

# **Behavior of Marine Fishes**

**Capture Processes and  
Conservation Challenges**

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**Part One**  
**Locomotion and Sensory**  
**Capabilities in Marine Fish**



# Chapter 1

## Swimming in Marine Fish

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### 1.1 INTRODUCTION

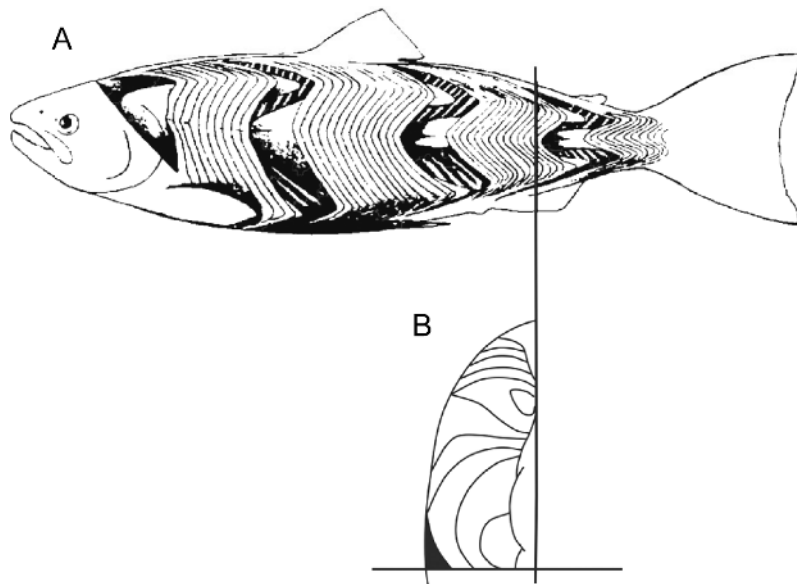
After 500 million years of natural selection, fish are extremely well adapted to various constraints set by the aquatic environment in which they live. In the dense fluid medium, they are usually neutrally buoyant and use body movements to induce reactive forces from the water to propel themselves. Animal movements are powered by contracting muscles, and these movements consume energy. The basic principles of fish locomotion are used by approximately 25,000 extant species. The variation in swimming styles, within the limits of these principles, is great. Swimming includes steady swimming at various speeds, accelerating, braking, maneuvering, jumping, diving downward, and swimming upward. Swimming behavior is different for every species and changes in each individual during growth from larva to adult. Speed, agility, and endurance maxima determine the chances for survival to a considerable extent. Peak performance in absolute terms is positively related to temperature and body length. Ultimately, performance affects the evolutionary fitness of each individual and is a significant factor that is directly related to capture by or escape from both active (e.g., trawls and seines) and passive (e.g., gillnet, longlines, and traps) fishing gear. This chapter reviews the current knowledge about fish swimming mechanisms and abilities to provide a background for discussions in later chapters.

### 1.2 THE SWIMMING APPARATUS

Fish are aquatic vertebrates with a skull, a vertebral column supporting a medial septum that divides the

fish into two lateral halves, and lateral longitudinal muscles that are segmentally arranged in blocks, or myotomes. The vertebral column is laterally highly flexible and virtually incompressible longitudinally. Consequently, contraction of the muscles on one side of the body bends the fish, and waves of curvature along the body can be generated by series of alternating contractions on the left and the right side (Videler and Wardle 1991). Fish vertebrae are concave fore and aft (amphicoelous) and fitted with a neural arch and spine on the dorsal side. In the abdominal region, lateral projections are connected with the ribs enclosing the abdominal cavity. The vertebrae in the caudal region bear a hemal arch and spine. Neural and hemal spines point obliquely backward. The number of vertebrae varies greatly among species—European eels (*Anguilla anguilla*) have 114 vertebrae, and the numbers in the large order of Perciformes vary between 23 and 40 (Ford 1937). The number is not necessarily constant within a species. Atlantic herring (*Clupea harengus*), for example, can have between 54 and 58 vertebrae (Harder 1975a, 1975b). The end of the vertebral column is commonly adapted to accommodate the attachment of the tail fin. Several vertebrae and their arches and spines are partly rudimentary and have changed shape to contribute to the formation of platelike structures providing support for the fin rays of the caudal fin. Most fish species have unpaired dorsal, caudal, and anal fins and paired pectoral and pelvic fins. Each fin is powered by intrinsic musculature.

The lateral muscles are usually the main target of the fishing industry. Relatively short lateral muscle

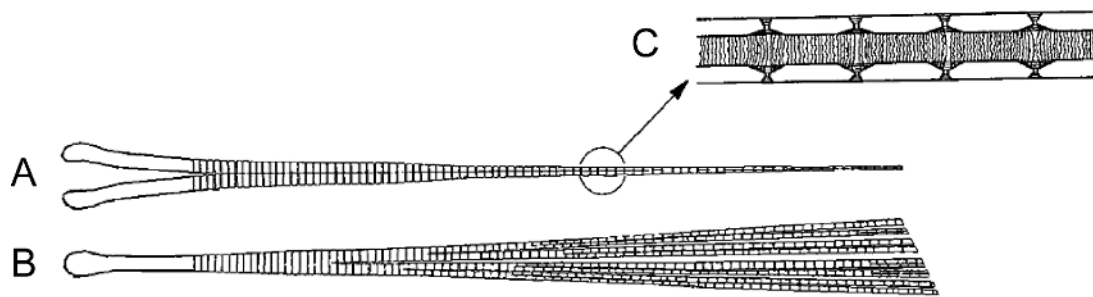


**Figure 1.1.** (A) The myotomes and myosepts on the left side of the king salmon. Myotomes have been removed at four places to reveal the complex three-dimensional configuration of the lateral muscles. [Redrawn after Greene and Greene (1913).] (B) A cross section through the upper left quarter of the caudal region of a salmon. Red muscle fibers are situated in the dark area near the outside. The lines represent the myosepts between the complex myotomes. [Based on Shann (1914).]

fibers are packed into myotomes between sheets of collagenous myosepts. The myotomes are cone shaped and stacked in a segmental arrangement on both sides of the median septum (Fig. 1.1A). In cross sections through the caudal region, the muscles are arranged in four compartments. On each side is a dorsal and a ventral compartment; in some groups, they are separated by a horizontal septum. The left and right halves and the dorsal and ventral moieties are mirror images of each other. In cross sections, the myosepts are visible as more or less concentric circles of collagen. The color of the muscle fibers may be red, white, or intermediate in different locations in the myotomes (Fig. 1.1B), which was first described by Lorenzini in 1678 (Bone 1966). Red fibers are usually situated directly under the skin. The deeper white fibers form the bulk of lateral muscles, and in some species intermediately colored pink fibers are found between the two. The red fibers are slow but virtually inexhaust-

ible and their metabolism is aerobic. They react to a single stimulus owing to the high density of nerve terminals on the fibers. The white fibers are fast, exhaust quickly, and use anaerobic metabolic pathways. White fibers are either focally or multiply innervated. Pink fibers are intermediate in most aspects. The red muscles of some large tuna and shark species are positioned well inside the white muscle mass, an arrangement that can increase the muscle temperature by as much as 10°C during swimming (Carey and Teal 1969). The final paragraph describes how this halves the twitch contraction time of the white muscles and doubles the maximum swimming speed.

