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Fish otoliths: do sizes correlate with taxonomic group, habitat and/or luminescence?

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Otoliths are dense structures in the ears of fishes that function in hearing and gravity perception. Otolith (sagitta) diameters, as percentages of standard length (% SL), are calculated for 247 marine fish species in 147 families and compared by taxonomic group (usually order), habitat and presence or absence of luminescence. Otolith sizes range from 0.4–31.4 mm and 0.08–11.2% SL. The eel and spiny eel orders Anguilliformes and Notacanthiformes have small to very small otoliths, as do the triggerfish order Tetraodontiformes, pipefish order Gasterosteiformes, billfish suborder Scombroidei and many of the dragonfish order Stomiiformes. The soldierfish order Beryciformes has moderate to very large otoliths. The perch order Perciformes has a wide range of otolith sizes but most have small to moderate otoliths 2–5% SL. Only 16 out of the 247 species have the relatively largest otoliths, over 7% SL. Seven out of these 16 species are also luminous from a variety of habitats. Luminous species have slightly to much larger otoliths than non-luminous species in the same family. Both beryciforms and luminous fishes live in low-light environments, where acute colour vision is probably impossible. Most fishes of the epipelagic surface waters have very small otoliths, perhaps due to background noise and/or excessive movement of heavy otoliths in rough seas. Bathypelagic species usually have small otoliths and regressed or absent swimbladders. Other habitats have species with a range of otolith sizes. While the relationship between hearing ability and otolith length is unknown, at least some groups with modified swim-bladders have larger otoliths, which may be associated with more acute hearing.

Keywords: otolith diameters; sagitta; luminescence

1. INTRODUCTION

Otoliths, or ear stones, are dense calcareous structures contained in three chambers associated with the ear in teleost fishes (Popper *et al.* 1988). The saccular otolith, the sagitta, is the largest in most fishes, while the lagenar otolith, the asteriscus, is second largest in most fishes and largest in most ostariophysian fishes. The smallest is the utricular otolith, the lapillus. All three otoliths are considered to be involved in both auditory and vestibular (gravity information) functions (Popper & Fay 1993). Fish ears can detect particle motion directly via the response of the otoliths to motion and indirectly via the fluctuations of swim-bladder volume in a pressure field; in some fishes this indirect detection is augmented by a direct connection of the swim-bladder to the ear (Popper *et al.* 1988; Popper & Fay 1993).

A review of the morphology of fish ears (Popper & Coombs 1982) indicated that most interspecific variation involves the larger two chambers of the ear, the sacculus and lagena. Variations in the size and shape of their two otoliths, particularly the sagitta, have long been known, and used as taxonomic features (i.e. Nafpaktitis & Paxton 1969). The variation in sagitta size is immense, ranging from pin-head sized in 1.5 m long dolphin fishes (family Coryphaenidae) to massive pieces of calcium carbonate at least 30 mm × 12 mm × 10 mm and weighing 4 g in one 2 m sciaenid. A number of the deep-sea lanternfishes (family Myctophidae) that are well known for their ability to luminesce also have relatively large otoliths, measuring up to 8.5% of the fish's standard length (SL).

The sagitta has long been thought to be involved primarily in hearing and it is tempting to correlate the variation in otolith sizes with hearing ability. The common names of croaker and drum for the Sciaenidae refer to the group's ability to produce sound. However, as the sagitta is now thought to have both auditory and vestibular functions, differences in otolith sizes may be influenced by at least two otolith functions. Knowledge of which aspects of a fish's life are correlated with variations in otolith sizes should be helpful in future considerations of otolith functions. The three questions asked here involve evolutionary histories, as evidenced by taxonomic grouping, habitat, here restricted to marine environments, and luminescence, which is not correlated restrictively with either taxonomy or habitat.

