

Using sagittal otoliths and eye diameter for ecological characterization of deep-sea fish: *Aphanopus carbo* and *A. intermedius* from NE Atlantic waters

VÍCTOR MANUEL TUSET ^{1,2}, SILVIA PIRETTI ¹,
ANTONI LOMBARTE ² and JOSÉ ANTONIO GONZÁLEZ ¹

¹ Departamento de Biología Pesquera, Instituto Canario de Ciencias Marinas (ICCM-ACIISI), P.O. Box 56, 35200 Telde, Las Palmas, Canary Islands, Spain. E-mail: victorta@iccm.rcanaria.es

² Institut de Ciències del Mar (CSIC), Passeig Marítim 37-49, 08003, Barcelona, Catalonia, Spain.

SUMMARY: The sagittal otolith and eye diameter of two sympatric species of the genus *Aphanopus*, *A. carbo* and *A. intermedius*, from North Atlantic waters were investigated. The study objectives were to find morphometric variables of otoliths to identify the two species and relate ecomorphological characters of otolith and eye diameter to the depth distribution of each species. The otoliths of the two species are very similar, although significant differences in shape, otolith height and weight and the *sulcus acusticus* area were detected. The ratio between eye diameter and cephalic length (*ED:CL* ratio) was also significantly different. In both analyses *A. carbo* obtained higher values, which suggests that *A. carbo* and *A. intermedius* live in different spatial niches, and that *A. carbo* inhabits deeper waters. The ratio between the *sulcus* and otolith areas (*S:O*) was low compared to other fish species, which suggests that the hearing capacity of *Aphanopus* spp. is adapted to low frequency sound. This adaptation may be related to the oceanographic conditions in which these species live, and in particular to the characteristics of sound transmission in the "SOFAR channel".

Keywords: ecology, morphometry, otolith, *Aphanopus carbo*, *Aphanopus intermedius*, teleosts.

RESUMEN: USO DEL OTOLITO SAGITA Y EL DIÁMETRO DEL OJO PARA LA CARACTERIZACIÓN ECOLÓGICA DE PECES DE PROFUNDIDAD: *APHANOPUS CARBO* AND *A. INTERMEDIUS* DEL ATLÁNTICO NORORIENTAL. – El otolito sagitta y el diámetro del ojo de dos especies simpátricas del género *Aphanopus*, *A. carbo* y *A. intermedius*, del Atlántico Norte fueron analizados. Los objetivos del estudio se centraron en encontrar las variables morfométricas del otolito que pudiesen ser empleadas en la diferenciación de ambas especies y en establecer una correspondencia entre la profundidad de distribución de las especies y las características ecomorfológicas del otolito y del diámetro del ojo. Los otolitos de ambas especies resultaron ser parecidos, si bien se detectaron diferencias significativas en la forma, en el peso y la anchura del otolito y en el área del *sulcus acusticus*. La proporción entre el diámetro del ojo y la longitud cefálica (*ED:CL*) también puso de manifiesto diferencias significativas entre ambas especies. En ambos análisis, los resultados indicaron que *A. carbo* alcanza valores mayores. Ello proporciona evidencias para poder afirmar que *A. carbo* y *A. intermedius* viven en nichos espaciales diferentes, habitando *A. carbo* aguas más profundas. La proporción entre el área del *sulcus* y el área del otolito (*S:O*) alcanzó valores bajos en comparación con otras especies, lo cual sugiere que la capacidad auditiva de *Aphanopus* spp. está adaptada a sonidos de baja frecuencia. Dicha adaptación podría estar relacionada con las condiciones oceanográficas donde viven estas especies y, en particular, con las características de la transmisión del sonido dentro del denominado "canal SOFAR".

Palabras clave: ecología, morfometría, otolito, *Aphanopus carbo*, *Aphanopus intermedius*, teleósteos.

INTRODUCTION

The black-scabbard fish *Aphanopus carbo* Lowe, 1843, has been commercially fished in the waters of the archipelago of Madeira for more than 150 years. This makes it the oldest deep-sea commercial fishery in the world (Shotton, 2005). Nowadays, it is also fished in continental fishing grounds off Sesimbra waters, Portugal (Bordalo-Machado *et al.*, 2009). This species also appears as by-catch in the trawl fishery in the west of the British Isles, along the Middle-Atlantic Ridge and at Corner Rise (Gordon, 2001). Its annual catches reach up to 14000 tonnes, reported mainly by the Portuguese and French fleets (Martins *et al.*, 1994; Martins and Ferreira, 1995; Morales-Nin *et al.*, 2002). Due to its commercial importance, many studies on fishery ecology have been carried out (Howe *et al.*, 1979; Clarke *et al.*, 2003; Gordo, 2009). These studies suggest that this species undergoes horizontal migration movements associated with its inner ontogenic cycle. In addition, juveniles probably move from the northwest of Scotland to the Portuguese continental coast in search for food during their first years of life. When they reach sexual maturity, they migrate to the Macaronesian archipelagos, the only known reproductive areas (Martins *et al.*, 1994; Machado *et al.*, 1998; Figueiredo *et al.*, 2003; Pajuelo *et al.*, 2008; Neves *et al.*, 2009). This means that the North Atlantic population may be considered as a population unit, independently of management and assessment aspects for regulating its fisheries.

At the beginning of the 1980s a series of descriptions of new species of *Aphanopus* started to appear; one of them, *A. intermedius* Parin, 1983, is partially

sympatric with *A. carbo* (Nakamura and Parin, 1993; Parin, 1995). Recent morphologic and genetic studies have demonstrated that the two species are present in the Azores, Madeira, the Canary Islands and off Morocco and the western Sahara (M. Biscoito, com. pers.). The external identification of these species is currently impossible, since it is necessary to count dorsal fins and vertebrae in order to distinguish them (Nakamura and Parin, 1993; Parin, 1995). The bathymetric distribution of *A. carbo* ranges between 200 and 2300 m, although the depth of the most frequent distribution is around 1000 m; whereas *A. intermedius* lives from 300 to 1500 m (Nakamura and Parin, 1993; Lorange *et al.*, 2001; Morales-Nin and Sena-Carvalho, 1996; Pajuelo *et al.*, 2008). However, due to the current confusion between the two species, it is not possible to confirm precisely the depth distribution of each species.