Fish fins consist of two layers of skin, usually supported by fin rays that are connected to supporting skeletal elements inside the main body of the fish. Intrinsic fin muscles find their origin usually on the supporting skeleton and insert on the fin rays. The fins of elasmobranchs (sharks and rays) are



**Figure 1.2.** The structure of a typical teleost fin ray. (A) Dorsal or ventral view: the left and right fin ray halves are each other's mirror image. (B) Lateral view; the size of the bony elements decreases to the right after each of the bifurcations in the various branches does not show a geometrically regular pattern. (C) Longitudinal section through the bony elements of the fin ray at a position indicated in (A). Note that a joint with densely packed collagenous fibers connects the elements. The collagenous fibers connecting the fin ray halves have a curly, serpentine appearance. [From Videler (1993).]

permanently extended and rather rigid compared with those of teleosts (bony fish). Elasmobranch fin rays consist of rows of longitudinally connected small pieces of cartilage in a juxtaposed arrangement. Intrinsic muscles on both sides of the rows running from the fin base to the edge bend these fins. Teleost fins can be spread, closed, and folded against the body. There are two kinds of teleost fin rays: spiny, stiff unsegmented rays and flexible segmented ones. Spiny rays stiffen the fin and are commonly used for defense. The flexible rays (Fig. 1.2) play an important role in adjusting the stiffness and camber of the fins during locomotion. They consist of mirror-image halves, each of which has a skeleton of bony elements interconnected by collagenous fibers. Muscles pulling harder on the fin ray head on one side will shift the two halves with respect to each other and bend the ray or increase the stiffness against bending forces from the water. In contrast to elasmobranch fins, there are no muscles on the fin itself.

The body shape of fish may vary greatly among species, but the best pelagic swimmers have a common form. Their bodies are streamlined, with gradually increasing thickness from the point of the snout to the thickest part at about one-third of the length. From that point, the thickness gradually decreases toward the narrow caudal peduncle. A

moving body in water encounters friction and pressure drag. Friction drag is proportional to the surface area, and pressure drag is proportional to the area of the largest cross section. A spherical body has the lowest friction for a given volume; a needle-shaped body encounters minimal amounts of pressure drag. An optimally streamlined body is a hybrid between a sphere and a needle and offers the smallest total drag for the largest volume. It has a diameter-to-length ratio between 0.22 and 0.24. The best pelagic swimmers have near-optimal thickness-to-length ratios (Hertel 1966).

The mechanically important part of fish skin is the tissue (the stratum compactum) underneath the scales, which consists of layers of parallel collagenous fibers (see Videler 1993 for a review). The fibers in adjacent layers are oriented in different directions, and the angles between the layers vary between 50 and 90 degrees, but the direction in every second layer is the same. The packing of layers resembles the structure of plywood, except that in the fish stratum compactum there are also radial bundles of collagen connecting the layers; the number of layers varies between 10 and 50. In each layer, the fibers follow left- and right-handed helices over the body surface. The angle between the fibers and the longitudinal axis of the fish decreases toward the tail. In some species, the

stratum compactum is firmly connected to the myosepts in the zone occupied by the red muscle fibers; in other fish, there is no such connection. The strongest fish skins that have been tested are those of eel and shark. Values of Young's modulus (the force per unit cross-sectional area that would be required to double the length) of up to 0.43 GPa (1 GPa =  $10^9$  N/m<sup>2</sup>) have been measured. This is about one-third of the strength of mammalian tendon, for which values of 1.5 GPa have been measured.

Scales are usually found at the interface between fish and water. Several swimming-related functions have been suggested. Scales might serve to prevent transverse folds on the sides of strongly undulating fish, keeping the outer surface smooth. Spines, dents, and tubercles on scales are usually arranged to form grooves in a direction of the flow along the fish. Roughness due to microstructures on scales in general creates small-scale turbulence, which could delay or prevent the development of drag-increasing large-scale turbulence (Aleyev 1977).

Fish mucus covering the scales is supposed to reduce friction with the water during swimming. This assumption is based on the idea that mucus shows the "Toms effect" (Lumley 1969), which implies that small amounts of polymers are released that preclude sudden pressure drops in the passing fluid. Measurements of the effects of fish mucus on the flow show contradictory results varying from a drag reduction of almost 66% (Pacific barracuda, *Sphyaena argentea*) to no effect at all (Pacific bonito, *Sarda chiliensis*) (Rosen and Cornford 1971). Experiments with rainbow trout showed that mucus increases the thickness of the boundary layer

(Daniel 1981). The layer of water around the fish is affected by the presence of the fish during swimming. Viscosity causes a layer of water close to the fish to travel with it at the speed of the fish. There is a gradient of decreasing water velocities in a direction away from the surface of the fish. The thickness of the boundary layer is defined as the distance from the surface of the fish to where the water is no longer dragged along. A thick boundary layer implies that the gradient is gradual, which reduces viscous friction. However, the penalty for a thicker boundary layer is that the fish has to drag along a larger amount of water. The conclusion might be that the effect of mucus is beneficial during slow-speed cruising but detrimental during fast swimming and acceleration (Videler 1995).

### 1.3 SWIMMING-RELATED ADAPTATIONS

Some fish species are adapted to perform some aspect of locomotion extremely well, whereas others have a more general ability to move about and are specialized for different traits not related to swimming. Generalists can be expected to have bodies that give them moderately good performance in various special functions. Specialists perform exceptionally well in particular skills. Fast accelerating, braking, high-speed cruising, and complex maneuvering are obvious examples. The special swimming adaptations shown in Figure 1.3 are only a few of a wealth of possible examples. A closer study of the swimming habits of a large number of species will show many more specialist groups than the dozen or so described here (e.g., Lindsey 1978).

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**Figure 1.3.** A representation of fish swimming specializations. See text for detailed explanation. (a) pike (*Esox lucius*), barracuda (*Sphyaena argentea*); (b) forkbeard (*Phycis phycis*), saithe (*Pollachius virens*); (c) bluefin (*Thunnus thynnus*), porbeagle shark (*Lamna nasus*); (d) angelfish (*Pterophyllum scalare*), butterfly fish (*Chaetodon* sp.); (e) sunfish (*Mola mola*), opah (*Lampris guttatus*), louvar (*Luvarus imperialis*); (f) swordfish (*Xiphias gladius*), sailfish (*Istiophorus platypterus*); (g) turbot (*Scophthalmus maximus*), skate (*Raja batis*); (h) moray eel (*Muraena Helena*), eel (*Anguilla anguilla*); (i) rainbow wrasse (*Coris julis*), sand eel (*Ammodytes tobianus*); (j) sea-horse (*Hippocampus ramulosus*), Atlantic flying fish (*Cheilopogon heterurus*), hatchet fish (*Gasteropelecus* sp.); cornet fish (*Fistsularia* sp.). [Modified from Videler (1993).]

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a Pike



Barracuda



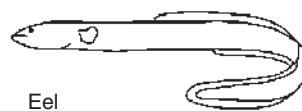
h Moray



b Forkbeard



Saithe



Eel



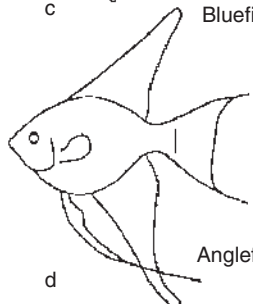
c Bluefin tuna



Porbeagle



i Rainbow wrasse

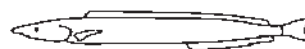


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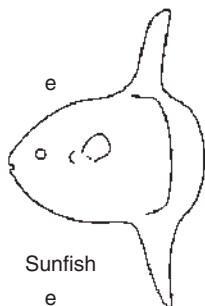
Angelfish



Butterflyfish



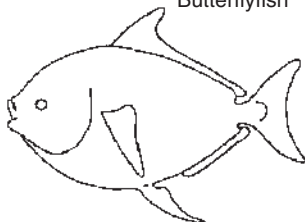
Sandeel



e

Sunfish

e



Opah



Louvar

j



Sea-horse



f Swordfish

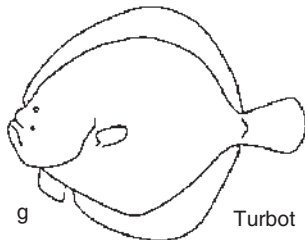


Sailfish

k

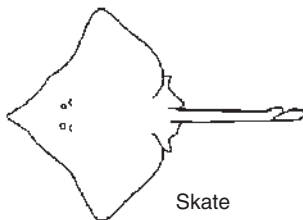


Atlantic flying fish



g

Turbot



Skate

l



Hatched fish



Cornet fish

Specialists in accelerating, such as the pike (*Esox lucius*) and the barracuda (Fig. 1.3a), are often ambush predators. They remain stationary or swim very slowly until a potential prey is within striking distance. These species have a reasonably streamlined body and large dorsal and anal fins positioned extremely rearward, close to the caudal fin. Acceleration during the strike is achieved by the first two beats of the tail, the effect is enlarged by the rearward position of the dorsal and anal fins. The relative skin mass of the pike is reduced, compared with that of other fish, increasing the relative amount of muscles and decreasing the dead mass that has to be accelerated with the fish at each strike. Maximum acceleration rates measured for pike vary between 40 and 150 m/s<sup>2</sup>, which is 4 to 15 times the acceleration due to gravity ( $G = 9.8 \text{ m/s}^2$ ). The highest peak acceleration value reported for pike is 25 times gravity (Harper and Blake 1990, 1991).

