Changing Structure and Function of the Ear and Lateral Line System of Fishes during Development

LEE A. FUIMAN

Marine Science Institute, University of Texas at Austin
750 Channel View Drive, Port Aransas, Texas 78373, USA

DENNIS M. HIGGS AND KIRSTEN R. POLING

Department of Biology, University of Windsor, Windsor, Ontario N9B 3P4, Canada

Abstract.—Adult fishes sense vibrations and disturbances in the water through the auditory and mechanosensory lateral line systems. The developmentally complete systems impart certain levels of sensitivity and acuity to a fish, but fish larvae hatch with rudimentary auditory and lateral line systems that confer poor sensory performance. The structures become more elaborate during ontogeny, with attendant improvement in performance. This review summarizes the ontogenetic changes in the peripheral anatomy of these sensory systems as well as the experimental work that has been undertaken to measure the changing functionality of each. In both systems, the number of end organs increases ontogenetically, roughly in proportion to somatic growth. Improvements in sensory function coincide with, and may be attributable to, these increases in end organs. Accessory structures that enhance functionality develop late in the larval period. Problems and recent advances in methodology as applied to larval fishes are discussed.

Introduction

Adult fishes sense vibrations and disturbances ("sounds") in the water through the ear and mechanosensory lateral line system (collectively known as the octavolateralis system). These systems in adults impart certain levels of sensitivity and acuity to a fish that enable it to gather information from the environment that is relevant to a wide range of activities. The auditory and lateralis systems of adult fishes have been the subject of detailed investigations for more than a century, from which much has been learned of their structure, functional mechanisms and capabilities, and ecological roles. Larval stages, by definition, are incompletely developed, yet they actively face challenges to survival that require sensory input. The incomplete state of larval organ systems at hatching and the gradual change toward the adult condition imply that larvae have different capabilities from adults but that their performance converges with that of the adult. This creates a dynamic relationship between a young fish and its environment.

Reviews and compendia are indispensable sources of information about various aspects of the auditory and lateralis systems of adult fishes (Fay 1988; Coombs et al. 1989; Montgomery et al. 1995; Fay and Popper 1999; Bretschneider et al. 2001; Mogdans and Bleckmann 2001; Myrberg and Fuiman 2002; Janssen 2003). Information on the systems in larvae is largely confined to a growing number of individual research papers and only a few reviews (Blaxter 1987; Higgs 2002; Myberg and Fuiman 2002; Whitfield et al. 2002). In this paper, we summarize relevant points about the adult systems in order to provide a context in which to understand how larval systems differ from, and ultimately converge with, adult systems. We then review the existing literature on the larval auditory and lateralis systems, emphasizing ontogenetic changes in form and function. Throughout, we attempt to maintain an ecological perspective because of the critical role of larval mortality in recruitment and population dynamics (Fuiman and Werner 2002).

Underwater Acoustics

The basic physics of sound propagation in water are well understood (see Kalmijn 1988, 1989; Rogers and Cox 1988). A sound wave has two components, particle displacement and pressure. For a pulsating (monopole) sound source, such as a resonating swim bladder, the magnitude of the displacement component is proportional to the inverse square of the distance from the source. If the sound source is moving back and forth (dipole), such as an oscillating fish body, particle displacement is proportional to the inverse cube of the distance. For both types of sound source, the pressure component is inversely proportional to the source diameter. Therefore, close to the sound source (acoustic near-field), the displacement component comprises most of the signal, but further away (far-field), most of the signal consists of the pressure component. In addition, an object moving at a constant velocity generates a hydrodynamically generated damming pressure front immediately in front of itself (Dijkgraaf 1989). Components of the octavolateralis system are sensitive to each of these characteristics of underwater sound.

Beyond the simple physics of sound waves, sound propagation in water is complex and varies greatly with the characteristics of the environment. Sound propagation through water is dependent on reflection of the sound wave from both the surface and the bottom, scattering of the sound wave by objects in the water, and refraction or bending of the sound wave in response to gradients in conduction velocity. There is little absorption (attenuation) of sound by water itself for frequencies within most of the hearing range of fishes, although this might be a factor for fishes that can detect ultrasonic frequencies (>20,000 Hz), such as American shad *Alosa sapidissima* (Mann et al. 1997, 1998, 2001).

Because of reflection, sound propagation is more complex in shallow waters. For a sound wave to travel a distance greater than its wavelength, it must repeatedly bounce off the bottom and surface, which distorts the waves. There are also absolute "cutoff frequencies" for each water depth, below which there is no undistorted propagation. For a 2000-Hz tone, the minimum water depth for propagation is 20–100 cm (depending on substrate composition), and for 500 Hz, the minimum water depth for undistorted propagation is more than 4 m (Rogers and Cox 1988). This means that in water shallower than about 1 m, most nonspecialist fishes (species that cannot hear above about 800 Hz) are effectively deaf to sounds propagating from any far source. Ostariophysan fishes can hear above 2,000 Hz, and it is thought that they evolved in shallow waters (Schellart and Popper 1992).

Adult Condition

The auditory and lateralis systems share a common functional mechanism within their end organ, the sensory hair cell. This innervated cell has one kinocilium and a graded series of stereocilia at the apical end of the cell. The direction of gradation defines the polarity of best response of the hair cell. The firing rate of the innervating neurons changes when the cilia are displaced, increasing or decreasing depending on the direction of displacement. Hair cells of the auditory and lateralis systems are located in different anatomical contexts, which impart different sensitivity characteristics. Although the systems operate in similar ways, they have separate neural pathways to the brain.

Auditory System

Anatomy and functional mechanism

For the purposes of this review, the auditory system encompasses the ear and any structural adaptations for transmitting sound sources to the ear. The basic patterns of the ear are well conserved among fishes, although there are many fine-scale differences between groups. Teleosts have three semicircular canals that are thought to be largely responsible for vestibular (balance) information. Although the sensory cells in the canals may also impart some auditory information, they will not be discussed further in this review, as their primary role is probably for balance. At the junction of the three semicircular canals sits the utricle, a sensory end organ that probably detects both vestibular and auditory signals, and it has a primary auditory role in many species (Popper and Fay 1999). The saccule and lagena lie ventral to the utricle and are predominantly auditory in nature but probably encode some vestibular information as well (Popper and Fay 1999). In this review, we will con-

sider the utricle, saccule, and lagena, the three auditory end organs of the ear.

All three end organs work the same way at the gross level (Popper and Fay 1999). Each end organ contains an otolith and a sensory epithelium consisting of hair cells, supporting cells, and basal cells (basal cells give rise to hair cells and supporting cells). Both the otoliths and the hair cells are integral to hearing. The hair cells are the sensory receptors that translate an acoustic stimulus to an action potential, allowing sounds to be detected by the fish. Each end organ consists of an enclosed sac with the sensory epithelium on one wall of the sac and the dense calcareous otolith floating nearby. There is a membrane between the otolith and the epithelium, perhaps attached to both, but this is unclear. When sound waves impinge upon a fish, they are transmitted through the body, displacing the center of the fish and the water at the same rate. Thus, there is little relative movement between the fish and the water. This would result in no, or very little, detection of sound waves. Because of the greater density of the otolith, however, its movement lags behind movement of the rest of the fish, causing relative motion between the otolith and the underlying sensory hair cells. The relative motion produces shear across the stereo- and kinocilia of the hair cells, causing ions to rush into the cell, polarizing the cell and resulting in an action potential in the innervating neuron. If relative motion of the otolith occurs in the direction of gradation, maximum stimulation occurs. If relative motion of the otolith occurs against the direction of gradation, minimum stimulation occurs (Popper and Fay 1999).

As noted above, the auditory system comprises more than just the ear itself. Just as mammals have evolved middle ear bones to increase sound transmission to the inner ear, many groups of fishes (termed "hearing specialists") have evolved mechanisms to increase the amount of auditory information transmitted to the ear. These mechanisms must also be considered when discussing hearing abilities. Because of the mechanics of sound travel in water and through the body of a fish, all of these specializations involve some coupling between the ear and a gas-filled structure that translates pressure of the sound wave to displacement information that the ear can detect. The different categories of specialization are (1) Weberian ossicles, a bony connection between the swim bladder and the ear (e.g., Cypriniformes, Characiformes, Gymnotiformes, and Siluriformes; von Frisch 1938; Chardon and Vandewalle 1997); (2) gas-filled extensions of the swim bladder that either approach or directly connect to the ear (e.g., Clupeiformes [O'Connell 1955; Denton et al. 1979]; some members of the Sciaenidae [Chao 1978; Ramcharitar et al. 2001]; some subfamilies of the Holocentridae [Nelson 1955]); and (3) a gas-filled chamber not connected to the swim bladder that is surrounded by, or in close proximity to, the ear (Anabantoidei, reviewed by Liem 1963; Mormyridae, von Frisch 1938; Fletcher and Crawford 2001). Fishes without any of these types of specializations are considered hearing generalists and generally do not hear frequencies much above about 800 Hz (Fay 1988). Fishes that have evolved one of these specializations can hear higher frequencies than hearing generalists. For example, species possessing Weberian ossicles can hear frequencies up to 4–5 kHz (Fay 1988), and at least two species with auditory bullae (gas-filled extensions of the swim bladder inside the ear of clupeoids) can hear up to 180 kHz (Mann et al. 1997, 1998, 2001).

Adult performance levels

Hearing generalists have a more restricted auditory bandwidth than specialists and do not detect frequencies above about 800 Hz, with peak sensitivities around 300–500 Hz (Fay 1988). While it is difficult to compare thresholds of different species obtained by different laboratories (Fay 1988; Higgs 2002), hearing generalists tend to have less sensitive hearing (higher thresholds) than specialists. Within the hearing specialists, auditory performance seems to depend upon the type of specialization present. Most species with Weberian ossicles (Ostariophysi) can detect pure tones up to 4,000–5,000 Hz (Fay 1988). Hearing abilities of those with swim bladder extensions, but no bony connection, vary depending upon the extent of swim bladder extension. Squirrelfishes (Holocentridae) that have a connection between the swim bladder and saccule (pearly soldierfish *Myripristis kuntee*) hear up to 3,000 Hz, while those with no connection (red and white striped squirrel fish *Adioryx xantherythrus*) do not detect sounds above 800 Hz (Coombs and Popper 1979). Clupeoid fishes all have gas-filled auditory bullae (Figure 1) that are directly connected
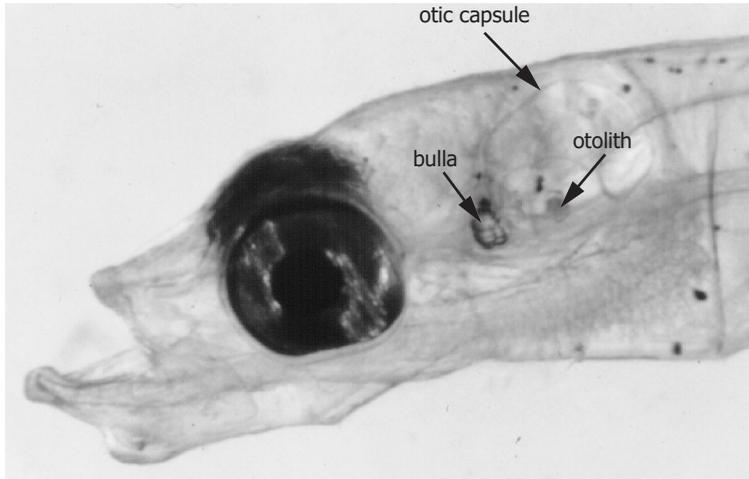
Figure 1. Head of larval Atlantic herring *Clupea harengus*, showing otic capsule with otoliths and inflated auditory bulla (photo by L. A. Fuiman).

to the utricular epithelium of the ear (O'Connell 1955; Allen et al. 1976; Best and Gray 1980). While audiograms are not available for many species of clupeoids, probably due at least partially to their extreme fragility, all species tested to date can detect pure tones up to at least 4,000 Hz (Mann et al. 1997, 1998, 2001). At least two species (American shad and gulf menhaden *Brevoortia patronus*) can detect pure tones of much higher frequencies, up to 180,000 Hz (Mann et al. 2001). This ability to detect ultrasound is not ubiquitous among clupeoid fishes, however, as at least three species (bay anchovy *Anchoa mitchilli*, scaled sardine *Harengula jaguana*, and Spanish sardine *Sardinella aurita*) do not detect ultrasound even though they also have auditory bullae (Mann et al. 2001). Finally, mormyrid and anabantoid fishes with a gas-filled chamber not directly connected to the swim bladder have also been shown to hear frequencies as high as 3,000–4,000 Hz, although deflation of these chambers results in a decrease of sensitivity but no change in auditory bandwidth in adults (Yan 1998; Yan and Curtsinger 2000; Yan et al. 2000; Fletcher and Crawford 2001).

Ecological functions of the adult auditory system

When thinking about the auditory system it is also necessary to consider to what fishes may be listening. That is, what are the major sources of sound underwater, and what relevance might these sources have to a fish. There are two schools of thought concerning which sounds are relevant to fish. One approach is to consider sounds produced by sources thought to be important to a fish, such as conspecific vocalizations or noises made by prey or predators, and test whether hearing is sensitive within that range. Some authors have found a match between dominant frequencies of auditory detection and vocalization in fishes (Cohen and Winn 1967; Myrberg and Spires 1980; Schellart and Popper 1992; Ladich and Yan 1998; Suzuki et al. 2002), which has led to the suggestion that the fish auditory system is tuned to conspecific vocalizations (Ladich and Yan 1998; Suzuki et al. 2002). Other authors have found no consistent match between sound source and detection (Fine 1981; Ladich 1999). Goldfish *Carassius auratus* have very sensitive hearing but are not known to communicate with sound, which suggests that communication did not drive the evolution of hearing in all fishes. A second school of thought argues that the fish ear did not evolve in conjunction with vocalization, but rather that hearing in fishes evolved to perform a sort of auditory scene analysis (Fay and Popper 2000). Under this hypothesis, fish "listen" to the complete suite of frequencies available in the environment, at least in the bandwidth in which their ear is sensitive, and extract information about the entire auditory scene. Specific features of the scene can then be extracted, ana-

lyzed, and interpreted by the auditory system, but the system did not evolve to be responsive to only a narrow portion of this scene. This type of analysis might be used by reef fish larvae to orient to coral reefs (Tolimieri et al. 2000, 2002; Leis et al. 2002), as discussed below.

