Development of Structure and Sensitivity of the Fish Inner Ear

Raquel O. Vasconcelos, Peter W. Alderks, and Joseph A. Sisneros

Abstract Fish represent the largest group of vertebrates and display the greatest diversity of auditory structures. However, studies addressing how the form and function of the auditory system change during development to enhance perception of the acoustic environment are rather sparse in this taxon compared to other vertebrate groups. An ontogenetic perspective of the auditory system in fishes provides a readily testable framework for understanding structure–function relationships. Additionally, studying ancestral models such as fish can convey valuable comparable information across vertebrates, as early developmental events are often evolutionary conserved. This chapter reviews the literature on the morphological development of the fish auditory system, with particular focus on the inner ear structures that evolve from an otic placode during early embryonic development and then continue to undergo differentiation and maturation in the postembryonic phase. Moreover, the chapter provides a systematic overview of how auditory sensitivity develops during ontogeny. Although most studies indicate a developmental improvement in auditory sensitivity, there is considerably species-specific variation. Lastly, the paucity of information and literature concerning the development of auditory capabilities for social communication in fishes is also discussed. Further investigation on the development of structure and function of the fish auditory system is recommended in order to obtain a deeper understanding of how ontogenetic morphological changes in the auditory pathway relate to modifications in acoustic reception, auditory processing, and the capacity to communicate acoustically.

Keywords Fish ontogeny • Auditory development • Auditory physiology • Ear morphology

R.O. Vasconcelos (✉)
Institute of Science and Environment, University of Saint Joseph, Macau, S.A.R., China
e-mail: raquel.vasconcelos@usj.edu.mo

P.W. Alderks
Department of Psychology, University of Washington, Seattle, WA 98195, USA

J.A. Sisneros
Department of Psychology, University of Washington, Seattle, WA 98195, USA

Department of Biology, University of Washington, Seattle, WA 98195, USA

1   Introduction

Studies on the auditory system have provided an unmatched wealth of information related to the evolution and function of sensory systems in vertebrates. The comparative data obtained from different levels of the auditory system, from the peripheral to the central auditory system, is by far the richest among all sensory systems. However, despite our growing knowledge in auditory system neuroscience, there are a number of fundamental questions related to the development and function of auditory structures that remain poorly understood across vertebrate taxa. For example, how does auditory reception and its neural processing change during ontogeny? Which morphological changes occur in the inner ear versus the central auditory system that may account for developmental improvements in hearing? What is the relationship between auditory development and vocal differentiation? Although some effort has been made to answer these questions in comparative studies from birds and mammals, the available information is scarce and in need of further investigation that includes also lower vertebrates such as fish. Such a research perspective will be needed in order to gain fundamental comparative insights into the evolution and ecology of the vertebrate auditory system.

The diversity of structure and function of fish sensory systems is exceptional, suggesting that through evolution species have found ways to become more adapted to their highly diverse aquatic environments. This diversity is particularly evident in the octavolateralis system of fishes that includes the lateral line and the inner ear (Braun and Grande 2008).

Fishes rely on their auditory system to extract biologically relevant information from the auditory scene, such as the presence of conspecifics, predators, prey, and to detect abiotic elements for orientation. The capacity to detect acoustic signals in the soundscape seems to start early in life in most species. Besides being important for the detection of food or danger, the auditory sense in juvenile fish is also important for intraspecific acoustic communication during agonistic interactions in the context of competition over food or space (Schneider 1964; Henglmüller and Ladich 1999; Amorim and Hawkins 2005; Kéver et al. 2012).

Studies that examine the ontogeny of hearing in fishes can ultimately provide an evolutionary perspective and deeper understanding of the mechanisms underlying the development of the auditory sense in all vertebrates. Many of the early developmental events in fishes appear to be evolutionarily conserved across all vertebrate groups in spite of the large diversity in auditory structure found in adult animals (Retzius 1884; Baird 1974; Henson 1974).

In this chapter we review the available information on the ontogenetic development of the inner ear morphology and sensitivity in fish. In addition, we briefly describe the available information on the development of auditory capabilities for social acoustic communication in this taxon, another area of research where information is still fairly limited.

## 2 Morphological Development of the Fish Auditory System

During ontogeny a number of important morphological changes occur in the otolithic end organs and peripheral auditory system of fishes. This section is meant as an overview of these structural changes that occur and likely influence auditory sensitivity, hearing perception, and communication and should not be considered a comprehensive review of the literature on this topic. The following sections briefly discuss the structure of the teleost inner ear, embryology, and early development of the auditory end organs, postembryonic development and changes to the peripheral auditory system.

2.1 The Teleost Inner Ear

Like other vertebrates, fish have ears that detect acoustic stimuli (Weber 1820; Parker 1903; von Frisch and Stetter 1932). The teleost inner ear is composed of three otolithic endorgans, the lagena, utricle, and saccule, which include otoliths and sensory epithelia, as well as three semicircular canals (see Fig. 1). All three otolithic end organs are thought to be capable of detecting both inertial stimuli and acoustic stimuli; however, it is likely that the three end organs differ in their relative contribution to motion detection and audition (Popper and Fay 1993; Popper et al. 2003). The saccule is the primary auditory end organ in most teleost fishes (Popper and Schilt 2008; Webb et al. 2008), whereas the other otolithic end organs seem to have either a vestibular role (von Frisch 1938; Platt 1983) or mixed auditory-vestibular functions (Popper et al. 1982; Schellart and Popper 1992).

The otolithic end organs respond to acoustic particle motion much like an accelerometer (Platt and Popper 1981; Popper and Tavolga 1981; Fay 1984). Here we describe how the otolithic end organs transduce vibrational energy using the saccule as our example. The saccule contains a dense otolith known as the sagitta, which is about three times more dense than the fish's body (de Vries 1950; Popper and Lu 2000). When sound passes through the fish, the sagitta moves at a different phase and amplitude than the saccular epithelium, which is attached to the sagitta by means of an otolith membrane (Dijkgraaf 1960; Fay and Popper 1975). A shearing motion results as the otolith and sensory epithelium move relative to one another during sound stimulation, causing the ciliary hair bundles to bend (Fay and Popper 1974; Popper and Fay 1993). Signal transduction occurs as the hair bundles bend toward the kinocilium and generate a receptor potential that can depolarize the hair cell and produce an action potential (Popper 1983; Fay and Popper 2000). Otolithic organs are most effective at responding to low frequencies below 1000 Hz (Fay 1988; Popper and Fay 1999).

Although we have described the most common features of the teleost inner ear, it is important to note that there is a great deal of variation and diversity of inner ear structures used for hearing in teleost fishes (Platt and Popper 1981). It is likely that
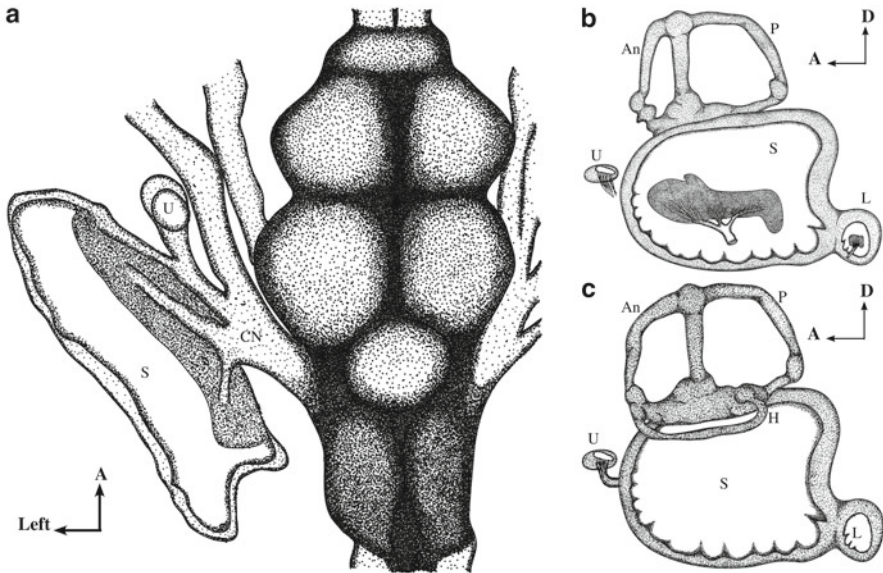
Fig. 1 The inner ear in the adult plainfin midshipman. *Porichthys notatus* (Batrachoididae) (**a**) depicts a dorsal view of the brain, auditory nerve (CN—VIIIth cranial nerve) and the inner ear (S—saccule, U—utricle). Notice the size of the saccule in relation to the brain. (**b**) and (**c**) show drawings of the right and left inner ears, respectively, in the plainfin midshipman. The three oto-lithic end organs (S—saccule, L—lagena, and U—utricle) as well as the three semi-circular canals (An—anterior, H—horizontal, P—posterior) are visible

