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Changes in otolith area: sensory area ratio with body size and depth

Antoni Lombarte
Institut de Ciències del Mar (CSIC), Passeig Nacional s/n, 08039 Barcelona, Catalonia, Spain

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Synopsis

The ratio between the sensory areas of the sulcus acusticus and the sagittal otolith (S : O ratio) in the species *Merluccius capensis* and *M. paradoxus* was analyzed using a digital image processing system. Sagittal growth in both species is negatively allometric with respect to total fish length but is more negative in the deeper-dwelling species, *Merluccius paradoxus.* In contrast, the sulcus acusticus undergoes a relative increase in size, that is, the S : O ratio increases with fish length. There was a clear relationship between the increase in the S : O ratio and depth.

Introduction

The otolith organs of teleost fishes, situated in the labyrinth of the inner ear, are peripheral mechanoreceptors that act as sound transducers (Schuijf 1981). The sagittal otolith, which is associated with auditory function, is located in the sacculus, which is one of the otolith organs of the pars inferior (Fay & Olsho 1979, Platt & Popper 1981). Both the sagitta and the sensory area associated with it, known as the saccular macula, are quite variable in shape (Hetch & Hetch 1978, Popper 1980, Schwarzhans 1980, Popper & Coombs 1982). Gauldie (1988) speculated on the possibility of a relationship between these morphological differences (ratio between the area of the sensory macula and the otolith area, M : O ratio) and hearing capabilities.

The ratio between the area of the sulcus acusticus and the area of the sagitta (S : O ratio) was calculated. This ratio has been regarded as closer to the M : O ratio, since the area of the sensory macula and that of the sulcus acusticus, the region of the sagitta associated with the sensory macula, are similar in gadiform fish (Gauldie 1988, Lombarte 1990).

Two sympatric demersal species from the Southeast Atlantic, *Merluccius capensis* (Castelnau, 1861) and *Merluccius paradoxus* (Franca, 1960) (Pisces, Gadiformes) were selected to perform this study, since they are, within the genus *Merluccius,* two phylogenetically-close species (Inada 1981) whose sagittae, additionally, have similar morphological characteristics and were thought to be interesting for comparative morphological studies. *M. capensis* inhabits depths between 50 and 450 m, and *M. paradoxus* between 150 and 800 m (Smith & Heemstra 1986, Turón et al. 1986). While there is some overlap in the distribution ranges of the two species, maximum abundance levels for each occur in areas bathymetrically and geographically distinct (Inada 1981, Macpherson et al. 1985, 1986, Mas-Riera et al. 1990). Furthermore, there is a neat relationship between the size of these fish and the depth they inhabit (Macpherson et al. 1985, 1986).

The object of this paper is to ascertain whether

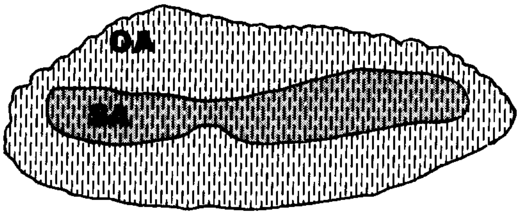

Fig. 1. Inner side of a right sagitta of *Merluccius capensis* with indication of the measured areas. OA: area of the sagittal otolith. SA: area of the sulcus acusticus.

there are differences in the S : O ratio between the two species and within each species during growth. Such differences may be adaptations of the different sizes of the fish to the environmental conditions occurring at different depths.

Materials and methods

Sagittae were collected from 239 specimens of *Merluccius capensis* and 225 specimens of *M. paradoxus* on combined oceanographic-fisheries surveys carried out off Namibia between 23° and 30° South latitude (Macpherson et al. 1985).

The sagittae were removed by cutting open the back of the heads of specimens. They were stored dry, and the total specimen length and the depth of the haul were recorded.

The sulcus area and the otolith area were measured using a digital image processing system. Such systems improve the speed, uniformity, and accuracy of measurements, especially in the case of non-linear measurements like areas.

The outline of each sagitta and of the sulcus acusticus was drawn with the aid of a camera lucida and a binocular microscope (Fig. 1), and the resulting image was digitalized. The sagittae were not used directly, because the tone was uniform and it was not possible to contrast the sulcus area with the rest of the otolith. The sagittal image was recorded using a video camera, digitalized, and calibrated in mm^2 in an image processor. The ratio between the sulcus area and sagittal area (S : O ratio) was then calculated.

The image analyzing system employed consisted of a high-resolution video camera and a VINIX digital processor equipped with a CYTIX morphometric and quantification package, property of the Centre de Tractament d'Imatges at the Universitat Autónoma in Barcelona.

