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Otolith size and its relationship with colour patterns and sound production

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A comparative, morphometric study was made of the 185 sagitta otoliths from 18 species belonging to four coastal perciform families of the north-west Mediterranean: the Labridae, Sparidae, Haemulidae and Sciaenidae. Species with relatively large otoliths belonged to groups considered specialists in sound production (sciaenids and haemulids), while those with small otoliths belonged to groups that rely on bright or contrasted colour patterns for visual communication (labrids). In sparids, species with clear body marks had smaller otoliths than species without dark stripes or dots. These findings support the hypothesis that otolith size is related to hearing ability in the inner ear.

Key words: ecomorphology; Haemulidae; Labridae; otolith area (OA); Sciaenidae; Sparidae.

INTRODUCTION

The otoliths are three pairs of calcareous structures, the sagittae, lapilli and asterisci, found in the inner ear of teleosts. They are associated with the saccule, utricle and lagena end organs respectively (Platt & Popper, 1981), which in turn are associated with vestibular (balance) and acoustic (sound detection) functions (Popper & Fay, 1993). These end organs perceive the two components of sound: particle displacement velocity (which they detect directly) and pressure variation (which they detect indirectly). It is largely unknown, however, how the great morphological variability of otoliths, especially of the saccular otoliths or sagittae, is involved in the capture and transduction of sound to the nervous system (Platt & Popper, 1981; Popper & Lu, 2000). Several hypotheses have been proposed. Platt & Popper (1981) suggested that shape (sculpture), which is species-specific, plays an important role in this. Volpedo & Echevarría (2003) indicated there was a relationship between overall otolith shape and preferred habitat. Gauldie (1988) suggested that a functional characteristic of the inner ear is the relationship between the size of the sagitta and that of its associated sensory macula [expressed as the area of the sulcus acusticus : area of the otolith (S : O)]. This hypothesis is supported by the fact that the sulcus acusticus, a

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depression on the medial face of the sagitta otolith, shows a clear relationship with the shape and size of the sensory macula (Lombarte & Fortuño, 1992; Torres *et al.*, 2000). Montgomery & Pankhurst (1997), indicated that relative otolith size is an adaptive factor associated with sensitivity to sound, while Paxton (2000) suggested that this is associated with the habitat occupied, and is therefore an adaptive character more involved with sound acuity (ability to discriminate between different frequencies) than sensitivity (range of frequencies that a species is able to hear). This suggests that there is a positive relationship between otolith size and sound production. There is a lack of quantitative data and conclusive evidence, however, to demonstrate a positive relationship between hearing ability (either sensitivity or acuity) and otolith size.

To determine and quantify the relationship between otolith size and adaptation to intraspecific communication based on sound production and colour pattern (visual communication), four Mediterranean families of the order Perciformes were selected [all characteristic of coastal waters (20–40 m depth) and all of which live in similar oceanographic conditions]: the Sciaenidae, Haemulidae, Labridae and Sparidae. In order to avoid phylogenetic interference (masked adaptive changes which appear when comparing morphological differences between phylogenetically separated groups) (Losos & Miles, 1994), three of the four families studied were phylogenetically very close (Sciaenidae, Haemulidae and Sparidae belonging to the suborder Percoidei) (Nelson, 1994).

The sciaenids (drums or croakers) and haemulids (grunts) are characterized by having specialized in acoustic communication. Their ability to produce sounds has long been known, as their common English names suggest. The sciaenids, which show well-developed soniferous muscles associated with the swimbladder (Moulton, 1963), use sound as a part of reproductive behaviour (Luczkovich *et al.*, 1999, 2000; Ramcharitar *et al.*, 2001; Holt, 2002).

The labrids (wrasses) are very different. This family is characterized by its great diversity in colourful body patterns. Labrids not only show marked interspecific differences in their liveries, but also show intraspecific differences that distinguish males from females, and adults from juveniles (Quignard & Pras, 1986; Corbera *et al.*, 1996). A bright or contrasted colouration is associated with an intraspecific visual based communication system for short distances (Voss, 1983; Michel *et al.*, 1984; Marshall, 2000; Siebeck & Marshall, 2000). In addition, Tavolga & Wodinsky (1963) confirmed that a brightly coloured labrid of the genus *Thalassoma* is not a sound producer.