Lateralis System

Anatomy and functional mechanism

The teleost lateralis system is composed of an array of neuromasts that are distributed over the body on the surface of the skin (superficial neuromasts) and inside canals (canal neuromasts). The structure and functional mechanism of neuromasts is similar to the sensory epithelium of ear end organs, consisting of a compact cluster of hair cells, supporting cells, and basal cells. Many stereocilia and a single kinocilium are arranged in a graded series at the apical end of each hair cell. Unlike the auditory epithelium, the stereocilia and kinocilium project into a gelatinous cupula (<300 μm long), which is in direct contact with fluid outside the body, either the water surrounding the fish or the fluid in the lateral line canals. Canal neuromasts generally are much larger and have more hair cells than superficial neuromasts (Münz 1989; Song et al. 1995; Wonsettler and Webb 1997; Engelmann et al. 2000; Northcutt et al. 2000), although superficial neuromasts have a higher density of hair cells and longer kinocilium (Song et al. 1995). As in the ear, shear across the stereocilia and kinocilia produces an action potential, and the direction of the shear is encoded in the signal produced. The difference between the ear and the lateralis mechanisms is that the shear results from water flow against the cupula (either directly or due to pressure differences along the canal), rather than differential movement of an otolith.

Neuromasts on the skin—also known as superficial, free, or naked neuromasts—are inconspicuous and often overlooked during cursory examination. They are grouped into short series (sometimes described as stitches) that are commonly found in five regions of the head in fishes. The anterior, middle, and posterior lines are located dorsal to the eye, otic, and postotic regions, respectively. Additional superficial lines occur on the cheek and lower jaw. The number and distribution of superficial neuromasts on the trunk vary greatly among species (Coombs et al. 1988; Münz 1989).

The usually prominent lateral line canal (or multiple canals) on the trunk is accompanied by a network of canals on the head. Canals of the head and trunk open to the surrounding water through numerous pores, and canal neuromasts lie inside the canals between pores. The typical configuration of lateral line canals in teleosts includes a trunk canal, which has a temporal segment in the otic and postotic regions of the head, and a main trunk segment that extends along the body to the base of the tail or even to the tip of the caudal fin. Trunk canals of the left and right sides of the body may be joined mid-dorsally by a supratemporal canal that emerges from the temporal segments of the trunk canals. Anteriorly, canals surround the eye: a supraorbital canal above, an infraorbital canal below. Canals also extend onto the cheek (preopercular canal) and lower jaw (mandibular) (Coombs et al. 1988; Münz 1989). Architecture of the canal system varies greatly among species, from a single, continuous trunk canal to a trunk canal broken into segments, shortened, or absent, or multiple trunk canals. Cephalic canals sometimes are very wide in species that live in lentic environments or highly branched, forming a complex network (Dijkgraaf 1963; Coombs et al. 1988; Janssen 2003). All of these variations in canal structure alter the physics involved in the movement of the neuromasts enclosed in the canals and, therefore, the response characteristics of the lateralis system. Additional details of phylogenetic variation in the distribution of canals and superficial neuromasts were provided by Coombs et al. (1988, 1992), Northcutt (1989), Bleckmann (1993), and Wonsettler and Webb (1997).

As with the ear, the lateral line canal system is functionally connected to the swim bladder in at least two groups of fishes. The best known of these connections is found in clupeoid fishes. The auditory bulla, the gas-filled extension of the swim bladder located in the ear (Figure 1), generates fluid displacements in the ear, which greatly improves sensitivity and bandwidth of the ear. The otic capsule is medially adjacent to the temporal segment of the trunk lateral line canal, from which it is separated by a compliant lateral recess membrane. This membrane conveys fluid movements in the ear to the fluid within the lateral line canals, providing an additional source of stimulation for the neuromasts contained within (Denton

and Blaxter 1976; Blaxter et al. 1981). Less well known is the laterophysic connection recently described in some chaetodontids (Webb 1998; Webb and Smith 2000). These butterflyfishes have paired projections of the swim bladder that extend anteriorly toward the otic region and contact a medial fossa in the lateral line canal contained within the supracleithrum. There is speculation that this close association between the swim bladder and lateral line canal system allows canal neuromasts to contribute to the fish's ability to sense variations in sound pressure (Webb and Smith 2000), as in the clupeoid system, although definitive experiments to test this function have not been reported.

Adult performance levels

The end organs of the lateralis system (superficial and canal neuromasts) are distributed across a fish's body to act as a sensor array. This arrangement of neuromasts is important to the spatial acuity of the system. Superficial neuromasts respond best to the velocity component of water flow across the cupulae, whereas canal neuromasts are more sensitive to accelerations (Kroese and Schellart 1987; Engelmann et al. 2000), although both types of neuromasts probably respond to velocity and acceleration to some degree. The response of superficial neuromasts is greatest at low frequencies, about 10–70 Hz, and they respond to flows as low as 0.03 mm/s (Münz 1985; Coombs and Janssen 1990). Since swimming activity results in low frequency flow across a fish's skin, functioning of superficial neuromasts may be compromised during swimming. Various behavioral strategies and structural and neural designs help reduce the problem of self-generated noise (Bleckmann 1993; Denton and Gray 1993; Montgomery and Bodznik 1994; Engelmann et al. 2000). Indeed, behavioral experiments suggest that fishes use superficial neuromasts for rheotaxis (Montgomery et al. 1997), although these results have been questioned (Janssen 2000).

Neuromasts within canals have different response properties from those of superficial neuromasts. The canals alter the nature of flow past the neuromasts so that they act as a high-pass or band-pass filter that attenuates lower frequencies (Denton and Gray 1989, 1993; Montgomery et al. 1995). Thus, canal neuromasts operate best at a higher range of frequencies (100–200 Hz)

than do superficial neuromasts (Münz 1985, 1989). The altered flow within the canals allows acceleration detection, with sensitivity in the range of 0.3–20 mm/s^2 (Münz 1985; Bleckmann and Münz 1990; Coombs and Janssen 1990). Lateral line system structure, including the extent of canals, their diameter and branching, flexibility of their walls, and size of neuromast cupulae relative to canal diameter, varies among species, locomotor habits, and habitats. For example, more active fishes and those that live in turbulent or lotic habitats tend to have more complex networks of canals and fewer superficial neuromasts; sedentary species from lentic habitats have fewer or wider canals but more superficial neuromasts (Dijkgraaf 1963; Vischer 1990; Janssen 2003).

Functions of adult lateral line system

The ability of the lateralis system to detect local water velocity and acceleration and to provide information about the location and strength of the stimulus source is useful in a variety of ecological contexts. Sensitivity to local water velocity is the basis of rheotaxis. Experiments on three ecologically and phylogenetically unrelated species provide evidence that superficial neuromasts play a role in rheotaxis (Montgomery et al. 1997). This ability to adjust swimming speed according to the local water current speed is not very different from being able to monitor swimming speed while moving. Based on the location of cupulae within a fish's hydrodynamic boundary layer (region of maximum velocity gradient), Blaxter (1987) suggested that fishes might use the lateralis system for this purpose. In support, Hassan et al. (1992) observed elevated swimming speeds in blind cave fish *Astyanax jordani* when neural activity of the lateral line was chemically reduced, as would be expected if a preferred swimming speed were achieved at a fixed level of lateral line activity.

Water is accelerated by the locomotor, feeding, social, reproductive, and other movements of aquatic animals. This provides an opportunity for the lateralis system to participate in a wide variety of interactions between a fish and other organisms. Numerous behavioral studies have confirmed that fishes use the lateral line to sense the presence and position of prey organisms, including other fishes (New et al. 2001), as well as planktonic (Janssen et al. 1995), benthic (Janssen

1990) and surface-dwelling (Bleckmann 1988) invertebrates. As we describe later, use of the lateralis system to sense approaching predators has been established in studies of larval fishes being attacked by larger fishes. The ability of schooling fishes to match the speed and maintain a distance from neighbors within the school is partly dependent upon input from the lateralis system (Pitcher et al. 1976; Partridge and Pitcher 1980). It is also likely that the water movements created during courtship, and aggressive interactions among individuals may be sensed by the lateralis system (Satou et al. 1991). The lateralis system can also be used for hydrodynamic imaging, in which the location of objects, including inanimate ones, is determined by the patterns of water flow around them (Hassan 1989). Finally, the low frequency swimming motions of animals create a hydrodynamic wake that may persist for several seconds (Bleckmann 1991) and be used by predators to locate prey (Dehnhardt et al. 2001). Regardless of the task, it is important to recognize that fishes rely on input from multiple sensory channels and that probably no ecological interactions are mediated entirely by neuromasts.

Development of Form and Function

Most of what is known about the octavolateralis system is based on the morphologically static adult condition whereby form and function relationships have been understood, in part, from comparisons of species that differ in morphology. Little of the adult sensory anatomy is present in larvae at hatching. Sensory anatomy develops gradually, implying that sensory capabilities are poor at hatching and improve steadily, at least until the sensory systems are complete. By examining changes in form and function during development within a species, larval fishes can be used as a natural experiment to ascertain the role of different structures without the confounding effects inherent in cross-species comparisons. By comparing species, it is possible to gain a better understanding of general trends as well as the ecological basis for variation in design of the system. The dynamic nature of development requires that comparisons of larvae be made at comparable stages of development. We use the ontogenetic index devised by Fuiman (1994) as the metric for interspecific comparisons of developing fishes, where

$$O_L = \frac{\log TL}{\log TL_{juv}} \times 100 \ .$$

Mathematically, this is equivalent to the logarithm of total length (TL) in base TL_{juv} (i.e., $\log_{TL_{juv}}$ (TL)), therefore it does not matter whether natural logarithms or base-10 logarithms are used in the calculation. This formulation expresses the ontogenetic state (O_L) of an individual as a percentage of its total ontogenetic period. It recognizes that TL is a better indicator of an individual fish's ontogenetic state than age (Fuiman et al. 1998) and that the rate of ontogenetic change within a species is roughly logarithmic (faster relative to TL early in the larval period than later). Scaling body size to the size at which a species becomes a juvenile (TL_{juv}) creates a common scale upon which multiple species can be compared. Thus, each species' developmental period fills one logarithmic cycle. In this paper, we use the size at complete squamation for TL_{juv}, whenever possible. For reference, the ontogenetic index takes a value of 100 at complete metamorphosis (complete squamation), and the value at hatching varies widely among species but is often approximately 25 for typical marine fish larvae and 50 for freshwater larvae.

Auditory System

Anatomical development

While the timing of ear development varies between species and is dependent upon temperature, food, and other environmental variables, even within a species (Higgs et al. 2002), available studies indicate that the pattern of ear development is highly conserved among species (Thornhill 1972; Waterman and Bell 1984; Sokolowski and Popper 1987; Vandewalle et al. 1990; Becerra and Anadón 1993a, 1993b; Haddon and Lewis 1996; Pankhurst and Butler 1996; Salem and Omura 1998a, 1998b; Bang et al. 2001; Bever and Fekete 2002). The molecular controls of this process are beyond the scope of this review but are ably reviewed by Whitfield et al. (2002). The ear forms from the otic placode, one of several bilaterally paired localized thickenings of the dorsolateral embryonic ectoderm. Soon after formation, the placode grows into a solid ball of cells. Cells in

the interior of the placode begin to migrate outward, leaving an empty space in the middle to form the lumen (Thornhill 1972; Haddon and Lewis 1996). This formation by cavitation is different from the process in birds and mammals, which form a lumen by invagination of the epithelial sheet first into a cup and then a lumen (Fritzsch et al. 1998). After a period of vesicle growth, protrusions grow from the wall of the lumen, eventually spanning the lumen to form three pillars of tissue. The space surrounding each pillar becomes a semicircular canal. Before the semicircular canals are complete, hair cells, supporting cells, and innervating neurons begin to develop. Sensory epithelial areas form from thickenings of the otic epithelium early in development. They are connected in one sheet, the macula communis. Within the macula communis, hair cells form as discrete, separated patches, one anterior (the presumptive utricular macula) and one posterior (the presumptive saccular macula). The epithelium within the sensory patches becomes stratified, with hair cell nuclei more apical and supporting cell nuclei more basal (Becerra and Anadón 1993b; Haddon and Lewis 1996). Once the first two auditory maculae have formed, the cristae of the semicircular canals form, with hair cells being clearly evident (Waterman and Bell 1984). Much later in development (many days posthatching), the lagena forms as an out-pocketing of the saccule (Sokolowski and Popper 1987; Haddon and Lewis 1996; Bever and Fekete 2002).

Addition of hair cells from basal cells in the sensory maculae continues throughout life. While few studies have quantified teleost hair cell numbers during development, some trends are evident (Figure 2). Hair cell addition in the saccule follows a similar function in all fish species examined to date, as well as in the macula neglecta (another type of sensory epithelium) of thornback ray *Raja clavata* (Corwin 1983). Thus, hair cell addition seems to track the growth of the fish, so that, within species, a larger fish will have more hair cells, although the number of hair cells differs between species for a given ontogenetic state (Figure 2). Unlike mammals (Ruben 1967), if the hair cells in the fish ear are damaged or destroyed, they can be replaced for the life of the animal (Corwin 1981, 1983; Popper and Hoxter 1984; Lombarte and Popper 1994; Higgs et al. 2002). When hair cells are added during the embryonic
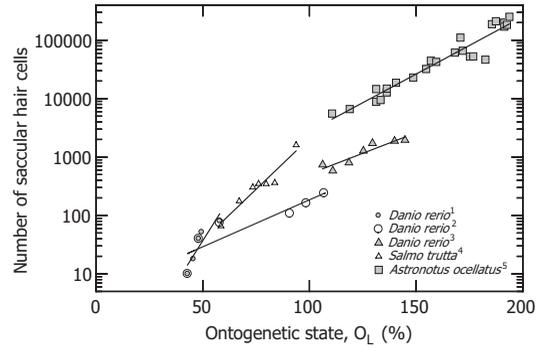
Figure 2. Hair cell addition to the saccule relative to the ontogenetic index (O_L) for zebra danio *Danio rerio* (three studies, TL_{juv} = 12 mm), brown trout *Salmo trutta* (TL_{juv} = 51 mm), and oscar *Astronotus ocellatus* (TL_{juv} = 15 mm). [1] Haddon and Lewis 1996; [2] Bang et al. 2001; [3] Higgs et al. 2002, 2003; [4] Becerra and Anadón 1993a; [5] Popper and Hoxter 1984.

period, the ciliary bundles of new hair cells form with a polarity different from that seen in adults (Sokolowski and Popper 1987). Bundle polarity changes to the adult pattern early in development, but whether this is due to reorientation or replacement remains unclear (Thornhill 1972; Sokolowski and Popper 1987).

In the early stages of ear development, most fish species start with two pairs of otoliths (Haddon and Lewis 1996; Pankhurst and Butler 1996; Bang et al. 2001; Bever and Fekete 2002). The more anterior of the two pairs becomes the lapilli (utricular otoliths), while the posterior pair becomes the sagittae (saccular otoliths). The lagenar macula forms last (see below) and the asterici (lagenar) are the last otoliths to form (Haddon and Lewis 1996; Pankhurst and Butler 1996; Bang et al. 2001; Bever and Fekete 2002). The relationship between otolith and somatic growth, and the problems therein, have been reviewed elsewhere (e.g., Jearld et al. 1992; Hoff and Fuiman 1993; Secor et al. 1995; Meekan et al. 1998; Cieri and McCleave 2000). This relationship has been used in many studies to estimate age and growth rates of wild fish (reviewed by Secor et al. 1995). Less well characterized are changes in otolith shape during development. When first forming, all otoliths are roughly round in shape, with little apparent difference between species (e.g., Jearld et al. 1992; Brown et al. 2001; Bever and Fekete 2002). During development, otoliths typically lose their round shape via addi-

tion of accessory growth centers, and they develop species-specific shapes (e.g., Sogard 1991; Brown et al. 2001). Some of these shape changes may be matched to life history events such as settlement (Jearld et al. 1992; Parmienter et al. 2002) or ontogenetic onset of characters, such as notochord flexion or full vertebral ossification (Brown et al. 2001). Unfortunately, there is little information available on functional consequences of these size and shape changes. It has recently been demonstrated mathematically that changes in otolith size might affect hearing abilities of fishes (Lychakov and Rebane 2000), but this has yet to be confirmed experimentally.