with inner ear otoliths acting as accelerometers all teleost fishes are able to detect the particle motion component of sound as discussed above, however several teleost groups have independently evolved specialized auditory structures that likely enhance hearing and/or make it possible for the additional detection of sound pressure (Fay and Popper 1975, 1980; Coombs and Popper 1979). For example, several groups have developed unique mechanisms that involve inner ear placement near a gas bladder, or by directly coupling the inner ear to a gas bladder that changes in volume in response to changes in sound pressure (Platt and Popper 1981). Additionally, there is a great deal of diversity in regard to the structure and morphology of teleost peripheral auditory system, such as the position of the inner ear within the braincase, the size and shape of each otolithic end organ and otoliths, as well as the size, shape, and ultrastructure of the sensory macula (Fay and Popper 1975; Platt and Popper 1981). All of these differences in auditory structure between various fish species likely reflect their high adaptation to specific environments that has been shaping the function of the auditory system. An ontogenetic perspective provides a readily testable framework for understanding the structure-function relationships within the auditory system.

2.2 Embryology and Early Development of the Auditory System

Auditory structures, like other sensory systems, arise early during development through a process closely linked with and influenced by the forming of the central nervous system and mesoderm of the embryo (Fig. 2). The first major event in the development of the inner ear is the induction of the otic placode in the ectoderm of the developing embryo. The otic placode then invaginates to form the otic pit and the subsequent closing of the otic pit forms the otocyst, which separates from the ectoderm. The otocyst polarizes and differentiates into the various end organs of the auditory and vestibular systems. Here we provide a brief review of these events in greater detail.
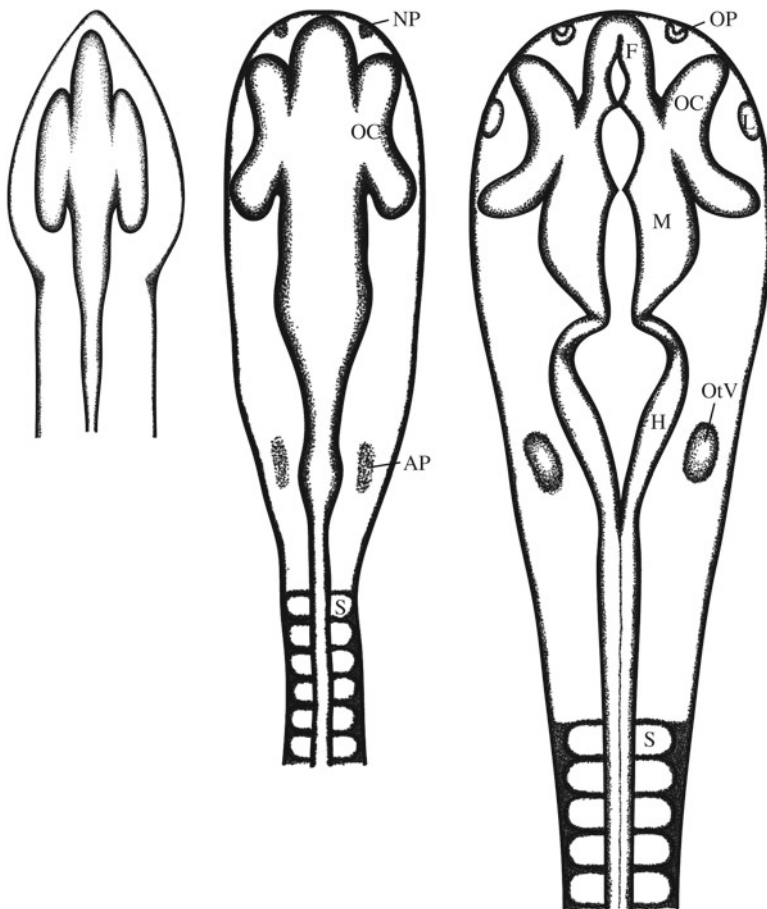

Fig. 2 Development of the brain and sensory organs in a fish embryo. NP—nasal placode, AP—auditory (otic) placode, OC—optic cup, S—somites, OP—olfactory pit, F—forebrain, M—midbrain, H—hindbrain, L—lens, OtV—otic vesicle (redrawn from Berrill and Karp 1976)

The otic placode, one of several dorsolateral placodes, is an epithelial thickening of the ectoderm near the middle of the developing hindbrain (Nelsen 1953; Kelly and Corwin 1992). The hindbrain develops from the neural tube and has a complex series of rhombomeres or bulges that have differential gene expression, particularly *Hox* gene expression, allowing for rhombomere specific differentiation, which in turn forms the basis of nerve patterning in the hindbrain (Keynes and Krumlauf 1994; Gilland and Baker 1993). The otic placode and later developing otocyst is located in close proximity to this rhombencephalon and the influence of the rhombencephalon is necessary and sufficient to induce the ectoderm to develop the otic placode (Model et al. 1981; Van De Water 1983; see Fig. 3). It is likely that molecular cues from the developing hindbrain are responsible for inducing the development of fish inner ear (Ekker et al. 1992). In addition to rhombencephalilization, the notochordal mesoderm, paraxial mesoderm and neural crest play a role in otic placode induction (Yntema 1955; Van De Water 1983; Jacobson and Sater 1988).

As the brain develops, the telencephalon and diencephalon begin to differentiate. Just after cephalic flexure increases, the otic pit forms as the otic placode invaginates. It has been demonstrated in amphibians that the axis polarity is fixed during early otic pit formation (Harrison 1945). This is likely true for all vertebrates including fish. Fixation of the anteroposterior axis occurs first, followed by the dorsoventral axis during otic pit formation (Yntema 1955). Once polarized, the locations for inner ear structures become fixed within the otic pit and disruptions in the orientation of the otic pit or later the otocyst will cause deformities in the inner ear (Harrison 1945; Detwiler and van Dyke 1950; Mansour et al. 1993).

The otic pit next separates from the ectoderm and closes to form the otocyst. As the otocyst forms, cells in the anteroventral portion of the otocyst give rise to the otic ganglia, which migrates away and breaks contact from the otocyst (Von Kupffer 1895; Webb and Noden 1993; Haddon and Lewis 1996). Populations of embryonic stem cells that make up part of the neural crest give rise to the support and glial cells found in the otic ganglion (Ayer-Le Liver and Le Douarin 1982; D'Amico-Martel and Noden 1983). Shortly after the otocyst separates from the ectoderm, there is a proliferation of undifferentiated epithelial cells along the ventro-medial surface of the otocyst. This proliferation of undifferentiated epithelial cells precedes segregation and differentiation of the otocyst into the various vestibular and auditory sensory epithelia. These undifferentiated epithelial cells later develop into hair and support cells within the otic endorgans. In amphibians transplantation and grafting experiments have demonstrated that the otocyst must be in close proximity to both the hindbrain and cephalic mesenchyme, at least during a critical period in an early stage otocyst, in order for differentiation to occur (Kaan 1930; Detwiler and van Dyke 1950). Although the length of this critical period varies among other vertebrate groups, it is likely that fish undergo a similar critical period where proximity to the hindbrain and cephalic mesenchyme is necessary for segregation and differentiation of the sensory epithelia.