Some of the Sparidae (porgies and sea breams) can produce sound while others cannot. For example, *Lagodon rhomboides* (L.), which often congregates in large groups (Robins & Ray, 1986), is a sound producer (Tavolga, 1974), while *Diplodus* (=*Sargus*) *annularis* (L.) is not (Dijkgraaf, 1952). The species of the genus *Diplodus* are characterized by their specific combinations of dark markings, suggesting that they specialize in visual communication.

MATERIALS AND METHODS

Specimens of 18 species belonging to the families Haemulidae, Labridae, Sciaenidae and Sparidae were captured during sampling cruises in the Catalonian Sea and around the Balearic Islands (north-west Mediterranean Sea) between 1995 and 2003. All the species analysed were coastal dwellers, and all were captured at depths of 20–40 m. The total body length (L_T) of all specimens was measured. The left sagittae were removed, cleaned, dried and stored. A total of 185 sagittae were analysed (Table I).

Of the Sciaenidae, brown meagre *Sciaena umbra* L., canary drum *Umbrina canariensis* Valenciennes and shi drum *Umbrina cirrosa* (L.) were selected for examination; of the Haemulidae, bastard grunt *Pomadasys incisus* (Bowdich) was selected; and of the Labridae, Mediterranean rainbow wrasse *Coris julis* (L.), brown wrasse *Labrus merula* L., pearly razor fish *Xyrichthys novacula* (L.) and peacock wrasse *Symphodus tinca* (L.) were chosen. Finally, 10 species of Sparidae were selected. These were divided into three subgroups depending on the type of their visually contrasting markings (stripes and dots). Group 1 (G1) included four species of the genus *Diplodus* [annular sea bream *D. annularis*, sharpsnout sea bream *Diplodus puntazzo* (Cetti), white sea bream *Diplodus sargus* (L.), common two-banded sea bream *Diplodus vulgaris* (Geoffrey Saint-Hilaire)] plus striped sea bream *Lithognathus mormyrus* (L.); all these have very contrasting markings running across the body, or along its length. It has been confirmed that *D. annularis* does not make sounds (Dijkgraaf, 1952). Group 2 (G2) included axillary sea bream *Pagellus acarne* (Risso), black sea bream *Spondyliosoma cantharus* (L.) and gilthead sea bream *Sparus aurata* L., which have small or medium black spots or poorly defined transversal markings. The third group (G3) included species with no markings (neither stripes nor spots), such as red porgy *Pagrus pagrus* (L.) and common pandora *Pagellus erythrinus* (L.).

The sagitta otolith area (A_O; mm^2) was used as the reference value for size since this is more representative than maximum diameter (Paxton, 2000). Measurements were made by taking digital images with a Sony High-res CCD video camera coupled to a Leica Wild binocular microscope and a PC. The processing of digital images, calibration and all analyses were performed using the Optimas v. 6.0 (Optimas Co. 1996) KRONO-MORPHOS programme (Morales-Nin *et al.*, 1998).

The comparative study of the relative increase in otolith area with respect to L_T was performed with two species representative of families that specialize in either visual or acoustic communication, the sciaenid *S. umbra* and the labrid *L. merula*, as well as two Sparidae species representative of the groups at the opposite extremes of colouration (G1 and G3), *D. sargus* (G1), characterized by its striped body design, and *P. erythrinus* (G3), with uniform colouring. The relationship between A_O and L_T was determined by fitting the data to the power equation $A_O = aL_T^b$. A *t*-test was used to compare the slopes for the different morphometric relationships, and to compare these with a value corresponding to isometry.

The relative sizes of the sagitta otoliths of the different families and of the Sparidae subgroups (G1, G2 and G3) were compared. For each species, the measurements obtained were standardized by removing the effect of L_T and allometry (by normalizing all measurements while taking allometric relationships into account) (Lombarte & Lleonart, 1993; Lleonart *et al.*, 2000). For each species, the allometric relationship between A_O and L_T was calculated using the standard equation $y = ax^b$. This was fitted by a ln-transformation to homogenize the residuals. Each measure for y (A_O) was then transformed into the term z according to $z = y(x_0\, x^{-1})^b$, where x is the original L_T of the fish, x_0 the reference L_T, and b is the allometric parameter relating the dependent variable y (A_O) to the independent variable x (L_T). z is the value of y if L_T is x_0. Based on the mean value for L_T of the specimens studied, a standard L_T of 20 cm (x_0) was selected for all species.