With respect to a developmental effect on hearing ability, the best studied peripheral specializations are the auditory bullae of clupeoid fishes (Figure 1). While the absolute timing of bulla formation and inflation differs between clupeiform species, the relative timing seems conserved. The first structure to form is the pro-otic bulla (Figure 1), first filled with gas at O_L = 60–75 for Atlantic menhaden *Brevoortia tyrannus* and bay anchovy (Hoss and Blaxter 1982; Higgs and Fuiman 1996), but not until an O_L = 80–85 in Atlantic herring (Allen et al. 1976; Fuiman 1989; Blaxter and Fuiman 1990). The pterotic bullae develop much later. The swim bladder begins to fill with gas after the pro-otic bulla fills (Allen et al. 1976). Swim bladder inflation is probably not important to functional aspects of hearing in this group, as the hearing effect is directly caused by sound waves vibrating the bullae, not being transmitted from the swim bladder (Denton et al. 1979).

The development of the Weberian apparatus of ostariophysan fishes has received some attention (Radermaker et al. 1989; Vandewalle et al. 1990; Bogutskaya 1991; Coburn and Futey 1996) but more as an examination of skeletal development than from an auditory perspective. The exact embryological origins of different elements of the Weberian ossicles remain unclear, although it is not known if the confusion arises because of interspecific variation or because of differences in methods employed (Chardon and Vandewalle 1997). Chondrification of individual Weberian elements begins early in the larval period (mean size of first appearance in cypriniforms about 6–8 mm standard length [SL]; Bogutskaya 1991; Coburn and Futey 1996), but Weberian apparatus formation is not complete until well into the juvenile period. Ontogeny of the apparatus begins with the appear-

ance of the anterior basidorsal and basiventral elements as extensions of the anterior vertebrae. In the African catfish (also known as sharptooth catfish) *Clarias gariepinus* and the barbel *Barbus barbus*, the four main Weberian elements (scaphium, intercalarium, tripus, and os suspensorium) appear to form as one unit (Rader-maker et al. 1989; Vandewalle et al. 1990), but in other species, the four units form separately and fuse once formed (Bogutskaya 1991; Coburn and Futey 1996). Regardless of the pattern observed, the four main elements do not connect to the ear and swim bladder until the juvenile period (Radermaker et al. 1989; Vandewalle et al. 1990; Bogutskaya 1991; Coburn and Futey 1996), thus probably limiting their role in hearing transduction until the elements have at least some contact with the ear (Higgs et al. 2003).

Larval performance levels

THRESHOLDS.—There are few published studies of the physiological response of the ear to stimuli during development in fishes. Existing studies can be divided into three types (Figure 3): those that show a clear increase in sensitivity with development (Corwin 1983; Kenyon 1996), those that show no change in sensitivity with development (Popper 1971; Higgs et al. 2002, 2003), and those that show inconsistent and small changes in auditory sensitivity with development (Iwashita et al. 1999; Wysocki and Ladich 2001). Because of differences in techniques and species used, it is best to discuss each type of study separately before looking for common patterns.

The two studies showing clear changes in sensitivity with development used very different techniques and species but obtained similar results. Using an isolated ear of the thornback ray, Corwin (1983) recorded physiological responses from the ramus neglectus (nerve innervating the macula neglecta) to vibratory stimuli of different frequencies. Corwin (1983) showed a clear decrease in threshold (increased sensitivity) with size (13.5–97 cm TL; O_L = 130–200) across all frequencies tested, with an almost 60-dB drop in threshold at the best frequency of 70 Hz (Figure 3). This increase in sensitivity was correlated with an increase in hair cell number and convergence of hair cells onto afferents in the macula neglecta sensory epithelium. A similar decrease in threshold across all detected frequencies was found in bicolor damselfish *Pomacentrus partitus* using a
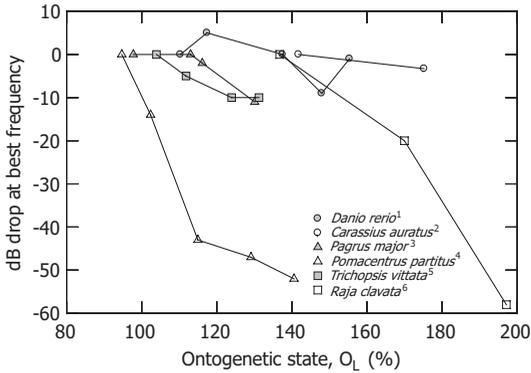
Figure 3. Developmental changes in threshold to frequencies of best sensitivity in *Danio rerio* (TL$_{juv}$ = 20 mm), *Carassius auratus* (TL$_{juv}$ = 15 mm), red seabream (also known as madai) *Pagrus major* (TL$_{juv}$ = 10 mm), *Pomacentrus partitus* (TL$_{juv}$ = 10 mm), croaking gourami *Trichopsis vittata* (TL$_{juv}$ = 20 mm), and thornback ray (TL$_{juv}$ = 100 mm). [1] Higgs et al. 2002, 2003; [2] Popper 1971; [3] Iwashita et al. 1999; [4] Kenyon 1996; [5] Wysocki and Ladich 2001; [6] Corwin 1983.

conditioned behavior paradigm (Kenyon 1996). Examining four size-classes of juveniles (from 12 to 38 mm SL; O$_L$ = 94–130) and one size-class of adults (>45 mm SL), Kenyon (1996) showed a consistent increase in sensitivity with development across all frequencies tested, with a 50-dB sensitivity decrease at the best frequency of 500 Hz (Figure 3). While morphological development was not examined, the changes in sensitivity fit a von Bertalanffy growth curve, which led Kenyon (1996) to suggest that a simple growth function, such as increasing hair cell numbers, could explain the changes seen in sensitivity.

The three studies showing no change in sensitivity with development were all done on one family of fish, Cyprinidae. Popper (1971) used avoidance conditioning to examine thresholds in goldfish of two size-classes: 45–48 mm SL (mean O$_L$ = 140) and 110–120 mm SL (mean O$_L$ = 175). There was no difference in threshold of these two size-classes across the range of frequencies tested (100–2,500 Hz; Figure 3), and the two averaged audiograms were virtually identical (Popper 1971). As pointed out by Kenyon (1996), larger goldfish in Popper's (1971) study tended to have slightly lower mean thresholds at frequencies between 100 and 1,000 Hz than the smaller fish, but the threshold ranges of these groups were overlapping, so the slight differences in means were

probably not real. Higgs et al. (2002) obtained similar results for juvenile and adult zebrafish (also known as zebra danio), using the auditory brainstem response (ABR). There was no difference in auditory threshold or bandwidth in this species between 25 and 50 mm total length (TL; O$_L$ = 130–155; Figure 3), despite significant increases in hair cell number. Examination of auditory performance over a broader developmental range (10–50 mm TL; O$_L$ = 98–155; Figure 3) did show changes in auditory bandwidth but not in sensitivity (Higgs et al. 2003). Larvae as small as 10–13 mm TL (O$_L$ = 98–103) could detect pure tones of 100 and 200 Hz with no differences in sensitivity from adults. As larvae developed, there was a significant improvement in auditory bandwidth (with maximum frequency expanding from 200 Hz in 10–13-mm-TL larvae up to 4,000 Hz in animals larger than 25 mm TL) but no change in threshold at which animals responded to the tone (Higgs et al. 2003). This increased bandwidth coincided with development of the Weberian ossicles, suggesting that once sound is transmitted to the ear by the developing ossicles, ears of larvae and adults are equally adept at sound detection.

Two other studies have shown less consistent differences in physiological measures of auditory performance with development. Iwashita et al. (1999) used conditioned avoidance behavior to examine audiograms of red seabream 0–2 years old and compared the data to a previous report for 3-year-old bream (O$_L$ = 130). Red seabream showed a decrease in threshold with age from 0 to 2 years old (mean O$_L$ = 95–115) for stimulation frequencies between 100 and 500 Hz, but an increase in threshold with age below 100 Hz and no differences above 500 Hz. Two-year-old bream (O$_L$ = 115) were more sensitive than 3-year-old fish from 100 to 500 Hz, and there appeared to be no significant change in threshold at the best frequency of 400 Hz (Figure 3). A similar mixed result has been found in the croaking gourami (Wysocki and Ladich 2001). Using ABR in fish of three size-classes (20–25.5 mm TL, O$_L$ = 100–108; 26–31.5 mm TL, O$_L$ = 109–115; and 32–51.5 mm SL, O$_L$ = 115–132), Wysocki and Ladich (2001) reported an ontogenetic increase in sensitivity to tones between 800 and 2,500 Hz, with no differences between size-groups at frequencies of 100–600 Hz, nor 3,000–5,000 Hz. There was a slight change in sensitivity at the best frequency of 2,000 Hz (Figure 3). When comparing their re-

sults to those of a previous study on adult gouramis, however, there was an ontogenetic increase in sensitivity only from 800 to 1,500 Hz, and adult fish were the least sensitive group at frequencies above and below this range (Wysocki and Ladich 2001). Finally, a similar mixed result has been found for clownfish (also known as saddle anenomefish) *Amphiprion ephippium* (S. Simpson, University of York, personal communication). Clownfish larvae show changes in auditory sensitivity, using ABR with development, but the sensitivity increase varies dependent upon frequency.

With so few studies available, it is difficult to identify and discuss broad trends in physiological sensitivity. Moreover, most of the existing data are for early juvenile or very late larval stages. Clearly, more examination of this question in other species and at earlier ontogenetic stages is required. The studies that show a clear change in sensitivity with ontogeny (Corwin 1983; Kenyon 1996) were conducted on hearing generalists, while those studies showing no change in sensitivity (Popper 1971; Higgs et al. 2002, 2003) were conducted on Ostariophysans, a group with a specialization for conducting sound to the ear. Higgs et al. (2003) speculated that development of the sound-conducting pathway (Weberian apparatus) in zebrafish works much like the development of the middle ear in mammals and birds. As the Weberian apparatus develops and becomes more connected, higher frequencies can be transmitted to the ear. Unlike mammals and birds, however, once these frequencies reach the ear, the sensory epithelium is just as sensitive in larvae as in adults. More work must still be done to settle this question.

BEHAVIOR.—Behavioral study of the ontogeny of hearing begins and ends largely with the work of Blaxter and collaborators. Thus, the Atlantic herring has received most research attention. As in other clupeoids, adult Atlantic herring have gas-filled auditory bullae directly connected to the utricular sensory epithelium (Allen et al. 1976; Denton and Gray 1979). Atlantic herring larvae hatch without a bulla. The bulla first forms around 18 mm TL (O_L = 74; Blaxter and Batty 1985) but does not fill with gas until 22–30 mm TL (O_L = 80–85; Allen et al. 1976; Blaxter et al. 1981; Blaxter and Batty 1985; Fuiman 1989; Blaxter and Fuiman 1990). Various tests show that this bulla inflation has dramatic effects on the audi-

tory performance of Atlantic herring larvae. Using fine-scale visualization of the bullae and auditory end organs, Blaxter et al. (1981) showed that, before the bulla inflates, there is no displacement of the perilymph by pressure waves. After the bulla fills with gas, however, pressure waves at frequencies of 30–4,000 Hz cause obvious deflections in the bullar membrane and the utricular epithelium, demonstrating the importance of the bullae to hearing. Blaxter et al. (1981) also showed that a gas-filled bulla is necessary to elicit startle responses by sound stimulation. Similarly, Blaxter and Batty (1985) never saw startle responses in Atlantic herring larvae without a bulla and only saw one startle response to auditory stimulation in a larva with a liquid-filled, but not a gas-filled, bulla. Using a more natural stimulus (an attacking fish), Fuiman (1989) and Blaxter and Fuiman (1990) found a dramatic increase in responsiveness coincident with the onset of bulla inflation in Atlantic herring, although this result may have been due to the connection between the bulla and the cephalic lateral line system. Finally, Blaxter and Hoss (1981) tested hearing in larvae before and after experimentally bursting the auditory bullae. While they saw no clear ontogenetic trends in auditory sensitivity in Atlantic herring larvae, they found a dramatic increase in threshold (decrease in sensitivity) after the auditory bullae were ruptured. Taken together, these studies show the importance of an ontogenetic change, bulla inflation, to hearing performance. Fuiman et al. (1999) also showed an ontogenetic increase in responsiveness of red drum *Sciaenops ocellatus* larvae to a 500-Hz tone burst, but did not associate it with any specific developmental changes in auditory morphology.

While it is generally assumed that development of auditory performance has important implications for larval ecology, ecological aspects of auditory development have only been carefully examined in the context of recruitment of larvae to coral reefs. In the last few years, there has been increased interest in the question of whether pelagic fish larvae use sound to locate and settle on reef habitats. Playback of recorded reef sounds results in significantly higher catches of some reef species (primarily *Fosterygion* sp.) in nearby light traps, but does not affect the catch of pelagic nonreef species, such as pilchard *Sardinops neopilchardus* (Tolimieri et al. 2000). Reef fish larvae (*Fosterygion* sp.) also show di-

rectional responses to reef sounds in controlled field experiments, moving toward the sound at night and away during the day (Tolimieri et al. 2002), perhaps to ensure settling on the reef only at night when vulnerability to predators would be expected to be reduced. Free-swimming damselfish (also known as blackfin chromis) *Chromis atripectoralis* larvae show directional responses to reef sounds but not white noise (artificial, broad band sounds; Leis et al. 2002). Thus, it is clear that larvae can detect reef sounds and that sounds emanating from the reef are a potent potential cue for settlement, although the actual use of sound as a settlement cue remains to be conclusively proven.

Lateralis System

Anatomical development

The general pattern of morphogenesis that gives rise to the lateralis system of most fishes has been described by Lekander (1949), Blaxter (1987), Northcutt et al. (2000), and others. The general consensus is that the lateralis system, both neuromasts and nerves, originates from dorsolateral ectodermal placodes located behind the eye (Northcutt 1997), although at least one report suggests that they originate from neural crest cells (Collazo et al. 1994). The anterior-most placode branches and elongates to form sensory ridges that surround the eye, ultimately forming the supraorbital and infraorbital lines (ultimately canals) and anterior superficial lines. A second placode anterior to the otic placode elongates into sensory ridges that produce the preopercular and mandibular lines. Placodes on either side of the otic placode give rise to the otic and postotic segments of the trunk canal and nearby lines of superficial neuromasts. A slightly posterior placode and sensory ridge produces the supratemporal series. The most posterior placode migrates caudally, ultimately traversing the length of the trunk.

