Review

Why otoliths? Insights from inner ear physiology and fisheries biology

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Abstract.   Otoliths are of interest to investigators from several disciplines including systematics, auditory neuroscience, and fisheries. However, there is often very little sharing of information or ideas about otoliths across disciplines despite similarities in the questions raised by different groups of investigators. A major purpose of this paper is to present otolith-related questions common to all disciplines and then demonstrate that the issues are not only similar but also that more frequent interactions would be mutually beneficial. Because otoliths evolved as part of the inner ear to serve the senses of balance and hearing, we first discuss the basic structure of the ear. We then raise several questions that deal with the structure and patterns of otolith morphology and how changes in otoliths with fish age affect hearing and balance. More specifically, we ask about the significance of otolith size and how this might affect ear function; the growth of otoliths and how hearing and balance may or may not change with growth; the significance of different otolith shapes with respect to ear function; the functional significance of otoliths that do not contact the complete sensory epithelium; and why teleost fishes have otoliths and not the otoconia found in virtually all other extant vertebrates.

Extra keywords: ageing, asteriscus, balance, biomechanics, ear, fish, hearing, lagena, lapillus, otoconia, saccule, sagitta, utricle.

Introduction

The vertebrate ear evolved very early in the history of the vertebrates, presumably as a mechanism for measuring motion and position of the head relative to gravity (see papers in Manley *et al*. 2004). With small changes, the ear has evolved into a device that could detect sound (van Bergeijk 1967).

All vertebrate ears contain several common features including three semicircular canals (other than in jawless vertebrates, which have one or two such canals) (Fig. 1). In addition, most non-mammalian vertebrates have three otolithic end organs: the saccule, utricle, and lagena. Each otolithic end organ contains calcium carbonate crystals (along with other structures described below). In most vertebrate species, the crystals are in the form of otoconial masses that are held together in a pasty mass. In teleost fishes, however, the calcium carbonate crystals are solidified into a single mass in each otolithic end organ, the otoliths.

The dense otoliths of teleost fishes are of considerable interest because of their intimate involvement in the function of the ear in the senses of balance and hearing. However, otoliths themselves are of interest because they provide information about the age and general biology of fishes and because they provide a good deal of information useful for understanding fish systematics and evolution.

It is rare that individual investigators from different disciplines are interested in all aspects of otolith biology, from their use in ageing to their role in enabling the ear to mediate the senses of hearing and balance. In effect, investigators interested in auditory neuroscience, fisheries biology, and/or systematics rarely interact with one another to share insights and data on otoliths. It is our contention, however, that investigators from these disciplines could benefit greatly from sharing knowledge, ideas, and questions, and that our overall understanding of the structure and function of otoliths would benefit from such collaborations.

The purpose of this paper, then, is twofold. First, we provide some background on the structure of the ears of fishes. Second, we set up several questions about the relationships between otolith structure and function that are at the interface between issues (e.g. otolith growth), which are of importance to the fields of fisheries, systematics, and neuroscience. In setting up these questions, we do not expect to provide
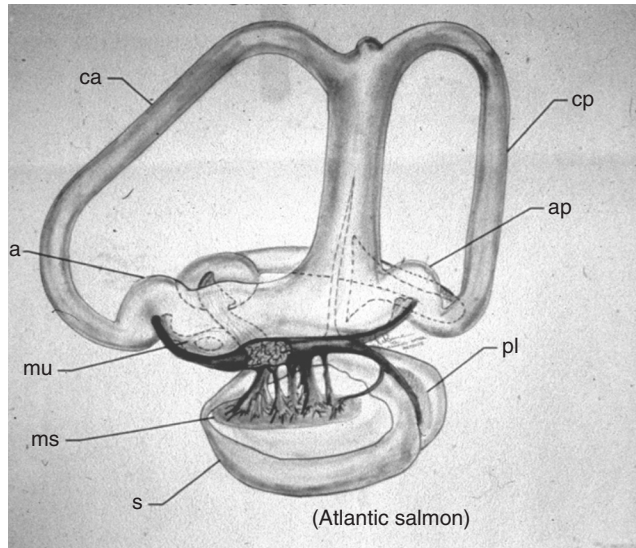
Fig. 1. The right ear of the Atlantic salmon (*Salmo salar*) (anterior to the left) redrawn from Retzius (1881). a, ap, cristae (sensory areas) of the semicircular canals; ca, cp, anterior and posterior semicircular canals (the horizontal canal is to the rear); ms, macula (sensory epithelium) of the saccule; mu, macula of the utricle; pl, sensory epithelium of the lagena; s, saccule.