Once the data were standardized, the mean A_O of the different families were compared by ANOVA, followed by the Scheffé test for multiple comparisons (STATISTICA 5.1, Stat. Soft Inc, 1998). The same procedure was used to examine the differences between the Sparidae groups G1, G2 and G3. In all cases, 95% CL were set.

RESULTS

ABSOLUTE OTOLITH SIZE

Total A_O varied from 1·25 mm^2 for the smallest labrid *C. julis* (80 mm L_T) up to 167 mm^2 for *U. cirrosa* [540 mm L_T (Sciaenidae)]. Table I shows that

TABLE I. Species, number of otoliths, total length range of specimens, absolute otolith area range, mean ± S.D. of otolith area and standardized mean otolith area

Species	Family	Number of otoliths	L_T range of fish (cm)	Otolith area		Standardized mean otolith area (mm^2)*
				Range	Mean ± S.D.	
Coris julis	Labridae	6	8–21	1·25–4·21	2·40 ± 1·06	4·27
Labrus merula	Labridae	9	10–33	1·80–6·73	5·16 ± 1·15	3·69
Symphodus tinca	Labridae	7	8–32	1·4–5·86	3·40 ± 1·63	3·94
Xyrichthys novacula	Labridae	6	12–17	4·32–6·68	5·99 ± 0·93	8·49
Pomadasys incisus	Haemulidae	9	13–21	16·82–30·55	23·27 ± 4·35	30·33
Sciaena umbra	Sciaenidae	15	15–49	33·64–148·99	99·95 ± 28·47	51·31
Umbrina canariensis	Sciaenidae	14	14–54	23·68–162·40	61·28 ± 33·42	41·93
Umbrina cirrosa	Sciaenidae	10	11–54	19·49–167	74·60 ± 52·91	35·92
Diplodus annularis	Sparidae (G1)	9	5–20	2·48–15·02	9·18 ± 3·74	15·96
Diplodus puntazzo	Sparidae (G1)	7	11–33	11·55–26·32	21·00 ± 4·79	18·19
Diplodus sargus	Sparidae (G1)	13	13–35	11·54–28·9	16·76 ± 4·87	13·99
Diplodus vulgaris	Sparidae (G1)	12	9–26	5·01–24·55	13·36 ± 5·98	16·23
Lithognathus mormyrus	Sparidae (G1)	7	13–35	8·57–25·55	17·95 ± 7·00	13·43
Pagellus acarne	Sparidae (G2)	12	9–24	6·4–20·79	13·52 ± 4·97	16·55
Sparus aurata	Sparidae (G2)	9	14–24	15·93–36·67	27·15 ± 7·03	26·88
Spondyliosoma cantharus	Sparidae (G2)	4	18–27	19·27–27·4	21·72 ± 3·81	20·23
Pagellus erythrinus	Sparidae (G3)	20	6–41	4·08–79·02	26·78 ± 23·30	26·88
Pagrus pagrus	Sparidae (G3)	16	11–35	13·78–58·11	34·95 ± 12·42	29·60

*Otolith area standardized to 20 cm L_T. G1, species with contrasting transverse stripes and spots; G2, species with small or medium spots or a few contrasting, transverse stripes; G3, species with neither spots nor stripes.

these families occupy the two extremes of A_O. The labrids (Fig. 1), with a maximum mean of 5·99 mm^2, had smaller sagittae in absolute terms than the sciaenids (Fig. 2) (mean $A_O = 99{\cdot}95$ mm^2 in *S. umbra*). The otoliths of the Sparidae (Figs 3 and 4) show intermediate values: 9·18 mm^2 for *D. annularis* and 34·95 mm^2 for *P. pagrus*. The representative species of the Haemulidae, *P. incisus* [Fig. 2(a)], had medium-high values (23·27 mm^2) similar to the largest Sparidae values.

THE RELATIONSHIP BETWEEN OTOLITH SIZE AND FISH SIZE

For *L. merula*, the otolith size and fish size relationship was $A_O = 0{\cdot}0157L_T^{1{\cdot}0293}$ ($r^2 = 0{\cdot}96$, $n = 9$) while for *S. umbra* $A_O = 0{\cdot}0515L_T^{1{\cdot}3023}$ ($r^2 = 0{\cdot}94$, $n = 15$) [Fig. 5(a)]. The relationship was allometric in both *L. merula* (*t*-test, d.f. = 7, $P < 0{\cdot}05$) and in *S. umbra* (*t*-test, d.f. = 13, $P < 0{\cdot}05$). A comparison of the slopes showed significant differences between sagitta growth in these two species (*t*-test, d.f. = 22, $P < 0{\cdot}05$).

