predation pressure on lower levels of the trophic web, so that species that have traditionally been given a low commercial value have increased in abundance and are all that is available. The sand eel illustrates this well. Until the early 1970s there was no significant fishery for sand eels in the North Sea. The growing demands for fish meal, generated by the poultry and pig production industries, created a market for previously unused species such as sand eels. Coupled with reduced catches of higher-valued species such as herring and cod, this stimulated fishermen to focus on sand eels and this, together with the continued sustained high levels of effort on the predators of sand eels is hastening the demise of the whole system. There have also been serious consequences for the sea bird populations that have suffered a number of years with little or no fledging of young.

See also

Benthic Organisms Overview. Coral Reef Fishes. Fisheries Overview. Fishery Management. Gelatinous Zooplankton. Large Marine Ecosystems. Mesopelagic Fishes. Pelagic Fishes. Plankton. Seabird Foraging Ecology. Upwelling Ecosystems.

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FISH HEARING, LATERAL LINES

A. N. Popper and D. M. Higgs,
University of Maryland, MD, USA

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Introduction

Fishes, like other vertebrates, have a variety of different sensory systems for gathering information from the world around them. Each sensory system provides information about certain types of signals, and all of this information is used to inform the animal about its environment.

Although each of the sensory systems may have some overlap in providing information about a particular stimulus (e.g. an animal might see and hear a predator), one or another sensory system may be most appropriate to serve an animal in a particular environment or condition. Thus, for example, visual signals are most useful when a fish is close to the source of the signal, in daylight, and the water is clear. Chemical signals travel slowly in water and diffuse in haphazard directions, and so they are generally only effective over short distances. Acoustic signals have a unique advantage in that they travel very rapidly in water and are not interfered with by low light levels or murkiness of the water. Acoustic signals also travel great distances without decreasing in intensity, and this provides the potential for two animals that are some distance apart to communicate quickly.

Since sound is potentially such a good source of information, fishes have evolved several mechanisms to detect sounds, and many species use sound for communication between members of the same species. Indeed, it is very possible that the vertebrate ability to detect sound arose in fish ancestors in order for these animals to hear nonbiological as well as biological sounds in their environment. Thus, the most primitive vertebrates may have evolved hearing in order to detect sounds that are produced by waves breaking on the shore, water movement around reefs, or the swimming sounds produced by predators. It was probably only later in evolution that fish (and the later evolving terrestrial vertebrates) evolved the ability to communicate with one another using sounds.

Fishes have two systems for detection of sound and hydrodynamic signals (water motion). The better known of these is the ear, which operates very much like the ears of other vertebrates. The second system is the lateral line, which consists of a series of receptors along the body of the fish both in canals and on the surface. Together, the two systems are known as the octavolateralis system. Although it was thought until quite recently that the two systems are related in embryonic origin, nervous innervation and function, it is now clear that the two systems probably evolved independently of one another, though with a common ancestral structure that included the one feature common to the two systems – the sensory hair cell.

Fish Hearing

What do Fish Hear?

It is possible to ask fish 'what they hear' by using behavioral methods to train fish to respond to the presence of a sound. These classical or operant conditioning paradigms are very similar to those used to train other animals. Using these methods, it is possible to determine the frequencies and intensities of sounds that a fish can detect by changing the signal parameters and seeing which signals the fish responds to and which they do not.

Hearing capabilities have been determined for about 75 species of fish (of the more than 25 000 extant species). **Figure 1** shows hearing capabilities of several species to illustrate the range and intensities of sound that different species can detect. By way of comparison, a young and normal human can generally detect sounds from 20 Hertz (Hz = cycles s^{-1}) to almost 20 000 Hz, which means that humans have a much wider hearing range than most fish, although sensitivity is not much better than the best hearing fish at low frequencies.