Braking is difficult while moving in a fluid medium. Fish use the unpaired fins and tail, usually in combination with the pectoral and pelvic fins, for braking. Gadoids with multiple or long unpaired fins are good at braking. Forkbeard (*Phycis phycis*) swims fast and close to the bottom with elongated pelvic fins extended laterally for the detection of bottom-dwelling shrimp. The fish instantly spreads the long dorsal and anal fins and throws its body into an S-shape when a prey item is touched. In the process, the fin rays of the tail fin are actively bent forward. Braking is so effective that the shrimp has not yet reached the caudal peduncle before the fish has stopped and turned to catch it. The highest deceleration rate measured is 8.7 m/s<sup>2</sup> for saithe (*Pollachius virens*) (Geerlink 1987). The contribution of the pectorals to the braking force is about 30%; the rest comes from the curved body and extended median fins (Geerlink 1987) (Fig. 1.3b).

Cruising specialists (Fig. 1.3c) migrate over long distances, swimming continuously at a fair speed. Many are found among scombrids and pelagic sharks, for example. Cruisers have highly streamlined bodies, narrow caudal peduncles with lateral keels, and high-aspect-ratio tails (aspect ratio is the tail height squared divided by tail surface area). The bluefin tuna (*Thunnus thynnus*), for example, is an extreme long distance swimmer, crossing the

Atlantic twice a year. The body dimensions are very close to the optimum values, with a thickness-to-length ratio near 0.25 (Hertel 1966). Cruising speeds of 3-m-long bluefin tunas measured in large enclosures reached 1.2 L/s (260 km/d), where L equals body length (Wardle et al. 1989). Angelfish (*Pterophyllum scalare*) and butterfly fish (*Chaetodon* sp.) (Fig. 1.3d) are maneuvering experts with short bodies and high dorsal and anal fins. Species of this guild live in spatially complex environments. Coral reefs and freshwater systems with dense vegetation require precise maneuvers at low speed. Short, high bodies make very short turning circles possible. Angelfish make turns with a radius of 0.065 L (Domenici and Blake 1991). For comparison, the turning radius of a cruising specialist is in the order of 0.5 L, an order of magnitude larger.

Sunfish (*Mola mola*), opah (*Lampris guttatus*), and louvar (*Luvarus imperialis*) are among the most peculiar fish in the ocean (Fig. 1.3e). They look very different from each other but they all have large body sizes. The sunfish reaches 4 m and 1500 kg, the opah may weigh up to 270 kg, and the louvar is relatively small with a maximum length of 1.9 m and weight of 140 kg. While little is known about the mechanics of their locomotion, they all seem to swim slowly over large distances. The opah uses its wing-shaped pectorals predominantly, and the louvar has a narrow caudal peduncle and an elegant high-aspect-ratio tail similar to those of the tunas. The sunfish has no proper tail, but the dorsal and ventral fins together form an extremely high-aspect-ratio propeller. Sunfish swim very steadily, moving the dorsal and ventral fins simultaneously to the left side and, half a cycle later, to the right side. The dorsal and ventral fins have a cambered wing profile in cross section with a rounded leading edge and a sharp trailing edge. The intrinsic fin muscles fill the main part of the body and insert on separate fin rays, enabling the sunfish to control the movements, camber, and profile of its fins with great precision. Although there are no measurements to prove this as yet, it appears that these heavy species specialize in slow steady swimming at low cost. Inertia helps them to keep up a uniform speed, while their well-designed propulsive fins generate just enough thrust to balance the drag as efficiently as possible.

Swordfishes (Xiphiidae) and billfishes (Istiophoridae) (Fig. 1.3f) show bodily features unique to these fish—the extensions of the upper jaws, the swords, and the shape of the head. They are probably able to swim briefly at speeds exceeding those of all other nektonic animals, reaching values of well over 100km/h (Barsukov 1960). The sword of swordfish is dorsoventrally flattened to form a long blade of up to 45% of the body length. The swords of billfish (including sailfish, spearfish, and marlin) are pointed spikes, round in cross section and shorter (between 14% and 30% in adult fish, depending on species) than those of swordfish. All swords have a rough surface, especially close to the point. The roughness decreases toward the head. One other unique bodily feature of the sword-bearing fishes is the concave head. At the base of the sword, the thickness of the body increases rapidly with a hollow profile up to the point of greatest thickness of the body. The rough surface on the sword reduces the thickness of the boundary layer of water dragged along with the fish (Hertel 1966). This reduces drag. The concave head probably serves to avoid drag-enhancing large-scale turbulence. The caudal peduncle is dorsoventrally flattened, fitted with keels on both sides. These features and the extremely high-aspect-ratio tail blades with rearward-curved leading edges are hallmarks of very fast swimmers.

The shape of the body of flatfish (Pleuronectiformes) and rays (Rajiformes) (Fig. 1.3g) offers the opportunity of hiding in the boundary layer of the seabed where speeds of currents are reduced. There is another possible advantage connected with a flat body shape. Both flatfish and rays can be observed swimming close to the bottom. These fish are negatively buoyant and, like flying animals, must generate lift (a downwash in the flow) at the cost of induced drag to remain “waterborne.” Swimming close to the ground could reduce the drag due to lift generation considerably, depending on the ratio between height off the ground and the span of the “wings” (Anderson and Eberhardt 2001).

Only a few species can swim both forward and backward. Eels (Anguillidae), moray eels (Muraenidae), and conger eels (Congeridae) (Fig. 1.3h) can quickly reverse the direction of the propulsive wave on the body and swim backward. The

common feature of these fish is the extremely elongated flexible body without a high tail fin. Swimming is usually not very fast; they prefer to swim close to the bottom and operate in muddy or maze-type environments.

Rainbow wrasses (*Coris julis*) and sand eels (*Ammodytes tobianus*) (Fig. 1.3i) sleep under a layer of sand—sand eels in daytime and rainbow wrasse during the night. Both species swim head-down into the sand using high-frequency low-amplitude oscillations of the tail. If the layer of sand is thick enough, the speed is not noticeably reduced. Body shapes are similar—that is, slender with a well-developed tail. The wrasses use their pectoral fins for routine swimming and move body and tail fin during escapes and to swim into the sand (Videler 1988).

Most neutrally buoyant fish species are capable of hovering in one spot in the water column. Some species can hardly do anything else. Seahorses (Fig. 1.3j) and pipefishes (Syngnathidae) rely on camouflage for protection from predators. They are capable of minute adjustments of the orientation of their body using high-frequency, low-amplitude movements of the pectoral and dorsal fins. Seahorses are the only fish with a prehensile tail.

Flying fish (Exocoetidae) (Fig. 1.3k) have exceptionally large pectoral fins to make gliding flights out of the water when chased by predators. Some species are four-winged because they use enlarged pelvic fins as well. The lower lobe of the caudal fin is elongated and remains beating the water during takeoff. Hatchet fishes (*Gasteropelecus* sp.) actually beat their pectoral fins in powered flight. The pectoral fins have extremely large intrinsic muscles originating on a greatly expanded pectoral girdle. Many additional species occasionally or regularly leap out of the water but they are not specially adapted to fly.