In the Sparidae, otolith size and fish size relationship was $A_O = 0{\cdot}0844L_T^{0{\cdot}9630}$ ($r^2 = 0{\cdot}7698$, $n = 13$) for *D. sargus* and $A_O = 0{\cdot}003L_T^{1{\cdot}7131}$ ($r^2 = 0{\cdot}9678$, $n = 20$) for *P. erythrinus* [Fig. 5(b)]. As above, the relationship was allometric in

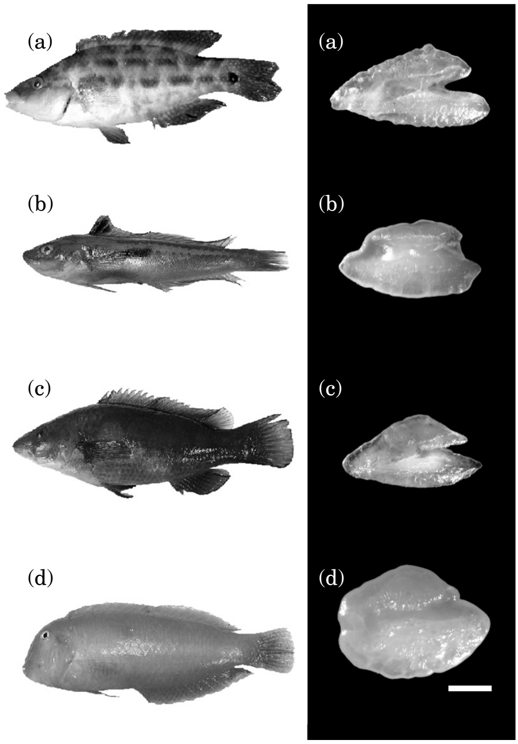

FIG. 1. Body patterns and left sagitta otoliths (medial view) of medium sized Labridae. (a) *Symphodus tinca* (20·5 cm L_T), (b) *Coris julis* (21 cm L_T), (c) *Labrus merula* (20·5 cm L_T) and (d) *Xyrichthys novacula* (17 cm L_T). Scale bar = 1 mm.

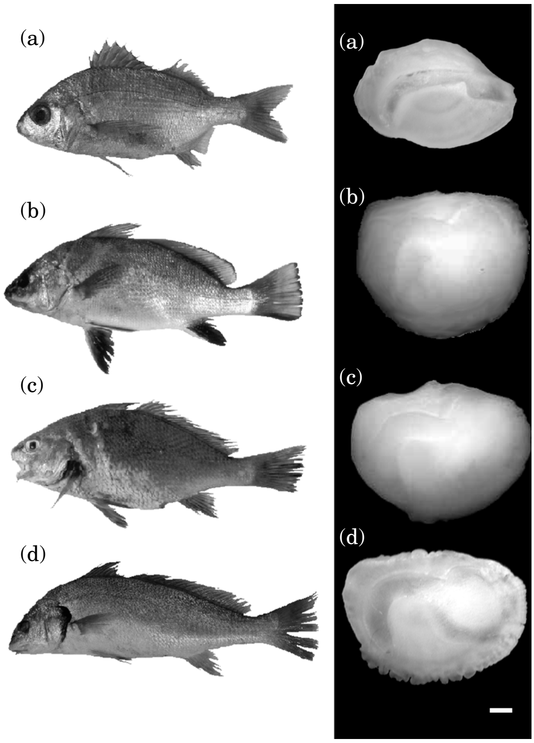

FIG. 2. Body patterns and left sagitta otoliths (medial view) of Haemulidae and Sciaenidae. (a) *Pomadasys incisus* (21 cm L_T), (b) *Sciaena umbra* (25 cm L_T), (c) *Umbrina canariensis* (28 cm L_T) and (d) *U. cirrosa* (26 cm L_T). Scale bar = 1 mm.