The goldfish is one of the most sensitive of all fish species and can detect sounds from below 50 Hz to about 3000 Hz. In contrast, other species such as tuna and salmon, only hear to several hundred Hertz and their sensitivity (lowest sound they can hear) is much poorer than the goldfish. Fish that hear particularly well, such as the goldfish, are called 'hearing specialists' since they have special structures, described below, that enhance their hearing capabilities. Other fishes, such as the salmon, are often called 'hearing generalists' since they have no special adaptation for hearing. Although these are data for a small proportion of all of the extant fish species, it appears that most fish fall into the 'hearing generalist' category, and this certainly includes most of the more common food fishes such as cod, haddock, trout, salmon, etc.

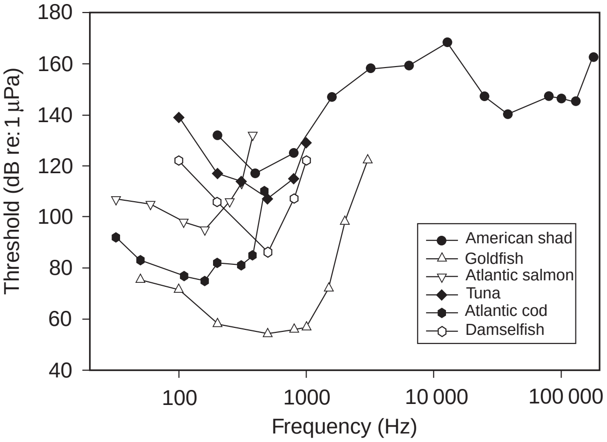

Figure 1 Hearing capabilities of representative teleost fishes measured using behavioral methods. The horizontal axis shows different frequencies and the vertical axis shows best sensitivity at each frequency. The widest hearing bandwidth has been shown for the American shad (*Alosa sapidissima*, Order Clupeiformes). Of the fishes shown, the most sensitive, in terms of detecting the lowest level sounds, is the goldfish (*Carassius auratus*). This fish can detect sounds from below 50 Hz to about 3 000 Hz and represents the hearing capabilities of many of the fishes that have specialized adaptations for sound detection. The goldfish also has a bandwidth that is typical of most hearing specialists, although the American shad clearly has the widest bandwidth of any fish studied to date. The Atlantic cod (*Gadus morhua*) also has low sensitivity at lower frequencies, its hearing bandwidth is not as great as that of the goldfish. The Atlantic salmon (*Salmo salar*) can only detect sounds to about 500 Hz, although recent studies have shown that it can also detect infrasound, signals to well below 30 Hz.

Of all fishes, those with by far the widest hearing range are some of the alewifes and shads (all members of the genus *Alosa*). These fishes have been shown to detect sounds from below 100 Hz to over 180 000 Hz, a range that is only reached by a few mammals such as some bats and dolphins. Although hearing in these fishes is not yet well understood, it has been suggested that they have evolved high frequency hearing in order to detect the echolocation sounds of one of their major predators, the dolphins.

In addition to being able to detect sounds, all vertebrates must be able to discriminate between sounds of different frequencies and intensities, detect the presence of a biological meaningful sound in the presence of biological and nonbiological noises, and determine the direction of a sound source. These capabilities are necessary if an animal is to be able to discriminate between different types of sound sources by their acoustic characteristics, and know where a sound is coming from in order either to escape a predator or find the sound source. Thus, it is not surprising that fish are able to perform all of these auditory tasks. Although they do not discriminate or localize sounds as well as mammals, the capabilities of fishes are sufficient to give them a good deal of information from acoustic signals.

How do Fish Hear?

Although fish have no external structures for hearing, as are found in many terrestrial vertebrates, they do have an inner ear which is very similar in structure and function to the inner ear of terrestrial vertebrates (**Figure 2**). Unlike terrestrial vertebrates, which require external structures to gather sound waves and change the impedance to match that of the fluid-filled inner ear, sound gets directly to the fish ear since the fish's body is the same density as the water. As a consequence, the fish ear, and the rest of the body, moves with the sound field. Although this might result in the fish not detecting the sound, the ear also contains very dense structures, the otoliths, which move at a different amplitude and phase from the rest of the body. This provides the mechanism by which fish hear.