Under these placodes and sensory ridges, neuroblasts appear that ultimately differentiate into ganglionic neurons. Peripheral processes contact the placode where rosette-shaped clusters of cells form neuromast primordia along the midline of the sensory ridge. Neuromasts erupt through the ectoderm, and their cupulae (Figure 4) are secreted by supporting cells within the neuromast (Northcutt 1997). Blaxter (1987) stated

that neuromasts of the superficial lines (i.e., those that do not ultimately become part of a canal series) differentiate secondarily from neuromasts of direct placodal origin. But, all superficial neuromasts may not have a common origin. A recent study of zebra danio provides details of how superficial lines in the trunk originate from the budding of founder neuromasts that have migrated from the main trunk line (Ledent 2002).

These developmental changes begin in the embryonic period, and even altricial fish larvae typically have a small number of neuromasts when they emerge from the egg. For example, the Japanese flounder (also known as olive flounder) *Paralichthys olivaceus* hatches at 2.5 mm TL (O_L = 31) with a single pair of otic neuromasts (Kawamura and Ishida 1985), and red sea bream hatches at 2.2 mm TL (O_L = 34) with four to seven pairs of neuromasts on the head and trunk (Okamoto et al. 1982). There may even be one or more neuromasts in the dorsal finfold at hatching, as in some sciaenids (Figure 4). In most cases, the more ontogenetically advanced a larva is at hatching, the more neuromasts it has. Ayu *Plecoglossus altivelis* hatches at 6.4 mm TL (O_L = 49) with 7 pairs of neuromasts on the head and 19 pairs on the trunk (Mukai et al. 1992). Chum salmon *Oncorhynchus keta* has 29 cephalic and 48 trunk neuromasts when it hatches at 20 mm TL (O_L = 84) (Disler 1960).

Proliferation of superficial neuromasts is a gradual process that occupies much of the larval period (Disler 1950; Peters 1973; Figure 5). Generally, as sensory ridges elongate and placodes migrate, neuromasts differentiate individually, but not in sequence along the ridge. For example, the main trunk series develops from head to tail, but it does so in successive waves. In the first wave, four or five neuromasts are deposited along the trunk, each separated by several myotomal segments. Successive waves deposit intervening neuromasts (Ledent 2002) until there is one neuromast per myomere in the main trunk line (Figure 4; Webb 1989a; Northcutt et al. 2000). Finally, more neuromasts appear, forming vertically aligned doublets or triplets along the main trunk line (Poling and Fuiman 1997). Assuming that these neuromasts are functional when they appear, this pattern of proliferation would establish a spatial array of receptors and hence greater functionality earlier than if the neuromasts developed sequentially down along the body in a single wave.
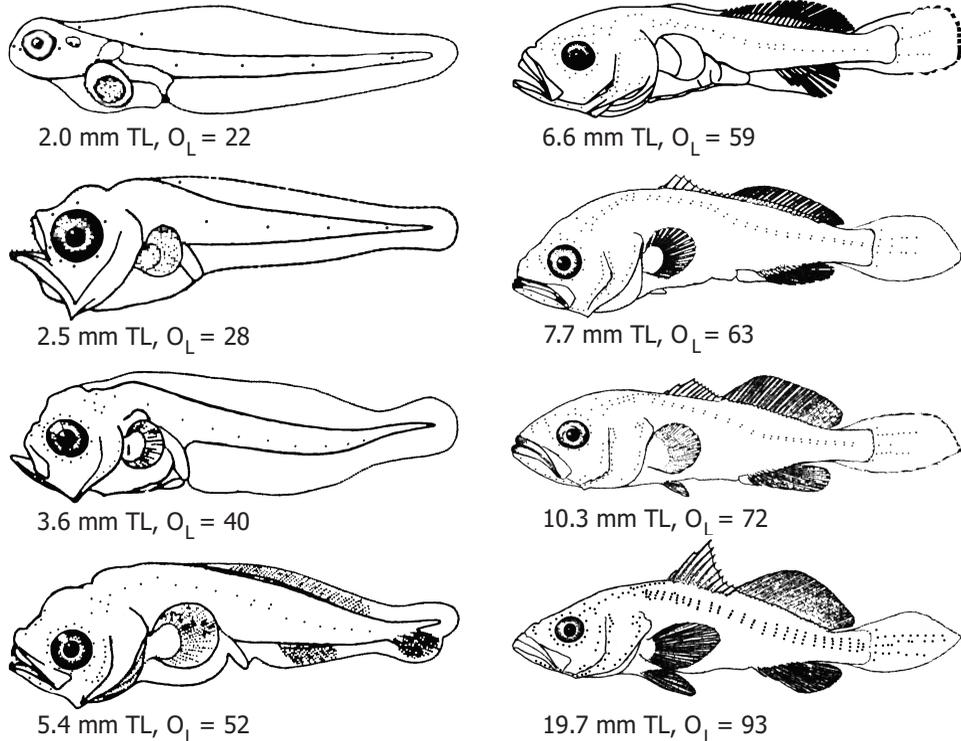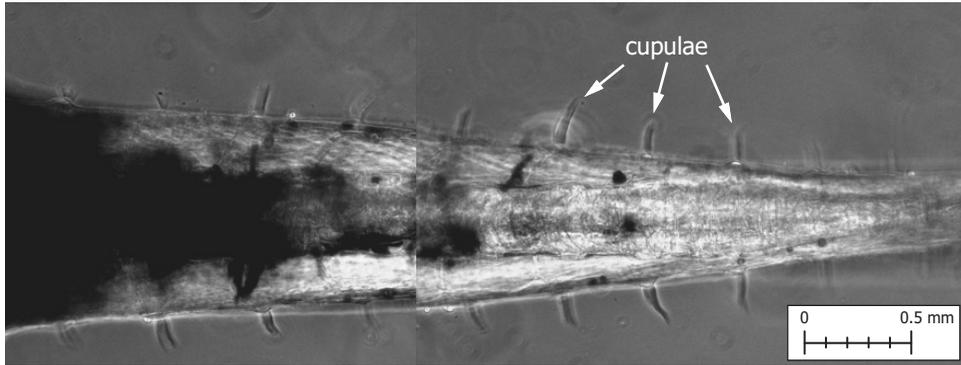
Figure 4. Photo: Dorsal view (anterior to the left) of the caudal peduncle of a larval red drum (6.4 mm TL), showing projecting neuromast cupulae. Drawings: Proliferation of superficial neuromasts (represented by dots) during development of spotted seatrout *Cynoscion nebulosus*. Sizes and ontogenetic state values refer to the distribution of neuromasts; drawings of fish only approximate these values. (Photo by B. Sarkisian. Drawings modified from Hildebrand and Cable 1934).

Neuromasts of the supraorbital and infraorbital series are among the first to appear in most species. Soon thereafter, the initial trunk neuromasts erupt, followed by the remaining presumptive canal neuromasts (Figure 4). The rate of addition of neuromasts is generally constant within a species, relative to ontogenetic state (O_L) or the logarithm of TL (correlation coefficient, $r = 0.81$–0.99 with a median of 0.96 for 24 species), but there are differences between species. Our analysis of published data for 24 species of freshwater and marine larvae reveals a compact group of 13 species with a relatively slow rate of neuromast proliferation. Their first neuromasts appear when the species is 20–50% developed (Figure 5). Another group of species
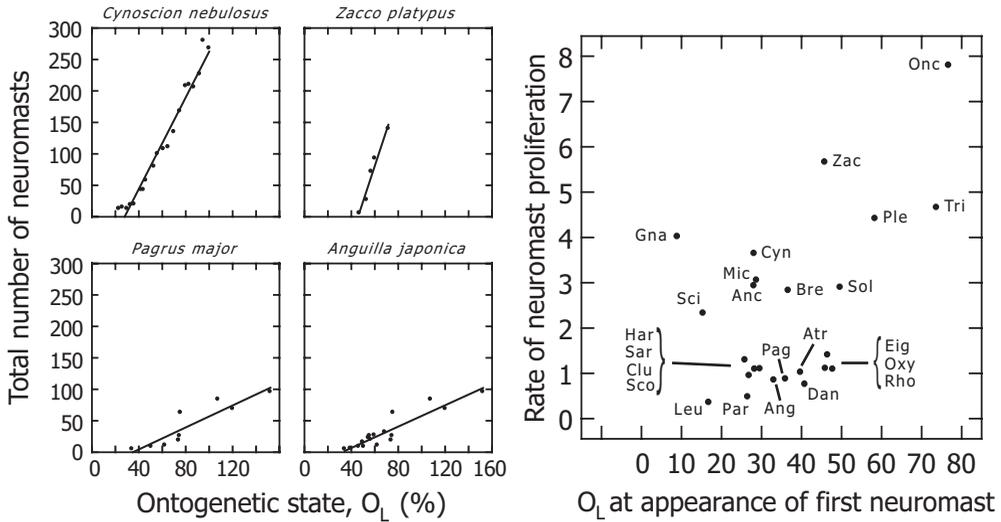
Figure 5. Proliferation of neuromasts during ontogeny in 24 species of marine and freshwater fish larvae. Four panels on left show increase in total number of neuromasts (one side of body) for representative species. Larger plot (right) shows regression statistics, expressed in terms of development, for all 24 species. Rate of neuromast proliferation is the slope of the regression of total neuromasts against ontogenetic index (O_L). O_L at appearance of first neuromast was calculated for each species from the same regression (i.e., O_L when $y = 1$). Species and data sources are: Anc – *Anchoa mitchilli*, Higgs and Fuiman 1998b; Ang – Japanese eel *Anguilla japonica*, Okamura et al. 2002; Atr – white seabass *Atractoscion nobilis*, Margulies 1989; Bre – *Brevoortia tyrannus*, Higgs and Fuiman 1998b; Clu - *Clupea harengus*, Blaxter et al. 1983; Cyn – *Cynoscion nebulosus*, Poling and Fuiman 1998; Dan – *Danio rerio*, Ledent 2002; Eig – glass knifefish *Eigenmannia virescens*, Vischer 1989; Gna – willow shiner *Gnathopogon elongatus caerulescens*, Mukai and Kobayashi 1995; Har – *Harengula jaguana*, Higgs and Fuiman 1998b; Leu – Eurasian dace *Leuciscus leuciscus*, Lekander 1949; Mic – Atlantic croaker *Micropogonias undulatus*, Poling and Fuiman 1998; Onc – *Oncorhynchus keta*, Disler 1960; Oxy – marble goby O*xyeleotris marmoratus*, Senoo et al. 1994; Pag – *Pagrus major*, Okamoto et al. 1982; Par – *Paralichthys olivaceus*, Kawamura and Ishida 1985; Ple – plaice *Pleuronectes platessa*, Harvey et al. 1992; Rho – greenback flounder *Rhombosolea tapirina*, Pankhurst and Butler 1996; Sar – *Sardinops melanostictus*, Matsuoka 2001; Sci – *Sciaenops ocellatus*, Poling and Fuiman 1998; Sco – turbot *Scopthalmus maximus*, Neave 1986; Sol – sole *Solea solea*, Harvey et al. 1992; Tri – Japanese dace *Tribolodon hakonensis*, Mukai and Kobayashi 1994; Zac – freshwater minnow *Zacco platypus*, Mukai and Kobayashi 1994.

develops neuromasts very rapidly, but species within that group vary in the ontogenetic state at which the first neuromast appears (10–80% developed). We are unable to see a phylogenetic or ecological pattern in the distribution of species among these groups. It would be interesting to explore the functional or ecological consequences of differing rates of neuromasts proliferation.

Characteristics of individual neuromasts also change during posthatching development. Newly differentiated neuromasts may have a single or very few hair cells, but the number of hair cells per neuromast increases rapidly (Harvey et al. 1992; Mukai and Kobayashi 1994; Northcutt 1997; Okamura et al. 2002). Similarly, the size of each neuromast, measured at the apical surface, increases during the larval period (Mukai and

Kobayashi 1994; Okamura et al. 2002). Even the cupulae increase in length during development, for example, from 60 to 70 mm to 175–190 mm in the knifefish *Eigenmannia* (Vischer 1989).

The last major developmental change to the lateralis system is the formation of canals. Canal formation begins when ectodermal ridges appear on both sides of a series of presumptive canal neuromasts, so that the neuromasts become contained within a groove. The ridges gradually close over the neuromasts but leave gaps that become lateral line pores (although there may be multiple neuromasts between pores, and not every neuromast occurs directly between pores) (Vischer 1989; Webb 1989b; Northcutt 1997). In all species where it is known, canal formation begins late in the larval period, at O_L of about 80 (range: 70–106 for 15 species reported in the literature).

The first canals to form are the supraorbital and infraorbital. Trunk canals begin to form somewhat later. It has been suggested that canals form when larvae are large and fast enough that the hydrodynamic boundary layer during routine swimming is no longer sufficient to protect the cupulae from overstimulation (Blaxter and Fuiman 1989). An alternative explanation is that canals do not develop earlier because their inside dimensions would be too small to allow flow sufficient to stimulate the enclosed neuromasts (Lara 1999).

Little is known about the development of the few accessory structures that link the lateralis system with the swim bladder. The lateral recess membrane, which functionally links the canal system to the ear and swim bladder, is capable of generating water movements in the canal of Atlantic herring larvae when they are 26 mm TL (O_L = 84) (Blaxter et al. 1983). Developmental timing of this feature is not known for any other clupeoids, but it cannot effectively move water within lateral line canals until the temporal lateral line canal closes. Nothing has been reported on the development of the laterophysic connection found in some chaetodontid fishes (Webb 1998; Webb and Smith 2000).

Larval performance

METHODS.—Several approaches have been employed to examine the changing function of the lateralis system through the larval period, each with a different degree of convenience, sophistication, animal manipulation, and potential bias. These approaches include associative studies that relate ontogenetic changes in one or more lateralis-mediated behaviors to the changing morphology of the lateralis system, and manipulative experiments that either alter the sensory environment of larvae or ablate neuromast function mechanically or chemically. Associative studies use the gradual recruitment of new neuromasts throughout the larval period and the late appearance of canals and accessory structures as a natural experiment in which some degree of sensory function is presumed absent in younger individuals because the necessary structures have not yet differentiated. Often, these associations of performance with morphology are made indirectly, by interpreting new performance data in the context of published studies of developmental morphol-

ogy. However, studies that combine direct observations of form and function are becoming more common (Margulies 1989; Higgs and Fuiman 1996; Poling and Fuiman 1997).