complete answers but perhaps will provide some insight into ways of thinking about otoliths and an ear that extends back in vertebrate evolution to the very earliest ostracoderms (e.g. Manley and Clack 2004 and papers in Manley *et al.* 2004).

The ear – a brief overview

The inner ear of modern teleost fishes is a membranous sac located in the cranial cavity, lateral to or below the hindbrain. Although all teleost ears have the same basic structure, there is substantial interspecific diversity in the size of the ears and their component parts (see Retzius 1881; for recent and extensive reviews see Popper *et al.* 2003; Ladich and Popper 2004).

The ears of fishes (and all vertebrates) have as their functional units mechanoreceptive sensory hair cells (Fig. 2*a*). These are found on specialised receptor surfaces, the sensory epithelia (Fig. 2*b*). These sensory hair cells are strikingly similar in the ears of all vertebrates and in the lateral line of fishes and amphibians (e.g. Chang *et al.* 1992; Coffin *et al.* 2004). The apical surface of each hair cell has a tuft of cilia upon which are located microscopic calcium channels (e.g. Hudspeth *et al.* 2000). Bending of the bundle of cilia opens channels and admits calcium, thus setting into action a cascade of events that ultimately causes the release of a neurotransmitter from the basal end of the cell that excites the afferent endings of the eighth cranial nerve and sends a signal to the brain about the presence of a mechanical event, which could be sound or movement of the head relative to gravity.

The ears of bony fishes and elasmobranchs have three semicircular canals (anterior, posterior, and horizontal) and

three otolithic end organs (saccule, lagena, and utricle) (Fig. 1) (e.g. Corwin 1981; Popper *et al.* 2003; Ladich and Popper 2004). Many, but not all, fishes have a seventh end organ, the macula neglecta, located near the utricle (Retzius 1881; Corwin 1981). Each semicircular canal has a sensory epithelial area, or crista, that is covered by a gelatinous cupula into which the very long ciliary bundles of the sensory cells are embedded. Thus, any motion of the cupula in response to angular acceleration of the head results in bending of the cilia and excitation of the sensory hair cells (Platt 1983; Popper *et al.* 2003).

Each of the otolithic end organs has a sensory epithelium (often called a 'macula') in the wall of the membranous chamber. The apical surface of the epithelium is separated from the overlying otolith by a thin otolithic membrane (Dunkelberger *et al.* 1980; Fig. 2*b*). Although the detailed structure of the otolithic membrane and the precise physical relationship between the otolith and sensory epithelium are not fully understood, there is evidence that the otolithic membrane attaches to microvilli on the supporting cells that surround the sensory cells of the sensory epithelium and to the rough surface of the otolith sulcus (e.g. Popper 1977; Dunkelberger *et al.* 1980). In effect, the otolithic membrane holds the otolith in place next to the epithelium.

The ciliary bundles of the sensory hair cells project through the otolithic membrane and may or may not have contact with the surface of the otolith. The otolithic end organs serve as an inertial system whereby a stimulus, whether it is head motion or sound, causes motion of the fish body relative to the otoliths (Fig. 2*b*). Because the otolith (or otoconial mass in non-teleost vertebrates) is approximately three times denser than the fish body, it moves at a different amplitude and phase than the sensory epithelium. As a result of the direct mechanical contact between the tips of the cilia and the otolith or indirect contact through the otolith membrane, the cilia bend as the otolith moves, leading to detection of the mechanical signal (reviewed in Popper *et al.* 2003; Ladich and Popper 2004).

