1 Locomotion

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CONTENTS

I. INTRODUCTION

With over 25,000 species of fishes living today, in addition to numerous extinct taxa,[160,196] it is perhaps not surprising that fishes display an impressive diversity of propulsive systems.[119,259,275] Access to a complex, three-dimensional medium with a wide diversity of habitats that include open oceans, coral reefs, high-velocity river flows, and crevices and muddy bottom substrates has subjected fishes to a panoply of selective regimes. The evolutionary result has been tremendous diversity in not only body and fin shapes but also in fundamental physiological features such as muscle fiber types and their distribution, muscle contractile properties, mechanics of joints, and supporting cardiovascular and metabolic systems. The diversity of functional solutions to movement through water makes fishes a particularly rewarding subject for physiological and biomechanical analyses of locomotion. With numerous well-documented evolutionary trends and considerable recent progress in phylogenetic analysis,[155,222,234,238] the diversity of fishes greatly facilitates comparative physiological study of closely related species as well as larger clades to better understand how locomotor traits have evolved.

Over the past 25 years, a variety of excellent review articles and book treatments covering the subject of fish locomotion have appeared, and these works provide a good introduction to research

au: Is "locomotor" used as a modifier throughout? I have left it as is in most places,except when I felt it referred to locomotion specifically. Please check.

up to the mid-to-late 1990s[1,2,26,46,131,163,259,275–277,280]; Wilga and Lauder[294] have recently reviewed locomotion in sharks and rays. The field of fish locomotor physiology continues to evolve rapidly, especially with new techniques driving a wide variety of approaches and providing novel results. The appearance of new findings has accelerated during the last 5 years; this chapter will provide a synthesis of the latest topics and developments in the study of fish locomotion by placing these new results in the context of classic work.

II.   DIVERSITY OF PROPULSIVE SYSTEMS

Biologists studying fish locomotion have been somewhat preoccupied with producing classification schemes. These classifications have been useful as a shorthand for referring to different types of swimming fishes and their general ecology, but the limitations of these schemes have become increasingly clear in recent years. In some cases, particular classifications give a seriously misleading impression of locomotor dynamics and physiology. Given the ubiquity of different classification schemes in the current literature, it is useful to consider in detail several of the classifications and discuss some of their drawbacks; most of these will be considered further at appropriate points in the remainder of this chapter.

There are at least six different classification schemes that have some currency. First, the classical plan of Breder[34] (also see Gray [117–119]) divides fish into categories based on their mode of locomotion named after exemplar species. This is something of a taxonomically based classification scheme but also reflects, at least nominally, some basic mechanical traits of locomotor dynamics. For example, fishes that are supposed to swim with relatively large undulations of the body are referred to as "anguilliform" after the eel *Anguilla*, progressing through subcarangiform, carangiform, and finally tunniform (after the tunas), referring to respectively decreasing portions of the body with significant lateral amplitude.[179] There are two difficulties with this scheme. The images accompanying discussions of this classification are often not based on quantitative analyses of locomotor kinematics; as will be discussed below, quantitative kinematic analyses of a variety of different fish species over the last 10 years shows that there are relatively minor differences among species in the pattern of body undulation and that the movement patterns shown for eels in particular have misleadingly large anterior amplitudes. In addition, classification of locomotor modes based on only a two-dimensional representation in the horizontal plane ignores the crucial three-dimensional geometry of fishes, especially the substantial changes in body area in the region of the caudal peduncle. Active thrust-generating movements seen in the dorsal and anal fins are also ignored. Other taxonomically based modes of swimming include, but are by no means limited to, balistiform (in which primarily the dorsal and anal fins are used together), gymnotiform (locomotion with the anal fin only), and labriform (swimming with pectoral fins).

A second method of classifying modes of fish propulsion is to locate fishes along a continuum from undulatory to oscillatory methods of generating propulsive forces.[179] In this scheme, rays (which undulate their pectoral fins), bowfins (which can swim by undulating their dorsal fins), and eels and anguilliform sharks would all be toward the undulatory end of the spectrum, while fishes that use primarily their pectoral, dorsal, anal, and caudal fins would be oscillatory swimmers. Of course, fishes such as trout or bluegill sunfish can swim slowly by oscillating their pectoral fins alone[76,105] and swim at faster speedsby undulating both the body and tail, thus confounding classification under this scheme.

A third way of considering fish locomotion is to classify fishes into groups based on fin use, which may also be correlated with speed or gait changes.[157,281,285] Hence, fishes swimming with their median fins (dorsal and anal) and paired fins (pectoral and pelvic) are termed MPF (median and paired fin) swimmers, while fishes using primarily the body and caudal fin would be classified as BCF (body and caudal fin) swimmers. Figure 1.1 illustrates median and paired fins in two teleost fishes with different body shapes and fin positions. MPF gaits can then be further divided into oscillatory and undulatory modes of swimming.

One difficulty with this scheme is that recent experimental data demonstrate that fishes swimming with body and caudal fin undulations may at the same time actively use the dorsal (and anal) fins to
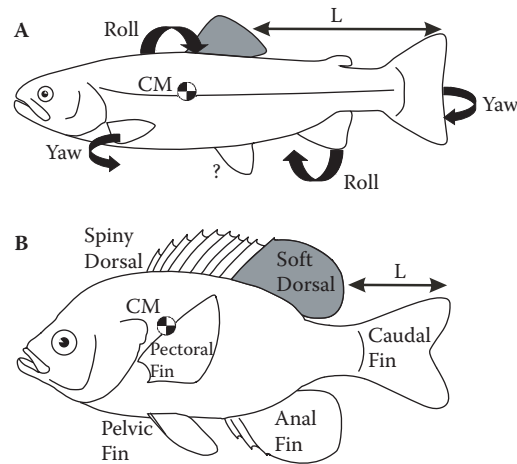
FIGURE 1.1 Body shapes in two representative teleost fishes, (A) trout (e.g., *Oncorhynchus mykiss*) and (B) bluegill (e.g., *Lepomis macrochirus*) illustrating the major median and paired fins and their positions. During locomotion, roll and yaw movements must be balanced around the center of mass by fin movements for fishes to execute steady rectilinear locomotion. The homologous soft-rayed portions of the dorsal fin in both species are shaded gray, and the approximate center of mass (CM) is located by the CM symbol. Note the differing locations of the dorsal and anal fins relative to the center of mass in trout and sunfish, and the gap (*L*) between the soft dorsal fin and the caudal fin. The role of the pelvic fins in locomotion is largely unknown and is indicated by a "?".

generate propulsive forces at any given speed.[73,166–168] The dorsal and anal fins are not simply stiff stabilizers resisting lateral movement of the body, remaining unused during swimming by body undulation. Instead, dorsal and anal fins are actively moved using intrinsic fin musculature to generate thrust and maneuvering forces. Even during steady forward propulsion, dorsal and anal fins play an important role by dynamically stabilizing the fish with actively generated lateral forces.[168]

Thus, as indicated in Figure 1.1, rectilinear locomotion requires a constant balancing of movements around the center of mass. Fishes swimming with caudal fins and body undulations use dorsal fins to counter the ventral roll movements produced by the anal fin or environmental perturbations, and similarly use anal fins to actively counter dorsal roll movements. Yaw movements generated by caudal fins are countered by movements generated by pectoral or pelvic fins. Thus, even fishes such as trout that are usually considered an exemplar of the BCF locomotion mode use dorsal and anal fins actively for body stabilization.[168]

A fourth method of classifying fish locomotion diversity is to use speed as an independent variable to quantify how fishes change locomotion patterns as they encounter increased drag forces.[67,68,157,202,281] At slow speeds, many fishes use pectoral fins exclusively, recruiting body and caudal fins only at higher speeds. Bluegill sunfish (*Lepomis macrochirus*) use their pectoral fins below a speed of about 1.1 body lengths per second (Ls^{-1}), while above this gait transition speed, they use the body, caudal fins, and dorsal and anal fins. Isolated pectoral fin beats may occur at any speed, but only intermittently above the gait transition. Webb[280,285] has emphasized the changing roles of fins with gaits and underscored that even station holding (which may involve a suite of novel behaviors to increase negative lift in currents, pushing fish into the bottom[10,279,282,297]), hovering,[76,287] and rapid escape behaviors constitute part of the natural diversity of gaits and speeds available to fishes. Also, fishes may radically alter their locomotion patterns when they encounter repeatable environmental turbulence. Liao et al.[172,173] have described a novel gait, termed the Karman gait (discussed in more detail below), observed when fishes swim in a vortex street shed behind obstacles in flowing water.

The classification of fish locomotion by speed has important implications for patterns of muscle function in fishes. Many studies have analyzed patterns of muscle fiber type recruitment with change of speed.[6,7,50,51,137,139,141,147,148,211,216,220] These results will be considered in more detail below. The

anatomical localization of different fiber types, as well as their changing patterns of activation with gait changes, is a hallmark of fish locomotor physiology.

A fifth perspective for understanding fish locomotion diversity is to categorize the various locomotion behaviors into steady and unsteady movements. The majority of locomotion analyses in fishes have focused on steady rectilinear swimming generated by repeated rhythmic movements, although unsteady escape responses (c-starts) have certainly received considerable attention also.[52,60,62,78,80,122,250,264,288] However, non-escape   maneuvering of lower speed and amplitude, which might also be termed "routine maneuvering," has hardly been studied. The few studies that have been done show novel fin uses and unexpected hydrodynamic patterns, including differentiation between the functions of right- and left-side fins.[72,73,75] Unsteady behaviors are important and in fact make up the majority of the locomotion budget in natural habitats, thus deserving of considerable future research.

Finally, fish locomotion diversity can be considered in an evolutionary context, in terms of major trends described and analyzed.[112,113,123,156,161,164,167,290] Several well-known trends characterize the evolution of fish locomotor design, two of which are summarized in Figure 1.2. Pectoral fin orientation in plesiomorphic ray-finned fishes is typically ventrolateral;[295] the more derived spiny-finned fishes (*Acanthopterygius*) have pectoral fins located laterally on their bodies, and these fins typically have a greater angle of attachment (see Figure 1.2A).[75] The dorsal fin of basal ray-finned fishes such as sturgeon is supported by flexible fin rays, while acanthopterygian fishes have a spiny dorsal fin located anterior to the soft-dorsal fin (see Figure 1.2B). These two dorsal fins may be separate or attached to each other (see Figure 1.2B). Pelvic fins in basal ray-finned fish taxa such as gar (*Lepisosteus*) and sturgeon (*Acipenser*) are typically located well posterior of the pectoral fins near the midbody region, while the derived teleost fishes possess pelvic fins that are located more anteriorly, almost under the pectoral fins. The caudal fins of fishes vary from the plesiomorphic heterocercal (externally asymmetrical) condition, with the upper lobe larger than the ventral lobe, to the homocercal condition with external symmetry.[84,161,164,246]

au: correct?

The functional significance of these evolutionary trends remains largely unknown (although some recent discoveries are discussed below). However, these large-scale patterns can serve as a focus for future studies and as a fertile source of hypotheses about the relative efficiency of different body and fin designs, the functional significance of major evolutionary changes, and the analysis of correlations among changes in morphological and physiological traits in evolution. Future students of fish loco-motion will be able to mine these evolutionary trends for profitable research directions and hypotheses that will be critical to understanding the diversity of locomotion patterns in fishes.
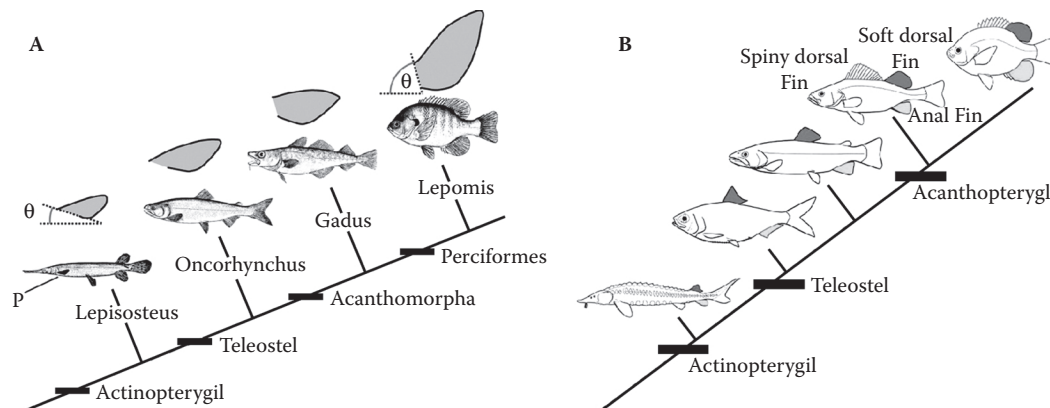

FIGURE 1.2 Evolutionary patterns to pectoral fin (A) and dorsal and anal fin (B) evolution in ray-finned fishes. Note especially the changing relationship of the pectoral fin (P) angle (Φ) and fin area relative to body length, and the changing position of the dorsal and anal fins relative to each other. Modified from Drucker and Lauder,[75] and Lauder and Drucker.[168]

None of the classification schemes discussed above was proposed with the idea that individual species would fit into only one category, that any one scheme is sufficient in and of itself to explain fish locomotor diversity, or that the complexity of underlying physiological or biomechanical mechanisms are reflected in any one scheme. Given that many of the above classification schemes need revision based on data from research in the last 10 years, these systems provide a general means of ordering the vast diversity of fish locomotion styles and generate hypotheses subject to experimental study.