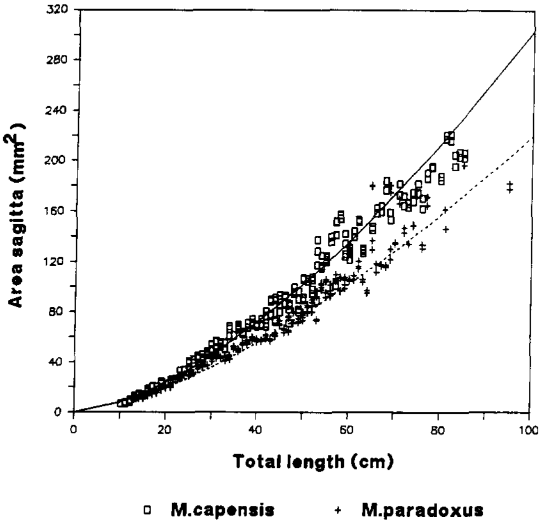

Fig. 2. Relationship between the area of the sagittal otolith (OA, mm^2) and total length (TL, cm) in *Merluccius capensis* (solid line, $OA = 0.22TL^{1.5668}$) and *Merluccius paradoxus* (broken line, $OA = 0.22TL^{1.5099}$).

A t-test was used to compare the slopes of the morphometric relationships between them and to the hypothetical value of isometry. The confidence limits for the parameter b (slope) were also calculated for the 95% level of significance.

Results

Growth of the area of the sagitta and the sulcus

In both species the relationship between the area of the sagitta and the area of the sulcus acusticus with total fish length and the relationship between sagittal area and sulcus area fit a power equation and yielded very high correlation coefficients ($r = 0.99$).

The growth of the sagittal area was negatively allometric with respect to total fish length in both species ($b = 1.5668 \pm 0.0003$, $t = 35.11$ $p < 0.0005$ in *M. capensis;* $b = 1.5099 \pm 0.0004$, $t = 36.66$, $p < 0.0005$ in *M. paradoxus*) (Fig. 2). The slopes were tested for isometry against a value of $b = 2$,

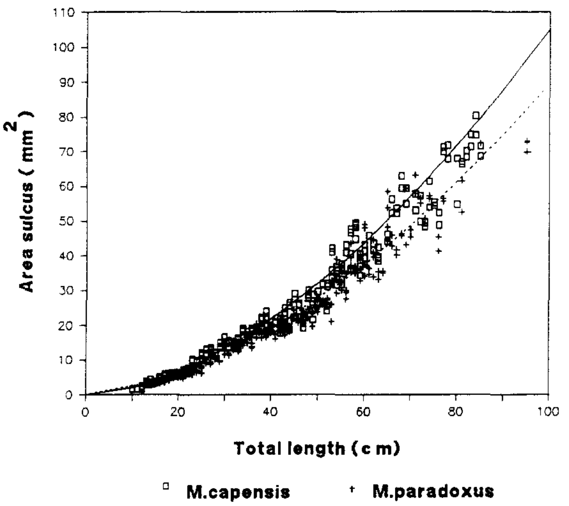

Fig. 3. Relationship between the area of the sulcus acusticus (SA, mm^2) and fish length (TL, cm) in *Merluccius capensis* (solid line, SA = $0.04TL^{1.7127}$) and *Merluccius paradoxus* (broken line, SA = $0.03TL^{1.7165}$).

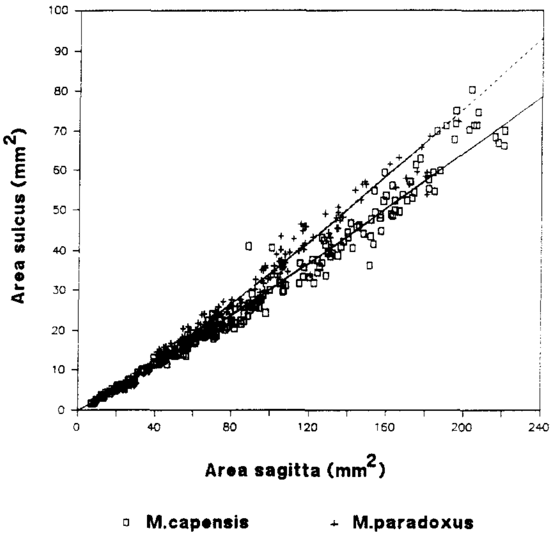

Fig. 4. Relationship between the area of the sulcus acusticus (SA, mm^2) and total sagittal area (OA, mm^2) in *Merluccius capensis* (solid line, SA = $0.20OA^{1.0934}$) and *Merluccius paradoxus* (broken line, SA = $0.18OA^{1.1317}$).

since it is a relationship between a linear value and a surface area value. These results indicate that the relative size of the sagittae decreases with fish length and that this decrease is more pronounced in *M. paradoxus* than in *M. capensis*. Both slopes were also significantly different between species ($t = 3.128$, $p < 0.001$).