As the otocyst develops and differentiates, the otic ganglia must grow distal processes to innervate the sensory epithelia of the auditory end organs. Studies in other vertebrate groups have demonstrated that the otocyst releases trophic factors to
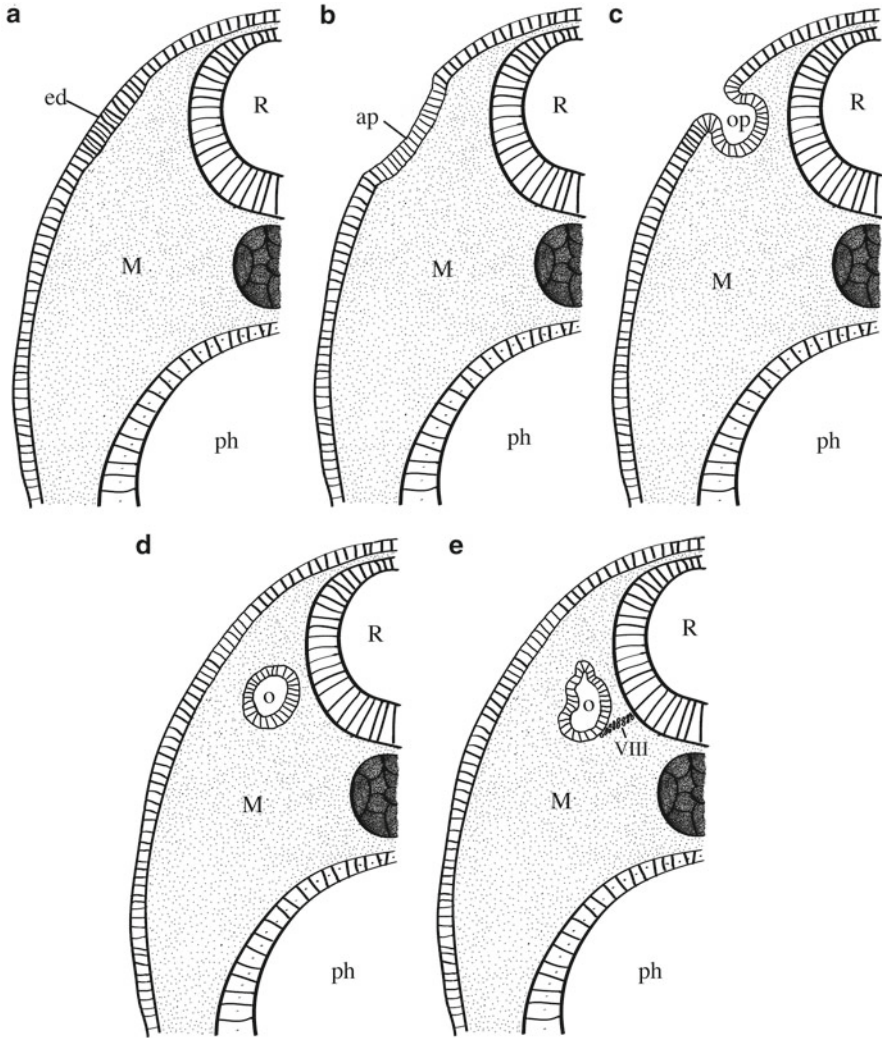
Fig. 3 Embryonic development of the auditory system in fishes. (**a**) Shows epithelial thickening in the ectoderm (ed) which is induced in (**b**) to form the auditory placode (ap) in the ectoderm of the developing embryo. In (**c**) the auditory placode invaginates to form the otic pit (op) and the subsequent closing of the otic pit in (**d**) forms the otocyst (o), which separates from the ectoderm. In (**e**) the otocyst polarizes and begins to differentiate into the various endorgans of the auditory and vestibular systems. R—rhombencephalon, M—head mesenchyme, ph—pharynx, ed—ecto-derm, ap—auditory placode, op—otic pit, o—otocyst, VIII—cranial nerve VIII

attract the growing ganglia toward the otocyst causing the neurons to enter at the appropriate sites (Hemond and Morest 1992; Bianchi and Cohan 1993). Although the exact timing of innervation by auditory afferents and efferents is not well stud-ied in fishes, nerve innervation appears to take place before functional maturation of

the hair cells in the sensory epithelium (Tanimoto et al. 2009). Afferent innervation does not appear to be necessary for hair cell differentiation, but it likely plays a role for long-term maintenance of individual hair cells (Sokolowski et al. 1993; Fritzsch et al. 2004). In the toadfish, *Opsanus tau*, cells located within the developing sensory epithelium that differentiate into hair cells have a layer of microvilli along the luminal surfaces, which elongate to form the stereocilia as the kinocilia begin to elongate (Lewis and Li 1973; Sokolowski and Popper 1988). Also, embryonic differentiation and hair cell addition in *O. tau* occurs throughout the saccule simultaneously and not only on the edges of the growing saccular macula (Sokolowski and Popper 1988). Once the processes of innervation, differentiation, and hair cell maturation have taken place in the auditory end organs, all of the structural components necessary for auditory perception are in place and transduction of acoustic stimuli can begin, however the auditory system continues to develop after fish hatch.

2.3 Postembryonic Development of the Peripheral Auditory System

Postembryonic sensory hair cell addition has been demonstrated in elasmobranch (Corwin 1981, 1983) and teleost fishes (Platt 1977; Popper and Hoxter 1984; Coffin et al. 2012). The size and shape of the sensory epithelia also change during ontogeny (Corwin 1983; Popper and Hoxter 1984; Lombarte and Popper 1994). Additional ontogenetic changes may include the density of sensory hair cells (Popper and Hoxter 1984; Lombarte and Popper 1994; Lu and DeSmidt 2013), and number of auditory nerve ganglion cells as well as the innervation patterns of the eighth nerve (Corwin 1983; Popper and Hoxter 1984), but at least in the European hake, *Merluccius merluccius*, it does not include orientation of the hair cells (Lombarte and Popper 1994).

Because the saccule is the main end organ of hearing in most teleost fishes, it has been the most extensively studied auditory end organ, however some data exists which suggests that the macula neglecta in elasmobranchs and other otolithic end organs such as the lagena and utricle in teleosts may also serve an auditory function. Popper and Hoxter (1990) found that sensory hair cells are added throughout the sensory macula of the saccule during normal development and not in a pattern similar to the annular growth rings of the sagitta found in *Astronotus ocellatus*. Hair cell addition was also observed throughout the lagenar and utricular sensory epithelia in *M. merluccius* (Lombarte and Popper 1994). This is in contrast to elasmobranchs, which have been shown to primarily add proliferating sensory hair cells to the margins of the sensory epithelium (Corwin 1981, 1983). Although hair cell proliferation appears to occur throughout the saccule in teleost fishes, in the European hake, *M. merluccius*, the caudal region of the saccule undergoes more hair cell proliferation than the rostral region of the saccule (Lombarte and Popper

1994), so there appears to be variation among fishes in where hair cells are added within the sensory epithelia.

Additionally, there is a large variation in the rate of hair cells addition during ontogeny in the auditory maculae of sexually immature juvenile fishes: 302 cells per day in the European Hake, *M. merluccius* (Lombarte and Popper 1994), 167 cells per day in the saccule of cichlid *Astronotus ocellatus* (Popper and Hoxter 1984), 13 hair cells per day in the zebrafish *Danio rerio* (Lu and DeSmidt 2013), and the elasmobranch *Raja calvata* adds 1–3 sensory hair cells per day to the macula neglecta (Corwin 1983). Lombarte and Popper (1994) also found significant postembryonic proliferation of hair bundles in the lagenar and utricular epithelia in *M. merluccius*, although at a much-reduced rate, 47 hair cells per day in the utricle, and 37 hair cells per day in the lagena. The only study to examine hair bundle orientation found no changes in orientation patterns or percentage of area occupied by different orientation groups in all three otolithic epithelia during ontogeny in the European hake (Lombarte and Popper 1994).

