

Form and Function in Fish Swimming

Some fishes are specialized for cruising, accelerating or maneuvering, but most are generalists with a combination of locomotor qualities. Recent work correlates each fish's form with its habit of swimming

by Paul W. Webb

Human beings have been reflecting on how fishes propel themselves through water for a remarkably long time. Some of the earliest thoughts on how fishes swim were recorded in India 2,500 years ago. In the Western world the hypotheses of Aristotle, although they were not very close to the mark, were generally accepted until late in the 19th century. Aristotle thought all vertebrate animals moved by pushing at a certain number of points of contact with the world. He hypothesized that fishes pushed against the water with two pairs of fins, four bends in the body or a combination of fins and bends. One reason his views prevailed for so long is that the study of fish swimming presents difficult problems of observation and analysis. The movements of the fish are quick and the fish can travel a long way in a short time. Moreover, the propulsive forces are complex and are exerted in a fluid medium, which makes them hard to measure.

By the end of the 19th century, however, much progress had been made in cinematography, which made it possible to begin examining in detail how fishes swim. At the same time advances were being made in the construction of wind tunnels and experimental water tanks and in the concepts of hydrodynamics. Such developments encouraged new work on the physical forces that have a role in fish swimming. As is true of any solid body that is being propelled, the forward motion of the fish is the net result of the forces that tend to advance it and the forces that tend to retard it. In the case of the fish the impelling force is the thrust generated by the swimming movements. The retarding forces come from inertial resistance or from the drag of the water.

By the 1930's Charles M. Breder of the American Museum of Natural History and Sir James Gray of the University of Cambridge had described swimming kinematics (the movements en-

tailed in swimming). By the 1960's Gray, Richard Bainbridge and John R. Brett of the Canadian Fisheries Research Board had made great contributions to the understanding of swimming energetics (the relations of force and energy generated by the propulsive movements). In the past 15 years particularly rapid progress has been made by building on the work of these pioneers. Quantitative theories formulated by Sir James Lighthill of Cambridge, T. Y. Wu of the California Institute of Technology and Daniel Weihs of the Israel Institute of Technology show how fishes generate thrust and how to calculate the magnitude of the thrust. The new theories also make clear how the form of the fish affects the thrust and the drag.

Thus the subject of how fishes swim presents a curious spectacle: it has been a source of interest for two and a half millennia but only in the past two decades has quantitative work begun to illuminate how a fish's form is related to its mode of swimming and its way of life. The interplay of thrust and resistance makes some body shapes much better than others for accelerating, some better for cruising and some better for maneuvering. These are the three main swimming functions. Some fishes have bodies specialized for one function. For example, the long, slender body of the pike is well suited to accelerating, which benefits the pike in preying on small fishes. In return for specialized abilities, however, the pike sacrifices peak performance in cruising and maneuvering.

Most fishes are not specialists, but generalists with bodies that give them moderately good performance in all three functions and superior performance in none. The bass can cruise, maneuver and accelerate fairly well but cannot accelerate as well as a pike, cruise as well as a tuna or maneuver as well as an angelfish. The work on fish swimming done in the past 15 years has made it possible to determine which fea-

tures of the fish's body make a significant contribution to its performance. Since the fish's behavioral options are largely determined by the animal's swimming ability, it has become possible for the first time to correlate in a precise way the design of a particular fish with its mode of life.

Undulation and Oscillation

Fishes clearly have a remarkable variety of shapes and sizes. At one extreme is the knifefish, a long, narrow, tapered animal resembling an eel. At another extreme is the triggerfish, a tropical fish with a body that is roughly diamond-shaped when it is viewed from the side and extremely narrow when it is viewed from the front or the rear. Not only fishes' bodies but also fishes' appendages are diverse. The knifefish has a fin that extends down the median line of the ventral (lower) surface of its body. The triggerfish, on the other hand, has many small fins with short bases on the dorsal (upper) and ventral surfaces of the body and also on the sides.

To make matters more complicated, every part of the body and every appendage is employed for swimming by some fish or other, including the body itself, the caudal fin (the tail), the paired fins on the sides of the body and the median fins on the dorsal and ventral surfaces. Such diversity would appear to make the task of understanding the functional morphology of fishes—the connection between the form of the animal and its way of swimming—a daunting one.

Fortunately for the ichthyologist the job is made easier by the fact that locomotion is underlain by unifying principles. Knowledge of these principles makes it possible to divide the fishes into large groups according to their mode of swimming. The first principle is the distinction between undulatory motion and oscillatory motion. In undulatory mo-

tion a wave passes along the propulsor, the structure that provides the propulsive force. Two types of structure can undulate: (1) the body and the caudal fin acting as a single unit and (2) fins attached to the body by a long base. Such long-based fins can be on the median line of the dorsal and ventral surfaces or in pairs on the sides. The mackerel, the shark, the salmon, the pike, the bass, the trout and the eel are propelled by the undulatory motion of the body and the caudal fin. The knife fish is propelled by the long-based undulatory fin on its ventral surface.

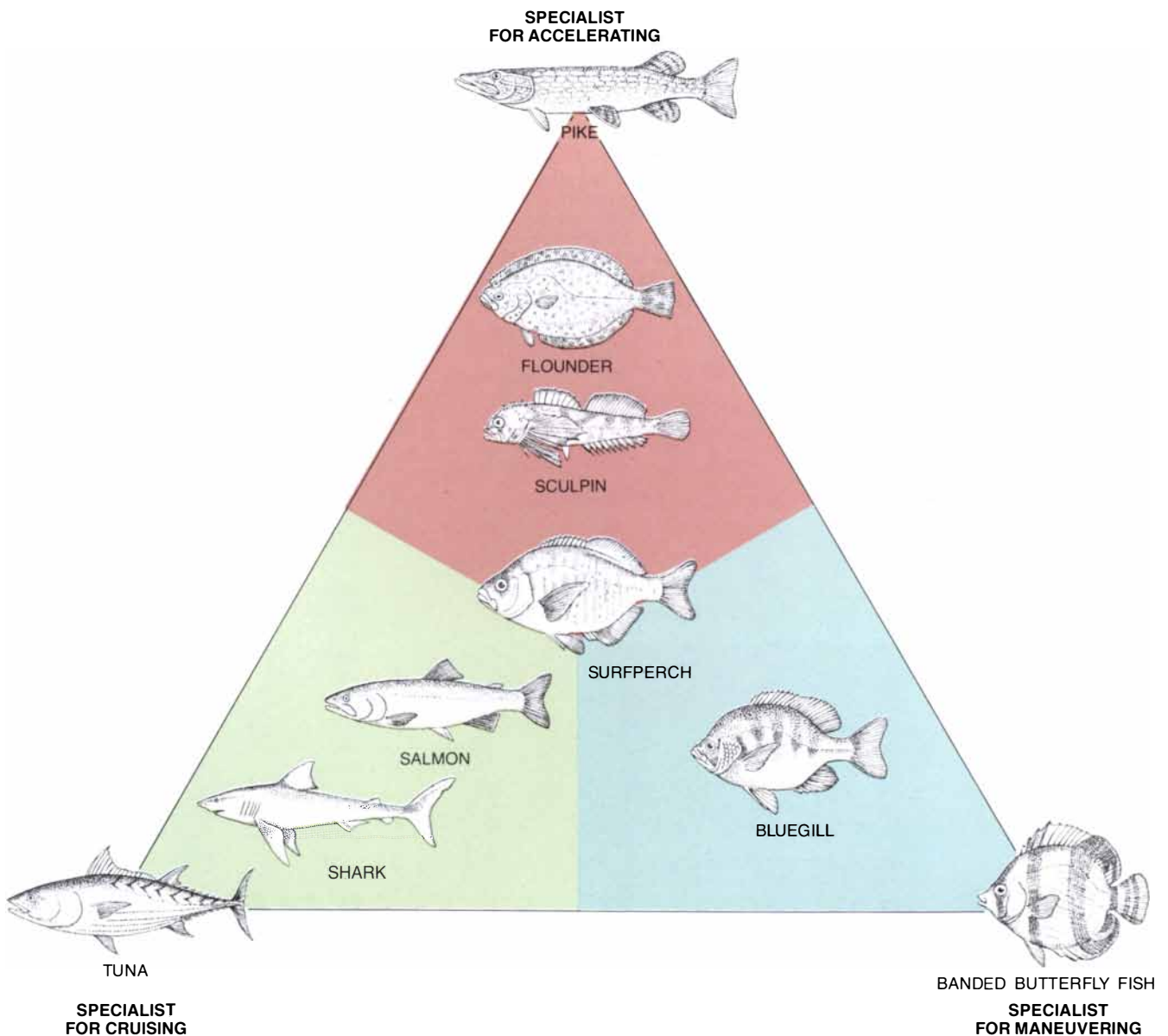
In oscillatory motion the part of the body that provides the propulsive force moves back and forth by pivoting on its

base, without the wave motion shown by undulatory structures. Fins attached to the body by a short base generally oscillate. As we shall see, there are two quite different physical principles by which oscillatory fins can generate a propulsive force. The surfperch and the mandarin fish are examples of fishes that rely on oscillatory fins for their main propulsive force. In general, oscillatory and undulatory fins unassisted by body movements are utilized at low speeds in situations where precise maneuvering makes a substantial contribution to the fish's feeding or to its survival. Faster swimming requires more power; therefore the myotomal muscle, the large mass of tissue on each side of the body,

is recruited for accelerating and high-speed swimming.

