Environmental Biology of Fishes 37: 297–306, 1993.

Otolith size changes related with body growth, habitat depth and temperature

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

Received 6.2.1992 Accepted 19.11.1992

Key words: Coelorhynchus, Merluccius, Morphometry, Fishes, Gadiformes, Allometry

Synopsis

Size variation in the sagittal otoliths of six species of the genus *Merluccius,* and five species of the genus *Coelorhynchus* was compared, using a digital image processing system and multivariate analysis. It is proposed that otolith growth occurs under dual regulation, overall shape is regulated genetically, and otolith size is influenced by environmental conditions. The decline of temperature with increasing habitat depth seems to be an important factor regulating the growth of otoliths in carbonate-saturated levels. The relative growth of the otoliths is usually negatively allometric.

Introduction

The otoliths of teleostean fishes are calcareous structures composed of aragonite crystals. Each individual possesses three pairs of otoliths in the inner ear, the largest of which are the sagittae. The sagittae are the most variable between species (Platt & Popper 1981). Morphology and morphometrics of sagittae have been used in trophic studies and in identification of populations or species (Saetersdal 1953, Templeman & Squire 1956, Botha 1971, Messieh 1972, Beamish 1979, Yefanov & Khorevin 1979), and to determine ages (Menon 1950, Boehlert 1985). Since the morphometry of otoliths is used for these different purposes, it is important to determine the factors that affect otolith variability.

Studies of morphology, especially of the outline shape and of the sulcus acusticus, found that the shape of otoliths is genetically determined and reflects phylogenetic relationships (Schmitt[1], Gaemers 1976, Nolf & Steurbaut 1989, Lombarte et al. 1991). However, morphology is not only directly related to genotype, but there is a strong variability related to environmental factors (Aldrich 1989). Thus, Wilson (1985) indicated that otolith growth and shape in abyssal fish is affected by undersaturation of the carbonates (this effect is produced by the low temperatures and high pressures of the abyssal habitat).

In this paper we investigate: (1) whether there is an environmental effect over otolith growth above the undersaturation levels, and therefore, whether this effect is independent of the carbonate saturation, (2) whether there exists a dual regulation (genetic and environmental) over the growth of the otoliths, in order to determine how each factor acts on otolith morphology. We analyze the intra- and interspecific growth variability of the sagitta among

---

[1] Schmitt, W. 1969. The otoliths as a means for differentiation between species of very similar appearance. Proc. Symp. Ocean. Fish. Resources of Sea tropical Atlantic, FAO and OUA: 339–396.

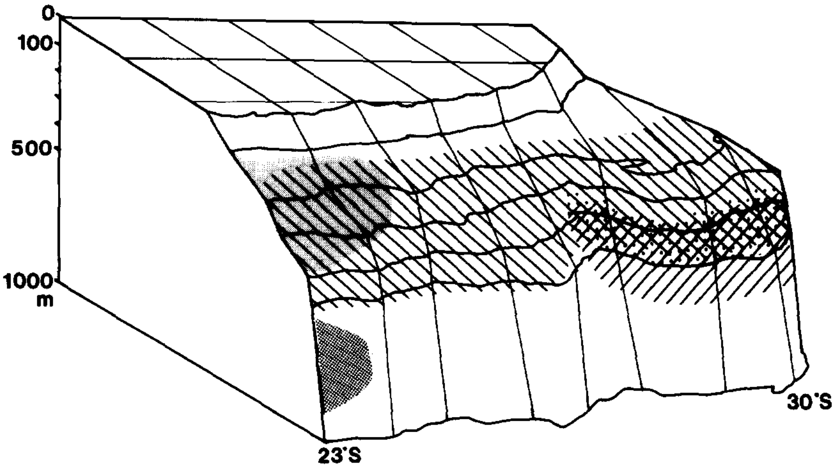

Fig. 1. Distribution of 5 species of the genus *Coelorhynchus* in SE Atlantic waters off Namibia. □ *C. coelorynchus,* ▧ *C. fasciatus,* ▨ *C. occa,* ⊡ *C. parallelus,* and ▩ *Coelorhynchus* sp.

closely phylogenetically related species using morphometric measurements. Depth/habitat effects were examined in the genus *Coelorhynchus* (Macrouridae) from the waters off Namibia (SE Atlantic) in five species which live above the carbonate undersaturation level. Six species from the genus *Merluccius* (Merluccidae), which have a worldwide distribution, were selected to study the relationships between otolith size and environmental factors. In a previous study, the otolith shape variability of these species of the genus *Merluccius* was analyzed independently of the otolith size. To accomplish this, the outlines of the otoliths were broken down numerically and classified according to numerical taxonomic methods (Lombarte & Castellón 1991).