As fish grow, so do the inner ears and the sensory maculae. In the zebrafish, *D. rerio*, the area of the otic vesicle as well as the area of saccular and utricular otoliths grow linearly, although the area of the saccular otolith grows at a greater rate than that of the utricular otolith (Lu and DeSmidt 2013). Lombarte and Popper (1994) found in *M. merluccius* that the utricular and lagenar epithelial areas grow at a slower rate than that of the saccular epithelial area, which grows isometrically with total length (TL). The shape of the sensory macula may or may not change as fish grow. In the ray, *R. clavata*, the macula neglecta elongates in the direction of the long axis of the posterior canal duct as the elasmobranch grows (Corwin 1983). This is in contrast to the zebrafish, which does not change shape during growth and development (Lu and DeSmidt 2013).

Another area where there seems to be variation in developmental patterns of the fish inner ear is hair bundle density. In the saccule of both *A. ocellatus* and *M. merluccius* hair bundle density decreased with age/size even though the total number of hair cells increased dramatically (Popper and Hoxter 1984; Lombarte and Popper 1994). In *M. merluccius*, the hair bundle density in the lagenar and utricular epithelia also decreased with size (Lombarte and Popper 1994). In *D. rerio*, hair bundle density in the saccule did not change in juvenile fish aged 3–18 months posthatch (Higgs et al. 2001), however during the first week of posthatched growth the density of hair cells increased linearly (Lu and DeSmidt 2013). It is possible during early postembryonic development that hair bundles rapidly increase in numbers relative to the growth of the sensory maculae causing an increase in density, which slows and reverses later during development due to a decrease in hair cell density as the area of the auditory macula grows and expands. More work is needed in other fishes over a broader range of developmental time periods to determine if this is the case.

Another area of the peripheral auditory system of fishes where ontogenetic plasticity has been demonstrated is the eighth cranial nerve. Relatively few data exists examining ontogenetic changes in the auditory nerve morphology, however Corwin (1983) found that the number of nerves that innervate the macula neglecta do not change in the skate, *Raja clavata*. In contrast, Barber et al. (1985) found that axon

number, total axon area, and hair cell number of the macula neglecta increased linearly with size/age of the skate, *R. ocellata*, and that there were significant differences in hair cell numbers of the macula neglecta in females and males for any given size of skate with females having a greater number of total hair cells. In the teleost *A. ocellatus*, the number of ganglion cells innervating the saccule increase 4.8-fold (Popper and Hoxter 1984). The rate of hair cell addition drastically outpaces nerve growth in *Astronotus ocellatus* and in both studies the disproportionate addition of hair cells results in an increase in neural convergence ratio of hair cells to auditory afferents (Corwin 1983; Popper and Hoxter 1984). By retrograde filling of the nerve axons using cobalt, Corwin (1983) found that each nerve innervates several hair cells with terminals that branch over a small area, with the greatest arborization in the center of the macula and lesser arborization at the periphery. These hair cells appeared to innervate by only one auditory afferent neuron (Corwin 1983). Corwin (1983) also found that as the ray grows, the axons increase in diameter and terminal field size.

2.4   Ontogenetic Structure-Function Relationships in the Fish Auditory System

The functional significance of many of the observed morphological changes in the fish auditory system during development is not known because relatively few studies have related quantified morphological changes to some measure of auditory sensitivity. It is likely, as shown in other vertebrate groups, that changes in some aspect of sensory morphology will be correlated with functional and/or sensitivity changes of the auditory system (Weiss et al. 1976; Lewis et al. 1985). In the elasmobranch *Raja clavata*, Corwin (1983) found a 500-fold increase in auditory nerve sensitivity that is likely due to the addition of sensory hair cells. This increase in sensory hair cells was not accompanied by a corresponding increase in auditory nerve innervation thus leading Corwin (1983) to postulate that the observed increase in auditory sensitivity resulted from the increased convergence ratio of sensory hair cells to auditory afferent neurons. In teleost fishes, Lu and DeSmidt (2013) found an increase in the microphonic response and sensitivity of the saccule in the zebrafish, *Danio rerio*, which correlated with increases in the number and density of saccular hair cells. In contrast, Higgs et al. (2001) found no changes in hearing sensitivity or bandwidth in *D. rerio* that correlated with hair cell addition. It is important to note that Lu and DeSmidt (2013) measured hearing sensitivity of the hair cells in the saccule, the end organ where the morphological changes were observed, whereas Higgs et al. (2001) measured hearing sensitivity using the auditory evoked potential (AEP) recording technique, which measures overall neural responses potentially including higher-order brain regions of the central auditory system (see next section). Lu and DeSmidt (2013) also used fish during an earlier stage of zebrafish development than Higgs et al. (2001), which may have allowed them to capture a period of

greater ontogenetic change. Additional studies looking at how other morphological changes relate to ontogenetic changes in auditory sensitivity would greatly improve our understanding of the structure function relationships between auditory structures and hearing sensitivity in fishes.

3 Development of Hearing in Fishes

In contrast to other vertebrate groups, there are only a few studies that have examined the development of hearing capabilities in fish. Most ontogenetic studies of fish hearing have focused on changes in auditory sensitivity in regard to thresholds of auditory evoked potentials (AEPs) across different-sized animals, although a few studies measured other functions such as changes in temporal encoding with age/size (e.g., Sisneros and Bass 2005).

Depending on the specific research question and species of fish examined, there has been a large degree of variability in the developmental stages investigated. While some studies tried to understand the functional role of specific morphological structures for hearing enhancement (e.g. Lechner et al. 2011; Webb et al. 2012; Caiger et al. 2013) or even the relationship between auditory sensitivity and the onset of vocal communication (e.g. Wysocki and Ladich 2001; Vasconcelos and Ladich 2008) over a wide range of fish sizes, others have only focused on larval stages to determine whether the auditory system is developmentally functional to enable fish larvae to find specific habitats for settlement using environmental acoustic cues (Wright et al. 2011).

This section provides a systematic overview of the studies concerning the development of fish hearing during ontogeny organized by taxa. Moreover, a final part will focus on how the hearing sense in fishes has evolved for the enhancement of social acoustic communication.

3.1 Diversity of Auditory Sensitivity

In order to study the development of auditory sensitivity in juvenile fish, investigators have employed different methods for the assessment of hearing ranging from behavioral to electrophysiological approaches. Likely due to the long training periods and difficulty of training small juvenile fish, only one study has used a behavioral conditioning method to investigate the ontogenetic development of auditory sensitivity (Kenyon 1996). One behavioral technique that has proved useful in determining whether or not the auditory system is functional during development is the acoustic startle or startle-like escape responses that consist of a stereotyped "tail-flip" response evoked by relatively loud sound stimuli (Blaxtey and Batty 1985; Fuiman et al. 1999; Zeddies and Fay 2005; Alderks and Sisneros 2013).

Alternatively, electrophysiology techniques have also been used, namely multiunit recordings from the auditory cranial nerve (Corwin 1983; Sisneros and Bass 2005) or measurement of evoked responses from populations of saccular hair cells (Alderks and Sisneros 2011), to characterize auditory sensitivity during ontogeny.