III. ANATOMY OF PROPULSIVE SYSTEMS

A hallmark of locomotor design in ray-finned fishes is the presence of numerous fins that project into the water and are actively used for propulsion and maneuvering. However, the design of these fins, their structure, and the mechanics by which they are actively controlled to generate and modulate propulsive forces have received very little attention. Shark fins, which have internal fin rays also (although of different structure than the fin rays of actinopterygian fishes), have hardly been studied.[208,294,297]

The fins of actinopterygian fishes are supported by bony fin rays termed lepidotrichia, which typically have an unsegmented region at the base, a segmented region in the middle and distal thirds and then branch toward the distal end (Figure 1.3A). A thin collagenous membrane spans adjacent fin rays (see Figure 1.3B) and allows the rays to collapse toward each other, thus reducing fin area, and
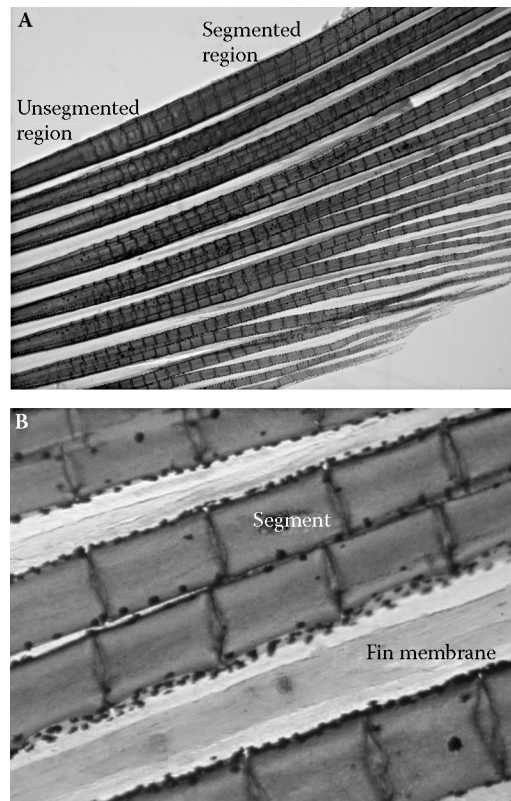

FIGURE 1.3 Fin ray structure in bluegill sunfish, representative of fin ray structure in ray-finned fishes in general. Panel A shows an overview of pectoral fin ray structure. The fin as a whole is composed of individual fin rays (lepidotrichia); each ray (often 12–14 total in each fin) is usually unsegmented at the base and transitions to a region with segments, and finally these segmented rays branch distally. Panel B: close view of fin ray segments and the thin collagenous membrane that connects adjacent rays.
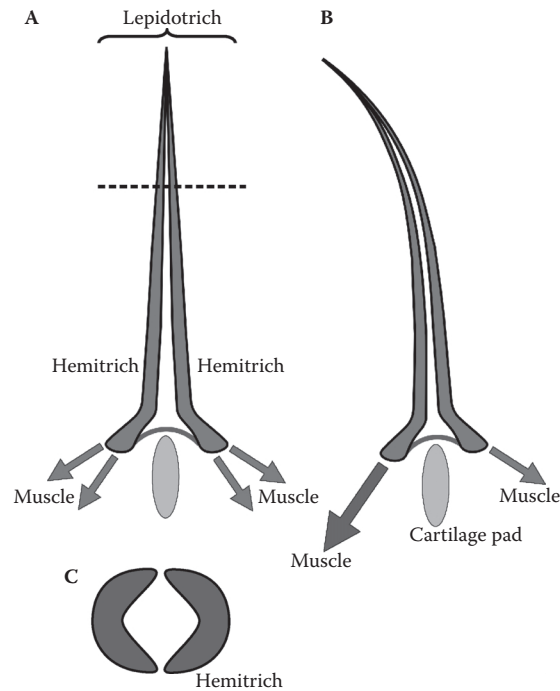
FIGURE 1.4 Mechanics of fin rays in ray-finned fishes. A: Each fin ray is composed of two bony halves, hemitrichia (singular, hemitrich) which are attached at their expanded bases by ligaments and supported by basal cartilage pads. The two hemitrichs together form a lepidotrich or fin ray and are attached at their distal ends. Typically, two muscles attach to the bases of each hemitrich. B: If unequal displacements are applied to the two hemitrichs, the lepidotrich curves to one side. C: Section through a lepidotrich at the level shown by the dashed line in panel A. The two hemitrichia are curved forming an interior space within the fin ray carrying nerves and vascular components and are connected by collagenous and elastic connective tissue.

to expand, thus increasing fin area when the membrane is extended to its limit. Fin ray segments are composed of membrane bone and are connected to each other by ligaments and elastic fibers. [9,93,96,159] Each lepidotrich has two halves, hemitrichs, which are separate at the base and attached to each other at their distal end (Figure 1.4A). Each hemitrich is lunate and curved toward its opposite half (see Figure 1.4B); blood vessels and nerves pass through the space between the hemitrich segments. In most fishes, four muscles attach to each fin ray, two at the expanded base of each hemitrich. In bluegill sunfish (*Lepomis macrochirus*), for example, each pectoral fin usually has 14 fin rays, and each ray has four muscles controlling its movement. With the inclusion of several other intrinsic fin muscles,[69,301] each sunfish pectoral fin has a total of 59 muscles or muscle bundles actuating the fin rays.

Unmineralized, unbranched actinotrichia are located at the ends of each fin ray and are composed of collagen polymerized into large fibers.[101,102,153,188] The actinotrichia are attached to the ends of the lepidotrichia, which thus cannot move relative to each other at their distal ends (see Figure 1.4A). The actinotrichia of ray-finned fishes have been proposed to be homologous to the unmineralized ceratotrichia which are the supporting rays in shark fins.[153]

The bilaminar structure of fin rays in ray-finned fishes has important implications for active control of fin ray curvature and thus for understanding the mechanics of locomotion (such control of fin conformation does not occur in sharks, as ceratotrichia are not bilaminar in structure). As shown in Figure 1.4B, activating the musculature attached to one hemitrich so as to cause unequal displacements of the two hemitrich bases causes the whole lepidotrich to bend to one side. Because the two hemitrichs are attached at their distal ends and cannot change length, the entire fin ray curves. Actively inducing curvature in a series of adjacent fin rays produces curvature of the fin surface. Active control of the

curvature of fins allows fishes to resist fin deformation imposed by fluid dynamic forces and to curve their fins *into* oncoming flow, with the potential of active camber adjustment to local flow conditions.

The fin ray structure described above occurs in all fins (dorsal, anal, caudal, pelvic, and pectoral) where the rays are segmented, but not in the spiny portions of dorsal and anal fins where the lepidotrichs are fused into rigid spines. This fin ray structure is diagnostic of ray-finned fishes, as observed even in the earliest clades, represented today by genera such as *Polypterus,* and retained in gar (*Lepisosteus*), sturgeon (*Acipenser*), and bowfin (*Amia*) as well as throughout the teleost radiation of bony fishes. Bilaminar fin ray structure allowing active conformational change is a remarkable innovation in propulsor design in contrast to the wings of insects and the feathers of bird wings which are not capable of such active bending.

Although fish fin rays have a complex and noteworthy structure, the segmented axial muscu-lature (myotomes or myotomes) of fishes may surpass fin rays in complexity of both structure and function. Written descriptions of the intricate w-shaped folding of axial white muscle segments in fishes invariably include the complexity of the collagenous myosepts that separate adjacent myo-tomes and the intricate muscle fiber trajectories within and among adjacent myotomes.[3,120,138,256,301] Gemballa and colleagues[97–100,260] have recently provided a series of elegant descriptions of seg-mented connective tissue and muscular elements in fishes and provide the clearest picture to date of the anatomical organization of fish axial muscle.

Figure 1.5 shows a schematic view of the location and orientation of segmented white fibers in fishes in relation to the vertebral column of teleost fishes. The w-shaped myotomes possess
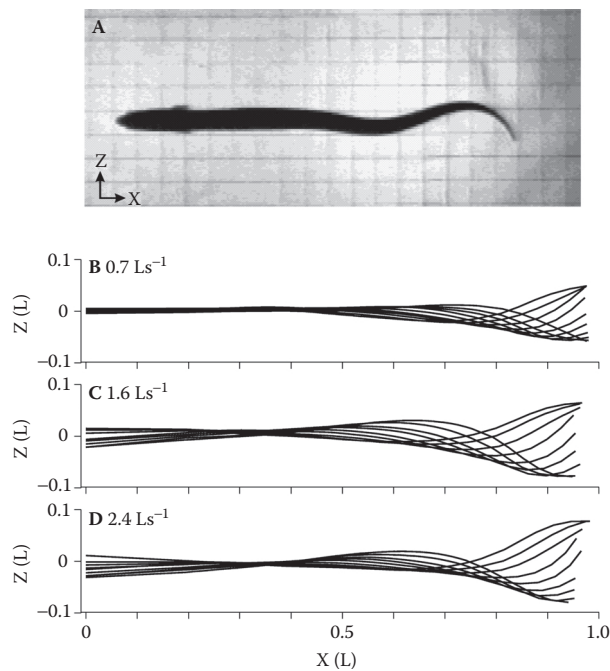

FIGURE 1.5 Myotomal structure in ray-finned fishes. A: location and w-shaped structure of the segmented axial locomotor musculature. Horizontal hatching indicates the portion of each myotome that lies at the body surface and attaches to the skin. B: Photograph of myotomal muscle segments on the left side of largemouth bass (*Micropterus salmoides*). Anterior is to the left and dorsal to the top of the image. Three myotomes have been removed from either side of the central myotome in the photograph. Each myotome has long thin arms extending anterodorsally (da) and anteroventrally (va), central large anteriorly pointing cones (ac), and posteriorly-directly pointing cones (pc). The horizontal septum (hs) dividing the musculature into epaxial and hypaxial portions is visible, as is the vertical septum (vs) separating the left and right sides of the fish. Panel A modified and redrawn from Wainwright,[263] and Panel B modified from Jayne and Lauder.[141]

anteriorly pointing central cones that attach to midline connective tissue or to the vertebral column as well as dorsal and ventral posterior cones. In addition, long thin arms of myotomal fibers reach anteriorly toward the dorsal and ventral margins of the body. Red fibers are located laterally near the midline horizontal septum and extend forward in a band from just anterior to the tail almost to the pectoral girdle. The function of axial musculature will be considered in detail below.

IV. BODY AND FIN MOTION DURING LOCOMOTION

A. BODY AND CAUDAL FIN PROPULSION

The availability of high-speed video technology over the last 15 years has allowed investigators to produce accurate quantitative descriptions of fish body movements at different swimming speeds. In addition, the use of flow tanks to accurately regulate the swimming speed of fishes allows this independent variable to be controlled within narrow limits. Kinematic patterns that result from body accelerations or turns can then be treated separately and not confused with steady swimming. As a result, there is now a solid database of kinematic information from a diversity of species to serve as input into models of body bending and muscle activation and to quantitatively define different modes of locomotion.

Figure 1.6 shows sample video and kinematic data on the steady swimming of an eel (*Anguilla*) and a largemouth bass (*Micropterus*) in a flow tank with low turbulence. The eel image demonstrates a key feature of steady swimming in virtually every fish species for which swimming is steady and rectilinear: at low speeds (up to about 1 Ls^{-1}), there is very little oscillation of the anterior half of the body.[107–109] Diagrams of anguilliform locomotion that show substantial head yaw and anterior body oscillation are most likely based on data obtained from accelerating animals, or animals not matching speed well. In many cases, figures showing eel body outlines are redrawn from the influential images published by Sir James Gray in the 1930s.[117] Unfortunately, these images (which have heavily influenced nearly 50 years of research on fish locomotor kinematics and modeling) appear to have been obtained from a small accelerating eel and thus do not reflect steady swimming kinematics.[169] Recent kinematic data indicate that at slow speeds, there is effectively no body bending and hence no muscle strain in either red or white muscles; locomotor forces must be generated by posterior body muscles.[48,50,216,220,231] Similar patterns are also seen in largemouth bass (see Figure 1.6B) at slower speeds,[140] whereas at higher speeds (>1.5 Ls^{-1}), noticeable yawing of the anterior half of the body occurs (see Figures 1.6C, D).[140] Similar results have been obtained for numerous other species, including needlefish, tuna, and mackerel.[63,66,171]

While most fishes show substantial increases in tail beat frequency with speed,[136,275] careful studies of tail beat amplitude also show a significant speed effect. Fish thus modulate both frequency *and* amplitude as speed increases. The bass midlines shown in Figure 1.6B illustrate this qualitatively, but statistical analyses of tail beat amplitudes versus speed during locomotion in needlefish, bass, mackerel, and sunfish all demonstrate amplitude effects, often as much as a doubling of amplitude as speed increases four times.[106,140,164,171]

Several studies have failed to detect amplitude increases with speed, but low-resolution ventral views make it difficult to detect amplitude differences, especially when the tail moves in a complex three-dimensional manner or when swimming speed and direction are poorly controlled.[161,164,167] Figure 1.7 shows a posterior view of caudal fin movement obtained by placing a small mirror downstream from swimming sunfish and mackerel in a flow tank. This posterior view clearly shows side-to-side motion of the tail and differential excursions of the dorsal and ventral tail lobes. The caudal fin is inclined to the horizontal plane during lateral movement, which suggests that the tail is generating lift in addition to thrust.[164] This asymmetrical motion within the tail is maintained at high speeds, even in fish such as mackerel that have symmetrical tail shapes (see Figure 1.7B).[106] The homocercal teleost tail thus can undergo complex three-dimensional deformations. Ventral views alone make it difficult to distinguish dorsal tail lobe motion from ventral tail lobe motion with changes in speed and changes in tail shape, which may mask amplitude increases.
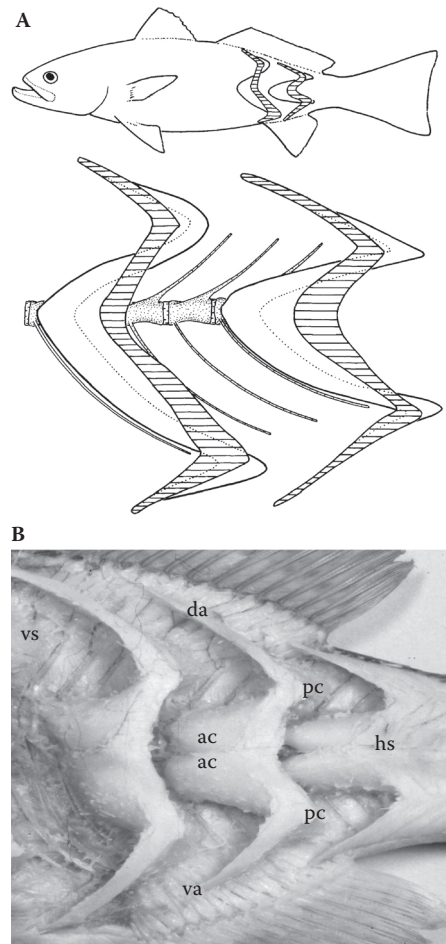
FIGURE 1.6 Kinematics of undulatory locomotion in fishes. A: Image from high-speed video of steady rectilinear locomotion in the American eel, *Anguilla rostrata* at a speed of 1.0 body lengths per second (Ls^{-1}). Note that the front half of the body is nearly straight and that body undulation is confined to the posterior half of the body. B–D: Midlines reconstructed from patterns of body bending during steady swimming in largemouth bass (*Micropterus salmoides*) over a speed range of 0.7–2.4 Ls^{-1}. Successive midlines are spaced equally in time during a half tail beat cycle. At the slower speed, body bending is confined to the posterior half of the body, but at higher speeds, the head begins to oscillate laterally. Z, lateral excursion in % body length (L); X, distance along the body, L. Panels B-D modified from Jayne and Lauder.[140]

