An 'average' fish larva has little chance for survival. Typically, numbers are reduced by three orders of magnitude during the larval stage. Thus, larval survivors may have special qualities, in addition to extraordinary luck. Individuals that behave appropriately or grow faster will survive because they are proficient at feeding and avoiding predators, and perhaps better at selecting favorable habitat (e.g. by vertically migrating). Favored or selected characteristics may be phenotypic or inherited. As an example of the former, there is evidence that in many species bigger larvae hatch from eggs spawned by larger and older females. Such larvae have higher survival potential. Thus, the fates of fish larvae may be partly programmed by genes from their parents, but also will depend on selective fishing practices that target the largest adults, in addition to the myriad environmental factors that normally act on larval populations.

See also

Conservative Elements. Fish Ecophysiology. Fish Feeding and Foraging. Fish Locomotion. Fish Migration, Horizontal. Fish Migration, Vertical. Fish Predation and Mortality. Fish Reproduction. Pelagic Fishes. Plankton. Population Dynamics Models. Small-scale Physical Processes and Plankton Biology. Zooplankton Sampling with Nets and Trawls.

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FISH LOCOMOTION

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Introduction

After one thousand million years of evolution 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 movements of the body to provoke reactive forces from the water to propel themselves. Propulsive forces overcome drag, are required for acceleration, and disturb the water. Animal movements are powered by contracting muscles and these consume energy. These basic principles of fish locomotion are used by more than 22 000 extant species. The variation in swimming styles, within the limits of these principles, is extremely large.

The Swimming Aparatus of Fish

Fish are aquatic vertebrates with a skull, a vertebral column supporting a medial septum dividing the fish into two lateral halves, and lateral longitudinal muscles 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 right side.

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 heamal arch and spine. Neural and haemal spines point obliquely backward. The number of vertebrae varies greatly among species: European eels have 114 vertebrae, and the numbers in the large perciform order vary between 23 and 40. The number is not necessarily constant within a species. Herring, for example, may have between 54 and 58 vertebrae. 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 finrays of the caudal fin. Most fish species have unpaired dorsal, caudal, and anal fins and paired pectoral and pelvic fins.

In fish, relatively short lateral muscle 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 (**Figure 1A**). In cross-sections through the caudal region the muscles are arranged in four compartments. On each side there is a dorsal and a ventral compartment, in some groups 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 (**Figure 1B**). Red fibers are usually situated 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 inexhaustible 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.

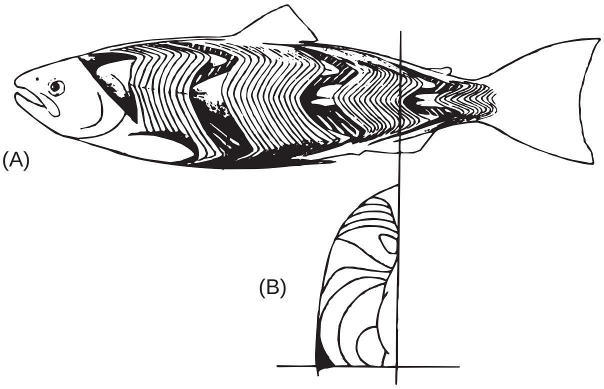


Figure 1 (A) The myotomes and myosepts on the left side of the king salmon. Myotomes have been removed at four places to reveal the complex three-dimensional configuration of the lateral muscles. (B) A cross-section through the upper left quarter of the caudal region of a salmon. Red muscle fibers are situated in the dark area near the outside. The lines represent the myosepts between the complex myotomes. (A) Redrawn after Greene and Greene, C. W. and Greene C. H. (The skeletal musculature of the King Salmon. *Bull. U.S. Bur. Fish.*, 1913 vol. 33); (B) based on Shann E. W. (On the nature of lateral muscle in teleostei. *Proc. 2001. Soc. Lond. vol. 22.*)

The red muscles of tuna and mackerel sharks are positioned well inside the white muscle mass, an arrangement that increases the muscle temperature by about 10°C during swimming. This halves the twitch contraction time of the white muscles and doubles the swimming speed.