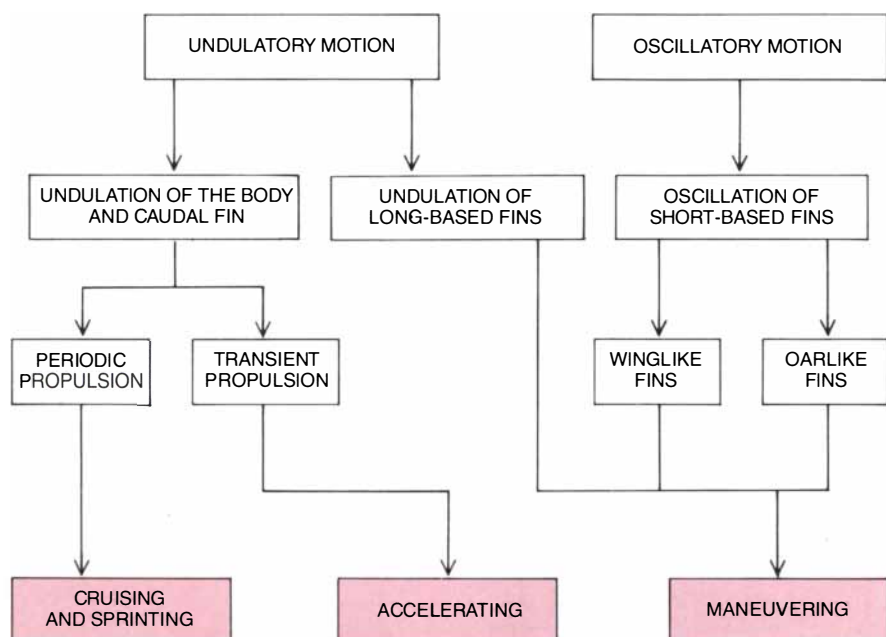
How does the undulation or oscillation of a part of the fish's body result in the thrust that propels the fish through the water? Much of the work that has been done in response to this question concerns undulatory movements, and the best-understood of these movements is the joint undulation of the body and the caudal fin. When the fish's body undulates, one or more half wavelengths travel from its head to its tail at a speed greater than the fish's speed with respect to the water.

In the undulation each propulsive element, or small segment of the body, moves laterally with respect to the head.

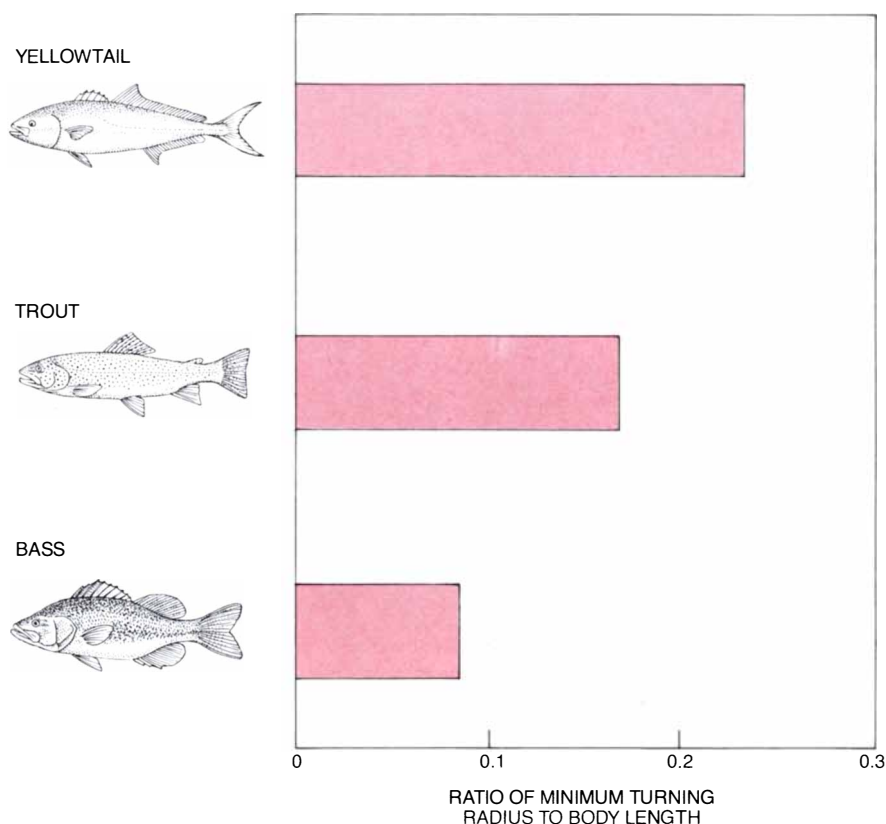


FUNCTIONAL-MORPHOLOGY PLANE for locomotion in fishes includes specialists and generalists. The fishes at the corners of the triangle are specialized for one swimming function: the tuna for sustained cruising, the pike for accelerating in quick strikes at prey and the banded butterfly fish for low-speed maneuvering in and around the coral reef. Each specialist performs poorly in the other two func-

tions. For example, the tuna does not accelerate or maneuver well. The surfperch, at the center of the triangle, is a generalist. It can accelerate, cruise and maneuver fairly well but does not perform any function as well as a specialist. Between the center of the triangle and the corners are fishes that are more specialized than the surfperch but are less specialized than the tuna, the pike or the butterfly fish.



TYPES OF PROPULSION utilized by fishes are shown in the boxes. In undulatory motion a wave passes down the length of the body part or the fin that provides the propulsive force. In oscillatory motion the anatomical structure moves back and forth. Cruising, sprinting and accelerating call for the coupled undulatory motion of the body and the caudal fin (the tail). In periodic propulsion, which is employed in cruising and sprinting, the swimming movements are repeated cyclically. In transient propulsion, which is employed in accelerating, the movements are not cyclical. Fishes that maneuver slowly utilize the oscillatory motion of fins with short bases (which operate like wings or like oars) or the undulatory motion of fins with long bases.



TRANSIENT SWIMMING PERFORMANCE can be measured by the ratio of the minimum turning radius of the center of body mass in a fast start to the length of the body. The smaller the ratio, the better the performance. Bass perform better in a quick start than trout or yellowtail. The reason for the superior performance of bass is that they have the largest body area in relation to their mass; the area is utilized for thrust whereas the mass resists the turn.

As the wave passes, the propulsive element accelerates the water nearby. The force generated by the muscles accelerates the water; an equal opposing force, called the reaction force, is exerted on the propulsive element by the water. The magnitude of the reaction force is equal to the product of the acceleration given to the water and the mass of the water accelerated. The force is perpendicular to the propulsive element and is inclined toward the head of the fish.

The force exerted on a propulsive element has two components. Consider a fish swimming in a straight line (meaning without turning). One component of the force on the propulsive element is parallel to the fish's overall direction of motion; this is the longitudinal force. The other component is perpendicular to the overall direction of motion; this is the side force. When the fish is swimming without turning, only the longitudinal component contributes to thrust.

Contributions to Thrust

The longitudinal force generated by the propulsive elements near the tail is greater than the force generated by the elements near the head. There are two reasons the caudal elements make a greater contribution to thrust. The first reason is that the caudal inclination of the segments near the tail is large.

To understand what caudal inclination means, imagine a line drawn along the axis of the propulsive element, that is, along the median line of the fish's body [see illustration on page 78]. When the propulsive wave passes down the body, the line corresponding to the axis of the element curves so that the side pushing against the water faces toward the tail. Now imagine a second line perpendicular to the first; the perpendicular line represents the reaction force that acts on each element and is directed toward the head. As the propulsive wave passes, the elements near the tail curve farther toward the rear than the elements near the head. As a result the reaction force on the rear elements has a direction closer to that of the overall motion of the fish, and more of the force exerted by the water on the element is parallel to the direction of motion.

The second reason the elements near the tail make a greater contribution to the thrust than the elements near the head is that as the wave passes, the rear elements traverse a greater distance than the forward ones. Hence the speed of the elements near the tail is greater and they accelerate the water more than the elements near the head of the fish.

The way thrust is generated by the propulsive elements as the wave moves down the body and the caudal fin has significant implications for the shape that most efficiently meets the needs of a particular fish. Swimming based on the

coupled motion of the body and caudal fin can be divided into two categories: transient swimming and sustained swimming. Transient swimming, which is the type of movement observed in fast starts and powered turns, entails propulsive movements that are brief and have a large amplitude. The movements can be as brief as tens of milliseconds and in them the tail can traverse a distance equal to half of the body length.