However, the most common electrophysiology technique used to determine hearing sensitivity in fish during ontogeny is the AEP recording technique, which was introduced and adapted for fish by Kenyon et al. (1998). This technique is used to measure the overall neural auditory responses evoked by auditory stimuli and consists of the summation of evoked field potentials from central brain regions, auditory nerve, and otolithic end organs over many presentations (for an extensive review of the use of the AEP technique in fish hearing, see Ladich and Fay 2013). The AEP technique has become a useful tool to assess the ontogenetic development of hearing in various marine and freshwater fishes.

In general, auditory thresholds of fishes have largely been characterized in terms of sound pressure, but it is now generally accepted that all fish species are capable of sensing particle motion via their otolithic end organs and only some fish species possess accessory hearing specializations that allow them to detect sound pressure. Most of the previous studies presented auditory threshold data in terms of sound pressure largely due to technical constraints, namely due to the difficulty of measuring particle motion directly and the commercial unavailability of neutrally buoyant underwater accelerometers. In addition, the reporting of auditory sensitivity in terms of sound pressure was a convenient mean of comparison with the sound spectra of conspecific vocalizations, which is typically characterized in terms of sound pressure.

Table 1 provides a systematic overview of the various fish species in which auditory sensitivity has been examined during ontogeny as well as the recordings techniques used in each study. The data in Table 1 reveals taxon-specific results, with most fish species exhibiting auditory sensitivity improvements with age/size during ontogeny. In addition to increased auditory sensitivity, some studies also report changes in peak frequency sensitivity and in the detectable frequency range or detection bandwidth.

3.1.1 Chondrichthyes (Cartilaginous Fishes)

Rajiformes

The first study to report changes in auditory sensitivity during development in fish was conducted by Corwin (1983) in the thornback skate *Raja clavata* (Chondrichthyes, Rajidae). By means of multiunit in vitro recordings of the macula neglecta (nonotolithic auditory end organ of the inner ear), the author showed a 500-fold increase in auditory sensitivity with age/size in skates from 21 to 91 cm total length (TL). This increase in auditory sensitivity was observed across the range of tested frequencies such that the filter shape of the audiogram remained similar but

Table 1 Systematic overview of the fish species studied regarding developmental changes in auditory sensitivity based on various measuring techniques

Order	Family	Species	Common name	Technique	Auditory changes	References
Rajiformes	Rajidae	*Raja clavata*	Thornback ray	SUR	+	Corwin (1983)
Clupeiformes	Clupeidae	*Alosa sapidissima*	American shad	AEP	=	Higgs et al. (2004)
	Clupeidae	*Clupea* spp.	Herring	ASR	+	Blaxtey and Batty (1985)
Cypriniformes	Cyprinidae	*Danio rerio*	Zebrafish	AEP	=	Higgs et al. (2001)
				AEP	=	Higgs et al. (2003)
				ASR	+	Zeddies and Fay (2005)
				ASR	+	Bhandiwad et al. (2013)
				HR	+	Lu and DeSmidt (2013)
Siluriformes	Mochokidae	*Synodontis schoutedeni*	Squeaker catfish	AEP	+	Lechner et al. (2010)
	Claroteidae	*Lophiobagrus cyclurus*	African bullhead catfish	AEP	+	Lechner et al. (2011)
Gadiformes	Gadidae	*Theragra chalcogramma*	Walleye pollock	AEP	=	Mann et al. (2009)
Batrachoidifomes	Batrachoididae	*Halobatrachus didactylus*	Lusitanian toadfish	AEP	+	Vasconcelos and Ladich (2008)
		Porichthys notatus	Plainfin midshipman fish	SUR	+	Sisneros and Bass (2005)
				SEP	=	Alderks and Sisneros (2011)
				ASR	=	Alderks and Sisneros (2013)

(continued)

Table 1 (continued)

Order	Family	Species	Common name	Technique	Auditory changes	References
Perciformes	Serranidae	*Epinephelus coioides*	Orange-spotted grouper	AEP	+	Wright et al. (2011)
		Epinephelus fuscoguttatus	Brown-marbled grouper	AEP	=	Wright et al. (2011)
	Carangidae	*Caranx ignobilis*	Giant trevally	AEP	+	Wright et al. (2011)
	Pomacentridae	*Abudefduf saxatilis*	Sergeant major damsefish	AEP	–	Egner and Mann (2005)
		Pomacentrus nagasakiensis	Nagasaki damsefish	AEP	+	Wright et al. (2005)
		Stegastes partitus	Bicolor damselfish	BC	+	Kenyon (1996)
		Amphiprion ephippium	Saddle anemonefish	HR	+	Simpson et al. (2005)
		Amphiprion rubrocinctus	Red anemonefish	HR	+	Simpson et al. (2005)
	Polyprionidae	*Polyprion oxygeneios*	Hapuka	AEP	+	Caiger et al. (2013)
	Gobiidae	*Neogobius melanostomus*	Round goby	AEP	=	Belanger et al. (2010)
	Osphronemidae	*Trichopsis vittata*	Croaking gourami	AEP	+	Wysocki and Ladich (2001)
	Sciaenidae	*Sciaenops ocellatus*	Red drum	ASR	+	Fuiman et al. (1999)
	Polynemidae	*Eleutheronema tetradactulum*	Indian salmon	AEP	+	Wright et al. (2011)
	Percichthyidae	*Macquaria novemaculeata*	Australian bass	AEP	+	Wright et al. (2011)
	Chaetodontidae	*Chaetodon ocellatus*	Spotfin butterflyfish	AEP	=	Webb et al. (2012)

AEP auditory evoked potentials, *ASR* acoustic startled response, *BC* behavioral conditioning, *SEP* saccular evoked potentials, *SUR* single-unit recordings, *HR* heart rate. Developmental changes in auditory sensitivity are indicated as (+) increase, (−) decrease, or (=) no changes

the thresholds decrease during ontogeny. Further studies need to be performed on other cartilaginous fish to determine whether these results are representative of hearing changes during development within this group of fishes.

3.1.2 Teleostomi/Osteichthyes (Bony Fishes)

Clupeiformes

Within this order that includes several species with high commercial value, such as herrings (*Clupea* sp.), sardines (*Dussumieria* sp., *Escualosa* sp. *Sardina* sp., *Sardinella* sp., and *Sardinops* sp.), shads (*Alosa* sp.), and anchovies (over 15 species with the most common being *Anchoa* sp., *Thryssa* sp., *Stolephorus* sp. and *Coilia* sp.), very little is known on development of their hearing capabilities. Many species that belong to this order are capable of ultra sound detection and understanding how their auditory sense is adapted throughout ontogeny would certainly provide valuable information for the fisheries industry and conservation.

In one of only two studies that have examined the development of hearing in fishes from this order, Blaxtey and Batty (1985) used a behavioral technique that examined the development of startle responses evoked by auditory stimuli in the larvae herring (*Clupea harengus*). These researchers found that the acoustic startle response (i.e., the Mauthner mediated C-start escape response) to auditory stimuli in herring larvae appeared after hatching. Herring larvae were observed to respond to sound at 22–36 mm TL, while only responding to touch stimuli during earlier stages of development at 10–12 mm TL.

In a second study, Higgs et al. (2004) conducted an ontogenetic physiological study to evaluate the onset of ultrasound detection in the American shad, *Alosa sapidissima*. According to the authors, once the developing shad was capable of detecting sounds, the auditory sensitivity as measured using the AEP technique was not observed to change with age/size. No improvements in sensitivity were registered with age/size, namely from larvae of 30–34 mm TL to adults greater than 100 mm TL over a frequency range of 0.1–90 kHz (Fig. 4). According to the authors, the onset of ultrasound detection was coincident with the early development and specialization of the utricle.

Cypriniformes

This order contains the Ostariophysian fishes that possess accessory morphological hearing structures (i.e., Weberian ossicles), which couple the inner ear to the anterior part of the swim bladder that enable the fish to detect sound pressure stimuli.