Interestingly, the basic morphology of the ear and its component parts is similar across extant-jawed vertebrates, although different vertebrate taxa may have modifications and specialisations that serve specific functions not necessarily found in bony fishes. Thus, all jawed vertebrates have semicircular canals and their associated cristae, and at least a utricle and saccule. The lagena is diminutive in birds and reptiles and is not present in mammals, and it has been suggested that the lagena may have given rise to the basilar papilla of reptiles and birds and the cochlea of mammals (Wever 1974).

The bottom line is that the function of the otolith in the vertebrate ear is to help stimulate the sensory hair cells of the otolithic organs. As a consequence, all issues raised about the structure of otoliths must be viewed in terms of ear function. It is probably fair to state that this system evolved over millions of years to optimise the detection of head motion and hearing.
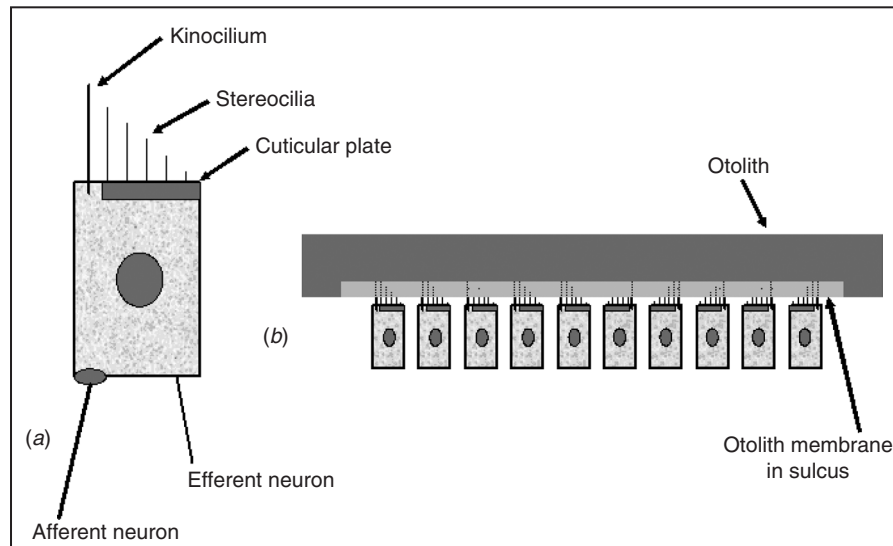
Fig. 2. Highly schematic views of a sensory hair cell (*a*) and the relationship between the otolith and the sensory epithelium (*b*). The sensory hair cell has an apical ciliary bundle made up of a single eccentrically located kinocilium and a series of stereocilia that are graded in size, with the longest closest to the kinocilium. The stereocilia have their bases embedded in a dense cuticular plate. The sensory cells are innervated by afferent and efferent neurons. The sensory cells are grouped into the sensory epithelium or macula. The epithelium sits within the sulcus of the otolith. A gelatinous otolithic membrane appears to connect the otolith to the epithelium. During sound stimulation, the fish's body, being the same density as water, moves with the water mass. However, the much denser otolith moves at a different amplitude and phase than the epithelium. Because the cilia are attached to the sensory cells and their tips contact the otoliths, the top and bottom of the cilia move differentially, resulting in a bending of the cilia. This produces a series of reactions that results in signal detection.

Hearing

Why hear?

Fish hearing has been reviewed several times recently (e.g. Popper and Carlson 1998; Fay and Megela Simmons 1999; Popper and Fay 1999; Popper *et al.* 2003; Ladich and Popper 2004), and so only a few observations are presented here because they provide some basis for discussions of the function of the otolith organs of the ear.

Fay and Popper (2000) argued that the auditory capabilities of fishes are quite sophisticated and that the basic functions of the fish auditory system are similar to those of terrestrial vertebrates including mammals. They pointed out that a major role of the auditory system is to provide an animal (or human) with a general sense of its acoustic environment and that this auditory scene (Bregman 1991) is of considerable value in providing an animal with information about things happening around it, but out of sight. Indeed, Fay and Popper (2000) suggest that hearing (one of the major functions of the ear) evolved to provide animals with information such as the presence and location of predators and prey, the location of coral reefs, and other distant information that was critical for survival.

