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Otolith size trends in marine fish communities from different depth strata

A. LOMBARTE* AND A. CRUZ

Institut de Ciències del Mar (CSIC), Passeig Marítim 37-49, 08003 Barcelona, Catalonia, Spain

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A comparison of 681 saccular otoliths (sagitta) from 134 species belonging to six demersal communities from different depth strata and the epipelagic community from the north-western Mediterranean Sea was made in order to study otolith relative size and function related morphologies. A relationship between otolith size composition, habitat and depth was found. The epipelagic community was characterized by species with very small and small otolith sizes (68% of the epipelagic species). In the demersal communities, the proportion of species with large sagitta increased with depth until 750 m (reached 50% of the species of the upper slope). The abyssal community (between 1000 and 2000 m), however, was characterized by a decrease in the mean otolith size and an increase in the proportion of species with very small otoliths. With exception of the abyssal community, endogenous causes (a mixture of geneaology, plesiomorph characters shared by the all species of the taxonomic group and recent adaptive ones) may be even more important than exogenous factors in determining the otolith relative size. Within the endogenous causes that condition sagitta size, the adaptive features associated with specialization in acoustic communication are relevant.

Key words: deep sea; ecomorphology; otolith size; phylogeny.

INTRODUCTION

The three otolith pairs in teleosts have a large morphological variability. This variability is especially true for the saccular otolith (sagitta) associated with the inner ear organ, sacculus, in non-ostariophsean fishes (Platt & Popper, 1981). The morphological differences affect both the size and shape of the otoliths (Paxton, 2000; Wright *et al.*, 2002; Volpedo & Echevarría, 2003). Different factors influence the size of the otolith in relation to fish size. Exogenous factors such as temperature, depth and food have well described effects (Simkiss, 1974; Campana & Neilson, 1985; Wilson, 1985; Morales-Nin, 1987; Lombarte & Lleonart, 1993). In closely related species or within populations, otoliths from inhabitants of more temperate waters are relatively larger and heavier than

*Author to whom correspondence should be addressed. Tel.: +34 93 2309563; fax: +34 93 230 9555; email: toni@icm.cat

those from colder water (Gauldie, 1993; Lombarte & Lleonart, 1993; Torres *et al.*, 2000). Otolith size differences could be caused by ontogenic factors, since there is usually a relationship between the growth of the otolith and the growth of the fish (Campana & Neilson, 1985; Secor & Dean, 1989; Secor *et al.*, 1989). There are also other endogenous factors that influence the otolith relative size, such as phylogeny (Gaemers, 1984; Nolf, 1985) and adaptive aspects related with the inner ear functions (Lychakov & Rebane, 2000; Paxton, 2000; Parmentier *et al.*, 2001).

In a recent ecomorphologic study, Cruz & Lombarte (2004) quantified a clear relationship between otolith size and communication strategies in four families of the order Perciformes in the Catalan Sea (north-western Mediterranean Sea). Species with relatively large otoliths belonged to groups that are considered specialists in sound production (sciaenids and haemulids), while those with small otoliths belonged to groups that rely on bright or contrasting colour patterns for visual communication (labrids).

In deep waters, visible light is rapidly weakened by scattering and absorption (Lythgoe, 1988). The light energy of some colours, such as red, orange and yellow, is absorbed nearer the sea surface (Munz & McFarland, 1977). In the Mediterranean Sea, environmental light was reduced to 50% at 20 m depth (Jerlov, 1977). As a consequence, the visual field is reduced and the possibility to communicate visually is decreased, with the exception of the bioluminescent species (Hastings, 1983). Therefore, with the increase in depth and turbidity in the water, there may be selection for alternative communication, such as chemical, electric and acoustic systems (Zakon, 1988; Cambray, 1994; Lombarte & Aguirre, 1997; Kotrschal *et al.*, 1998; Buran *et al.*, 2005), which compensate for the reduced environmental light intensity.

If a relative large otolith size reflects adaptation to sound communication (Ramcharitar *et al.*, 2001, 2004; Cruz & Lombarte, 2004) there should be an increase in the number of species with large otoliths in poor light environments. To determine whether this relationship exists, the relative sizes of the otolith in different communities of the north-western Mediterranean Sea were compared. The differences in size of the four main taxonomic groups were also compared in order to determine if there are phylogenetic effects on the relative otolith size.

MATERIAL AND METHODS

A total of 681 otoliths from 134 fish species, belonging to 56 families and 13 orders (Appendix) were selected from six demersal communities of different depth strata (between 5 and 2000 m) and one epipelagic community from the north-western Mediterranean Sea (Catalan Coast and Balearic Islands) (Fig. 1). The otoliths used in this study were obtained from ICM Barcelona (CSIC) collection integrated in AFORO database http://www.cmima.csic.es/aforo/(Lombarte *et al.*, 2006).