B. PECTORAL FIN MOVEMENT

Pectoral fin movements in fishes during steady swimming have been the subject of numerous papers[25,67,76,94,105,223,266,268,270,271,274,292,296,297] as well as several recent reviews[75,162,269,291,294] and hence will not be considered in detail here. Pectoral fins are used extensively by fishes for maneuvering and propulsion, and labriform locomotion in particular has proven to be a fruitful avenue for studying the relationship among fin shape, locomotor speeds, and performance, with links to ecological patterns on coral reefs.[17,18,90,262] Walker has analyzed the movement of pectoral fins in sticklebacks in detail and has compared and contrasted flapping and rowing modes of pectoral fin propulsion[267,269,271] (also see Vogel[261]). Sticklebacks, in which the planes of fin abduction and adduction are largely horizontal, use an extreme rowing stroke of the pectoral fins. In contrast, a more stereotypical flapping pectoral fin stroke is exemplified by wrasses,[268,292,293] in which the stroke

A   1.2 Ls^{-1}
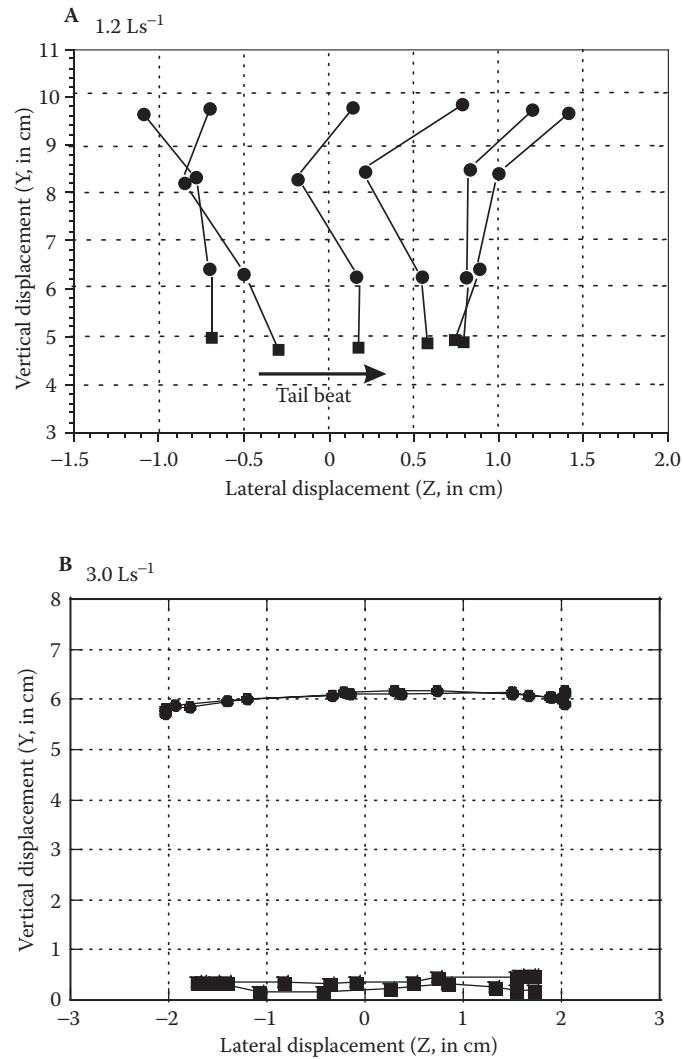

B   3.0 Ls^{-1}

FIGURE 1.7 Tail kinematics in bluegill sunfish, *Lepomis macrochirus* (A) and mackerel, *Scomber japonicus* (B) as seen in a posterior (YZ plane) view. In sunfish, four points along the tail trailing edge were digitized, and lines connecting adjacent points approximate the shape of the tail. In mackerel, only the excursions for dorsal and ventral tips of the tail are shown. In both species, the tail moves asymmetrically even during steady forward undulatory locomotion, with greater lateral (Z) excursion of the upper (dorsal) lobe and with the tail surface inclined at an angle to the vertical during lateral motion. Modified from Lauder[164] and Gibb et al..[106]

plane is mostly vertically oriented. Many fishes, such as bluegill sunfish, show pectoral fin move-ments that fall between these extremes and may thus utilize fluid dynamic mechanisms of force generation with features of both drag-based and lift-based propulsion.[70,105]

In contrast to the large volume of literature on pectoral fin propulsion, very little information is available on the movements of pectoral fins as fishes execute maneuvers.[87,127,227,283] Drucker and Lauder[72] analyzed the kinematics and hydrodynamics of yawing turns in sunfish and showed that during relatively low-speed turns (5 to 0 degrees s^{-1}), in the range of routine turning velocities frequently exhibited by maneuvering fishes, the left and right pectoral fins function very differently. During a turn to the right, for example, the left-side fin is rapidly abducted and then adducted, while the right-side fin shows delayed abduction. During this time, the body undergoes primarily

rotational movements in the horizontal plane. Then, the left-side fin adducts causing body translation. The two pectoral fins thus appear to have distinct roles: one causing rotation and the other translation. The combined effect of both fin motions is a yawing turn accompanied by body movement away from the stimulus.

Hovering[76] and braking[95] can also be considered types of maneuver effected by pectoral fins,[34,287] but few studies have considered fin function under these circumstances. Trout and sunfish show alternating movements of pectoral fins to maintain body station in the water column; braking, however, involves rapid abduction of the pectoral fins to generate a forward flow.[75,76] Trout and sunfish differ dramatically in the directions of forces generated by their pectoral fins during braking.[75] Harris[128] and Breder[34] had suggested that sunfish could avoid rotational moments by directing the forward braking jets of water at an angle such that the mean reaction force from fin movement passes through the center of mass. Drucker and Lauder[75] used flow imaging to show that this hypothesis is corroborated for sunfish, while trout braking induces substantial rotational movements about the center of mass. The pectoral fin designs in these two species result in dramatic differences in braking function.

The pectoral fins of sharks also play an important role in maneuvering.[294,296,297] Most research to date has focused on vertical maneuvers, and studies on leopard sharks have shown that active changes in pectoral fin conformation result in directed lift forces that induce body rotation. To move down in the water column, for example, leopard sharks elevate the posterior region of the pectoral fins, causing an upward water flow and a pitching movement that tilts the body down.[296]

C. DORSAL AND ANAL FIN MOVEMENTS

Dorsal fin function in fishes has been studied experimentally in only a very limited number of species, and yet recent experimental data show that this fin, along with the anal fin, may play a critical role during both steady swimming and maneuvering.[168] Dorsal and anal fins have been viewed as relatively simple stabilizers, resisting fluid forces that might otherwise promote roll movements of the body (see Figure 1.1).[34,126] This description might apply to the spiny dorsal fin of acanthopterygian fishes (see Figures 1.1 and 1.2), which is erected rapidly during high-speed turns. But the soft dorsal fin in species such as sunfish and trout plays an active role in generating propulsive force during both propulsion and turning maneuvers.[73,168] As swimming speed increases, the height of the soft dorsal fin above the body decreases, and the dorsal fin generates thrust as well as lateral forces; at a speed of 1.1 Ls^{-1}, the dorsal fin of sunfish provides roughly 12% of total thrust force. During turns, the soft dorsal fin of sunfish contributes almost 35% of the lateral force generated by all fins during the turn.[73] In trout, the dorsal fin produces strong lateral pulses of flow to the right and left sides even during steady forward locomotion,[168] suggesting that trout actively use the dorsal fin to maintain a stable body position.

Basic kinematic patterns of dorsal and anal fin use have also been described for tetraodontiform fishes[11,132] and needlefish[171]. In tetraodontiform species, multiple fins are used simultaneously to generate thrust, and pectoral fins may move in an alternating fashion even at the highest swimming speeds; in needlefish, the dorsal and anal fins move synchronously with each other.

Electromyographic studies of dorsal fin function in sunfish executing a variety of behaviors[144] confirm that the inclinator muscles (which control side-to-side fin ray movement) are active and function either to increase fin resistance to imposed hydrodynamic loads or to bend the dorsal fin into oncoming flow.

V.   BODY MUSCLE FUNCTION DURING LOCOMOTION

Patterns of muscle activation in fishes during swimming have been the subject of many studies, with the primary focus on patterns of red and white fiber recruitment and on determining the physiological characteristics of muscle fibers and their power production along the length of the

body.[5,6,50,53,64,79,81,145,148,152,154,211,220,232,241,242,249,257,272] Within the white myotomal fibers, complex acti-
vation patterns occur that reflect the intricate anatomical structures of the myotomes. White fiber
activation within the myotomes has been studied much less than red fiber activation, in part due
to the relatively high swimming speeds needed to activate these fibers and also because of the
difficulty of localizing electrode positions with individual myotomes. Figure 1.8A shows the results
of recording electrical activity patterns from three different myotomes along the body of largemouth
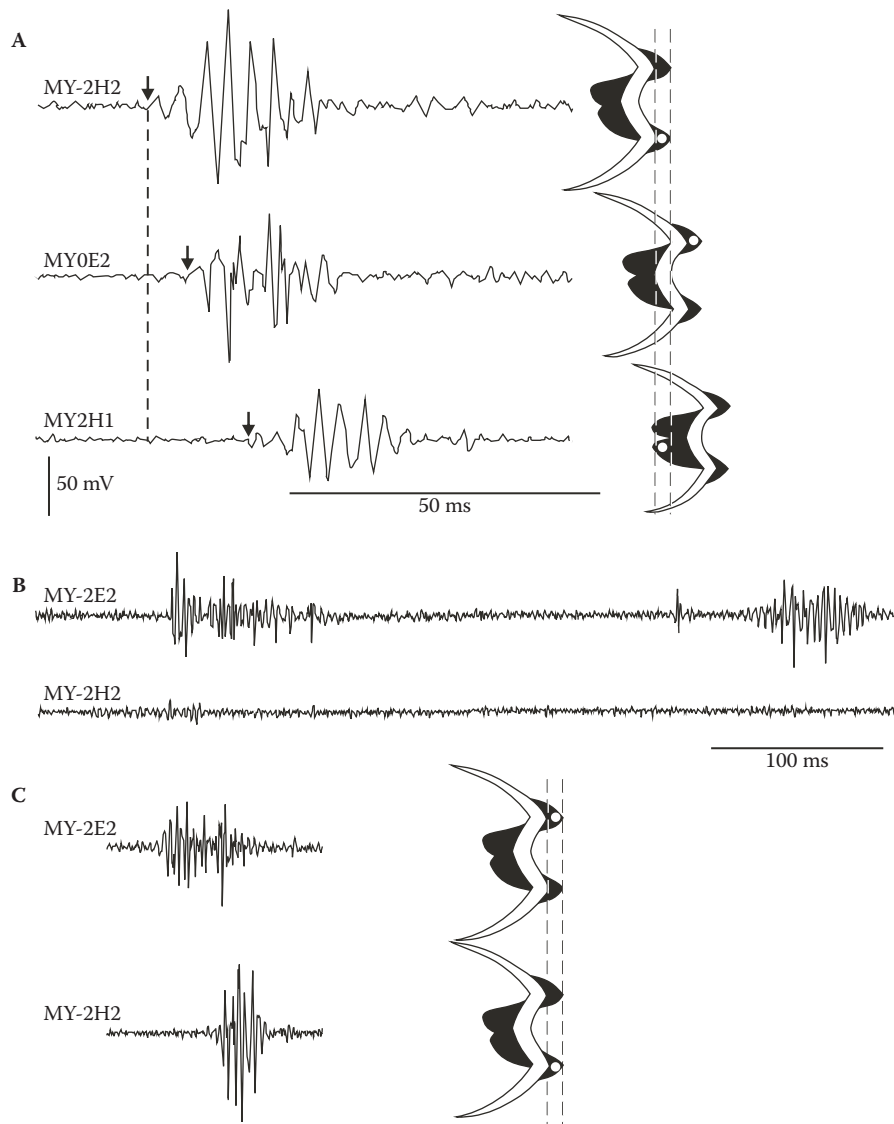
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FIGURE 1.8 Function of white myotomal musculature in largemouth bass (*Micropterus salmoides*). A:
Muscle activity patterns recorded simultaneously from three locations (white dots) within myotomes spanning
six vertebral segments. The upper and lower traces are from electrodes at the same longitudinal location but
differ in onset by 10 minutes (ms) (arrows indicate the start of muscle fiber electrical activity). B, C: Further
recordings from the same individual during slower unsteady swimming and kick-and-glide locomotion,
respectively. Note the differential activity of fibers in the dorsal and ventral posterior cones. Labels refer to
relative myotome number along the vertebral axis (e.g., MY-2 is two segments anterior to MY-0), and to the
epaxial (E) and hypaxial (H) regions (1 or 2) of the myotome. Modified from Jayne and Lauder.[141]

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bass swimming with a high-speed burst-and-glide mode. Electrodes at the same longitudinal location (see Figure 1.8A, upper and lower traces) show substantial differences in onset timing, reflecting their positions in the myotomes three segments apart. Electrical activity in the central myotome cones thus corresponds to sequential activation of myotomes down the body, not to the simultaneous activation of muscle tissue at a single longitudinal location.[141] Considerable differentiation of activity was also observed within single myotomes (see Figure 1.8B): an electrode in a dorsal posterior cone could be fully active (and thus recruited at a lower swimming speed) without any activity detected in an electrode in a ventral posterior cone of the same myotome. At higher speeds (see Figure 1.8C), activity is seen in both dorsal and ventral cones, but with substantially different onset times.

These data reflect the complexity of myotome structure in fishes, and as yet there is no clear description of how myotomes function to bend the body. Two adjacent vertebrae can have muscle fibers from up to six different myotomes spanning the intervertebral joint and hence able to effect bending at that joint. An individual myotome with long anterior arms and posterior cones can span up to one third the length of the axial skeleton and thus cause bending of many vertebrae simultaneously. Mathematical models of myotome function are becoming increasingly sophisticated, but more studies need to be undertaken before we understand why fibers within a single myotome should show differential activity and how controlled bending is achieved when only parts of myotomes are activated at any given moment.[3,12,256]

Unexpected complexities of muscle fiber activation in fishes have also emerged in the pattern of red, pink, and white fiber recruitment as speed increases.[50,51,139] The pattern of muscle fiber type recruitment in fishes was first clarified in experiments by Bone,[30–32] who showed clearly that red fibers (with slower contraction times) were activated to power slow swimming, while at faster speeds, white fibers (with shorter contraction times) are activated to power the more rapid body movements needed to overcome drag (also see[133,207]). Rome and colleagues [211,212,216–218] demonstrated the effect of temperature on recruitment patterns; in addition, patterns of changing strain and activation down the body have now been reported for a number of species.[6,23,50,51,64,232] These results initially suggested an additive model of fiber recruitment, in which white fibers are recruited after the red fibers have been maximally activated at the highest swimming speed for which they can produce power to match drag. At high swimming speeds, red fibers are active *in addition to* white fibers.

