

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

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

John R. Paxton

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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 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 (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. O 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 Nota 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, pipef 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 Stomiif 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 Per 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 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 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 t 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 env 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 wat 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 i 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. Oth 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 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,

Keywords: otolith diameters; sagitta; luminescence

1. INTRODUCTION

Otoliths, or ear stones, are dense calcareous structures contained in three chambers associated with the ear in
contained in three chambers associated with the ear in primarily in hearing and it is tempting to correlate the
contained in three chambers associated with the ear in 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 t 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 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 ostarion by since \sum 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 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 an 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 19 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 (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 fluctua-
tions of swim-bladder volume in a pressure field ears can detect particle motion directly via the response
of the otoliths to motion and indirectly via the fluctua-
tions of swim-bladder volume in a pressure field; in some
fishes this indirect detection is augmented by a 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 tions 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 $\&$ Fav 1993) fishes this indirect detectio

connection of the swim-blaa

1988; Popper & Fay 1993).

A review of the mornho mnection of the swim-bladder to the ear (Popper *et al.* m
88; Popper & Fay 1993). tiv
A review of the morphology of fish ears (Popper &
nombs 1982) indicated that most interspecific variation

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 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 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 bee 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. Nafnaktitis 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, 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 nin-head sized in 1.5 m long dolphin fishes 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
Corvaphenidae) to massive pieces of calcium carbon 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 from pin-head sized in 1.5 m long dolphin fishes (family Coryphaenidae) to massive pieces of calcium carbonate at least $30 \text{ mm} \times 12 \text{ mm} \times 10 \text{ mm}$ and weighing 4 g in one 2 m sciencid. A number of the deep-sea lan Coryphaenidae) to massive pieces of calcium carbonate
at least $30 \text{ mm} \times 12 \text{ mm} \times 10 \text{ mm}$ and weighing 4 g in one
 2 m sciaenid. A number of the deep-sea lanternfishes
(family Myctophidae) that are well known at least $30 \text{ mm} \times 12 \text{ mm} \times 10 \text{ mm}$ 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) 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 ility to luminesce also have relatively large otoliths,
easuring up to 8.5% of the fish's standard length (SL).
The sagitta has long been thought to be involved
imarily in hearing and it is tempting to correlate the

utricular otolith, the lapillus. All three otoliths are vestibular functions, differences in otolith sizes may be considered to be involved in both auditory and vestibular influenced by at least two otolith functions. Know The sagitta has long been thought to be involved primarily in hearing and it is tempting to correlate the 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 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 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 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 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. Knowle 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 v 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 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 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 enviro of otolith functions. The three questions asked here involve evolutionary histories, as evidenced by taxonomic grouping, habitat, here restricted to marine environinvolve evolutionary histories, as evidenced by taxonomic
grouping, habitat, here restricted to marine environ-
ments, and luminescence, which is not correlated restric-
tively with either taxonomy or habitat grouping, habitat, here restricted to
ments, and luminescence, which is not c
tively with either taxonomy or habitat. **2. MATERIAL AND METHODS**

The *Otolith atlas of southern African marine ¢shes* (Smale *et al.* 1995) provided scanning electron micrograph images of otoliths 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, teacher with 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

(www.lly longth negaly height) 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, (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. (10 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 191 families, were included in Smale *et al.* (1995), following Nelson (1994)) and 147 of the 181 families, were entered in a spreadsheet. Usually the *Phil. Trans. R. Soc. Lond.* B (2000) **355**, 1299–1303 1299 (2000) **1299** C 2000 The Royal Society

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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 species in seven isn ian missis.

