that also receives tendons from the abductor superficialis (AS) muscle (arrow). (B) Dissection reveals that the AS has two distinct layers—superficial ( $AS_1$ ) and deep ( $AS_2$ ) and that each layer is itself composed of separate discrete bundles of fibers. (C) Each fiber bundle condenses to a well-developed tendon that attaches to the head of the fin ray (arrow).

bones and insert on the heads of pectoral fin rays. The abductor muscle often has separate deep and superficial sections, and each muscle group may be divided into discrete bundles that insert on the fin rays. An example of such an organization is shown in Fig. 8, in which two separate abductor muscle layers are illustrated along with a detailed view of the attachment of each discrete bundle to the fin rays. Medially located fin adductor musculature has a similar structure to the lateral abductor muscles, with two discrete layers. There are two arrector muscles (ventralis and dorsalis) that insert on the leading (first) fin ray. These muscles have a complex function, and allow expansion of the

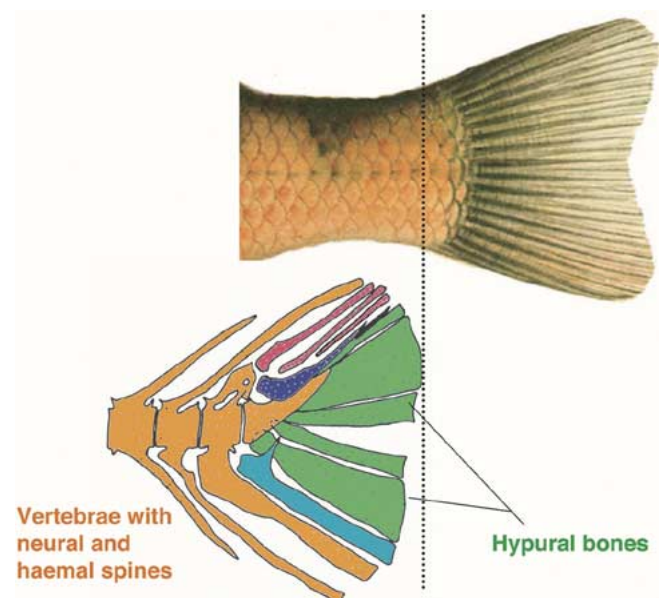


Fig. 9. Caudal fin skeleton of a sunfish to illustrate the major supporting elements of the fin rays. The axial skeleton ends at the location indicated by the dotted line. The tail proper consists of fin rays that articulate with the flattened hypural bones.

fin surface by pulling anteriorly on the first ray, accelerate and decelerate the fin, and assist in controlling dorsoventral movement of the fin [52]. The leading edge of the pectoral fin plays a critical role during locomotion, as demonstrated by kinematic analyses of fin movement which show that the first fin ray leads the remaining rays during the fin beat cycle [8], [9], [53].

#### D. Median Fin Anatomy: Osteology and Musculature

The anatomy of median fins in fish is even more complex than that of the paired fins, as numerous muscles attach to a variety of cartilaginous and bony elements. In sharks the caudal skeleton consists of unpaired expanded cartilaginous neural and haemal arches supporting the ceratotrichia [48]. The tail is heterocercal in shape in the vast majority of shark taxa [54], although several species possess lunate tuna-like tails [55]. There are currently no detailed anatomical studies of how tendons from the myotomal body musculature insert on the tail skeletal elements, or of intrinsic tail ligaments or muscle fibers (but see [4], [6], and [56]).

In teleost fish the tail skeleton is composed of median flattened hypural bones (Fig. 9) as well as flattened haemal and neural spines [56]–[58]. The distal edges of the hypural bones support a cartilage pad onto which the heads of the caudal fin rays attach. Dorsally, median epural and paired uroneural elements fill the gap between the hypurals and neural spines. Caudal fin musculature in teleost fish allows precise control of tail movement and is divided into two major layers, each with distinct muscle elements [26], [46], [56]. Dorsally and ventrally, extensions of the myotomal epaxial and hypaxial fibers insert on the smaller procurent rays anterior to the complete fin rays (Fig. 10). Paired supracarinalis and infracarinalis muscles also attach dorsally and ventrally and enable the expansion of the tail by exerting anterior force on the marginal rays. The main lateral myotomal musculature is highly modified in the region of the tail and flattens into a broad lateralis superficialis

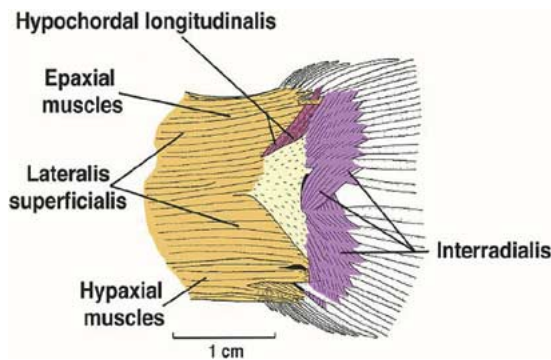


Fig. 10. Superficial dissection of the musculature controlling caudal fin rays in sunfish. The lateralis superficialis muscle is the flattened extension of the superficial myotomal (lateral body) muscles. Interradialis muscles allow caudal fin rays to be adducted (drawn together).

muscle which condenses into distal discrete bundles that attach to the heads of the caudal fin rays. Also visible in a superficial dissection of the caudal fin are the interraddialis muscles that interconnect adjacent fin rays and allow compression of the caudal fin and a reduction in fin area (Fig. 10). Deeper dissections (Fig. 11) show that teleost fish tails have numerous muscles that allow fine control over tail conformation. Deep flexor muscles separately move the dorsal and ventral fin rays, and an off-axis hypochordal longitudinalis muscle arises from the ventral tail skeleton and inserts on the dorsal-most three to four fin rays (Fig. 11). This muscle in particular allows fish to move the dorsal tail margin separately from the ventral margin, effectively turning the dorsal fin rays into a leading edge. Kinematic and electromyographic studies have shown that during steady locomotion, the hypochordal longitudinalis muscle is in fact active to tilt the caudal fin at an angle to the vertical [26]. In some fish, especially those known for high-speed locomotion such as tuna, the caudal skeleton is considerably reduced via fusion of the numerous separate elements present in more generalized species [4], [6]. In such cases, there is also considerable reduction of intrinsic tail musculature, and the hypochordal longitudinalis muscle may be absent.

Dorsal and anal fins are typically anchored in sharks by expanded cartilages termed basals, which in turn support numerous segmented radials attaching to the ceratotrichia. Some shark species have dorsal fin spines located at the anterior margin of the fin, and when such spines are present they are anchored to the basal cartilages [59]. Paired lateral sheets of muscle arise from the basals and insert on the heads of median fin ceratotrichia [48].

In the majority of teleost fish, median fins possess a more elaborate musculature, with fin ray erector, depressor, and inclinator muscles all present on each side of the body for each fin ray in the soft dorsal fin [46], [60]. The dorsal fin inclinator muscles are remarkable in their origin from the surface of the connective tissue covering the epaxial myotomal musculature, and electromyographic experiments have shown that these muscles play an active role during a wide variety of locomotor behaviors [60]. There are as yet no experimental studies of median fin erector and depressor muscles. Teleost fish thus possess considerable active control over fin height and lateral position, a fact that is critical to understanding the hydrodynamics of dorsal fin

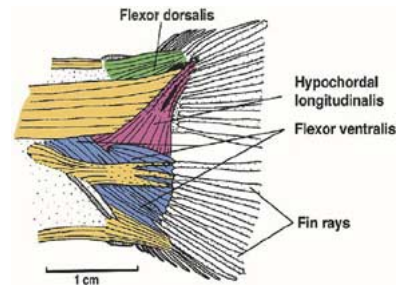


Fig. 11. Deep dissection of the musculature controlling caudal fin rays in sunfish. The dorsal and ventral flexor muscles attach to the heads of fin rays. Note especially the hypochordal longitudinalis muscle which allows asymmetrical tail function via its oblique line of action to the body axis. This muscle inserts on the four dorsal fin rays.

function described below. In fish with an anterior spiny dorsal fin, inclinator muscles are absent in the spiny region. The dorsal and anal fins in fish are supported by median bony pterygiophore elements located in between the neural and haemal spines, which are in turn embedded in the dorsal and ventral connective tissue septa [61]–[64].

### III. EXPERIMENTAL HYDRODYNAMICS OF FISH FIN CONTROL SURFACES

#### A. Overview of Experimental Approaches

Until very recently, most studies of fish fin hydrodynamic function were highly inferential, relying on patterns of fin movement, shape, or possibly the flow of dye around the fin, to infer the hydrodynamic role of fins in locomotion. The two books by Aleev [65], [66] summarize a large early literature on the biomechanics of fish fins, and describe a variety of experimental approaches used to determine the hydrodynamic function of fish fins. Of particular recent concern has been the inability to quantify the forces exerted by fins on the water, and hence the inability to determine precisely how individual fins are contributing to propulsion and maneuvering. In the last five years, experimental studies have begun to appear that examine the hydrodynamic function of fish fins using the techniques of digital particle image velocimetry (DPIV). Recent examples of such work include [5], [12], [17], [32], and [67]–[71]. This approach has made it possible to examine the function of individual fins, determine possible hydrodynamic interactions among fins, and calculate forces generated by fins during in vivo locomotion (see reviews in [72] and [73]). A schematic diagram of the experimental arrangement used to record DPIV data from freely swimming fish is presented in Fig. 12. Validation of force calculations from DPIV has been accomplished both for lift and drag forces estimated from the vortex wake of swimming sunfish and mackerel [5], [68]. In addition, quantification of wake flow patterns using DPIV has often been accompanied by detailed kinematic analyses obtained through high speed video records of fin movement taken simultaneously with DPIV data acquisition (Fig. 12). This allows correlation of wake flow patterns and fin forces with body and fin movement.