Table 1. Distribution, length range (TL), and sample size of intraspecific and interspecific analyses of the species of the genus *Merluccius* studied.

Species	Geographic distribution	TL (cm)	Sample size	
			intra	inter
M. bilinearis	NW Atlantic	15–50	27	10
M. capensis	SE Atlantic	15–80	239	10
M. gayi	SE Pacific (Chile)	8–71	13	8
M. gayi	SE Pacific (Peru)	11–76	24	7
M. merluccius	NW Mediterranean	6–78	74	13
M. paradoxus	SE Atlantic	15–85	225	13
M. productus	NE Pacific (Canada)	37–69	19	6
M. productus	NE Pacific (USA)	18–74	23	8

Materials and methods

The six species of the genus *Merluccius* selected were: *M. productus* (Ayres, 1855), *M. gayi* (Guichenot, 1848), *M. bilinearis* (Mitchill, 1814), *M. merluccius* (Linnaeus, 1758), *M. capensis* Castelnau, 1861 and *M. paradoxus* Franca, 1960. The length range and the geographical distribution of each species is shown in Table 1.

The five species of the genus *Coelorhynchus* selected were *C. coelorhynchus* Risso, 1810, *C. fasciatus* (Günther, 1878), *C. occa* (Goode & Bean, 1886), and *C. parallelus* (Günther, 1877). The fifth species, *Coelorhynchus* sp., was well differentiated from the other species of this genus, but it was not possible to identify it to species level (possibly *C. flabellispinis*). The depth distribution range is different for all the species considered (Turón et al. 1986, Table 2, Fig. 1).

One and two dimensional measures of otoliths were obtained using a digital image-processing system. Such systems have been used in previous biometric studies of otoliths with good results, in terms of measurement uniformity and accuracy, particularly in the case of two dimensional measurements (Lombarte 1992). The outline of each sagitta and the sulcus acusticus was drawn with the aid of a camera lucida and a binocular microscope, and the resulting image was recorded using a video camera, digitized, and calibrated in square millimeters. The image analyzing system used was a high-resolution video camera and a VINIX digital processor equipped with a CYTIX morphometric and quantification package.

The following measurements were taken on each otolith: maximum sagitta length (mm), maximum sagitta height (mm), areas of the sagitta and the sulcus acusticus (mm^2), perimeters of the sagitta and sulcus acusticus (mm) (Fig. 2). Sagitta weight (mg) was also determined.

To carry out the statistical analyses, fish body size and allometry effects were avoided by normalizing all measurements to a standard body size, taking into account the allometric relationships. For each of the seven otolith measurements (2 linear lengths, 2 perimeter lengths, 2 surfaces and 1 weight) the allometric relationship with body length of the fish was calculated. For *Merluccius,* the total body length as an independent variable was used. Due to the weakness of the tail of *Coelorhynchus,* the preanal length was used as the independent variable for specimens of this genus. The equation used was the standard $Y = aX^b$, fitted using logarithmic transformation to homogenize residuals. Each measure Y_{ij}, where $i = 1,7$ is the variable and j the individual, is transformed into Z_{ij} according to

$$Z_{ij} = Y_{ij}\left[\frac{X_0}{X_j}\right]^{b_i},$$

where X_j is the body length of the individual j, X_0 is the reference body length, and b_i is the allometric parameter relating the dependent variable Y_i with the independent variable X. Z_{ij} is the value that would measure Y_{ij} if the fish length were X_0, considering its allometric growth and residual. For *Merluccius* 40 cm was used as reference length (X_0), for *Coelorhynchus* the preanal reference length was 8 cm.

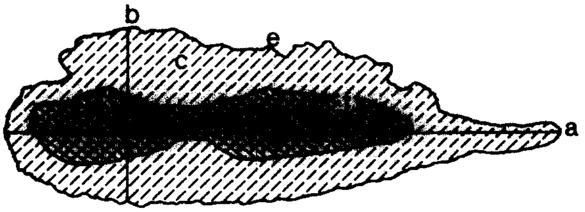

Fig. 2. Measurements taken on each otolith by a digital image-processing system: a – maximum sagitta length (mm), b – maximum sagitta height (mm), c – area of the sagitta (mm^2), d – area of the sulcus acusticus (mm^2), e – perimeter of the sagitta (mm), f – perimeter of the sulcus acusticus (mm).