The orientation of the muscle fibers in the myotomes is roughly parallel to the longitudinal axis of the fish. However, a more precise analysis of the fiber direction shows a complex helical pattern. Fiber directions may make angles as large as 80° with the main axis of the fish. A possible function of this arrangement could be that it ensures equal strain rates during lateral bending for fibers closer to and farther away from the median septum. The purpose of the complex architecture of fish lateral muscles is not yet fully understood.

Fish fins are folds of skin, usually supported by fin rays 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) are permanently extended and rather rigid compared to those of teleosts (bony fish). The fin rays consist of rows of small pieces of cartilage. 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 (**Figure 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 inserting on the fin ray heads can change the bending of the rays or the stiffness against bending forces.

The body shape of fish may vary greatly among species, but the best pelagic swimmers have a

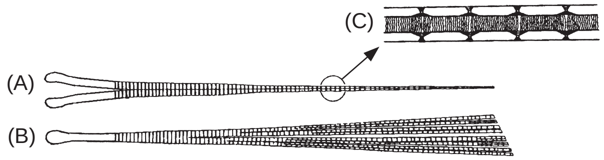


Figure 2 The structure of a typical teleost fin ray. (A) Dorsal or ventral view: the left and right fin ray halves are each other's mirror image. (B) Lateral view; the size of the bony elements decreases to the right after each of the bifurcations. The position of the bifurcations in the various branches 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.

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 towards the narrow caudal peduncle. A moving body in water encounters friction and pressure drag. Friction drag is proportional to the surface area, pressure drag 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.

The mechanically important part of fish skin is the tissue (the stratum compactum) underneath the scales, which consists of layers of parallel collagenous fibers. The fibers in adjacent layers are oriented in different directions, the angles between the layers vary between 50° and 90°, 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 towards 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 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 ($1\,\mathrm{GPa} = 10^9\,\mathrm{N\,m^{-2}}$) have been measured. This is about one-third of the strength of mammalian tendon, for which values of 1.5 GPa have been measured. The oblique fiber direction and the relative weakness of the structure make it difficult to understand how the stratum compactum could transmit forces from anterior muscles toward the tail, but it is possible that strong skin plays such a mechanical role in swimming.

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.

Fish mucus is supposed to reduce friction with the water during swimming. This assumption is based on the idea that mucus shows the 'Toms effect,' 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) to no effect at all (California bonito). Experiments with rainbow trout showed that mucus increases the thickness of the boundary layer, which implies that viscous friction is reduced. 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.

Swimming-related Adaptations

Various 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. Swimming economically, top speed sprinting, making use of ground effect, backward swimming, swimming in sandy bottoms, precise position keeping, flying, and straight acceleration by recoil reduction are less apparent. These special swimming adaptations shown in **Figure 3** are only a few out of a wealth of possible examples. A closer study of the locomotory habits of a large number of species will show many more specialist groups than the dozen or so described here.

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° phase shift between the left and right side. 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. The wavelength of the body curvature of slender eel-like fish is about $0.59L$ ($L =$ body length), 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 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. 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 linearly related to the swimming speed. 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 $0.7L$. Many species reach values between 0.5 and $0.6L$ during steady swimming bouts.

Swimming with appendages includes pectoral fin swimming and median fin propulsion. Pectoral fin movements of for example labrids, shiner perches, and surfperches 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.