The zebrafish (*Danio rerio*), a well-studied model, belongs to this taxon. This species has become a significant biomedical research model for investigating human hearing and vestibular disorders as it combines genetics, embryology, and excellent in vivo visualization all in a single organism (Whitfield et al. 2002; Lu and
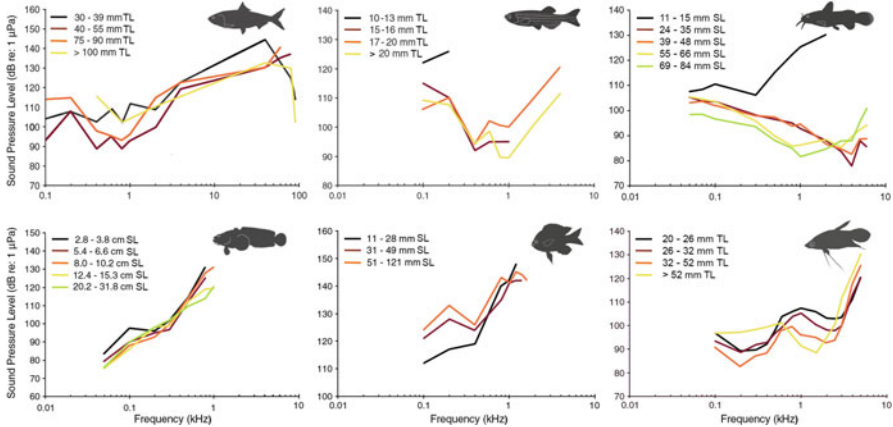
Fig. 4 Development of auditory sensitivity in various teleost fish species, namely: *upper row*, from *left to right*—American shad (*Alosa sapidissima*), zebrafish (*Danio rerio*), African bullhead catfish (*Lophiobagrus cyclurus*); *lower row*, from *left to right*—Lusitanian toadfish (*Halobatrachus didactylus*), sergeant major damselfish (*Adudefduf saxatilis*), croaking gourami (*Trichopsis vittata*). After Higgs et al. (2004), Higgs et al. (2003), Lechner et al. (2011), Vasconcelos and Ladich (2008), Egner and Mann (2005) and Wysocki and Ladich (2001), respectively

DeSmidt 2013).The first study to investigate the ontogeny of hearing in zebrafish was conducted by Higgs et al. (2001) using AEP recordings, and reported an absence of improvements in auditory sensitivity or bandwidth with growth and development, despite continuous hair cell production with age/size (body length tested: 25–34 mm up to 45–50 mm TL) (Fig. 4). According to this study, hearing sensitivity is not necessarily related to the number of sensory cells in the ear in juvenile or adult fish. Subsequently, Higgs et al. (2003) focused on zebrafish during earlier developmental stages (10–45 mm TL) and reported an increase in the maximum detectable frequency from 200 Hz (at 10 mm TL) to 4000 Hz (at 45 mm TL), which coincided with the development of the Weberian ossicles and sensitivity to sound pressure. Again, no differences were found regarding auditory sensitivity, response latency, or response amplitude with age/size for zebrafish across the size range tested.

Using a different technique based on observation of acoustic startle responses evoked by auditory/vibratory stimuli, Zeddies and Fay (2005) found that the stimulus thresholds and frequency bandwidth to which zebrafish responded was similar from 5 dpf (days post fertilization) to the adult stage. However, the authors also found that deflating the swim bladder in adults decreased their startle-like responses, while the same procedure in larval fish did not affect hearing, indicating that acoustic startle response thresholds are adjusted as the fish develop in order to maintain appropriate reactions to relevant stimuli. According to this study, zebrafish seem to switch from particle motion sensitivity, at the larvae stage, to sound pressure sensitivity during the juvenile and adult stages, which possess a fully developed ear containing Weberian ossicles.

Recently, Lu and DeSmidt (2013) recorded evoked potentials from saccular hair cells (microphonic responses) from zebrafish larvae at 2–7 dpf using particle motion stimulation delivered by a displacement-driven piezoelectric probe placed adjacent to the inner ear. Saccular potentials increased with stimulus intensity and frequency while auditory thresholds (at 200 Hz) decreased gradually during fish growth with age/size. Such developmental changes were correlated with the increases in the number and density of saccular hair cells. The results reported in this study are in contrast with the previously published data on the same species (Higgs et al. 2001, 2003), however the latter investigation by Lu and DeSmidt (2013) used zebrafish larvae during the first week of development, a period of rapid anatomical and physiological changes in the inner ear, which could explain the changes in ontogenetic auditory sensitivity.

Siluriformes

Within this taxon (also otophysines), two catfish species have been investigated, namely the squeaker catfish (*Synodontis schoutedeni*) (Mockokidae) and the African bullhead catfish (*Lophiobagrus cyclurus*) (Bagridae) (Lechner et al. 2010, 2011). Based on AEP recordings, both species exhibited considerable improvement in auditory sensitivity and changes in best frequency sensitivity range with increases in size/age (Lechner et al. 2010). According to Lechner et al. (2010), the smallest juveniles *S. schoutedeni* with 22–37 mm standard length (SL) had relatively poor hearing ability in comparison with larger juveniles and adults that range up to 127 mm SL (tested over a frequency range of 0.5–1 kHz). The authors reported an ontogenetic increase in auditory sensitivity of 26 dB re 1 μPa and a change in the range of lowest thresholds from 2–3 kHz in juveniles of 22–37 mm SL to 0.3–1 kHz in larger fish of 62–127 mm SL.

In the bullhead catfish (*L. cyclurues*), auditory sensitivity was reported to increase up to 40 dB re 1 μPa during ontogeny (Lechner et al. 2011) (Fig. 4). The smallest juveniles (11–15 mm SL) were unable to detect frequencies higher than 2–3 kHz while being most sensitive to frequencies of 0.05–2 kHz, whereas larger individuals (>24 mm SL) showed best sensitivity to higher frequencies of 4–6 kHz. According to the authors, the increase in auditory sensitivity and maximum detectable frequency was posited to be due to the development of interossicular ligaments between the Weberian ossicles.

Gadiformes

The single representative species of this order studied so far is the walleye pollock (*Theragra chalcogramma*) (Gadidae). Mann et al. (2009) showed that there were no significant differences in AEP sensitivity between three different size groups tested that ranged from 14 to 26 cm TL. The three size groups of walleye pollock had best hearing sensitivity from 100 to 200 Hz with thresholds of approximately 75 dB re 1 μPa. Although there were no significant differences in thresholds among the three

size groups, the authors did find a significant interaction between frequency and age/size, as well as, a trend (but not significant) which indicated that older fish may have slightly lower thresholds. The same study also described a substantial increase in the size of the saccular otolith and associated saccular epithelia of the inner ear during development, suggesting that a large increase in the size of the inner ear size does not necessarily lead to a significant change in auditory sensitivity.

Batrachoidiformes

This order includes the midshipman fish and toadfishes, which rely on acoustic communication for social behaviors and, therefore, their auditory system has been focus of attention in many studies including ontogeny.

According to Vasconcelos and Ladich (2008), the Lusitanian toadfish *Halobatrachus didactylus* (Batrachoididae) exhibits slight developmental increases in auditory sensitivity and maximum detectable frequency with age/size. Using the AEP recording technique, the authors found that the smallest group analyzed (3–4 cm SL) was circa 11 dB less sensitive at 100 Hz compared to larger size groups and had a lower maximum detectable frequency (800 Hz). The remaining size groups, which ranged from 5–7 to 20–32 cm SL, responded at all frequencies tested (50–1000 Hz) with similar thresholds (Fig. 4).

Another member of Batrachoididae, the plainfin midshipman (*Porichthys notatus*), has also been investigated regarding ontogenetic changes in auditory capabilities using electrophysiology and behavioral methods. Sisneros and Bass (2005) conducted extracellular single unit recordings from saccular afferents in different-sized midshipman fish, from small juveniles (3–5 cm SL) to the adults (>10 cm SL). Both resting discharge rate and auditory sensitivity increased with fish size, while the temporal encoding of the tested frequencies at an iso-intensity of 130 dB re 1 μPa did not show any significant developmental shifts.