One key area in which we lack data is the three-dimensional (3-D) body trajectory analysis during maneuvering locomotion. Some three-dimensional data have recently been presented showing how the body moves during turning and braking



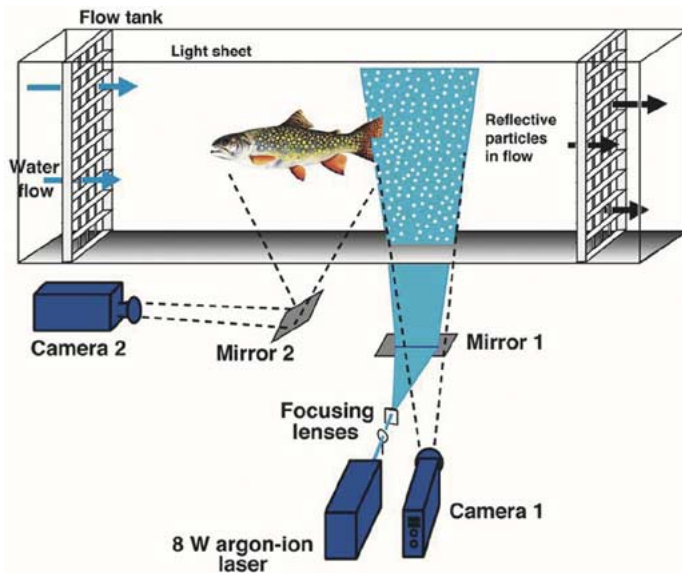


Fig. 12. Schematic diagram of experimental arrangement used to study the hydrodynamics of fish fins during in vivo locomotion. Fish swim in a recirculating flow tank with either median or paired fins intercepting a laser light sheet to allow quantification of wake flow patterns. Two simultaneous video systems are used: one images the fish and fin movement and the second captures images of the fin wake.

maneuvers in trout [31], but a much wider variety of data on different species performing a diversity of locomotor behaviors would be of considerable value in understanding how forces generated by fish fins control maneuvering and stability in fish.

Below we review recent data on the experimental hydrodynamics of fish fin function, treating separately studies done on the paired and median fin control surfaces. Hydrodynamic function is intimately tied to kinematic patterns, and although details of fish fin kinematics are reviewed elsewhere in this volume [74], we will address kinematic data here where needed to interpret hydrodynamic function.

### B. Function of Paired Fins

This section will focus on the function of pectoral fins as very little is known about the function of pelvic fins. Gosline [33], Harris [37], and Breder [21] present hypotheses of pelvic fin function based on anatomy and simple models, but no experimental hydrodynamic analyses of pelvic fin function have yet been conducted. From recent analyses of turning and maneuvering in fish it is clear that fish actively use their pelvic fins as control surfaces during turning maneuvers (see [31, Fig. 3]), but there are currently no quantitative hydrodynamic analyses of pelvic fin function in any species of fish. Hence, the remainder of this section will focus on pectoral fin control surfaces for which there is a growing body of experimental hydrodynamic data that addresses maneuvering behaviors.

1) *Pectoral Fin Function in Sharks and Sturgeon:* Sharks and sturgeon are characterized by relatively ventrolaterally located pectoral fins with a horizontally oriented body attachment and aspect ratios, in most species, of 1.5–2.5, although some pelagic shark species may have pectoral fin aspect ratios as high as 5. Pectoral fins in the majority of shark and sturgeon species have the appearance of lateral wings which, according to classical textbook hypotheses, function to enhance body stability

and to generate lift during rectilinear locomotion [75]. Under this view, ventrolateral wing-like pectoral fins function as relatively static hydrofoils that generate lift to counter the moments induced by lift force generated by the heterocercal tail (see review in [76]). This classical view of pectoral fin function has received some support from video analyses of sharks swimming in large aquaria which show that the fins may be held in a configuration concordant with the hypothesis that lift is produced during steady swimming [77].

Harris [38] conducted extensive wind-tunnel tests on the stability of a model dogfish shark in which pectoral fins (as well as dorsal, caudal, and pelvic fins) were sequentially added and removed to examine their effect on body pitch and yaw moments. This exemplary early work provides a wealth of hypotheses for experimental test today. But as Harris himself noted, the positions of the fins used for his analysis were fixed and need not correspond to fin positions in freely swimming sharks. In addition, Harris performed fin amputation experiments and noted that pectoral fin amputation produced a significant disturbance in body pitch control.

However, laboratory studies of both three-dimensional kinematics and water flow patterns in the wake of pectoral fins in shark and sturgeon species show that pectoral fins undergo complex active changes in three-dimensional conformation during locomotion (Fig. 13). During steady rectilinear swimming the pectoral fins are held at a slight negative angle of attack and lack downwash behind the fin [15]–[17]. The pectoral fin in leopard sharks, for example, is cupped in a concave-downward configuration with a mean chord angle of  $-5^\circ$  during steady horizontal locomotion (Fig. 4) [17]. This is a very different position of the pectoral fins than that used by Harris [38] in his studies of shark casts. Furthermore, electromyographic analysis of sturgeon pectoral fin musculature shows that effectively no muscle activity is present in the pectoral fin muscles during rectilinear swimming, although fin muscles are active to reorient the trailing edge to effect maneuvers [16]. These data suggest that the pectoral fins of shark and sturgeon species studied to date do not generate lift during propulsion, in contrast to the classical view. The key finding from the research on pectoral fin function in freely swimming sharks and sturgeon is that these low-aspect ratio pectoral fins are used primarily for maneuvering locomotion, to effect changes in body orientation relative to incident flow. Indeed, analyses of pectoral fin conformation and wake flow patterns show a very good correlation between fine movement and alterations in body pitch [17]. An important additional finding is that the pectoral fins are held at a significant negative dihedral angle relative to the body. In this position, the pectoral fins are predicted to destabilize the body during propulsion and promote instability [17]. While this may necessitate corrective movements from other fins during steady propulsion, the negative dihedral pectoral fin angle enhances maneuverability, a critical function that is discussed in more detail below.

The new view that emerges of elongate-body fish such as shark and sturgeon with low-aspect ratio fins is that these species are designed to be unstable. Fin position on the body and activation by fin muscles are related to maneuvering both horizontally and vertically. A corollary of this point is the demonstration that the overall force balance during locomotion occurs via

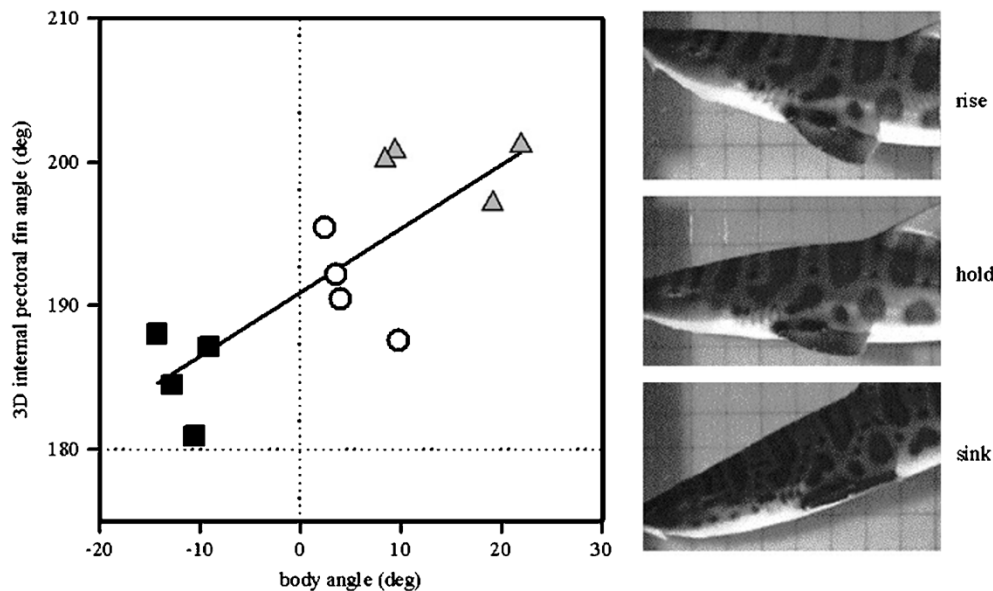


Fig. 13. Graph of three-dimensional internal pectoral fin angle versus body angle for each of three locomotor behaviors during locomotion at 1.0 body lengths per second. Circles indicate steady propulsion, triangles show upward vertical maneuvering, and squares show maneuvering toward the bottom. Each point represents the mean of five sequences for each of four individuals. Images to the right show sample head and pectoral fin positions during rise, hold, and sink behaviors. Pectoral fin angles equal to  $180^\circ$  indicate that the fin is planar in shape with no appreciable internal deformation; angles less than  $180^\circ$  show that the fin surface is concave dorsally; angles greater than  $180^\circ$  indicate that the fin surface is concave ventrally. The 3-D internal pectoral fin angle is significantly different among the three maneuvering behaviors. (From [17].)

modulation of body angle. Sharks and sturgeon swim horizontally with their body held at a constant positive angle of attack ( $5$  to  $10^\circ$ ). Body torques are balanced (without use of pectoral fins) to achieve this [16], [39]. Alteration of body angle (pitch) during vertical maneuvering occurs by active changes in pectoral fin conformation which induces positive and negative anterior torques about the center of mass to reposition the body (by altering pitch) for vertical movement.