According to ecomorphological premises, some characters should have a close relationship with the environmental factors that form the habitat of the organism (Bock, 1990; Norton *et al.*, 1995). Therefore, the study of morphological features related to the sensorial perception of environmental stimuli (Blaxter, 1988; Weissburg, 2005) may help us to understand which adaptive features can indicate a certain ecological segregation (Schoener, 1974; Lombarte and Aguirre, 1997; Seehausen *et al.*, 2008).

The sensorial characters with ecological implications most studied are: i) the eye size and the eye's inner structures (Fernald, 1988; Bozzano *et al.*, 2001), and ii) the sagittal otoliths, the main structure of the inner ear in Teleostean non-ostariophysian fish (Aguirre and Lombarte, 1999; Volpedo and Echevaría, 2003; Tuset *et al.*, 2003; Lombarte and Cruz, 2007). Lombarte (1992) indicated differences in relative size of the *sulcus acusticus* between *Merluccius capensis* and *M. paradoxus*, and concluded that the species that lives at greater depths, *M. paradoxus*, obtained higher values. Schulz-Mirbach *et al.* (2008) also found differences in otolith morphology between surface and cave populations of *Poecilia mexicana*. Consequently, the goal of this paper is to hypothesize on the spatial niche of the two species by analyzing (i) the otolith morphometry, (ii) the ratio between the *sulcus acusticus* area and otolith area, and (iii) the ratio between the eye diameter and cephalic length, in order to determine whether these characters can indicate the ecological segregation of the two species.

MATERIALS AND METHODS

Sampling and data collection

A total of 137 specimens of *Aphanopus carbo* and *A. intermedius* were collected off Sesimbra (mainland Portugal), the Azores, Madeira, the Canary Islands and off the coasts of Morocco and the western Sahara (Fig. 1). The individuals from Sesimbra, the Azores and Madeira were taken randomly from the commercial fishery. In the other locations, specimens were

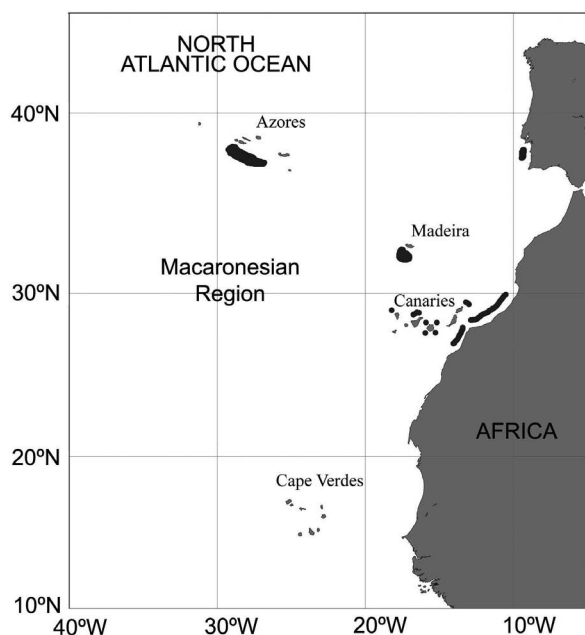


FIG. 1. – Map of the study area in the NE Atlantic Ocean showing the locations where specimens of *A. carbo* and *A. intermedius* were collected.

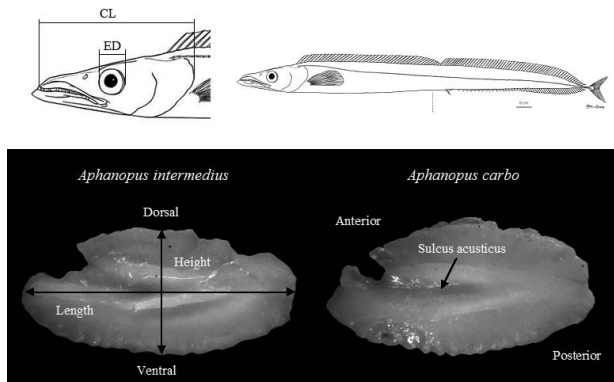


FIG. 2. – Schematic drawings of *Aphanopus* spp. showing head measurements used in the present study (adapted from Nakamura and Parin, 1993) and the mesial surface of sagittal otoliths of *A. carbo* and *A. intermedius* illustrating various features.

obtained from experimental fishing. As it is difficult to distinguish the species using external morphologic characters, all specimens were genetically identified according to the method developed by Stefanni and Knutsen (2007).

Cephalic length (CL in mm) and eye diameter (ED in mm) were measured (Fig. 2) for all individuals (the total, standard and furcal lengths were not considered for this study because in many specimens the posterior end was damaged), and otoliths were removed, washed, dried and stored in plastic vials. The otoliths of the two species were described morphologically according to the terminology proposed by Tuset *et al.* (2008).

All otoliths were weighed (OW) to the nearest 0.01 mg. Otoliths from the right side of the fish were

orientated with the *sulcus* side up. Their images were digitized using a microscope attached to an image analyzer with a magnification of 1.5–2.5× depending on the size of the otolith. Otolith area (OA in mm²), length (OL in mm), height (OH in mm) and perimeter (OP in mm) and *sulcus* area (SA in mm²) (Fig. 2) were measured using Image-Pro Plus version 4.1.0 software (Media Cybernetics, Inc.). To avoid fish size effecting the analyses, the individuals were truncated from 173 mm CL.