The relationship between the area of the sulcus acusticus and total fish length (Fig. 3) was also negatively allometric ($b = 1.7127 \pm 0.0007$, $t = 15.87$, $p < 0.0005$ in *M. capensis* and $b = 1.7165 \pm 0.0004$ ($t = 19.95$, $p < 0.0005$) in *M. paradoxus*). No significant differences were detected in the slopes when comparing the growth curves for the two species ($t = 0.162$). The slopes for the relationship between sulcus area and sagittal area were greater than 1 in both species ($b = 1.0934 \pm 0.0001$, $t = 12.54$, $p < 0.0005$ in *M. capensis,* and $b = 1.1317 \pm 0.0002$, $t = 15.34$, $p < 0.0005$ in *M. paradoxus*). Since for an isometric relationship between the two areas the value of the slope b would be 1, growth of sulcus area is positively allometric with respect to otolith area in both species (Fig. 4). Such a relationship implies higher growth of the sulcus relative to that of the sagitta, such that the S : O ratio increases with otolith size. Comparison of the relationship between the growth of these two areas in both species showed that the value of the slope of the curve was significantly higher in *M. paradoxus* than in *M. capensis* ($t = 3.36$, $p < 0.0005$), hence the relative growth of the sulcus would appear to be greater in *M. paradoxus* than in *M. capensis*.

Relationship between the S : O ratio and total fish length

In both species the relationship between S : O ratio and total fish length fit a significant regression line ($r^2 = 0.66$, $t = 12.84$, $p < 0.0005$ in *M. capensis;* $r^2 = 0.73$, $t = 16.18$, $p < 0.0005$ in *M. paradoxus*) (Fig. 5). The S : O ratio increased with fish length in both species, but the slope of the regression line was significantly higher in *M. paradoxus* ($b = 0.0016 \pm 1.95e^{-8}$) than in *M. capensis* ($b = 0.0010 \pm 1.28e^{-8}$) ($t = 4.49$, $p < 0.0005$), hence interspecific differences in the S: O ratio became larger with fish length.

Relationship between the S : O ratio and depth

The relationship between the S : O ratio (for both

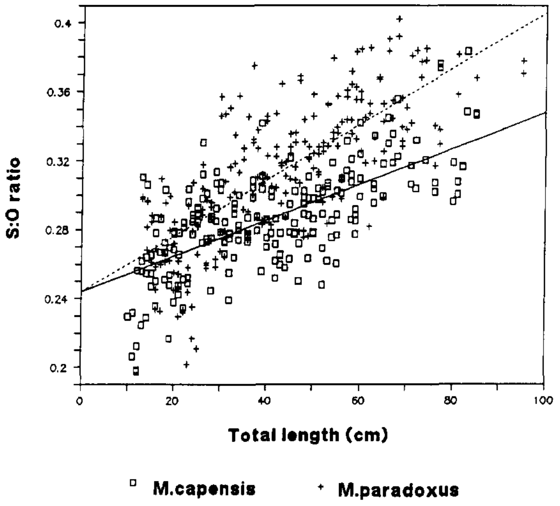

Fig. 5. Relationship between the S : O ratio (S : Or) and total fish length (TL, cm) in *Merluccius capensis* (solid line, S : Or = 0.24 + TLO.00103) and *Merluccius paradoxus* (broken line, S : Or = 0.24 + TLO.00165).