largest specimen for which both otolith and specimen lengths

unce given wes wed for each engains. A number of species were 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 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 aposite in 24 families and s 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 longth is convented to SL wh luminous species in 24 families and eight orders were included.
Total length is converted to SL where necessary by multiplying 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
veriety of fish illustrations Variety of fish 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). Habi-
tats include inchere, corre by 0.8, based on a tail-length range of 12–26% total length in a
variety of fish illustrations in Smith & Heemstra (1986). Habi-
tats include inshore, coral reef, shelf, slope, epipelagic, meso-
pelogic and bethunologic an variety of fish illustrations in Smith & Heemstra (1986). Habitats include inshore, coral reef, shelf, slope, epipelagic, meso-
pelagic and bathypelagic and are determined from knowledge of
the fish familias and/or data pr pelagic 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, the fish families and/or data presented in Smith & Heemstra 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 polative stalith (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 arbit-
regiliu very small 0.01 The following relative otolith size ranges are categorized arbit-
rarily: 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 S. RESULTS
The complete data set is too large to present in this
small paper, but is available as an Excel file from the
suthor. Otolith diameter ranges from 0.08% SI in the 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 pipesmall 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 pine-
cone fish (Monocentridae) while in absolute size otoliths author. Otolith diameter ranges from 0.08% SL in the swordfish (Xiphiidae) to 11.2% SL in the luminous pine-
cone fish (Monocentridae), while in absolute size otoliths
range from 0.4 mm in a pinefish (Symmathida swordfish (Xiphiidae) to 11.2% SL in the luminous pine-
cone fish (Monocentridae), while in absolute size otoliths
range from 0.4 mm in a pipefish (Syngnathidae) to
 31.4 mm in *Araynsomus hololehidatus* of the croake cone fish (Monocentridae), while in absolute size otoliths of
range from 0.4 mm in a pipefish (Syngnathidae) to St
31.4 mm in *Argyrosomus hololepidotus* of the croaker-drum (1^{.4}
family Sciaenidae, However, this latter s 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 SI of 1.08 m and the otolith is a relatively small $2.$ 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 family Sciaenidae. However, this latter specimen has a
SL of 1.08m and the otolith is a relatively small 2.9% SL.
The breakdown of the 247 species in the data set by The breakdown of the 247 species in the data set by *Phil. Trans. R. Soc. Lond.* B (2000)

relative size is very small, 14.5% ; small, 36.3% ; moderate, 31.5% ; large, 11.3% ; and very large, 6.4% relative size is very small, 14.5%; small, 36.3
31.5%; large, 11.3%; and very large, 6.4%.
A few taxonomic groups are correlated wit ative size is very small, 14.5%; small, 36.3%; moderate, 5%; large, 11.3%; and very large, 6.4%.
A few taxonomic groups are correlated with sagitta size.
ithin the supercrear Elonomorpha, the eel order Anguil.

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 Anguil-
liformes represented by 11 species in six families, have A few taxonomic groups are correlated with sagitta size.
Within the superorder Elopomorpha, the eel order Anguil-
liformes, represented by 11 species in six families, have
relatively small to very small otoliths $0.17-2.4$ Within the superorder Elopomorpha, the eel order Anguil-
liformes, represented by 11 species in six families, have
relatively small to very small otoliths, 0.17–2.43% SL, with liformes, 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% SI. The single species of the spiny ee 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 Nota-
canthiformes also has a very small otolith at only two of the 11 species having otoliths larger than 1% SL. The single species of the spiny eel order Nota-
canthiformes also has a very small otolith at 0.47% SL.
Another group with small to very small otoliths is the 1% SL. The single species of the spiny eel order Nota-canthiformes also has a very small otolith at 0.47% SL.
Another group with small to very small otoliths is the canthiformes 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 si 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
0.49–9.13% SL. In the ninefish order Gaster 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 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 otolities $\lt 1\%$ SL. Not surprisingly the l 0.42–2.13% SL. In the pipefish order Gasterosteiformes,
four of the five species and families have very small
otoliths, $\lt 1\%$ SL. Not surprisingly, the large and diverse
order Perciformes represented by 58 species in 4 four of the five species and families have very small otoliths, $\langle 1\% \rangle$ SL. Not surprisingly, the large and diverse order Perciformes, represented by 58 species in 41 families otoliths, $\langle 1\%$ 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,
0.08–775% SL. The suborder Scombroidei repres 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 gen 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, $0.08-3.27\%$ SI : only the slope g 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 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 $2-5\%$ SI. Fight species in five famil *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. St 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% SI 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. omiiformes, considered one family, Stomiidae, by Nelson
194), all have otoliths smaller than 1.5% SL.
To determine which taxonomic groups have the largest
pliths the l6 species with the largest relative otoliths all

(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 spec 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
other species (grey).

are in the squirrelfish order Beryciformes, in the families
Holocentridae, and Trachichthyidae (two species each) are in the squirrelfish order Beryciformes, in the families
Holocentridae and Trachichthyidae (two species each),
Monocentridae and Diretmidae The other ten species in 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 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 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 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 Acropomatida 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), Arg with very large otoliths include Perciformes (two out of two species of Apogonidae, one out of two Acropomatidae), Myctophidae), Argentini-
Myctophiformes (two out of six Myctophidae), Argentini-
formes (one out of two Oni Myctophiformes (two out of six Myctophidae), Argentini-
formes (one out of two Opisthoproctidae), Stomiiformes Myctophiformes (two out of six Myctophidae), Argentini-
formes (one out of two Opisthoproctidae), Stemiiformes
(one out of three Melamphaidae), Zeiformes (one out of formes (one out of two Opisthoproctidae), Stomiiformes
(one out of four Sternoptychidae), Stephanoberyciformes
(one out of three Melamphaidae), Zeiformes (one out of five
capacidae), and Scorpaeniformes (one out of five (one out of four Sternoptychidae), Stephanoberyciformes
(one out of three Melamphaidae), Zeiformes (one out of
one Caproidae) and Scorpaeniformes (one out of five
Scorpaenidae) Scorpaenidae). one Caproidae) and Scorpaeniformes (one out of five Scorpaenidae).
Seven out of the 16 species with the relatively largest