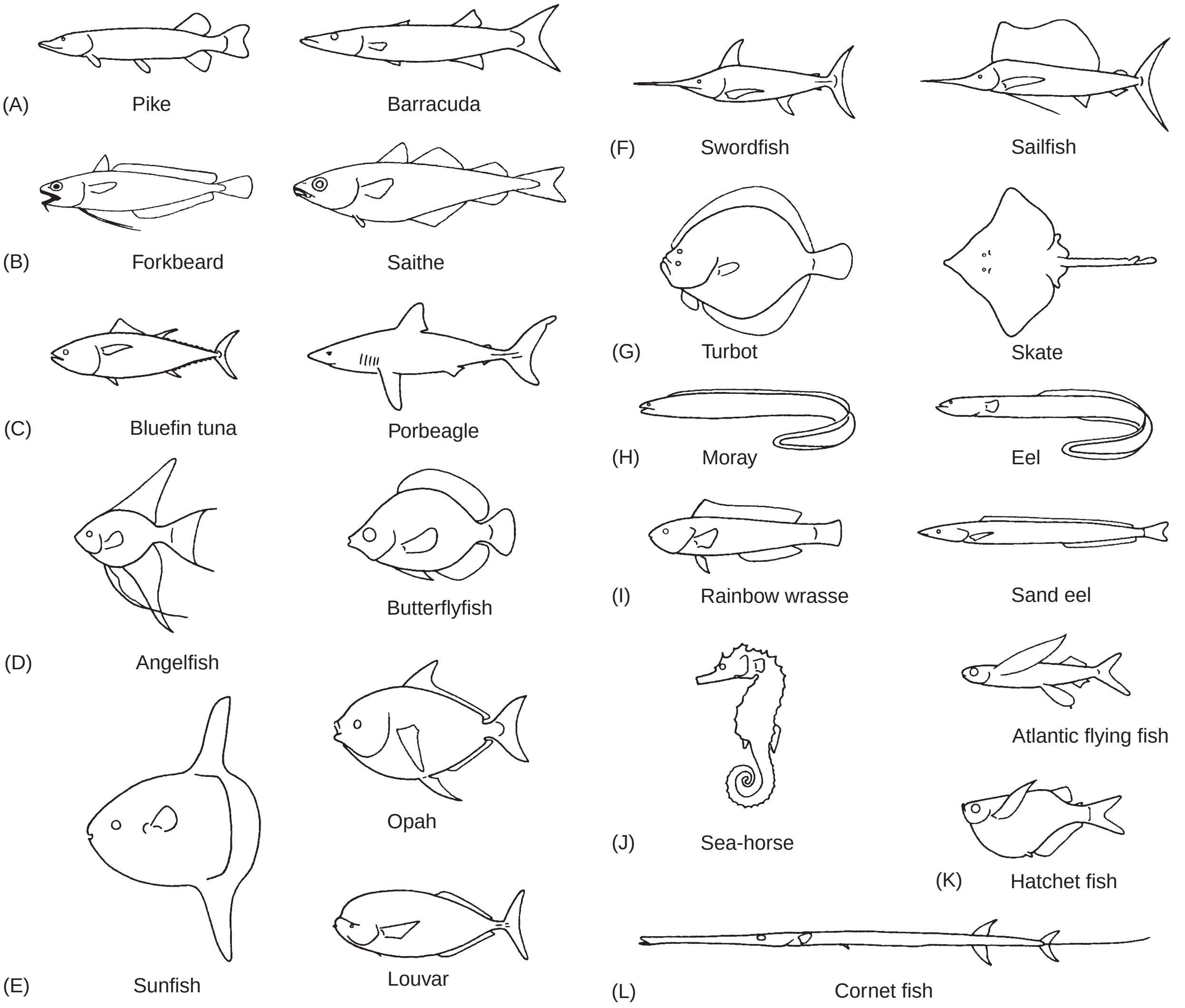
Undulations of long dorsal and anal fins can propel fish forward and backward and are used in combination with movements of the pectoral fins and the tail. In triggerfish, for example, tail strokes aid during fast swimming and the pectorals help while maneuvering. There is usually more than one wave on each fin (up to 2.5 waves on the long dorsal fin of the African electric eel). The stride lengths obtained by this mode of propulsion are low, with values in the order of one-quarter of the body length.

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 thrust forces by adding momentum to the water. Quantitative flow visualization techniques have been successfully applied to reveal the flow patterns near fish using body undulations to propel themselves. The interaction between undulating bodies and the water results in flow patterns along and behind the swimming animals. Hydrodynamic approaches usually focus on the flow generated by the tail. A schematic three-dimensional impression of the wake behind a fish is shown in **Figure 4**. This shows the dorsal and ventral tip vortices generated by the tail 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 halfstroke 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 halfstroke the tail changes direction and builds up high 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 medio-frontal 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 medio-frontal plane of swimming fish reveal that this picture of the wake is correct (**Figure 5**).