Also using the midshipman fish model, Alderks and Sisneros (2011) recorded evoked saccular potentials to investigate potential ontogenetic changes in saccular sensitivity across a wider range of animals from small juveniles (1.9–3.1 cm SL) to adults (9–22.6 cm SL). The authors showed an ontogenetic retention of saccular sensitivity with size (see Fig. 5). They also reported an increase in the maximum detectable frequency with age/size such that larger fish were more likely to detect frequencies greater than 385 Hz. Subsequently, Alderks and Sisneros (2013) reported the development of the acoustic startle-like response in different-sized groups of midshipman fish larvae that ranged in size from 1.5 to 3.2 cm TL. The acoustic startle response was first observed in larvae at a size of 1.4 cm TL; above 1.8 cm TL, all larvae responded to a broadband stimulus of 154 dB re 1 μPa. Larval fish from the medium size group (1.9–2.4 cm TL) had significantly lower acoustic startle-like thresholds at 75–145 Hz than the other size groups, which may be related to differential growth and development of the saccule during different time points during early larval development (Fig. 5). Future work will be needed to determine the mechanisms responsible for the observed differences in acoustic startle-like response among the size groups tested for this species.
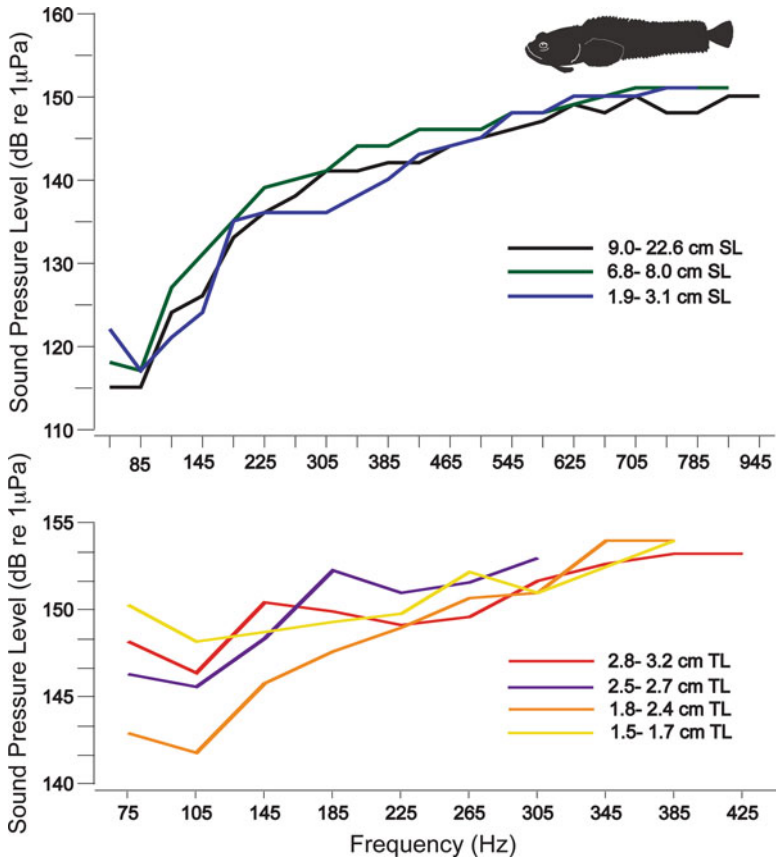
Fig. 5 Auditory sensitivity in the plainfin midshipman (*Poricithys notatus*) throughout development: *top*, tuning curves derived from saccular potential recordings in three size classes of fish. Notice the similar tuning profile from all three size groups, however larger fish are able to detect higher frequencies; *bottom*, tuning curves derived from auditory evoked behavioral responses in four different size groups of fish. Again notice the similar shape in the tuning curves from all four size groups. However larval fish in the 1.9–2.4 cm TL size group had significantly lower acoustic startle-like thresholds at 75–145 Hz than the other size groups, which may be related to differential growth and development of the saccule during different time points during early larval development

Perciformes

Within this highly diverse order, representatives of several families have been investigated. One research question that has received recent interest is whether the biotic sounds of reef habitats serve as important sound orientation cues for pelagic larvae and facilitate the localization and recruitment to appropriate settlement habitats.

Although it is clear that settlement-stage fish larvae can detect reef sound at distances of a few 100 m (Wright et al. 2010), it is less understood how such auditory sensitivity develops throughout the larval phase and how the auditory abilities vary between species.

The early hearing capabilities in several pelagic reef Pomacentrid species have been examined during larval stages with mixed results. Using AEP recordings, Egner and Mann (2005) reported an ontogenetic change in the auditory sensitivity of the sergeant major damselfish (*Abudefauf saxatilis*, Pomacentridae) (Fig. 4). Curiously, at 100 and 200 Hz there was a significant effect of size on hearing thresholds with auditory sensitivity decreasing with standard fish length. In addition, maximum detectable frequency increased with SL with the larger fish (>50 mm SL) being more responsive at higher frequencies (1000–1600 Hz). This study suggests that sound may play a role in short-range orientation (<1 km) of pelagic larvae to reefs.

In contrast, both hearing improvement and absence of developmental changes have been described among other species within the Pomacentridae family. Kenyon (1996), through classical conditioning experiments conducted in a standing wave tube to control sound pressure and particle motion cues, showed that the bicolor damselfish (*Stegastes partitus*) exhibit an ontogenetic increase in auditory sensitivity, up to 45 dB re 1 µPa at their most sensitive frequency of 300 Hz. Likewise, Wright et al. (2005) also reported increases in AEP responses of roughly 8 dB re 1 µPa at 100 and 600 Hz between pre-settlement (12–15 mm SL) and post-settlement (15–17 mm SL) in juvenile damselfish (*Stegastes nagasakiensis*).

Simpson et al. (2005) investigated sound detection in early embryonic stages of two clownfish species, the saddle anemone fish (*Amphiprion ephippium*) and the red anemone fish (*A. rubrocinctus*, Pomacentridae), by measuring the heart rate of embryos while exposed to sounds in the range of 100–1200 Hz at 80–150 dB (re 1 µPa at 1 m). The authors found that after 3 dpf the heart rate of larvae increased significantly in response to sound. Throughout development, larvae responded to sound via changes in heart rate to large range of frequencies from 400–700 Hz at 3 dpf and 100–1200 Hz at 9 dpf. Larval auditory sensitivity was also shown to increase during development approximately 51 dB re 1 µPa at 700 Hz.

More recently, Wright et al. (2011) described using AEP recordings ontogenetic increases in auditory sensitivity ranging up to 25 dB re 1 µPa in three pelagic coral-reef fish species. Ontogenetic increases in auditory sensitivity were demonstrated for larval stages of carangid (*Caranx ignobilis*), serranid (*Epinephalus coioides*), and polynemid (*Eleutheronema tetradactulum*) fishes ranging from 9 to 28 mm TL. However, fish larvae from two other species examined, *Epinephelus fuscoguttatus* (Serranidae) and *Macquaria novemaculeata* (Percichthyidae), did not show any ontogenetic changes in auditory sensitivity across different-sized groups. Such species-specific variation in auditory sensitivity during ontogeny suggests that both the developmental stage and species are important factors to consider when investigating whether sound may be a salient cue used by pelagic larvae for navigation and orientation to reef habitats.

Fuiman et al. (1999) used acoustic startle responses to investigate hearing in the sciaenid *Sciaenops ocellatus* (red drum) and observed an increase in sensitivity to acoustic stimuli, as well as to visual stimuli, throughout ontogeny (mostly in early larval stages with less than 8 mm TL). Several variables, such as response magnitude, frequency, duration, speed, and distance (to the auditory stimulus source) increased considerably during early development.