The need to glean information about the sounds around the animal would have evolved early in the course of evolution

of the vertebrate ear, argue Fay and Popper (2000). In effect, just knowing that a sound is present is not of much value to an animal. It is far more important to know where a sound is coming from, to be able to discriminate one sound from another, and to pick out the biologically relevant sounds from the cacophony of sounds that make up any environment. Presumably, it was only later in vertebrate evolution that animals started to emit their own species-specific sounds for communication. Supporting the usefulness of sound, even in animals that do not make or use sound for intraspecific communication, are data showing that the goldfish (*Carassius auratus*) is not known to make sounds. Yet, it has excellent hearing and can detect sounds to over 3000 Hz with good sensitivity (Fay 1988).

In considering that the auditory system (including the otolith organs and the auditory part of the brain) not only has to detect the presence of sound but also has to discriminate between sounds that differ in frequency and/or intensity; determine the direction of sounds in three-dimensional space (sound source localisation); and detect signals in the presence of other, unwanted (masking) sounds, one could assume that the ear must be fairly sophisticated in how it does its job. Thus, the structure of the ear, its shape, the shape and size of its sensory epithelia, and the shape and size of its otoliths,

are likely to be intimately tied to these detection and analysis processes. Moreover, considering the diversity of fishes and the diversity of fish ears (e.g. Retzius 1881), it is reasonable to suggest that fishes have 'invented' multiple ways to do the same basic auditory tasks. In considering the structure of the ear (and their otoliths), it is imperative to keep these auditory tasks in mind.

What sounds do fish hear?

Studies of hearing capabilities of fishes have resulted in hearing assessments in ~100 species (see Fay 1988; Fay and Megela Simmons 1999; Popper *et al.* 2003 for reviews). Figure 3 shows a set of audiograms, or measures of fish hearing sensitivity, for a group of fishes in order to demonstrate certain aspects of fish hearing. Most species can detect sounds from below 50 Hz to perhaps 1000 or 1500 Hz, as represented in Fig. 3 by the Atlantic croaker (*Micropogonias undulatus*), Atlantic cod (*Gadus morhua*), and Atlantic salmon (*Salmo salar*). In contrast, there are some species such as goldfish (*Carassius auratus*) and silver perch (*Bairdiella chrysoura*) that can detect sounds to over 3000 Hz (Fay 1988; Ramcharitar and Popper 2004) and a few others, all in the genus *Alosa*, that can detect sounds to over 180 kHz (Mann *et al.* 2001). The first group of fishes is referred to in the literature as hearing 'generalists' or 'non-specialists,' whereas the fish in the latter group are referred to as hearing 'specialists.' Not only do specialists have a wider bandwidth of hearing than generalists, but they also are often able to detect lower intensity sounds.

The basis for the better hearing by specialists is that all such species have evolved enhancements that improve hearing. Generally, these species acoustically couple a pressure-detecting device such as the swim bladder or other air bubble that may be located close to the ear. This results in specialists being able to detect both the pressure and particle velocity component of sound (see Kalmijn 1988; Rogers and Cox 1988), as opposed to primarily (but not only) particle velocity detection in generalists.