The ear of a fish (**Figure 2**) has three semicircular canals that are involved in determining the angular movements of the fish. The ear also has three otolith organs, the saccule, lagena and utricle, that are involved in both determining the position of the fish relative to gravity and detection of sound. Each of the otolith organs contains an otolith that lies in close proximity to a sensory epithelium.

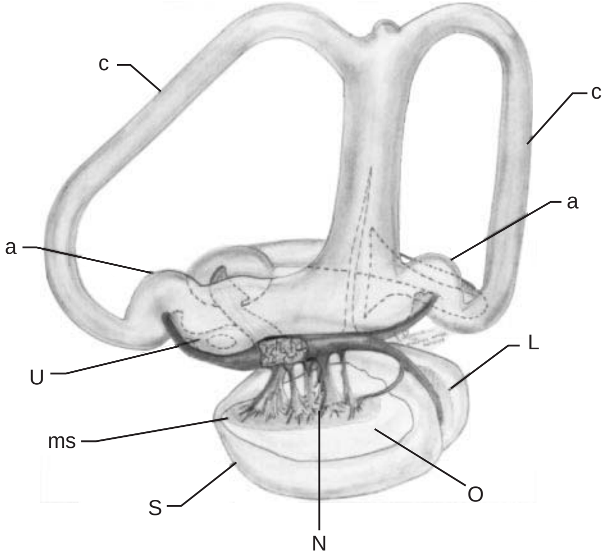

Figure 2 Drawing of the right ear of the Atlantic salmon (*Salmo salmo*). Anterior is to the left and dorsal to the top. The figure shows the three semicircular canals (c) and their sensory regions, the ampullae (a). The three otolithic organs, the utricle (U), saccule (S), and lagena (L) each have a single otolith (O) and sensory epithelium (best seen in the saccule, ms). The ear is innervated by the eighth cranial nerve (N). Redrawn from Retzius (1881) *Das Gehörorgan der Wirbelthiere*, vol. I. Stockholm: Samson and Wallin.

The sensory epithelium in fish contains mechanoreceptive sensory hair cells that are virtually the same as those found in the mechanoreceptive cells of the lateral line (see below) and in the inner ear of terrestrial vertebrates. All parts of the ear have the same kind of cell to detect movement, whether it be sound or of the head relative to gravity.

The sensory hair cells (**Figure 3**) are not very different from other epithelial cells of the body, except that on their apical (top) ends they have a set of cilia (sometimes called 'hairs,' hence the name of the cell) that project into the space above the epithelium and contact the otolith. Each cell has many cilia. Generally these are graded in size, with the longest being at one end of the ciliary bundle. The sensory hair cell responds to bending of the ciliary bundle by a change in its electrical potential. This in turn, causes release of chemical signals (neurotransmitters) which excite neurons of the eighth cranial nerve which innervate the hair cells. These neurons then send signals to the brain to indicate detection of a signal.

Bending of the ciliary bundles results from the relative motion between the sensory epithelium (and the fish's body) and the overlying otolith. There is evidence suggesting that the motion of the otolith relative to the body of the fish depends on the direction of the sound source. Since the sensory hair cells are responsive to bending in only certain directions, they can detect the direction of motion of the otolith and provide the fish with information about the direction, relative to the fish, of a sound source.

Why do Fish Hear?

Fish use information from sound stimuli for many reasons but perhaps the most well studied is to detect sounds produced by other fish, and particularly other fish of the same species. Many species of fish make and use sounds for communication. These sounds are generally pulses or short bursts of signal that range in frequency from below 30 Hz to above 500 Hz. The exact frequency range and pattern of the sound varies by species, and sometimes even within species, where different sounds may be used for different functions.