Among the family Osphronemidae, the croaking gourami (*Trichopsis vittata*) has been investigated by Wysocki and Ladich (2001), which revealed an increase in auditory sensitivity with size/age (from 20 mm to greater than 52 mm TL) for a frequency range of 0.8–3 kHz. The authors also reported a shift in the most sensitive frequency during development from 2.5 to 1.5 kHz (Fig. 4). According to Wysocki and Ladich (2001), such developmental changes in hearing sensitivity are most likely related to morphological changes in the air-breathing apparatus of the suprabranchial chamber that functions as an accessory hearing organ.

In contrast, the round goby (*Neogobius melanostomus*) belonging to the family Gobidae has been investigated by Belanger et al. (2010) and showed similar AEP thresholds with no changes in sensitivity during development across different size stages ranging from 40 mm TL to greater than 120 mm TL. The authors of this study suggest that the lack of size effects on auditory sensitivity is likely due to the concurrent growth of both otolith (sulcus) area and auditory epithelium, which results in maintaining hair cell density in the auditory macula during development.

In the spotfin butterflyfish (*Chaetodon ocellatus*, family Chaetodontidae), Webb et al. (2012) also reported the absence of ontogenetic changes in auditory sensitivity to sound pressure in fish of 21–31 mm SL. However, the authors did report a significantly higher sensitivity of larvae from this species compared to other similar-sized larvae of other coral reef species that lack the swim bladder horns found in *C. ocellatus*. The absence of developmental hearing improvements in *C. ocellatus* may be due to the fact that the swim bladder horns (accessory morphological hearing structures) are established earlier in development prior to a size of 21 mm SL.

More recently, Caiger et al. (2013) investigated the hearing abilities of hapuka (*Polyprion oxygeneios*, family Polyprionidae) using AEP recordings and described increases in both ontogenetic auditory sensitivity (up to 27 dB re 1 µPa) and in auditory bandwidth (from maximum of 800 up to 1000 Hz) within the first year of development (from 10 to 262 mm fork length). The authors suggested that the development of rostral extensions of the swim bladder to the otic capsule may explain the increased auditory sensitivity of this species during development.

3.2   Development of Auditory Capabilities for Social Communication

Communication requires both a sender and receiver, thus one must analyze both the development of auditory sensitivity and sound production when investigating how acoustic communication develops in fishes. Only three non-related species have

been investigated regarding the development of auditory capabilities and sound production in the context of acoustic communication, namely the croaking gourami (*T. vittata*, Osphronemidae) (Wysocki and Ladich 2001), the Lusitanian toadfish (*Halobatrachus didactylus*, Batrachoididae) (Vasconcelos and Ladich 2008), and the squeaker catfish (*Synodontis schoutedeni*, Mochokidae) (Lechner et al. 2010). In each of these species, ontogenetic improvements in auditory sensitivity were coincident with changes in the spectral features of sound production, such as dominant frequency and amplitude.

More specifically, as mentioned before, in the croaking gourami (*Trichopsis vittata*), auditory sensitivity increased up to 14 dB re 1 μPa between 0.8 and 3.0 kHz and the most sensitive frequency within this range shifting from 2.5 to 1.5 kHz (Wysocki and Ladich 2001). The authors of this study also reported that sound production in *T. vittata* began early in development (at 17.5 mm SL) and the dominant frequency of vocalizations shifted from 3 to 1.5 kHz accompanied by an increase in amplitude of 43 dB re 1 μPa. Such results suggested the onset of acoustic communication occurs only after improvements in both auditory sensitivity and vocal amplitude around the same frequencies (circa 1.5 kHz).

In the Lusitanian toadfish (*H. didactylus*), the best hearing sensitivity was found at 50 Hz for all sizes analyzed (from 3 to 32 cm SL) and auditory sensitivity improved at 100 Hz, as well as, at higher frequencies such as 800 and 1000 Hz with age/size (Vasconcelos and Ladich 2008). Comparing auditory thresholds with sound spectra within each size group revealed that smaller juveniles were potentially barely able to detect agonistic vocalizations of similar-sized fish, contrary to larger fish. The authors suggested that the onset of acoustic communication occurs when juveniles were able to generate grunts of higher sound amplitude and lower dominant frequency.

Finally, in the squeaker catfish (*S. schoutedeni*), auditory sensitivity increased at higher frequencies during ontogeny, namely at 5 and 6 kHz, and comparisons between audiograms and sound spectra revealed a match between that the most sensitive hearing frequencies and the dominant frequencies of agonistic sounds for all sizes analyzed (Lechner et al. 2010). This study showed that *S. schoutedeni* could detect conspecific vocalizations at all developmental stages examined, most likely due to the presence of the Weberian apparatus.

In these studies, all juvenile fishes vocalized in agonistic context, showing similar changes in sound features despite possessing different sound production mechanisms. In all three studies the dominant frequency decreased with fish development, whereas sound pressure levels and pulse periods increased throughout ontogeny. In both the croaking gourami and the squeaker catfish sound duration also increased throughout ontogeny. Future studies should analyze how the vocal repertoire changes during development, especially in highly vocal species such as the toadfishes, and whether vocal differentiation parallels auditory improvements.

4 Conclusions and Future Directions

Fish represent the largest extant group of vertebrates and display the greatest diversity of structures of the vertebrate auditory system. Thus, this taxon has the potential to provide valuable insights into the ecology and evolution of the vertebrate auditory system. However, despite the greater than 30,000 known fish species only a relatively small number has been examined in terms of ontogenetic development of structure and sensitivity of the auditory system. Thus, more studies should be performed on representatives of diverse species and families with different anatomical hearing specializations. The remarkable diversity of inner ear morphologies and accessory hearing structures in fishes should provide a rich source for future comparisons to gain insights on the selective pressures that have shaped the evolution of fish auditory systems.

There remain many important questions and areas of research that should be addressed in future work, several of which are briefly detailed below:

1. Although the saccule is the main auditory end organ in most teleost species, more physiology studies are needed for the other putative auditory end organs, the lagena and utricle, and their characterization in terms of ontogenetic changes in morphology, sensitivity, and contribution to the development of hearing in fishes. Compared to the numerous studies for the fish saccule, there are only a limited number of studies for the lagena and utricle regarding their potential contribution to hearing during ontogeny (Higgs et al. 2004; Webb et al. 2012; Inoue et al. 2013).

2. Another topic that needs further study concerns the ontogenetic morphological changes in hair cell addition and bundle density in the three putative auditory end organs (saccule, lagena, and utricle). Questions that should be addressed include: (1) Are there differences in hair cell addition and bundle density in the saccule, lagena, and utricle during different stages of development? (2) How do changes in hair cell bundle density relate to the auditory sensitivity of the end organ? (3) In addition to ontogenetic changes, are there seasonal differences in the proliferation and density of hair cells in these auditory end organs across different stages of the reproductive cycle? Recently a study by Coffin et al. (2012) reported seasonal changes in hair cell density in the saccules of female plainfin midshipman fish (*Porichthys notatus*) that did not occur in the other two end organs (lagena or utricle). The saccular-specific changes in hair cell density were correlated with reproductive state-dependent changes in auditory saccular sensitivity of female midshipman. Additional studies should be performed in other vocal and non-vocal species to determine how widespread this phenomenon is among fishes.

3. Very few studies have examined the concurrent development of the auditory system and sound production in fishes in the context of social acoustic communication. In order to better understand how the vocal motor system develops together

with the auditory system for acoustic communication, future studies should analyze the ontogenetic development of the vocal-auditory pathways. In these studies, a particular focus should be given to highly vocal species exhibiting vocal differentiation, which might be influenced by developmental changes in the central auditory circuitry.

4. Finally, the effects of the acoustic environment, including sounds from conspecifics and self-generated vocalizations, on early development of the fish auditory system remain to be investigated.

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