The 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 20 joules per ml oxygen used. 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 between species. The highest levels of energy consumption measured in fish are about $4\,\mathrm{W\,kg^{-1}}$. Fast streamlined fish can increase their metabolic rates up to 10 times resting levels during swimming at the highest sustainable speeds. Short-burst speeds powered by anaerobic white muscles can cost as much as 100 times resting rates. Most of the energy is required to generate enough 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 meters per second (**Figure 6**). 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 meter ($\mathrm{J\,s^{-1}}$ divided by $\mathrm{m\,s^{-1}}$). To make



◀ **Figure 3** (A) Specialists in accelerating, such as the pike and the barracuda, are often ambush predators. They remain stationary or swim very slowly until a potential prey occurs within striking distance. Colour patterns adapted to each specific environment provide the essential camouflage to make them hardly visible against the background. 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 caused by the first two beats of the tail, which is in effect enlarged by the rearward position of the dorsal and anal fins. The relative skin mass of the pike is reduced, compared with 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 $\mathrm{m\,s^{-2}}$ which equals 4 to 15 times the acceleration due to gravity ($g = 9.8\,\mathrm{m\,s^{-2}}$). The highest peak acceleration value reported for pike is 25 g. (B) Braking is difficult while moving in a fluid medium. Gadoids with multiple or long unpaired fins are good at it. The forkbeard 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. Braking is so effective that the shrimp has not yet reached the caudal peduncle before the fish has stopped and turned to catch it. Fish use the unpaired fins and tail, usually in combination with the pectoral and pelvic fins, for braking. In the process, the fin rays of the tail fin are actively bent forward. The highest deceleration rate measured is 8.7 $\mathrm{m\,s^{-2}}$ for saithe. The contribution of the pectorals to the braking force is about 30%, the rest comes from the curved body and extended median fins. (C) Cruising specialists 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 keels, and high-aspect-ratio tails (aspect ratio being the tail height squared divided by tail surface area). The bluefin tuna, for example, crosses the Atlantic twice a year. The body dimensions are very close to the optimum values, with a thickness-to-length ratio near 0.25. Cruising speeds of 3 m long bluefin tunas measured in large enclosures reached 1.2L per second (260 $\mathrm{km\,d^{-1}}$). (D) Angelfish and butterflyfish are maneuvering experts with short bodies with 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 0.065L. For comparison, the turning radius of a cruising specialist is in the order of 0.5L, an order of magnitude larger. (E) Sunfish, opah, and louvar are among the most peculiar fish in the ocean. They look very different but have large body sizes in common. 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. Little is known about the mechanics of their locomotion. They all seem to swim slowly over large distances. The opah will use 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 are an extremely high-aspect-ratio propeller. Sunfish swim very steadily, moving the dorsal and ventral fins simultaneously to the left and, half a cycle later, to the right side. The dorsal and ventral fins have an aerodynamic profile in cross-section. 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 looks as though 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. (F) Swordfishes (Xiphiidae) and billfishes (Istiophoridae) show bodily features that no other fish has: 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 100 $\mathrm{km\,h^{-1}}$. The sword of swordfish is dorsoventrally flattened to form a long blade (up to 45% of the body length). The billfish (including sailfish, spearfish, and marlin) swords are pointed spikes, round in cross-section and shorter (between 14% and 30% in adult fish, depending on species) than those of swordfish. All the 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. 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. (G) The shape of the body of flatfish and rays offers the opportunity of hiding in the boundary layer close to 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 induced drag considerably, depending on the ratio between height off the ground and the span of the 'wings'. (H) Only a few species can swim both forward and backward. Eels, moray eels, and congers 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. Swimming is usually not very fast; they prefer to swim close to the bottom and operate in muddy or maze-type environments. (I) Sand eels and rainbow wrasse 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, i.e. 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. (J) Most neutrally buoyant fish species are capable of hovering in one spot in the water column. Some species can hardly do anything else. Sea-horses 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. (Sea-horses are the only fish with a prehensile tail.) (K) Flying fish 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 take-off. Hatchet fishes (Gasteropelecidae) actually beat their pectoral fins in powered flight. The pectoral fins have extremely large intrinsic muscles originating on a greatly expanded pectoral girdle. The flying gurnards (Dactylopteridae) have tremendously enlarged pectoral fins, usually strikingly colored. There is still some dispute over their ability to use these large pectorals when airborne. Many more species occasionally or regularly leap out of the water but are not specially adapted to fly. (L) Cornet fishes (Fistulariidae) are predators of small fish in the littoral of tropical seas, most often seen above seagrass 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 there is a long thin caudal filament. They 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. 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. Based on Videler (1993) with figures (B) added.