D. sargus (*t*-test, d.f. = 11, $P < 0{\cdot}05$) and in *P. erythrinus* (*t*-test, d.f. = 18, $P < 0{\cdot}05$). Comparison of the slopes again showed significant differences in sagitta growth in these species (*t*-test, d.f. = 31, $P < 0{\cdot}05$).

RELATIVE OTOLITH SIZE

An ANOVA of the standardized mean A_O of the four families (Table I) showed that they were significantly different (Table II). The Scheffé test for multiple comparisons showed significant differences between the A_O of the Sparidae, Labridae, Sciaenidae and Haemulidae. The labrids had smaller otoliths than the remaining families (Fig. 6). The sparids had standardized $A_O > 20\,\text{mm}^2$, the haemulids had values of $30\,\text{mm}^2$, while the sciaenids had the largest values at $40–45\,\text{mm}^2$.

An ANOVA showed the A_O of the three Sparidae subgroups, G1, G2 and G3, to be significantly different (Table III). This is confirmed by the Scheffé test for multiple comparisons. The mean A_O of these subgroups are shown in Fig. 7. The otoliths of G1 (*Diplodus* spp. and *L. mormyrus*) are characterized by smaller values than those of G2 and G3. The otoliths of G2 (*P. acarne*, *S. cantharus* and *S. aurata*) are intermediate between G1 and G3, though clearly different to G1. G3 otoliths (those of *P. pagrus* and *P. erythrinus*) show the largest relative size.

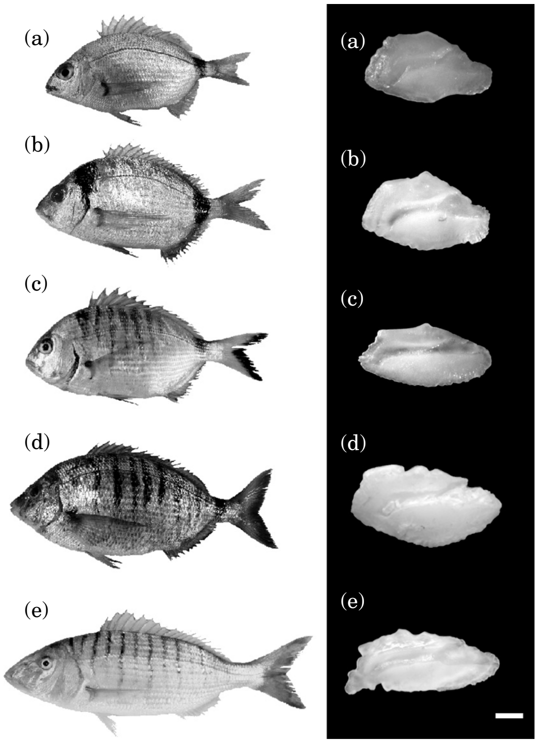

FIG. 3. Body patterns and left sagitta otoliths (medial view) of Sparidae (G1; see Table I) with transverse body stripes and spots. (a) *Diplodus annularis* (20 cm L_T), (b) *Diplodus vulgaris* (20·5 cm L_T), (c) *Diplodus sargus* (21·5 cm L_T), (d) *Diplodus puntazzo* (21 cm L_T) and (e) *Lithognathus mormyrus* (24 cm L_T). Scale bar = 1 mm.

DISCUSSION

The results show statistical differences between relative otolith size in species from families which differ in body colouration, and species belonging to a group which produce sounds. Those species with relatively large otoliths belong to groups specialized in sound production (associated with acoustic communication, Myrberg, 1981), while those with small otoliths show bright or contrasted colour patterns (related to visual communication). As indicated by Paxton (2000), the otoliths of the Sciaenidae, whose members can produce sounds and who show highly developed intraspecific acoustic communication (Luczkovich *et al.*, 1999, 2000; Holt, 2002), were particularly large. In the present study, sciaenid and haemulid otoliths had the largest relative size. Sciaenids had standardized otoliths means which were 1·5 times larger than those of sparids and 6·5 times larger than those of labrids.

The labrids, like other day-feeding coastal and shallow water pelagic species had relatively small otoliths. Paxton (2000) offered several reasons for this, including the suggestion that rough, but well-lit, surface waters may generate so much background noise that acute colour vision may have become more important than sound perception (Marshall, 2000).