But recordings of white and red muscle fibers in fishes swimming in high-speed burst-and-glide movements show interesting differences from this additive model. Figure 1.9A illustrates the diversity of fiber type recruitment as speed increases. In bluegill sunfish, during slow to rapid steady swimming (0 to 2.0 Ls^{-1}), red fibers are active and electrical activity is propagated posteriorly (compare onset times in red anterior and posterior channels of Figure 1.9A). There is no activity in white fibers at this time. During rapid unsteady movements, white fibers are recruited, and red fibers are *deactivated* relative to the amount of activity seen at slower swimming speeds. During moderate-speed unsteady activity (at a speed intermediate to the two previous conditions), both red and white fibers are active, but the white fibers show onset times that lag substantially behind the red fibers, despite having similar offset times (see Figure 1.9A).[139]

These data suggest a nonadditive model for fiber type recruitment (see Figure 1.9B), in which red fibers alone are activated at slow swimming speeds, both red and white fibers are activated at higher speeds, and red fiber activity *decreases* and white fiber activity is maximal at even higher speeds. Derecruitment of red fibers has also been demonstrated in embryonic zebrafish muscle during fast fictive swimming.[41] The lag in the onset time of white fibers relative to that of red fibers may be due to their shorter contraction times, providing a rough synchronization of maximal force production at a given longitudinal location. Coughlin[50,51] further showed that pink fibers, present in many fishes in a layer between the superficial red fibers and the deeper white fibers, are delayed in activity onset compared with red fiber activity onset. This suggests that there is a relationship between fiber contraction speed and the delay in activity onset, with faster fibers at the same longitudinal position becoming active later in time.
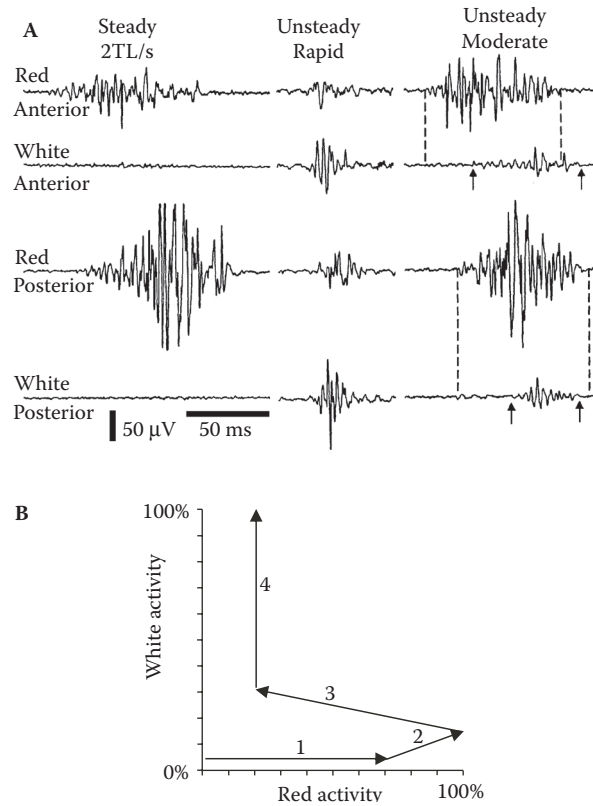
FIGURE 1.9 A: Muscle activity patterns recorded simultaneously from four locations on the same side of one individual bluegill sunfish (*Lepomis macrochirus*) during three locomotor behaviors. During relatively fast steady swimming, only red muscle fibers are active and show clear longitudinal propagation from anterior to posterior. During rapid unsteady body movements preceding a glide, white fibers are strongly active, while red fibers show reduced activity. At speeds intermediate between these two traces, both sets of muscle fibers are recruited, but white fibers are active at a later onset time than red. B: Schematic diagram summarizing the pattern of muscle fiber recruitment in swimming bony fishes indicated by experimental data. Numbers show the order of speed increase during locomotion from slow swimming (1) to the fastest unsteady speed (4). See text for discussion. Modified from Jayne and Lauder.[139]

A schematic summary of muscle activity patterns in red and white muscles during both steady swimming and unsteady c-start escape behaviors is shown in Figure 1.10. During steady swimming, the electrical wave of activity in red muscle fibers propagates from anterior to posterior. At certain times during steady swimming, red muscle fibers are active along nearly the entire length of the fish.[137,142] In bluegill sunfish, which have 23 myotomes, electromyographic recordings show that at a swimming speed of 1.6 Ls^{-1}, activity is seen in red fibers corresponding to 21 segments at a time.[143] Rapid escape responses in fishes are referred to as c-starts, as the body of the escaping fish bends (more or less) into a c-shape.[59,61,62,77,78,80,121,122,137,233,264,288] This behavior is well described kinematically and involves an interesting pattern of muscle activity. At the beginning of the startle response, both red and white muscle fibers are synchronously active along one side of the body and bend the majority of the body into a c-shape (see Figure 1.10, Stage 1). The tail region often bends back against the flow due to hydrodynamic loading, which cannot be overcome by the reduced mass of muscle near the tail, and the body thus assumes an s-shape at the end of stage 1 of the c-start.[137] This activity is followed by activation of both red and white muscles on the opposite side to bend the body back to the contralateral side and initiate the propulsive phase (see Figure 1.10,
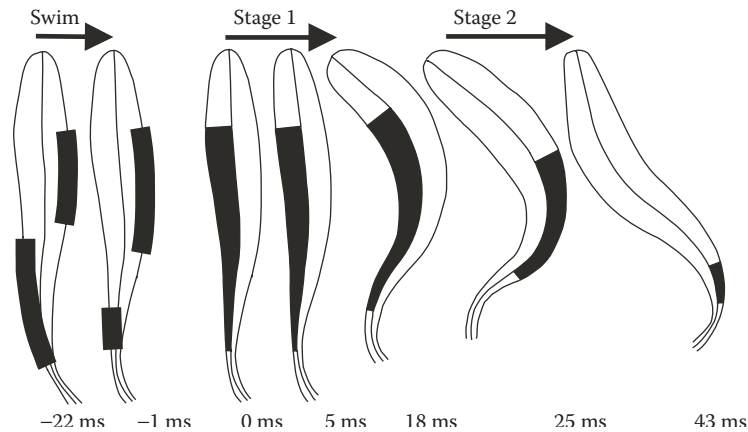
Swim　　　　　　　Stage 1　　　　　　Stage 2

−22 ms　　−1 ms　　　0 ms　　5 ms　　18 ms　　　25 ms　　　43 ms

FIGURE 1.10 Schematic summary of body movement patterns and red and white muscle activity during steady swimming and a c-start escape response in bluegill sunfish (*Lepomis macrochirus*). Time (in ms) relative to the start of the escape response (0 ms) is indicated at the bottom. Thin black regions laterally indicate activity of red fibers during steady swimming, while white fiber activity is indicated by black regions that extend to the midline; during stages 1 and 2 of c-starts, both red and white muscle fibers are active. This escape response was elicited from a sunfish swimming steadily. See text for discussion. Modified from Jayne and Lauder.[137]

Stage 2). One interesting feature of this pattern is that the speed of the body bending during stage 1 is greater than the contraction time of red muscle fibers, which cannot then contribute to the bending: the white fibers are compressing the red fibers faster than they can actively shorten. Nonetheless, these red fibers are active, which may reflect their role in stiffening the body or explain the constraints — which prevent separate rapid activation of white fibers alone — on neural circuit activation during the rapid escape response.[137]

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Another approach to understanding body muscle function during locomotion is to quantify muscle activity and strain *in vivo* and then separately measure muscle power output using the *in vitro* work loop technique.[151] This permits determination of how much power is available relative to the power needed to execute behaviors such as steady swimming and rapid burst-and-glide movements. Work loop measurements can be done with *in vivo* strain and phase relationships to mimic swimming, but a variety of strains and phases also can be used to determine if the *in vivo* values produce maximal power output. This approach has been applied to the study of numerous species over the past 15 years. Data from locomotion at steady swimming speeds ranging from $0.7\ Ls^{-1}$ to high-speed, unsteady, burst-and-glide swimming are shown for largemouth bass in Figure 1.11. Estimated muscle strains of +/–6% were consistently found for red fibers at all steady swimming speeds. However, during unsteady burst-and-glide swimming, red fiber strains approached +/–15%. During slow swimming, red fibers at the posterior end of the body (just anterior to the caudal peduncle) were electrically active for part of the time while they were shorter than resting length; however, during rapid locomotion, the same fibers were activated while they were longer than resting length (see Figure 1.11). This phase change between activation and shortening results in red muscle fibers achieving maximal power at a tail beat frequency of 3 Hz and cannot contribute significantly greater power at higher frequencies seen during burst-and-glide swimming (Figure 1.12).

If the total power required for fishes to swim at a given speed (calculated from energy studies measuring oxygen consumption) is compared with the power available from red muscle as determined from work loop measurements in largemouth bass (see Figure 1.12),[145] then it is clear at tail beat frequencies in the range of 2 to 4 Hz that the power available from red muscle substantially exceeds the power needed. This suggests that not all of the red fibers need to be recruited to power locomotion at these speeds and that electromyographic activity in red fibers at these speeds should be less than maximal (which is indeed the case, as shown in Figure 1.9). At very slow swimming
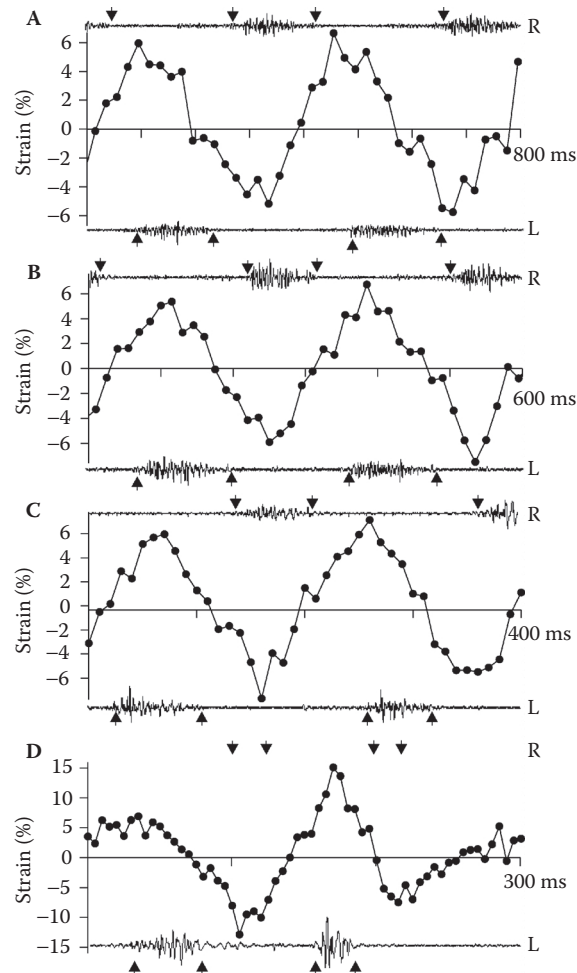
FIGURE 1.11 Pattern of electrical activity and calculated muscle strain during locomotion in largemouth bass (*Micropterus salmoides*) at 0.7 (A), 1.6 (B), 2.4 Ls^{-1} (C), and unsteady kick-and-glide swimming (D). Note differing time scales on the horizontal axis as swimming speed increases. Arrows indicate approximate muscle activity onset and offset times. From Johnson et al.[145]

speeds, when many fish use their pectoral fins, there is a large power excess available from red myotomal fibers and locomotor power comes from pectoral fin muscles. At tail beat frequencies above 4 Hz, the power required to overcome drag exceeds that available from red muscle fibers, and fishes must therefore recruit white fibers (see Figure 1.12). The speed limit to rapid steady locomotion may thus be set by the power available from red fibers.[145]

There has been some controversy in recent years over the region of the body where red fibers generate the positive work needed for locomotion in teleost fishes. One early proposal[257] was that anterior red fibers produced most of the positive *in vivo* work for body bending and that posterior fibers were electrically active as they lengthened, doing mostly negative work and transmitting force from anterior muscles to the tail. In light of a spate of recent studies that show predominately positive work from posterior red lateral fibers and questions about the methodology of the earlier studies,[47,50] it seems well established now that for most teleost species, red muscle on the posterior half of the body produces positive work powering swimming at steady cruising speeds.[48,145,154,213-215,220] Indeed, numerous kinematic analyses of the body bending during locomotion (e.g., Figure 1.6) show that at speeds less than about 1.5 Ls^{-1}, there is very little body bending (and hence strain) along the
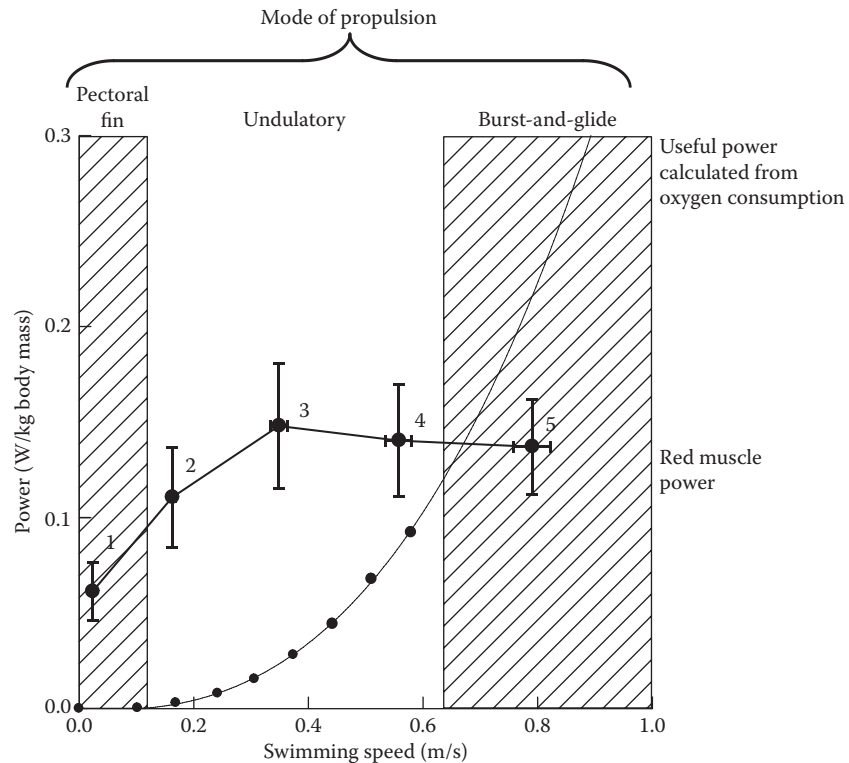
FIGURE 1.12 Power requirements for swimming calculated from oxygen consumption, compared with power available from red muscle as determined from work loop experiments. Error bars are standard errors. Numbers above the red muscle data indicate tail beat frequencies at the given absolute swimming speed. Modified from Johnson et al.[145]

anterior half of the body. Small strains greatly limit the power that red muscle can produce and further indicate that power for steady swimming is produced mostly by posterior red fibers in teleost fishes.[49,219,220]

An interesting new finding in leopard sharks by Donley and Shadwick[64] suggests that, at least in this species, red fibers along the entire length of the body may do positive work to power steady swimming. They found a *consistent* phase between red muscle activity and strain along the body, in contrast to the result, seen in all teleost species studied to date, of *decreases* in activity duration in more posterior red fibers. The generality of this finding to other elasmobranch species remains unknown, but this result currently represents an intriguing contrast between shark and teleost fish muscle function during locomotion.