Cornet fishes (*Fistularia* sp.) (Fig. 1.3l) are predators of small fish in the littoral of tropical seas, most often seen above sea grass beds or sandy patches between coral reefs. They seem to have two tails; the first one is formed by a dorsal and anal fin, and the second one is the real tail. Beyond the tail is a long, thin caudal filament. These fish hunt by dashing forward in one straight line without any side movements of the head, using large-amplitude

strokes of the two tail fins and the trailing filament (J.J.V., personal observations). It looks as though the double-tail fin configuration with the trailing filament serves to allow fast acceleration without recoil movements of the head. Precise kinematic measurements are needed to provide evidence for this assumption.

#### 1.4 STYLES OF SWIMMING

Most fish species swim with lateral body undulations running from head to tail; a minority use the movements of appendages to propel themselves. The waves of curvature on the bodies of undulatory swimmers are caused by waves of muscle activations running toward the tail with a 180-degree phase shift between the left and the right side (Videler and Wardle 1991). The muscular waves run faster than the waves of curvature, reflecting the interaction between the fish's body and the reactive forces from the water. The swimming speed varies between 0.5 and 0.9 times the backward speed of the waves of curvature during steady swimming (Videler and Hess 1984). The wavelength of the body curvature of slender eel-like fish is about  $0.6L$ , indicating that there is more than one wave on the body at any time. Fast-swimming fish such as mackerel and saithe have almost exactly one complete wave on the body, and on short-bodied fish such as carp and scup, there is less than one wave on the length of the body during steady swimming. The maximum amplitude (defined as half the total lateral excursion) may increase toward the tail linearly, as in eels and lampreys, or according to a power function in other species (Wardle et al. 1995). The increase in maximum amplitude is concentrated in the rearmost part of the body in fast fish like tuna. The maximum amplitude at the tail is usually in the order of  $0.1L$  with considerable variation around that value. The period of the waves of curvature determines the tail beat frequency, which is normally linearly related to the swimming speed (Bainbridge 1958). The distance covered per tail beat is the "stride length" of a fish. It varies greatly between species but also for each individual fish. Maximum values of more than one body length have been measured for mackerel; the least distance covered per beat of the same individual was reported to be  $0.7L$  (Videler and Hess 1984; Wardle and

1988). Many species reach values between 0.5 and  $0.6L$  during steady swimming bouts.

Left-right undulations of the body from head to tail are used by fish varying in body shape from eel to tuna. However, the amplitudes of the undulations and the way in which they are generated greatly differ among species. In eel-like fishes, there is a fairly tight connection between the position of the backward-moving bend and muscle shortening on the concave side of the bend. One-sided waves of muscle contraction run from head to tail, causing the local bending of the body with a slight delay. There is always more than one complete wavelength present on the body of these fish between the head and tail (Wardle et al. 1995). Mackerel-type fishes, on the other hand, have only one wavelength on the body at all times, and the lateral muscles on one side of the body from head to tail are activated simultaneously (Wardle and Videler 1993). Simultaneous muscle activity would result in a C-shaped lateral bending of the body if it took place outside the water. However, during swimming, water reacts more strongly to sideward movements of the high tail than to the movements of the rounded side of the rest of the body. Lateral muscles in the anterior part of the body actually shorten when activated, but muscles in the rear part and especially in the caudal peduncle are active when they are being stretched by the sideward push of the water against the tail. Muscles there produce negative work by resisting being stretched. This type of muscle activity provides higher forces and power per unit cross-sectional area. Therefore, the rear part of these fishes can be narrower (to contribute to a streamlined body) and still transmit the high forces from the anterior muscle mass to the tail blade (Wardle and Videler 1993; Wardle et al. 1995).

Fish locomotion using paired and median fins was reviewed by Blake (1983). Swimming with appendages includes pectoral fin swimming and median fin propulsion. Pectoral fin movements of, for example, labrids (Labridae), shiner perches (*Cymatogaster aggregata*), and surfperches (Embiotocidae) make an elegant impression. The beat cycle usually consists of three phases. During the abduction phase, the dorsal rays lead the movement away from the body and downward. The adduction phase brings the fin back to the body surface led by

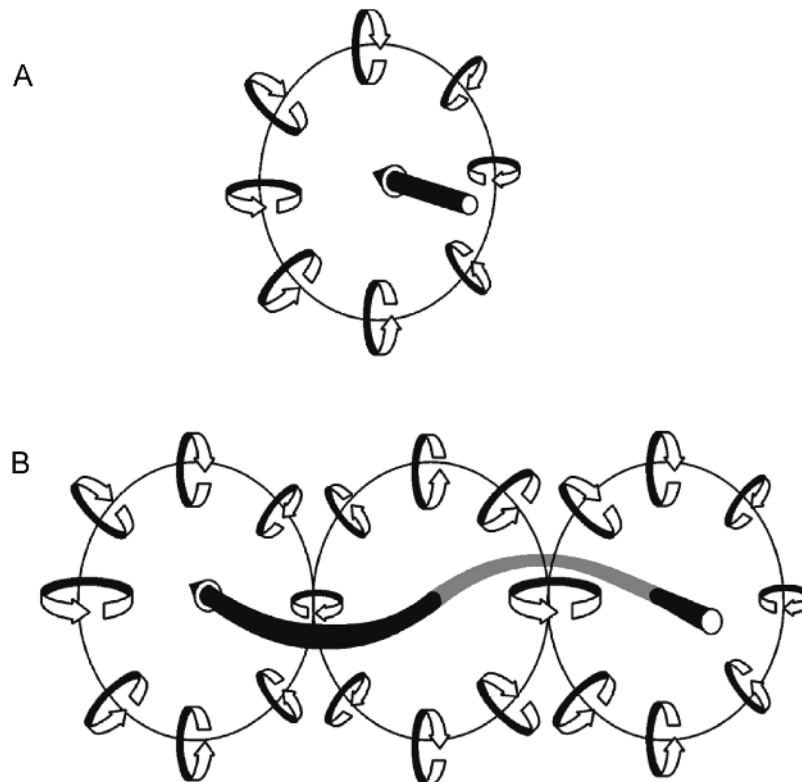
horizontal movement of the dorsal rays. During the third phase, the dorsal rays rotate close to the body back to their initial position. Stride lengths vary with speed and may reach more than one body length at optimal speeds. Undulations of long dorsal and anal fins can propel fish forward and backward and are used in combination with movements of the pectoral fins and the tail. There is usually more than one wave on each fin (e.g., up to 2.5 waves on the long dorsal fin of the African electric eel, *Gymnarchus niloticus*).

### 1.5 INTERACTIONS BETWEEN FISH AND WATER: FISH WAKES

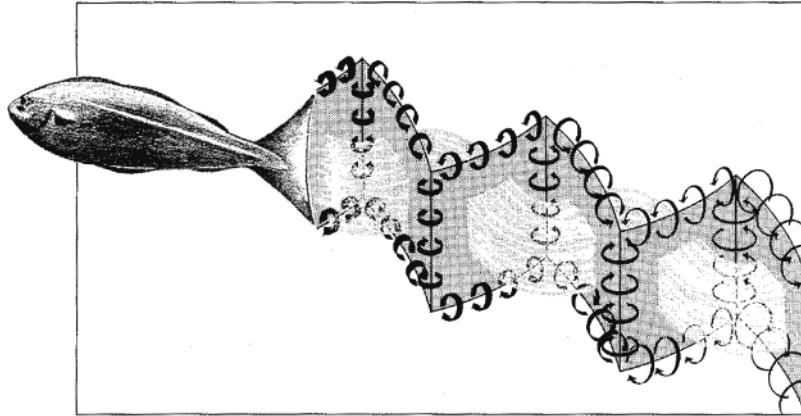
Every action of the fins or the body of a fish will, according to Newton's third law, result in an equal

but opposite reaction from the surrounding water. A swimming fish produces forces in interaction with the water by changing water velocities locally. The velocity gradients induce vortices, being rotational movements of the fluid. Vortices either may end at the boundary of the fluid or may form closed loops or vortex rings with a jet of water through the center (Videler et al. 2002). Furthermore, vortex rings can merge to form chains (Fig. 1.4).