The sounds are produced in a variety of different ways, none of which involves movement of air across a membrane, as happens in terrestrial

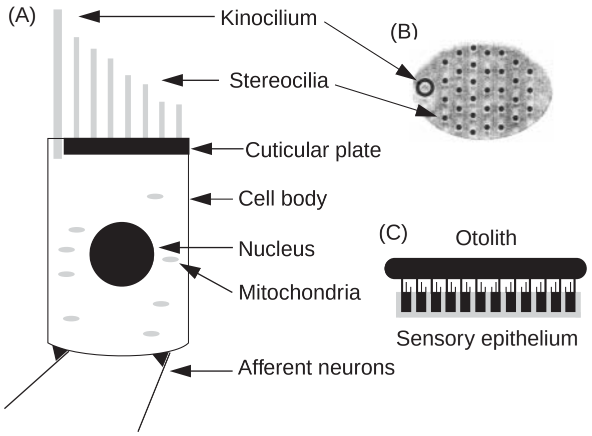

Figure 3 Schematic drawing of a sensory hair cell typical of those found in the ear and lateral line of fishes, and the ears of other vertebrates. (A) Side view of a sensory hair cell showing the apically located kinocilium and stereocilia (collectively called the ciliary bundle). These structures penetrate the apical cell membrane. The kinocilium terminates in basal bodies in the cytoplasm (not shown) while the stereocilia terminate in the dense cuticular plate. Other components of the sensory hair cell are represented by the nucleus and mitochondria, but other organelles found in typical epithelial cells are also found in hair cells. The hair cell is typically innervated by afferent neurons of the eighth cranial nerve that carry information from the cell to the brain. Many cells may also have efferent innervation (not shown), which is thought to carry signals from the brain to the hair cell, which modulate their responses to signals. Each cell has a single kinocilium and many stereocilia. Typically, the stereo cilia are graded in height, with the longest lying closest to the kinocilium. (B) Top view of the apical membrane of the sensory hair cell showing the eccentric position of the kinocilium and the rows of stereocilia. The sensory hair cell is stimulated when the ciliary bundle is bent. Bending of the ciliary bundle in the direction directly from the kinocilium to the stereocilia causes maximum response of the sensory cell, whereas bending in the opposite direction results in least response. Bending in other directions causes a response proportional to a cosine function of the direction relative to the axis of maximum stimulation of the sensory cell. (C) Side view of the sensory epithelium with sensory hair cells and the overlying otolith a thin otolith membrane lies between the otolith and epithelium to keep the two structures next to one another. Relative motion between the otolith and the sensory epithelium in a sound field, resulting from their very different masses, results in bending of the ciliary bundle. Since the hair cells on different epithelial regions are oriented with their kinocilium in different directions (as shown here), motion of the otolith in different directions relative to the sensory cells will give different response levels from different hair cell groups. This information can be used by the fish to tell sound source direction.

animals. Sounds in some species are produced by two bony structures hitting or rubbing against one another. In other cases, as in the well-known system of the toadfish (*Opsanus tau*), there are special muscles located on the swim bladder, a bubble of air in the abdominal cavity. These muscles contract at up to several hundred times per second and produce a sound which is amplified by the air in the swim bladder. In still other cases, such as several marine catfish (e.g. *Arius felis*), a muscle from the skull contracts and pulls on another bone which then hits the swim bladder, thereby producing sounds.

Fish sounds are used in a variety of different behavioral situations. The toadfish has a repertoire of two different sound types. One sound, which is generally pulsed, is made by both males and females year-round. A second, long, moan-like sound, called the boat whistle, is produced only by males during the breeding season. This signal, which sounds very much like a low-frequency boat horn, is used to attract females to the male's nest for breeding purposes. Sounds produced by some species of squirrelfish (Holocentridae) are used to warn of potential enemies in the vicinity, whereas damselfish (Pomacentridae) males produce sounds to try and scare potential predators away from a nest.