By way of comparison, although hearing generalists generally detect sounds to above 1 kHz and specialists to ~3 kHz, the few data available for sharks suggest that they can detect sounds to only ~800 Hz (Corwin 1981; Fay 1988). In contrast, birds generally detect sounds to several thousand hertz, whereas young humans are able to detect sounds to 20 kHz (Fay 1988). Many other mammals can detect sounds to 60 Hz or better, whereas certain specialised mammals such as bats and toothed whales can detect sounds to over 100 kHz (Fay 1988). Still, perhaps the best 'hearing' vertebrates are members of the teleost genus *Alosa* (shads and menhaden), which can detect sounds to over 200 kHz (Mann *et al.* 2001) and that may use this high-frequency detection to avoid dolphin predators by detecting the echolocation signals that these mammals use to find fish schools (Plachta and Popper 2003).
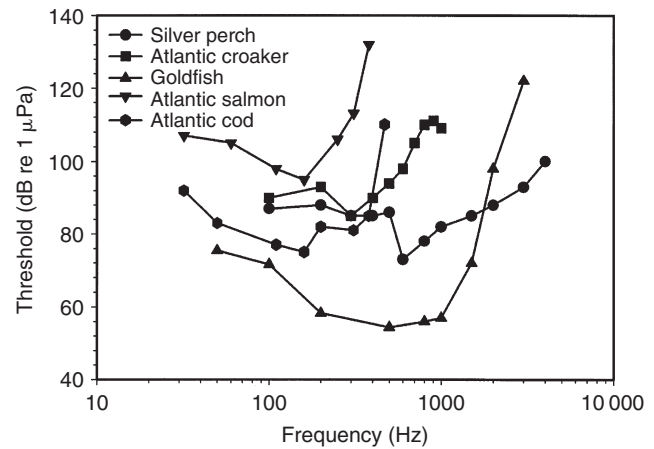

Fig. 3. Audiograms from several representative teleost species. The data are plotted as frequency *v.* the lowest sound level that is detectable by the species (threshold). Although these data give a general sense of the hearing capabilities of these species, many were determined using different behavioural or physiological methods using different types of experimental tanks. As a consequence, some of the differences in thresholds may be the result of experimental methods and not to differences between species or the differences may actually be greater but are hidden by different methods. These data do, however, show the range of hearing encountered in hearing studies and illustrate some of the differences between hearing specialists (goldfish, *Carassius auratus*) and silver perch (*Bairdiella chrysoura*; Ramcharitar *et al.* 2004) and hearing generalists such as the Atlantic salmon (*Salmo salar*; Hawkins and Johnstone 1978), Atlantic cod (*Gadus morhua*; Chapman and Hawkins 1973), and Atlantic croaker (*Micropogonias undulatus*; Ramcharitar and Popper 2004).

Inner ear diversity

One of the most striking aspects of fish ears is the interspecific diversity in structure that ranges from the gross structure of the ear to details in the structure of sensory hair cells. The gross shape of the ear may be partly related to the size of the fish but may also be related to ear function. However, nothing is known about the functional significance of the shape of the ear. More significantly, there is substantial diversity in the shape and size of the otoliths (Fig. 4). Although the functional significance of these differences is not known, it has been noted that there is much more diversity in the shape of the saccular otoliths than in the otoliths in the utricle and lagena. Interestingly, the saccule is the otolithic end organ most often implicated in hearing, and fishes with specialisations in hearing tend to also show some specialisations in otolith structure (e.g. Ladich and Popper 2004). For example, the silver perch, a species that detects sounds up to several kilohertz, has several specialisations of its otoliths including enlargement of the saccular and utricular otoliths, close proximity between these otoliths, and a deeply grooved sulcus in the saccular otolith (Ramcharitar *et al.* 2004).