To compare the effect of depth, six communities were selected at different depth strata between the Catalan and Balearic coast: 1) the coastal community [stratum A between 5 and 20 m of three different locations: Medes Islands (A1), Mallorca Island (A2) and off Calafell (A3) on Fig. 1], 2) the upper continental shelf (stratum B, between 40 and 80 m), 3) the lower continental shelf (stratum C between 90 and 200 m), 4) the upper slope (stratum D, between 300 and 450 m), 5) the middle slope (stratum E, between 600 and 750 m) and 6) the abyssal community (stratum F, between 1000

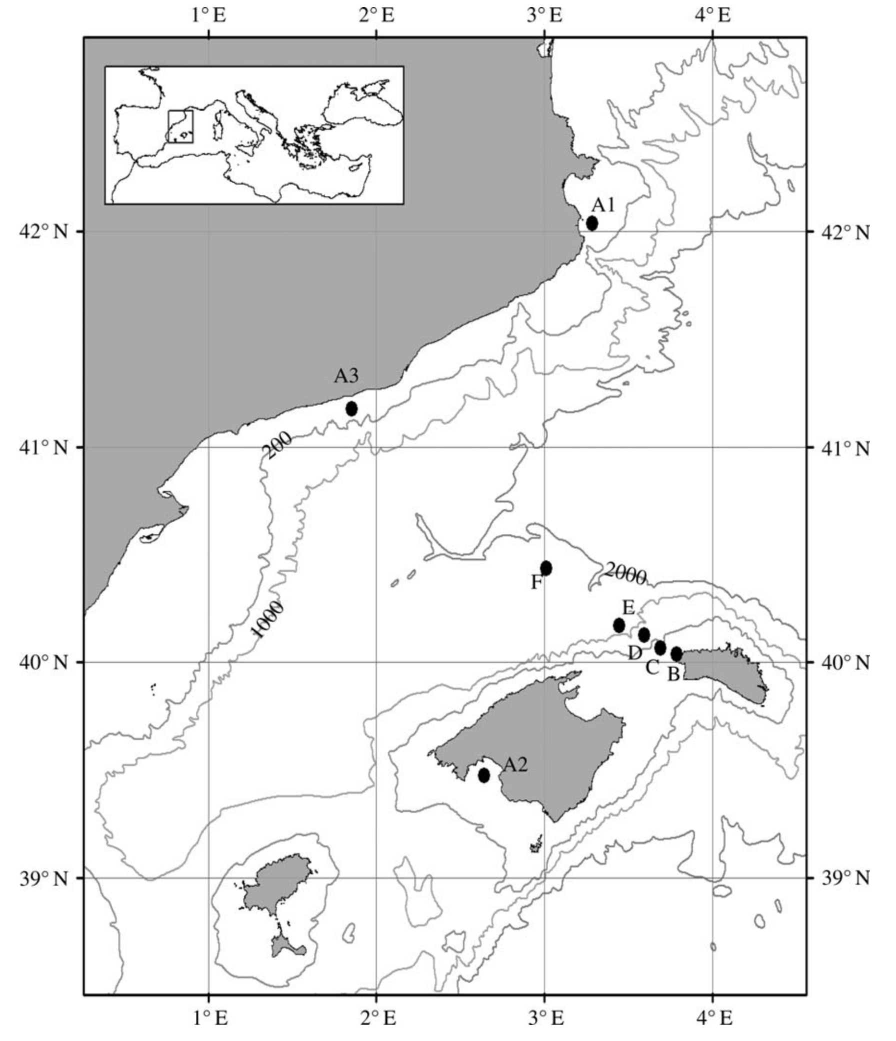

FIG. 1. Location of the different communities studied in the north-western Mediterranean Sea (Balearic Sea). A1, littoral rocky bottom in Medes Islands at 5–15 m; A2, *Posidonia* seagrass meadows off Mallorca Island at 10–20 m; A3, mixed rocky and muddy sand area at 10–20 m off Calafell; B, upper continental shelf community at 40–80 m; C, lower continental shelf at 90–200 m; D, upper slope 300–450 m; E, middle slope 600–750 m; F, abyssal community 1000–2000 m.

and 2000 m). In each community the most abundant species were selected (Stefanescu, 1991; García-Rubíes, 1997; Moranta *et al.*, 1998; Massutí & Reñones, 2005; Recasens *et al.*, 2006) (Appendix).

Left saccular otoliths were digitized and the area of their orthogonal projection on the medial side (sulcus acusticus side) was measured. Processing, calibration and measuring of digital images were done using the Optimas v. 6.0 (Optimas Co., Houston, TX, U.S.A.) KRONOMORPHOS software (Morales-Nin *et al.*, 1998). The length (O_L) and area (O_A) of the inner side of the sagitta was used as the reference value for size (Paxton, 2000; Cruz & Lombarte, 2004).

For each species the measurements obtained were standardized by removing the effect of allometry (by normalizing all measurements while taking allometric relationships into account) (Lleonart *et al.*, 2000). In order to remove the otolith shape effect, an index of otolith relative size (O_R) was calculated for each otolith according to $O_R = 1000 O_A L_T^{-2}$, where L_T = fish total length (mm). The otolith relative size value of each species was calculated using the index O_R. Also, the relationship $O_L L_T^{-1}$ was taken into account for each species (Appendix).