Although many species of fish can make sounds, and presumably use the sounds for communication, this has been hard to study for several reasons. Often, fish in a tank will not make sounds, and even when they do the tank walls tend to distort the sounds so badly that the sounds are abnormal. When studying fish acoustic communication in the open waters, such as on a reef, it is often hard for divers to hear sounds since humans, unlike fish and marine mammals, are not adapted to easily detect, or determine the location of, sound under water. Thus, even if divers hear a sound, they are not able to tell which fish is making the sound (fish generally have no movements associated with sound production). It is possible to use underwater microphones, called hydrophones, to listen to fish, but these are generally not directional and so it is still not easy to tell which individual fish is making a sound.

Adaptations for Improvement of Hearing

As shown in **Figure 1**, some fish are hearing specialists. Although it is still not clear how the American shad and other related species hear very high frequency sounds (ultrasound), it is clear that hearing specialists, such as the goldfish, have special adaptations that improve hearing compared to other fishes.

Most species of fish detect sounds by detecting relative motion between the otoliths and the sensory hair cells. However, other fishes, most notably the hearing specialists, also detect sounds using the air-filled swim bladder in the abdominal cavity. The swim bladder is used for a variety of functions in fish. It probably evolved as a mechanism to maintain buoyancy in the water column. In effect, fish can adjust the volume of gas in the swim bladder and make themselves neutrally buoyant at any depth in the water. In this way, they do not have to expend extra energy to maintain their vertical position.

The other two roles of the swim bladder are in sound production and hearing. In sound production, the air in the swim bladder is energized by the sound-producing structures, and serves as a radiator of the sound. Because it is filled with air, the swim bladder has a very different density from the rest of the fish body. Thus, in the presence of sound the gas starts to vibrate in response to some pressure changes. This is capable of re-radiating sound and is potentially able to stimulate the inner ear by moving the otolith relative to the sensory epithelium. However, in hearing generalists the swim bladder is quite far from the ear, and any re-radiated sound attenuates a great deal before it reaches the ear. Thus, these species probably do not detect these sounds. There is some evidence to suggest that fishes that use the swim bladder for sound detection hear a wider range of sounds, and sounds of lower intensity, than fishes that cannot use the signals re-radiated from the swim bladder.

Hearing specialists always have some kind of acoustic coupling between the swim bladder and the inner ear to reduce attenuation and assure that the signal from the swim bladder gets to the ear. In the goldfish and its relatives (e.g. catfish), there is a series of bones, the Weberian ossicles, which connect the swim bladder to the ear. When the walls of the swim bladder vibrate in a sound field, the ossicles move and carry the sound directly to the inner ear. Removal of the swim bladder or ossicles in these fishes results in a drastic loss of hearing range and sensitivity.

Other fishes have evolved a number of different strategies to enhance hearing. Most notably, the swim bladder often has anterior projections that actually contact one of the otolith organs. In this way, the motion of the swim bladder walls directly couples to the inner ear of these species. In thealewifes, development of these anterior projections coincides with a dramatic increase in the ability of these fish to detect and avoid their predators, strongly suggesting the natural function of this specialization. Finally, some species have extra air bubbles next to the ear. For example, in the bubble-nest builders, a bubble of air, analogous to the swim bladder, is trapped in the mouth near the ear. Removal of this air-bubble can make the fish temporarily deaf to certain frequencies of sounds.

The Lateral Line

The lateral line has been one of the most enigmatic of all vertebrate sensory systems. Over the past 150 years various investigators have suggested that the lateral line is involved in hearing, temperature reception, chemoreception, touch, and a variety of other functions. However, in the last few years it has finally become clear that the lateral line is involved as a sensor of water motion, or hydrodynamic stimulation, arising within a few body lengths of a fish. In other words, the lateral line detects the presence of nearby animals and objects that cause or disrupt water flow.

The lateral line is involved with schooling behavior, where fish swim in a cohesive formation with many other fish. The lateral line tells the fish where the other fish are in the school, and helps the fish maintain a constant distance from its nearest neighbor. In experiments where the lateral line is temporarily disabled, the ability of fish to school is disrupted and fish tend to swim more closely together. The lateral line is also used to detect the presence of nearby moving objects, such as food, and to avoid obstacles, especially in fishes that cannot rely on light for such information, such as the cave-dwelling fishes.