Data analysis

To detect the specific ontogenetic changes in otolith morphometry and visual perception, all variables were fitted by a power function $Y = aX^b$. Statistical differences in the regression slopes between species were tested by means of an ANCOVA, treating species as the main factor and length (or otolith height) as the covariate. One-way (ANOVA) was used to compare the eye diameter:cephalic length (ED:CL) and sulcus area:otolith area (S:O) ratios among size groups (CL in mm, <200, 201–240, 241+) and a post-hoc Tukey's test was applied; whereas a Student's *t*-test was used for comparisons according to species and size class (Zar, 1996).

RESULTS

The otolith morphology of the two species is very similar. According to Tuset *et al.* (2008): the ventral margin is sinuate to crenate. Sulcus acusticus: heter-

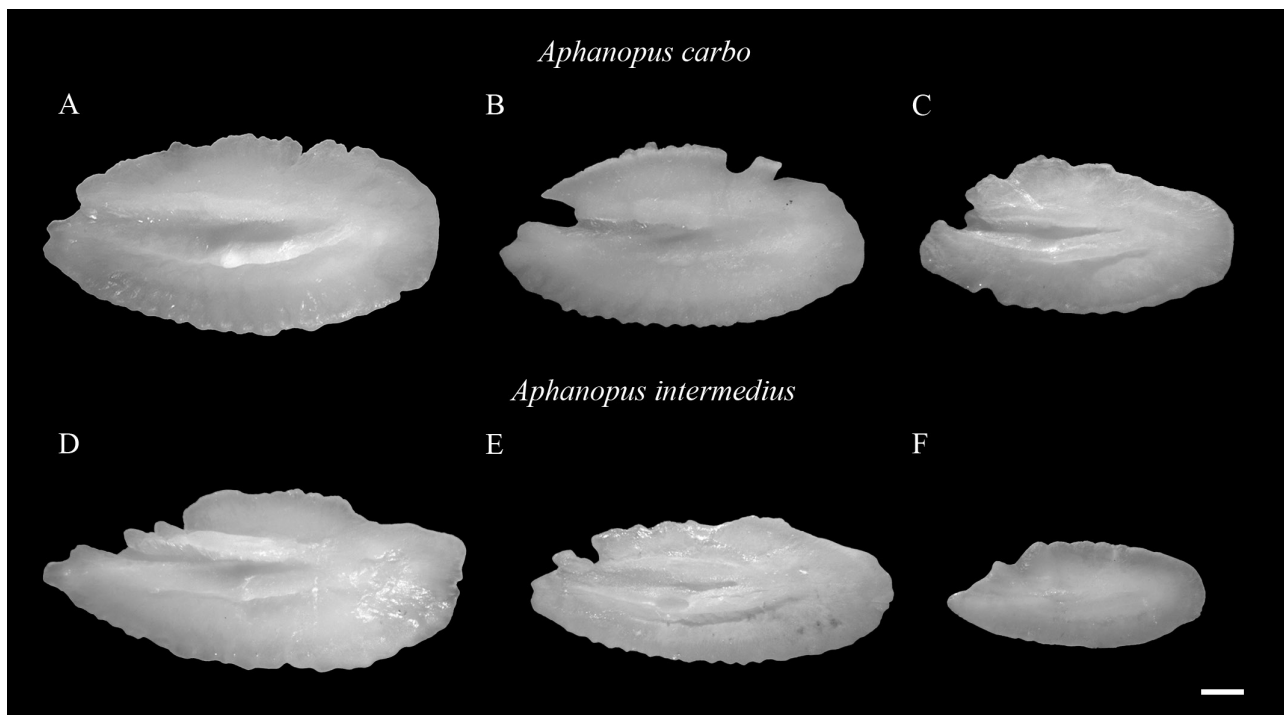


FIG. 3. – Sagittal otoliths of *A. carbo* (A–C) and *A. intermedius* (D–F). A, 118.8 cm; B, 107.0 cm; C, 90.5 cm; D, 129.6 cm; E, 96.3 cm; F, 63.8 cm. All measurements in SL.

TABLE 1. – Descriptive statistics of fish and otolith variables in *Aphanopus* spp. CL, cephalic length; ED, eye diameter; OA, otolith area; OH, otolith height; OL, otolith length; OP, otolith perimeter; OW, otolith weight; SA, sulcus area.

Variables	n	<i>Aphanopus carbo</i>				n	<i>Aphanopus intermedius</i>			
		Min.	Max.	Mean	sd		Min.	Max.	Mean	sd
CL	71	174	250	210.89	17.65	42	173	270	212.55	27.2
ED	71	33	59	46.5	5.74	42	30	62	43.01	7.27
OA	71	19.01	35.16	25.43	3.54	42	15.99	30.06	22.75	3.82
OH	71	3.26	4.69	3.97	0.36	42	2.97	4.64	3.68	0.35
OL	71	7.35	10.59	8.69	0.6	42	6.82	9.89	8.43	0.77
OP	71	17.98	24.97	21.49	1.6	42	16.54	24.56	20.42	1.99
OW	71	22.4	72.00	42.22	13.09	42	17.6	59.4	31.93	10.91
SA	71	0.99	5.03	2.32	0.94	42	0.73	3.79	2.03	0.8

osulcoid, ostial, median. Ostium: funnel-like, shorter than the cauda. Cauda: tubular, straight, ending half way to the posterior margin. Anterior region: peaked; rostrum short, broad, pointed; antirostrum absent or short, narrow, pointed; excisura wide with or without a deep and acute notch. Posterior region: round. Nevertheless, it seems clear that the otolith shape is different for the two species, as *A. carbo* is more oblong and less elliptic than *A. intermedius* (Fig. 3).

The descriptive statistics of all variables are summarized in Table 1. Although the mean cephalic length was higher in *A. intermedius*, the mean of the rest of variables was greater in *A. carbo*. No significant variations were detected in the mean of the *ED:CL* ratio amongst size classes for *A. carbo* (ANOVA, $F = 1.735$, $P = 0.184$) and *A. intermedius* ($F = 0.374$, $P = 0.691$). However, the Student's *t*-test showed significant differences ($t = 3.844$, $P < 0.001$) between species, and *A. carbo* obtained higher values (mean and standard deviation, 0.221 ± 0.022) than *A. intermedius* (0.203 ± 0.026) (Fig. 4).