Quantitative flow visualization techniques have been successfully applied to reveal the flow patterns near fish using body undulations to propel themselves (Müller et al. 1997). The interaction between undulating bodies and moving fins and the water results in complex flow patterns along and behind the swimming animals (Videler 1993). A schematic



**Figure 1.4.** Schematic drawings of vortex ring structures. (A) A single vortex ring. The ring shaped centre of rotation is drawn as a line. The rotations of the vortex ring structure draw a jet of water through the centre of the ring, indicated by the arrow. (B) A 3-D reconstruction of a chain of three connected vortex rings. A resulting jet of fluid undulates through the centre of the vortex rings building the chain. [From Videler et al. (2002).]



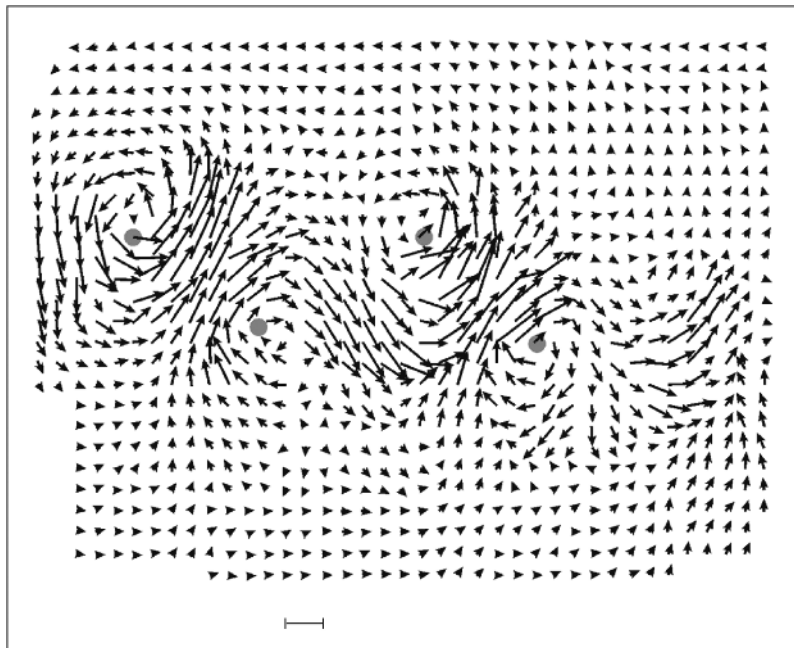
**Figure 1.5.** Artist's impression of the flow behind a steadily swimming saithe. The tail blade is moving to the left and in the middle of the stroke. At the end of each half-stroke a column vortex is left behind when the tail blade changes direction. Tail tip vortices are shed dorsally and ventrally when the tail moves from side to side. Together the vortices form a chain of vortex rings (as shown schematically in Fig. 1.4) with a jet of water winding through the centers of the rings in the opposite swimming direction. [From Videler (1993).]

three-dimensional impression of the wake generated by the tail behind a steadily swimming fish is shown in Figure 1.5. This shows the dorsal and ventral tail tip vortices generated during the tail beat as well as the vertical stop–start vortices left behind by the trailing edge of the tail at the end of each half-stroke. During a half-stroke, there is a pressure difference between the leading side of the fin and the trailing side. Dorsal and ventral tip vortices represent the water escaping at the fin tips from the leading side, with high pressure to the trailing side where the pressure is low. At the end of the half-stroke, the tail changes direction and builds up pressure on the opposite side of the fin, leaving the previous pressure difference behind as a vertical vortex column. These vertical, dorsal, and ventral vortex systems form a chain through which a jet of water undulates opposite the swimming direction. If we concentrate on what happens in a mediofrontal plane through the fish and the wake, we expect to see left and right stop–start vortices with an undulating backward jet between them. The rotational sense should be anticlockwise on the right of the fish and clockwise on the left. Visualizations of the flow in the mediofrontal plane of swimming fish

reveal that this picture of the wake is correct (Fig. 1.6) (Müller et al. 1997). Flow patterns around fish using paired and unpaired fins, as well as the tail and those near maneuvering fish, are much more complex systems of jets and vortex rings. Such complex flow patterns have been published for a number of species during recent years (Lauder and Tytell 2006).

## 1.6 ENERGY REQUIRED FOR SWIMMING

Swimming fish use oxygen to burn fuel to power their muscles. Carbohydrates, fat, and proteins are the common substrates. A mixture of these provides about 20J/ml oxygen used (Videler 1993). Measurements of energy consumption during swimming are mainly based on records of oxygen depletion in a water tunnel respirometer. Respiration increases with swimming speed, body mass, and temperature and varies considerably among species. The highest levels of energy consumption measured in fish are about 4W/kg (Videler 1993). Fast, streamlined fish can increase their metabolic rates up to 10 times resting levels during swimming at the highest sustainable speeds. Short-burst speeds

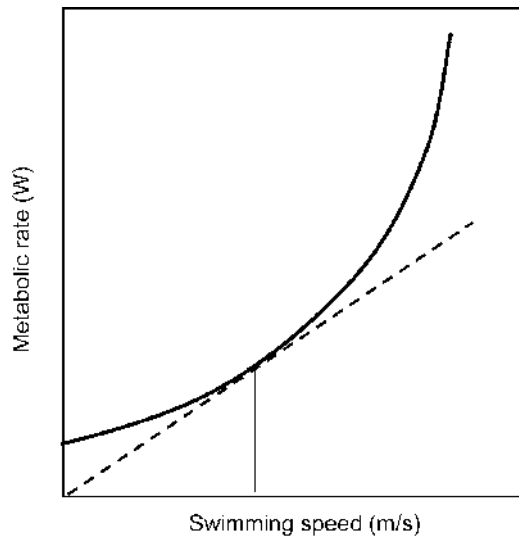


**Figure 1.6.** The wake of a continuously swimming mullet. The arrows represent the flow velocity in mm/s scaled relative to the 10 mm/s bar on the bottom. The shaded circles indicate the centers of the column vortices. The picture represents a horizontal cross-section half way down the wake drawn in Figure 1.5. [Based on Müller et al. (1997).]

powered by anaerobic white muscles can cost as much as 100 times resting rates. Most of the energy during swimming at a constant speed is required to generate sufficient thrust to overcome drag. The drag on a steadily swimming fish is proportional to the square of the swimming speed—the energy required increases as the cube of the speed. In other words, if a fish wants to swim twice as fast, it will have to overcome four times as much drag and use eight times as much energy. A fair comparison of the energy used requires standardization of the speed at which the comparison is made. The energetic cost of swimming is the sum of the resting or standard metabolic rate and the energy required to produce thrust. Expressed in watts (joules per second), it increases as a J-shaped curve with speed in m/s (Fig. 1.7) (Videler 1993). The exact shape of the curve depends mainly on the species, size, temperature, and condition of the fish. Owing to the shape of the curve, there is one optimum speed at which the ratio of metabolic rate over speed reaches a minimum. This ratio represents the amount of work a fish has to do to cover 1 m (J/s divided by m/s). To make fair comparisons possible, the

optimum speed ( $U_{opt}$ ), where the amount of energy used per unit distance covered is at a minimum, is used as a benchmark. Series of measurements of oxygen consumption at a range of speeds provide the parameters needed to calculate  $U_{opt}$  and the energy used at that speed. The energy values are normalized by dividing the active metabolic rate at  $U_{opt}$  (in  $W = J/s = Nm/s$ ) by the weight of the fish (in N) multiplied by  $U_{opt}$  (in m/s), to reach a dimensionless number for the cost of transport. Hence, COT represents the cost to transport one unit of weight over one unit of distance at  $U_{opt}$ .