According to O_R, otoliths were divided into four categories: very small ($O_R < 0{\cdot}10$), small (0·10–0·32), medium (0·33–0·65) and large (>0·65) and the percentage of each otolith size category was calculated in each community. For each community, the mean of the otolith relative sizes (O_R) for the characteristic species in the communities studied were calculated (Appendix). The mean index O_R value and the proportion of the different size categories in the four main taxonomic groups studied (Gadiformes, Perciformes, Pleuronectiformes and Scorpaeniformes) were also calculated to determine possible phylogentic effects on the otolith relative size.

An ANOVA was carried out to evaluate differences between mean sagitta size of different communities and taxonomic groups. Independence of saccular otolith size groups with environmental factors (depth) and phylogeny were tested by a χ^2 contingency table (STATISTICA 5.1). In both analyses a confidence level of 99% was set.

RESULTS

The mean otolith area at transformed L_T (mean L_T in mm) and the relative size category for each species studied are shown in Appendix. The otolith relative size ranged between $O_R = 0{\cdot}01$ for *Lepidopus caudatus* (Euphrasen) to 1·84 for the deep water dwelling *Hoplostethus mediterraneus mediterraneus* Cuvier.

ANOVA of mean relative otolith size of the seven communities (six epipelagic and one pelagic) showed significant differences ($F_{6,188}$, $P < 0{\cdot}01$). The χ^2 contingency table indicated that sagitta size composition of the community was dependent on depth strata (Pearson χ^2, d.f. = 18, $P < 0{\cdot}01$).

The epipelagic community was characterized by having a greater proportion (37·5%) of species with very small sagittae ($O_R < 0{\cdot}10$) compared with the demersal communities and the absence of these with large otoliths [Fig. 2(a)]. Comparing demersal communities at different depths, an increase in the proportion of species with large sagittae was observed. In the continental shelf communities (strata A, B and C) the percentage of species with large sagittae varied between 11 and 24%. In the upper slope this percentage (stratum D) increased to 33%, and reached 50% of the species in the depth range of 600–750 m (stratum E). In the abyssal community (F), however, the percentage of species with large sagittae decreased to 20%. There was also a decrease in the percentage of species with small sagittae [Fig. 2(a)]. The proportion of small otoliths decreased from 51% of the species in stratum A (between 5 and 20 m) to 13% of the species in stratum F. The proportion of very small otoliths increased in the deepest stratum (F) and reached 26% in the abyssal community. When comparing the continental shelf communities (B and C strata), medium sized sagittae were clearly more abundant than small and large ones. When the mean relative size of the sagitta was compared between the different communities, epipelagic species clearly had relatively smaller otoliths than the demersal ones [Fig. 2(b)]. Comparing demersal communities, there was a significant tendency for the mean relative sagitta size to increase with depth, except for the abyssal species, where there was a decrease in size compared with the slope species.