To date, experimental hydrodynamic work on shark and sturgeon pectoral fins has demonstrated their role in inducing changes in body pitch, effecting roll, and maintaining body trim during propulsion. No data are yet available on how these fish control yaw movements, which may be primarily induced by changes in bending of the body and hence effected by the lateral myotomal musculature.

Sharks also use their pectoral fins to aid in maintaining station on the bottom in a current. Strong elevation of the posterior margin of the pectoral fins generates clear vortical structures in the wake, which produce force pressing the shark toward the bottom [15].

**2) Pectoral Fin Function in Teleost Fish:** Teleost (bony) fish which use their pectoral fins extensively for propulsion and maneuvering typically have shorter body lengths (relative to fin length) than sharks and sturgeon. Within the bony fish there is considerable variation in pectoral fin design, ranging from the ventral fin position with a relatively horizontal fin base seen in basal taxa (such as trout) to a more lateral fin position with a relatively vertical fin base seen in perch-like fish such as sunfish [34, Fig. 2A]. While much has been made of fin base orientation as an indicator of potential fin motion, it is clear from recent experimental work that most fish can actively reorient the pectoral fin to a previously unsuspected degree during the natural range of fin movement that accompanies their diverse locomotor

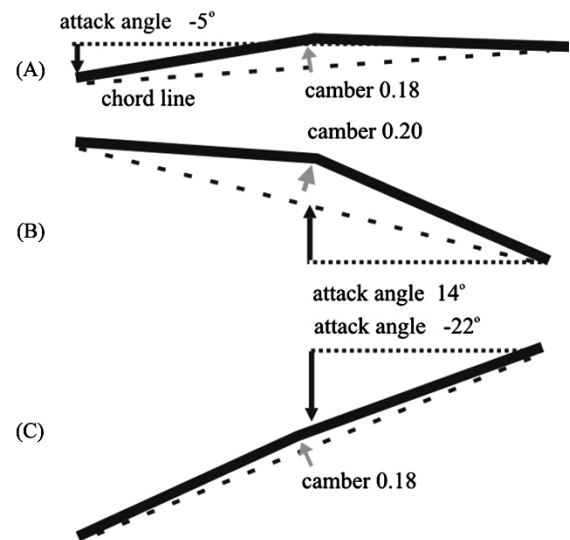


Fig. 14. Schematic diagram of pectoral fin chord, camber, and orientation during hold, rise, and sink behaviors in leopard sharks. Note that during steady horizontal swimming (holding behavior) the pectoral fin has a negative angle of attack and is inclined downward with respect to the flow which is parallel to the horizontal dotted line. The angle of attack is measured between the chord line (dashed line) and the flow (dotted line). From [17]. (A) Hold, (B) rise, and (C) sink.

repertoire [31]. This appears to reflect motion of the radial bones at the base of the fin. During maneuvering in trout, for example, the fin base may rotate up to  $30^\circ$  (see Fig. 5). This movement is most likely the result of fin ray 1 rotating on its socket joint with the scapula to depress the leading edge of the fin, while the posterior fin rays are relatively elevated via posterodorsal rotation of the distal radials (Fig. 4).

During steady swimming in microturbulent flow, the pectoral fins may be completely inactive in species such as trout [31],



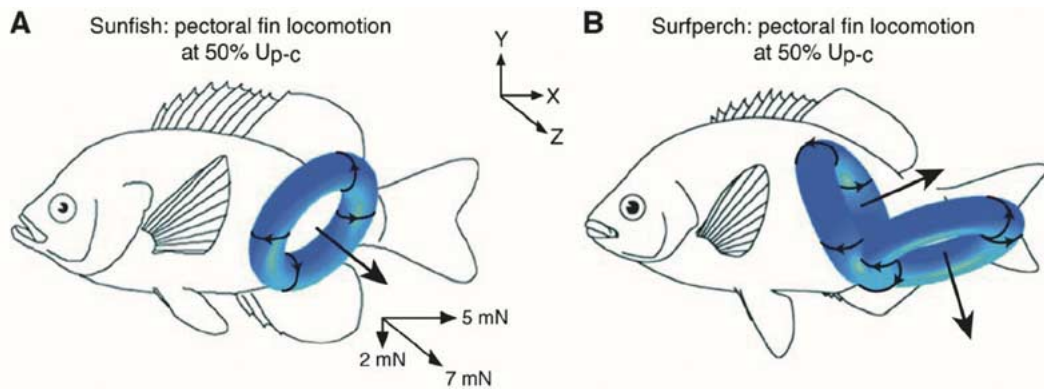


Fig. 15. Vortex wakes of sunfish and surfperch swimming with their pectoral fins. Vortex generation is a hallmark of fluid force production, and fish fins shed vortex rings into the wake during locomotion. (A), (B) Bluegill sunfish and black surfperch swimming at 50% of their maximal pectoral-fin swimming speed  $U_{p-c}$ ; curved arrows represent vortices observed in vertical and horizontal laser light sheets. These species shed wakes consisting, respectively, of discrete vortex rings and linked vortex rings, each with central high-velocity jet flow (large straight arrows). Average wake force components calculated from DPIV data for the left pectoral fin of sunfish are shown in A. (From [79].)

TABLE I  
KINEMATIC AND HYDRODYNAMIC MEASUREMENTS FOR PECTORAL-FIN TURNING BY BLUEGILL SUNFISH AND RAINBOW TROUT

Measurement	Sunfish	Trout	<i>t</i> -value
Angular velocity of body rotation (degrees $s^{-1}$ )	10.9±2.0	13.5±2.4	-0.75 (34)
Wake jet angle (degrees)	91.6±5.5	121.4±5.0	-3.15* (27)
Wake momentum, lateral component (g cm $s^{-1}$ )	1151.7±245.0	42.6±8.8	4.25* (15)
Force, lateral component (mN)	20.9±6.5	2.7±0.9	2.61* (15)
Lateral force/Fin area (mN $cm^{-2}$ )	2.9±0.9	0.8±0.3	2.07* (15)

Data tabulated as mean±S.E.M.. Interspecific comparisons made with unpaired *t*-tests (asterisks indicate significant differences at the Bonferroni-adjusted  $\alpha=0.01$ ; degrees of freedom shown in parentheses).

Wake measurements are from frontal-plane velocity fields. Jet angle is measured relative to longitudinal body axis. Wake forces are stroke-averaged measurements reported per fin. Dividing lateral force by fin area corrects for interspecific variation in propulsor size (mean pectoral fin area in sunfish and trout: 7.2 and 3.2  $cm^2$ , respectively).

or fish may swim steadily using only their pectoral fins [8], [9], [22], [53], [68], [78], [79]. In trout, the introduction of turbulence or well-defined vortical structures can induce pectoral fin activity which is correlated with corrective motions that aid fish in maintaining station in vortex streets [80].

To date, experimental hydrodynamic data are only available for two species of fish that swim steadily using their pectoral fins: sunfish and surfperch [68], [79]. In these species, each fin beat generates either a single or double vortex ring depending on speed (Fig. 15). The most striking finding from these studies is the relatively high lateral force generated by the fin during propulsion. In sunfish, lateral force exceeds thrust force when fish swim at 0.5 L/s. For example, a 20-cm-long sunfish swimming at 10 cm/s generates with each pectoral fin a thrust of 5 mN, lift of 2 mN (to balance body weight), and lateral force of 7 mN (Fig. 15). As propulsive speed increases, sunfish rotate vortex rings laterally (presumably to increase stability) and lateral forces increase. Thrust generated by the pectoral fins decreases nearly to zero, and the thrust force necessary to counter drag is produced by other fins, primarily the tail.

During low-speed yawing maneuvers in sunfish, there is significant differentiation between the hydrodynamic function of the pectoral fins on each side of the body [12]. If a stimulus is presented on the left side of a sunfish, the fish will execute a yawing turn to the right. The left pectoral fin generates a laterally directed force, anterior to the center of mass, that yaws the

body to the right. Then, the right-side fin generates a posteriorly directed force that acts to translate the fish away from the stimulus. This decoupling of hydrodynamic function between left- and right-side fins is a key mechanism by which fish execute turning maneuvers which include both pure yaw as well as translation. In trout, the pectoral fins play a generally similar role but generate less force than in sunfish, even when adjusted for interspecific variation in fin area (Table I). However, trout invariably also generate negative thrust with their pectoral fins when turning as a significant component of pectoral fin force is directed anteriorly. This may be due to the relatively horizontal orientation of the pectoral fin which necessitates an elevation of the trailing edge and cupping of the fin to generate yawing movements.