Otolith length was not a good predictor of otolith weight ($r^2 < 0.60$), while the variation in otolith height values was greater than 77% for both species (Table 2, Fig. 5). The ANCOVA test showed significant differences between species for both relationships (*OH-OW*, $F = 3.350$; *OL-OW*, $F = 19.849$; $P < 0.05$). However, all otolith variables showed significant correlations with cephalic length. The variable most strongly related to fish size was the otolith weight, with 84.9% of the variability in *A. intermedius* and 69.5% in *A. carbo* explained by the model. The comparison with the slopes

indicated significant differences between species for the *CL-OH* (ANCOVA, $F = 5.663$, $P < 0.05$), *CL-OW* ($F = 5.106$, $P < 0.05$) and *CL-SA* ($F = 9.368$, $P < 0.05$) relationships, although slopes of all equations were higher for *A. carbo* (Table 2, Fig. 6). In this sense, more noticeable differences were detected in the relative increase in weight and the *sulcus acusticus* area, as the distance between slopes increased as the cephalic length became larger.

The *S:O* ratio did not vary significantly among size classes in *A. carbo* (ANOVA, $F = 2.914$, $P = 0.061$), although a positive tendency was observed with the increase in fish size. However, significant differences were detected in *A. intermedius* (ANOVA, $F = 3.334$, $P = 0.046$). The Tukey's test grouped the size classes 180-220 and 220-260 (Fig. 7). Finally, the ratio analysis did not show significant differences between species for each size class (Student's *t*-test, $t = 0.609$ in 180 mm, $t = 0.493$ in 220 mm, $t = 1.956$ in 260 mm, $P > 0.05$) (Fig. 7).

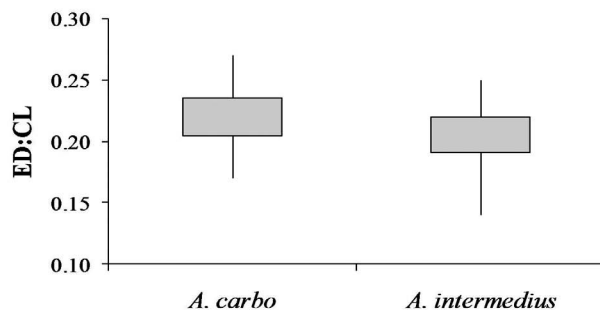
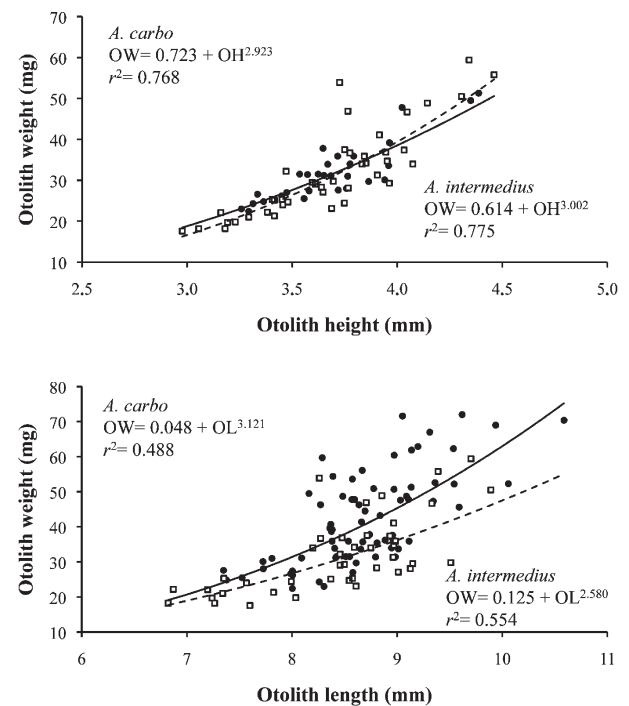
FIG. 4. – Box plots (maximum, minimum, upper and lower quartiles) for the eye diameter:cephalic length ratio (*ED:CL*) in *Aphanopus* spp.FIG. 5. – Power relationships between otolith weight and otolith length and height in *A. carbo* (black dots) and *A. intermedius* (white squares).

TABLE 2. – Regression parameters of the relationships by species and ANCOVA test comparing the slopes between species. CL, cephalic length; OA, otolith area; OH, otolith height; OL, otolith length; OP, otolith perimeter; OW, otolith weight; SA, sulcus area.