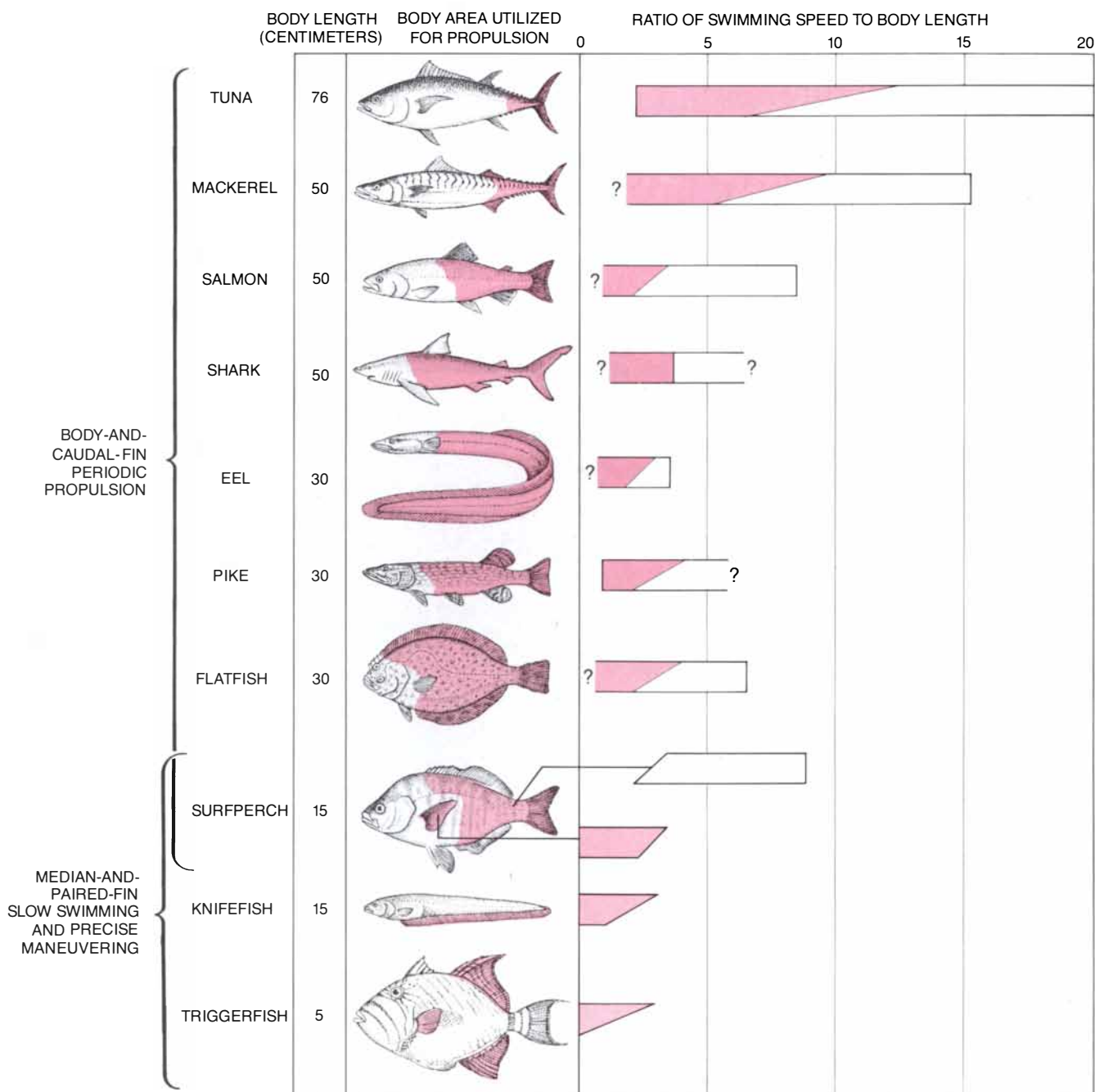
Sustained swimming, on the other hand, is any propulsion with cyclically

repeated swimming movements; such movements generally include several beats of the tail. Sustained swimming can itself be divided into several types according to the duration of the propulsion. For example, cruising is a type of swimming that can be sustained for an hour or more. Sprinting, another type of sustained swimming, may last for only a few seconds. The mechanism whereby thrust results from the wavelike motion of the body has implications for transient swimming different from those it

has for sustained swimming, and as a result fishes that rely mainly on quick acceleration have a shape different from that of fishes that cruise large areas of the ocean at a steady pace.

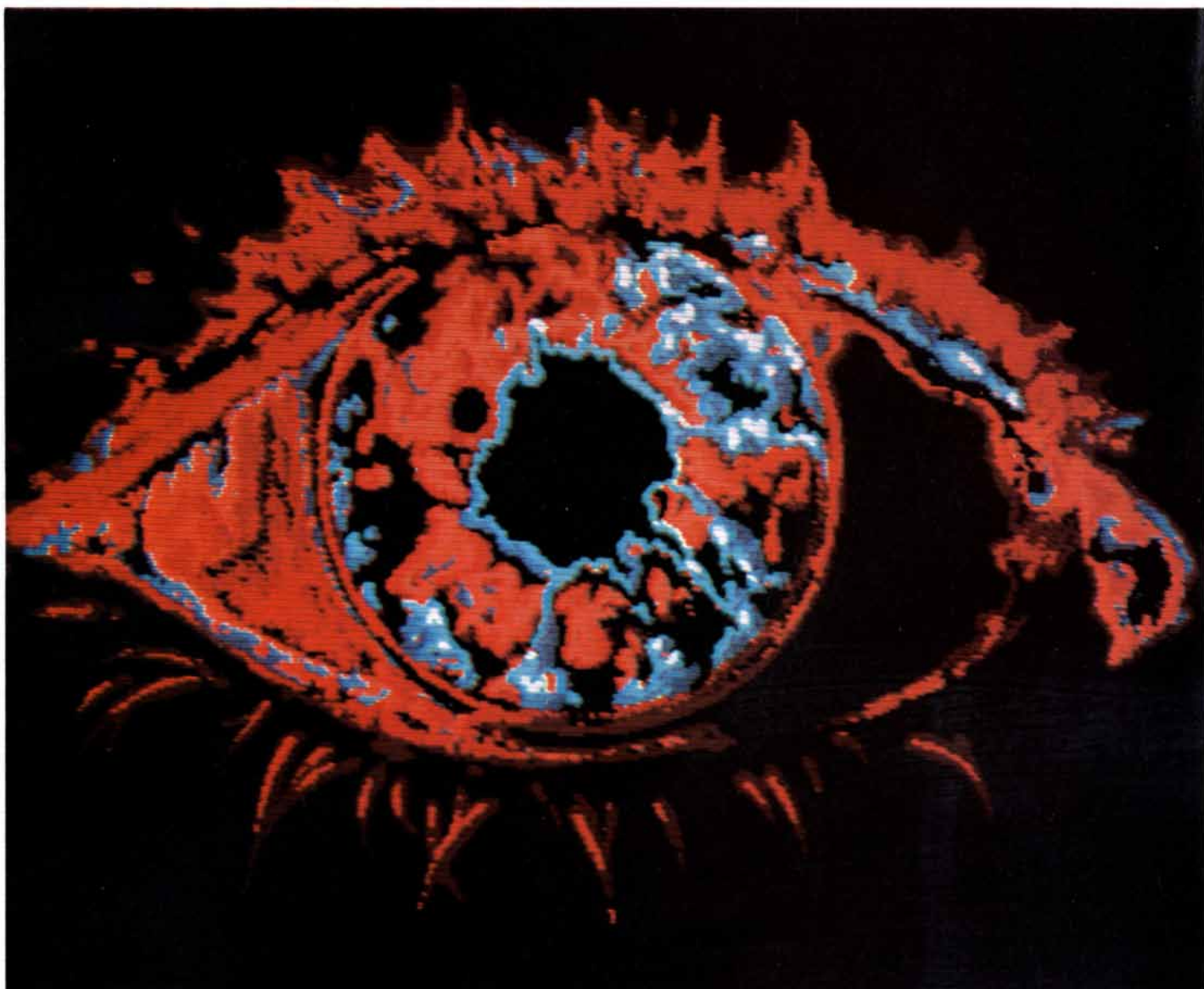
Transient Swimming

For transient swimming one of the most significant implications of the method of thrust generation is the shape of the silhouette seen from the side. When the propulsive element moves, it



PERIODIC SWIMMING AND MANEUVERING can be accomplished with almost any part of the body. This illustration shows the structures utilized for propulsion (color) by some periodic swimmers and maneuverers. Also shown are the range of speed in cruising (colored part of bar) and the range in sprinting (open part of bar); maneu-

verers tend to cruise at low speeds. Question marks indicate that the limits of performance are not known with precision. The surfperch can be either a periodic swimmer or a maneuverer: it employs the motion of the body and the caudal fin for sprinting and the oscillatory motion of the paired pectoral fins for cruising and maneuvering.



The human eye, greatest of natural sensors, is a key model for Hitachi electronic devices that translate environmental conditions into signals machines can act on.

SENSOR

Hitachi began giving the powers of perception to machines long ago. More than 50 years ago, in fact, with the development of a bimetal thermostat to control cooling temperatures in electric refrigerators back in 1928. The legacy: Electrical equipment capable of seeing, hearing and even touching as humans do, but with much greater acuteness and accuracy.

Electronic eyes, ears, nose and nerves

Today, the results of Hitachi research can be seen all around you. Automobile fuel injection systems with uniquely designed sensor feedback circuits to control air flow electronically. Voice-pattern recognition units and smoke sensors for office building security. Welding robots that use "wrist-mounted" sensors to detect changes in workpiece dimensions.

Our engineers have applied new semiconductor technology to pressure gauges, photocells and pickup tubes. They have reduced sensor size, yet increased sensitivity and control, while creating better materials and production processes that improve energy efficiency and ensure absolute quality.

In fact, we are constantly coming up with innovations and new applications. Most recently: The world's first MOS image sensor for much lighter, more compact video cameras with

exceptional solid-state color and clarity.

These are just a few of the ways in which Hitachi puts sensor technology to work for you. Developing practical tools that meet your needs...and those of professionals in manufacturing, medicine, and virtually every other field you can name.

The best of worlds is yet to come

Our vision of the future includes intelligent robots that learn through 3D optical sensors. Health detectors that monitor patients' life functions and report changes to computer-aided medical centers. Carbon dioxide sensors for regulating atmospheric conditions in agricultural complexes. Nutrient detectors that determine food freshness. And much, much more.

We'd like you to share in the benefits of our scientific research, covering the next generation of lasers, optical transmitters, liquid crystal displays and other electronic devices. For improved business efficiency. For a higher quality of life. Two goals we've pursued for 74 years as part of our commitment to a better world through electronics.