One final area of current study is the change in red fiber contractile properties and muscle protein isoforms down the body. Red fibers along the length of fishes appear to differ in properties, which may help explain interspecific differences in power production[7,248,249] (also see[146,149,150]).

au: should this be "inter-species"?

VI. EXPERIMENTAL HYDRODYNAMIC ANALYSES OF LOCOMOTION

A. BODY POSITION AND SHAPE

As fishes change speed and maneuver, they typically alter their body posture, and this can play a critical role in the overall hydrodynamic force balance during swimming. Only recently has the hydrodynamic importance of body posture control been fully recognized, although many studies have noted that fishes often swim with the body axis at an angle to the horizontal plane, even

during steady rectilinear locomotion.[1,2,106,129,183,184,195,295] For example, Gibb et al.[106] as well as Nauen and Lauder[195] noted that mackerel (*Scomber japonicus*) swam at speeds greater than 1.0 Ls^{-1} with a slight (1 to 5°) downward tilt to the body. Body angle is significant, in part because alterations in this angle affect the movement of the force generated by the tail around the center of mass, and hence needed compensatory hydrodynamic forces from other fins. At slower speeds, many fishes tilt the body at a positive angle of attack toward oncoming flow to generate hydrodynamic lift.

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A particularly clear example of body angle adjustment during locomotion is seen in the leopard shark (*Triakis semifasciata*) as speed increases from 0.5 to 2.0 Ls^{-1} (Figure 1.13A).[296] Body angles in leopard sharks declined over this speed range from a mean of 11° to 0.6°, presumably because a lower body angle of attack is needed in faster flow to generate the lift forces to counter body weight. In addition, fishes adjust body angle during maneuvering (see Figure 1.13B). Sharks, for example, may use pectoral fins to generate movements around the center of mass that pivot the body up at a positive angle to move upward in the water column or down as they move toward the bottom. The body angle of attack toward oncoming flow is the main reason leopard sharks move vertically in the water, since the direction of force produced by the tail does not change.[296,298]

Bartol et al.[13,14] provide a good example of how body shape can affect flow patterns that aid in stability during swimming, as in boxfishes, which have a rigid "carapace" of fused scales. Ridges
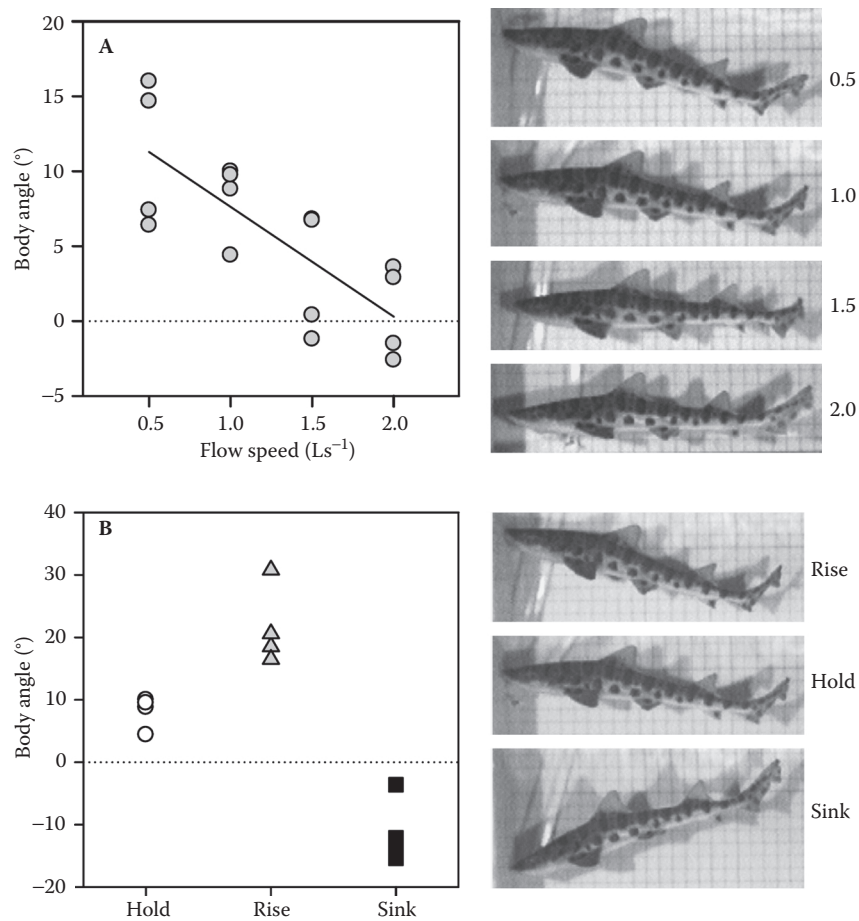

FIGURE 1.13 Sharks change body angle with speed (A) and during vertical maneuvers in the water column (B). Speeds in A range from 0.5 to 2.0 Ls^{-1}, and rise, hold, and sink behaviors correspond to positive (up), zero, and negative (down) vertical maneuvers. Modified from Wilga and Lauder.[296]

along the body generate longitudinal vortices which, with their accompanying low pressure, act to stabilize the body and bring it back into trim in response to externally induced pitching moments. Body shape thus generates self-correcting movements about the center of mass and acts to maintain stability during locomotion.

B. FIN AND BODY HYDRODYNAMICS

Within the last 10 years, a new area of research into the locomotion of fishes has emerged: experimental hydrodynamics of freely swimming fishes. While the seminal theoretical contributions of Sir James Lighthill in the 1960s and 1970s [175–178] and the influential models of G. I. Taylor[244] provided the initial basis for studying the fluid dynamics of fish locomotion,[46,130,203,276,303] in recent years, the advent of increased computational power and relatively inexpensive high-power lasers for laboratory use has opened up new avenues in the study of the dynamics of fish locomotion. It is now possible to directly visualize the flow generated by the body and fins of actively swimming fishes (not just models) and to quantify these flows by generating a matrix of velocity vectors that characterizes the flow in a two-dimensional slice of fluid.[14,70,71,74,124,164–166,168,189,235,302] This technique is called Digital Particle Image Velocimetry (DPIV).

Lauder and colleagues[165–168] provide an overview of DPIV as it applies to the study of fish locomotion, and sample data and their interpretation are shown in Figure 1.14. Flow is visualized by using a laser to generate a light sheet that typically is 1 to 2 mm thick and 10 to 20 cm wide. This light sheet is projected into a flow tank or aquarium, and small reflective particles that reflect light back to one or more high-speed cameras are mixed into the water.[70,72,75] Fish swim with their body or fins cutting through the light sheet, and the flow over the surface of the body and fins and in the wake can be seen by following the positions of particles in high-speed video frames. Successive images in time are analyzed with cross-correlation to reconstruct a matrix of velocity vectors that represents an estimate of flow in that slice of fluid during the time between frames.[85,165,166,300] From these velocity vector matrices, a wide variety of quantities can be calculated: the location of vortex centers, fluid dynamic circulation (a measure of vortex strength), vorticity (measuring the angular velocity of fluid), momentum, force, work, and power.[165] Reorientation of the light sheet into orthogonal orientations (see Figure 1.14) allows the flow to be analyzed in three separate perpendicular planes, which greatly aids three-dimensional reconstruction of fluid structures shed by the fins and body. While the bulk of recent studies have been limited to studying flow in a single two-dimensional flow slice at a time, Nauen and Lauder[194] used a stereo-DPIV technique to image simultaneously the three components of flow velocity (x, y, z) in a 2-mm thick light sheet.

By analyzing orthogonal planes in the wake behind the pectoral fin in bluegill sunfish, Drucker and Lauder[70] showed that each plane illustrates counterrotating centers that reflect slices through a vortex ring (see Figures 1.14B and 1.14C). Each beat of the sunfish pectoral fin thus generates an isolated vortex ring (see Figure 1.14D) that represents momentum transferred from the pectoral fin to the fluid. These vortex rings have a central momentum jet that is directed downward, posteriorly, and laterally. For an approximately 20-cm long bluegill sunfish swimming at 0.5 Ls^{-1}, the posterior component (generated by both fins) of 11 mN balances a total drag of approximately 10.6 mN on the fish during steady swimming. The total downward component of 3.2 mN balances the weight of the sunfish (3.4 mN). An unexpected finding from this work is the large lateral force generated: 6.7 mN per fin relative to a thrust of 5.5 mN. Thus, each sunfish pectoral fin is producing more lateral force than thrust, inefficient for steady forward locomotion but possibly necessary for stability and useful for rapidly generating large turning movements.

Vortex ring structure and/or orientation can change as speed increases (Figures 1.15A and 1.15B)[70] and as fishes maneuver;[72,76,296] differences in vortex ring morphology among species swimming with their pectoral fins at the same relative speed have also been observed.[71] Interspecific changes in vortex ring orientation with speed are particularly instructive in the analysis of why fishes change gaits as speed increases. Certainly, the analysis of red muscle power described earlier
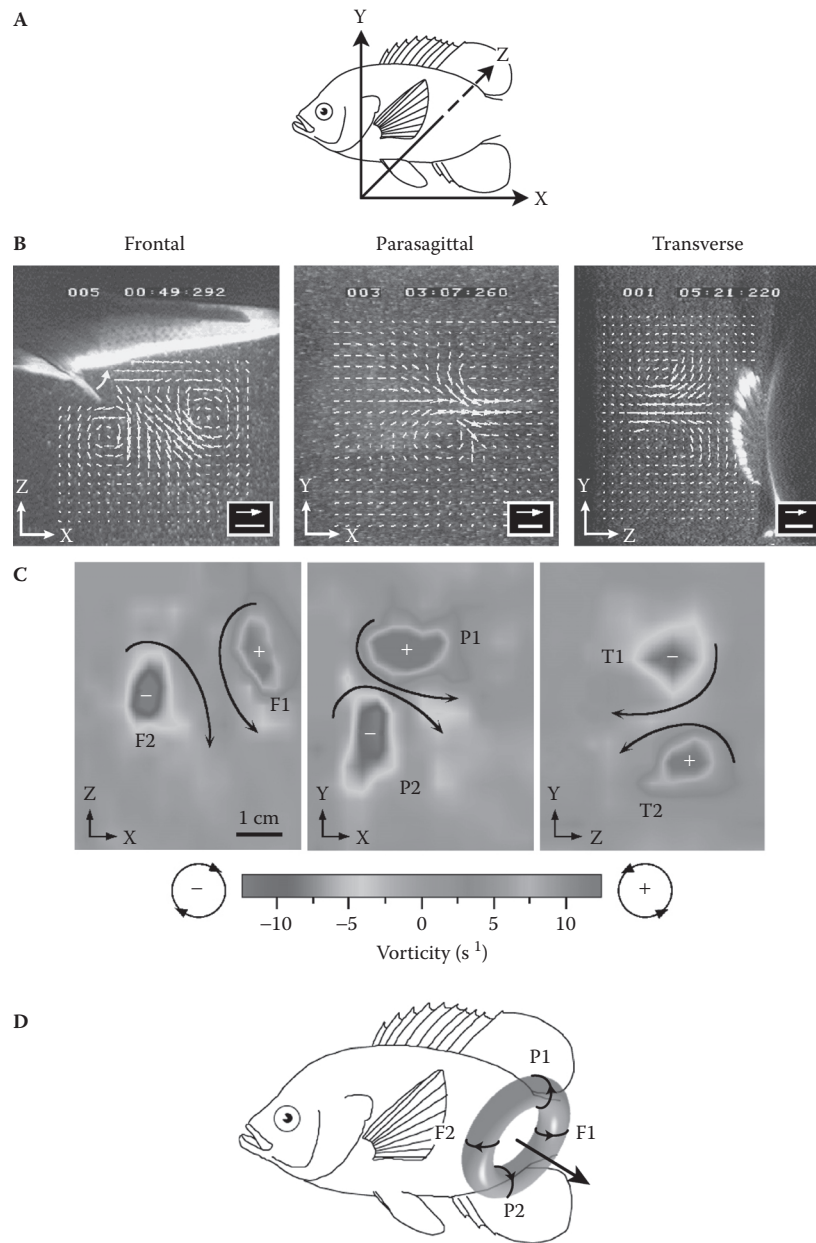
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FIGURE 1.14 Experimental approach for analyzing the hydrodynamic wake structure in three dimensions during locomotion in freely swimming fishes, illustrated for the pectoral fin wake in bluegill sunfish (*Lepomis macrochirus*). A: Analyses are conducted in three separate perpendicular planes, frontal (XZ), parasagittal (XY), and transverse (YZ). B: Representative data from each of these planes showing velocity vectors (in white) superimposed on the background image of the fish and laser light reflections from 12-μm particles suspended in the water. C: Vorticity calculation based on the velocity vector fields. Note that each plane has two discrete centers of counterrotating flow in the indicated directions. D: Inferred vortex ring structure in the wake of bluegill sunfish swimming at 0.5 Ls⁻¹ with pectoral fins alone. The wake consists of a single vortex ring that is shed with each fin beat. In panels C and D, F1-2, P1-2, and T1-2 indicate the centers of vorticity observed in the wake. The straight arrow shows the direction of the central momentum jet that passes through the center of the vortex ring. Scales for panel B: Arrow = 120 cm s⁻¹; bar = 1 cm. Modified from Drucker and Lauder.[70,74]
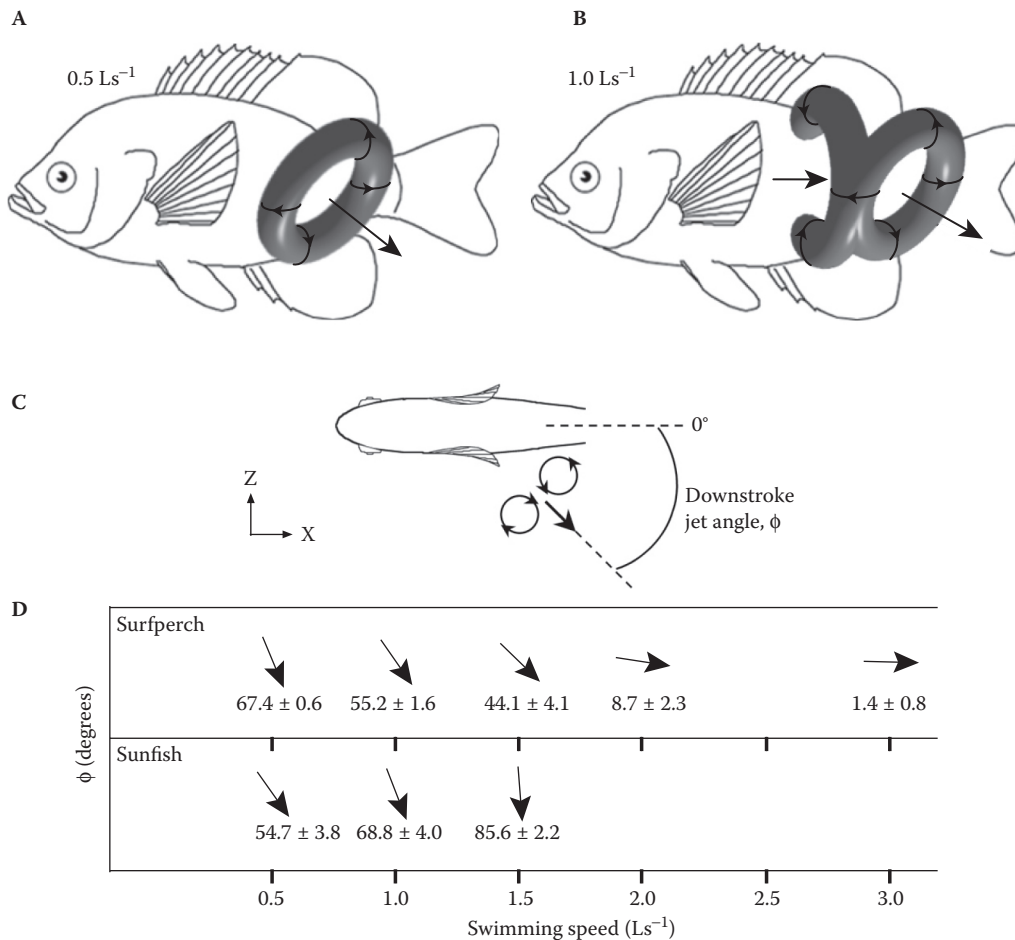
FIGURE 1.15 A, B: Vortex wake structure changes with speed during pectoral fin locomotion in bluegill sunfish (*Lepomis macrochirus*). Note the additional vortex structure present at higher speed of 1.0 Ls^{-1}. C: Convention for measuring the angle of the central vortex momentum jet in the horizontal (XZ) plane: Φ is measured relative to the axis of travel (0°) and is 90° when the jet is aimed laterally. D: Comparison of vortex jet angle (in degrees) in bluegill sunfish with those produced by surfperch, *Embiotoca jacksoni*. Note that as speed increases, sunfish vortex jets turn almost directly laterally, while those of surfperch are increasingly aimed downstream. See text for discussion. Modified from Drucker and Lauder.[71]