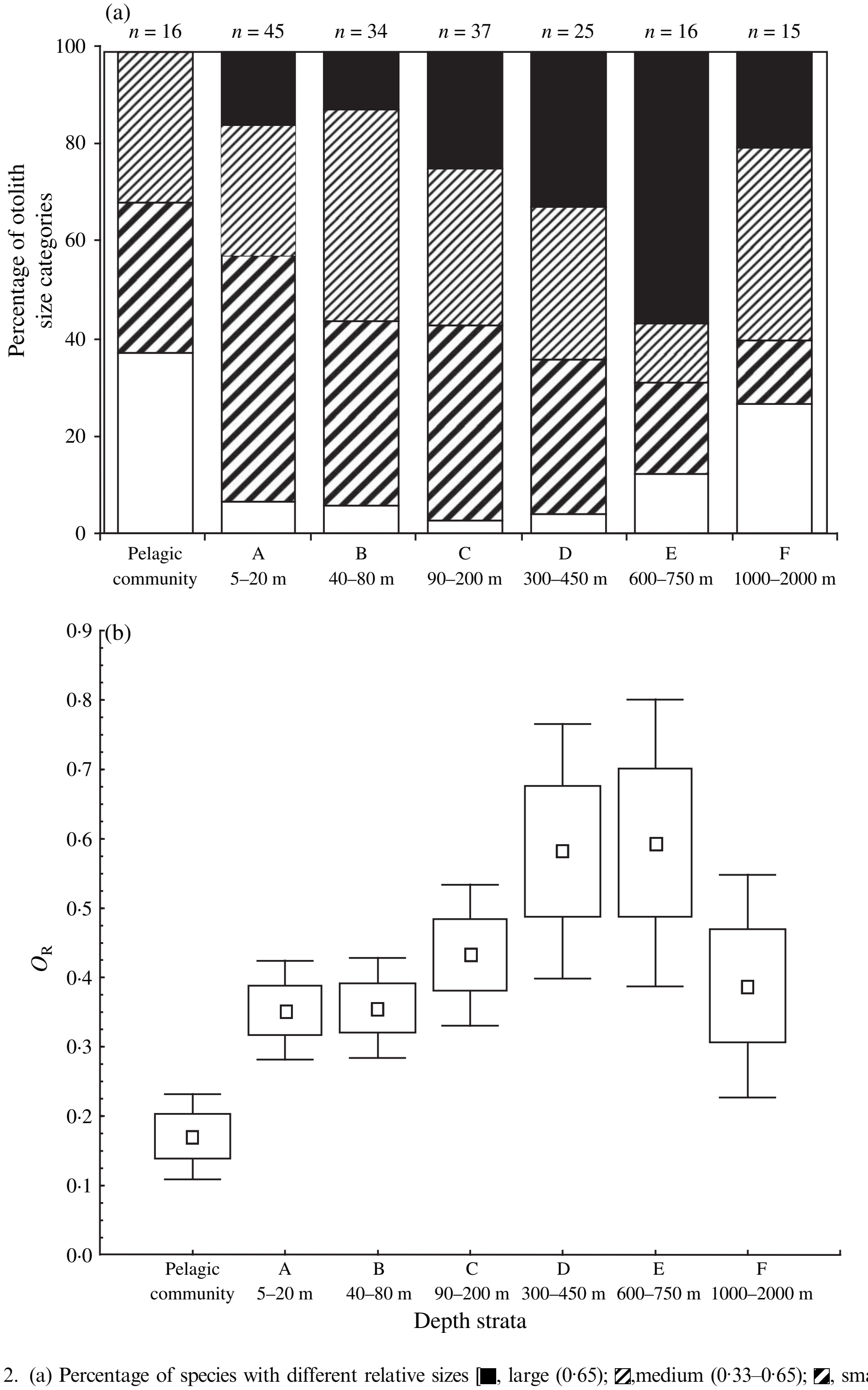

FIG. 2. (a) Percentage of species with different relative sizes [■, large (0·65); ▨,medium (0·33–0·65); ◪, small (0·10–0·32); □, very small (<0·10)] of the saccular otolith (sagitta). (b) A box-whisker plot (⊤, ±1·96 S.E.; ▭, ±1·00 S.E.; □, mean) of the relative otolith size (O_R; see Appendix) in different depth strata of demersal and epipelagic communities. n, number of species analysed. Taxa by each strata are indicted in Appendix.

ANOVA of mean relative otolith size of the four groups showed significant differences ($F_{3,104}$, $P < 0.01$). The χ^2 contingency table indicated that sagitta size composition of the community was dependent of the taxonomic group (Pearson χ^2, d.f. = 9, $P < 0.01$).

When comparing the four main taxonomic groups studied (Gadiformes, Perciformes, Pleuronectiformes and Scorpaeniformes), significant differences in the proportion of the sagittae relative size were observed in the gadiforms, which are generally characterized by large otoliths (62·5% of total of gadiform species) (Fig. 3). The pleuronectiforms showed a larger number of species with small otoliths than other groups (76·5%), and scorpaeniforms and perciforms were characterized by a large variety of sizes, with more medium and small otoliths. The order perciforms included some epipelagic species with very small sagittae (Fig. 3).

DISCUSSION

A relationship between sagitta size composition, habitat and depth was found. When comparing the distribution of the sagitta relative sizes between communities there was an increase in the mean otolith relative size, relating to an increase in the percentage of species with large otoliths, as the depth of the community increased. The only exception was related to the abyssal depths. The communities of the upper and medium slope located between 300 and 750 m included numerous species with large otoliths.

To explain the interspecific size differences that were observed it is relevant to take into account that otoliths are a very important part of the fish's inner ear (Platt & Popper, 1981) and play an important role in the sound transduction process (Popper & Fay, 1993). Variability in otolith size is an indicator of the way how the teleostean inner ear functions, as suggested by Gauldie (1988), Lychakov & Rebane (2000), Paxton (2000) and Parmentier *et al.* (2001). This morpho-functional interpretation suggests that the importance of acoustic communication is correlated with a large otolith size in deep waters in order to compensate for the reduction of light with depth. The present results coincide with the enlargement of the regions of brain associated with the octavolateralis system (Kotrschal *et al.*, 1998), the recent description of sound production in deep-sea fish species (Mann & Jarvis, 2004) and the description of ultrastructural adaptations in the inner ear of deep water fish species (Buran *et al.*, 2005).

A similar increase in otolith size exists for species that are nocturnally active, such as many coastal species like sciaenids and holocentrids. These groups all display soniferous behaviour, and there is a similar relationship between large otolith relative size and acoustic communication (Lugli *et al.*, 1995; Luczkovich *et al.*, 1999; Paxton, 2000). Furthermore, brightly coloured species like labrids, callionimids, dactylopterids, blennids and others, which live in littoral waters are characterized by relatively small sagittae (see Appendix). Epipelagic species are also characterized by small sagittae (Klingenberg & Ekau, 1996; Paxton, 2000). Paxton (2000) associated this small saccular otolith relative size with the diverse adaptive aspects of a high luminosity and noisy epipelagic environment near the sea surface. In epipelagic fishes visual communication is especially relevant (Fernald, 1988).