WE BELIEVE SENSORS ARE THE LINK BETWEEN HUMAN NEEDS AND TECHNOLOGY



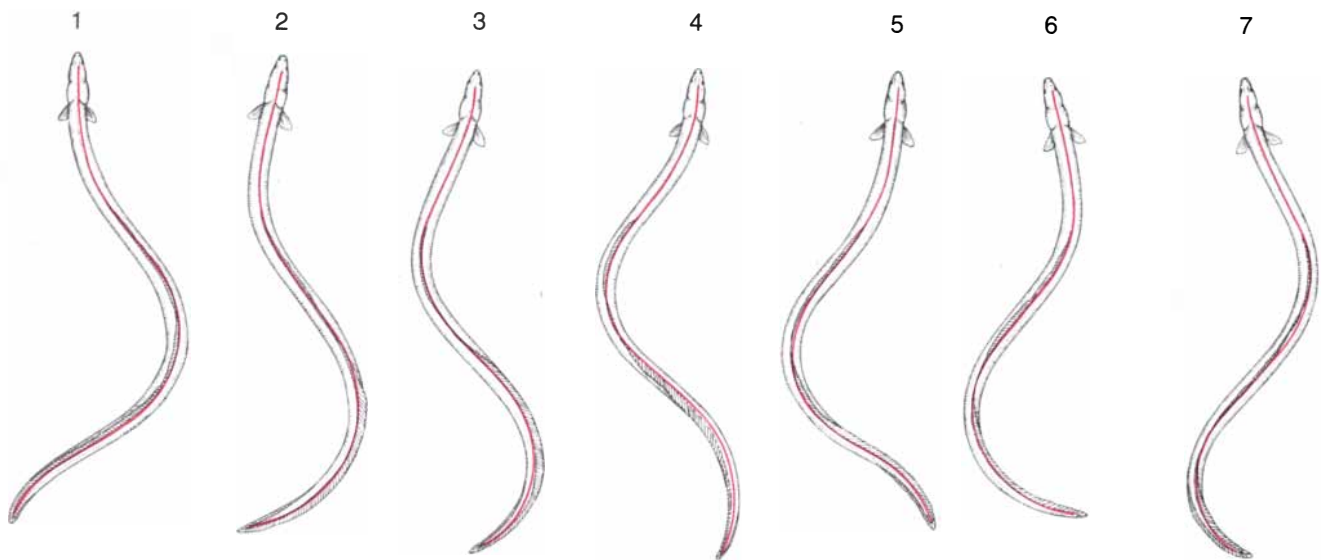
accelerates a quantity of water that is referred to as the added mass. The magnitude of the added mass is approximated by the mass of the water contained in a cylinder with a diameter equal to the depth of the propulsive element (measured from the upper edge of the body or fin to the lower edge) and a small length.

It follows that to maximize the thrust each propulsive element should be as deep as possible, which would yield a very deep silhouette for any fish that relies on the body and the caudal fin for propulsion. As it happens, a deep silhouette maximizes thrust only when each propulsive element makes an independent contribution to the thrust, that is,

when there is no significant interaction among the elements. In sustained swimming the action of one element has a considerable effect on the action of the other elements; the interaction has a profound influence on the silhouette that yields the best performance. In transient swimming, however, there is little interaction among elements, and a deep silhouette leads to an increase in thrust. The result is a very deep body and median fin, such as those of flatfishes and sculpins, fishes that are frequent transient swimmers.

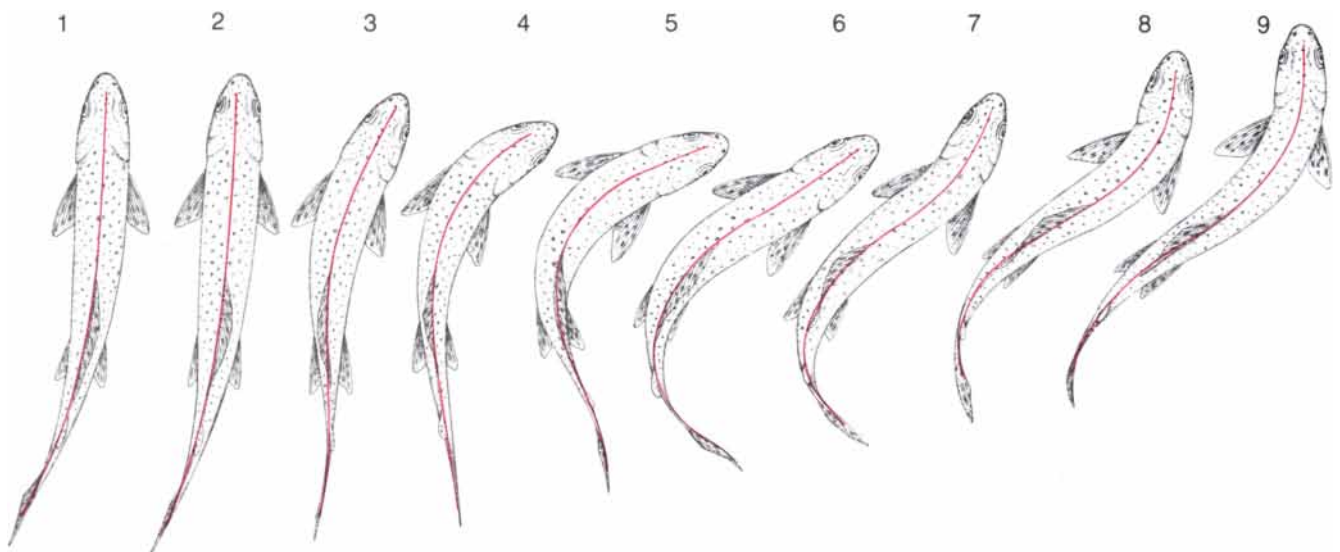
The level of performance made possible by a particular body form does not depend solely on the magnitude of the

thrust. On the contrary, performance depends on the net balance between the thrust and the resistance. As is the case with thrust, the factors that determine resistance in transient swimming are different from those that determine resistance in sustained swimming. In transient swimming the rate of acceleration is high and resistance comes mainly from inertia. The effect of inertia can be minimized by making the nonmuscle dead weight (the body weight contributed by tissues other than skeletal muscle) as small as possible. Indeed, the myotomal muscle in a fish specialized for transient swimming can contribute 60 percent of the total body mass.



CRUISING EEL bends into more than one complete wavelength as it moves through the water. In the two illustrations on this page the numbered figures at the left are based on frames of a motion picture made at short intervals. The panel at the right shows the position of

the centerline of the fish during the propulsive movements. In every type of body-and-caudal-fin swimming the propulsive wave travels along the body at a speed higher than the net speed of the fish with respect to the water. In periodic propulsion, such as that of the cruising



ACCELERATING TROUT bends its body into only part of a complete wavelength as it increases speed from a standing start. In such

transient swimming the overall propulsive movement is not repeated cyclically. Like most transient swimmers, the trout combines a fast

The analysis of transient swimming in the preceding paragraphs suggests there is an optimum design for fishes with a mode of life that relies heavily on quick starts. The design includes a body flexible enough to bend into a wave of large amplitude, a body and fins with a large area and a body that is mostly muscle. Although this would appear to be an advantageous combination, no fish has all these features. Nonlocomotor factors, in particular factors related to feeding, exert an influence. As a result the optimum design for transient swimming is not necessarily the best design for the overall welfare of the fish.

Rather than showing all the features

of the optimum design, many transient swimmers have a form in which one feature predominates. For example, the sculpin is a transient swimmer with a design that maximizes thrust. It has large dorsal and ventral fins that give the fish a deep silhouette along the length of its body. The design of the sculpin, however, does not yield the maximum proportion of myotomal muscle. The reason is that the sculpin's head is large and heavy, with a geometry that is valuable in feeding on bottom animals. As a result the nonmuscle dead weight cannot be reduced to the minimum and only 30 percent of the body mass of the sculpin is myotomal muscle.

The Pike

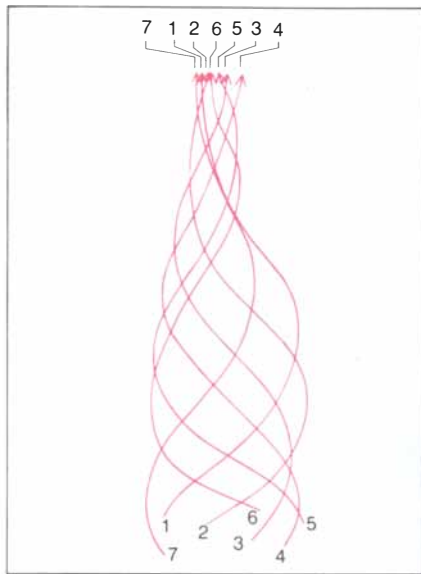
The design specifications of the pike, another acceleration specialist, result in low resistance. The body of the pike is from 55 to 60 percent muscle; the fish even has a thin skin. The minimizing of nonmuscle dead weight is not surprising in a predator that catches its prey by rapid acceleration. Yet the pike does not conform to the optimum design for transient swimming because its silhouette is deep only near the tail; near the head the silhouette is shallow.

Since a deep silhouette all along the body offers maximum thrust in a quick start, the shallowness of the pike's silhouette near the head does not appear to make sense for catching small prey. To ascertain what other factors influence the design of the pike several of my students at the University of Michigan and I compared the strike of the tiger muskie, a hybrid relative of the pike with a shape similar to that of the pike, with the strike of the trout, the bass and the rock bass.