strongly suggests that for undulatory locomotion, red fibers simply cannot generate the power needed to overcome drag at high speeds and hence white muscles are recruited at or near the transition to a kick-and-glide gait. However, gait transitions at lower speeds, from pectoral fin propulsion to undulatory swimming, may have a different explanation. Figures 1.15C and 1.15D illustrate a comparison between vortex ring orientation in bluegill sunfish (*Lepomis macrochirus*) and that in surfperch (*Embiotoca jacksonii*) as both species increase speed. By measuring the angle of the central vortex momentum jet in the horizontal plane in both species as speed increased, Drucker and Lauder[71] found that surfperch reorient vortex ring momentum to an increasingly downstream orientation (see Figure 1.15D). This provides for additional momentum transfer to the water as speed increases. Surfperch are able to maintain pectoral-fin-based propulsion up to a speed of 3.0 Ls^{-1}, at which point the vortex momentum jet is oriented nearly directly downstream. In contrast, sunfish swim at slow speeds of 0.5 Ls^{-1}, with pectoral fin vortex jets directly at about a 55° angle to the path of motion, but rotate these jets *laterally* as speed increases. As a result, at

1.5 Ls^{-1}, sunfish have virtually no downstream momentum remaining in the jet as it points nearly directly to the side (see Figure 1.15D); additional fins or the body *must* be recruited starting at about 1.1 Ls^{-1} to provide the thrust needed to overcome drag. Sunfish thus change gait from pectoral propulsion to undulatory propulsion because they can no longer generate enough force with the pectoral fins due to the lateral orientation of the vortex rings. The inability of sunfish to reorient the vortex rings to provide needed downstream momentum may be a consequence of pectoral fin anatomy or possibly a requirement for body stability as speed increases.

Sharks use their pectoral fins to reorient body position and to generate rotational movements, but not for propulsion (Figure 1.16). Three-dimensional kinematic analysis shows that during steady
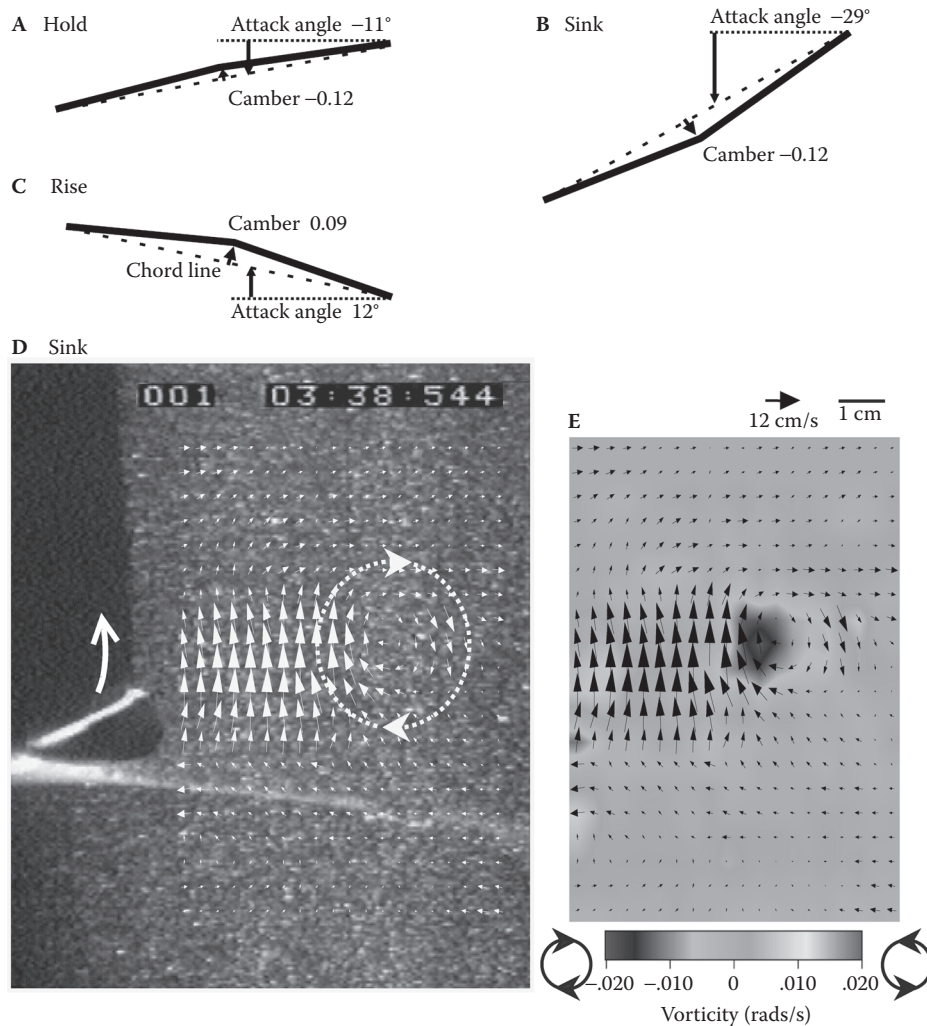
FIGURE 1.16 Summary of pectoral fin kinematics and hydrodynamics during locomotion in sturgeon, *Acipenser transmontanus*. A: During steady horizontal swimming (holding vertical position), the pectoral fins are held at a negative angle of attack. During sinking (B) and rising (C) in the water column, pectoral fin angles change to an average –29° and +12°, respectively. D: Fluid dynamic analysis of pectoral fin function using digital particle image velocimetry shows that during sinking, sturgeon pectoral fins flip up (white solid arrow) and shed a large vortex (white dotted circle) into the fluid, creating a movement about the center of mass that rotates the head down. The vorticity plot (E) shows the large center of vorticity associated with the upward fin flip. Modified from Wilga and Lauder.[295]

FIGURE 1.17 Analysis of the dorsal fin wake in bluegill sunfish (*Lepomis macrochirus*). A: Schematic diagram of the horizontal laser light sheet used to image flow shed by the dorsal fin trailing edge. A high-speed video camera is aimed a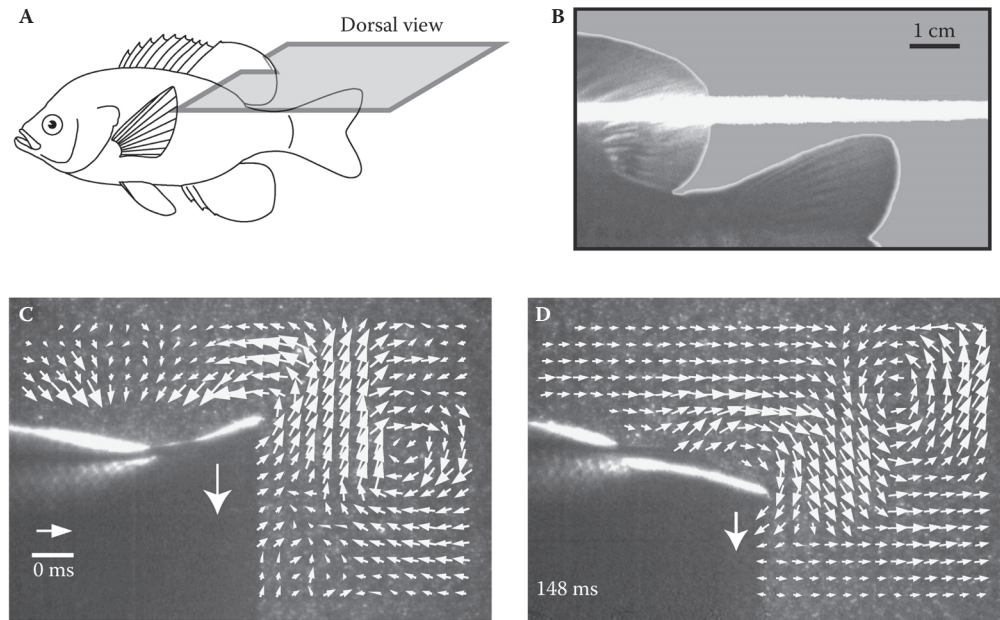t the laser light sheet from above. B: Lateral view image of the sunfish caudal and dorsal fins with the laser light sheet seen edge-on as a thick white line. C, D: Flow fields in the wake of the dorsal fin at time 0 and 148 ms corresponding to the duration of a half-stroke of the fin during steady swimming at 1.1 Ls^{-1}. The dorsal fin is moving in the direction of the large white arrow. The dorsal fin actively generates a strong wake that has both lateral and downstream components. Modified from Drucker and Lauder.[73]

horizontal swimming, leopard sharks hold their pectoral fins at a slightly negative angle of attack and that this angle changes significantly as vertical maneuvers are executed.[296] An upward flip of the pectoral fins is used to induce upward flow and shed a vortex (see Figures 1.16D and 1.16E) that pitches the head of the shark downward and initiates powered sinking in the water column.

Experimental hydrodynamic analysis of the dorsal fin (Figure 1.17) demonstrates that, at least in bluegill sunfish, this fin generates both significant lateral and thrust forces. At a speed of 1.1 Ls^{-1}, the dorsal fin produces roughly 12% of the total thrust needed to overcome body drag,[73] and an analysis of intrinsic muscle activity in the dorsal fin indicates that this wake is generated actively.[144] The dorsal fin is thus an active component of the locomotor repertoire in fishes and not merely a passive stabilizer used to prevent roll instabilities. In addition, the wake from the dorsal fin passes back and is encountered by the tail, which moves through flow that is accelerated and moving at a significant angle toward freestream flow.[73,168,193] The effect of the substantial narrowing of the body just anterior to the tail is to direct flow toward the tail centerline in the vertical plane. In the horizontal plane, the tail encounters flow that contains strong vortices and has a higher speed than freestream flow. This suggests several mechanisms of thrust enhancement.[73,187] The tail generates greater thrust in the presence of a dorsal fin wake due to enhancement of leading edge vortices than it could with freestream flow alone.[73,187]

Perhaps the most general result to emerge from integrated kinematic and experimental fluid dynamic analyses of flow impinging on the tail is that the caudal fin does not move through undisturbed water. Rather, the flow encountered by the caudal fin, and especially the upper and lower lobes of the tail, is radically different from undisturbed freestream flow. Computational models of propulsion in fishes need to account for the effect of active movement of both the dorsal and anal fins on the fluid and for the effect of rapid body narrowing just before the tail.
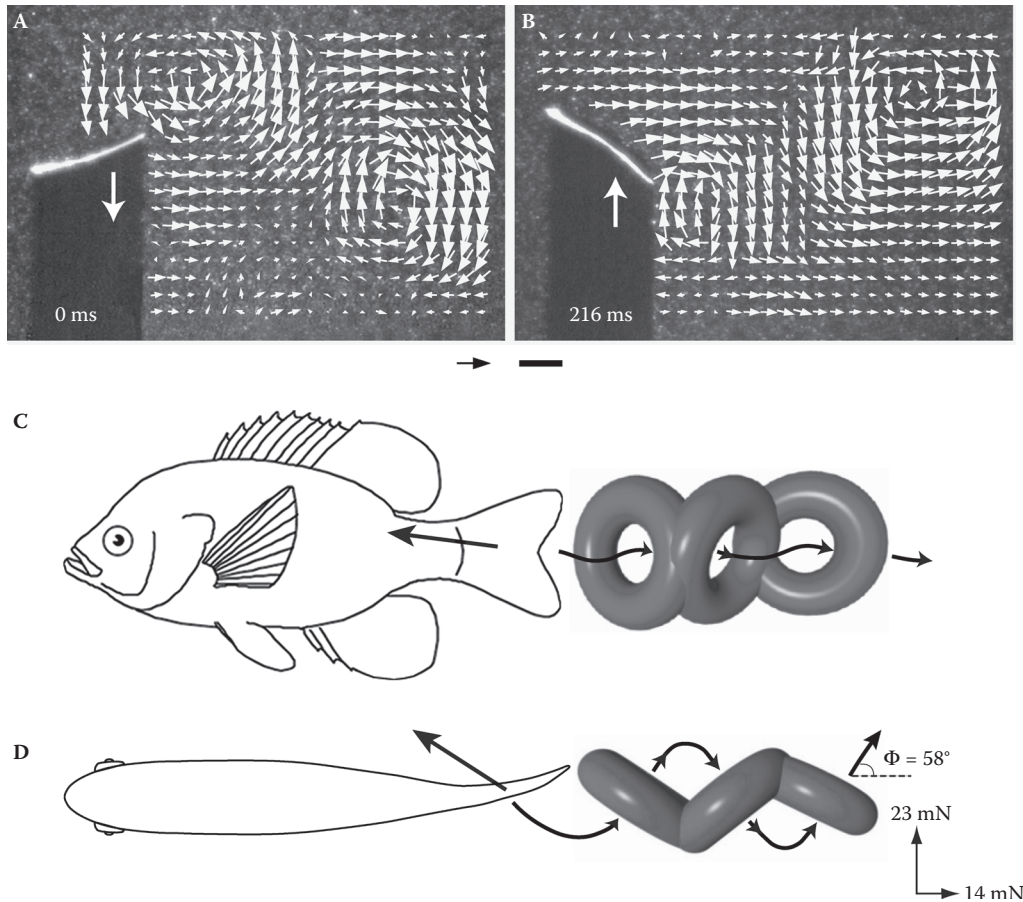
FIGURE 1.18 Caudal fin wake in bluegill sunfish (*Lepomis macrochirus*). A, B: Flow fields at time 0 and 216 ms later corresponding to roughly one half-stroke of the caudal fin during swimming at 1.1 Ls^{-1}. Two counterrotating centers of vorticity are clearly visible. Arrow represents flow of 10 cm s^{-1} (freestream velocity has been subtracted), and the scale bar is 1 cm. C, D: Schematic lateral and dorsal views respectively of the vortex wake of sunfish swimming at about 1.5 Ls^{-1}. Curved arrows represent central jet flow, while is the angle of the jet to relative to the path of motion. For a sunfish 20 cm long, the caudal fin generates 14 mN thrust and 23 mN lateral force. Straight arrows represent the direction of the reaction force on the fish from the wake vortex rings. Modified from Drucker and Lauder.[73,165]

The caudal fin in fish species with a well-defined narrowing of the body at the peduncle serves as an additional propulsive surface that is at least partially independent of the body (Figure 1.18).[164,166,167] The wake generated by the caudal fin consists of a linked chain of vortex rings that results from the combined action of oscillatory side-to-side tail movement (and the consequent shedding of start-stop vortices) and the rollup of tip vortices shed by the dorsal and ventral tail margins (see Figure 1.18). As was the case with flows generated by sunfish pectoral fins, the caudal fin also generates large lateral forces, often twice the value of thrust.