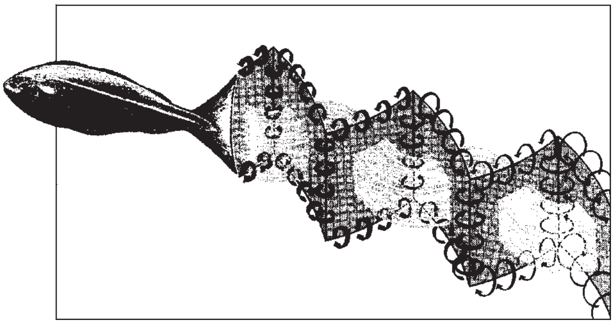


Figure 4 Artist's impression of the flow behind a steadily swimming saithe. The tail blade is moving to the left and in the middle of the stroke. At the end of each half-stroke a column vortex is left behind when the tail blade changes direction. Tail tip vortices are shed dorsally and ventrally when the tail moves from side to side. Together the vortices form a chain of vortex rings with a jet of water winding through the centers of the rings in the opposite swimming direction Videler (1993).

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 $\mathrm{W} = \mathrm{J\,s^{-1}} = \mathrm{wt\,m\,s^{-1}}$) by the weight of the fish (in newtons (N)) times u_{opt} (in $\mathrm{m\,s^{-1}}$), to reach a dimensionless number for the cost of transport (COT expressed in $\mathrm{J\,N^{-1}\,m^{-1}}$). Hence, COT represents the cost to transport one unit of weight over one unit of distance.

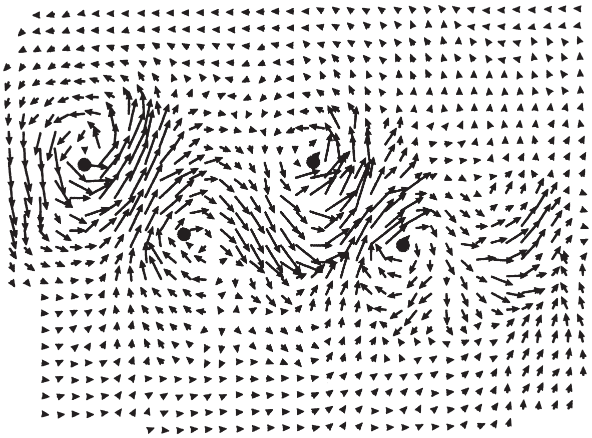


Figure 5 The wake of a continuously swimming mullet. The arrows represent the flow velocity in mm $\mathrm{s^{-1}}$ scaled relative to the field of view of 195 × 175 mm. The shaded circles indicate the centers of the column vortices. The picture represents a horizontal cross-section through the wake drawn in **Figure 4**. (Based on Müller *et al.* (1997).)

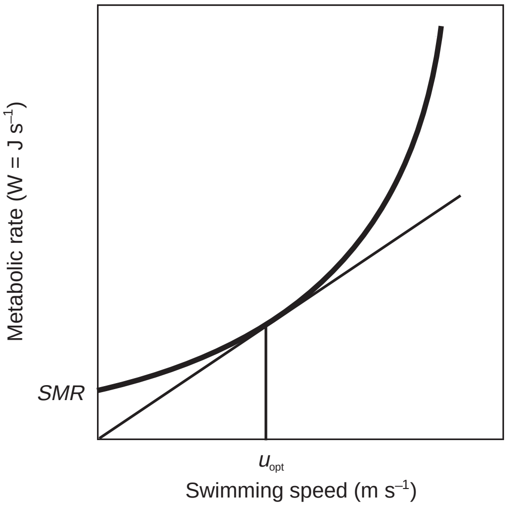


Figure 6 A theoretical curve of the rate of work as a function of swimming speed. SMR is the standard or resting metabolic rate at speed 0. The amount of work per unit distance covered ($\mathrm{J\,m^{-1}}$) is at a minimum at u_{opt} (Videler (1993).)