The lateral line consists of two groups of receptors located on the body surface. One group is in canals, and are called canal organs (**Figure 4**), whereas other groups are located on the body surface and are called surface organs. The canal organs are primarily involved in detection of low frequency (e.g. below 100 Hz) hydrodynamic movements of other fish, whereas the surface receptors appear, at

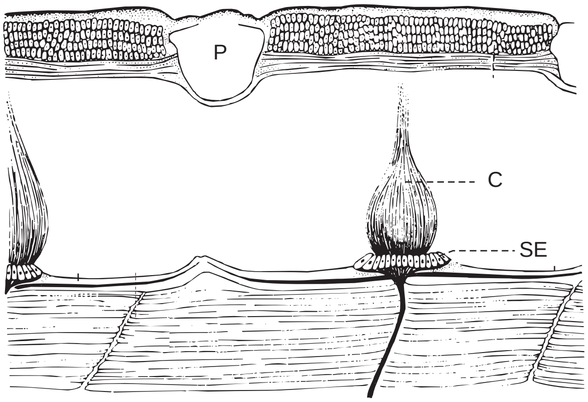

Figure 4 Longitudinal section of a lateral line canal. Each fluid-filled canal is open to the outside via a pore (P). A canal neuromast (SE) with its overlying cupula (C) sits on the floor of the canal, with one neuromast between each pore. The canal neuromasts are innervated by a cranial nerve. (Redrawn from Grassé PP (1958) L'oreille et ses annexes. In: Grassé PP (ed.) *Traité de Zoologie*, vol. 13, pp. 1063–1098. Paris: Masson.

least in some species, to provide fish with information about general water motion and assist the fish in swimming with or against currents.

The lateral line receptors consist of the same sensory hair cells as found in the ear. However, the hair cells are organized into small groups called neuromasts, with (perhaps) up to 100 cells per neuromast. The cilia from the neuromasts protrude into a gelatinous sail-like structure called a cupula. Bending of the cupula caused by the movement of water particles results in bending of the cilia on the hair cell, and the firing of the neurons which take signals to the lateral line region of the brain. In essence, the lateral line hair cells are stimulated as a result of the net difference between the motion of the fish and the surrounding water particles.

There is considerable variation in the exact pattern of the lateral line in different species. Some species have a single canal along the (lateral) trunk, whereas other species have multiple canals, or even no canals at all on the trunk. The most elaborate canal system, and the most variable, is on the head of fish. The lateral line segments on the head enable surface-feeding fish to detect and locate the source of surface waves produced by prey and may be important for making fine-scale adjustments in position in fish that form particularly tight schools.

Interactions Between the Ear and Lateral Line

It is generally thought that the ear and lateral line may be complementary systems. Both detect water motions, but whereas the ear can detect signals that come from great distances, the lateral line only detects signals that are very close to the fish. Significantly, the frequency range over which the two systems appear to work overlaps from about 50 to 150 Hz, although the ear can detect sounds to much higher frequencies and the lateral line can detect hydrodynamic signals to below 1 Hz. Both systems send their signals into near-by regions of the brain. Although the initial points of connection in the brain are close to one another, they are not identical, but the two systems interact at higher connections in the brain. In addition, the lateral line canals on the head of some species (clupeoids) converge in a structure called a lateral recess, a thin membrane situated just above the ear. This may allow the lateral line to be stimulated by vibrations in or around the ear. The functional significance of these connections is not yet known, but their presence supports the idea that fish can use the two systems together to gain a good deal of information about signals in the environment.