Manipulative experiments have used various stimuli and responses mediated by the lateralis system, including artificial devices that emit simplified sensory signals (an advancing hand-held probe, suction or water jets from a pipette, or an electronically controlled vibrating sphere) and biological stimuli with realistic, but very complex and variable, sensory characteristics (prey or predators). Mechanical ablation of neuromast function has been achieved by dislodging cupulae (and possibly kinocilia and stereocilia) with the turbulence created by vigorous aeration (Blaxter and Fuiman 1989), scraping the skin (Disler 1960; Coombs et al. 2001), or inserting a thread into the lateral line canals of larger fishes (Abdel-Latif et al. 1990; Janssen 1996). The obvious difficulty of applying physical damage to delicate fish larvae without unintended impairments or death leaves chemical methods as the more realistic approach for blocking neuromast function. Larvae can be placed into solutions containing cobalt ions or an aminoglycoside antibiotic, such as streptomycin, gentamycin, neomycin, and kanamycin, to inhibit hair cell transduction (Wersäll and Flock 1964; Karlsen and Sand 1987). The effect of cobalt and aminoglycosides can be reversed, making these methods especially good for confirming the role of the lateralis system in a given response. The action of both classes of chemicals is antagonized by calcium, so their efficacy in seawater, where calcium is very abundant, can be problematic. Thus, higher concentrations of cobalt or antibiotic are required in seawater.

When using chemical treatments, caution must be exercised to guard against unwanted side effects. Karlsen and Sand (1987) showed that long-term exposure (1–2 weeks) to cobalt ions at 1 mmol/L was lethal to fish, perhaps due to osmoregulatory dysfunction, and thus, recommended Co^{2+} levels no higher than 0.1 mmol/L. Similar toxicity results have been found for shorter term Co^{2+} exposure. Janssen (2000) reported that Co^{2+} concentrations of 2 mmol/L (the same as used in earlier studies of lateral line function; Montgomery et al. 1997; Baker and Montgomery 1999), were toxic to fish by 17 h exposure. This led Janssen to question the results of studies that used

high concentrations of Co^{2+} to disrupt lateral lines, due to general health effects. In the case of Montgomery et al. (1997) and Baker and Montgomery (1999), fish were exposed to cobalt for only 3 h, and the behavior of treated fish was identical to those with physically damaged superficial neuromasts, suggesting that health effects of cobalt treatment were not the main cause of patterns seen. Such careful comparisons must also be made by experimenters treating fish with aminoglycosides. While there is no current evidence that aminoglycosides affect transduction of hair cells of the ear, that potential problem does exist (Lombarte et al. 1993). In that regard, Janssen's (2000) warning is worth bearing in mind. Whenever chemical treatment is used, careful observation is required to ensure that only healthy fish are used for behavioral experiments. This is especially important when adapting doses previously used in adult fishes for use on larval fishes, since chemical concentrations recommended for large fishes may not be safe for larvae (J. Janssen, University of Wisconsin, personal communication).

Several studies have drawn conclusions about the function of the lateralis system in fish larvae (and later life stages) based on the presumption that all neuromasts are ablated as a result of brief exposure to an aminoglycoside antibiotic. The finding that gentamycin damages hair cells in canal neuromasts, but not superficial neuromasts, of an adult fish (Song et al. 1995) raises important questions and may have serious ramifications for these studies. Do other aminoglycoside antibiotics (streptomycin, neomycin, kanamycin, etc.) have the same differential effect on canal and superficial neuromasts? Wersäll and Flock (1964) showed that streptomycin suppresses canal neuromast responses, while Montgomery et al. (1997) and Baker and Montgomery (1999) showed that streptomycin treatment has the same effect as superficial neuromast ablation, suggesting streptomycin disrupts all lateral line function. Also, since it is not the canals themselves that make their neuromasts more susceptible to gentamycin (Song et al. 1995), do presumptive canal neuromasts have the same response to gentamycin before canal formation? Differences in embryological origin and morphology (size, shape, number of hair cells) suggest that the two classes of neuromasts are distinct even before canal formation. Depending on the answers to these two questions, it is possible that the antibiotic treatments

that were intended to ablate all neuromasts in larvae actually ablated only the presumptive canal neuromasts and left the other neuromasts functional. If so, the responses that were reduced or eliminated in larvae by treatment with the antibiotic may have been mediated solely by presumptive canal neuromasts lying outside of canals. Reinterpretation of prior experiments would be premature at this time, but the implications of the significant discovery of Song et al. (1995) must be kept in mind.

The body of literature that contributes to our understanding of the developmental changes in form and function of the lateralis system is larger than that for the auditory system. It is best summarized from an ecological and behavioral perspective. The nature of the stimulus applied or the response observed places each study in one of four ecological contexts: rheotaxis, schooling, feeding, and predator evasion.

Rheotaxis and schooling.—Rheotaxis and schooling are behaviors that require a fish to maintain position as water flows across its body and therefore have the potential to involve the lateralis system. In rheotaxis, water flows past the fish at a more or less constant velocity, whereas in schooling, water is accelerated by the swimming motions of nearby school members or by a fish's own changes in velocity. Therefore, the velocity sensitivity of superficial neuromasts is appropriate for rheotaxis, as suggested for adult fishes by the experimental results of Montgomery et al. (1997), and the sensitivity of canal neuromasts to water accelerations is more appropriate for schooling (Pitcher et al. 1976; Partridge and Pitcher 1980).

Rheotaxis in larvae has not received much research attention. In both largemouth bass *Micropterus salmoides* and Nile tilapia *Oreochromis nilotica*, rheotaxis appears to begin relatively early in the larval period, at 2.5 and 5 d after hatching (Kawamura and Washiyama 1989). Striped jack *Pseudocaranx dentex* larvae as small as 4.5 mm TL ($O_L = 44$) exhibited positive rheotaxis in a flow of 1.7 cm/s, but the response was not consistent among individuals until they reached 6 mm TL ($O_L = 53$) (Masuda and Tsukamoto 1996). Kawamura and Washiyama (1989) inferred that rheotaxis requires functional superficial neuromasts because the response appeared after at least some neuromasts were present on the skin, although the authors did not describe the methods

they used to determine the presence of rheotaxis. Lateral line canals clearly are not necessary because rheotaxis occurs in all three species long before canals form.

Some of the earliest research on the development of form and function of the lateralis system was conducted by Cahn and colleagues, who examined the relationship between schooling behavior and lateral line development in Atlantic silverside *Menidia menidia* and inland silverside *M. beryllina*. They observed that, during the larval period, schooling stabilized once the larvae were able to maintain position in a current and when neuromasts became innervated and lateral line canals began to form (Cahn and Shaw 1965; Cahn et al. 1965). Specifically, schooling behavior first appeared in larvae greater than or equal to 9 mm in length ($O_L = 84$), the same stage at which the grooves that precede closure of lateral line canals on the head began to form. Cahn et al. (1968) reported that some, but not all, neuromasts were innervated by the time grooves formed, but that all neuromasts in closed canals were innervated. Cahn et al. (1965) suggested that a functional lateralis system (which they believed occurred when canals formed) is an accessory to the visual system in control of schooling in fishes.

The work of Cahn and her colleagues is often cited to support the notion that lateral line canal system functionality is a prerequisite of schooling, even though the conclusion was based entirely on associative observations and vaguely described methods. Although it is true that both schooling behavior and lateral line canals develop relatively late in fishes, the association between behavioral and morphological development is not so precise. Atlantic herring and northern anchovy *Engraulis mordax* form highly organized schools as adults, and this behavior appears at lengths of 25–35 mm TL ($O_L = 83$–91) for herring (Rosenthal 1968; Gallego and Heath 1994) and 13–15 mm TL for anchovy (Hunter and Coyne 1982). In contrast, lateral line canals begin to form at 18 mm TL in both species, which is $O_L = 74$ for herring (Allen et al. 1976; Hunter and Coyne 1982). A study of the morphological development of sense organs and corresponding behavioral changes in two freshwater species, largemouth bass and Nile tilapia, demonstrated that, in both species, schooling appeared before any lateral line canals developed but after the first superficial neuromasts formed (Kawamura and Washiyama 1989).

Many of these associative studies failed to provide a definition of schooling or the criteria used for determining when schooling was present. This makes it difficult to compare studies because they may have used different definitions. Masuda and Tsukamoto (1999) greatly reduced the subjectivity of determining whether a group of striped jack larvae was schooling by measuring separation angle and interindividual distance. They found that schooling appeared when larvae were about 16 mm TL ($O_L = 82$), much later than the onset of rheotaxis ($O_L = 44$) and about the time that cephalic lateral line canals were complete (18 mm TL, $O_L = 85$). They felt that the time lag between the onsets of rheotaxis and schooling was not satisfactorily explained by development of external sensory (or locomotor) structures, so they reared a related jack species, buri *Seriola quinqueradiata*, on a diet depleted of docosahexaenoic acid (DHA) to impair normal development of the central nervous system. Larvae reared on the DHA-deficient diet failed to form schools when they reached the size at which schooling normally occurred, even though visually mediated taxis (optokinetic response) developed as normal. Based on these results, Masuda and Tsukamoto (1999) suggested that, in striped jack larvae, taxis operates through the peripheral nervous system, whereas schooling behavior operates through the central nervous system.

FEEDING.—The zooplankton and benthic invertebrates that comprise much of the prey of larval fishes generate water disturbances as they move. The relatively low frequencies of swimming movements and the short distance over which this predator–prey interaction takes place are ideal for involvement of the lateralis system.

Superficial neuromasts were implicated in larval fish feeding based on experiments that used the acidic properties of the anesthetic tricaine methansulfonate (MS-222) to disrupt neuromast cupulae in willow shiner larvae. Mukai et al. (1994) found that neuromast cupulae were removed and feeding success in the dark was reduced by treatment with MS-222. The effect appeared to be caused by the acidity of the anesthetic, as larvae treated with buffered MS-222 (pH = 7.3) were significantly more successful feeding in the dark than larvae treated with unbuffered anesthetic (pH = 4.2). Regeneration of cupulae was complete after about 24 h, and feeding success of larvae in the

dark improved steadily as the length of the regenerating neuromasts increased. The feeding response might also be explained, however, by recovery from the physiological effects of the anesthetic or its acidity. These results also reveal that acidic anesthetics, such as MS-222, may be inappropriate for general use if lateral line function is necessary after the fish are revived.

There are anecdotal reports of fish larvae feeding in darkness in the laboratory or collected in the field late in the night with food in their guts. The implication of these observations is that such feeding was mediated by the lateralis system, as it is in adult fishes (Janssen et al. 1995). Experimental studies have confirmed this. Salgado and Hoyt (1996) isolated sensory systems in fathead minnow *Pimephales promelas* larvae and found that larvae from 3 d posthatching (first feeding, 5.4 mm TL, $O_L = 51$) to 7 d posthatching (about 7 mm TL, $O_L = 58$) were able to feed in the dark and did so more frequently on live prey (*Artemia* sp.) than dead prey. Salgado and Hoyt (1996) indicated that fathead minnows have neuromasts on the head and body surface at hatching. Although they did not describe the timing of canal development, canals were probably not present in the young larvae they studied. Jones and Janssen (1992) found that mottled sculpin *Cottus bairdi* larvae were able to locate moving prey (*Artemia* sp.) in the dark unless their neuromasts were ablated by streptomycin treatment. As canals formed, the distance at which sculpins responded to prey decreased, reflecting a decrease in sensitivity of the lateralis system. This decrease in sensitivity was assumed to be temporary; however, studies of adult sculpins have demonstrated that biting and orienting responses are largely meditated by canal neuromasts (Coombs and Janssen 1989; Coombs et al. 2001). Using similar techniques, Batty and Hoyt (1995) found that, although both sole and plaice were able to feed on live copepods (*Tigriopus* sp.) in the dark, the feeding rate of plaice was reduced in the dark, while sole fed equally well under both conditions. Streptomycin treatment resulted in significantly reduced feeding activity in sole, but not plaice. Interestingly, sole, and to a lesser extent plaice, were able to feed in the dark without the use of the lateralis system, presumably via chemoreception. These studies were conducted on recently metamorphosed flatfishes (19–21 mm TL, $O_L = 118–123$).

PREDATOR EVASION.—Laboratory experiments have shown that the responsiveness of fish larvae of many species to attacks by predatory fishes improves with development (Fuiman 1994). Fewer studies have combined such experiments with detailed analysis of the developing sensory systems. In one of the most comprehensive of these studies, Margulies (1989) not only examined development of the lateralis and visual systems in white seabass, but also compared responsiveness of larvae to attacks by different types of predatory fishes. Adult northern anchovy attacked larval seabass at relatively high speed, whereas juvenile white seabass attacked larvae more slowly and initiated their attack from a shorter distance than anchovy. Responsiveness of seabass larvae increased with development regardless of the predator species. By comparing these observations with sensory development, Margulies (1989) attributed the general ontogenetic increase in responsiveness of larvae to an increase in the number of superficial neuromasts and improvements in the visual system. He suggested that responses by larvae less than 4.5 mm SL ($O_L = 55$) were mediated by superficial neuromasts because visual acuity is poor at that stage and lack of gas in the swim bladder would reduce auditory inputs. Margulies (1989) suggested that the increasing responsiveness of seabass larvae greater than 5–7 mm SL ($O_L = 56–68$) was due to improvements of the lateralis and visual systems.

Margulies (1989) also found that responsiveness of smaller larvae was the same for both species, but larvae greater than 7.5 mm SL ($O_L = 70$) were more responsive to attacks by juvenile seabass than to attacks of the faster anchovy. He attributed the higher responsiveness of larvae attacked by juvenile seabass to the slower speed of those attacks (giving larvae more time to respond). Differences in the stimuli emitted by the two predator species may also have been important, especially if the juvenile seabass used suction and adult anchovy did not. The importance of suction as a stimulus was evident in the data of Yin and Blaxter (1987), who found that Atlantic herring, Atlantic cod *Gadus morhua*, and flounder (also known as European flounder) *Platichthys flesus* larvae, prior to lateral line canal formation, were more responsive to suction applied through a pipette (in the light) than to the approach, and even touch, of a hand-held probe.

Other studies have used a hand-held probe to

elicit evasive responses in fish larvae, but with the specific goal of determining the role of the lateralis system in the response. Young Atlantic herring, cod, and plaice larvae (8.6, 4.7, and 4.3 mm TL; O_L = 55, 41, and 59) responded to an advancing probe in the dark at distances of 1–3 mm from the probe (Blaxter and Fuiman 1989). Treatment of larvae with streptomycin eliminated these distance responses in all three species. Comparable methods applied to larvae of five other species, two clupeoids (Higgs and Fuiman 1998a) and three sciaenids (Poling and Fuiman 1999), confirmed that the lateralis system contributes to responses to an advancing probe in the dark.