The hydrodynamics of braking have been studied in sunfish and trout [31], [34]. Fish may execute braking maneuvers in response to a stimulus in front of them, but also in the course of natural behaviors such as feeding. When sunfish capture prey, for example, they brake as they open their mouth to position themselves accurately relative to the prey. Both pectoral fins move rapidly and synchronously out from the body and generate a well-defined anteroventrally directed jet that rapidly stops body motion. The reaction force to this braking movement is directed through the center of mass of the sunfish, which thus do not experience any rotational moments as a result of braking (Fig. 16). This supports the hypothesis

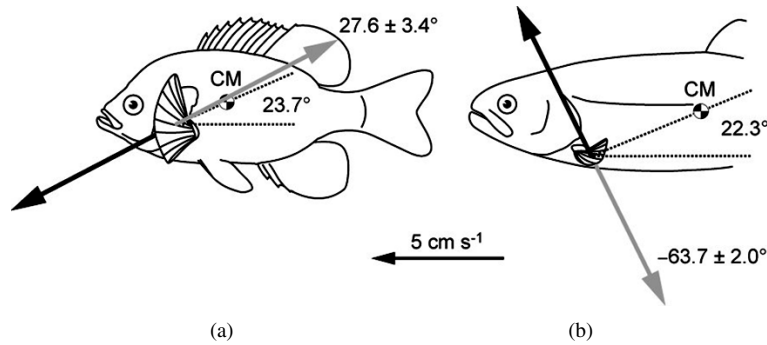


Fig. 16. Interspecific comparison of pectoral fin braking jet velocity and force orientation in (a) sunfish and (b) trout. Average orientation of the braking-force line of action (with standard error of the mean), defined by the mean momentum jet angle. Black vectors represent braking forces; gray vectors denote reaction forces. Dashed lines indicate the angle of inclination of the center of mass of the body (CM) above the horizontal. In sunfish, the reaction force experienced by the pectoral fins during braking is directed through the center of mass. In trout, braking induces pitching of the body as the reaction force is directed nearly  $90^\circ$  to the center of mass moment arm. (From [34].)

of Harris [81] who first proposed that perch-like fish might direct pectoral fin reaction forces during braking through the center of mass. In trout, however, braking is accomplished by a dorsal cupping of the fin and elevation of the posterior fin margin. The fluid jet produced from this movement is directed anteriorly and dorsally, and the reaction force thus has a large pitching moment about the center of mass. As a result, trout do not show a pure braking movement and invariably braking is accompanied by downward movement of the body [31]. Trout use other fins (pelvic, anal, and dorsal) to compensate for pitching movements during braking.

Fish also hover with their pectoral fins although invariably other median and paired fins are also involved in maintaining body position which results from a balance of forces among all fins. To date, the only experimental hydrodynamic analysis of hovering behaviors is for trout [31]. Trout hover using alternating movements of their left and right pectoral fins which are held below the body and twisted along their length. Hovering appears to be the only behavior in trout during which the pectoral fins generate positive thrust. During hovering, alternating left and right fin movements result in one fin generating positive thrust while the opposite fin generates negative thrust. Hovering pectoral fin movements also likely generate downward force to counter body weight.

An additional pectoral fin behavior exhibited by teleost fish is benthic station holding [82]–[84]. Trout, for example, attempt to maintain station while on the bottom by cupping their pectoral fins in a manner very similar to that described above in sharks.

The first well-developed computational research on pectoral fin function was the blade-element approach taken by Blake and his colleagues (e.g., [85]–[87]). This work provided valuable predictions for experimental measurements and formed the theoretical framework for early kinematic work [8]. Modern computational fluid dynamic research on fish pectoral fin function has just begun, but initial results are promising [88]. The ability to compute, in three dimensions, fluid flow patterns and fin forces and to manipulate fin shapes and movement patterns interactively would represent a considerable advance. Detailed kinematic analyses are needed (e.g., [22], [53]), however, to provide inputs into computational models, and to date no models have addressed maneuvering locomotion.

Experimental hydrodynamic work to date has focused on the structure of the wake and fin-stroke averaged forces as a means of understanding basic mechanisms of finned propulsion. As a result, we have effectively no data for any species on the pattern of fluid flow over the fin surface and on instantaneous forces at times within the fin beat cycle. Thus, the fluid dynamic mechanisms by which fin surface pressures and fluid flows are generated remain largely unknown.

Based on their experimental data on sunfish pectoral-fin wake flow patterns and the experimentally determined vortex ring structures that result from fin movement, as well as previous three-dimensional kinematic data on the same species [8], Drucker and Lauder [68] presented hypothesized mechanisms by which the pectoral fin generates locomotor forces (see [68, Figs. 8 and 9]). These mechanisms can be summarized as follows. As the sunfish pectoral fin beat begins, the fin is oriented vertically and held flat against the body. The leading edge of the fin peels off the body and moves down and to the side [ventrolaterally, as seen in Fig. 17(A)]. As this occurs, a leading edge vortex (LEV,  $a$ ) is hypothesized to develop and remain attached throughout the majority of fin abduction. This LEV forms a center of low pressure on the anterior third of the pectoral fin which contributes to both lift and thrust as the leading edge fin ray pulls the fin ventrally and anteriorly. Most fish, including sunfish, are not neutrally buoyant and lift is required to balance body weight. As the entire fin is abducted, a trailing region of high vorticity (the tip vortex) is shed leaving behind a counterclockwise vortex  $P1$  [Fig. 17(A)], which has been visualized experimentally. Kelvin's theorem dictates that the circulation in  $a$  and  $P1$  are equal and opposite in magnitude.

As the fin decelerates [Fig. 17(B)], water begins to circulate in a clockwise direction around the trailing edge due to both the acceleration reaction and fin rotation (Fig. 17(C)). This results in a strong clockwise circulation  $P2$ . As the fin completes its rotation and begins the upstroke, two additional centers of circulation are shed.  $P3$  has the same sense as  $P2$  and merges with it to form a single large vortex [Fig. 17(D)]. If fin adduction is strong during higher speed pectoral fin swimming,  $P4$  is shed as a discrete vortex center and forms part of a second linked ring [68]. The upstroke also involves production of the central fluid jet through the center of the vortex [Fig. 17(E), light gray

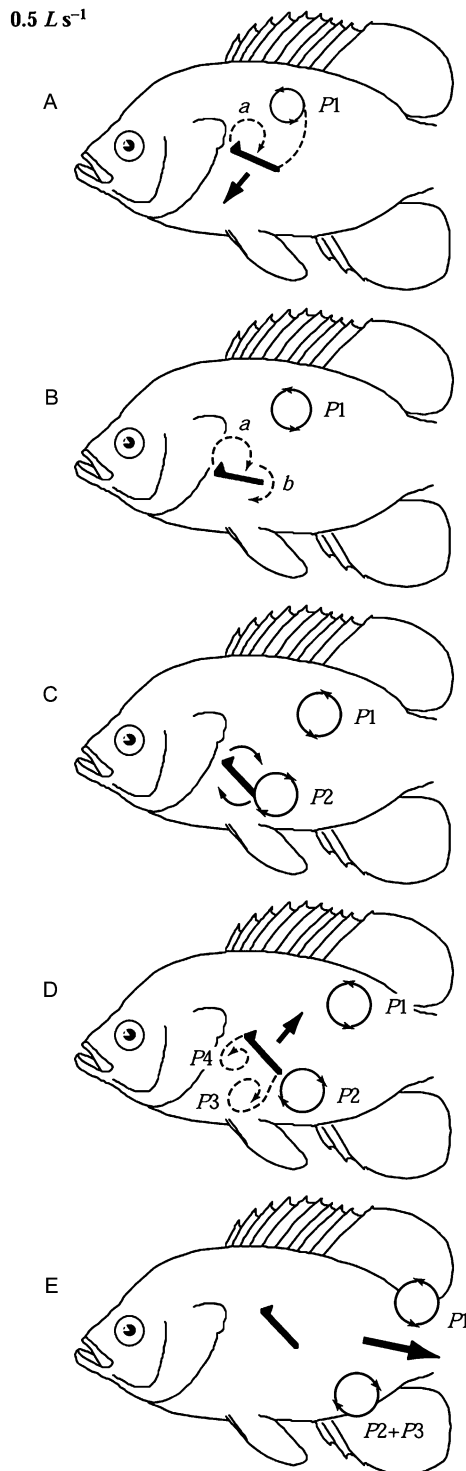


Fig. 17. Schematic hypothesis of the primary mechanism of force production by the pectoral fin of bluegill sunfish during steady rectilinear locomotion at 0.5 L/s. Thin black arrows indicate the direction of fin movement; light gray arrow shows final high-velocity jet through the center of the shed vortex ring. *a* attached leading edge vortex; *b* clockwise flow around fin trailing edge induced by acceleration reaction; *P1*, *P2*, *P3* vorticity shed in the parasagittal (vertical) plane. (Modified from [68].) (A) Early downstroke  $t = 136$  ms, (B) end of downstroke  $t = 288$  ms, (C) stroke reversal  $t = 338$  ms, (D) early upstroke  $t = 464$  ms, and (E) end of upstroke  $t = 592$  ms.

arrow] as the fin approaches the body. This could be viewed as a drag-based component of thrust production by the fin.

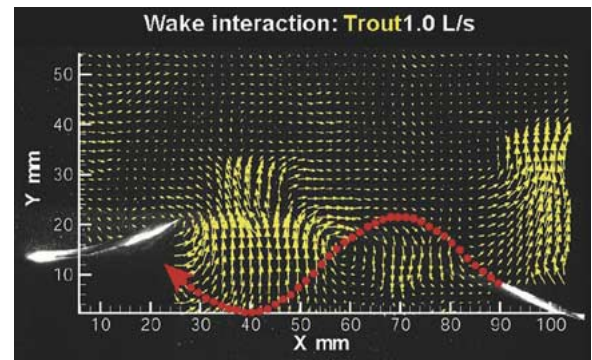


Fig. 18. Results from a DPIV analysis of the dorsal fin wake in rainbow trout swimming steadily at 1.0 L/s. Red dots show the path of the tail which passes directly through the centers of shed dorsal fin wake vortices. During turning maneuvers, the trout soft dorsal fin generates a strong unilateral vortex ring. In sunfish the tail encounters significantly increased wake flow and vortices shed from the dorsal fin are staggered in the classical reverse Karman pattern.