Available data show that u_{opt} is positively correlated with mass (proportional to mass$^{0.17}$); u_{opt} decreases with mass if it is expressed in L per second (proportional to mass$^{-0.14}$). The variation measured is large but $2L$ per second 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 with an exponent of -0.38 (**Figure 7**). Fish use on average $0.07\,\mathrm{J\,N^{-1}}$ to swim their body length at u_{opt}. If the weight and the size of the animals is taken into account as well by calculating the energy needed to transport the bodyweight over

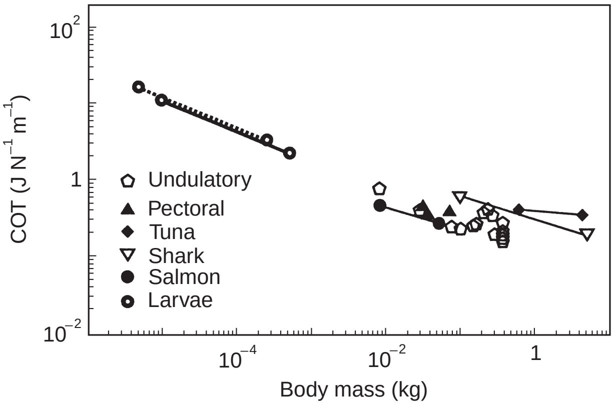


Figure 7 Doubly logarithmic plot of dimensionless COT, being the energy needed to transport one unit of mass over one unit of distance ($\mathrm{J\,N^{-1}\,m^{-1}}$) during swimming at u_{opt}, related to body mass. The connected points indicate series of measurements of animal groups indicated separately; 'undulatory' and 'pectoral' refer to measurements of fish using body plus tail and pectoral fins respectively, for propulsion.

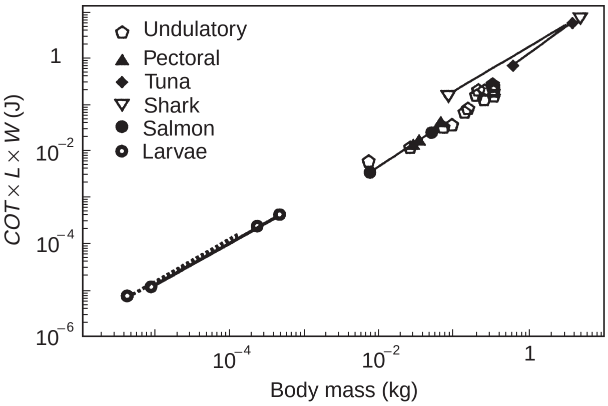


Figure 8 Doubly logarithmic plot of the energy needed by a swimming fish to transport its body weight over its body length as a function of body mass. Symbols as in **Figure 7**. Based on Videler (1993).

the length, the amount of energy used to swim at u_{opt} increases in proportion to body mass with an exponent of 0.93 (**Figure 8**).

Energy-Saving Swimming Behaviors

Burst-and-coast (or kick-and-glide) swimming behavior is commonly used by several species. 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 9** 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. The model predictions are based on a 3-fold difference in drag between a rigid body and an actively moving fish.

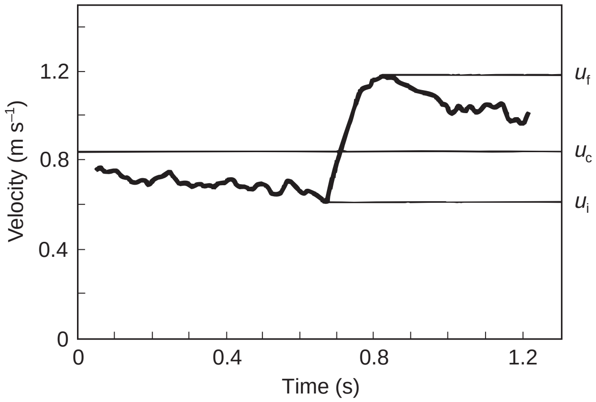


Figure 9 Part of a velocity curve during burst-and-coast swimming of cod. The average speed u_c was 3.2L per second. The initial speed and the final velocity of the acceleration phase are indicated as u_i and u_f, respectively. From Videler (1993).