The heterocercal tail of sharks also generates a vortex wake,[298] but due to the temporal lag between lateral movements of the upper and lower lobes and the movement-inclined trailing edge, the vortex wake consists of a ring-within-a-ring structure (Figure 1.19).[299] The larger outer vortex rings are themselves linked to each other in a manner similar to the vortices shed by the externally symmetrical tail of bony fishes. The generality of this vortex wake morphology among sharks or even ray-finned fishes with heterocercal tails is currently unknown, as is the functional significance
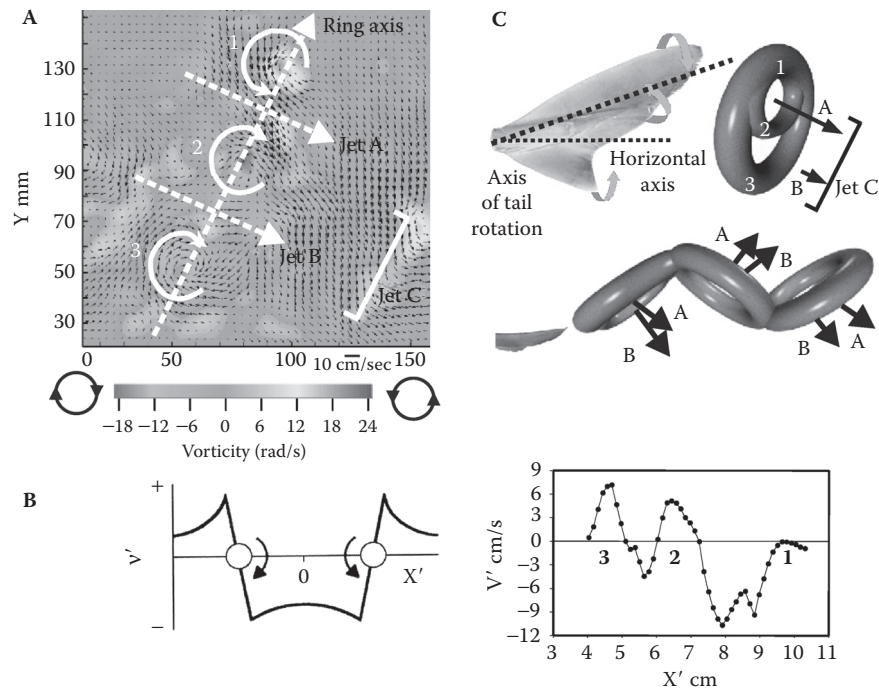
FIGURE 1.19 Analysis of the vortex wake from the tail of spiny dogfish (*Squalus acanthias*) swimming steadily while maintaining vertical position. A: Vorticity plot of a vertical slice through the wake showing three centers of vorticity: center 1 rotating counterclockwise in this view, and centers 2 and 3 with clockwise rotation. Fluid jets through these vortex rings (jets A and B) develop and merge into a single larger jet C. B: Analysis of a transect along the ring axis shown in A. Theoretically predicted velocity distribution is shown on the left, and the actual graph from the time shown in panel A is given on the right, showing the three centers. C: Reconstruction of the vortex wake as a ring-within-a-ring structure. Modified from Wilga and Lauder.[299]

of the ring-within-a-ring structure. Sharks might be able to actively direct flow through the upper ring by adjusting tail angle or by the action of intrinsic muscles, but experimental data from leopard sharks suggest that at least this species is not capable of such control.[298]

A recent detailed study of the vortex wake of eels (*Anguilla*) swimming steadily[253] has shown that there is effectively no downstream component of momentum in the wake (Figure 1.20). Rather, a series of vortices are shed by the eel tail with flow between the vortex centers directed laterally. This contrasts sharply with the wake of subcarangiform swimmers, which invariably contains downstream momentum in the vortex jets. The lateral wake jets of an eel swimming steadily form just anterior to the tail tip, and the alternating sign of the lateral flows results in an unstable shear layer that rolls up into two or more secondary vortices approximately one tail beat later (see Figure 1.20).[253] The eel wake does not form as a result of acceleration of fluid along the entire length of the animal, but rather the vast majority of fluid momentum is acquired in the region centered 15% of body length anterior to the tail.[253] This produces a wake pattern that resembles two unlinked vortices with central jet flows directed to each side.

Tytell and Lauder[253] explained the differences between the eel wake and that of subcarangiform swimmers (and that of pectoral fin swimming), described above, with an analogy of a boat with a propeller. A swimming mackerel, for example, incurs the vast majority of drag on the body like a boat hull does, while the tail generates thrust like the propeller on a boat. Like a boat with a propeller, there will be a thrust signature in the wake because of spatial separation between the major drag-producing structure (the body or the hull) and the thrust-generating structure (the tail or the propeller). Eels may be balancing drag and thrust along the body to a greater extent than
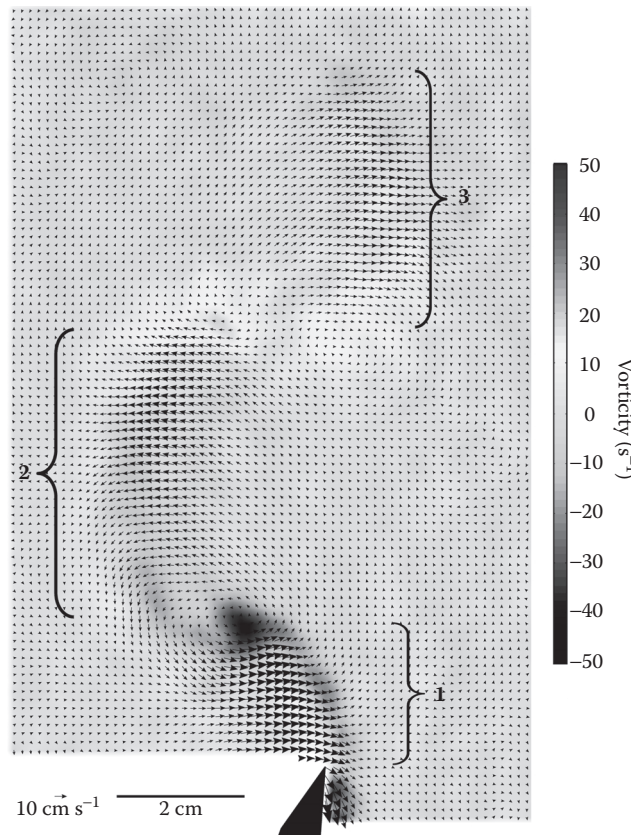
FIGURE 1.20 Hydrodynamic wake behind a steadily swimming eel, *Anguilla rostrata*, swimming at 1.4 Ls^{-1}. The flow field shown is a phase average of 14 tail beats. Black vectors show the direction of water flow. Three prominent lateral jets are shown labeled 1 to 3 from anterior to posterior. The tail tip of the eel is shown at the bottom of the figure. Freestream flow is subtracted. Note the lack of a posteriorly directed jet flow between adjacent vortices; flow generated by body and tail movement is predominately lateral. Modified from Tytell and Lauder.[253]

fish such as mackerel or sunfish.[228] Eels lack the substantial longitudinal shape change anterior to the tail, seen in most carangiform swimmers with a thrust wake; eels lack a morphologically discrete propeller. Indeed, differences in body shape along the posterior third of swimming fishes, not the relatively minor differences in midline kinematics, may be the dominant explanation for the different wake patterns observed between anguilliform and subcarangiform locomotion.

As swimming eels increase speed, the basic pattern of the wake with its lateral jets does not change.[251] But when eels perform linear accelerations, a wake very similar to that of mackerel and sunfish is seen: vortex jets point downstream adding momentum to the water to sustain body acceleration.[252]

Most experimental hydrodynamic studies on swimming fishes to date have focused on the wake or flow near the caudal peduncle or over the tail. The nature of flow over the body of a freely swimming fish has yet to be fully examined, but the recent careful and detailed analysis by Anderson et al.[8] has provided the first quantitative data on boundary layer characteristics of freely swimming fishes. By obtaining video images of flow close to the body surface in scup (*Stenotomus*) and dogfish (*Mustelus*), Anderson et al. were able to generate high-resolution boundary layer velocity profiles along the body midline for both species. They found no separation of the boundary layer

at speeds around 1.5 Ls^{-1} for scup, strongly suggesting that pressure drag on steadily swimming scup is minimal. The majority of drag is incurred in the form of friction drag. Boundary layer profiles were laminar at slow swimming speeds and turbulent at higher-speed locomotion. Total drag calculated from shear stresses estimated for the whole body was approximately two to four times that calculated or measured from rigid body drag experiments. These results provide the first empirical data from freely swimming fishes, supporting Lighthill's original view that swimming fishes incur increased drag as a result of body undulation.[177]

C. ENVIRONMENTAL VORTICES AND FISH LOCOMOTION

Turbulence at a variety of scales is a characteristic feature of the environment for fishes swimming in natural habitats.[44,82,173] Rarely do fishes encounter the steady microturbulent flows characteristic of laboratory flow tanks. Instead, fishes in natural habitats are faced with a variety of obstacles in flowing waters that shed vortices and large-scale turbulent eddies. But studying fish locomotion in such turbulent flows is a difficult challenge: only relatively limited experimental measurements can be made under field conditions. Laboratory flow tanks are, however, not generally designed to generate appropriate turbulence. One way around these difficulties is to introduce into laboratory flow tanks known obstacles that generate fluid dynamically in well-understood large-scale turbulent flow structures. For example, a D-section cylinder is known to produce a well-defined Karman vortex street even at relatively large Reynolds numbers (up to 50,000). (The Reynolds number indicates the ratio of inertial to viscous forces in moving fluids, and hence the amount of turbulence that can be expected.[261]) So, it is possible to place such a cylinder in a flow tank (Figure 1.21A), generate a Karman vortex street downstream of the cylinder, and observe fish swimming in the resulting structured turbulence. The experimental arrangement depicted in Figure 1.21A has one noteworthy advantage. Because cylinders shed columnar arrays of vortices, two high-speed video cameras can be used: one for imaging the fish in ventral view silhouetted against the laser light and another to simultaneously film from above using a mirror to quantify the pattern of vortices. In this manner, both kinematics and the position of the body in the vortex street can be obtained without any blockage of the light sheet by swimming fish.

Results from the experiments performed by Liao et al.[173] are shown in Figures 1.21B and 1.21C, where the outline of a swimming trout can be seen slaloming between oncoming vortex centers. Trout swimming in a vortex street, well downstream of the D-cylinder in the flow, adopt a gait termed the Karman gait,[172] with large lateral oscillations of the center of mass compared with freestream swimming. Figures 1.22A and 1.22B compare the pattern of movement of trout swimming in freestream flow with that of the same trout swimming in the Karman vortex street generated by the D-cylinder. The most characteristic feature of the Karman gait is the large lateral oscillation of the entire body, which appears to move, in a largely passive way, from side to side between oncoming vortices. Body amplitudes and curvatures are much larger than in steady swimming at equivalent speeds, and tail beat frequencies are much lower: body motion is tuned to synchronize with oncoming vortices.[172] Recordings of red and white muscle activity during the Karman gait confirm that this gait is, indeed, largely passive: no white muscle activity is observed, and only the anterior red fibers are active (see Figure 1.22C).[174] When pectoral fins are used to make minor adjustments in body position in the vortex street, even this anterior red muscle activity is absent, and all body musculature is electically inactive.