2. MATERIAL AND METHODS

The *Otolith atlas of southern African marine fishes* (Smale *et al.* 1995) provided scanning electron micrograph images of otoliths (sagitta for all but the Siluriformes) of 972 fish species in 181 families, together with the largest diameter of the otolith (usually length, rarely height) and the standard or total length of the specimen. Some 247 species, representing 12 superorders, 29 orders, 11 suborders of the order Perciformes (all that were included in Smale *et al.* (1995), following Nelson (1994)) and 147 of the 181 families, were entered in a spreadsheet. Usually the

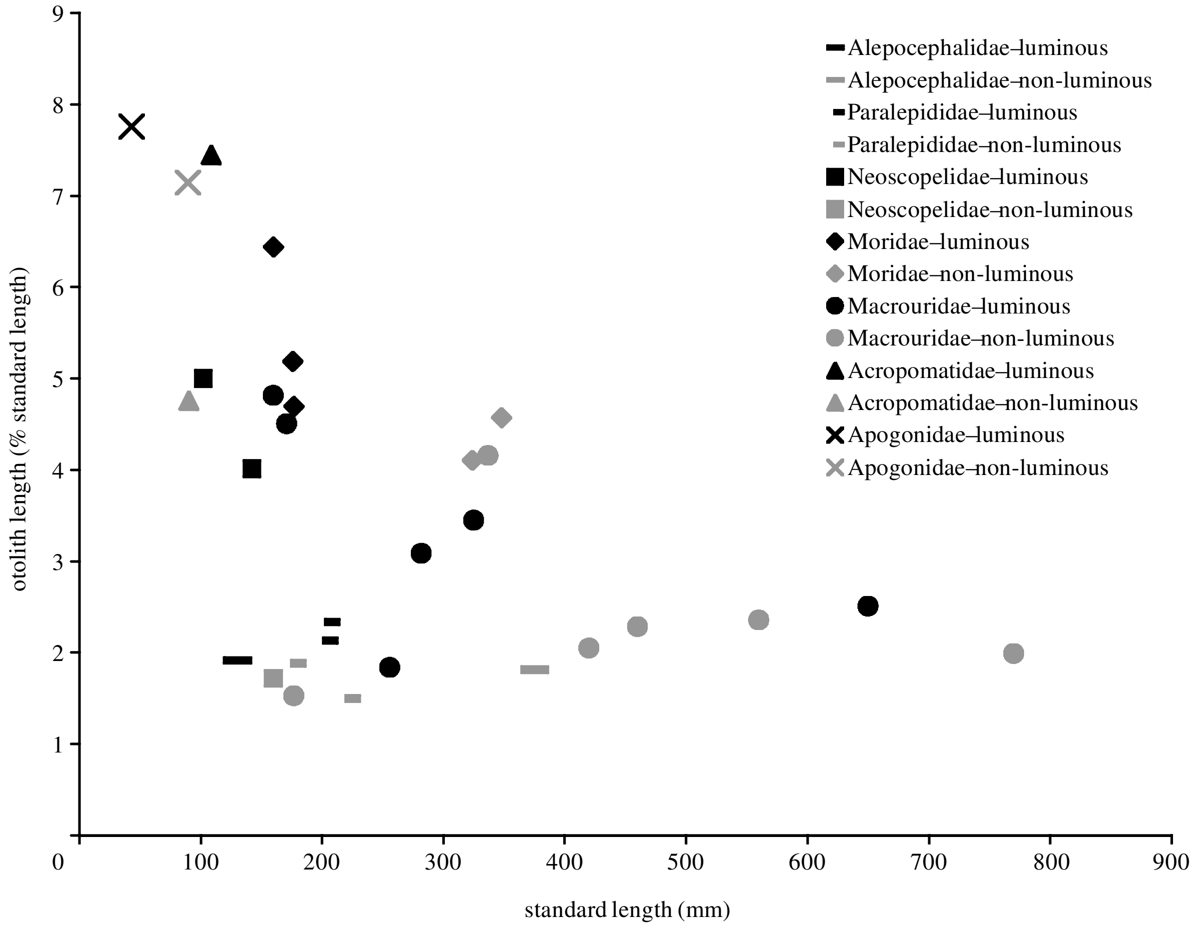

Figure 1. Otolith sizes as percentage standard length versus standard length in millimetres of luminous (black) and non-luminous (grey) species in seven fish families.