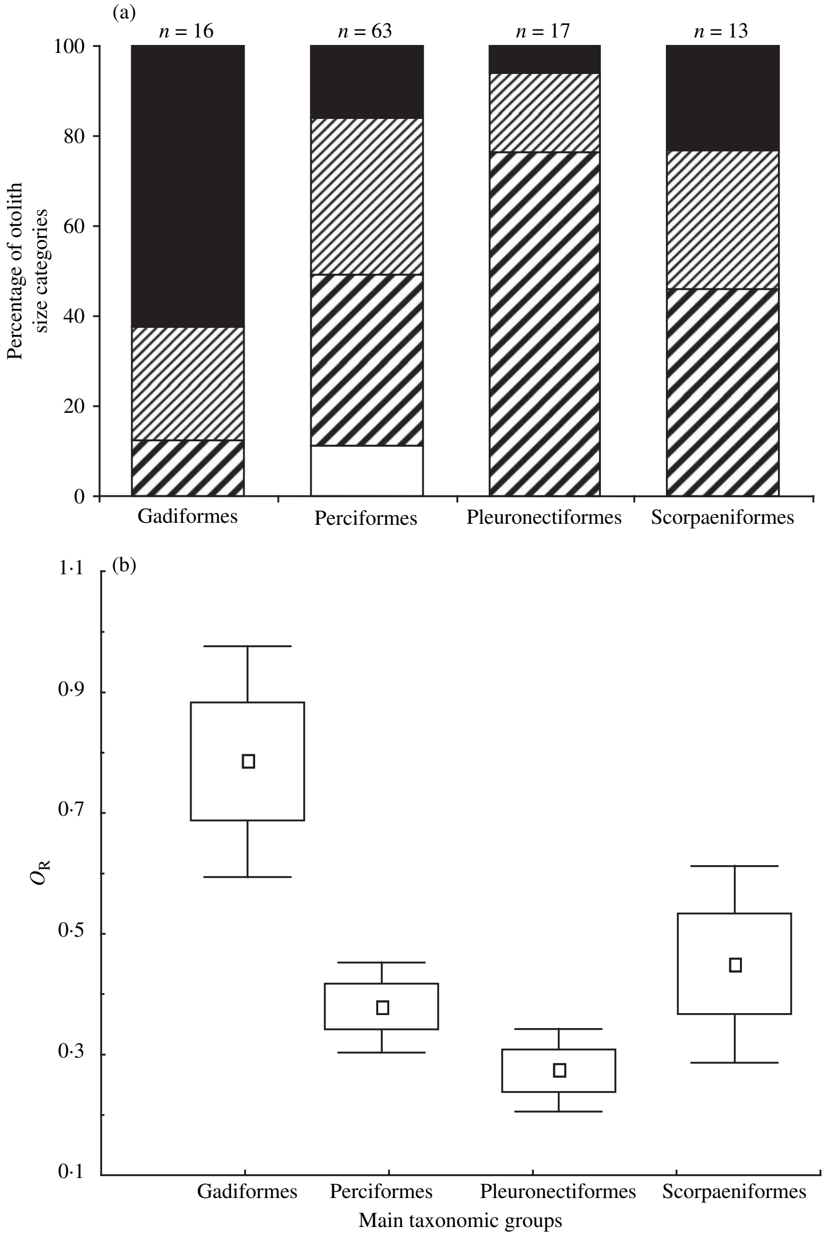

FIG. 3. (a) The percentage of species with different relative sizes [■, large (>0·65); ▨, medium (0·33–0·65); ◩, small (0·10–0·32); □, very small (<0·10)] of saccular otolith (sagitta). (b) The box-whisker plot (⌶, ±1·96 S.E.; ▭, ±1·00 S.E.; □, mean) of the otolith relative size (O_R; see Appendix) in the main four taxonomic groups. *n*, number of species analysed.

There is a clear relationship between taxonomic groups and otolith relative size (Nolf, 1985). In the present results some taxonomic groups like gadiforms tend to have medium or large sagittae, and others such like pleuronectiforms showed the opposite tendency. As pleuronectiforms have a wide range of depth distributions, this tendency could be related with a plesiopmorph feature shared by all species of this order (historical or genealogical character) on otolith size, which is independent of the recent adaptations. Gadiforms, however, are the dominant group between 200 and 700 m. The scorpaeniforms and especially the perciforms, with their great ecological and morphological variability (Nelson, 1994), exhibit a wide range of otolith sizes. Despite this variability, the sagittae of epigonids, the deepest species of perciforms, are characterized by a larger O_R (0·94–1·02).

Some authors have suggested that differences in sagitta size are related to the body growth rate of the fish (Secor & Dean, 1989), but closely related species with similar otolith sizes show very different growth rates (K). This is the case of some Mediterranean coastal labrids with relatively small otoliths. Gordoa *et al.* (2000) described very different growth rates for each species based on daily rings in otoliths of *Labrus merula* L. ($K = 0{\cdot}358$), *Symphodus tinca* (L.) ($K = 0{\cdot}808$) and *Coris julis* (L.) ($K = 0{\cdot}107$). This last value of K is close to the *Merluccius merluccius* (L.) growth rate ($K = 0{\cdot}12$), which is a species with a medium-large otolith relative size (Recasens *et al.*, 1998). So, the body growth rate of the fish cannot be considered a determining factor in the interspecific differences in relative otolith size.