Diversity is also found in the shape and size of the sensory epithelia (Popper 1977; Ramcharitar *et al.* 2004) and the relationship between the otolith and the epithelia (Popper *et al.*
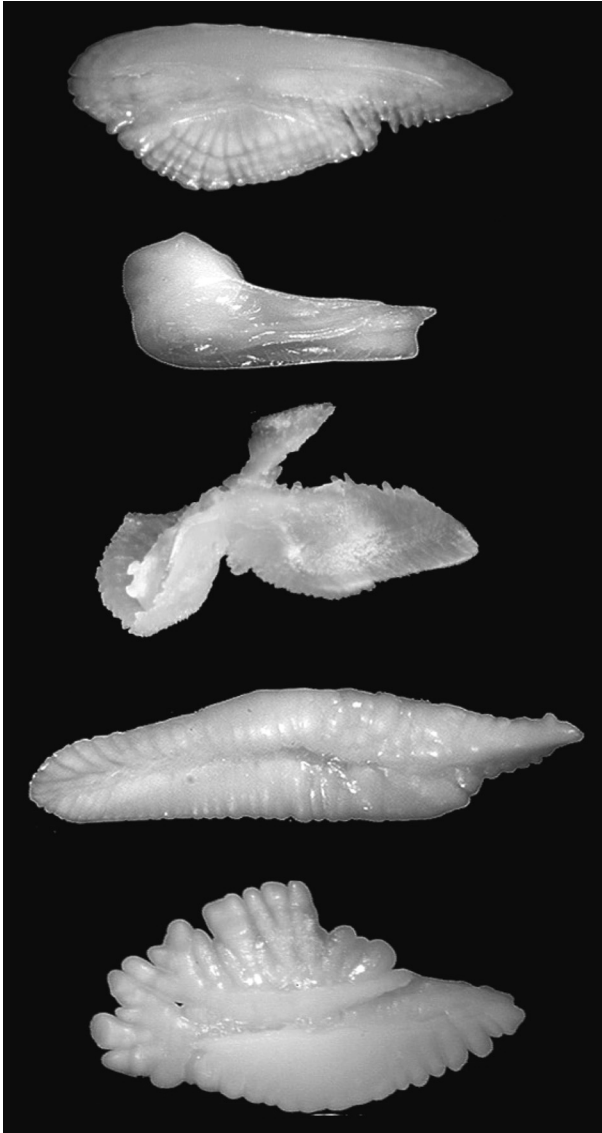
Fig. 4. Examples of the diversity of otolith shapes present among teleosts. Shown from top to bottom (not to scale) are sagittal otoliths of *Merluccius bilinearis*, *Halargyreus johnsoni*, *Lampris guttatus*, *Urophycis tenuis* and *Lopholatilus chamaeleonticeps*.

2003). In some species, the saccular epithelia fit fully within the sulcus of the otolith, whereas in other species, a portion of the epithelium is not covered by the otolith (e.g. Popper 1980). Additionally, there are interspecific variations in the depth of the sulcus, as exemplified in sciaenid fishes (Chao 1978; Ramcharitar *et al*. 2004).

Finally, there is diversity in the microstructure of the sensory hair cells themselves. There are very substantial differences in the length of the cilia in different epithelial regions. Although the functional significance of different cilia lengths has not been fully explored in fishes, there is some evidence that length is correlated with the frequency-response characteristics of the hair cells in different epithelial

regions (Platt and Popper 1984; Lanford *et al*. 2000). There is also evidence that there are interepithelial differences in the organelles in hair cells (Chang *et al*. 1992), some of which may be related to the energetics of the cells as well as to the number of cilia on hair cells in different epithelial regions (Ramcharitar *et al*. 2001).

Questions

The questions posed about otoliths by fisheries biologists and neuroscientists may appear to be quite different, but when analysed in detail, they are often similar questions taken from different perspectives. Thus, a fisheries biologist will ask questions about the significance of otolith growth increments and how they develop, whereas the neuroscientist will ask about the impact of growth on the senses of hearing and balance and the functional significance of specific otolith shapes. Yet, both groups are basically interested in otolith shape, size, growth, and diversity. Indeed, the interests of both groups led to a series of questions that are of basic importance in understanding otoliths, their physiology, and their function, and these are outlined below.

What is the significance of otolith size?

Some otolith size differences are related to fish growth, but otoliths in very large fishes can be much smaller than those in very small fish and vice versa (e.g. Campana 2004). Moreover, otoliths vary dramatically in size between different species. We would predict that otoliths of different sizes (and masses) would have differences in resonance frequency (and thus in movement characteristics) relative to the sensory epithelium. For example, large otoliths may be more sensitive to low-frequency sounds than small otoliths are (Lychakov and Rebane 1993, 2000). However, there are virtually no experimental data that directly relate otolith size and function in balance and hearing.