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 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) Sternontychidae (Stomijformes) otoliths, over 7.0% SL, are luminous: two Myctophidae (Myctophiformes) and one each of Opisthoproctidae (Argentiniformes), Sternoptychidae (Stomiiformes), Monocentridae (Bervciformes) Acronomatidae and Apogonidae (Perciformes). They occupy the following 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 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 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 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 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 Stomiiformes. % SL, including the vast majority of the 14 species of omiiformes.
To examine more closely these luminous species, 30
ecles are plotted from the seven families that have both

To examine more closely these luminous species, 30
species are plotted from the seven families that have both
luminous and non-luminous representatives (Alepocepha-
lidae two species: Paralenididae four species: Neoscopespecies are plotted from the seven families that have both
luminous and non-luminous representatives (Alepocepha-
lidae, two species; Paralepididae, four species; Neoscope-
lidae, three species: Moridae, five species: Macr luminous and non-luminous representatives (Alepocepha-lidae, two species; Paralepididae, four species; Neoscope-lidae, three species; Moridae, five species; Macrouridae, *Phil. Trans. R. Soc. Lond.* B (2000)

12 species; Acropomatidae, two species; and Apogonidae, two species). In all families except the Macrouridae, all of 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 two species). In all families except the Macro
the luminous species have slightly to much la
than their non-luminous relatives (figure 1).
Otolith sizes were also compared by babits e luminous species have slightly to much larger otoliths
an their non-luminous relatives (figure 1).
Otolith sizes were also compared by habitat, with most
owing a great range of sizes: inshore 23 species 0.13–

(Myctophiformes) and one each of Opisthoproctidae species). The otoliths are small to very small, $\lt 1.4\%$ SL, (Argentiniformes), Sternoptychidae (Stomiiformes), in all but the Beloniformes, where three flying fishes an 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– 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– showing a great range of sizes: inshore, 23 species, 0.13–6.09% SL; scral reef, 22 species, 0.48–7.75% SL; shelf, 62 species, 0.96–11.2% SL; slope, 74 species, 0.45–9.30% SL; mesonelagic 40 species 0.13–8.55% SI : and bat 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 mesopelagic, 40 species, $0.13-8.55\%$ SL; and bathy-
pelagic, 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% SI (figure pelagic, 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 I ampridiformes (three sp 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),
Lophiformes (one species), Beloniformes (five spe 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 (species are in the orders Lampridiformes (three species),
Lophiformes (one species), Beloniformes (five species),
Perciformes (five species) and Tetraodontiformes (one
species) The otoliths are small to very small $\leq 1.$ 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 f Perciformes (five species) and Tetraodontiformes (one species). The otoliths are small to very small, $\langle 1.4\% \rangle$ SL, in all but the Beloniformes, where three flying fishes and an oceanic halfbeak have moderate-sized oto species). The otoliths are small to very small, $\langle 1.4\% \rangle$ 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% SI in all but the Beloniform
an oceanic halfbeak have
from 3.51 to 4.25% SL.

4. DISCUSSION

To examine more closely these luminous species, 30 provided data, A. hololepidotus and Atractoscion aequidens,
species are plotted from the seven families that have both the three specimens of each species had a decreasing Most fish species apparently have some allometric 4. **DISCUSSION**
Most fish species apparently have some allometric
growth of otoliths, sometimes significant. In the two
largest species of Sciencidae for which Smale et al. (1995) 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 holalehidatus and Atractoscian agained 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 largest species of Sciaenidae for which Smale et al. (1995) provided data, A. hololepidotus and Atractoscion aequidens, provided data, A. hololepidotus and Atractoscion aequidens,
the three specimens of each species had a decreasing rela-
tive otolith size with increasing SL $(5.3\%$ of 112.8 mm SL,
 4.5% of 180 mm SL and 1.9% of 1348 the three specimens of each species had a decreasing rela-
tive otolith size with increasing SL $(5.3\% \text{ of } 112.8 \text{ mm SL},$
 4.5% of 180 mm SL and 1.9% of 1348 mm SL; and 6.5%
of 56.8 mm SI , 5.0% of 144.8 mm SI , an tive 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