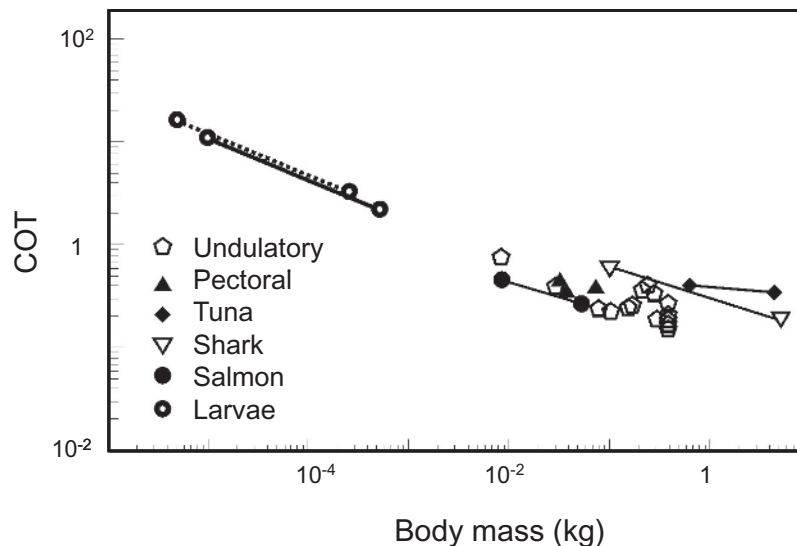
Available data show that  $U_{opt}$  is positively correlated with mass ( $M$ ) and proportional to  $M^{0.17}$ . The value of  $U_{opt}$  decreases, however, with mass if  $U_{opt}$  is expressed in L/s and is proportional to  $M^{-0.14}$ . While there is great variation in measured  $U_{opt}$ , 2L/s can serve as a reasonable first estimate of the optimum speed in fish. At  $U_{opt}$  the COT values are negatively correlated with body mass ( $M^{-0.38}$ ) (Fig. 1.8). Fish use an average of 0.07 J/N to swim their body length at  $U_{opt}$ . If the weight and the size of the animals are taken into account as well by calculating the energy needed to transport the body weight



**Figure 1.7.** A theoretical curve of the rate of work as a function of swimming speed. SMR is the standard or resting metabolic rate at speed 0. The amount of work per unit distance covered (J/m) is at a minimum at  $U_{opt}$ . [From Videler (1993).]

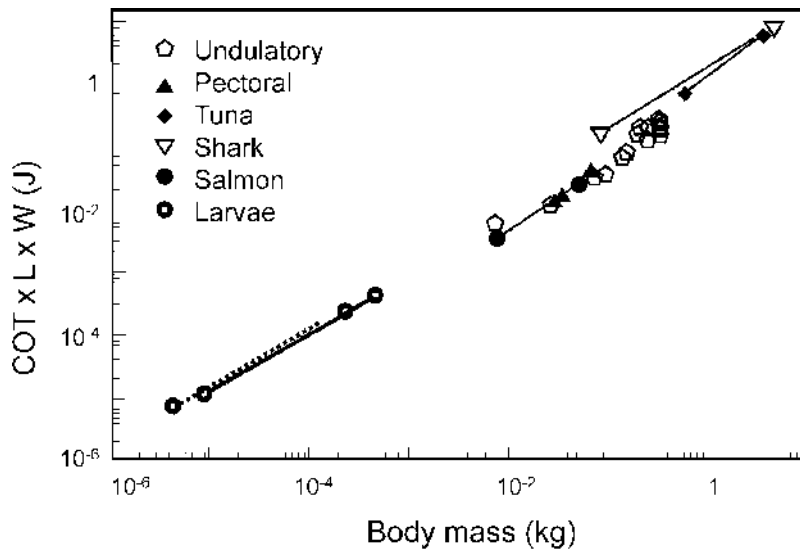
over the length, the amount of energy used to swim at  $U_{opt}$  increases in proportion to  $M^{0.93}$  (Fig. 1.9) (Videler 1993).

Burst-and-coast (or kick-and-glide) swimming behavior is commonly used by several species (Weihs 1974; Videler and Weihs 1982). It consists of cyclic bursts of swimming movements followed by a coast phase in which the body is kept motionless and straight. The velocity curve in Figure 1.10 shows how the burst phase starts off at an initial velocity ( $U_i$ ) lower than the average velocity ( $U_c$ ). During a burst, the fish accelerates to a final velocity ( $U_f$ ), higher than  $U_c$ . The cycle is completed when velocity  $U_i$  is reached at the end of the deceleration during the coast phase. Energy savings in the order of 50% are predicted if burst-and-coast swimming is used during slow and high swimming speeds instead of steady swimming at the same average speed (Videler and Weihs 1982). The model predictions are based on the assumption that there is a three-fold difference in drag between a rigid gliding body and an actively moving fish.

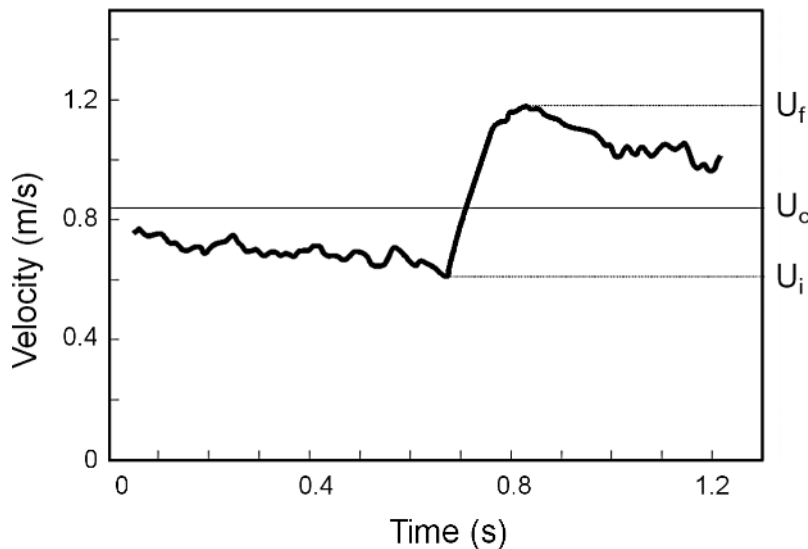


**Figure 1.8.** Doubly logarithmic plot of dimensionless COT, being the energy needed to transport one unit of mass over one unit of distance during swimming at  $U_{opt}$ , related to body mass. The connected points indicate series of measurements of animal groups indicated separately; "undulatory" and "pectoral" refer to measurements of fish using body plus tail and pectoral fins respectively, for propulsion. [From Videler (1993).]





**Figure 1.9.** Doubly logarithmic plot of the energy needed by a swimming fish to transport its body weight over its body length as a function of body mass. Symbols as in Figure 1.7. [Based on Videler (1993).]



**Figure 1.10.** Part of a velocity curve during burst-and-coast swimming of cod. The average speed  $U_c$  was 3.2L/s. The initial speed and the final velocity of the acceleration phase are indicated as  $U_i$  and  $U_f$ , respectively. [From Videler (1993).]