Schooling behavior probably has energy saving effects. **Figure 4** – 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. 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 been confirmed by actual observations. However, energetic benefits for school members have been confirmed by indirect evidence. It has been observed that the tail beat frequency of schooling Pacific mackerel is reduced compared with solitary mackerel swimming at the same speed. In schools of sea bass, trailing individuals used 9–14% 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.

Swimming Speed and Endurance

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 10** relates swimming speed, endurance and the cost of swimming for a 0.18 m sockeye salmon at 15°C. At low speeds this fish can swim continuously without showing any signs of fatigue. The optimum speed u_{opt} is between 1 and 2L per second. Limited endurance can be measured at speeds higher than the maximum sustained speed (u_{ms}) of somewhat less than 3L per second. For these prolonged speeds, the logarithm of the time to fatigue 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 speed in this case is in the order of 7L per second.

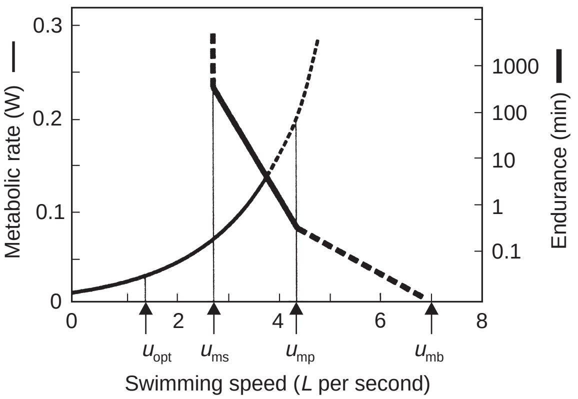


Figure 10 The metabolic rate (linear scale) and the endurance (logarithmic scale) of a 0.18 m, 0.05 kg sockeye salmon as functions of swimming speed in *L* per second. The water temperature was 15°C. The optimum swimming speed (u_{opt}), the maximum sustained speed (u_{ms}), the maximum prolonged speed (u_{mp}) and an estimate of the maximum burst speed (u_{mb}) are indicated. From Videler (1993).

A comparison of published data reveals that u_{ms} for fish varying in size between 5 and 54 cm is on the order of 3*L* per second and that u_{mp} is about twice that value. A 15 cm carp is capable to swim at 4.6*L* per second for 60 minutes and at 7.8*L* per second during 0.2 minutes. Within a single species, u_{ms} and u_{mp} expressed in *L* per second decline with increasing length, and so does endurance.

Demersal fish living in complex environments have shallower endurance curves than pelagic long-distance swimmers, which fatigue more quickly when they break the limit of the maximum sustained speed. 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 meters per second increases linearly with body length; the slope is about three times as steep as that of the maximum sustained and prolonged speeds. The average relative value is about 10*L* per second, a figure that turns out to be a fairly good estimate for fish between 10 and 20 cm long. Small fish larvae swim at up to 60*L* per second during startle response bursts. Speed record holders in meters per second are to be found among the largest fish. Unfortunately, reliable measurements are not usually available. The maximum burst speed of fish depends on the fastest twitch contraction time of the white lateral muscles. 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 and the maximum tail beat frequency. Muscle twitch contraction times halve for each 10C temperature rise and the burst speed doubles. Larger fish of the same species have slower white muscles than smaller individuals. The burst swimming speed decreases with size with a factor of on average 0.89 for each 10 cm length increase. Estimates based on muscle twitch contraction times and measured stride length data for 226 cm long bluefin tuna vary between 15 and 23 $\mathrm{m\,s^{-1}}$ (54–83 $\mathrm{km\ h^{-1}}$). Estimates for 3 m long swordfish exceed 30 $\mathrm{m\,s^{-1}}$ (108 $\mathrm{km\,h^{-1}}$). Measured values for burst speeds are difficult to find. The maximum swimming speed ever recorded in captivity is that of a 30 cm mackerel swimming at 5.5 $\mathrm{m\ s^{-1}}$ (20 $\mathrm{km\ h^{-1}}$). Its tail beat frequency was 18 Hz and the stride length 1 L.

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 above cruising speeds are swum. The variation in performance between species is large and details have been hardly investigated so far.

See also

Fish Migration, Horizontal. Fish Migration, Vertical. Fish Predation and Mortality.

Further Reading

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