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772 mm SL, respectively). Clearly the otoliths are growing
much more slowly than the rest of the fishes With 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 772 mm SL, respectively). Clearly the otoliths are growing dr
much more slowly than the rest of the fishes. With in
maximum sagitta sizes for these specimens of 31.4 mm are
and 21.7 mm respectively it is unlikely that hear 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 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. Perhans some otolith size threshold that is relate 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 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 age. Perhaps so
function is read
growth slows.
One aspect of growth slows.
One aspect of the present study may distort some of the

growth slows. 6%

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 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-hodied species and underempha 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 relativel 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 Angu 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 Anguilli-
formes is partly an artefact of the methodology Ho the size in long-bodied forms. Thus, the relatively small
otolith of the eel orders Notacanthiformes and Anguilli-
formes is partly an artefact of the methodology. However,
comparison of the actual otolith sizes for the 12 otolith of the eel orders Notacanthiformes and Anguilli-
formes is partly an artefact of the methodology. However,
comparison of the actual otolith sizes for the 12 eel
species in these two orders $(0.8-2.5 \text{ mm})$ (eight s formes is partly an artefact of the methodology. However,
comparison of the actual otolith sizes for the 12 eel
species in these two orders $(0.8-2.5 \text{ mm})$ (eight species)
and $3.5-4.1 \text{ mm}$ (four species)) with actual ot comparison of the actual otolith sizes for the 12 eel
species in these two orders $(0.8-2.5 \text{ mm})$ (eight species)
and 3.5-4.1mm (four species)) with actual otolith sizes of
the 15 species of the order Bervciformes with re species in these two orders $(0.8-2.5 \text{ mm})$ (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 $(4.2-6.54 \text{ mm})$ (three speci and 3.5–4.1 mm (four species)) with actual otolith sizes of
the 15 species of the order Beryciformes with relatively
large otoliths $(4.2-6.54 \text{ mm})$ (three species) and $7.0-$
 17.0 mm (12 species)) indicates that the 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 si large otoliths $(4.2-6.54 \text{ mm})$ (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 $\S 3$ give a totally false picture of relative otolith sizes.
The taxonomic comparison of otolith sizes given in $\S 3$
is limited to the bigger picture at the ordinal level, where
eels have relatively small otoliths and soldier The taxonomic comparison of otolith sizes given in $\S 3$
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 o 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 deen sea. Many have fresh 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 numbe 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, 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 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 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 hearing. pear to have a more important sense of smell than
aring.
With the soldierfish order, Beryciformes, it is not
ssible to separate the evolutionary bistory as evidenced

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 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 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 spec 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 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 mesonelagic or bathynelagic waters species in the mesopelagic or bathypelagic waters (Anoplogastridae); those species associated with coral reefs slope (Berycidae, Trachichthyidae) or as free-swimming
species in the mesopelagic or bathypelagic waters (Anoplo-
gastridae); those species associated with coral reefs
(Anomalopidae, Holocentridae) or the shelf (Monocen-(Anomalopidae, Holocentridae) or the shelf (Monocengastridae); those species associated with coral reefs
(Anomalopidae, Holocentridae) or the shelf (Monocentridae) are almost always nocturnal (Paxton 1998). Most
have large eves as well as large otoliths and it appears that (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 bearing are beightened. At tridae) 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
seme helocentrids have hearing augmented by a have large eyes as well as large otoliths, and it appears that specimen may contribute. Most of the other eight bathysenses of both sight and hearing are heightened. At least pelagic species have small otoliths. Not includ senses of both sight and hearing are heightened. At least
some holocentrids have hearing augmented by an with
otophysic connection with the swim-bladder (Popper & ve
Coombs 1982) A senarate analysis of all species of Holosome holocentrids have hearing augmented by an otophysic connection with the swim-bladder (Popper & Coombs 1982). A separate analysis of all species of Holo-centridae in Smale *et al.* (1995) indicates the three general 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 Myrinistinae, with a two-chambered Coombs 1982). A separate analysis of all species of Holo-
centridae in Smale *et al.* (1995) indicates the three genera (Nelson 1994) are included, these also have small otoliths.
of the subfamily Myripristinae, with a two swim-bladder (Nelson 1994) and otophysic connection, 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 singleswim-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 wh 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 r two genera of the subfamily Holocentrinae with a single-
chambered swim-bladder (six species, $3.0-4.7\%$ SL when
one specimen, $\lt 80$ mm SL, is excluded). While the rela-
tionship between hearing ability and otolith len chambered swim-bladder (six species, $3.0-4.7\%$ SL when
one specimen, $\lt 80$ mm SL, is excluded). While the rela-
tionship between hearing ability and otolith length is
unknown at least some groups with modified swimunknown, at least some groups with modified swimtionship 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 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 hearing. 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 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 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 sound production of this group, known as croakers and
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drums, is evident. Popper & Coombs (1982, p.322)
indicated the goby family Gobiidae is characterized by drums, is evident. Popper & Coombs (1982, p.322)
indicated the goby family, Gobiidae, is characterized by
an exceptionally large sacculus. The data analysed here 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 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 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 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 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 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 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 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 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 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 hased on the three very elo small or very small otoliths (figure 2). A possible criticism
of this analysis, based on the three very elongate species 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 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. 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 eninelagic fishes may b 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: the average to very-small end of
very-small otoliths of epipelagic
of one or more of the following:

- 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 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: (Popper *et al.* 1988) and
may generate so much
hearing is impossible;
rough seas may cause 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
- hearing is impossible;
rough seas may cause heavy otoliths to move too
much in the sacculus (R. McCauley, personal
communication): communication); much in the sacculus (R. McCauley, personal
communication);
(iii) acute colour vision in well-lit surface waters (many
enjnelagic fishes have large eves) may be so import-
- (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
ordities the majority of intertidal fishes on the open coast If rough seas are a significant disadvantage to large
otoliths, the majority of intertidal fishes on the open coast
should have small otoliths If rough seas are a signified
otoliths, the majority of inter-
should have small otoliths.
Montgomery $\&$ Pankhu 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, 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 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. Sig pardenskioldii, has very large 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% SI There are often exceptions to any gener 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 generaliza-Melamphaidae, *Sio nordenskjoldii*, has very large otoliths,
9.63% SL. There are often exceptions to any generaliza-
tion, although allometry in this small, 40 mm SL,
specimen may contribute. Most of the other eight bathy- 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 bathy-
pelagic species have small otolities. Not included is tion, although allometry in this small, 40 mm SL,
specimen may contribute. Most of the other eight bathy-
pelagic species have small otoliths. Not included is the
whalefsh family Cetomimidae with some 35 species and 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 bathworlagic ceration anglerfis 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 otoli 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 genera the 150 species of bathypelagic ceratioid anglerfish (Nelson 1994) are included, these also have small otoliths. (Marshall 1979). Small otoliths in most bathypelagic fishes may be correlated with the inability to use the (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 mesofishes 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 meso-
pelagic Stomiidae also lack swim-bladders (Marshall indirect method of pressure-wave detection due to swim-
bladder absence. The predatory members of the meso-
pelagic Stomiidae also lack swim-bladders (Marshall
1979) and have very small sagittas (see 8.3) bladder absence. The predatory members of the meso-
pelagic Stomiidae also lack swim-bladders (Marshall 1979) and have very small sagittas (see $\S 3$). lagic Stomiidae also lack swim-bladders (Marshall
79) and have very small sagittas (see § 3).
Montgomery & Pankhurst (1997) indicated that
pribonelagic slope fishes have larger sagittas and many

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 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 abused precise, counled with 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 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 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 denth may make vibration difficult or imall otoliths despite the presence of swim-bladders. They suggested that decreasing elasticity of swim-bladders at increasing depth may make vibration difficult, or

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increased gas density may lessen their efficiency as sound
resonators resonators. The indication that many lessen their efficiency as sound
sonators.
The indication that many luminous fishes have large
pliths is initially surprising (figure 1). However, the

The indication that many luminous fishes have large otoliths is initially surprising (figure 1). However, the presence of luminescence indicates the absence or great 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 a 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 s 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 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 othe 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. Howe 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 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 such an advantage does not explain why most lun
species have larger otoliths than non-luminous spec
the same family. A more detailed survey is needed.
The conclusions reached above are by necessity ecies have larger otoliths than non-luminous species in
e same family. A more detailed survey is needed.
The conclusions reached above are by necessity specu-
ive as the relationship between otolith size and hearing

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 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 kn lative 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
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lengths of some eels, dragonfish or oarfish. Use of otolith
area or mass could provide more sensitive discrimination
than maximum diameter 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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Marshall and Shaun Collin kindly provided an inv stimulating discussion and Art Popper much advice and references (but the remaining errors are all the author's). Justin Marshall and Shaun Collin kindly provided an invitation to this enlightening conference ences (but the remaining err
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