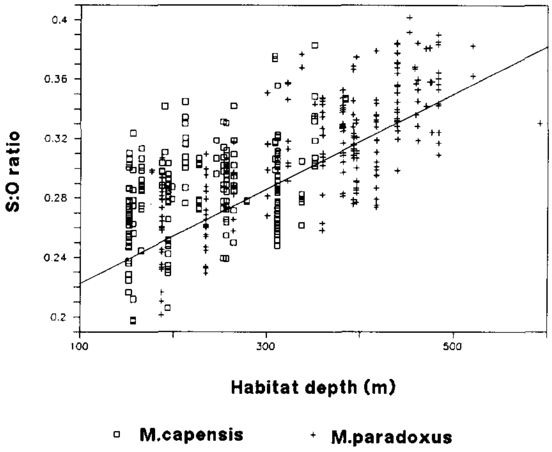

Fig. 6. Relationship between the S : O ratio (S : Or) and water depth of the habitat (D, m) in *Merluccius capensis* and *Merluccius paradoxus* (S : Or = 0.24 + DO.00027).

species combined) and depth of capture showed a significant relationship (Fig. 6) ($r^2 = 0.69$; $b = 0.00026 \pm 3.38e^{-10}$, $t = 19.76$, $p < 0.0005$). The S : O ratio increased with increasing depth. The value of the S : O ratio was larger for the deeper-dwelling species, *M. paradoxus,* and for the larger length groups, which inhabit greater depths than the smaller individuals (Table 1). The lowest mean value of the S : O ratio (0.24) was for the smallest length group of *M. capensis* (< 20 cm), which had a depth distribution between 50 and 200 m; intermediate mean S : O values (0.27–0.29) corresponded to *M. capensis* 21–40 cm and 41–60 cm long and *M. paradoxus* < 20 cm and 21–40 cm long, which showed a depth distribution between 100–400 m; the highest mean S : O values (0.32–0.35) were for *M. capensis* > 60 cm long and *M. paradoxus* 41–60 cm and > 60 cm long, with a depth distribution between 300 and 800 m.

Discussion

In both these species of the genus *Merluccius* the growth in the sagittal area and sulcus acusticus area was negatively allometric with respect to fish length. This relationship would appear to be common to the order Gadiformes, to which *Merluccius* belongs, since it has been reported in all studies on otolith growth carried out for this group (Saetersdal 1953, Beamish 1979, Frost & Lawry 1981, Wilson 1985, Lombarte & Morales 1989) and for other

Table 1. Mean values and standard deviations (σ) for the S : O ratio by depth range (in m) and length group (total length in cm).

Species	Length group cm	Depth range m	Sample size	S/O ratio mean	S/O ratio σ
M.capensis	≦ 20	50–200	38	0.24	0.03
	21 - 40	100–400	79	0.28	0.02
	41 - 60	150–400	76	0.28	0.03
	> 60	250–450	46	0.32	0.03
M.paradoxus	≦ 20	150–300	30	0.27	0.02
	21 - 40	200–400	75	0.29	0.04
	41 - 60	350–700	77	0.33	0.03
	> 60	450–800	43	0.35	0.03

groups of teleost fishes (Southward 1962, Bori 1986).

Comparison of otolith growth and sulcus growth in relation to total fish length indicated that the negative allometry with respect to fish length was considerably greater for saggital growth than for sulcus growth, such that, with fish growth, there was not only a decrease in the relative size of the sagitta but an increase in sulcus size in relation to sagittal size.

There is a relationship between fish size and depth, with larger individuals occurring at greater depths (Macpherson et al. 1985, 1986, Gordoa 1989). The decrease in the relative size of the sagitta and the increase in the relative size of the sulcus with fish growth was also related with depth. The relative size of the sagitta was smaller and the S : O ratio greater in *M. paradoxus,* which dwells at greater depths, than in *M. capensis.*

Similar effects between relative otolith size and depth have also been reported for Arctic gadids (Frost & Lawry 1981) and abyssal macrurans (Wilson 1985) and have been associated with physical alterations in water conditions. These environmental changes, especially temperature, probably affect the physiological process of deposition of material on the otoliths, lower temperatures slowing down otolith growth (Morales-Nin 1987).

The relative increase in the size of the sulcus with respect to sagittal size (S : O ratio) with fish length and in species dwelling at greater depths would seem to indicate that sulcus growth differs from that of the rest of the otolith.

Although the data reported by Gauldie (1988) were not indicative of changes in the S : O ratio (or the M: O ratio) with growth, the length range considered in that study was considerably more limited than the range considered herein. For instance, this author examined *Hoplostethus atlanticus* of sizes ranging between 5 and 35 cm, whereas the present study dealt with *M. capensis* 10–85 cm in length and *M. paradoxus* 13–95 cm in length and also took into account the different depth distributions for the various length groups.

The values of the S : O ratios and the corresponding length ranges were: for *Merluccius capensis* from 0.24 (< 20 cm) to 0.32 (> 60 cm), and for *M. paradoxus* from 0.27 (< 20 cm) to 0.35 (> 60 cm). These were slightly lower than the value of 0.36 for the S : O ratio in another gadiform, *Gadus morhua* (Gauldie 1988).

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