Schooling behavior probably has energy-saving effects (Weihs 1973). As seen in Figure 1.5, the wake of a steadily swimming fish shows an undulating jet of water in the opposite swimming direction through a chain of vortex rings. Just outside this system, water will move in the swimming direction. Theoretically, following fish could make use of this

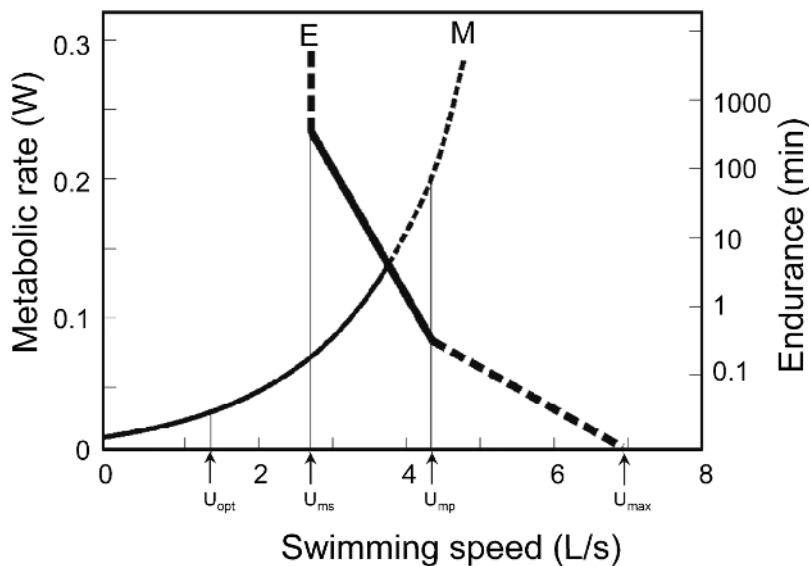
forward component to facilitate their propulsive efforts (Weihs 1973). One would expect fish in a school to swim in a distinct three-dimensional spatial configuration in which bearing and distance among school members showed a distinct constant diamond lattice pattern and a fixed phase relationship among tail beat frequencies. This has not,

however, been confirmed by actual observations. On the other hand, energetic benefits for school members have been confirmed by indirect evidence. It has been observed that the tail beat frequency of schooling Pacific mackerel (*Scomber japonicus*) is reduced compared with solitary mackerel swimming at the same speed (Fields 1990). In schools of sea bass, trailing individuals used 9% to 14% lower tail beat frequencies than fish in leading position. There is also some evidence showing that fast swimming fish in a school use less oxygen than the same number of individuals would use in total in solitary swimming at the same speed (Herskin and Steffensen 1998).

### 1.7 SWIMMING SPEEDS AND ENDURANCE

The relationship between swimming speed and endurance is not straightforward due to the separate use of red, intermediate, and white muscle. Virtually inexhaustible red muscles drive slow cruising speeds; burst speeds require all-out contraction of

white muscles lasting only a few seconds. Endurance decreases rapidly when speeds are above cruising speeds. Maximum swimming speeds of fish are ecologically important for obvious reasons. However, slower swimming speeds and the stamina at these speeds represent equally important survival values for a fish. Figure 1.11 relates swimming speed, endurance, and the cost of swimming for a 0.18-m sockeye salmon (*Oncorhynchus nerka*) at 15°C (Videler, 1993). At low speeds, this fish can swim continuously without showing any signs of fatigue. The optimum speed  $U_{opt}$  is between 1 and 2 L/s. Limited endurance can be measured at speeds higher than the maximum sustained speed ( $U_{ms}$ ) in this case, somewhat less than 3 L/s. For these prolonged speeds, the logarithm of the time to fatigue (endurance) decreases linearly with increasing velocity up to the maximum prolonged speed ( $U_{mp}$ ) where the endurance is reduced to a fraction of a minute. Along this endurance trajectory, the fish will switch gradually from partly aerobic to totally anaerobic metabolism. The maximum burst



**Figure 1.11.** The metabolic rate (linear scale) and the endurance (logarithmic scale) of a 0.18-m, 0.05-kg sockeye salmon as functions of swimming speed in L per second. The water temperature was 15°C. The optimum swimming speed ( $U_{opt}$ ), the maximum sustained speed ( $U_{ms}$ ), the maximum prolonged speed ( $U_{mp}$ ) and an estimate of the maximum burst speed ( $U_{max}$ ) are indicated. [From Videler (1993).]

speed in this case is in the order of 7L/s for sockeye salmon (Brett 1964).

A comparison of published data for some marine species reveals that values for  $U_{ms}$  for fish varying in size between 10 and 49 cm are between 0.9 and 9.9L/s, with larger fish achieving less  $U_{ms}$  in L/s (Table 1.1). For example, 17-cm-long haddock (*Melanogrammus aeglefinus*) are capable of swimming at 2.6L/s for longer than 200 min, but 41-cm-long haddock can only swim at 1.5L/s for the same period of time (Breen et al. 2004).

Bottom-dwelling demersal fish living in complex environments usually have shallower endurance curves than pelagic long-distance swimmers, which fatigue more quickly when they break the limit of the maximum sustained speed (Videler 1993). Endurance in fish swimming at prolonged speeds is limited by the oxygen uptake capacity. Higher speeds cause serious oxygen debts.

The maximum burst speed in m/s increases with body length (Fig. 1.12). Average relative values for adult fish are between 10 and 20L/s. Small fish larvae swim at up to 50L/s during startle response bursts (Fuiman 1986). Speed record holders in m/s are to be found among the largest fish. Unfortunately, reliable measurements are usually not available. The maximum burst speed of fish depends on the fastest twitch contraction time of the white lateral muscles (Wardle 1975). For each tail beat, the muscles on the right and on the left have to contract once. Hence, the maximum tail beat frequency is the inverse of twice the minimum contraction time. The burst speed is found by multiplying the stride length by the maximum tail beat frequency. Muscle twitch contraction times halve for each 10°C temperature rise, and the burst speed doubles (Videler 1993). Larger fish of the same species have slower white muscles than smaller individuals. The burst swimming speed in L/s decreases with size with a factor of on average 0.89 for each 10cm length increase. Estimates based on muscle twitch contraction times and measured stride length data for 2.26m long blue fin tuna vary between 15 and 23m/s (Wardle et al. 1989). Estimates for 3 m long swordfish exceed 30m/s (Barsukov 1960). Measured values for burst speeds are difficult to find. The maximum swimming speed in terms of L/s ever recorded in captivity is that of a 30cm mackerel

swimming at 18L/s (or 5.4m/s, Wardle and He 1988). At that speed, the tail beat frequency was 18Hz and the stride length was 1L.

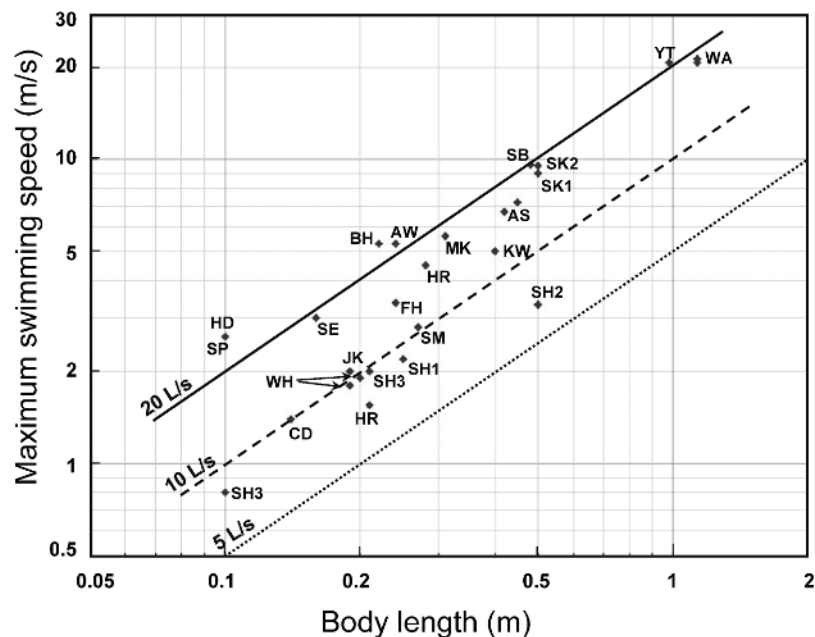
## 1.8 CONCLUDING REMARKS

Understanding fish swimming performance involves studies of the functional morphology of the swimming apparatus and requires insight in swimming-related adaptations. Undulations of body and tail propel the majority of species; others predominantly use movements of paired and unpaired fins. Hydrodynamic interactions between the moving fish and water represent the forces required. Visualization of the flow patterns reveals the vortex systems, pressure distributions, and forces. The energy used to swim is obtained by muscles burning fuel and can be as high as 4W/kg. The metabolic rate increases exponentially with speed. Fair comparisons among species can be made by looking at the most economic swimming performance at the speed where the energy used per unit weight and unit distance is at a minimum. These dimensionless costs of transport decrease with body mass. The amount of work that needs to be done to transport the weight of a body over its length increases with body mass. Schooling behavior may reduce the costs of transport. Pelagic fish commonly use red lateral muscle during steady swimming at low speeds and white lateral muscle during burst swimming. The stride length of these fish is more or less constant and therefore swimming speed can be predicted from the tail beat frequency which in turn is directly related to the contraction times of the lateral the muscles. Swimming speeds can be classified as sustained speeds, prolonged speeds and burst speeds. Endurance of swimming is reduced at higher swimming speeds during prolonged swimming. Temperature has a profound effect on the swimming capacity with both endurance and swimming speed reduced at lower temperatures. Maximum swimming speeds double for every 10°C increase in temperature. The maximum swimming speed of many marine fish species is between 10 and 20L/s. Swimming performance affects the evolutionary fitness of a species. For each individual, it is a significant factor directly related to capture by or escape from fishing gears.