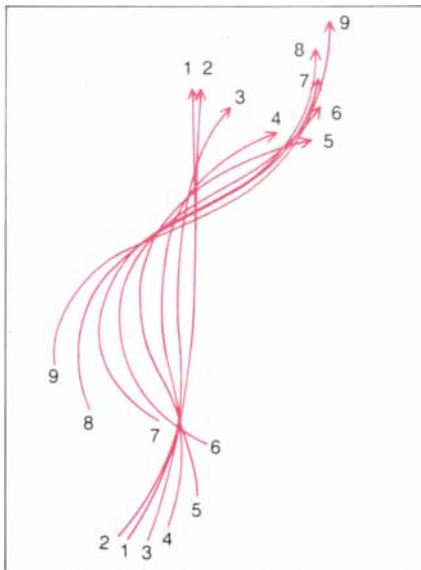
It was found that prey fish were much slower in responding to the muskie than they were in responding to the other predators, with the result that in 70 to 80 percent of the strikes the muskie caught its prey before the smaller fish responded by moving away. The prey were much quicker to evade the other predators: only about 30 percent of the strikes of the trout and the two kinds of bass were successful.

The disparity in the response threshold of the prey is due largely to the shape of the lateral cross section of the predator's body, which is the outline the prey responds to when the predator strikes. Trout and bass have a lateral cross section that resembles a vertically aligned ellipse. Fishes are extremely sensitive to that shape. The pike, however, has a lateral cross section more like a disk, because its dorsal fins end well behind the head. Thus in the body of the pike the optimum design for locomotion is compromised to accommodate sensory factors in the prey.

In sustained swimming the interaction



eel, the movements are cyclical. The undulatory movements of the eel were first described by Sir James Gray in the 1930's; much of the current work draws on Gray's observations.



start with a power turn. In transient swimming the propulsive movements are small and brief.

Science in the first person

THE ALFRED P. SLOAN
FOUNDATION SERIES

Jerome Bruner IN SEARCH OF MIND ESSAYS IN AUTOBIOGRAPHY

"For those who want to understand the current burst of interest in cognitive science...there is no better place to start than this book....It is a fascinating life story related by one of the most literate and imaginative thinkers of our time."

—Howard Gardner,
The New Republic

"An insider's guide to major developments in psychology and allied fields in the past 50 years."

—Maya Pines,
Washington Post Book World



Stanley Seligson

S.E. Luria A SLOT MACHINE, A BROKEN TEST TUBE AN AUTOBIOGRAPHY

A Nobel Prize-winner in Medicine/Physiology, "Luria manages to convey the excitement of science....The entire book is interesting in all of its many facets, not only because Luria

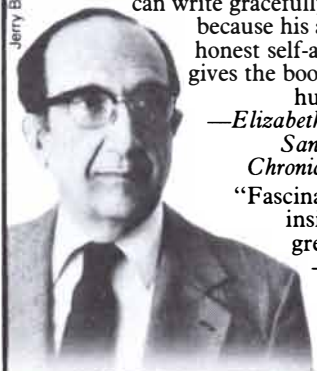
can write gracefully, but also because his attempt at honest self-assessment gives the book texture, humor, life"

—Elizabeth Wilhelm,
San Francisco Chronicle Review

"Fascinating: rare insight into a great spirit."

—Anthony Lewis,
New York Times

Jerry Bauer



NOW IN PAPERBACK

Hendrick B.G. Casimir HAPHAZARD REALITY:
Half a Century of Science
Freeman Dyson DISTURBING THE UNIVERSE
P.B. Medawar ADVICE TO A YOUNG SCIENTIST

At bookstores or call TOLL FREE
(800) 638-3030

Harper & Row



1817

**Your
family's
software
grows
on the
Peachtree.®**

And it couldn't be in better hands.

Only one software company so completely covers home, education and business.

Only one has behind it the resources of the world's largest independent producer of mainframe software, Management Science America, Inc. (MSA).

And only one offers you the most complete line for microcomputers. Peachtree Software®. The leader that's still leading. With 25 new products this season, 67 in all. With applications for IBM, Apple and most leading microcomputers.

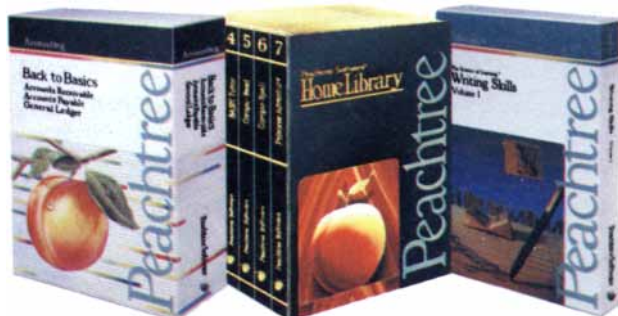
For instance: our new Home Library. A complete home package, including word processing, financial spread sheet, home accounting system, the basics of how to write your own programs, a game, and an educational bundle to improve reading and writing skills for all ages.

For instance: our new five-volume Writing Skills System. Created to correct common writing problems; teaches writing for all levels through the development of editing skills.

For instance: our new Back to Basics Accounting System. Perfect for a business conducted at home. For your PCjr™, Apple, Atari, Commodore or almost any leading microcomputer. Lets you set up a basic accounting system even if you have little or no previous accounting knowledge.

Whether it's for home, business or education, America's software grows on the Peachtree. Look for all our products wherever software is sold, or send us the coupon for a free brochure.

Your family's software grows on the Peachtree. Reach for it.



**America's Software
grows on the Peachtree.**

PCjr is a trademark of International Business Machines Corporation.
Peachtree and Peachtree Software are registered trademarks of Peachtree Software Incorporated, an MSA Company. © 1984



Peachtree Software

3445 Peachtree Road N.E.
Atlanta, GA 30326 • 1-800-554-8900

Please send me more information about Peachtree Software.
I'm interested in software for () business, () home, () education.

Name _____

Address _____

City _____ State _____ Zip _____

Phone _____

CA4

of the fish's body and the surrounding medium leads to optimum body and fin shapes quite different from those of the sculpin and the pike. In cruising and sprinting the propulsive movements are repeated cyclically. Because of the repeated movements, sustained swimming is also referred to as periodic propul-

sion. In cruising and sprinting the amplitude of the tail beat is smaller than it is in transient propulsion. The tail moves a distance that rarely exceeds 20 percent of the body length, and so it is possible for the body to be bent into a larger number of wavelengths.

In periodic propulsion the water ac-

celerated by a propulsive element is immediately affected by the action of the next element toward the rear of the fish. As we have seen, the rear elements travel faster than the forward ones, and the caudal inclination of the elements toward the rear is greater than the inclination of the elements toward the head. Therefore the effect of the rear propulsive element is to increase the magnitude of the acceleration given to the water by the element in front of it. In periodic propulsion the propulsive elements interact, and the last element at the tail (corresponding to the trailing edge of the fish) determines the net acceleration imparted to the water. In most fishes the movement of the trailing edge also determines the final added mass. Hence in thrust generation the trailing edge of the tail is the most crucial element. It follows that it is valuable for the tip of the tail to be as deep as possible.

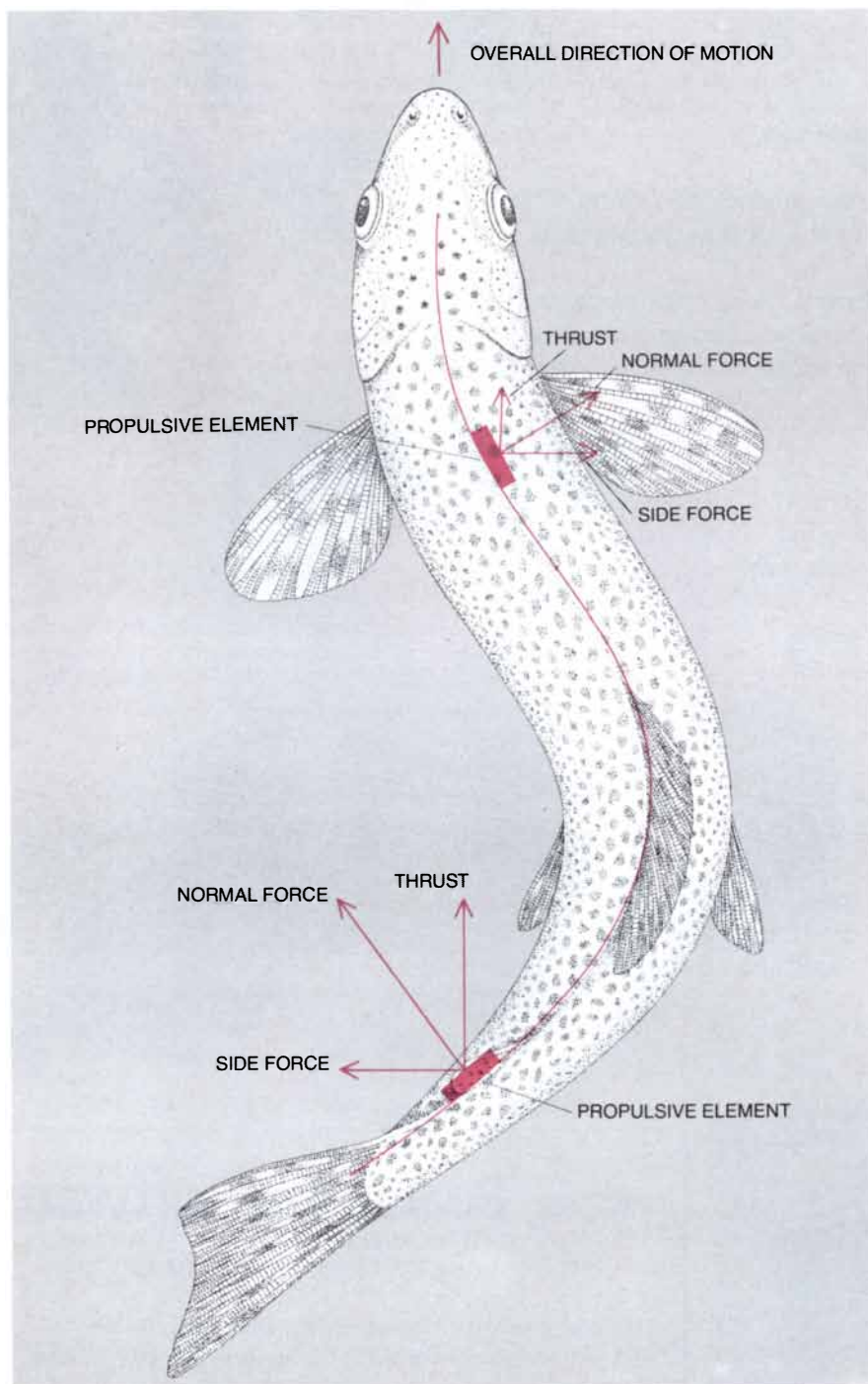
Because the action of the rear propulsive elements is of great significance in sustained swimming, it would appear that the optimum design for a fish that spends much time cruising would include a deep rear silhouette, perhaps something like the rear silhouette of the pike. There are several reasons, however, for this not being so. Indeed, it can be shown that among the optimum design features for periodic swimming is the scooping out of the body in front of the tail to form a narrow caudal peduncle: a slender stem to which the tail is attached. Lighthill calls such a tail design narrow necking and the design is a characteristic feature of fishes that spend their lives cruising.