The asymmetry of upstroke and downstroke motion is important to this mechanism, as is the fin position starting near the flat body. This hypothesized mechanism of force production involves both a high-lift mechanism via the LEV, and drag-based production of the central vortex jet, but most aspects of this proposal remain to be confirmed experimentally.

### C. Function of Median Fins

The median fins of fish can be considered as three separate control surfaces, or groups of control surfaces, consisting of the anal, dorsal, and caudal fins. In many fish, as discussed further below, the dorsal fin may be separated into two or more discrete fins. While this section will largely treat each of these groups of fins separately to facilitate discussion of the experimental hydrodynamic data, in freely swimming fish the median fins function in concert. For example, Breder [21] illustrated a common pattern of median fin use in perch-like fish during braking in which the dorsal and anal fins are curved to one side while the tail is curved to the opposite side. This results in laterally symmetrical forces on the body and allows braking without yaw or pitch. Furthermore, there are hydrodynamic interactions that potentially could result from flow over the dorsal and anal fins subsequently encountering the tail. This aspect of integrated median fin function is treated in more detail below.

Virtually nothing is known about anal fin function, and so we will focus on the locomotor roles of the dorsal and caudal fins. However, recent experiments on dorsal fin function have suggested a number of explicit hypotheses involving anal fin function and its role in maintaining body stability, and these are discussed below.

*1) Dorsal Fin Function:* The dorsal fin of fish plays an active role during both propulsion and maneuvering (e.g., [13], [89]–[91]). Experimental measurement of muscle activity in dorsal inclinator muscles during a variety of locomotor behaviors has shown that these muscles are active to move the soft portion of the dorsal fin during steady swimming, turning, and braking [60]. A key point is that the dorsal fin of fish cannot be treated as simply an extension of the body, moving in phase with and at the same frequency as the body surface at the equivalent longitudinal position. Rather, the soft dorsal fin



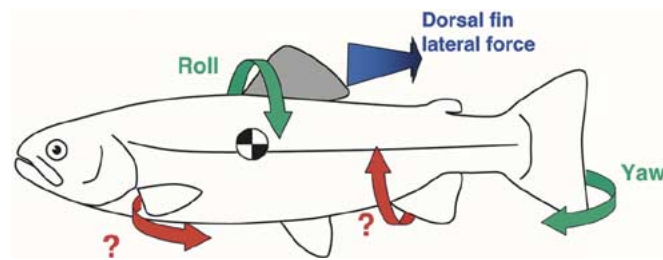


Fig. 19. Schematic diagram to illustrate the overall body balance of torques required by new data showing that the trout dorsal fin generates lateral forces during propulsion. Compensatory torques must be generated by the tail, anal, and pectoral fins, although values for these torques are currently unknown.

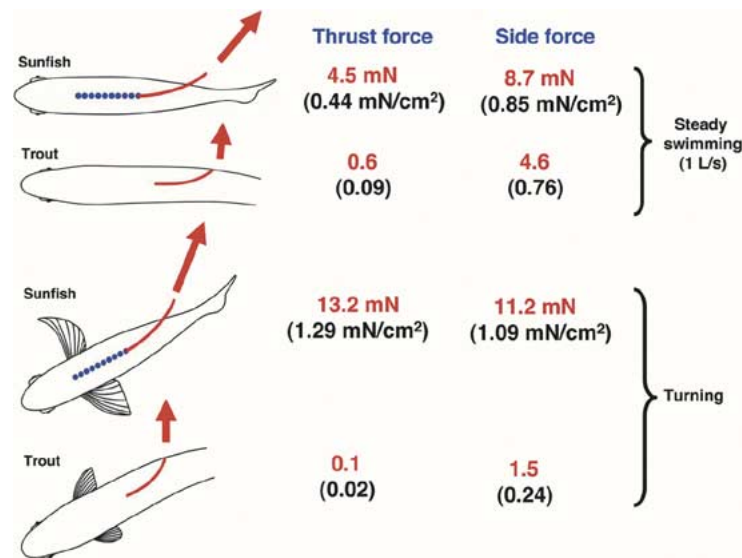


Fig. 20. Summary of experimentally measured dorsal fin forces in trout and sunfish during steady swimming and maneuvering locomotion. Normalized values (force per unit fin area) are given in parentheses.

of fish functions as its own active control surface independent of the body, and the trailing edge of the dorsal fin thus sheds vorticity in patterns not well predicted by simply considering the dorsal fin as moving with the body.

In trout, the dorsal fin generates strong alternating lateral jets with a negligible thrust component during propulsion (Fig. 18). The tail takes a path directly through the center of the dorsal fin's shed vortices. This result suggests that the trout dorsal fin may play a critical role in maintaining body stability during propulsion, acting to counter minor perturbations induced by oncoming flow and acting in concert with other fins, all of which are simultaneously generating opposing lateral forces and contributing to the overall force balance. One hypothesis for the action of multiple fins during propulsion that emerges from the experimental data on trout dorsal fins is shown in Fig. 19. The lateral forces generated by the dorsal fin induce both roll and yaw torques. Roll torque must be countered by action of the anal fin, while yaw torques must be countered by the pectoral fins anterior to the center of mass and by the tail posterior to the center of mass (Fig. 19). Thus, even during steady rectilinear locomotion, the median and paired fins must all be active to stabilize body position.

This view is rather different from the traditional representation of body and caudal fin based fish propulsion, with median fins functioning as ancillary thrust generators or as passive elements. In most fish, the center of buoyancy is below the center

of mass, and most fish are negatively buoyant [92]. Hence, most fish are inherently unstable and this instability is exacerbated by freestream turbulence as it is encountered by fish. As a result, carangiform swimmers such as trout need constant adjustment of torques and this is achieved by median fin lateral force generation, in addition to as yet undetermined activity of median-fin pelvic and pectoral fins.

When maneuvering, trout activate their dorsal fin to produce an asymmetrical jet flow that is aimed posterolaterally. Trout dorsal fin maneuvering forces act posterior to the center of mass to induce yawing moments (Figs. 19 and 20).

Sunfish, in contrast, generate significant thrust as well as lateral force during steady propulsion with their soft dorsal fin [7]. The dorsal fin wake is more posteriorly oriented and the tail moves through a region of altered flow angle and increased flow velocity relative to the free stream. When executing yawing turns (Fig. 20), sunfish generate substantial forces with their dorsal fin with roughly equivalent thrust and lateral components. The forces generated by sunfish are greater both absolutely when compared to same-size trout and when corrected for differences in fin area.

2) *Finlets*: Some teleost fish, notably those in the scombrid (tuna) clade, possess modified dorsal fin-like elements called finlets [6], [93]–[95]. Finlets are small nonretractable fins located on the dorsal and ventral margins of the body between the dorsal and anal fins anteriorly and the tail posteriorly. This

region is termed the caudal peduncle, and between five and 12 finlets are found on both the dorsal and ventral margins of the peduncle depending on species. Finlets are triangular in shape and possess fin rays as internal supports. In addition, the base of each finlet serves as the attachment site for tendons which are themselves attached to musculature that appears to be homologous to the inclinor, erector, and depressor muscles of generalized bony fish [93]. Finlets are thus under active control by scombrid fish, and kinematic data show that mackerel execute low-speed turns by actively reorienting finlets. Three-dimensional kinematic studies of finlet movement during propulsion and analyses of water flow over finlets in freely swimming mackerel [96], [97] have been used to test existing literature hypotheses of finlet function and suggest new hypotheses. For example, finlets may act to increase vorticity entrained into the caudal fin vortex prior to its being shed from the tail trailing edge. Even a small increase in tail vortex circulation could have significant energetic consequences given the large number of tail beats that scombrid fish execute over a lifetime of oceanic locomotion.

**3) Caudal Fin Function:** The vast majority of research on the function of the tail in fish has been directed at the role that the tail plays in propulsion, and a large amount of work on a variety of fish with a diversity of tail shapes has recently addressed the mechanisms by which thrust is generated by the tail [2], [5], [23], [30], [37], [67], [69], [74], [92]. Much of this literature has previously been reviewed [26], [30], [40], [98]. Four key points will be summarized here. First, kinematic measurements of tail conformation in freely swimming fish have shown that the caudal fin moves in a complex three-dimensional pattern, not as a single vertical flat plate with side-to-side oscillation. Even morphologically symmetrical homocercal tails in scombrid fish are inclined to the fluid as they move laterally, generating lift as well as thrust [2]. These lift forces at the tail induce torques that must be countered by holding the body at a positive angle of attack or by using pectoral fins. Second, lateral forces generated by the tail are high, frequently equaling or even exceeding thrust forces. Third, the measurement of significant streamwise momentum added to the wake of carangiform swimmers that balances expected drag forces suggests that the tail of carangiform swimmers acts like a propeller, generating thrust discretely from the primary locus of drag incurred by the body. Fourth, heterocercal tails in sharks generate inclined vortex rings with substantial downward momentum [39] fitting the classical view of shark tail function [75]. However, the heterocercal tail of sturgeon moves very differently from that of sharks [26] and as a result momentum added to the water has only a negligible lift component [32], with an overall reaction force that passes through the center of mass. This underscores the dangers in attempting to infer hydrodynamic function from external morphology alone.