**Table 1.1.** Maximum Sustained Swimming Speed ( $U_{ms}$ ) and Endurance at Prolonged Speeds of Some Marine Fish Species.

Species	Length (cm)	$U_{ms}$ (cm/s)	$U_{ms}$ (L/s)	E-U Relation	Method	T (°C)	Source
Atlantic cod	40	42	1.1	...	FT	0.8	He (1991)
<i>Gadus morhua</i>	49	45	0.9	...		0.8	
Atlantic cod	36	75	2.1	$\log E = -0.99 \cdot U + 3.99$	FT	5	Beamish
<i>Gadus morhua</i>	36	90	2.5	$\log E = -1.13 \cdot U + 4.96$		8	(1966)
Atlantic herring <i>Clupea harengus</i>	25	102	4.1	$\log E = -1.43 \cdot U + 8.37$	AT	13.5	He and Wardle (1988)
Atlantic mackerel <i>Scomber scombrus</i>	31	110	3.6	$\log E = -0.96 \cdot U + 5.45$	AT	11.7	He and Wardle (1988)
American shad <i>Alosa sapidissima</i>	42			$\log E = -1.78 \cdot U + 19.02$	FT		Castro-Santos (2005)
Haddock <i>Melanogrammus aeglefinus</i>	17	44	2.6	...	AT	9.9	Breen et al. (2004)
	24	53	2.2	...			
	31	58	1.9	...			
	34	57	1.7	...			
	41	60	1.5	...			
Jack mackerel <i>Trachurus japonicus</i>	14	90	6.4	$\log E = -7.2 \cdot \log U + 9.3$	FT	19	Xu (1989)
	21	90	4.3				
Japanese mackerel <i>scomber japonicus</i>	10	99	9.9	$\log E = -0.62 \cdot U + 4.38$	FT	19	Beamish (1984)
Redfish <i>Sebastes marinus</i>	17	52	3.1	$\log E = -0.25 \cdot U + 1.71$	FT	5	Beamish
	16	52	3.3	$\log E = -0.23 \cdot U + 1.70$	FT	8	(1966)
	16	52	3.3	$\log E = -0.42 \cdot U + 2.94$	FT	11	
Saithe <i>Pollachius virens</i>	25	88	3.5	$\log E = -1.63 \cdot U + 5.60$	AT	14.4	He and Wardle (1988)
	34	100	2.9	$\log E = -1.52 \cdot U + 5.91$			
	42	106	2.5	$\log E = -1.36 \cdot U + 6.16$			
	50	110	2.2	$\log E = -1.17 \cdot U + 5.95$			
Striped bass <i>Morone saxatilis</i>	42-57			$\log E = -0.69 \cdot U + 10.65$	FT		Castro-Santos (2005)

Note. T, temperature; FT, flume tank; AT, annular tank; E, endurance (in min); U, swimming speed (in m/s).



**Figure 1.12.** Maximum swimming speed of some marine species in relation to their body length. Letter symbols, sources, and temperatures (when available) are as follows: AS—American shad, *Alosa sapidissima*, Castro-santos (2005); AW—Alewife, *Alosa pseudoharengus*, Castro-santos (2005); BH—blueback herring, *Alosa aestivalis*, Castro-santos (2005); CD—cod, *Gadus morhua*, 9.5° to 12°C, Blaxter and Dickson (1959); FH—flathead, *platycephalus bassensis*, 20°C, Yanase *et al.* (2007); HD—haddock, *Melanogrammus aeglefinus*, 12°C, Wardle (1975); HR—Atlantic herring, *Clupea harengus*, 10° to 15°C, Misund (1989); JK—jack mackerel, *Trachurus japonicus*, 23°C, Xu (1989); KW—kawakawa, *Euthunnus affinis*, 25°C, cited in Beamish (1978); MK—Atlantic mackerel, *Scomber scombrus*, 12°C, Wardle and He (1988); SB—striped bass, *Morone saxatilis*, Castro-santos (2005); SE—seabass, *Dicentrarchus labrax*, 20°C, Nelson and Claireaux (2005); SH1—saithe, *Pollachius virens*, Videler (1993); SH2—saithe, 10.8°C, He (1986); SH3—saithe, 14° to 16°C, Blaxter and Dickson (1959); SK1—skipjack tuna, *Katsuwonus pelamis*, Walters and Fierstine (1964); SK2—skipjack tuna, cited in Magnuson (1978); SP—sprat, *Sprattus sprattus*, 12°C, Wardle (1975); WA—wahoo, *Acanthocybium solandrei*, >15°C, Fierstine and Walters (1968); WH—whiting, *Gadus merlangus*, 9° to 13°C, Blaxter and Dickson (1959); YJ—yellowfin tuna, *Thunnus albacares*, Fierstine and Walters (1968). Lines for 20 L/s (solid), 10 L/s (dashed), and 5 L/s (dotted) are drawn to indicate swimming speed in L/s. (Modified from He, 1993).

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**SPECIES MENTIONED IN THE TEXT**

African electric eel, *Gymnarchus niloticus*  
 alewife, *Alosa pseudoharengus*  
 American shad, *Alosa sapidissima*  
 angelfish, *Pterophyllum scalare*  
 Atlantic cod, cod, *Gadus morhua*  
 Atlantic flying fish, *Cheilopogon heterurus*  
 Atlantic herring, *Clupea harengu*  
 Atlantic mackerel, *Scomber scombrus*  
 blueback herring, *Alosa aestivalis*  
 bluefin tuna, *Thunnus thynnus*  
 butterfly fish, *Chaetodon* sp.  
 cornet fishes, *Fistsularia* sp.  
 European eel, eel, *Anguilla anguilla*  
 flathead, *Platycephalus bassensis*  
 forkbeard, *Phycis phycis*  
 haddock, *Melanogrammus aeglefinus*  
 hatchet fish, *Gasteropelecus* sp.  
 jack mackerel, *Trachurus japonicus*  
 Japanese mackerel, *Scomber japonicus*  
 kawakawa, *Euthunnus affinis*  
 louvar, *Luvarus imperialis*  
 moray eel, *Muraena helena*  
 opah, *Lampris guttatus*

Pacific barracuda, barracuda, *Sphyaena argentea*  
 Pacific bonito, *Sarda chiliensis*  
 Pacific mackerel, *Scomber japonicus*  
 pike, *Esox lucius*  
 porbeagle shark, *Lamna nasus*  
 rainbow wrasse, *Coris julis*  
 redfish, *Sebastes marinus*  
 sailfish, *Istiophorus platypterus*  
 saithe, *Pollachius virens*  
 sand eel, *Ammodytes tobianus*  
 seabass, *Dicentrarchus labrax*  
 seahorse, *Hippocampus ramulosus*  
 shiner perch, *Cymatogaster aggregata*  
 skate, *Raja batis*  
 skipjack tuna, *Katsuwonus pelamis*  
 sprat, *Sprattus sprattus*  
 striped bass, *Morone saxatilis*  
 sunfish, *Mola mola*  
 swordfish, *Xiphias gladius*  
 turbot, *Scophthalmus maximus*  
 wahoo, *Acanthocybium solandrei*  
 whiting, *Gadus merlangus*  
 yellowfin tuna, *Thunnus albacares*