largest specimen for which both otolith and specimen lengths were given was used for each species. A number of species were included for each family with luminous species; in total, 49 luminous species in 24 families and eight orders were included. Total length is converted to SL where necessary by multiplying by 0.8, based on a tail-length range of 12–26% total length in a variety of fish illustrations in Smith & Heemstra (1986). Habitats include inshore, coral reef, shelf, slope, epipelagic, mesopelagic and bathypelagic and are determined from knowledge of the fish families and/or data presented in Smith & Heemstra (1986). Different sets (taxa, habitats, luminescence) are plotted, usually as otolith size (% SL) versus SL (mm) (figures 1 and 2). The following relative otolith size ranges are categorized arbitrarily: very small, 0.01–0.99% SL; small, 1–2.99% SL; moderate, 3–4.99% SL; large, 5–6.99% SL; and very large, 7–12% SL.

3. RESULTS

The complete data set is too large to present in this small paper, but is available as an Excel file from the author. Otolith diameter ranges from 0.08% SL in the swordfish (Xiphiidae) to 11.2% SL in the luminous pinecone fish (Monocentridae), while in absolute size otoliths range from 0.4 mm in a pipefish (Syngnathidae) to 31.4 mm in *Argyrosomus hololepidotus* of the croaker–drum family Sciaenidae. However, this latter specimen has a SL of 1.08 m and the otolith is a relatively small 2.9% SL. The breakdown of the 247 species in the data set by relative size is very small, 14.5%; small, 36.3%; moderate, 31.5%; large, 11.3%; and very large, 6.4%.

A few taxonomic groups are correlated with sagitta size. Within the superorder Elopomorpha, the eel order Anguilliformes, represented by 11 species in six families, have relatively small to very small otoliths, 0.17–2.43% SL, with only two of the 11 species having otoliths larger than 1% SL. The single species of the spiny eel order Notacanthiformes also has a very small otolith at 0.47% SL. Another group with small to very small otoliths is the puffer and triggerfish order Tetraodontiformes, represented by seven species in six families with an otolith size range of 0.42–2.13% SL. In the pipefish order Gasterosteiformes, four of the five species and families have very small otoliths, < 1% SL. Not surprisingly, the large and diverse order Perciformes, represented by 58 species in 41 families and 13 suborders, has a wide range of otolith sizes, 0.08–7.75% SL. The suborder Scombroidei, represented by four species including bill fishes and tuna, have generally small otoliths, 0.08–3.27% SL; only the slope gemfish *Rexea* has an otolith exceeding 1.1% SL. The majority of perciforms in this data set have small- to moderate-sized otoliths, 2–5% SL. Eight species in five families within the Stomiiformes, considered one family, Stomiidae, by Nelson (1994), all have otoliths smaller than 1.5% SL.

To determine which taxonomic groups have the largest otoliths, the 16 species with the largest relative otoliths, all > 7% SL, were compared by order. Of these 16, six species