These same three studies examined the ontogeny of responses in the dark. Blaxter and Fuiman (1989) found that responsiveness of Atlantic herring larvae remained relatively constant up to about 11.3 mm TL (O_L = 62), but decreased sharply at 13.2 mm TL (O_L = 66). The distance at which herring larvae responded decreased continually during development (prior to lateral line canal formation), from about 3 mm at 9.7 mm TL (O_L = 58) to 1–2 mm at 13.2 mm TL (Blaxter and Fuiman 1989). The decreases in responsiveness and reactive distance suggest an ontogenetic decrease in sensitivity for this species. In contrast, data of Higgs and Fuiman (1998a) for Atlantic menhaden and bay anchovy, and Poling and Fuiman (1999) for spotted seatrout, Atlantic croaker, and red drum showed that responsiveness remained constant or increased slightly throughout the larval period in four of the species. The exception was bay anchovy, in which responsiveness decreased ontogenetically. Reactive distance in the dark increased steadily during development for all five species, increasing from 1 to 2 mm in recently hatched larvae to 4–16 mm closer to metamorphosis, suggesting a strong increase in sensitivity of the lateralis system. All five species in which reactive distance increased ontogenetically were among the group of species characterized by a rapid rate of neuromast proliferation relative to O_L, and the only species with decreasing reactive distance (herring) was in the group of species that had a slow rate of neuromast proliferation (Figure 5). This suggests that, since O_L directly reflects body size, neuromast density (for example, number per unit body length or area) has functional consequences for sensitivity (reactive distance, but not responsiveness). Higgs and Fuiman (1998b) provided data on ontoge-

netic changes in neuromast density and suggested the possibility that neuromast density, rather than total number, may be functionally (and ecologically) important.

Despite the advantages of being able to control an artificial stimulus such as a hand-held probe, a predator presents a much more complex and variable suite of stimuli to which a larva may respond. Nevertheless, it is possible to combine selective sensory ablation with a natural stimulus to come to a better understanding of the role of the various senses in ecological interactions. Atlantic herring are unusual in that for much of the larval period (from hatching until O_L = 85 or 27 mm TL) responsiveness to an attacking fish is very low and constant (approximately 6%), after which it increases abruptly, reaching 65% by O_L = 89 or 32 mm TL (Fuiman 1989). Noting that this rapid increase corresponded to the time when gas appeared in the auditory bullae, Fuiman (1989) compared the responsiveness of 32 mm TL larvae that had gas in the bullae with that of a few 32 mm TL larvae that still had not filled the bullae. Larvae without gas in the bullae never responded to the predator's attack, whereas those with gas in the bullae responded to 68% of attacks. Since the bullae of clupeoids provide an indirect pathway to both the ear and the lateralis system, imparting pressure sensitivity to both systems, it was apparent that the pressure component of the predator's approach might play a major role in triggering a response, but it remained unclear whether the lateralis system contributed to this sudden increase in responsiveness.

Ablation of neuromasts with streptomycin had no significant effect on responsiveness of herring larvae to a predatory fish up to O_L = 74 (18 mm TL). At O_L = 89 (32 mm TL), with gas-filled auditory bullae and complete cephalic lateral line canals, ablation of neuromasts resulted in responsiveness of 43%, as compared to 69% for control fish of the same size (Blaxter and Fuiman 1990). Further experiments on three size-groups of larvae within the span of development in which the bullae fill with gas and lateral line canals form verified the role of the canal neuromasts. Responsiveness of larvae averaging 21.7 mm TL (without gas in the bullae, O_L = 90) was low (9–15%) and unaffected by streptomycin. Slightly larger larvae, which had gas in the bullae but no lateral line canals (23.9 mm TL), also had low responsiveness (14%). Larger larvae (29.6 mm TL, O_L =

100), which had gas in the bullae and neuromasts enclosed in cephalic lateral line canals, were significantly more responsive (59%), unless the neuromasts were ablated with streptomycin (21%). Reactive distance to an attacking predator in the light was short (2–4 cm) but considerably greater than the reactive distance of most species to an approaching probe in the dark. These results confirm that neuromasts within lateral line canals mediate the response of Atlantic herring larvae to an attacking fish (Blaxter and Fuiman 1990).

Conclusions and Needs for Further Research

Our review of the developmental changes in morphology of the peripheral components of the octavolateralis system in fishes highlights a few major ontogenetic patterns. In both the auditory and lateralis systems, the number of end organs (hair cells and neuromasts) increases gradually throughout the larval period, roughly in proportion to somatic growth. Accessory structures that enhance each system's function (swim bladder, Weberian ossicles, auditory bullae, lateral line canals) develop late in the larval period. Published studies provide evidence that these major ontogenetic trends in morphology have demonstrable functional consequences. In some hearing generalists, for example, auditory sensitivity increases possibly as a result of the increasing number of hair cells in the maculae. Sensitivity of the lateralis system appears to be related to the density of neuromasts. Species that exhibit a high rate of superficial neuromast proliferation relative to somatic growth achieve an increasing level of functionality, whereas lateralis-system performance diminishes in at least one species with a low rate of neuromast proliferation. In hearing specialists (Cyprinidae, Clupeoidei), an expansion of auditory bandwidth (but not sensitivity) coincides with development of otophysic connections (Weberian ossicles, auditory bullae).

Experimental studies indicate that the auditory system, the lateralis system, or both play a role in a variety of ecological activities of larval fishes. Studies also verify the presumption that the ontogenetic increase in sensory system complexity expands a larva's behavioral repertoire and improves its ability to participate in ecological activities and thereby withstand ecological

challenges. For example, larvae respond better to prey and predators as components of the octavolateralis system elaborate. There are preliminary indications that perception of sounds emanating from reefs may enable planktonic reef fish larvae to find their settlement habitat. Although schooling is mediated primarily by visual cues, formation of lateral line canals appears to improve coordination of school members. Ecological interpretations of results from studies of octavolateralis function must always recognize that animals normally act on information received simultaneously from multiple sensory channels. Responses obtained under restricted sensory conditions may be very different from responses in nature, where more and different types of information are available.

The two components of the adult lateral line systems—superficial neuromasts and canal neuromasts—have different response properties and appear to subserve different ecological functions. It is not clear, however, whether the differences in neuromast response properties exist in larvae before canals enclose some of the neuromasts. That is, do the response properties result from fundamental differences in the neuromasts or differences in their environment (enclosed in canals or not). By virtue of the fact that all neuromasts in larvae are exposed on the epidermis until canals form, those neuromasts have been called superficial neuromasts and assumed to function uniformly and in the same manner as the superficial neuromasts in adult fishes. Differences in embryological origin, morphology, and response to pharmacological agents suggest that there may be at least two distinct classes of neuromasts. An important question is whether they function differently before canals form. If so, a new terminology, based on response properties, will need to be applied so that the different classes of neuromasts can be distinguished in larvae. One immediate research need is to clarify the effects of aminoglycoside antibiotics. It must be determined whether the differential effects of gentamycin on superficial and canal neuromasts (Song et al. 1995) are characteristic of related compounds and whether the same effects can be demonstrated in earlier stages of lateralis system ontogeny. Differences in methods of administering antibiotics also must be examined. Song et al. (1995) bathed oscar cichlids in a 0.002% solution of gentamycin sulfate in freshwater for a pe-

riod of 1–4 d and observed physical damage to the apical cilia of canal neuromasts, but not superficial neuromasts. Typical doses of streptomycin used in studies of behavior in marine fish larvae are necessarily higher (5–10 mmol/L, 0.73–1.46%) but much more brief (2–5 min; Blaxter and Fuiman 1989, 1990; Higgs and Fuiman 1996, 1998a; Poling and Fuiman 1997, 1999). The brief exposures given larvae may produce only a general physiological effect that may include hair cells of all neuromasts (A. N. Popper, personal communication).

While still challenging, it is now possible to examine developmental changes in auditory and lateral line systems with physiological recordings (using the ABR technique). This line of research should be pursued more vigorously in the future. Examination of changes in sensory physiology as structures develop can provide a great deal of information on sensory capabilities in larvae and the role discrete structures play in larval and adult responses. Similar approaches have been conducted in birds and mammals and have provided useful insights into the function of different portions of the auditory system and central circuitry (e.g., Ehret and Romand 1981; Gray and Rubel 1985; Walsh et al. 1986; Dmitrieva and Gottlieb 1992). A similar approach in developing fishes would more conclusively delineate the role of sensory hair cell addition, swim bladder inflation, and canal enclosure, for example, in the functioning of auditory and lateral line systems and their integration. Coupling of physiological experiments with behavioral trials would further increase the utility of this approach. Differences seen between physiological and behavioral results can ascertain whether there is a direct effect of structural development or if developmental changes are more integrative in nature.

The majority of research on teleosts has examined either the acoustic or lateralis systems in isolation. A few studies have examined development of more than one system, but to our knowledge, no research has yet been done on the development of multi-modal sensory integration in fishes. An object of potential biological relevance to a fish can simultaneously emit visual, olfactory, auditory, mechano-sensory, and even electrical cues. Each of these cues will impinge on a fish simultaneously, causing the fish to integrate information from a variety of sensory receptors to decide whether the object is to be eaten, escaped from, mated with, or ignored. Adult fishes clearly can integrate information from multiple sensory modalities (Bastian 1982; Schellart 1983; Schellart et al. 1987; New et al. 2001). The ontogeny of multi-modal sensory integration would have important implications for larva survival and, therefore, recruitment, ecology, and aquaculture. Until more effort is devoted to examining integration of information from multiple sensory modalities, we will remain ignorant as to how a larval fish perceives and responds to its world.

Regardless of the approach taken, much more attention must be paid to responses using natural stimuli, especially in the auditory system. Artificial stimuli have been used with success to tell us much about auditory and lateral line function, but it is difficult to extrapolate from these laboratory studies to questions of ecological relevance of auditory and lateral line capabilities. The aquatic environment is inherently noisy, both in terms of auditory and mechanosensory stimuli, and yet fish are clearly able to extract useful information from high levels of background noise. The mechanics of how the auditory and lateralis systems extract signals from noise have been examined using artificial maskers and tones, but the ecological relevance of this ability is still unclear. We suggest more studies should be designed to, first, identify what signals are of interest to fishes, second, how these signals may differ in different habitats or between species, and third, using these signals in laboratory and field studies to investigate how fish respond to these signals. This will provide a more realistic view of how fish interpret natural signals at physiological and behavioral levels to interact with their environment.

Acknowledgments

References

Abdel-Latif, H., E. S. Hassan, and C. von Campenhausen. 1990. Sensory performance of blind Mexican cave fish after destruction of the canal neuromasts. Naturwissenschaften 77:237–239.

Allen, J. M., J. H. S. Blaxter, and E. J. Denton. 1976. The functional anatomy and development of the swimbladder – inner ear – lateral line system in herring and sprat. Journal of the Marine Biological Association of the United Kingdom 56:471–486.

Atema, J., R. R. Fay, A. N. Popper, and W. N. Tavolga, editors. 1988. Sensory biology of aquatic animals. Springer-Verlag, New York.

Baker, C. F., and J. C. Montgomery. 1999. The sensory basis of rheotaxis in the blind Mexican cave fish, *Astyanax fasciatus*. Journal of Comparative Physiology A 184:519–527.

Bang, P. I., W. F. Sewell, and J. J. Malicki. 2001. Morphology and hair cell type heterogeneities of the inner ear epithelia in adult and juvenile zebrafish (*Danio rerio*). Journal of Comparative Neurology 438:173–190.

Bastian, J. 1982. Vision and electroreception: integration of sensory information in the optic tectum of the weakly electric fish *Apteronotus albifrons*. Journal of Comparative Physiology 147:287–297.

Batty, R. S., and R. D. Hoyt. 1995. The role of sense organs in the feeding behaviour of juvenile sole and plaice. Journal of Fish Biology 47:931–939.

Becerra, M., and R. Anadón. 1993a. Development of the inner ear of the brown trout (*Salmo trutta fario*): I. Gross morphology and sensory cell proliferation. Journal of Morphology 216:209–223.

Becerra, M., and R. Anadón. 1993b. Development of the inner ear of the brown trout (*Salmo trutta fario*): II. Cytodifferentiation and innervation of sensory cells. Journal of Morphology 216:241–257.

Best, A. C. G., and J. A. B. Gray. 1980. Morphology of the utricular recess in the sprat. Journal of the Marine Biological Association of the United Kingdom 60:703–715.

Bever, M. M., and D. M. Fekete. 2002. Atlas of the developing inner ear in zebrafish. Developmental Dynamics 223:536–5443.

Blaxter, J. H. S. 1987. Structure and development of the lateral line. Biological Reviews 62:471–514.

Blaxter, J. H. S., and D. E. Hoss. 1981. Startle response in herring: the effect of sound stimulus frequency, size of fish and selective interference with the acoustico-lateralis system. Journal of the Marine Biological Association of the United Kingdom 61:871–879.

Blaxter, J. H. S., E. J. Denton, and J. A. B. Gray. 1981. Acousticolateralis system in clupeid fishes. Pages 39–59 in W. N. Tavolga, A. N. Popper, and R. R. Fay, editors. Hearing and sound communication in fishes. Springer-Verlag, New York.

Blaxter, J. H. S., J. A. B. Gray, and A. C. G. Best. 1983. Structure and development of the free neuromasts and lateral line system of the herring. Journal of the Marine Biological Association of the United Kingdom 63:247–260.

Blaxter, J. H. S., and R. S. Batty. 1985. The development of startle responses in herring larvae. Journal of the Marine Biological Association of the United Kingdom 65:737–750.

Blaxter, J. H. S., and L. A. Fuiman. 1989. Function of the free neuromasts of marine teleost larvae. Pages 481–499 in Coombs et al. (1989).

Blaxter, J. H. S., and L. A. Fuiman. 1990. The role of the sensory systems of herring larvae in evading predatory fishes. Journal of the Marine Biological Association of the United Kingdom 70:413–427.

Bleckmann, H. 1988. Prey identification and prey localization in surface-feeding fish and fishing spiders. Pages 619–641 in Atema et al. (1988).

Bleckmann, H. 1991. Orientation in the aquatic environment with the aid of hydrodynamic stimuli. Verhandlungen Deutsche Zoologische Gesellschaft 84:105–124.

Bleckmann, H. 1993. Role of the lateral line in fish behaviour. Pages 201–246 in T. J. Pitcher, editor. Behaviour of teleost fishes. 2nd edition. Chapman and Hall, London.

Bleckmann, H., and H. Münz. 1990. Physiology of lateral-line mechanoreceptors in a teleost with highly branched, multiple lateral lines. Brain, Behavior and Evolution 35:240–250.

Bogutskaya, N. G. 1991. Development of the Weberian apparatus during ontogeny of some species of Cyprinidae. Journal of Ichthyology 31:109–120.

Bretschneider, F., A. V. van den Berg, and R. C. Peters. 2001. Mechanoreception: hearing and lateral line. Pages 215–253 in G. von der Emde, J. Mogdans, and B. G. Kapoor, editors. The senses of fishes: adaptations for the reception of natural stimuli. Narosa Publishing House Pvt. Ltd., New Delhi.

Brown, A. L., M. S. Busby, and K. L. Mier. 2001. Walleye pollock *Theragra chalcogramma* during transformation from the larval to juvenile stage: otolith and osteological development. Marine Biology 139:845–851.

Cahn, P. H., and E. Shaw. 1965. A method for studying lateral line cupular bending in juvenile fishes. Bulletin of Marine Science 15:1060–1071.