Despite this lack of data, one speculation is that otolith size is more influential with regard to balance and swimming than to hearing. Several observations support this argument. For example, some of the largest ocean fishes (e.g. swordfishes, tunas) have very small otoliths relative to body size, whereas many shallow-water reef fishes have relatively large otoliths. The only existing study on large pelagic fishes suggested that tunas are hearing generalists (Iversen 1967). Although it is possible that hearing capabilities are inversely related to otolith size, we consider it more likely that the selective pressures on otolith size and ear function are more related to the response to the rapid motions of the animals rather than to hearing. Tunas and swordfishes are fast, agile swimmers capable of rapid turns. In such fishes, overly sensitive detection of changes in angular motion could be a disadvantage rather than an advantage. For example, a recent study on fossil and extant cetaceans found that the arc of the semicircular canals in whales and dolphins was approximately one-third that of terrestrial mammals when corrected for differences

in body mass (Spoor *et al.* 2002). Indeed, the canals of the blue whale were smaller than those of an average human. The reduced canal arc radius made the cetaceans less sensitive to changes in angular acceleration, which is in keeping with their greater capability for rapid rotation and movements relative to comparably sized land mammals (Spoor *et al.* 2002). If similar evolutionary pressures were at work with teleosts, it might explain why large fast fish like tunas have relatively small inner ears (and otoliths) compared with more sedentary ground fishes where small changes in angular sensitivity would be more important.

In contrast, a theoretical analysis of otoliths of several different teleost species suggests some correlation exists between otolith size and the upper limit of hearing capabilities, with larger otoliths being associated with a narrower range of hearing than smaller otoliths (Finneran and Hastings 2000; Lychakov and Rebane 1993, 2000). Supporting this argument is the finding that a marine catfish, *Arius felis*, has excellent low-frequency hearing but does not detect sounds above ∼900 Hz (Popper and Tavolga 1981). In contrast, other catfish species have somewhat poorer low-frequency hearing than *Arius* but they can detect sounds to over 3 kHz (Fay 1988). The difference is that *Arius* has an exceptionally large utricular otolith compared with other catfish species, suggesting that the larger otolith functions are an accelerometer for low-frequency signals (Popper and Tavolga 1981).

Although the two ideas proposed here to account for the functional significance of otolith size may appear to be mutually exclusive within an individual fish, they may well explain many of the differences among species. Clearly though, only experimental data will help discriminate between these hypotheses, and there may, indeed, be other explanations to explain the significance of otolith size. The critical point here, however, is that additional data are needed if we are to understand the functional significance of otolith size.

How does growth affect ear function?

Both the otoliths and the sensory epithelia grow for much of the life of most fishes. Significantly, the growth in the sensory epithelium is combined with the addition of sensory hair cells so that large fishes may have substantially more sensory hair cells than smaller fishes (e.g. Lombarte and Popper 1994). Although it has been suggested that the increased size and number of sensory cells help fishes maintain stable hearing sensitivity as the fish grows (Popper *et al.* 1988; Rogers *et al.* 1988), this idea has yet to be tested, and it is possible that there is a continual change in hearing sensitivity and/or range of hearing with fish growth. In contrast, there appears to be a stable allometry between otolith size (and presumably epithelium size) and fish size through most of the lifetime (Campana 2004), supporting the view that hearing sensitivity is maintained.

An intriguing situation concerns the function of the ear once the fish's growth rate is reduced to very low levels in old individuals. Despite the negligible somatic growth of the fish, the otolith continues to increase in mass as growth increments continue to be accreted (Boehlert 1985). Most of this additional mass is added to the medial (sensory epithelial) side of the sensory otolith (Beamish 1979). Based on the limited data in the literature, it is likely that once fishes stop growing, they no longer add sensory hair cells to the sensory epithelia (e.g. Higgs *et al.* 2001). Thus, if the mass of the otolith changes without an increase in the number of sensory cells, does the increased mass mean a change in ear function with age?

What is the reason for the complex shapes in otoliths?

As can be seen in any atlas of otolith structure (and Fig. 4), the shape of saccular otoliths vary greatly, and although some are simple ellipsoids, others have highly complex patterns with various projections and invaginations that are species specific. Although one can speculate that the different otolith patterns have no meaning in terms of function of the ear, it is also possible to argue from parsimony and suggest that the complex shapes are biologically meaningful. Thus, the shape may impose specific motion dynamics on the otoliths in response to acoustic or vestibular stimuli that are more complex than one would get from a more ellipsoid otolith.