The caudal fin is also important during maneuvering, as recent experiments have provided evidence that some fish can vector thrust from the tail to contribute to changes in body position during maneuvering. Evidence of thrust vectoring comes from experimental hydrodynamic analyses of sturgeon locomotion which demonstrated that these fish alter the angle between

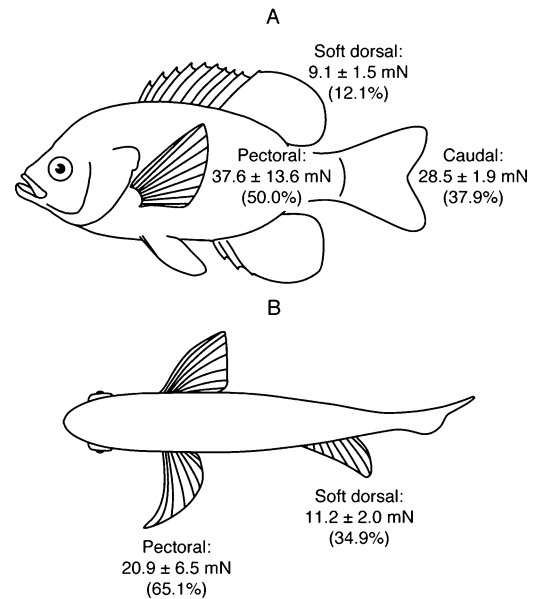


Fig. 21. Summary of the components of wake force contributed by different fins of bluegill sunfish during steady swimming and turning behavior. All forces are stroke-averaged and reported as mean  $\pm$  s.e.m. For each behavior, the percentage of total force generated by each fin is given in parentheses. (A) Thrust generated during steady swimming at  $1.1$  body length  $s^{-1}$  by the soft dorsal fin, tail and both pectoral fins together (per complete stroke cycle). (B) Laterally oriented force produced by a single pectoral fin during the early stage of a turning maneuver and by the soft dorsal fin during the latter stage of the turn. The partitioning of force among fins in A and B underlines the ability of teleost fish to use multiple propulsors simultaneously and independently during locomotion. The observed contribution of the soft dorsal fin to locomotor force (12% of thrust; 35% of lateral force) supports an active role of this fin in propulsion for perciform fish.

the body axis and vortex rings shed from the tail as they maneuver vertically and change body pitch [32].

#### 4) Hydrodynamic Interactions Among Median Fins:

Evidence from both computational fluid dynamics [91] and experimental studies of dorsal and caudal fin flow patterns [7] indicates that fish may derive a benefit in the form of increased thrust as the tail passes through the wake shed by the dorsal fin, relative to thrust generated by the tail acting alone. Presumably similar benefits will occur from anal fin wakes, although no data are available to demonstrate this. Together, the dorsal and anal fins may significantly influence flow over the tail, and demonstrating this through a combination of experimental and computational work is a key area for future research.

**5) Thrust Partitioning Among Fins:** The multiple control surfaces present on fish and their simultaneous use while they swim and maneuver indicates clearly that individual fins cannot be studied in isolation if we are to understand the complexities of maneuvering and propulsion in fish. To date, fin forces during locomotion have been measured for the caudal, dorsal, and pectoral fins in sunfish, and a summary of thrust partitioning among these fins is shown in Fig. 21. When sunfish swim at a speed of  $1.1$  L/s, they use the caudal, dorsal, and pectoral fins to generate thrust. At this speed, the dorsal fin accounts for 12%, the caudal 38%, and the pectoral fins 50% of total thrust force. The as-yet unstudied anal fin presumably contributes also to developing total thrust needed to overcome body and fin drag.

During maneuvering, both the pectoral fins and the soft dorsal fin are recruited to generate turning moments (Figs. 20 and 21). The study of thrust partitioning among fins is in its infancy, and this is a key area for future investigation.

#### IV. LESSONS FROM FISH FINS FOR AUV DESIGN

This overview of the morphology and experimental hydrodynamics of fish fin control surfaces suggests a number of implications for the design of AUVs. While practical aspects of AUV design may prohibit current implementation of all of these lessons, new technologies such as artificial polymer muscle actuators and new materials may in the future remove many current limitations. Hence, we present these “lessons learned” from fish without regard to current practicality, and as a general guide to potential benefits available from studying biological systems. The overarching conclusion to emerge from experimental study of fish fin control surfaces to date is that fish are unstable and are constantly using their numerous fins to generate opposing and balancing forces in addition to thrust. For example, the primary function of the trout dorsal fin during propulsion appears to be generation of lateral forces to assist other nonpropulsive fins in maintaining body posture.

The first lesson from experimental studies of fish fins for AUV design is to use multiple control surfaces, varying in size and shape, and distribute them around the center of mass so that large moments can be generated with relatively little force. Multiple control surfaces are present from the very origin of fish over 500 million years ago, and the versatility of this design has been proven in the remarkably diverse evolutionary radiation of fish which has occurred in part due to their ability to maneuver with precision in the three-dimensional aquatic habitat.

Second, while the shape of fins is certainly important for fine-tuning locomotor performance, the degrees of freedom of control surface movement is a far more important parameter to enhance. The direction and magnitude of force application by fish fins appears to be significantly improved by increasing the range of motion at the fin base and the ability of fin muscles to reorient the fin. The remarkable performance of fish fins is due largely to the flexibility of attachment to the body, and the consequent ability of fish to rapidly reorient the fin surface in the  $x$ ,  $y$ , and  $z$  planes to suit a variety of locomotor requirements.

Third, the ability of fish to modulate fin surface conformation greatly facilitates small adjustments in body trim and low-speed maneuvers with only minor changes in fin orientation. Fish achieve this with musculature that either attaches to discrete fin-ray elements or fans out into the fin surface itself. Fins can be undulated and trailing edges raised and lowered without resorting to gear-like systems or joints. This design permits a fine level of control that has yet to be successfully developed in current AUV technology, but one that is well suited to artificial polymer muscles.

Fourth, fish make use of multiple control surfaces simultaneously and appear able to modify the performance of one propulsor by positioning it in the wake of upstream propulsors. To the extent that AUVs are able to use similar control surface designs, they may experience enhanced performance both in propulsion and maneuvering.

Fish have a remarkably sophisticated control system for their fins that receives input from body sensors such as the lateral line and inner ear. Even mimicking only the hovering motions of a perch-like fish represents a tall technical hurdle, as all fin surfaces are in constant low-amplitude motion to control body position in space. Developing a similar control system for AUVs is likely to be a major challenge, but one that ultimately must be overcome if biomimetic AUVs are to achieve similar levels of performance to fish.

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#### REFERENCES

- [1] G. V. Lauder and K. F. Liem, “The evolution and interrelationships of the actinopterygian fish,” *Bull. Museum Comp. Zool.*, vol. 150, pp. 95–197, 1983.
- [2] A. C. Gibb, K. A. Dickson, and G. V. Lauder, “Tail kinematics of the chub mackerel *Scomber japonicus*: Testing the homocercal tail model of fish propulsion,” *J. Exper. Biol.*, vol. 202, pp. 2433–2447, 1999.
- [3] J. Donley and K. A. Dickson, “Swimming kinematics of juvenile Kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*),” *J. Exper. Biol.*, vol. 203, pp. 3103–3116, 2000.
- [4] M. Westneat and S. A. Wainwright, “Mechanical design for swimming: Muscle, tendon, and bone,” in *Tuna: Physiology, Ecology, and Evolution*, B. Block and E. D. Stevens, Eds. San Diego, CA: Academic, 2001, pp. 271–311.
- [5] J. C. Nauen and G. V. Lauder, “Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae),” *J. Exper. Biol.*, vol. 205, pp. 1709–1724, 2002.
- [6] H. L. Fierstine and V. Walters, “Studies in locomotion and anatomy of scombroid fish,” *Memoirs South. Calif. Acad. Sci.*, vol. 6, pp. 1–31, 1968.
- [7] E. G. Drucker and G. V. Lauder, “Locomotor function of the dorsal fin in teleost fishes: Experimental analysis of wake forces in sunfish,” *J. Exper. Biol.*, vol. 204, pp. 2943–2958, 2001.
- [8] A. Gibb, B. C. Jayne, and G. V. Lauder, “Kinematics of pectoral fin locomotion in the bluegill sunfish *Lepomis macrochirus*,” *J. Exper. Biol.*, vol. 189, pp. 133–161, 1994.
- [9] E. G. Drucker and J. S. Jensen, “Pectoral fin locomotion in the striped surfperch. I. Kinematic effects of swimming speed and body size,” *J. Exper. Biol.*, vol. 199, pp. 2235–2242, 1996.
- [10] G. V. Lauder and B. C. Jayne, “Pectoral fin locomotion in fish: Testing drag-based models using three-dimensional kinematics,” *Amer. Zool.*, vol. 36, pp. 567–581, 1996.
- [11] J. A. Walker and M. W. Westneat, “Mechanical performance of aquatic rowing and flying,” in *Proc. Roy. Soc. London*, vol. 267, 2000, pp. 1875–1881.
- [12] E. G. Drucker and G. V. Lauder, “Wake dynamics and fluid forces of turning maneuvers in sunfish,” *J. Exper. Biol.*, vol. 204, pp. 431–442, 2001.
- [13] J. R. Hove, L. M. O’Byrne, M. S. Gordon, P. W. Webb, and D. Weihs, “Boxfish (Teleostei: Ostraciidae) as a model system for fish swimming with many fins: Kinematics,” *J. Exper. Biol.*, vol. 204, pp. 1459–1471, 2001.
- [14] J. A. Walker and M. Westneat, “Performance limits of labriform propulsion and correlates with fin shape and motion,” *J. Exper. Biol.*, vol. 205, pp. 177–187, 2002.
- [15] C. D. Wilga and G. V. Lauder, “Functional morphology of the pectoral fins in bamboo sharks, *Chiloscyllium plagiosum*: Benthic versus pelagic station holding,” *J. Morphol.*, vol. 249, pp. 195–209, 2001.
- [16] —, “Locomotion in sturgeon: Function of the pectoral fins,” *J. Exper. Biol.*, vol. 202, pp. 2413–2432, 1999.
- [17] —, “Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in leopard sharks *Triakis semifasciata*,” *J. Exper. Biol.*, vol. 203, pp. 2261–2278, 2000.
- [18] J. Lighthill and R. Blake, “Biofluidynamics of balistiform and gymnotiform locomotion. Part 1. Biological background and analysis by elongated-body theory,” *J. Fluid Mech.*, vol. 212, pp. 183–207, 1990.