Cahn, P. H., E. H. Atz, and E. Shaw. 1965. Lateral line nerve differentiation correlated with schooling in

the marine fish, *Menidia*. American Zoologist 5:225.

Cahn, P. H., E. Shaw, and E. H. Atz. 1968. Lateral-line histology as related to the development of schooling in the atherinid fish, *Menidia*. Bulletin of Marine Science 18:660–670.

Chao, L. N. 1978. A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). NOAA NMFS Technical Report Circular 415:1–61.

Chardon, M., and P. Vandewalle. 1997. Evolutionary trends and possible origin of the Weberian apparatus. Netherlands Journal of Zoology 47:383–403.

Cieri, M. D., and J. D. McCleave. 2000. Discrepancies between otoliths of larvae and juveniles of the American eel: is something fishy happening at metamorphosis? Journal of Fish Biology 57:1189–1198.

Coburn, M. M., and L. M. Futey. 1996. The ontogeny of supraneurals and neural arches in the cypriniform Weberian apparatus (Teleostei: Ostariophysi). Zoological Journal of the Linnean Society 116:333–346.

Cohen, M. J., and H. E. Winn. 1967. Electrophysiological observations on hearing and sound production in the fish, *Porichthys notatus*. Journal of Experimental Zoology 165:355–370.

Collazo, A., S. E. Fraser, and P. M. Mabee. 1994. A dual embryonic origin for vertebrate mechanoreceptors. Science 264:426–430.

Coombs, S., P. Görner, and H. Münz, editors. 1989. The mechanosensory lateral line: neurobiology and evolution. Springer-Verlag, New York.

Coombs, S., and A. N. Popper. 1979. Hearing differences among Hawaiian squirrelfish (Family Holocentridae) related to differences in the peripheral auditory system. Journal of Comparative Physiology 132:203–207.

Coombs, S., J. Janssen, and J. F. Webb. 1988. Diversity of lateral line systems: Evolutionary and functional considerations. Pages 553–593 *in* Atema et al. (1988).

Coombs, S., and J. Janssen. 1989. Peripheral processing by the lateral line system of the mottled sculpin (*Cottus bairdi*). Pages 299–319 *in* Coombs et al. (1989).

Coombs, S., and J. Janssen. 1990. Behavioral and neurophysiological assessment of lateral line sensitivity in the mottled sculpin, *Cottus bairdi*. Journal of Comparative Physiology, A 167:557–567.

Coombs, S., J. Janssen, and J. C. Montgomery. 1992. Functional and evolutionary implications of peripheral diversity in lateral line systems. Pages 267–294 *in* D. B. Webster, R. R. Fay, and A. N. Popper, editors. The evolutionary biology of hearing. Springer-Verlag, New York.

Coombs, S., C. B. Braun, and B. Donovan. 2001. The orienting response of Lake Michigan mottled sculpin is mediated by canal neuromasts. Journal of Experimental Biology 204:337–348.

Corwin, J. T. 1981. Postembryonic production and aging of inner ear hair cells in sharks. Journal of Comparative Neurology 201:541–553.

Corwin, J. T. 1983. Postembryonic growth of the macula neglecta auditory detector in the ray, *Raja clavata*: continual increases in hair cell number, neural convergence, and physiological sensitivity. Journal of Comparative Neurology 217:345–356.

Dehnhardt, G., B. Mauck, W. Hanke, and H. Bleckmann. 2001. Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). Science 293:102–104.

Denton, E. J., and J. H. S. Blaxter. 1976. The mechanical relationships between the clupeid swimbladder, inner ear and lateral line. Journal of the Marine Biological Association of the United Kingdom 56:787–807.

Denton, E. J., and J. A. B. Gray. 1979. The analysis of sound by the sprat ear. Nature (London) 282:406–407.

Denton, E. J., J. A. B. Gray, and J. H. S. Blaxter. 1979. The mechanics of the clupeid acoustico-lateralis system: frequency responses. Journal of the Marine Biological Association of the United Kingdom 59:27–47.

Denton, E. J., and J. A. B. Gray. 1989. Some observations on the forces acting on neuromasts in fish lateral line canals. Pages 229–246 *in* Coombs et al. (1989).

Denton, E. J., and J. A. B. Gray. 1993. Stimulation of the acoustico-lateralis system of clupeid fish by external sources and their own movements. Philosophical Transactions of the Royal Society of London 341:113–127.

Dijkgraaf, S. 1963. The functioning and significance of the lateral-line organs. Biological Reviews of the Cambridge Philosophical Society 38:51–105.

Dijkgraaf, S. 1989. A short personal review of the history of lateral line research. Pages 7–14 *in* Coombs et al. (1989).

Disler, N. N. 1950. Development of the sense organs of the lateral-line system of the perch and ruff. Trudy Instituta Morfologii Zhivotnykh im A. N. Severtsova 2:85–139. [Translation by Gosline and Gosline, Bureau of Commercial Fisheries, Ichthyolology Laboratory, U.S. National Museum, Washington, D.C.]

Disler, N. N. 1960. Lateral line sense organs and their importance in fish behaviour. Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 1971.

Dmitrieva, L. P., and G. Gottlieb. 1992. Development

of brainstem auditory pathway in mallard duck embryos and hatchlings. Journal of Comparative Physiology A 171:665–671.

Ehret, G., and R. Romand. 1981. Postnatal development of absolute auditory thresholds in kittens. Journal of Comparative Physiology and Psychology 95:304–311.

Engelmann, J., W. Hanke, J. Mogdans, and H. Bleckmann. 2000. Hydrodynamic stimuli and the fish lateral line. Nature (London) 408:51–52.

Fay, R. R. 1988. Hearing in vertebrates: a psychophysics databook. Hill-Fay Associates, Winetka, Illonois.

Fay, R. R., and A. N. Popper. 1999. Comparative hearing: fish and amphibians. Springer-Verlag, New York.

Fay, R. R., and A. N. Popper. 2000. Evolution of hearing in vertebrates: the inner ears and processing. Hearing Research 149:1–10.

Fine, M. L. 1981. Mismatch between sound production and hearing in the oyster toadfish. Pages 257–263 in W. N. Tavolga, A. N. Popper, and R. R. Fay, editors. Hearing and sound communication in fishes. Springer-Verlag, New York.

Fletcher, L. B., and J. D. Crawford. 2001. Acoustic detection by sound-producing fishes (Mormyridae): the role of gas-filled tympanic bladders. Journal of Experimental Biology 204:175–183.

Fritzsch, B., K. F. Barald, and M. I. Lomax. 1998. Early embryology of the vertebrate ear. Pages 80–145 in E. W. Rubel, A. N. Popper, and R. R. Fay, editors. Development of the auditory system. Springer-Verlag, New York.

Fuiman, L. A. 1989. Vulnerability of Atlantic herring larvae to predation by yearling herring. Marine Ecology Progress Series 51:291–299.

Fuiman, L. A. 1994. The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. Journal of Fish Biology 45(Supplement A):55–79.

Fuiman, L. A., K. R. Poling, and D. M. Higgs. 1998. Quantifying developmental progress for comparative studies of larval fishes. Copeia 1998:602–611.

Fuiman, L. A., M. E. Smith, and V. N. Malley. 1999. Ontogeny of routine swimming speed and startle responses in red drum, with a comparison of responses to acoustic and visual stimuli. Journal of Fish Biology 55(Supplement A):215–226.

Fuiman, L. A., and R. G. Werner, editors. 2002. Fishery science: the unique contributions of early life stages. Blackwell Scientific Publications, Oxford, UK.

Gallego, A., and M. R. Heath. 1994. The development of schooling behaviour in Atlantic herring *Clupea harengus*. Journal of Fish Biology 45:569–588.

Gray, L., and E. W. Rubel. 1985. Development of absolute thresholds in chickens. Journal of the Acoustical Society of America 77:1162–1172.

Haddon, C., and J. Lewis. 1996. Early ear development in the embryo of the zebrafish, *Danio rerio*. Journal of Comparative Neurology 365:113–128.

Harvey, R., J. H. S. Blaxter, and R. D. Hoyt. 1992. Development of superficial and lateral line neuromasts in larvae and juveniles of plaice (*Pleuronectes platessa*) and sole (*Solea solea*). Journal of the Marine Biological Association of the United Kingdom 72:651–668.

Hassan E. S. 1989. Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. Pages 217–228 in Coombs et al. (1989).

Hassan. E. S., H. Abdel-Latif, and R. Biebricher. 1992. Studies on the effects of Ca^{++} and Co^{++} on the swimming behavior of the blind Mexican cave fish. Journal of Comparative Physiology A 171:413–419.

Higgs, D. M. 2002. Development of the fish auditory system: how do changes in auditory structure affect function. Bioacoustics 12:180–182.

Higgs, D. M., and L. A. Fuiman. 1996. Ontogeny of visual and mechanosensory structure and function in Atlantic menhaden *Brevoortia tyrannus*. Journal of Experimental Biology 199:2619–2629.

Higgs, D. M., and L. A. Fuiman. 1998a. Associations between behavioral ontogeny and habitat change in clupeoid larvae. Journal of the Marine Biological Association of the United Kingdom 78:1281–1294.

Higgs, D. M., and L. A. Fuiman. 1998b. Associations between sensory development and ecology in three species of clupeoid fish. Copeia 1998:133–144.

Higgs, D. M., M. J. Souza, H. R. Wilkins, J. C. Presson, and A. N. Popper. 2002. Age- and size-related changes in the inner ear and hearing ability of the adult zebrafish (*Danio rerio*). Journal of the Association for Research in Otolaryngology 3:174–184.

Higgs, D. M., A. K. Rollo, M. J. Souza, and A. N. Popper. 2003. Development of form and function in peripheral auditory structures of the zebrafish (*Danio rerio*). Journal of Acoustic Society of America 113:1145–1154.

Hildebrand, S. F., and L. E. Cable. 1934. Reproduction and development of whitings or kingfishes, drum, spot, croakers, and weakfishes or seatrouts, Family Sciaenidae. U.S. Bur Fish Bull 48(16):41–117.

Hoff, G. R., and L. A. Fuiman. 1993. Morphometry and composition of red drum otoliths: changes associated with temperature, somatic growth rate, and age. Comparative Biochemistry and Physiology 106A:209–219.

Hoss, D. E., and J. H. S. Blaxter. 1982. Development and

function of the swimbladder–inner ear–lateral line system in the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe). Journal of Fish Biology 20:131–142.

Hunter, J. R., and K. M. Coyne. 1982. The onset of schooling in northern anchovy larvae, *Engraulis mordax*. California Cooperative Oceanic Fisheries Investigations Reports 23:246–251.

Iwashita, A., M. Sakamoto, T. Kojima, Y. Watanabe, and H. Soeda. 1999. Growth effects on the auditory threshold of red sea bream. Nippon Suisan Gakkaishi 65:833–838.

Janssen, J. 1990. Localization of substrate vibrations by the mottled sculpin (*Cottus bairdi*). Copeia 1990:349–355.

Janssen, J. 1996. Use of the lateral line and tactile senses in feeding in four Antarctic nototheniid fishes. Environmental Biology of Fishes 47:51–64.

Janssen, J. 2000. Toxicity of Co^{2+}: implications for lateral line studies. Journal of Comparative Physiology, A 186:957–960.

Janssen, J. 2003. Lateral line sensory ecology. Pages 231–264 *in* G. von der Emde, J. Mogdans, and B. G. Kapoor, editors. The senses of fishes: adaptations for the reception of natural stimuli. Narosa Publishing House Pvt. Ltd., New Delhi.

Janssen, J., W. R. Jones, A. Whang, and P. E. Oshel. 1995. Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences 52:358–363.

Jearld, A. Jr., S. L. Sass, M. F. Davis. 1992. Early growth, behavior, and otolith development of the winter flounder *Pleuronectes americanus*. Fishery Bulletin, U.S. 91:65–75.

Jones, W. R., and J. Janssen. 1992. Lateral line development and feeding behavior in the mottled sculpin, *Cottus bairdi* (Scorpaeniformes: Cottidae). Copeia 1992:485–492.

Kalmijn, A. J. 1988. Hydrodynamic and acoustic field detection. Pages 83–130 *in* Atema et al. (1988).

Kalmijn, A. J. 1989. Functional evolution of lateral line and inner ear sensory systems. Pages 187–215 *in* Coombs et al. (1989).

Karlsen, H. E., and O. Sand. 1987. Selective and reversible blocking of the lateral line in freshwater fish. Journal of Experimental Biology 133:249–262.

Kawamura, G., and K. Ishida. 1985. Changes in sense organ morphology and behaviour with growth in the flounder *Paralichthys olivaceus*. Bulletin of the Japanese Society of Scientific Fisheries 51:155–165.

Kawamura, G., and N. Washiyama. 1989. Ontogenetic changes in behavior and sense organ morphogenesis in largemouth bass and *Tilapia nilotica*. Transactions of the American Fisheries Society 118:203–213.

Kenyon, T. N. 1996. Ontogenetic changes in the auditory sensitivity of damselfishes (Pomacentridae). Journal of Comparative Physiology A 179:553–561.

Kroese, A. B. A., and N. A. M. Schellart. 1987. Evidence for velocity- and acceleration-sensitive units in the trunk lateral line of the trout. Journal of Physiology 394:13.

Ladich, F. 1999. Did auditory sensitivity and vocalization evolve independently in otophysan fishes? Brain, Behavior and Evolution 53:288–304.

Ladich, F., and H. Y. Yan. 1998. Correlation between auditory sensitivity and vocalization in anabantoid fishes. Journal of Comparative Physiology A 182:737–746.

Lara, M. R. 1999. Sensory development in settlement-stage larvae of Caribbean labrids and scarids – a comparative study with implications for ecomorphology and life history strategies. Doctoral dissertation, College of William and Mary, Williamsburg, Virginia.

Ledent, V. 2002. Postembryonic development of the posterior lateral line in zebrafish. Development 129:597–604.

Leis, J. M., B. M. Carson-Ewart, and D. H. Cato. 2002. Sound detection *in situ* by the larvae of a coral-reef damselfish (Pomacentridae). Marine Ecology Progress Series 232:259–268.

Lekander, B. 1949. The sensory lateral line system and canal bones in the head of some Ostariophysi. Acta Zoologica 30:1–131.

Liem, K. F. 1963. The comparative osteology and phylogeny of the Anabantoidei (Teleostei, Pisces). Illinois Biological Monographs 30.

Lombarte, A., H. Y. Yan, A. N. Popper, J. S. Chang, and C. Platt. 1993. Damage and regeneration of hair cell ciliary bundles in a fish ear following treatment with gentamicin. Hearing Research 64:166–174.

Lombarte, A., and A. N. Popper. 1994. Quantitative analyses of postembryonic hair cell addition in the otolithic endorgans of the inner ear of the European hake, *Merluccius merluccius* (Gadiformes, Teleostei). Journal of Comparative Neurology 345:419–428.