There are no empirical data to support this argument. However, there is no doubt that asymmetric and convoluted otoliths would have a very different centre of mass than would a more symmetrical otolith. As such, it might be argued that otolith shape is more influential on balance and orientation than on hearing. The fact that otolith shape in the region of the sulcus (which is the point of attachment of the sensory epithelium) is relatively invariant supports the view that variations in the centre of mass are the primary result of variations in otolith shape. Conversely, if otolith shape had no effect on hearing or vestibular functions, one would not expect shape to be so consistent within a species.

What is the significance of 'incomplete' otoliths?

Some otoliths are incomplete relative to the sensory epithelium. In other words, there are many species in which the caudal end of the saccular epithelium is contained within the sulcus, whereas the rostral end may not be covered by the otolith at all (e.g. Popper 1980). What does this mean in terms of stimulation of the epithelium? Are the epithelial regions 'covered' by the otolith stimulated in different ways than the epithelial regions not lying directly under the otolith? Could incomplete otoliths provide a broader range of sensitivity than complete otoliths? Clearly, detailed physiological experiments are required to resolve this issue.

Otoliths v. otoconia

Why do bony fishes have a single fused calcified structure, whereas primitive fishes, elasmobranchs, and all tetrapods

(including marine mammals) have otoconia? Virtually no work has been conducted on the functional differences of otoconial masses *v.* otoliths. The very limited behavioural data for elasmobranchs suggests a narrow hearing bandwidth (Fay 1988), but these data are in need of replication and do not necessarily form the basis for suggesting any differences in otoconial *v.* otolith ears. Although it would be tempting to use tetrapod data to help understand otolith function, the roles of the otolith organs are generally different in tetrapods than in fishes, and so such extrapolation is probably not appropriate.

Of the three crystalline forms of calcium carbonate found in otoliths and other calcified structures, it is the metastable aragonite form that makes up almost all otoliths (a conspicuous exception being asteriscii, which are often composed of vaterite). Among vertebrates, only the otoliths of teleosts and the otoconia of poikilothermic vertebrates are aragonitic; fish more primitive than teleosts have otoconia composed of either calcite or hydroxyapatite, whereas mammals have calcitic otoconia (Mann *et al.* 1983). In addition, it is only aragonitic otoliths that serve as useful age indicators; otoconia do not form growth increments. There is no obvious reason why this should be nor is there any known physiological advantage of an aragonitic otolith over other crystal morphs of calcium carbonate. However, it is tempting to speculate that the combination of species-specific shapes, aragonitic composition, and unique method of calcification is indirectly responsible for the time-keeping and environmental recording properties of otoliths (Campana and Thorrold 2001).

The chemical purity of aragonitic otoliths is striking, with ∼97% of it being made up of pure calcium carbonate and the remainder being a small percentage of organic material and a smattering of trace elements (Campana 1999). Although comparable tests are not available for calcitic otoconia, hydroxyapatite is very unlikely to be as pure. The significance of this purity is unknown.

In summary, teleost otoliths are markedly different than otoconia in several features: otoliths are generally aragonitic, chemically pure, relatively large, are of a detailed and species-specific shape, are acellular, and form discrete growth increments. In contrast, otoconia are formed of either calcite or hydroxyapatite, are relatively small and of unstructured shape, may be cellular or acellular, and do not form growth increments. The differences may be, in part, functionally related to the hearing and balance demands of the environment (aquatic *v.* terrestrial), but this cannot account for the very different morphology of cetacean ears. Clearly, more research is required here.

Summary and conclusions

The questions raised in this paper are common to both the fisheries biologist and the neuroscientist. Answers to these questions would enhance our understanding of fish biology and would improve our understanding of the structure and function of the ear. Answers to none of these questions will be easy to come by, but it is reasonable to suggest that achieving these answers and moving forwards in our understanding of otolithic systems would benefit greatly from an increased interaction between biologists from the different disciplines. The goal of this paper, then, would be achieved if it helps to start a dialogue that would ultimately bring together individuals with diverse interests in otoliths and otolithic systems and to share knowledge and perhaps design experiments that would enable a fuller understanding of 'why otoliths.'

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