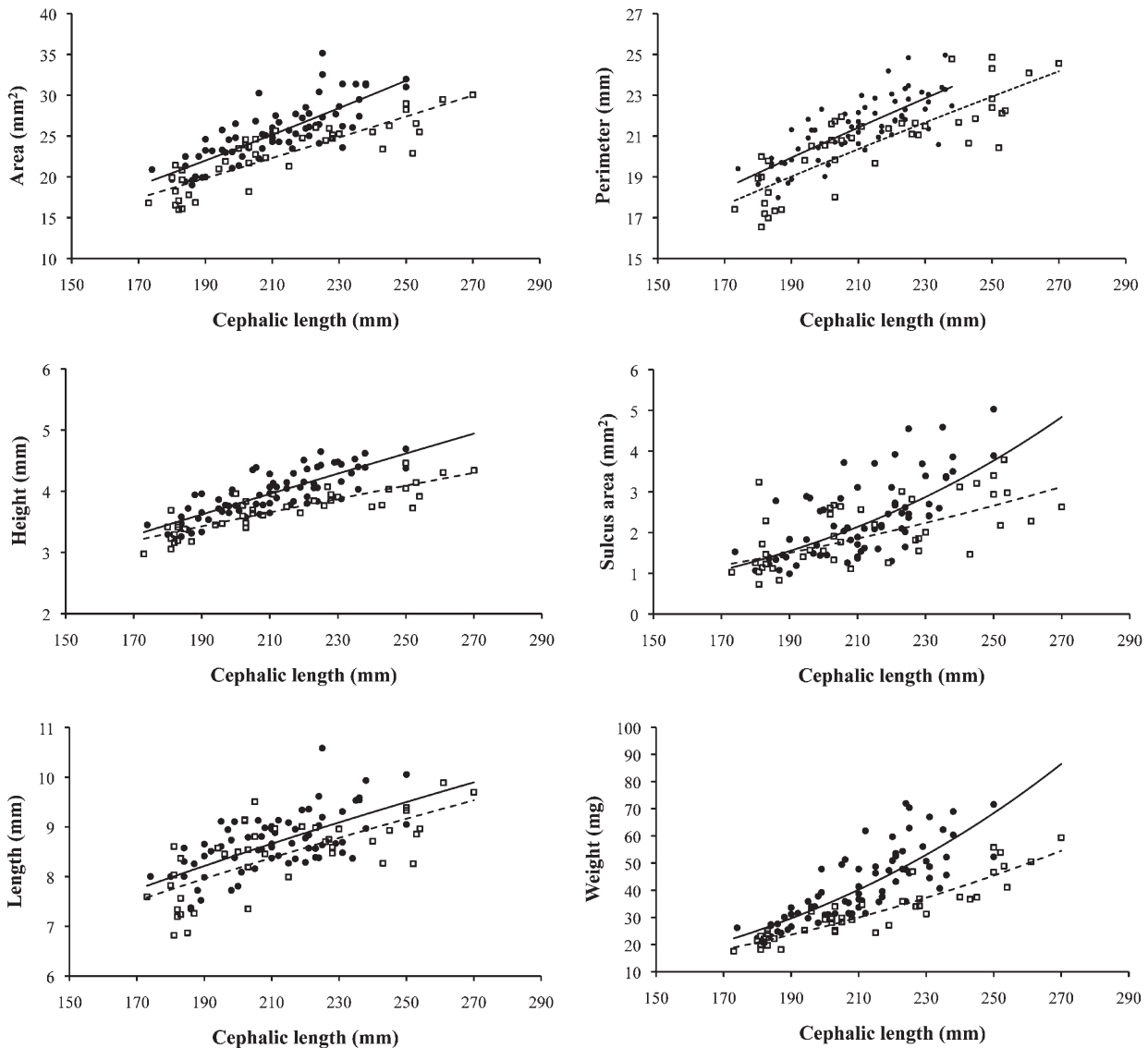
Relationship	n	<i>Aphanopus carbo</i>					n	<i>Aphanopus intermedius</i>					ANCOVA
		a	b	se (b)	r ²	P		a	b	se (b)	r ²	P	
CL-OA	71	0.019	1.341	0.115	0.662	<0.01	42	0.420	1.176	0.116	0.719	<0.01	1.042 ns
CL-OH	71	0.035	0.886	0.078	0.653	<0.01	42	0.115	0.647	0.062	0.730	<0.01	5.663 <0.05
CL-OL	71	0.508	0.530	0.075	0.420	<0.01	42	0.535	0.515	0.084	0.485	<0.01	0.020 ns
CL-OP	71	0.469	0.715	0.063	0.651	<0.01	42	0.652	0.643	0.071	0.670	<0.01	0.592 ns
CL-OW	71	3.4*10 ⁻⁶	3.048	0.243	0.695	<0.01	42	8.9*10 ⁻⁵	2.381	0.159	0.849	<0.01	5.106 <0.05
CL-SA	71	6.3*10 ⁻⁸	3.243	0.476	0.420	<0.01	42	2.7*10 ⁻⁵	2.080	0.412	0.389	<0.01	9.368 <0.05
OL-OW	71	0.048	3.121	0.385	0.488	<0.01	42	0.125	2.580	0.373	0.544	<0.01	19.849 <0.001
OH-OW	71	0.723	2.923	0.193	0.768	<0.01	42	0.614	3.002	0.256	0.775	<0.01	3.350 <0.05

DISCUSSION

The present study provides evidence to assert that *A. carbo* and *A. intermedius* are adapted to living in different spatial niches, which confirms the previous assumption that *A. carbo* inhabits deeper waters,

although overlapping occurs (Nakamura and Parin, 1993; Morales-Nin and Sena-Carvalho, 1996).

Fish have a variety of different sensory receptors that enable them to glean a good deal of information about their sensory environment (Atema *et al.*, 1988). The vision of deep-sea animals inhabiting different

FIG. 6. – Power relationships between cephalic length and otolith variables in *A. carbo* (black dots) and *A. intermedius* (white squares).

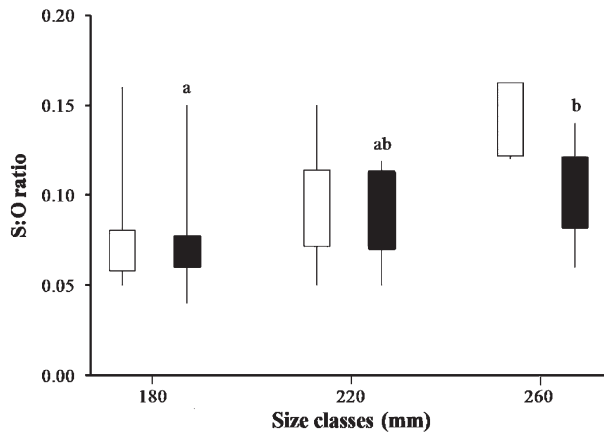


FIG. 7. – Box plots (maximum, minimum, upper and lower quartiles) for the sulcus area:otolith area ratio ($S:O$) by size class (CL) in *A. carbo* (white boxes) and *A. intermedius* (black boxes). Means with different superscript are significantly different ($P > 0.05$).