Lychakov, D. V., and Y. T. Rebane. 2000. Otolith regularities. Hearing Research 143:83–102.

Mann, D. A., Z. Lu, and A. N. Popper. 1997. A clupeid fish can detect ultrasound. Nature (London) 389:341.

Mann, D. A., Z. Lu, M. C. Hastings, and A. N. Popper. 1998. Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). Journal of the Acoustical Society of America 104:562–268.

Mann, D. A., D. M. Higgs, W. N. Tavolga, M. J. Souza, and A. N. Popper. 2001. Ultrasound detection by clupeiform fishes. Journal of the Acoustical Society of America 109:3048–3054.

Margulies, D. 1989. Size-specific vulnerability to predation and sensory system development of white seabass, *Atractoscion nobilis*, larvae. Fishery Bulletin, U.S. 87:537–552.

Masuda, R., and K. Tsukamoto. 1996. Morphological development in relation to phototaxis and rheotaxis in the striped jack, *Pseudocaranx dentex*. Marine and Freshwater Behaviour and Physiology 28:75–90.

Masuda, R., and K. Tsukamoto. 1999. School formation and concurrent developmental changes in carangid fish with reference to dietary conditions. Environmental Biology of Fishes 56:243–252.

Matsuoka, M. 2001. Development of sense organs in the Japanese sardine. Fisheries Science 67:1036–1045.

Meekan, M. G., J. J. Dodson, S. P. Good, and D. A. J. Ryan. 1998. Otolith and fish size relationships, measurement error, and size selective mortality during the early life of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55:1663–1673.

Mogdans, J., and H. Bleckmann. 2001. The mechanosensory lateral line of jawed fishes. Pages 181–213 *in* B. G. Kapoor and T. J. Hara, editors. Sensory biology of jawed fishes: new insights. Science Publishers, Inc., Endfield, New Hampshire.

Montgomery, J. C., and D. Bodznick. 1994. An adaptive filter that cancels self-induced noise in the electrosensory and lateral line mechanosensory systems of fish. Neuroscience Letters 174:145–148.

Montgomery, J., S. Coombs, and M. Halstead. 1995. Biology of the mechanosensory lateral line in fishes. Reviews in Fish Biology and Fisheries 5:399–416.

Montgomery, J. C., C. F. Baker, and A. G. Carton. 1997. The lateral line can mediate rheotaxis in fish. Nature (London) 389:960–963.

Mukai, Y., H. Kobayashi, and H. Yoshikawa. 1992. Development of free and canal neuromasts and their directions of maximum sensitivity in the larvae of ayu, *Plecoglossus altivelis*. Japanese Journal of Ichthyology 38:411–417.

Mukai, Y., and H. Kobayashi. 1994. Development of free neuromasts in larvae of cyprinid fish. Memoirs of the Faculty of Agriculture of Kinki University 27:1–14.

Mukai, Y., H. Yoshikawa, and H. Kobayashi. 1994. The relationship between the length of the cupulae of free neuromasts and feeding ability in larvae of the willow shiner *Gnathopogon elongatus caerulescens* (Teleostei, Cyprinidae). Journal of Experimental Biology 197:399–403.

Mukai, Y., and H. Kobayashi. 1995. Development of

free neuromasts with special reference to sensory polarity in larvae of the willow shiner, *Gnathopogon elongatus caerulescens*. Zoological Science 12:125–131.

Münz, H. 1985. Single unit activity in the peripheral lateral line system of the cichlid fish *Sarotherodon niloticus* L. Journal of Comparative Physiology, A 157:555–568.

Münz, H. 1989. Functional organization of the lateral line periphery. Pages 285–297 *in* Coombs et al. (1989).

Myrberg, A. A. Jr. and J. Y. Spires. 1980. Hearing in damselfishes: an analysis of signal detection among closely related species. Journal of Comparative Physiology 140:135–144.

Myrberg, A. A., Jr., and L. A. Fuiman. 2002. The sensory world of coral reef fishes. Pages 123–148 *in* P. F. Sale, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California.

Neave, D. A. 1986. The development of the lateral line system in plaice (*Pleuronectes platessa*) and turbot (*Scophthalmus maximus*). Journal of the Marine Biological Association of the United Kingdom 66:683–693.

Nelson, E. M. 1955. The morphology of the swimbladder and auditory bulla in the Holocentridae. Fieldiana: Zoology 37:121–130.

New, J. G., L. A. Fewkes, and A. N. Khan. 2001. Strike feeding behavior in the muskellunge, *Esox masquinongy*: contributions of the lateral line and visual sensory systems Journal of Experimental Biology 204:1207–1221.

Northcutt, R. G. 1989. The phylogenetic distribution and innervation of craniate mechanoreceptive lateral lines. Pages 17–78 *in* Coombs et al. (1989).

Northcutt, R. G. 1997. Evolution of gnathostome lateral line ontogenies. Brain, Behavior and Evolution 50:25–37.

Northcutt, R. G., P. H. Holmes, and J. S. Albert. 2000. Distribution and innervation of lateral line organs in the channel catfish. Journal of Comparative Neurology 421:570–592.

O'Connell, C. P. 1955. The gas bladder and its relation to the inner ear in *Sardinops caerulea* and *Engraulis mordax*. Fishery Bulletin, U.S. 56:501–533.

Okamoto, R., H. Matsunaga, K. Funae, and M. Hisaoka. 1982. Biological studies on the mass production of juvenile red sea bream *Chrysophrys major* Temmink et Schlegel. - I. Development of lateral-line organs and its bearing on behavioral changes. Bulletin of Nansei National Fisheries Research Laboratory 14:19–31.

Okamura, A., H. P. Oka, Y. Yamada, T. Utoh, N. Mikawa, N. Horie, and S. Tanaka. 2002. Development of

lateral line organs in leptocephali of the freshwater eel *Anguilla japonica* (Teleostei, Anguilliformes). Journal of Morphology 254:81–91.

Pankhurst, P. M., and P. Butler. 1996. Development of the sensory organs in the greenback flounder, *Rhombosolea tapirina*. Marine and Freshwater Behaviour and Physiology 28:55–73.

Parmienter, E., F. Lagardère, and P. Vandewalle. 2002. Relationships between inner ear and sagitta growth during ontogenesis of three Carapini species, and consequences of life-history events on the otolith microstructure. Marine Biology 141:491–501.

Partridge, B. L., and T. J. Pitcher. 1980. The sensory basis of fish schools: relative roles of lateral line and vision. Journal of Comparative Physiology 135:315–325.

Peters, H. M. 1973. Anatomie und Entwicklungsgeschichte des Lateralissystems von *Tilapia* (Pisces, Cichlidae). Zeitschrift für Morphologie der Tiere 74:89–161.

Pitcher, T. J., B. L. Partridge, and C. S. Wardle. 1976. A blind fish can school. Science 194:963–965.

Poling, K. R., and L. A. Fuiman. 1997. Sensory development and concurrent behavioural changes in Atlantic croaker larvae. Journal of Fish Biology 51:402–421.

Poling, K. R., and L. A. Fuiman. 1998. Sensory development and its relation to habitat change in three species of sciaenids. Brain, Behavior and Evolution 52:270–284.

Poling, K. R., and L. A. Fuiman. 1999. Behavioral specialization in developing sciaenids and its relationship to morphology and habitat. Environmental Biology of Fishes 54:119–133.

Popper, A. N. 1971. The effects of size on auditory capacities of the goldfish. Journal of Auditory Research 11:239–247.

Popper, A. N., and B. Hoxter. 1984. Growth of a fish ear: 1. Quantitative hair cell and ganglion cell proliferation. Hearing Research 15:133–142.

Popper, A. N., and R. R. Fay. 1999. The auditory periphery in fishes. Pages 43–100 *in* R. R. Fay and A. N. Popper, editors. Comparative hearing: fish and amphibians. Springer-Verlag, New York.

Radermaker, F., C. Surlemont, P. Sanna, M. Chardon, and P. Vandewalle. 1989. Ontogeny of the Weberian apparatus of *Clarias gariepinus*. Canadian Journal of Zoology 67:2090–2097.

Ramcharitar, J., D. M. Higgs, and A. N. Popper. 2001. Sciaenid inner ears: a study in diversity. Brain, Behavior and Evolution 58:152–162.

Rogers, P. H., and M. Cox. 1988. Underwater sound as a biological stimulus. Pages 131–149 *in* Atema et al. (1988).

Rosenthal, H. 1968. Observation on the development of schooling behavior in larvae of the herring, *Clupea harengus*. Marine Biology 2:73–76.

Ruben, R. J. 1967. Development of the inner ear of the mouse: a radioautographic study of terminal mitoses. Acta Otolaryngologia Supplement 220:1–44.

Salem, M. A., and Y. Omura. 1998a. Light and electron microscopic studies on the development of the inner ear and otolith of the ayu *Plecoglossus altivelis*. Fisheries Science 64:259–264.

Salem, M. A., and Y. Omura. 1998b. Embryonic development of the inner ear and otolith of the rainbow trout *Oncorhynchus mykiss*. Archives Histology and Cytology 61:179–187.

Salgado, S. D., and R. D. Hoyt. 1996. Early behavior formation in fathead minnow larvae, *Pimephales promelas*: implications for sensory function. Marine and Freshwater Behaviour and Physiology 28:91–106.

Satou, M., A. Shiraishi, T. Matsushima, and N. Okumoto. 1991. Vibrational communication during spawning behavior in the hime salmon (landlocked red salmon, *Oncorhynchus nerka*). Journal of Comparative Physiology A 168:417–428.

Schellart, N. A. M. 1983. Acousticolateral and visual processing and their interaction in the torus semicircularis of the trout, *Salmo gairdneri*. Neuroscience Letters 42:39–44.

Schellart, N. A. M., M. Kamermans, and L. J. A. Nederstigt. 1987. An electrophysiological study of the topographical organization of the multisensory torus semicircularis of the rainbow trout. Comparative Biochemistry and Physiology 88A:461–469.

Schellart, N. A. M. and A. N. Popper. 1992. Functional aspects of the evolution of the auditory system of actinopterygian fish *in* D. B. Webster, R. R. Fay, and A. N. Popper, editors. The evolutionary biology of hearing. Springer-Verlag, New York.

Secor, D. H., J. M. Dean, and S. E. Campana, editors. 1995. Recent developments in fish otolith research. University of South Carolina Press, Columbia, South Carolina.

Senoo, S., K. J. Ang, and G. Kawamura. 1994. Development of sense organs and mouth and feeding of reared marble goby *Oxyeleotris marmoratus* larvae. Fisheries Science 60:361–368.

Sogard, S. M. 1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. Canadian Journal of Fisheries and Aquatic Sciences 48:1862–1871.

Sokolowski, B. H. A., and A. N. Popper. 1987. Gross and ultrastructural development of the saccule of

the toadfish *Opsanus tau*. Journal of Morphology 914:323–348.

Song, J., H. Y. Yan, and A. N. Popper. 1995. Damage and recovery of hair cells in fish canal (but not superficial) neuromasts after gentamicin exposure. Hearing Research 91:63–71.

Suzuki, A., J. Kozloski, and J. D. Crawford. 2002. Temporal encoding for auditory computation: physiology of primary afferent neurons in sound-producing fish. Journal of Neuroscience 22:6290–6301.

Thornhill, R. A. 1972. The development of the labyrinth of the lamprey (*Lampetra fluviatilis* Linn. 1758). Proceedings of the National Academy of Sciences 181:175–198.

Tolimieri, N., A. Jeffs, and J. C. Montgomery. 2000. Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. Marine Ecology Progress Series 207:219–224.

Tolimieri, N., O. Haine, J. C. Montgomery, and A. Jeffs. 2002. Ambient sound as a navigational cue for larval reef fish. Bioacoustics 12:214–217.

Vandewalle, P., F. Radermaker, C. Surlemont, and M. Chardon. 1990. Apparition of the Weberian characters in *Barbus barbus* (Linné 1758) (Pisces Cyprinidae). Zoologischer Anzeiger 225:362–376.

Vischer, H. A. 1989. The development of lateral-line receptors in *Eigenmannia* (Teleostei, Gymnontiformes). I. The mechanoreceptive lateral-line system. Brain, Behavior and Evolution 33:205–222.

Vischer, H. A. 1990. The morphology of the lateral line system in 3 species of Pacific cottoid fishes occupying disparate habitats. Experientia 46:244–250.

von Frisch, K. 1938. The sense of hearing in fish. Nature (London) 141:8–11.

Walsh, E. J., J. McGee, and E. Javel. 1986. Development of auditory-evoked potentials in the cat. I. Onset of response and development of sensitivity. Journal of the Acoustical Society of America 79:712–724.

Waterman, R. E., and D. H. Bell. 1984. Epithelial fusion during early semicircular canal formation in the embryonic zebrafish, *Danio rerio*. Anatomical Record 210:101–114.

Webb, J. F. 1989a. Developmental constraints and evolution of the lateral line system in teleost fishes. Pages 79–97 *in* Coombs et al. (1989).

Webb, J. F. 1989b. Neuromast morphology and lateral line trunk canal ontogeny in two species of cichlids: an SEM study. Journal of Morphology 202:53–68.

Webb, J. F. 1998. Laterophysic connection: a unique link between the swimbladder and the lateral-line system in *Chaetodon* (Perciformes: Chaetodontidae). Copeia 1998:1032–1036.

Webb, J. F., and W. L. Smith. 2000. The laterophysic connection in chaetodontid butterflyfish: morphological variation and speculations on sensory function. Philosophical Transactions of the Royal Society of London: Biological Sciences 355:1125–1129.

Wersäll, J., and Å. Flock. 1964. Suppression and restoration of the microphonic output from the lateral line organ after local application of streptomycin. Life Sciences 3:1151–1155.

Whitfield, T. T., B. B. Riley, M-Y. Chiang, and B. Phillips. 2002. Development of the zebrafish inner ear. Developmental Dynamics 223:427–458.

Wonsettler, A. L., and J. F. Webb. 1997. Morphology and development of the multiple lateral line canals on the trunk in two species of *Hexagrammos* (Scorpaeni-formes: Hexagrammidae). Journal of Morphology 233:195–214.

Wysocki, L. E., and F. Ladich. 2001. The ontogenetic development of auditory sensitivity, vocalization, and acoustic communication in the labyrinth fish *Trichopsis vittata*. Journal of Comparative Physiology A 187:177–187.

Yan, H. Y. 1998. Auditory role of the suprabranchial chamber in gourami fish. Journal of Comparative Physiology A 183:325–333.

Yan, H. Y., and W. S. Curtsinger. 2000. The otic gasbladder as an ancillary auditory structure in a mormyrid fish. Journal of Comparative Physiology A 186:595–602.

Yan, H. Y., M. L. Fine, N. S. Horn, and W. E. Colón. 2000. Variability in the role of the gasbladder in fish audition. Journal of Comparative Physiology A 186:435–445.

Yin, M. C., and J. H. S. Blaxter. 1987. Escape speeds of marine fish larvae during early development and starvation. Marine Biology 96:459–468.