Narrow Necking

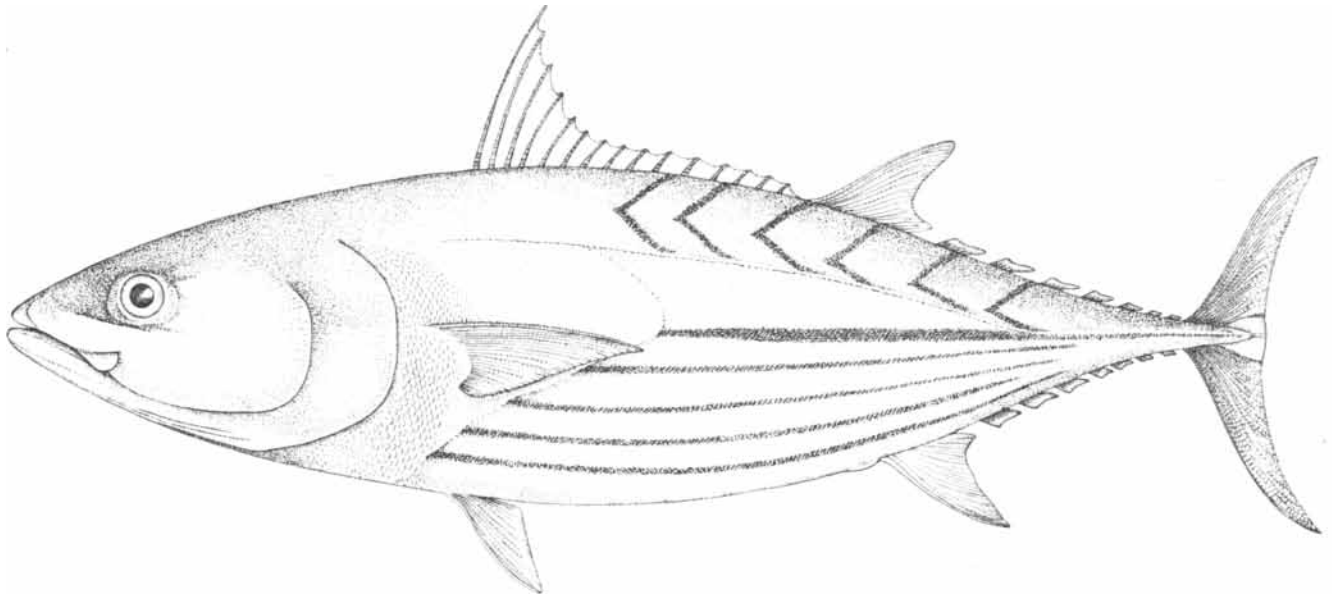
Why is narrow necking so valuable? One reason is related to the side force, the component of the reaction force that does not contribute to the forward motion of the fish but turns the body to the side. The side force tends to make the part of the body near the head recoil, or oscillate laterally. In periodic swimming the side force can lead to the waste of considerable energy. If all the propulsive elements were of equal depth, the side force would be greatest in the rear elements. With a decrease in the depth of the body in front of the tail the wasteful side force is reduced.

The lateral oscillation is reduced further by an increase in the mass of the body near the head. The resistance of the forward part of the body to the effect of the side force is also increased by a fin on the upper surface of the body, which helps to explain the presence of forward median fins in many aquatic animals.

Narrow necking also contributes to the lowering of resistance. The major source of resistance in sustained swimming, in contrast to the resistance in transient swimming, is drag that arises

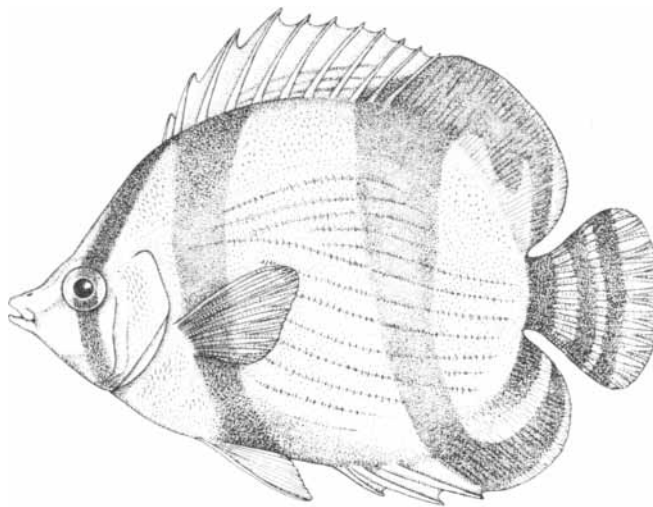


THRUST IS GENERATED by propulsive elements: small segments of the body. The forces operating on two propulsive elements are shown. As the propulsive wave passes, each element moves laterally and accelerates the water nearby. The element is inclined toward the tail, and so the water is accelerated toward the tail. The normal force, which is equal and opposite to the force exerted on the water, presses against the propulsive element. The normal force has two components: the side force is perpendicular to the overall motion of the fish and the thrust is parallel to the overall motion. The combined thrust from all the propulsive elements propels the fish. The magnitude of the thrust contributed by each element increases toward the tail.



SKIPJACK TUNA is a superior cruiser with a design that approximates the optimum for periodic swimming. It has a stiff body with a "streamlined" shape that is deepest about halfway between the head

and the tail. The deep, narrow caudal fin generates a strong thrust. The caudal fin is connected to the body by a slender peduncle. Such a design serves to maximize the thrust while reducing the drag force.



BANDED BUTTERFLY FISH has a design that approximates the optimum for low-speed maneuvering. The disk-shaped body is quite short, which facilitates rotating movements in the median vertical plane. The oscillating fins that provide the propulsive force are dis-

tributed all around the center of the body mass, and so small, precise thrusts can be delivered in any plane. Such a form is of considerable advantage to the fish in geometrically complex habitats such as the coral reef, where many specialists for low-speed maneuvering live.

from the viscosity of the water. The viscous drag force depends on the rate at which the fluid is distorted. The rate of distortion is greatest in the boundary layer: the thin layer of fluid immediately adjacent to the surface of any body moving through a fluid.

The viscous drag force is proportional to the square of the velocity and the surface area of the body. Propulsion that depends on flexing the body increases the viscous drag force because the motion of the propulsive elements increases their velocity with respect to the surrounding fluid (in comparison with the corresponding elements of a rigid body). In addition, the propulsive movements

modify the local flow patterns and increase the distortion of the fluid, which increases the frictional force.

Reducing Viscous Drag

As a result of such factors the drag on a self-propelled flexing object such as a fish can be greater at the tail by an order of magnitude than the drag on a rigid body in the corresponding position. If the drag is summed along the entire body, it is found that the average drag on the fish is from two to four times greater than the drag on a rigid body. Viscous drag is reduced if the area of the moving body is minimized. Moreover,

the reduction is particularly great if the area is reduced in the region in front of the tail, because it is there that the effect of body movement leads to the greatest increase in drag. The result is narrow necking. In addition a narrow tail section makes it possible for the forward part of the body to be more rigid and for the body to be fusiform ("streamlined"), which also decreases the drag.

The interaction of the propulsive elements in periodic swimming and the benefits associated with decreased viscous drag suggest that there is an optimum design for fishes that rely on sustained swimming. The design includes a stiff body attached by a slim caudal pe-

duncle to a deep, narrow tail. The body itself has a fusiform shape: it is deepest at a point that is between a third and a half of the distance from the head to the tail and narrows gently to the tail. Perhaps the best approximation of the optimum sustained-swimming design is the form of the tuna. A similar morphology is found in sharks, dolphins, whales and even in ichthyosaurs, a group of extinct swimming reptiles. All these animals show a specialization for fast, efficient cruising.

As with transient swimmers, there are deviations from the optimum locomotor design among fishes that live by cruising. The most notable deviations are observed in the sharks. Although most sharks depend heavily on cruising for their livelihood, only a few have a body shaped like the body of a tuna. The reason for the divergence is that in spite of the fact that both the shark and the tuna are cruising fishes, most sharks have a mode of swimming quite different from the tuna's. Indeed, it appears that the swimming movements common among sharks are more like those of the eel than they are like those of the tuna.