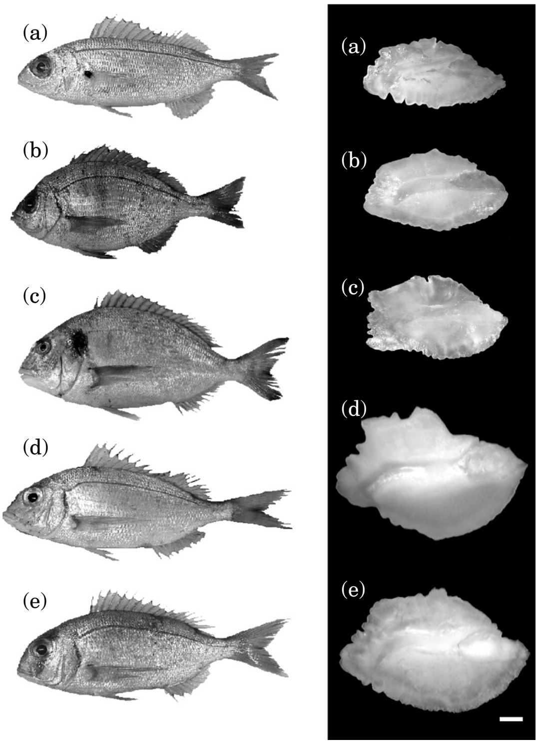

FIG. 4. Body patterns and left sagitta otoliths (medial view) of Sparidae (G2, G3; see Table I) with small spots or no body markings. (a) *Pagellus acarne* (20 cm L_T), (b) *Spondyliosoma cantharus* (20·5 cm L_T), (c) *Sparus aurata* (23·5 cm L_T), (d) *Pagellus erythrinus* (21 cm L_T) and (e) *Pagrus pagrus* (23 cm L_T). Scale bar = 1 mm.

The Sparidae possess neither very specialized visual behaviour nor acoustic behaviour. They show no differences in the colouration of adults and juveniles, nor any that distinguish males from females. Neither do they show any territorial posturing behaviour (Corbera *et al.*, 1996). Some of these species are sound producers while others are not (Dijkgraaf, 1952; Tavolga, 1974). The A_O of this family were found to be intermediate between those of the labrids and sciaenids, but were smaller in those species with transverse, coloured body markings, *e.g.* those of *Diplodus* spp. and *L. mormyrus*. *Diplodus annularis* does not seem to be able to make sounds (Dijkgraaf, 1952). Those sparid species with relatively large otoliths (*P. pagrus* and *P. erythrinus*), however, show no contrasting colouration. According to the hypothesis proposed by Paxton (2000), these species ought to be sound producers, as experimentally shown for other species of this family (Tavolga, 1974). Research to determine sound production capabilities in these Mediterranean species is required to confirm this hypothesis.

Paxton (2000) and Volpedo & Echevarría (2003) found a relationship between otolith size and habitat and behaviour. The sciaenids of the Mediterranean coast are nocturnal species with a preference for muddy bottoms (characterized by turbid waters) (Corbera *et al.*, 1996). Other nocturnal species, like *Ophidion*