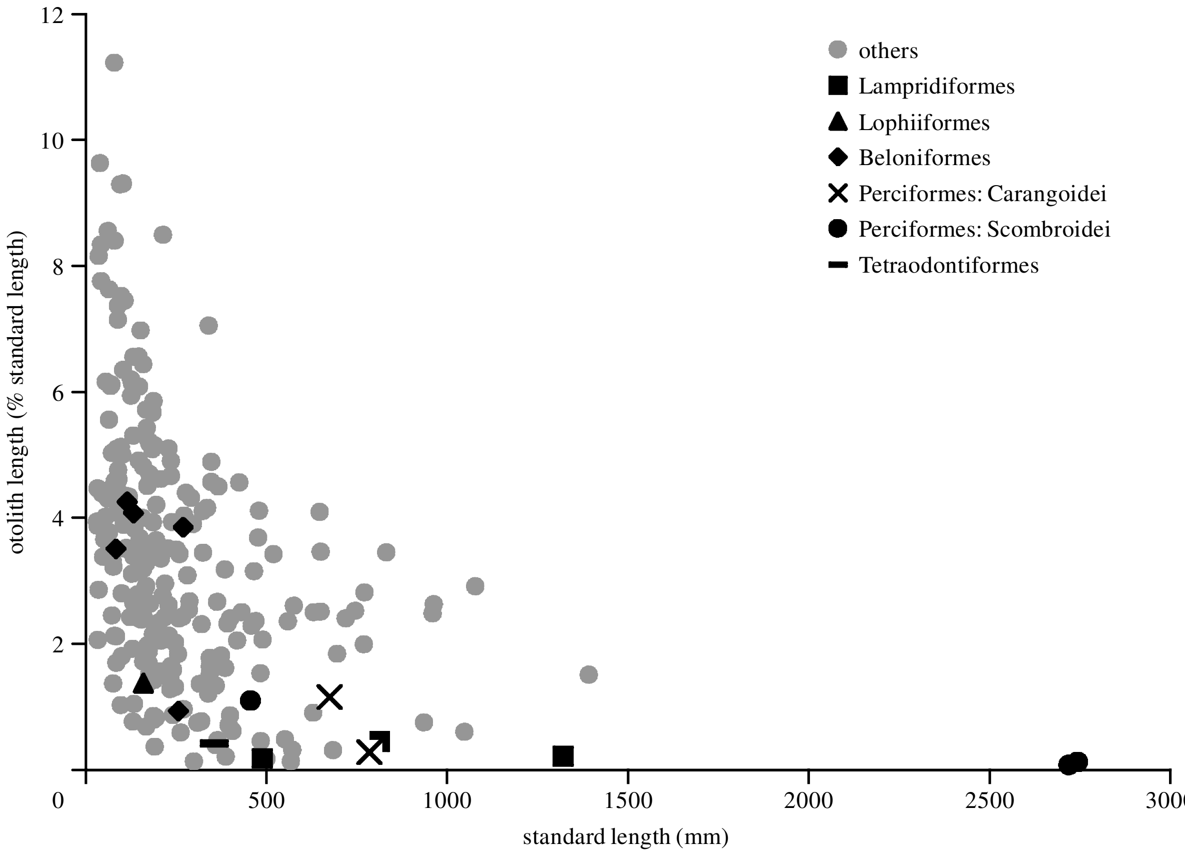

Figure 2. Otolith sizes as percentage standard length versus standard length in millimetres of epipelagic species (black) versus all other species (grey).

are in the squirrelfish order Beryciformes, in the families Holocentridae and Trachichthyidae (two species each), Monocentridae and Diretmidae. The other ten species in the Beryciformes have otoliths ranging from 3.55 to 6.97% SL, of moderate to large relative size. Other orders with very large otoliths include Perciformes (two out of two species of Apogonidae, one out of two Acropomatidae), Myctophiformes (two out of six Myctophidae), Argentiniformes (one out of two Opisthoproctidae), Stomiiformes (one out of four Sternoptychidae), Stephanoberyciformes (one out of three Melamphaidae), Zeiformes (one out of one Caproidae) and Scorpaeniformes (one out of five Scorpaenidae).

Seven out of the 16 species with the relatively largest otoliths, over 7.0% SL, are luminous: two Myctophidae (Myctophiformes) and one each of Opisthoproctidae (Argentiniformes), Sternoptychidae (Stomiiformes), Monocentridae (Beryciformes), Acropomatidae and Apogonidae (Perciformes). They occupy the following habitats: mesopelagic (three species), slope (two species), shelf and coral reef (one species each). However, when all 48 luminous species are considered, the majority are found to have very small to moderate otoliths, less than 4% SL, including the vast majority of the 14 species of Stomiiformes.

To examine more closely these luminous species, 30 species are plotted from the seven families that have both luminous and non-luminous representatives (Alepocephalidae, two species; Paralepididae, four species; Neoscopelidae, three species; Moridae, five species; Macrouridae, 12 species; Acropomatidae, two species; and Apogonidae, two species). In all families except the Macrouridae, all of the luminous species have slightly to much larger otoliths than their non-luminous relatives (figure 1).