The body of the shark, however, is more fusiform than the body of the eel. In addition, whereas the eel has no significant median fins, the shark has several and they are sizable. The median fins on the dorsal surface of the body are particularly pronounced. There is generally a large forward dorsal fin and a somewhat smaller rear dorsal fin. The upper extension of the tail is also large. Between the three dorsal appendages there are substantial spaces.

The combination of the shark's swimming movements and the large gaps between the median fins is of great mechanical significance. The effect arises from the fact that any fin with a sharp rear edge trails a wake behind it. Furthermore, because of the periodic motion of sustained swimming the wake follows a sinusoidal path.

The Fins of the Shark

Consider the wake of the shark's fin in a frame of reference that has the same velocity as the fish and is moving in the direction the fish moves. In such a frame the wake will appear to be traveling downstream, or toward the tail of the fish. The velocity of the wake with respect to the fish will be equal to that of the fish when the fish is viewed by an observer in the normal frame of reference. The propulsive wave is also traveling toward the tail but, as we have seen, the velocity of the propulsive wave is greater than that of the fish. Since the propulsive wave travels faster than the wake, there is a phase difference between the two sinusoidal paths. If the fish is swimming at a steady pace, then the phase difference will be constant at any point that is downstream from the fin.

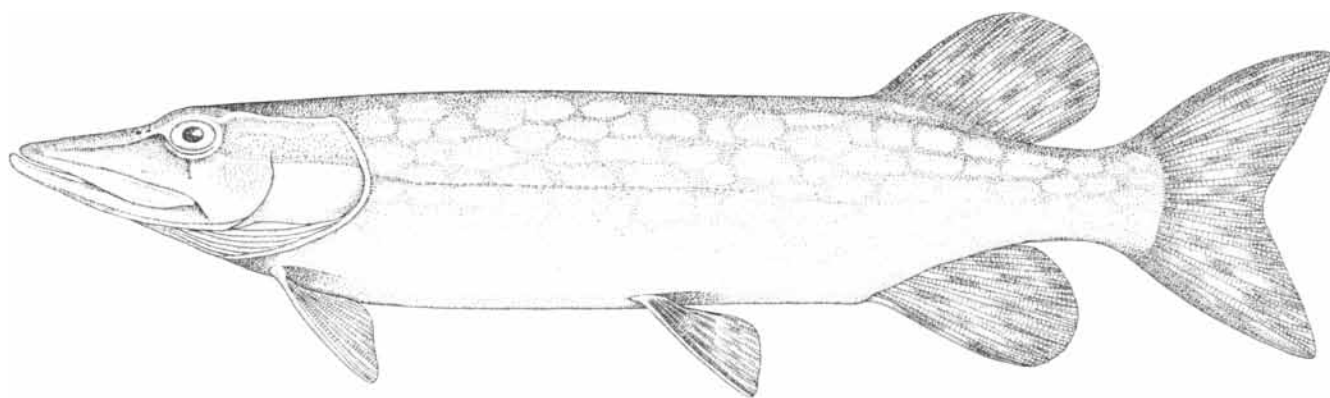
Next consider a second fin closer to the tail than the first. If at the second fin the phase difference between the propulsive wave and the wake has the right magnitude, the wake begins to move inward just as the second fin is moving outward. If that is the case, the thrust resulting from the motion of the second fin can be considerably increased. The

effect is roughly analogous to reaching out to push a swinging door just as the door is pushed from the other side.

As it happens, the minimum phase difference, or the difference in the position of the sinusoidal paths, needed to yield the thrust-enhancing effect is 90 degrees. With Raymond Keyes of Sea World in San Diego I studied six species of shark at the shark facility of Sea World to find out whether the phase difference between the trailing wake and the downstream fin is large enough for the thrust-enhancing interaction to take place. We found that all six species swim in such a way that the forward fin and the rear fin can interact to increase the thrust.

One reason sharks rely on thrust-enhancing mechanisms rather than on the specialized refinement of the tuna design is the material of which the shark's skeleton is composed. The skeleton of sharks is not bony but cartilaginous. Although the skeleton is in many instances reinforced with stronger, calcium-containing materials, the cartilaginous members cannot sustain as much bending as the bone found in most other fishes. This is one reason the few sharks that look like tunas cannot swim as fast as tunas can.

The differences in functional morphology between sharks and tunas reflects far-reaching differences in the ecology of the two groups of fishes. James F. Kitchell of the University of Wisconsin at Madison analyzed the pattern of energy utilization by tunas and concluded that they are "energy speculators." Tunas expend considerable energy swimming continuously at high



NORTHERN PIKE is a specialist for acceleration with a design that yields the minimum resistance. In transient swimming the resistance comes mostly from inertia. The inertia with respect to the magnitude of the propulsive force can be reduced by having the nonmuscle component of the body mass as small as possible: the pike has a body mass that is 60 percent muscle. The pike's long, slender body can

bend into a large-amplitude wave, which is advantageous in accelerating. The silhouette of a pike viewed from the side is deep near the tail, yielding considerable thrust in darting strikes at small prey fish. Near the head, however, the silhouette is shallow. The author has found that the rounded lateral cross section near the head aids the pike because prey fishes are comparatively insensitive to that shape.

speed over great distances searching for prey and breeding sites. The continuous high-speed swimming is facilitated by endothermy: internal regulation of body temperature. Conversely, continuous swimming and endothermy call for much energy in the form of food, hence tunas must search the ocean at a steady high speed.

Sharks: Energy Conservatives

Sharks, on the other hand, are much more conservative in the management of their energy accounts. Sharks are rarely endothermic. Indeed, their metabolic rate is low compared with the rates of most other fishes. Sharks often stop swimming and rest on the bottom. Their low energy requirements enable them to be opportunistic predators: by stopping and waiting they can take advantage of food sources that are unpredictable. Alternative patterns of energy acquisition and consumption such as those shown by tunas and sharks influence the form and behavior of organisms throughout the animal kingdom.

Undulatory swimming with the body and caudal fin together has been subjected to more intensive scrutiny than any other mode of fish swimming. Many fishes, however, rely on the oscillatory motion of short-based fins for propulsion, without any body motion. Such a mode of swimming is characteristic of fishes that rely on precise maneuvers at low speed to get food and to hide in small spaces. Many of the tropical fishes living in coral reefs show specialization for maneuvering.

Oscillatory swimming is not as well

understood as undulatory swimming but it is currently being examined by Robert W. Blake of the University of British Columbia. Much of the work concerns the two distinct mechanisms that underlie the operation of oscillatory fins. The principles could be called the oar principle and the wing principle. Both types of short-based fin are found in pairs on the sides of the body. The paired fins generally operate symmetrically. The oscillatory motions of the two types, however, are different.

Fins that are like oars move back and forth horizontally much as the oars of a small boat do, alternating the power stroke and the recovery stroke. During the power stroke the fin moves in the direction opposite to the direction of overall motion. The fin blade is broadside to the fish's direction of motion and moves faster than the fish's body. During the recovery stroke the fin moves in the same direction as the body. The power stroke generates a substantial drag force that can be oriented to thrust the fish in the direction it chooses. In the recovery stroke no thrust is generated and the fin blade adds to the resistance that retards the motion of the fish through the water. The resistance contributed by the fin in the recovery is reduced by collapsing the fin blade and twisting it parallel to the water flow.

The shape of the fin has considerable influence on how much thrust the blade can be made to yield. Imagine the fin divided into narrow strips like the propulsive elements employed in the analysis of undulatory propulsion. The contribution of each blade element to the thrust is proportional to the area of the

element and the square of its relative velocity (the velocity measured with respect to the body of the fish).

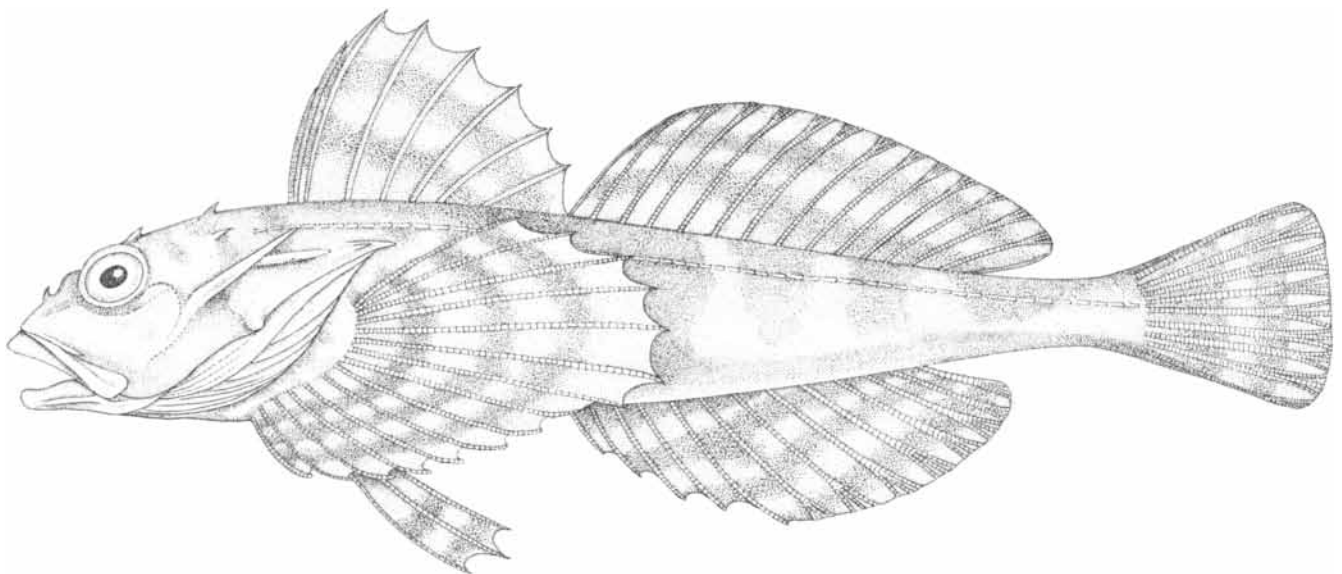
The blade elements farthest from the body (the ones at the end of the fin blade) traverse the greatest distance during the power stroke. Therefore such elements make the greatest contribution to the thrust. Indeed, elements close to the base of the fin sometimes move so slowly that they actually generate resistance rather than thrust. Hence the optimum shape for a fin that operates like an oar is a triangle with the apex at the fin base.