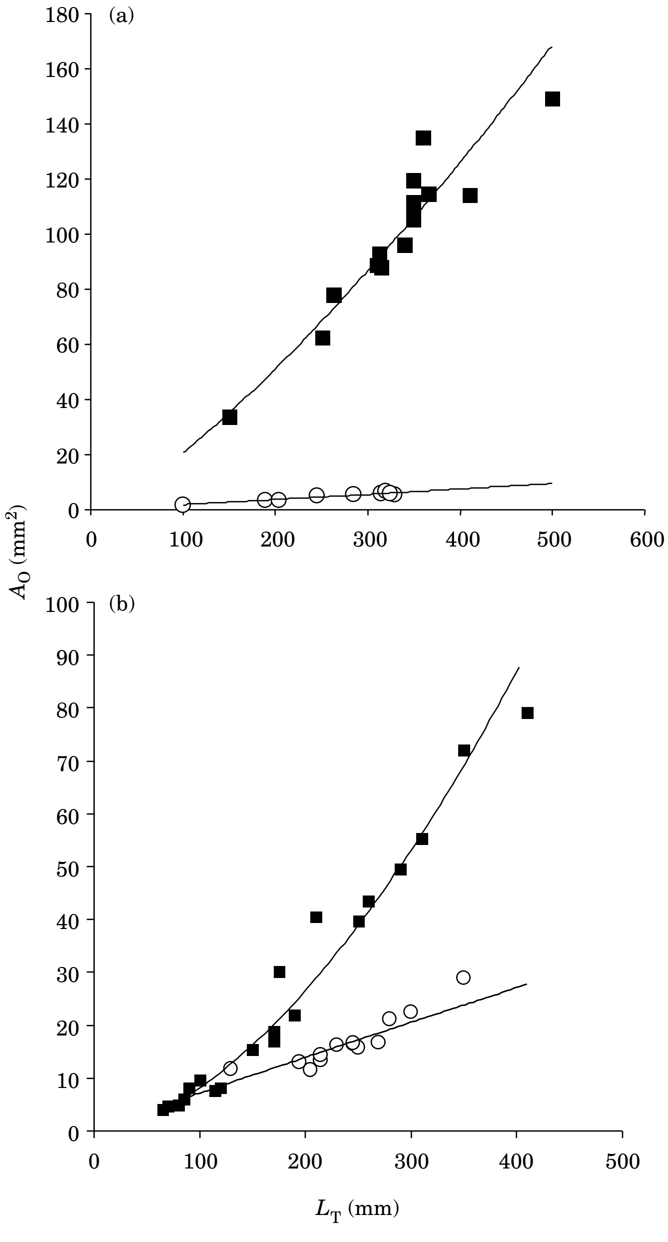

FIG. 5. The relationship between otolith area and total length in (a) *Labrus merula* (Labridae) (○; $y = 0{\cdot}0157x^{1{\cdot}0293}$; $r^2 = 0{\cdot}96$) and *Sciaena umbra* (Sciaenidae) (■; $y = 0{\cdot}0515x^{1{\cdot}3023}$; $r^2 = 0{\cdot}94$) and (b) *Diplodus sargus* (Sparidae G1; see Table I) (○; $y = 0{\cdot}084x^{0{\cdot}963}$; $r^2 = 0{\cdot}77$) and *Pagellus erythrinus* (Sparidae G3; see Table I) (■; $y = 0{\cdot}003x^{1{\cdot}713}$; $r^2 = 0{\cdot}97$).

marginatum (De Kay), display soniferous behaviour (Rountree & Bowers-Altman, 2002). Consequently, these species carry out their activities in a light-limited environment, a condition which could favour non-visual communication (acoustic or chemical). On the contrary, the members of the Labridae are

TABLE II. Results of ANOVA and the Scheffé test for multiple comparisons of relative otolith size (area). Otolith area was standardized for a total fish length of 20 cm

ANOVA

SS effect	d.f. effect	MS effect	SS error	d.f. error	MS error	*F*	*P*
27224·50	3	9074·83	8493·95	181	46·93	193·38	0·00

Scheffé test

Family	Sparidae Mean = 20·864	Labridae Mean = 4·9067	Sciaenidae Mean = 43·995	Haemulidae Mean = 30·334
Sparidae		0·000000*	0·000000*	0·001598*
Labridae	0·000000*		0·000000*	0·000000*
Sciaenidae	0·000000*	0·000000*		0·000006*
Haemulidae	0·001598*	0·000000*	0·000006*	

*, $P < 0.05$.

day-feeders who prefer shallow waters with a rocky bottom or where there is thick sand or sea grass. These environments are characterized by their wide range of light wavelengths in which intraspecific communication can be based on colour. In sympatric, brightly coloured species, differences in colour are essential components of sexual selection (Seehausen *et al.*, 1998).

Relationships between otolith size, habitat and behaviour are also seen in other groups. In notothenioids (Perciformes), benthonic species have larger otoliths than pelagic ones (Klingenberg & Ekau, 1996; Lombarte *et al.*, 2003). Like the sciaenids, the holocentrids (Beryciformes; nocturnal, coastal species which show interspecific