Otolith sizes were also compared by habitat, with most showing a great range of sizes: inshore, 23 species, 0.13–6.09% SL; coral reef, 22 species, 0.48–7.75% SL; shelf, 62 species, 0.96–11.2% SL; slope, 74 species, 0.45–9.30% SL; mesopelagic, 40 species, 0.13–8.55% SL; and bathypelagic, 11 species, 1.28–9.63% SL. Only the epipelagic showed a significant trend towards small otoliths, with 15 species ranging from 0.08 to 4.25% SL (figure 2). These species are in the orders Lampridiformes (three species), Lophiiformes (one species), Beloniformes (five species), Perciformes (five species) and Tetraodontiformes (one species). The otoliths are small to very small, < 1.4% SL, in all but the Beloniformes, where three flying fishes and an oceanic halfbeak have moderate-sized otoliths ranging from 3.51 to 4.25% SL.

4. DISCUSSION

Most fish species apparently have some allometric growth of otoliths, sometimes significant. In the two largest species of Sciaenidae for which Smale *et al.* (1995) provided data, *A. hololepidotus* and *Atractoscion aequidens*, the three specimens of each species had a decreasing relative otolith size with increasing SL (5.3% of 112.8 mm SL, 4.5% of 180 mm SL and 1.9% of 1348 mm SL; and 6.5% of 56.8 mm SL, 5.0% of 144.8 mm SL and 2.8% of

772 mm SL, respectively). Clearly the otoliths are growing much more slowly than the rest of the fishes. With maximum sagitta sizes for these specimens of 31.4 mm and 21.7 mm, respectively, it is unlikely that hearing or some other otolith function becomes less important with age. Perhaps some otolith size threshold that is related to function is reached at an early age, after which otolith growth slows.

One aspect of the present study may distort some of the data on relative otolith sizes. The use of otolith maximum diameter as a percentage of SL exaggerates the relative otolith size in short-bodied species and underemphasizes the size in long-bodied forms. Thus, the relatively small otolith of the eel orders Notacanthiformes and Anguilliformes is partly an artefact of the methodology. However, comparison of the actual otolith sizes for the 12 eel species in these two orders (0.8–2.5 mm (eight species) and 3.5–4.1 mm (four species)) with actual otolith sizes of the 15 species of the order Beryciformes with relatively large otoliths (4.2–6.54 mm (three species) and 7.0–17.0 mm (12 species)) indicates that the distortion does not give a totally false picture of relative otolith sizes.

The taxonomic comparison of otolith sizes given in § 3 is limited to the bigger picture at the ordinal level, where eels have relatively small otoliths and soldierfish relatively large otoliths. Eels inhabit a variety of environments from freshwater to the deep sea. Many have modifications of the nostrils, some spectacular, and a number of deep-sea species have sexual dimorphism of the nasal organ, with macrosomatic males (McCosker 1998). As a group, eels appear to have a more important sense of smell than hearing.

With the soldierfish order, Beryciformes, it is not possible to separate the evolutionary history, as evidenced by the taxonomic grouping, completely from the habitat. This order is restricted almost entirely to the dim or dark waters of the deep sea, either as benthic species on the slope (Berycidae, Trachichthyidae) or as free-swimming species in the mesopelagic or bathypelagic waters (Anoplogastridae); those species associated with coral reefs (Anomalopidae, Holocentridae) or the shelf (Monocentridae) are almost always nocturnal (Paxton 1998). Most have large eyes as well as large otoliths, and it appears that senses of both sight and hearing are heightened. At least some holocentrids have hearing augmented by an otophysic connection with the swim-bladder (Popper & Coombs 1982). A separate analysis of all species of Holocentridae in Smale *et al.* (1995) indicates the three genera of the subfamily Myripristinae, with a two-chambered swim-bladder (Nelson 1994) and otophysic connection, have larger otoliths (nine species, 5.5–9.3% SL) than the two genera of the subfamily Holocentrinae with a single-chambered swim-bladder (six species, 3.0–4.7% SL when one specimen, < 80 mm SL, is excluded). While the relationship between hearing ability and otolith length is unknown, at least some groups with modified swim-bladders, like the Myripristinae and Sciaenidae, have larger otoliths, which may be associated with more acute hearing.