- [19] J. Lighthill, "Biofluidynamics of balistiform and gymnotiform locomotion. Part 3. Momentum enhancement in the presence of a body of elliptic cross-section," *J. Fluid Mech.*, vol. 213, pp. 11–20, 1990.
- [20] J. Lighthill and R. Blake, "Biofluidynamics of balistiform and gymnotiform locomotion. Part 2. The pressure distribution arising in two-dimensional irrotational flow from a general symmetrical motion of a flexible flat plate normal to itself," *J. Fluid Mech.*, vol. 213, pp. 1–10, 1990.
- [21] C. M. Breder, "The locomotion of fish," *Zoologica NY*, vol. 4, pp. 159–256, 1926.
- [22] M. W. Westneat, "Functional morphology of aquatic flight in fish: Kinematics, electromyography, and mechanical modeling of labriform locomotion," *Amer. Zool.*, vol. 36, pp. 582–598, 1996.
- [23] P. W. Webb, "Kinematics of pectoral fin propulsion in *Cymatogaster aggregata*," *J. Exper. Biol.*, vol. 59, pp. 697–710, 1973.
- [24] H. Hertel, *Structure, Form and Movement*. New York: Reinhold, 1966.
- [25] G. V. Lauder, "Caudal fin locomotion in ray-finned fish: Historical and functional analyses," *Amer. Zool.*, vol. 29, pp. 85–102, 1989.
- [26] —, "Function of the caudal fin during locomotion in fish: Kinematics, flow visualization, and evolutionary patterns," *Amer. Zool.*, vol. 40, pp. 101–122, 2000.
- [27] P. W. Webb, "Swimming," in *The Physiology of Fishes*, D. H. Evans, Ed. Boca Raton, FL: CRC Press, 1993, pp. 47–73.
- [28] —, "The biology of fish swimming," in *Mechanics and Physiology of Animal Swimming*, L. Maddock, Q. Bone, and J. M. V. Rayner, Eds. Cambridge, U.K.: Cambridge Univ. Press, 1994, pp. 45–62.
- [29] V. Arreola and M. W. Westneat, "Mechanics of propulsion by multiple fins: Kinematics of aquatic locomotion in the burrfish (*Chilomycterus schoepfii*)," *Philos. Trans. Roy. Soc. London B*, vol. 263, pp. 1689–1696, 1997.
- [30] G. V. Lauder, J. Nauen, and E. G. Drucker, "Experimental hydrodynamics and evolution: Function of median fins in ray-finned fishes," *Integr. Compar. Biol.*, vol. 42, pp. 1009–1017, 2002.
- [31] E. G. Drucker and G. V. Lauder, "Function of pectoral fins in rainbow trout: Behavioral repertoire and hydrodynamic forces," *J. Exper. Biol.*, vol. 206, pp. 813–826, 2003.
- [32] J. Liao and G. V. Lauder, "Function of the heterocercal tail in white sturgeon: Flow visualization during steady swimming and vertical maneuvering," *J. Exper. Biol.*, vol. 203, pp. 3585–3594, 2000.
- [33] W. A. Gosline, *Functional Morphology and Classification of Teleostean Fishes*. Honolulu: Univ. of Hawaii Press, 1971.
- [34] E. G. Drucker and G. V. Lauder, "Wake dynamics and locomotor function in fishes: Interpreting evolutionary patterns in pectoral fin design," *Integr. Compar. Biol.*, vol. 42, pp. 997–1008, 2002.
- [35] D. E. Rosen, "Teleostean interrelationships, morphological function, and evolutionary inference," *Amer. Zool.*, vol. 22, pp. 261–273, 1982.
- [36] A. J. Schrank, P. W. Webb, and S. Mayberry, "How do body and paired-fin positions affect the ability of three teleost fish to maneuver around bends?," *Can. J. Zool.*, vol. 77, pp. 203–210, 1999.
- [37] J. E. Harris, "The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins," *J. Exper. Biol.*, vol. 16, pp. 32–47, 1938.
- [38] —, "The role of the fins in the equilibrium of the swimming fish. I. Wind tunnel tests on a model of *Mustelus canis* (Mitchell)," *J. Exper. Biol.*, vol. 13, pp. 476–493, 1936.
- [39] C. D. Wilga and G. V. Lauder, "Function of the heterocercal tail in sharks: Quantitative wake dynamics during steady horizontal swimming and vertical maneuvering," *J. Exper. Biol.*, vol. 205, pp. 2365–2374, 2002.
- [40] G. V. Lauder, E. G. Drucker, J. Nauen, and C. D. Wilga, "Experimental hydrodynamics and evolution: Caudal fin locomotion in fishes," in *Vertebrate Biomechanics and Evolution*, V. Bels, J.-P. Gasc, and A. Casinos, Eds. Oxford, U.K.: Bios Scientific, 2003, pp. 117–135.
- [41] P. Mabee, P. Crotwell, N. Bird, and A. Burke, "Evolution of median fin modules in the axial skeleton of fish," *J. Exper. Zool.*, vol. 294, pp. 77–90, 2002.
- [42] P. Wainwright, D. R. Bellwood, and M. Westneat, "Ecomorphology of locomotion in labrid fish," *Environ. Biol. Fishes*, vol. 65, pp. 47–62, 2002.
- [43] K. V. Kardong, *Vertebrates. Comparative Anatomy, Function, Evolution*, 2nd ed, Dubuque: W. C. Brown, 1998.
- [44] G. S. Arita, "A re-examination of the functional morphology of the soft-rays in teleosts," *Copeia*, vol. 1971, pp. 691–697, 1971.
- [45] W. Harder, *Anatomy of Fishes*, Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, 1975.
- [46] R. Winterbottom, "A descriptive synonymy of the striated muscles of the Teleostei," in *Proc. Acad. Natural Sci. Phila.*, vol. 125, 1974, pp. 225–317.
- [47] A. Grenholm, *Studien über die flossenmuskulatur der teleostier*, Uppsala: Almqvist and Wiksells, 1923.
- [48] K. F. Liem and A. P. Summers, "Muscular system. Gross anatomy and functional morphology of muscles," in *Sharks, Skates, and Rays. The Biology of Elasmobranch Fishes*, W. C. Hamlett, Ed. Baltimore, MD: Johns Hopkins Univ. Press, 1999, pp. 93–114.
- [49] Q. Bone, "Muscular system: Microscopical anatomy, physiology, and biochemistry of elasmobranch muscle fibers," in *Sharks, Skates, and Rays. The Biology of Elasmobranch Fishes*, W. C. Hamlett, Ed. Baltimore, MD: Johns Hopkins Univ. Press, 1999, pp. 115–143.
- [50] L. Rosenberger and M. W. Westneat, "Functional morphology of undulatory pectoral fin locomotion in the stingray *Taeniura lymma* (Chondrichthyes: Dasyatidae)," *J. Exper. Biol.*, vol. 202, pp. 3523–3539, 1999.
- [51] L. Rosenberger, "Pectoral fin locomotion in batoid fish: Undulation versus oscillation," *J. Exper. Biol.*, vol. 204, pp. 379–394, 2001.
- [52] E. G. Drucker and J. S. Jensen, "Kinematic and electromyographic analysis of steady pectoral fin swimming in the surfperches," *J. Exper. Biol.*, vol. 200, pp. 1709–1723, 1997.
- [53] J. A. Walker and M. W. Westneat, "Labriform propulsion in fish: Kinematics of flapping aquatic flight in the bird wrasse *Gomphosus varius* (Labridae)," *J. Exper. Biol.*, vol. 200, pp. 1549–1569, 1997.
- [54] K. S. Thomson and D. E. Simanek, "Body form and locomotion in sharks," *Amer. Zool.*, vol. 17, pp. 343–354, 1977.
- [55] W.-E. Reif and D. B. Weishampel, "Anatomy and mechanics of the lunata tail in lamnid sharks," *Zool. Jb. Anat.*, vol. 114, pp. 221–234, 1986.
- [56] G. V. Lauder, "Structure and function of the caudal skeleton in the pumpkinseed sunfish, *Lepomis gibbosus*," *J. Zool. London*, vol. 197, pp. 483–495, 1982.
- [57] W. A. Gosline, "Functional morphology of the caudal skeleton in fish," *Ichthyolog. Res.*, vol. 44, pp. 137–141, 1997.
- [58] G. S. Helfman, B. B. Collette, and D. E. Facey, *The Diversity of Fishes*. Malden, MA: Blackwell Science, 1997.
- [59] L. J. V. Compagno, "Endoskeleton," in *Sharks, Skates, and Rays. The Biology of Elasmobranch Fishes*, W. C. Hamlett, Ed. Baltimore, MD: Johns Hopkins Univ. Press, 1999, pp. 69–92.
- [60] B. C. Jayne, A. Lozada, and G. V. Lauder, "Function of the dorsal fin in bluegill sunfish: Motor patterns during four locomotor behaviors," *J. Morphol.*, vol. 228, pp. 307–326, 1996.
- [61] T. H. Eaton, "Skeletal supports of the median fins of fish," *J. Morphol.*, vol. 76, pp. 193–212, 1945.
- [62] P. J. Geerlink, "Joints and muscles of the dorsal fin of *Tilapia nilotica* L. (Fam. Cichlidae)," *Netherlands J. Zool.*, vol. 24, pp. 279–290, 1974.
- [63] C. Lindsey, "Evolution of meristic relations in the dorsal and anal fins of teleost fish," *Trans. Roy. Soc. Can.*, vol. 49, pp. 35–49, 1955.
- [64] R. D. Mooi and A. C. Gill, "Association of epaxial musculature with dorsal-fin pterygiophores in acanthomorph fish, and its phylogenetic significance," *Bull. Br. Museum (Natural History)*, vol. 61, pp. 121–137, 1995.
- [65] Y. G. Aleev, *Function and Gross Morphology in Fish*. Jerusalem, Israel: Keter, 1969.
- [66] —, *Nekton*. The Hague, the Netherlands: Junk Publishers, 1977.
- [67] J. C. Nauen and G. V. Lauder, "Quantification of the wake of rainbow trout (*Oncorhynchus mykiss*) using three-dimensional stereoscopic digital particle image velocimetry," *J. Exper. Biol.*, vol. 205, pp. 3271–3279, 2002.
- [68] E. G. Drucker and G. V. Lauder, "Locomotor forces on a swimming fish: Three-dimensional vortex wake dynamics quantified using digital particle image velocimetry," *J. Exper. Biol.*, vol. 202, pp. 2393–2412, 1999.
- [69] U. K. Muller, B. Van den Heuvel, E. J. Stamhuis, and J. J. Videler, "Fish foot prints: Morphology and energetics of the wake behind a continuously swimming mullet (*Chelon labrosus* Risso)," *J. Exper. Biol.*, vol. 200, pp. 2893–2906, 1997.
- [70] I. K. Bartol, A. M. Gordon, M. Gharib, J. R. Hove, P. Webb, and D. Weihs, "Flow patterns around the carapaces of rigid-bodied, multipropulsor boxfish (Teleostei: Ostraciidae)," *Integr. Compar. Biol.*, vol. 42, pp. 971–980, 2002.
- [71] M. J. Wolfgang, J. M. Anderson, M. Grosenbaugh, D. Yue, and M. Triantafyllou, "Near-body flow dynamics in swimming fish," *J. Exper. Biol.*, vol. 202, pp. 2303–2327, 1999.
- [72] G. V. Lauder and E. G. Drucker, "Forces, fishes, and fluids: Hydrodynamic mechanisms of aquatic locomotion," *News Physiolog. Sci.*, vol. 17, pp. 235–240, 2002.
- [73] E. G. Drucker and G. V. Lauder, "Experimental hydrodynamics of fish locomotion: Functional insights from wake visualization," *Integr. Compar. Biol.*, vol. 42, pp. 243–257, 2002.