The environments occupied by each species can influence otolith growth (Morales-Nin, 1987), which is closely related to temperature and depth (Simkiss, 1974; Wilson, 1985). Closely related species or populations from temperate or shallower waters have relatively larger otoliths than those from colder or deeper water (Gauldie, 1993; Torres *et al.*, 2000). The differences in otolith relative size described for the species that live in different environmental conditions (depth, temperature), however, are not as extensive (Lombarte & Lleonart, 1993) as those observed in the present study, with the exception of the abyssal communities below 1000 m depth. In this last case, exogenous factors such as the low temperature and high pressure in abyssal waters cause carbonate under-saturation, which affects otolith shape and relative size (Wilson, 1985). Furthermore, exogenous factors alone cannot explain the high degree of size variation within each community, as species develop in similar environmental conditions. It is evident that other endogenous factors act on otolith size (Mosegard *et al.*, 1988).

In conclusion, aspects related to their phylogeny [a mixture of geneaology, plesiomorph characters shared by the all species of the taxonomic group and recent adaptive ones (Losos & Miles, 1994)] may be even more important than exogenous factors in determining the sagitta relative size. Within the phylogenetic causes that condition sagitta size, the adaptive features associated with specialization in acoustic communication are important.

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APPENDIX. Species, depth and bottom distribution, number of otoliths (n), mean fish total length (L_T), mean relative otolith size ($O_L L_T^{-1}$ and $O_R = 1000 O_A L_T^{-2}$), and size category (C) in relation to O_R (vs, very small; s, small; m, medium; l, large, see Fig. 2). P, epipelagic community; O_L, mean otolith length; O_A, otolith area. Taxonomic classification follows Nelson (1994)

Order	Strata											
Family	P	A	B	C	D	E	F		Mean L_T	Relative size		
Species		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m	n	(mm)	$O_L L_T^{-1}$	O_R	C
Anguilliformes												
Congridae												
Conger conger		X	X					5	464	0·02	0·08	vs
Nettastomidae												
Nettastoma melanurum							X	5	519	0·01	0·03	vs
Albuliformes												
Notacanthidae												
Nothacantus bonapartei						X	X	5	221	0·01	0·02	vs
Polyacanthonotus rissoanus						X	X	2	220	0·01	0·02	vs
Clupeiformes												
Clupeidae												
Alosa fallax	X							1	435	0·01	0·03	vs
Sardina pilchardus	X							8	131	0·02	0·13	s
Sardinella aurita	X							1	132	0·02	0·10	s
Engraulidae												
Engraulis encrasicholus	X							9	132	0·02	0·18	s
Osmeriformes												
Argentinidae												
Glossanodon leiglossus				X	X			5	111	0·04	0·52	s

APPENDIX. Continued

Order / Family / Species	Strata P	A	B	C	D	E	F	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	O_R	C
		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m					
Alepocephalidae												
Alepocephalus rostratus							X	8	212	0·03	0·24	s
Aulopiformes												
Chlorophthalmidae												
Chlorophthalmus agassizii					X	X		3	102	0·04	0·43	m
Ipnopidae												
Bathypterois mediterraneus							X	8	125	0·02	0·22	s
Synodontidae												
Synodus saurus		X	X					3	295	0·02	0·10	s
Ophidiiformes												
Carapidae												
Carapus acus				X				3	95	0·02	0·21	s
Echiodon dentatus						X		5	157	0·03	0·26	s
Ophidiidae												
Ophidion barbatum				X				3	143	0·03	0·78	l
Bythitidae												
Cataetyx alleni							X	5	206	0·04	0·43	m
Cataetyx laticeps							X	4	206	0·03	0·42	m

APPENDIX. Continued

Order	Strata											
Family	P	A	B	C	D	E	F		Mean L_T	Relative size		
Species		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m	n	(mm)	$O_L L_T^{-1}$	O_R	C
Gadiformes												
Moridae												
Lepidion lepidion						X	X	6	207	0·06	0·98	l
Mora moro						X	X	8	269	0·05	0·74	l
Phycidae												
Phycis blennoides					X	X	X	10	310	0·05	0·40	m
Phycis phycis		X						8	288	0·05	0·68	l
Merlucciidae												
Merluccius merluccius			X	X	X			25	340	0·04	0·53	m
Gadidae												
Gadiculus argenteus					X			7	69	0·06	1·70	l
Micromesitius poutassou					X			2	200	0·08	1·23	l
Trisopterus minutus				X				7	164	0·05	0·94	l
Lotidae												
Gaidropsarus biscayensis					X			3	112	0·03	0·20	s