Fins that Are like Wings

Whereas a rowboat is propelled by a drag force, the wing of an airplane raises the craft by means of a lifting force. Because of the difference in the propulsive force, there are differences in design between fins that operate as oars do and fins that operate as wings do. When an oarlike fin moves, thrust is generated in the same plane as the plane of motion of the fin blade. Lift, on the other hand, is generated in a plane perpendicular to the direction of motion: when an airplane travels through the air, the lift is vertical although the wing is moving horizontally.

Therefore in order to propel the fish forward a lifting fin must move up and down in a plane that is roughly perpendicular to the long axis of the fish's body. Since the lift is generated at right angles to the plane of the fin blade, no recovery stroke is necessary. The fins generate lift on the upstroke and on the downstroke.

As is the case for drag, lift is propor-



SCULPIN is a specialist for acceleration with a design that yields the maximum thrust. The silhouette of a sculpin viewed from the side is quite deep. Fins on the upper and lower surfaces increase the area of the silhouette, thereby yielding the greatest thrust in transient swimming. The body is long and flexible, so that the fish can bend into a large-amplitude wave. The nonmuscle mass of the sculpin, however,

is not small. The fish's body is only about 30 percent muscle, which implies that in fast starts the propulsive force is small compared with the inertial resistance. One reason for the increased inertia is the form of the head. The head is large and heavy, with a geometry that is advantageous in feeding on bottom animals. Thus the optimum design for transient swimming is compromised by nonlocomotor factors.

tional to the area of the fin blade and the square of the velocity of the blade. The lift force, however, can be an order of magnitude greater than the drag force generated by a fin blade with the same area. As a result of such factors the thrust yielded by lift-based fins is larger and more continuous than the thrust yielded by drag-based fins. Hence the fastest oscillatory swimmers have fins that operate like wings; these include the surfperch, the wrasses and the ocean sunfish. In contrast to oarlike fins, wing-like fins are not limited to placement on the sides of the body; they can also be on the dorsal and ventral surfaces.

The shape of a fin that generates lift tends to be different from the shape of a fin that generates drag. One reason is the need to minimize crossflow, which is the flow around the tip of the fin. The same pattern is observed in air flowing around the tip of an airplane wing. In both instances crossflow leads to a decrease in lift and an increase in drag.

Airplane designers minimize crossflow by making the tip of the wing as narrow as possible. This is generally done by tapering the wing from the base to the tip. A fin cannot be tapered along its entire length because the fin must be narrow at the base in order to oscillate freely. Therefore lifting fins tend to be diamond-shaped, with a taper at the inboard end and at the outboard end.

Oscillating fins and long-based undulatory fins serve for slow swimming and precise maneuvering in structurally complex habitats such as weed beds and coral reefs. In such environments fishes hide in small spaces and pluck food from surfaces where it is growing or has settled. The surfaces are oriented in all directions, and in order to be able to put its mouth in the right place the fish must be capable of delivering small propulsive thrusts with considerable precision.

This implies that the fins should be flexible and should have the capacity to bend and rotate precisely in several directions. In addition, for slow swimming and delicate maneuvering some overall body forms appear to be better than others. Fishes that are successful in geometrically complex environments tend to have laterally flattened bodies with the outline of a disk or a diamond.

Such shapes offer the least resistance to rotation in the median vertical plane of the body. Moreover, many successful reef fishes have top and bottom fins that extend over the tapering rear segment of the body. There are paired pectoral fins high on the body and paired pelvic fins low on the body. Thus the propulsive appendages are distributed around the center of mass of the body and thrust can be directed in any plane. The butterfly fish is an example of a reef fish with such an optimum design for maneuvering. Fishes with that morphology tend to displace other species in habitats where

precise maneuvering is at a premium.

My analysis of the three basic locomotor designs—for transient swimming, for sustained swimming and for maneuvering—suggests a fundamental conclusion: that it is not possible to combine all the optimum features for the different types of swimming in one fish. I call this the principle of the mutual exclusion of optimum designs. Theoretical and experimental work shows that the design elements resulting in the best transient-swimming performance and the elements resulting in the best periodic-swimming performance are mutually exclusive. There are also good reasons to think the optimum design for maneuvering excludes the elements that favor high performance in accelerating or in sprinting and cruising.

The butterfly fish, a maneuvering specialist, could not perform optimally in transient swimming and periodic swimming. During periodic propulsion the large area of its body and fins exacts a high price in increased drag. The shortness of the body leaves little room for muscle and therefore there is considerable dead weight, which impairs performance in a quick start. Moreover, with this type of body the large-amplitude movements needed for rapid acceleration are difficult to execute.

Conversely, fishes that are specialists in body-and-caudal-fin swimming are not particularly adept at slow swimming and maneuvering. Periodic swimmers have stiff fins that serve as keels for stability and hydroplanes for regulating the depth of the fish in the water; such stiff fins are of little use for delivering the small, precise thrusts needed in low-speed maneuvering. The elongated body of the transient-swimming specialist reduces its ability to turn in habitats with a complex geometry.

The Functional-Morphology Plane

Therefore it appears that there are three basic optimum designs for swimming and that the designs are mutually exclusive. It would be foolish, however, to conclude that all fishes should conform to one of the three basic designs. Even the most perfunctory examination of the shapes of fishes shows that most of them have locomotor designs with a combination of the design elements of the specialists. Hence the majority of fishes are locomotor generalists rather than locomotor specialists.

Such generalists clearly perform better than any specialist in the two broad types of swimming the specialist sacrifices to achieve high performance. No generalist, however, can perform as well as a specialist in the specialist's domain. Therefore in spite of the fact that few fishes approximate the optimum design for a particular swimming function the principle of the three basic designs is

not invalidated. Instead the three fundamental designs should be regarded as defining a locomotor functional-morphology plane with the shape of a triangle.

Most fishes have a position on the functional-morphology plane, with the position depending on the particular combination of specialized design elements each fish shows. Some fishes, however, cannot be put on the plane. Among them are fishes with modes of life in which swimming has a secondary role, such as the anglerfish, which lives deep in the ocean and relies on mouth suction to catch its prey.

The Qualities of the Generalists

Straight line segments drawn across the triangular plane, from the specialists at the corners to the generalists in the middle, pick out groups of fishes with swimming qualities arranged in a continuum that is based on differences in the resources exploited by the fishes. One such pattern is shown in the success rate of the strike at prey. The tuna, at one corner of the triangle, catches from 10 to 15 percent of the fish it strikes at. The reason is that the specialized design of the tuna, which is excellent for cruising, limits acceleration and maneuverability. By cruising widely at high speed, however, the tuna can increase the number of prey it encounters and thereby increase the number of strikes it makes.

As we have seen, fishes shaped like the pike, which are at another corner of the triangle, catch from 70 to 80 percent of the fish they strike at. Because the pike is not able to cruise, however, it must wait for prey, which limits the number of prey it encounters and the number of strikes it can make. Fishes such as the trout and the bass, which are intermediate in form between the pike and the tuna, are also intermediate in the rate of successful strikes. Such generalists eventually catch from 40 to 50 percent of the fish they attack, and because they are generalists, they can also cruise looking for prey. Their compromises in design open up feeding opportunities that are closed to the specialists.

The biomechanical approach to the biology of fishes has thrown light on aspects of the animals' lives that could hardly have been illuminated in any other way. As a result it is becoming possible to correlate precise measurements of performance in the water with the fish's way of swimming and its way of life. One hallmark of a successful scientific model is that it leads to new knowledge that would have been overlooked in the absence of the model. The significance of hydromechanical models in understanding the lives of aquatic animals is an example of such success. In a general way it shows the role biomechanics can have in elucidating fundamental biological puzzles.



RENAULT ALLIANCE

It was a long road from the concept stage to reality. But the achievement is clear: Renault Alliance is a success. A success in making European technology affordable. In turning pedestal seats and independent suspension into the best, most comfortable, ride ratings in its class.* A success in designing electronic fuel injection to deliver **52** EST HWY, **38** EPA EST MPG** *Built in America.*

So successful in bringing it all together for **\$5,959**†, it became the best-selling new American-built car line launched in the 1983 model year. Take it for a ride. Like nine out of ten owners who said they would buy another,†† you're sure to make a successful decision.

SUCCESS



Alliance 2-door

RENAULT

THE ONE TO WATCH

*1983 New Car Buyers Study conducted by Factline, Inc., for Newsweek. Ratings by individual car owners. **Use for comparison. Your mileage may vary with speed, trip length, weather. Actual highway and CA figures lower. †Manufacturer's suggested retail price for 2-door. Tax, license, destination charges, optional or regional equipment extra. ††Based on June 1983 Alliance Owners Poll by Popular Mechanics. Built by American Motors. Safety belts save lives.