- [74] J. A. Walker, "Kinematics and performance of maneuvering control surfaces in teleost fish," *IEEE J. Oceanic Eng.*, to be published.
- [75] R. M. Alexander, *Functional Design in Fishes*. London, U.K.: Hutchinson, 1967.
- [76] L. A. Ferry and G. V. Lauder, "Heterocercal tail function in leopard sharks: A three-dimensional kinematic analysis of two models," *J. Exper. Biol.*, vol. 199, pp. 2253–2268, 1996.
- [77] F. E. Fish and L. D. Shannahan, "The role of the pectoral fins in body trim of sharks," *J. Fish Biol.*, vol. 56, pp. 1062–1073, 2000.
- [78] E. G. Drucker and J. S. Jensen, "Pectoral fin locomotion in the striped surfperch. II. Scaling swimming kinematics and performance at a gait transition," *J. Exper. Biol.*, vol. 199, pp. 2243–2252, 1996.
- [79] E. G. Drucker and G. V. Lauder, "A hydrodynamic analysis of fish swimming speed: Wake structure and locomotor force in slow and fast labriform swimmers," *J. Exper. Biol.*, vol. 203, pp. 2379–2393, 2000.
- [80] J. Liao, D. N. Beal, G. V. Lauder, and M. S. Triantafyllou, "The Kármán gait: Novel body kinematics of rainbow trout swimming in a vortex street," *J. Exper. Biol.*, vol. 206, pp. 1059–1073, 2003.
- [81] J. E. Harris, "The mechanical significance of the position and movements of the paired fins in the Teleostei," *Pap. Tortugas Lab.*, vol. 31, pp. 173–189, 1937.
- [82] G. P. Arnold and D. Weihs, "The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa*)," *J. Exper. Biol.*, vol. 75, pp. 147–169, 1978.
- [83] C. L. Gerstner and P. W. Webb, "The station-holding performance of the plaice *Pleuronectes platessa* on artificial substratum ripples," *Can. J. Zool.*, vol. 76, pp. 260–268, 1998.
- [84] P. W. Webb, "Station-holding by three species of benthic fish," *J. Exper. Biol.*, vol. 145, pp. 303–320, 1989.
- [85] R. W. Blake, "The mechanics of labriform locomotion. I. Labriform locomotion in the angelfish (*Pterophyllum eimekei*): An analysis of the power stroke," *J. Exper. Biol.*, vol. 82, pp. 255–271, 1979.
- [86] —, "The swimming of mandarin fish *Synchropus picturatus* (Callinjiidae: Teleostei)," *J. Marine Biol. Assoc. U.K.*, vol. 59, pp. 421–428, 1979.
- [87] —, "The mechanics of labriform locomotion. II. An analysis of the recovery stroke and the overall fin-beat cycle propulsive efficiency in the angelfish," *J. Exper. Biol.*, vol. 85, pp. 337–342, 1980.
- [88] R. Ramamurti, W. C. Sandberg, R. Lohner, J. A. Walker, and M. Westneat, "Fluid dynamics of flapping aquatic flight in the bird wrasse: Three-dimensional unsteady computations with fin deformation," *J. Exper. Biol.*, vol. 205, pp. 2997–3008, 2002.
- [89] B. Wright, "Form and function in aquatic flapping propulsion: Morphology, kinematics, hydrodynamics, and performance of the triggerfish (Tetraodontiformes: Balistidae)," in *Department of Organizational Biology and Anatomy*. Chicago, IL: Univ. of Chicago, 2000, p. 303.
- [90] M. A. Ashley-Ross, "Mechanical properties of the dorsal fin muscle of seahorse (Hippocampus) and pipefish (Syngnathus)," *J. Exp. Zool.*, vol. 293, pp. 561–577, 2002.
- [91] Q. Zhu, M. J. Wolfgang, D. K. P. Yue, and G. S. Triantafyllou, "Three-dimensional flow structures and vorticity control in fish-like swimming," *J. Fluid Mech.*, vol. 468, pp. 1–28, 2002.
- [92] P. W. Webb and D. Weihs, "Hydrostatic stability of fish with swim bladders: Not all fish are unstable," *Can. J. Zool.*, vol. 72, pp. 1149–1154, 1994.
- [93] J. C. Nauen and G. V. Lauder, "Locomotion in scombrid fish: Morphology and kinematics of the finlets of the Chub mackerel *Scomber japonicus*," *J. Exper. Biol.*, vol. 203, pp. 2247–2259, 2000.
- [94] B. Collette and C. E. Nauen, "Scombrids of the world. FAO species catalog vol 2," *FAO Fish Synopsis*, vol. 125, pp. 1–137, 1983.
- [95] B. Block and E. D. Stevens, "Tuna: Physiology, ecology, and evolution," in *Fish Physiology*, W. Hoar, D. J. Randall, and A. P. Farrell, Eds. San Diego, CA: Academic, 2001, vol. 19.
- [96] J. C. Nauen and G. V. Lauder, "Three-dimensional analysis of finlet kinematics in the Chub mackerel (*Scomber japonicus*)," *Biol. Bull.*, vol. 200, pp. 9–19, 2001.
- [97] —, "Locomotion in scombrid fish: Visualization of flow around the caudal peduncle and finlets of the Chub mackerel *Scomber japonicus*," *J. Exper. Biol.*, vol. 204, pp. 2251–2263, 2001.
- [98] M. S. Triantafyllou, G. S. Triantafyllou, and D. K. P. Yue, "Hydrodynamics of fishlike swimming," *Annu. Rev. Fluid Mech.*, vol. 32, pp. 33–53, 2000.
- [99] J. S. Nelson, *Fishes of the World*, 2nd ed. New York: Wiley, 1984.
- [100] L. J. V. Compagno, *Sharks of the Order Carchariniiformes*. Princeton, NJ: Princeton Univ. Press, 1988.



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