Correlations Between Structure and Habitat

By examining the structure of the lateral line and ear in fishes occupying a variety of different habitats, some information can be obtained as to the functional significance of specializations in these two systems. In general, species with many superficial neuromasts seem to live in quieter waters whereas those in running and noisier waters tend to have fewer superficial neuromasts and a better developed canal system. Extensively branched lateral-line canals are also commonly found in schooling fishes, possibly allowing for fine spatial discrimination of signals coming from many sources (other fish in the school). These correlations suggest that canals may have evolved as a mechanism to reduce extraneous ‘noise’ in hydrodynamic stimuli. Fewer correlative studies have been done comparing fish hearing to habitat, but it appears that fish with the highest discrimination ability tend to live in shallower, soft bottom habitats whereas those with less fine-tuned hearing abilities tend to be found in noisier habitats. Although there are numerous exceptions to these trends, examination of the lateral line and ears of fish is one way to predict where and how a fish might live.

The habitat in which a fish lives also seems to dictate how important hearing or lateral line inputs can be. This is most evident in fishes such as blind cavefish and blind catfishes (family Ictaluridae) that spend their entire life in the dark. These animals have no need for vision, and rely much more heavily on the lateral line and hearing. They have very well-developed neuromasts and canal systems and also tend to have a greater proportion of their brain area devoted to receiving hydrodynamic inputs. In deep sea fishes, the lateral line and hearing are highly developed as compared to visual senses, again showing how these senses can take over when others are not available.

See also

Bioacoustics. Coral Reef Fishes. Eels. Fish Feeding and Foraging. Fish Locomotion. Fish Migration, Vertical. Fish Predation and Mortality. Fish Schooling. Fish Vision. Salmonids.

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FISH LARVAE

E. D. Houde, University of Maryland, Solomons, MD, USA

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Introduction

Most marine teleost (bony) fishes produce thousands to millions of planktonic eggs and larvae. Newly hatched larvae, usually 1–5 mm in length, are delicate, poorly developed, and retain many embryonic characteristics. They usually hatch with undeveloped mouth parts, fins, and eyes. Larvae drift and disperse in the sea. Most die before transforming into the juvenile stage. The larval stage originates as a nonfeeding, yolk-sac larva that derives nutrition from stored yolk and develops into an actively feeding larva that eventually transforms to a juvenile morphologically resembling a small adult. Transformation, which occurs from a few days to more than a year after hatching, often involves major changes in morphology (e.g. eels, flounders, herring) or may be less dramatic (e.g. cods, basses, sea breams). Lengths at metamorphosis are usually < 25 mm, but can range from a few millimeters to many centimeters (some eels). The diverse, sometimes bizarre, suite of larval types that are collected represents a range of adaptations that promote survival and fitness in marine environments ranging from estuaries to the deep sea (**Figure 1**).

Fisheries scientists and managers are concerned about growth and survival during the earliest life stages of fishes because variability in those processes can lead to 10-fold or greater differences in numbers of recruits that survive to catchable size. Causes of mortality are seldom evaluated. Since early in the twentieth century, scientists have realized that ocean circulation, frontal systems, and turbulence might be key physical factors controlling larval survival. Biological factors, especially larval nutrition and predation also are major controllers of survival and growth. The physical and biological factors combine to determine success of the reproductive effort, termed 'recruitment' by fisheries scientists. Recruitment processes are not confined to the larval stage but act on earlier (eggs) and later (juveniles) stages. The larval stage is important but does not stand alone as a 'critical stage', and its relative importance in determining recruitment success can vary annually and seasonally.

Fish Larvae and the Plankton

Larvae of marine fishes, termed ichthyoplankton, usually are pelagic, drifting in the sea and interacting with pelagic predators and planktonic prey. Most fish larvae, even of species that ultimately are herbivores as juveniles or adults, are primarily carnivorous during the larval stage, feeding upon smaller planktonic organisms. In turn, larval fishes are the prey of larger nektonic and planktonic organisms. Escape from the precarious larval stage is accomplished via growth and ontogeny. Only a few individuals from thousands of newly hatched larvae survive the ever-present threats of starvation and predation during planktonic life.

Eggs and larvae of marine fishes are collected in fine-meshed plankton nets or specially designed traps. Surveys at sea estimate distributions,