depths are matched to a gradual change in visual scene from an extended source to point source. Species living in the mesopelagic zone (150–1000 m), which is dimly lit by down-welling daylight, have comparatively large eyes relative to head size (Warrant and Locket, 2004). It is known that *A. carbo* — or *A. intermedius* due to the current confusion in the North Atlantic — migrates vertically at night to the upper water layer to feed on crustaceans, cephalopods and benthopelagic, mesopelagic and pelagic fish depending on its ontogenic cycle (Mauchline and Gordon, 1984; Pshenichny *et al.*, 1986; Figueiredo *et al.*, 2003). This circadian migration to layers with more light should affect the vision pattern as this is influenced by daylight. In fact, the morphology and size of the eyes in *Aphanopus* spp. is similar to other trichiurids from shallower waters. Although they live below 1000 m, the following premise could apply to them: larger eyes (relative to body size) are related to a deeper depth distribution. Our results show that the eyes of *A. carbo* are larger, and therefore it can be hypothesized that either it inhabits deeper waters or it does not reach surface waters in vertical migration, or both. The reason why *Aphanopus* spp. occurs in deeper waters in the Canary Islands and Madeira may be in order to avoid overlapping with the trophic niches of other trichiurids as well as other species, such as *Promethichthys prometheus* (Pajuelo *et al.*, 2008).

Previous studies have concluded that otolith size is related to the habitat and behaviour of species (Paxton, 2000; Tuset *et al.*, 2003; Volpedo and Echevarría, 2003). In most cases, it has been demonstrated that an increase in the depth distribution of species that live below 1000 m also implies an increase in otolith size (Lombarte and Cruz, 2007; Schulz-Mirbach *et al.*, 2008). In the present study, statistical differences were detected in the otolith morphometry between *A. carbo* and *A. intermedius* for otolith weight and height and sulcus area. The otoliths of *A. carbo* clearly grow more in size and weight, which suggests that this species inhabits deeper waters.

The inner ear is considered to be the most important structure for detecting distant sound sources, and the $S:O$ ratio is related to the hearing capabilities of fish and changes in food, spatial niches and depth (Gauldie, 1988; Aguirre and Lombarte, 1999; Popper and Lu, 2000). However, the biological meaning of ontogenic changes in the $S:O$ ratio is controversial. Some studies have not found significant allometric changes with fish growth as in *Hoplostethus atlanticus*, *H. mediterraneus*, *Tachurus declivis* (Gauldie, 1988), *Pomatoschistus lozanoi* (Arellano *et al.*, 1995), *Mullus barbatus* (Aguirre and Lombarte, 1999) and *Serranus* spp. (Tuset *et al.*, 2003) and *A. carbo* (present study). In other species, such as *Merluccius capensis* and *M. paradoxus* (Lombarte, 1992), *Pomatoschistus lozanoi* (Arellano *et al.*, 1995), *Mullus surmuletus* (Aguirre and Lombarte, 1999) and *A. intermedius* (present study) the relationship is noticeable. In the particular case of *Merluccius* spp., it has been demonstrated that the adults have a wider depth distribution, reach deeper waters for feeding mainly on fish (Recasens *et al.*, 1998), and show an increase in the $S:O$ ratio and in the number of hair cells (Lombarte, 1992; Lombarte and Popper 1994; Torres *et al.*, 2000). Other studies have suggested a positive association between $S:O$ area ratio and mobility (Gauldie, 1988; Lombarte and Popper, 1994; Arellano *et al.*, 1995). As previously commented, *Aphanopus* spp. are great swimmers, with horizontal and vertical migrations. The analysis of the $S:O$ ratio did not reveal significant differences between species, although the values obtained for *A. carbo* were always higher in each size group which might imply major physical activity, a better hearing capability or a wider spatial niche.

It is possible to distinguish two types of hearing in fish: specialist and generalist. Specialists detect the sound with both direct and indirect pathways, whereas generalists tend to have a narrower hearing bandwidth and poorer sensitivity (Fay, 1988). Most of species are generalist and usually do not detect sound above 1000 Hz, and their sensitivity at lower frequencies is also poorer (Fay, 1988; Popper and Lu, 2000). Gauldie (1988) demonstrated that the $S:O$ ratio may be correlated with auditory frequency; hence, species with a higher ratio can discriminate higher frequencies. The $S:O$ ratio in *Aphanopus* spp. is low (around 0.8–1) compared with other species, e.g. 0.28 to 0.31 in *Merluccius* spp. (Lombarte, 1992), 0.36 in *Gadus morhua*, 0.20 in *Hoplostethus mediterraneus* (Gauldie, 1988) and 0.23 to 0.28 in *Mullus* spp. (Aguirre and Lombarte, 1999), and similar to *Pomatoschistus* spp. (Arellano *et al.*, 1995). Hence, it appears that the hearing capability of *Aphanopus* spp. is adapted to low frequency sound. They live in an environment where low-frequency signals produce long sound wavelengths which may travel thousands of kilometres before dissipating. This happens due to a layer of water called the “SOFAR channel” which lies between 800 and 1000 m below the sea surface at low and middle latitudes, and which

is deeper in the subtropics and close to the surface in high latitudes (Rogers and Cox, 1988). It seems logical to consider that the development of the *sulcus acusticus* is an adaptation to habitat, since different preys will produce signals that can be detected from closer or farther away. There are aspects of the otolith structure, such as its thickness, the depth of the *sulcus* and the shape of the otolith itself, that do not have a known impact on the hearing capabilities (Popper and Lu, 2000; Reichenbacher *et al.*, 2007). Future research should be focused on developing three-dimensional techniques to help us better understand the relation between fish ecology and otolith morphology and hearing capabilities.