APPENDIX. Continued

Order	Strata											
Family	P	A	B	C	D	E	F		Mean L_T	Relative size		
Species		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m	*n*	(mm)	$O_L L_T^{-1}$	O_R	C
Macrouridae												
Caelorhinchus caelorhincus					X			5	224	0·06	0·84	l
Caelorhinchus mediterraneus							X	4	210	0·05	0·64	m
Coryphaenoides guentheri							X	4	219	0·03	0·41	m
Coryphaenoides mediterraneus							X	4	223	0·03	0·29	s
Hymenocephalus italicus					X	X		6	123	0·04	1·21	l
Nezumia aequalis						X		5	145	0·04	0·84	l
Trachyrincus scabrus						X	X	7	341	0·04	0·93	l
Lophiiformes												
Lophiidae												
Lophius budegassa				X	X			4	370	0·02	0·17	s
Lophius piscatorius				X	X			4	251	0·02	0·13	s
Mugiliformes												
Mugilidae												
Chelon labrosus		X						5	480	0·02	0·21	m
Liza aurata		X						8	475	0·02	0·18	s

APPENDIX. Continued

Order / Family / Species	P	A	B	C	D	E	F	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	Relative size O_R	C
		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m					
Beryciformes												
Trachichthydae												
Hoplostethus mediterraneus mediterraneus					X	X		7	155	0·06	1·84	l
Zeiformes												
Caproidae												
Capros aper				X	X			6	77	0·03	0·52	m
Zeidae												
Zeus faber				X				1	150	0·01	0·06	vs
Scorpaeniformes												
Dactylopteridae												
Dactylopterus volitans		X	X					3	297	0·01	0·04	vs
Scorpaenidae												
Helicolenus dactylopterus				X	X	X		7	155	0·05	0·75	l
Scorpaena elongata					X			3	120	0·06	0·99	l
Scorpaena notata		X	X	X				9	148	0·05	0·86	l
Scorpaena porcus		X	X					8	194	0·04	0·54	m
Scorpaena scrofa		X	X					8	249	0·05	0·50	m

APPENDIX. Continued

Order / Family / Species	Strata P	A 5–20 m	B 40–80 m	C 90–200 m	D 300–450 m	E 600–750 m	F 1000–2000 m	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	Relative size O_R	C
Triglidae												
Aspitrigla cuculus			X	X				3	135	0·02	0·23	s
Lepidotrigla cavillone			X	X				8	124	0·03	0·32	s
Trigla lyra				X	X			4	143	0·02	0·28	s
Trigloporus lastoviza			X					4	155	0·02	0·23	s
Peristediidae												
Peristedion cataphractum					X			1	95	0·03	0·41	m
Liparidae												
Paraliparis leptochirus						X		2	60	0·02	0·24	s
Perciformes												
Serranidae												
Anthias anthias				X				4	157	0·03	0·35	m
Epinephelus marginatus		X						1	390	0·03	0·25	s
Serranus cabrilla		X	X	X				3	127	0·01	0·40	m
Serranus hepatus			X	X				6	88	0·04	0·79	l
Serranus scriba		X						5	140	0·05	0·39	m

APPENDIX. Continued

Order	Strata											
Family	P	A	B	C	D	E	F		Mean L_T	Relative size		
Species		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m	*n*	(mm)	$O_L L_T^{-1}$	O_R	C
Callanthiidae												
Callanthias ruber			X					3	131	0·03	0·62	m
Epigonidae												
Epigonus denticulatus					X			5	112	0·05	1·02	l
Epigonus telescopus						X		4	130	0·04	0·94	l
Carangidae												
Lichia amia	X							1	265	0·01	0·04	vs
Seriola dumerili	X							3	340	0·01	0·05	vs
Trachurus mediterraneus	X							3	203	0·03	0·29	s
Trachurus picturatus	X							1	230	0·03	0·21	s
Trachurus trachurus	X							5	172	0·03	0·33	m
Sparidae												
Boops boops	X		X	X				11	212	0·03	0·33	m
Dentex dentex		X						3	467	0·03	0·41	m
Diplodus annularis		X	X					9	131	0·04	0·42	m

APPENDIX. Continued

Order / Family / Species	Strata P	A 5–20 m	B 40–80 m	C 90–200 m	D 300–450 m	E 600–750 m	F 1000–2000 m	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	Relative size O_R	C
Diplodus cervinus		X						1	280	0·03	0·39	m
Diplodus puntazzo		X	X					2	315	0·02	0·21	s
Diplodus sargus		X						13	241	0·03	0·29	s
Diplodus vulgaris		X	X					12	169	0·03	0·46	m
Lithognatus mormyrus		X						7	253	0·03	0·28	s
Pagellus acarne		X	X					12	170	0·04	0·46	m
Pagellus bogavareo					X			5	186	0·03	0·48	m
Pagellus erythrinus		X	X	X				20	183	0·04	0·69	l
Pagrus pagrus			X					5	234	0·03	0·58	m
Spondylosoma cantharus		X	X					4	216	0·03	0·47	m
Centracanthidae												
Centracanthus cirrus				X				1	170	0·03	0·34	m
Spicara smaris			X	X				4	113	0·03	0·41	m