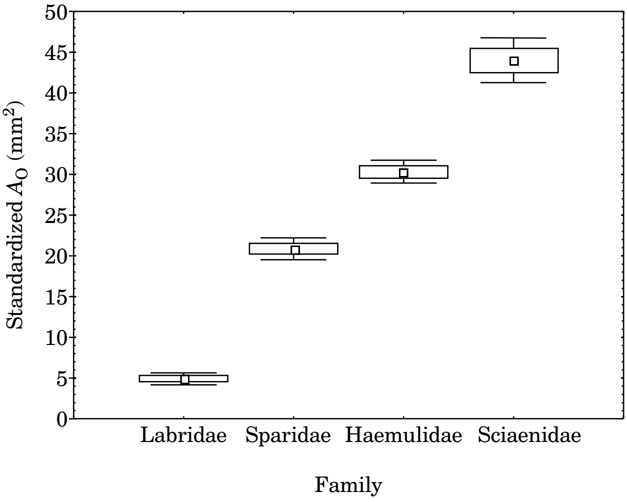

FIG. 6. Box-whisker plot of the relative otolith size (mm^2) of the families studied. □, standardized means; ▭, ± 1·00 S.E. and ⌶, ± 1·96 S.E.

TABLE III. Results of ANOVA and the Scheffé test for multiple comparisons of relative otolith size (area) by subgroups of Sparidae (see Table I). Otolith area was standardized for a total fish length of 20 cm

ANOVA

SS effect	d.f. effect	MS effect	SS error	d.f. error	MS error	*F*	*P*
3283·15	2	1641·58	2177·12	106	20·54	79·93	0·00

Scheffé test

Group	G1 Mean = 15·452	G2 Mean = 20·854	G3 Mean = 28·085
G1		0·000026*	0·000000*
G2	0·000026*		0·000000*
G3	0·000000*	0·000000*	

*, $P < 0{\cdot}05$.

differences in the production of sounds), demonstrate a similar relationship between large relative otolith size and acoustic communication (Paxton, 2000). The sciaenids are considered 'hearing generalists', however, since they possess no direct connection between the swimbladder and the internal ear (Schellart & Popper, 1992), and since they show a narrower hearing bandwidth and have less acoustic sensitivity than specialists such as the Holocentridae (Schellart & Popper,

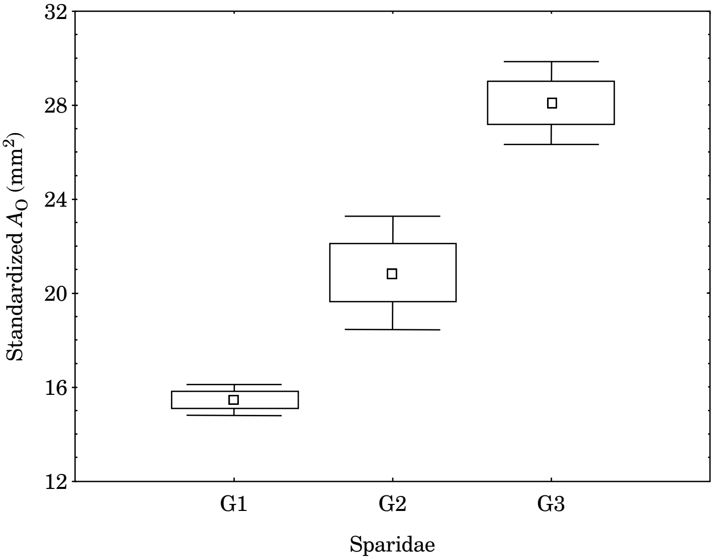

FIG. 7. Box-whisker plot of the relative otolith size (mm^2) for the three Sparidae subgroups (see Table I). □, standardized means; ▭, ± 1·00 S.E. and ⌶, ± 1·96 S.E.

1992). Nevertheless, several different species live in the north-west Atlantic, each with a characteristic sonogram (Luzckovich *et al.*, 1999; Ramcharitar *et al.*, 2001). The greater otolith size in sound-producing species could, therefore, be more related to sound acuity than sound sensitivity (defined by a low threshold and a wide range of sound frequency responses). Sound acuity is needed to be able to discriminate sounds made by different species within the soundscape. A similar situation exists among the freshwater Gobiidae, characterized by their relative very large otoliths (Popper & Coombs, 1982) and their ability to produce sounds with very clear interspecific variation (Lugli *et al.*, 1995).

The present results support the hypothesis that greater relative otolith size improves the hearing capabilities related with sound acuity, as suggested by Gauldie (1988), Paxton (2000) and Lychakov & Rebane (2000, 2002). Otolith size, however, does not appear to be associated with the threshold and bandwidth of sound sensitivity, a factor closely related to the presence of specialized structures connecting the swimbladder and the internal ear (Platt & Popper, 1981; Schellart & Popper, 1992).

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