ACKNOWLEDGEMENTS

Many people helped us in the data collection and sampling involved in this study. We thank José Ignacio Santana, José Antonio Pérez-Peñalvo, Olga Ayza, and Antonio García-Mederos from the Instituto Canario de Ciencias Marinas (Gran Canaria, Spain); Manuel Bischoito from the Museu Municipal do Funchal (História Natural) (Madeira, Portugal); Dalila Sena-Carvalho and João Delgado from the Direcção de Serviços de Investigação das Pescas (Madeira, Portugal); and Dr. Eduardo Isidro from the University of the Azores (Azores, Portugal). This study was co-funded by the research project *PESCPROF 3* (ref: 05/MAC/4.2/M11 and co-financed by EU Interreg III-B programme), and pursued in collaboration with the pilot projects RAI-AP-36/2005 and 37/2005 co-financed by the EU and the Spanish Government. We would like to thank the reviewers for their comments and suggestions.

REFERENCES

- Aguirre, H. and A. Lombarte. – 1999. Ecomorphological comparisons of sagittae in *Mullus barbatus* and *M. surmuletus*. *J. Fish Biol.*, 55: 105-114.
- Arellano, R.V., O. Hamerlynck, M. Vinex, J. Mees, K. Hostens and W. Gijssels. – 1995. Changes in the ratio of the *sulcus acusticus* area to the sagitta area of *Pomatoschistus minutus* and *P. lozanoi* (Pisces, Gobiidae). *Mar. Biol.*, 122: 355-360.
- Atema, J., R.R. Fay, A.N. Popper and W.N. Tavolga. – 1988. *Sensory biology of aquatic animals*. Springer-Verlag, New York.
- Blaxter, J.H.S. – 1988. Sensory performance, behavior and ecology of fish. In: J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga (eds.), *Sensory biology of aquatic animals*, pp. 203-222. Springer-Verlag, New York.
- Bock, W.J. – 1990. From biologicische anatomie to ecomorphology. *Netherlands J. Zool.*, 40: 254-277.
- Bozzano, A., R. Murgia, S. Vallergera, J. Hirano and S. Archer. – 2001. Functional adaptations of the photoreceptor system in the retinae of two species of dogfish: relationships with feeding habits and depth distribution. *J. Fish Biol.*, 59: 1258-1278.
- Clarke, M.W., C.J. Kelly, P.L. Connolly and J.P. Molloy. – 2003. A life history approach to the assessment and management of deepwater fisheries in the Northeast Atlantic. *J. Northwest Atl. Fish. Sci.*, 31: 401-411.
- Fay, R.R. – 1988. *Hearing in vertebrates, a psychophysics data-book*. Heffernan Press, Massachusetts.
- Fernald, R.D. – 1988. Aquatic adaptation on eye design. In: J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga (eds.), *Sensory biology of aquatic animals*, pp. 435-466. Springer-Verlag, New York.
- Figueiredo, I., P.B. Machado, S. Reis, D. Sena-Carvalho, T. Blasdale, A. Newton and L.S. Gordo. – 2003. Observations on the reproductive cycle of the black scabbardfish (*Aphanopus carbo* Lowe, 1839) in the NE Atlantic. *ICES J. Mar. Sci.*, 60(4): 774-779.
- Gauldie, R.W. – 1988. Function, form and time-keeping properties of fish otoliths. *Comp. Biochem. Physiol.*, 91: 395-402.
- Gordo, L.S. – 2009. Black scabbardfish (*Aphanopus carbo* Lowe, 1839) in the southern Northeast Atlantic: considerations on its fishery. *Sci. Mar.*, 73S2: 11-16.
- Gordon, J.D.M. – 2001. Deep-water fisheries at the Atlantic Frontier. *Cont. Shelf Res.*, 21: 987-1003.
- Howe, K.M., D.L. Steine and C.E. Bond. – 1979. First records off Oregon of the pelagic fishes *Paralepis atlantica*, *Gonostoma atlanticum* and *Aphanopus carbo*, with notes on the anatomy of *Aphanopus carbo*. *Fish. Bull.*, 77(3): 700-703.
- Lombarte, A. – 1992. Changes in otolith area: sensory area ratio with body size and depth. *Environ. Biol. Fish.*, 33: 405-410.
- Lombarte, A. and A. Popper. – 1994. Quantitative analyses of postembryonic hair cell addition in the otolithic end organs of the inner ear of the European hake, *Merluccius merluccius* (Gadiformes, Teleostei). *J. Comp. Neurol.*, 345: 419-428.
- Lombarte, A. and H. Aguirre. – 1997. Quantitative differences in the chemoreceptors systems in the barbels of two species of Mullidae (*Mullus surmuletus* and *M. barbatus*) with different bottom habitats. *Mar. Ecol. Prog. Ser.*, 150: 57-64.
- Lombarte, A. and A. Cruz. – 2007. Otolith size trends in marine communities from different depth strata. *J. Fish. Biol.*, 71: 53-76.
- Lorance, P., S. Souissi, F. Uiblein and R. Castillo-Eguia. – 2001. Distribution and density of carnivorous fish species around Lanzarote and Fuerteventura, Canary Islands. *Sci. Coun. Res. Doc. NAFO*, 01/168: 1-14.
- Martins, M.R. and C. Ferreira. – 1995. Line fishing for black scabbardfish *Aphanopus carbo* Lowe, 1839 and other deep water species in the eastern mid Atlantic to the north of Madeira. In: A.G. Hoppe (ed.), *Deep Water Fisheries of the North Atlantic Oceanic Slope*, pp. 323-325. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Martins, M.M., M.R. Martins and F. Cardador. – 1994. Evolution of the Portuguese fishery of black scabbard fish *Aphanopus carbo* Lowe, 1839 during the period 1984-1993. pp. 1-12 (ICES CM 1994/G: 28).
- Mauchline, J. and J.D.M. Gordon. – 1984. Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. *ICES J. Cons.*, 41: 239-247.
- Morales-Nin, B. and D. Sena-Carvalho. – 1996. Age and growth of the black scabbard fish *Aphanopus carbo* off Madeira. *Fish. Res.*, 2: 239-251.
- Morales-Nin, B., A. Canha, M. Casas, I. Figueiredo, L.S. Gordo, J.M. Gordon, D. Gouveia, C.G. Piñeiro, S. Reis, A. Reis and S.C. Swan. – 2002. Intercalibration of age readings of deepwater black scabbardfish, *Aphanopus carbo* (Lowe, 1839). *ICES J. Mar. Sci.*, 59: 352-364.
- Nakamura, I. and N.V. Parin. – 1993. FAO Species Catalogue, vol. 15. Snake mackerels and cutlassfishes of the world (Families Gempylidae and Trichiuridae). An annotated and illustrated catalogue of the snake mackerels, snoeks, escolars, gemfishes, sackfishes, domine, oilfish, cutlassfishes, scabbardfishes, hairtails, and frofishes known to date. *FAO Fish. Synop.*, 125: 1-136.
- Neves, A., A.R. Vieira, I. Farias, I. Figueiredo, V. Sequeira and L.S. Gordo. – 2009. Reproductive strategies in black scabbardfish (*Aphanopus carbo* Lowe, 1839) from the NE Atlantic. *Sci. Mar.*, 73S2: 19-31.
- Norton, S.F., J.J. Luczkovich and P.J. Motta. – 1995. The role of ecomorphological studies in the comparative biology of fishes. *Environ. Biol. Fish.*, 44: 287-304.
- Pajuelo, J.G., J.A. González, J.I. Santana, J.M. Lorenzo, A. García-Mederos and V.M. Tuset. – 2008. Biological parameters of the bathyal fish black scabbardfish (*Aphanopus carbo* Lowe, 1839) off the Canary Islands, Central-east Atlantic. *Fish. Res.*, 92: 140-147.
- Parin, N.V. – 1995. Three new species and new records of cutlassfishes of the genus *Aphanopus* (Trichiuridae). *J. Ichthyol.*, 35(2): 128-138.
- Paxton, J.R. – 2000. Fish otoliths: do sizes correlate with taxonomic group, habitat and/or luminescence? *Philos. Trans. R. Soc. Lond. B*, 355: 1299-1303.
- Popper, A.N. and Z. Lu. – 2000. Structure-function relationships in