APPENDIX. Continued

Order / Family / Species	P	A 5–20 m	B 40–80 m	C 90–200 m	D 300–450 m	E 600–750 m	F 1000–2000 m	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	Relative size O_R	C
Sciaenidae												
Sciaena umbra		X						14	345	0·04	0·88	l
Umbrina canariensis		X						14	260	0·04	0·88	l
Mullidae												
Mullus barbatus			X	X				5	179	0·03	0·16	s
Mullus surmuletus		X	X	X				5	175	0·02	0·19	s
Cepolidae												
Cepola macrophthalma				X				5	267	0·02	0·14	s
Pomacentridae												
Chromis chromis		X						4	73	0·05	0·88	l
Labridae												
Coris julis		X	X					6	128	0·02	0·14	s
Labrus merula		X						8	277	0·01	0·07	vs
Labrus viridis		X						2	150	0·02	0·10	s
Symphodus cinereus		X						5	79	0·02	0·20	s
Symphodus doderteini		X						4	83	0·02	0·23	s

APPENDIX. Continued

Order	Strata											
Family	P	A	B	C	D	E	F		Mean L_T	Relative size		
Species		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m	*n*	(mm)	$O_L L_T^{-1}$	O_R	C
Symphodus mediterraneus:		X						6	90	0·02	0·19	s
Symphodus ocellatus		X						5	74	0·02	0·19	s
Symphodus roissali		X						1	80	0·02	0·17	s
Symphodus rostratus		X						5	93	0·02	0·19	s
Symphodus tinca		X						7	175	0·02	0·11	s
Thalassoma pavo		X						1	92	0·03	0·25	s
Zoarcidae												
Melanostigma atlanticum							X	3	95	0·01	0·05	vs
Trachinidae												
Trachinus draco								4	156	0·05	0·63	m
Trachinus radiatus								2	315	0·04	0·36	m
Uranoscopidae												
Uranoscopus scaber		X	X	X				7	176	0·04	0·66	l

APPENDIX. Continued

Order / Family / Species	P	A	B	C	D	E	F	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	O_R	C
		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m					
Blenniidae												
Blennius ocellaris			X	X				5	98	0·01	0·17	s
Callionymidae												
Callionymus maculatus				X				5	99	0·02	0·13	s
Synchiropus phaeton				X	X			2	133	0·02	0·14	s
Gobiidae												
Deltentosteus quadrimaculatus				X				4	83	0·04	1·19	l
Gobius bucchichi		X						2	73	0·04	0·60	m
Gobius cruentatus		X						5	117	0·04	0·64	m
Lesueurigobius friesii				X				5	61	0·04	1·42	l
Sphyraenidae												
Sphyraena sphyraena	X							4	415	0·03	0·21	s
Trichiuridae												
Lepidopus caudatus					X			7	632	0·01	0·01	vs
Scombridae												
Sarda sarda	X							7	607	0·01	0·02	vs
Scomber colias	X							7	300	0·02	0·08	vs

APPENDIX. Continued

Order / Family / Species	P	A	B	C	D	E	F	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	Relative size O_R	C
		5–20 m	40–80 m	90–200 m	300–450 m	600–750 m	1000–2000 m					
Scomber scombrus	X							7	304	0·01	0·04	vs
Centrolophidae												
Schedophilus medusophagus	X							1	500	0·03	0·35	m
Stromateidae												
Stromateus fiatola	X							1	260	0·03	0·34	m
Pleuronectiformes												
Citharidae												
Citharus linguatula			X	X				10	176	0·03	0·35	m
Bothidae												
Arnoglossus imperialis			X					1	105	0·02	0·20	s
Arnoglossus laterna				X				2	108	0·02	0·28	s
Arnoglossus ruepellii				X				2	103	0·02	0·27	s
Arnoglossus thori			X					3	88	0·03	0·35	m
Bothus podas		X	X					2	173	0·01	0·10	s
Scophthalmidae												
Lepidorhombus boscii				X	X			4	225	0·02	0·29	s

APPENDIX. Continued

Order / Family / Species	Strata P	A 5–20 m	B 40–80 m	C 90–200 m	D 300–450 m	E 600–750 m	F 1000–2000 m	n	Mean L_T (mm)	Relative size $O_L L_T^{-1}$	Relative size O_R	C
Lepidorhombus whiffiagonis				X	X			1	340	0·02	0·12	s
Psetta maxima		X						5	224	0·02	0·20	s
Scophthalmus rhombus		X						6	235	0·02	0·21	s
Soleidae												
Bathysolea profundicola					X			2	108	0·02	0·25	s
Monochirus hispidus				X				4	86	0·03	0·52	m
Solea kleini			X					1	230	0·01	0·13	s
Solea senegalensis		X						7	314	0·01	0·11	s
Solea solea		X						7	265	0·02	0·15	s
Cynoglossidae												
Symphurus ligulatus						X		3	80	0·03	0·66	b
Symphurus nigrescens					X	X		5	96	0·02	0·24	s
Total species 134	16	45	34	37	25	16	15	681				
Mean relative size (O_R) 0·41	0·17	0·34	0·36	0·43	0·57	0·59	0·39					