Detailed analyses of otolith sizes by family have not been attempted here. The very large otoliths of the family Sciaenidae are well known and correlation with the sound production of this group, known as croakers and drums, is evident. Popper & Coombs (1982, p. 322) indicated the goby family, Gobiidae, is characterized by an exceptionally large sacculus. The data analysed here for two species indicate a sagitta of moderate length, 4.26–4.46% SL. None of the other 13 South African species of Gobiidae for which otolith diameter is presented (Smale *et al.* 1995) have otoliths greater than 6% SL, and nine species have relatively moderate otolith lengths of 3.03–4.97% SL. However, these otoliths are almost round or square, and total area or mass may be more important than overall length.

Otolith size is apparently correlated with at least one habitat, the epipelagic. Here, the majority of species have small or very small otoliths (figure 2). A possible criticism of this analysis, based on the three very elongate species of Lampridiformes in the epipelagic, is at least partially deflected by their absolute otolith sizes of 0.9–3.7 mm, at the average to very-small end of the scale. The small to very-small otoliths of epipelagic fishes may be the result of one or more of the following:

(i) a low signal-to-noise ratio limits signal detection (Popper *et al.* 1988) and rough seas in surface waters may generate so much background noise that acute hearing is impossible;
(ii) rough seas may cause heavy otoliths to move too much in the sacculus (R. McCauley, personal communication);
(iii) acute colour vision in well-lit surface waters (many epipelagic fishes have large eyes) may be so important that the disadvantages of (i) and (ii) outweigh the advantage of acute hearing in calm weather.

If rough seas are a significant disadvantage to large otoliths, the majority of intertidal fishes on the open coast should have small otoliths.

Montgomery & Pankhurst (1997) stated that the sagitta in bathypelagic fishes is small. The data set here, of 11 species in six families, is too small to generalize. However, one of the three species of the bathypelagic Melamphaidae, *Sio nordenskjoldii*, has very large otoliths, 9.63% SL. There are often exceptions to any generalization, although allometry in this small, 40 mm SL, specimen may contribute. Most of the other eight bathypelagic species have small otoliths. Not included is the whalefish family, Cetomimidae, with some 35 species and very small otoliths (Paxton 1989); while only three out of the 150 species of bathypelagic ceratioid anglerfish (Nelson 1994) are included, these also have small otoliths. The swim-bladders of bathypelagic fishes in general, including anglers and whalefish, are lacking or regressed (Marshall 1979). Small otoliths in most bathypelagic fishes may be correlated with the inability to use the indirect method of pressure-wave detection due to swim-bladder absence. The predatory members of the mesopelagic Stomiidae also lack swim-bladders (Marshall 1979) and have very small sagittas (see § 3).

Montgomery & Pankhurst (1997) indicated that benthopelagic slope fishes have larger sagittas and many are sound producers. They cited studies that showed lack of sound production in abyssal species, coupled with small otoliths despite the presence of swim-bladders. They suggested that decreasing elasticity of swim-bladders at increasing depth may make vibration difficult, or increased gas density may lessen their efficiency as sound resonators.

The indication that many luminous fishes have large otoliths is initially surprising (figure 1). However, the presence of luminescence indicates the absence or great diminution of one important environmental variable, sunlight, in the habitats of these species. As a result, acute colour vision is probably impossible. The loss of such an important sense may give added adaptive advantage to the heightened development of more than one other sense, in these cases both hearing and dim-light vision. However, such an advantage does not explain why most luminous species have larger otoliths than non-luminous species in the same family. A more detailed survey is needed.

The conclusions reached above are by necessity speculative as the relationship between otolith size and hearing acuity is unclear, and are based on a superficial analysis of sagitta diameters in only about 1% of the known fish species. A more detailed study using many more species may give more insight into the sensory perception of fishes. In such a study, the possible distortion caused by using SL or total length could be lessened by using head length, as few head lengths are as extreme as the body lengths of some eels, dragonfish or oarfish. Use of otolith area or mass could provide more sensitive discrimination than maximum diameter.

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