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These data demonstrate that fishes can take advantage of low-pressure vortices in oncoming flow to maintain station in downstream flows of 2.5 Ls^{-1} or greater without expending significant muscular energy by tuning body kinematics to the external flow environment. The Karman gait differs from the interesting entrainment behaviors in which fishes maneuver into the low-pressure suction region immediately behind small cylinders placed in the flow.[239,284]

FIGURE 1.21 Analysis of locomotor mode and hydrodynamic wake of rainbow trout (*Oncorhynchus mykiss*) when swimming in a vortex street generated by a D-section cylinder in a flow tank (A). Trout body movement was visualized with a ventral camera (camera 2), while simultaneously a dorsal camera (camera 1) imaged the flow generated by the cylinder undisturbed by trout body movement. Laser light was focused into a horizontal light sheet to image water flow with digital particle image velocimetry. In this way, the interaction of trout and environmental vortices could be directly observed. B: Time series of body outlines (heavy line) and midlines (thin line) of trout encountering the Karman vortex street shed by the D-section cylinder (grayscale vorticity background) with calculated water velocity vectors superimposed as black arrows to show the direction of flow. Background grayscale plots show vorticity centers. D: Midlines of trout swimming from right to left for seven tail beats illustrating that trout slalom in between vortex centers (indicated by + and – symbols), and do not intercept vortices directly. Modified from Liao et al.[173]
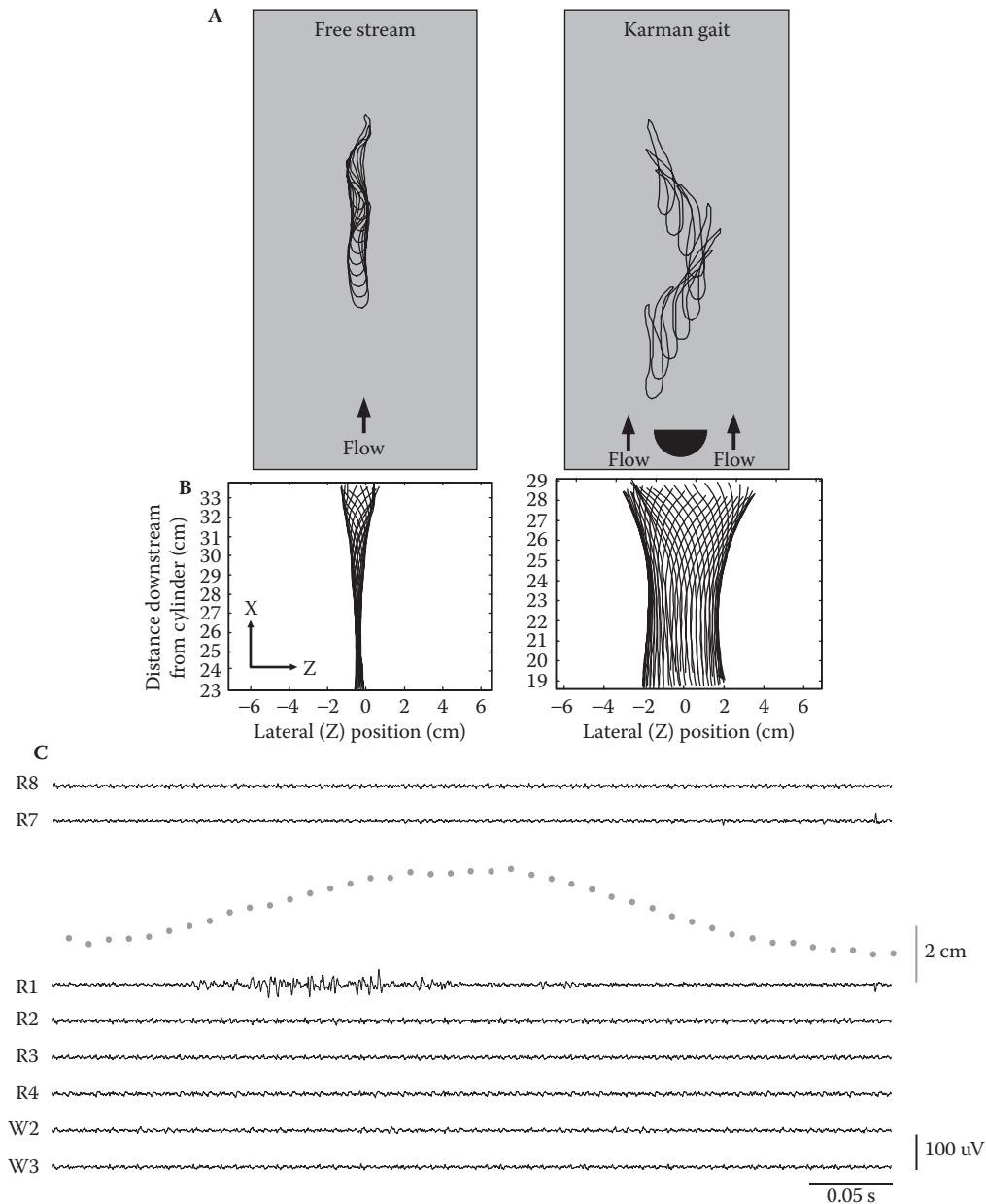
FIGURE 1.22 A: Comparison of body motion in rainbow trout (*Oncorhynchus mykiss*) when swimming in freestream flow at 4.5 Ls[-1] compared with body oscillation in the flow deficit within the Karman vortex street behind a D-section cylinder. Large amplitude body oscillations in a vortex street, with lateral center of mass excursions six times that of freestream movements, are termed the Karman gait.[172–174] B: Comparison of midline motion of freestream locomotion versus the Karman gait. C: Pattern of muscle activity during Karman gait locomotion. Red muscle electrodes R1 to R4, from anterior to posterior, show little activity except at the anterior-most site (R1). Neither white muscle electrodes nor red muscle on the contralateral side to center of mass movement (R7, R8) show activity. The Karman gait is thus largely passive. Modified from Liao et al.[172,174]

VII.   EMERGING NEW DIRECTIONS

In the past 10 years, a number of new avenues for research have emerged that provide an interesting direction to the next decade of research in fish locomotion. Several of these areas have a significant history, but recent developments or initiatives offer renewed potential. Here, I focus briefly on each of six different areas which promise particularly interesting new findings in the near future.

A.   ONTOGENY OF LOCOMOTION

The vast majority of research on fish locomotion is undertaken on adult or subadult individuals. But a number of authors have noted that locomotion patterns in larval fishes could be significantly different due to the low Reynolds number at which they swim.[88,89,134,135,191,198,199,258,278] Larval fishes are small and swim with low velocities, a situation that suggests that viscous forces should be relatively large.

Figure 1.23 presents data demonstrating a substantial change in the Reynolds number for zebrafish coasting between bouts of active swimming locomotion.[186] Zebrafish traverse almost four orders of magnitude of the Reynolds number as they develop and change shape from larvae through juvenile stages to full adult morphology. Body size increase is accompanied by changes in fin shape and area (see Figure 1.23A) as well as behavioral changes. Teasing apart changes in shape, internal changes in physiology,[41] sensory system development,[273] and behavioral alterations to better understand the ontogeny of locomotion dynamics in fishes is a key challenge for the years ahead.
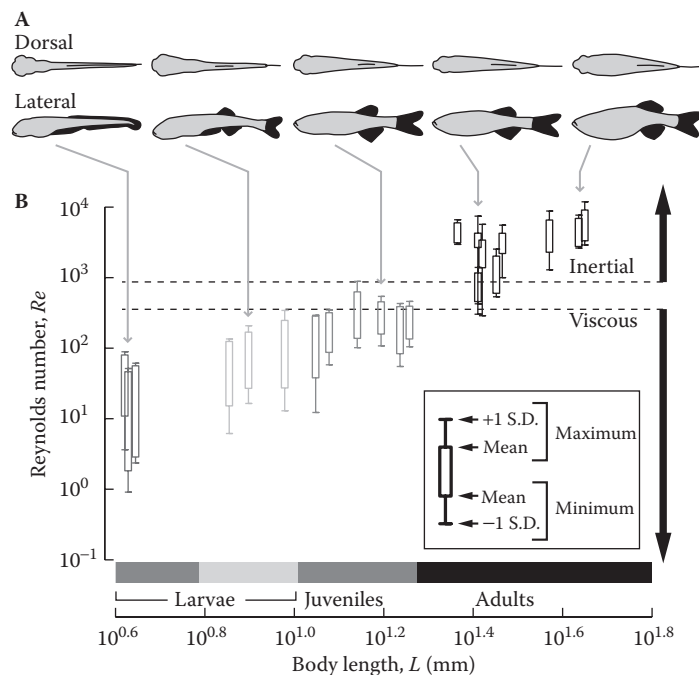
FIGURE 1.23 Ontogeny of gliding behavior in zebrafish showing the Reynolds numbers spanned by zebrafish of different size. A: Dorsal and lateral views of the body outline (gray) and fins (black) at different stages of growth. B: The range of Reynolds numbers experienced during gliding in zebrafish of different sizes. The upper and lower edges of vertical bars and error bars denote the mean and 1 standard deviation (SD) of maximum and minimum values, respectively, for three glides per fish. The hydrodynamic regimes (dashed lines) quantified by experimentally measuring drag on preserved fish of different ontogenetic stages are shown to the right. Modified from McHenry and Lauder.[186]

B. LOCOMOTOR PERFORMANCE

The study of the performance abilities of fishes (i.e., the ability of different species to perform specific tasks, such as traversing a section of fast-moving stream, negotiating an underwater maze, or responding to an imposed destabilizing stimulus) is one of the most understudied aspects of fish locomotion and yet holds great promise to clarify the comparative locomotor abilities of fishes. Exemplary studies of this kind have been conducted by Webb and colleagues,[103,226,227,283,286] who have tested fishes of different body shapes and fin positions for their ability to maneuver around bends and through small vertical and horizontal openings.

A further critical area for the examination of locomotor performance in fishes requires moving them out of small laboratory flow tanks and into large-scale test facilities that mimic field conditions or into the field itself where the fluid dynamic challenges facing fishes can be severe. Castro-Santos and Haro[42–44,125] describe locomotion research using a large-scale (24 m long by 1 m square) flume using diverted Connecticut river water to achieve flow speeds of up to 4.5 m s^{-1}. An additional important feature of this test platform is that fishes ascend through the flow volitionally as part of their annual upstream migration, and not in response to laboratory prodding. Fishes use swimming speeds much higher than those studied in the laboratory for much longer periods and adopt novel behavioral strategies when faced with such severe locomotor challenges.[44]

Field studies of fishes navigating severe rapids and currents (up to 5 m s^{-1}) also provide a great deal of insight into the locomotor performance envelope, the energetic requirements for such intense activity, and behavioral strategies that fishes employ when faced with severe natural obstacles.[236,237] We know remarkably little about the routine locomotor behavioral repertoire in fishes, natural locomotor budgets, and the habitats that fishes use when performing specific locomotor behaviors.

C. LOCOMOTOR ECOLOGY, BEHAVIOR, AND EVOLUTION

The study of locomotor ecology and behavior of fishes has enjoyed a renaissance recently, as the experimental systems exemplified by Trinidad guppies and North American sticklebacks have been developed to shed light on patterns of natural selection and the evolutionary response to predation. These studies are part of a broader trend toward the experimental study of selection and evolution.[19,83,209,210,221] Locomotor performance has clear variables (e.g., maximum acceleration, critical speed) that can be quantified and tracked over generations. Escape responses are rapid and well-defined events, making fish locomotion an excellent experimental system for the study of selection. Recent studies on guppy locomotion in the context of population differentiation and selection include those pioneered by Reznick and colleagues,[45,104,197,200] while analyses of stickleback morphology and locomotor performance provide a fascinating case study of recent population differentiation.[16,92,170,192,224,225,240,243,245,265] The study of

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intraspecific differentiation in locomotor function and its environmental and historical correlates will continue to be an important avenue for future investigation.

A second significant new effort in fish locomotor ecology and behavior involves the study of migratory patterns in large pelagic fishes such as tunas and sharks. The advent of pop-up tags with information that can be downloaded via satellite is providing a wealth of new data on where fish go, their long-term average speeds, and sites of reproduction.[27–29,33,182] There is still much to learn about the movements of fishes in the open ocean, and tracking and telemetry of behavioral and physiological data will provide a wealth of new information over the next decade.

D. COMPUTATIONAL MODELING

Although experimental kinematic and hydrodynamic analyses of fish locomotion provide considerable insight into the mechanisms by which propulsive forces are generated, these approaches are limited to what can be practically measured in freely swimming fishes. For example, it will most likely not be possible for many years to experimentally measure the pressure distribution on the surface of fish fins at more than one or two locations simultaneously.

The ability to directly calculate such pressures as a continuous function of fin surface area, as well as wake properties and relevant lift, drag, and added mass forces, would be a tremendous advantage in understanding not only the fundamental mechanisms of propulsion but also the results of mathematical manipulations which enable alternative kinematic patterns and morphologies (including those not found in nature) to be analyzed. Such approaches are just now becoming feasible as exemplified by the recent detailed work on anguilliform locomotion and pectoral fin propulsion.[180,181,187,206,302]

E. ENERGETICS

Energetics studies of fish locomotion are hardly new and have played an important role in studies of fish locomotion since the early work of Brett[35–38] (also see[15,86,110,111,157,158,275,285]). But several recent studies have made noteworthy contributions. Van den Thillart et al.[254] and van Ginneken et al.[255] measured the energy cost of locomotion in European eels (*Anguilla anguilla*) "migrating" for three months at 0.5 Ls^{-1} in their laboratory flow tank. They demonstrated that the energy cost of locomotion was very low (37 mg O^2 kg^{-1} h^{-1}) and was met primarily via the mobilization of fat stores. The amount of body fat present in their eels was more than sufficient to power migration over the 6000-km distance between the spawning grounds and the European coast.

The energetics costs of different gaits in fishes have only recently been addressed. Liao et al.[173,174] showed that trout adopting the Karman gait in a vortex street are able to greatly reduce muscle activity compared with freestream locomotion, suggesting that they achieve considerable energy savings. Korsmeyer et al.[157] studied parrotfish and triggerfish locomotor energetics as they transitioned between pectoral and dorsal fin locomotion, respectively, and body and caudal fin oscillatory propulsion. They concluded that median and paired fin locomotion is relatively efficient and that use of the body incurs additional costs beyond what would be predicted based on the cost of swimming with pectoral or dorsal fins at higher speeds.

In recent years, a wide diversity of papers have appeared on the locomotor physiology of tuna and their relatives, with the result that a great deal is now known about the kinematics of swimming, the physiology of tuna muscle fibers, and energetics costs of locomotion in tuna and related scombrids.[4,27,54–58,63,66,113–115,229,230] Indeed, our understanding of tuna physiology and the convergences with lamnid sharks[20–22,65] now exceeds that of most other fish groups.

Finally, the important issue raised by Webb[285] concerning the energetics cost of maintaining stability in fishes has yet to be fully addressed. Swimming at less than 1.0 Ls^{-1} appears to incur elevated metabolic costs, perhaps due to the need to maintain body stability at these slow speeds. This is certainly consistent with the large lateral forces generated by pectoral and dorsal fins described earlier in this chapter. But a direct link between the generation of stabilizing hydrodynamic forces with median and paired fins and increased costs of low-speed swimming has not yet been established. Coordinated experimental hydrodynamic and energetic analyses of fish locomotor gaits would be a valuable future direction for research.

F. LOCOMOTION IN MODEL FISH SYSTEMS

Zebrafish have become a model system for the study of vertebrate development, and future studies of zebrafish locomotion will benefit greatly from the libraries of mutants that provide a diverse array of morphologies and physiological functions.[116,201] Interest in zebrafish locomotion is already well established, with analyses of locomotor dynamics, muscle function, developing sensory systems, and development of the skeleton and musculature, to cite just a few areas of current interest.[24,39–41,88,91,185,186,190,204,205,247,289] Other model fish systems, such as guppies and sticklebacks, are developing into major research areas in developmental and evolutionary biology. The potential for zebrafish to clarify issues in locomotor biomechanics and physiology remains largely untapped.

ACKNOWLEDGMENTS

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