- fish otolith organs. *Fish. Res.*, 46: 15-25.
- Pshenichny, B.P., A.N. Kotlyar, and A.A. Glukhov. – 1986. Fish resources of the Atlantic Ocean thalassobathyal. In: *Biological resources of the Atlantic Ocean*, pp. 230-252. Nauka Press, Moscow.
- Recasens, L., A. Lombarte, B. Morales-Nin and G. Torres. – 1998. Spatio-temporal variation in the population structure of the European hake in the NW Mediterranean. *J. Fish. Biol.*, 53: 387-401.
- Reichenbacher, B., U. Sienknecht, H. Küchenhoff and N. Fenske. – 2007. Combined otolith morphology and morphometry for assessing taxonomy and diversity in fossil and extant Killifish (*Aphanius*, †*Prolebias*). *J. Morph.*, 268: 898-915.
- Rogers, P.H. and M. Cox. – 1988. Underwater sound as a biological stimulus. In: J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga (eds.), *Sensory biology of aquatic animals*, pp. 131-149. Springer-Verlag, New York.
- Schoener, T.W. – 1974. Resource partitioning in ecological communities. *Science*, 1985: 27-39.
- Schulz-Mirbach, T., C. Stransky, J. Schlickeisen and B. Reichenbacher. – 2008. Differences in otolith morphologies between surface- and cave-dwelling populations of *Poecilia mexicana* (Teleostei, Poeciliidae) reflect adaptations to life in an extreme habitat. *Evol. Ecol. Res.*, 10: 537-558.
- Seehausen, O., Y. Terai, I.S. Magalhaes, K.L. Carleton, H.D.J. Mrosso, R. Miyagi, I. Van der Sluijs, M.V. Schneider, M.E. Maan, H. Tachida, H. Imai and N. Okada. – 2008. Speciation through sensory drive in cichlid fish. *Nature*, 455: 230-625.
- Shotton, R. – 2005. Pesquerías en aguas profundas. In: Examen de la situación de los recursos pesqueros marinos mundiales. *FAO Doc. Téc. Pesca*, 457: 1-260.
- Stefanni, S. and H. Knutsen. – 2007. Phylogeography and demographic history of the deep-sea fish, *Aphanopus carbo* (Lowe, 1839), in the NE Atlantic: vicariance followed by secondary contact or speciation? *Mol. Phylog. Evol.*, 42: 38-46.
- Torres, G.J., A. Lombarte and B. Morales-Nin. – 2000. Variability of the sulcus acusticus in the sagittal otolith of the genus *Merluccius* (Merluciidae). *Fish. Res.*, 46: 5-13.
- Tuset, V.M., A. Lombarte, J.A. González, J.F. Pertusa and M.J. Lorente. – 2003. Comparative morphology of the sagittal otolith in *Serranus* spp. *J. Fish Biol.*, 63: 1491-1504.
- Tuset, V.M., A. Lombarte and C.A. Assis. – 2008. Otolith atlas for the western Mediterranean, north and central eastern Atlantic. *Sci. Mar.*, 72S1: 1-203.
- Volpedo, A.V. and D.D. Echeverría. – 2003. Ecomorphological patterns of the sagitta in fish on the continental shelf off Argentine. *Fish. Res.*, 60: 551-560.
- Warrant, E.J. and A. Locket. – Vision in the deep sea. *Biol. Rev.*, 79: 671-712.
- Weissburg, M.J. – 2005. Sensory biology: linking the internal and external ecologies of marine organisms. Introduction. *Mar. Ecol. Prog. Ser.*, 287: 263-265.
- Zar, J.H. – 1996. Biostatistical Analysis. New Jersey: Prentice-Hall International.
- Scient. ed.: J. Lleonart.
- Received March 9, 2009. Accepted April 15, 2010.
- Published online September 23, 2010.