Table 2. Preanal length range of the individuals studied, depth distribution range, and sample size of intraspecific and interspecific analyses of the species of the genus *Coelorhynchus* from SE Atlantic.

Species	Preanal length range (cm)	Depth range (m)	Sample size	
			intra	inter
C. coelorhynchus	6–9	100–350	10	10
C. fasciatus	2–13	150–600	41	10
C. occa	5–9	350–700	10	9
C. parallelus	3–12	375–475	38	9
Coelorhynchus sp.	6–16	600–900	10	10

Standardized weights of otoliths from *Coelorynchus* and *Merluccius* of SE Atlantic (off Namibia) were employed to study the relationship between size and temperature. The bottom temperature of each trawl was either directly measured with a CTD device after each trawl or estimated after Shannon (1985) and Masó & Manríquez (1987).

Results

Intraspecific variability

For each species, all allometric relationships between otolith measurements and size of fish were calculated (Table 3, 4). The correlation coefficients and standard errors of b are within expected ranges. The majority of allometries obtained were negative. *Merluccius merluccius* yielded allometric values near isometry. The only examples showing positive allometry were the length of the sagitta of *M. bilinearis* and the area and the perimeter of the sulcus of *M. merluccius.*

Interspecific variability

Two principal components analyses (PCA) on correlation matrices of the seven standardized measurements of otoliths are presented to analyze interspecific variability. One was applied to otolith variability in the sympatric species of Macrouridae, the second was used to study otolith variability in *Merluccius* spp. In all PCAs only the first and second axes are presented since the third, and following axes, never have eigenvalues greater than 1, so they explain less variance than the first two variables (Table 5). The axes were not rotated.

Otolith size variability in the genus Coelorhynchus

PCA was performed on standardized data from a total of 48 otoliths from 5 species of *Coelorhynchus*. The first component (accumulating 85.4% of total inertia) placed the otoliths according to their relative size (Fig. 2). *C. coelorhynchus* and *C. fasciatus* have a large relative otolith size, *C. parallelus* has an intermediate size, and *C. occa* and *Coelorhynchus* sp. a small size. The second component (6.8%) ordered the otoliths according to more or less elongated shape. Rounded otoliths, as in *C. coelorhynchus* and *C. occa,* have positive values, whereas elongated otoliths (*C. fasciatus* and *Coelorhynchus* sp.) have negative values (Fig. 3).

Otolith size variability in the genus Merluccius

A total of 75 otoliths from 6 species of *Merluccius* were analyzed. Analysis of the standardized varia-

Table 3. a and b parameters for the equation $Y = aX^b$, and standard error of b (σ). x = total length of the individual in cm and y each of the biometric variables of the otoliths for the following species of *Merluccius:* MBI *M. bilinearis,* MCA *M. capensis,* MGG *M. gayi* from Chile, MGP *M. gayi* from Perú, MME *M. merluccius,* MPA *M. paradoxus,* MPC *M. productus* from Canada, MPU *M. productus* from USA.

		MBI	MCA	MGG	MGP	MME	MPA	MPC	MPU
Sample size		27	239	13	24	74	225	19	23
length	a	0.47	0.76	0.69	0.63	0.51	0.72	0.58	0.69
sagitta	b	1.01	0.83	0.86	0.90	0.98	0.82	0.90	0.86
(mm)	σ	0.03	0.01	0.02	0.02	0.01	0.01	0.06	0.02
height	a	0.62	0.42	0.40	0.44	0.27	0.43	0.70	0.77
sagitta	b	0.62	0.73	0.78	0.74	0.92	0.63	0.62	0.58
(mm)	σ	0.03	0.01	0.02	0.03	0.01	0.01	0.09	0.04
area	a	0.25	0.22	0.20	0.20	0.09	0.22	0.38	0.44
sagitta	b	1.55	1.57	1.62	1.62	1.90	1.51	1.43	1.39
(mm^2)	σ	0.05	0.01	0.03	0.04	0.02	0.01	0.11	0.06
perimeter	a	1.29	2.04	1.89	1.77	1.29	2.03	1.78	1.95
sagitta	b	0.98	0.82	0.85	0.87	0.98	0.81	0.86	0.83
(mm)	σ	0.03	0.03	0.02	0.02	0.01	0.03	0.05	0.02
area	a	0.05	0.04	0.04	0.03	0.01	0.03	0.04	0.06
sulcus	b	1.67	1.71	1.80	1.80	2.23	1.72	1.75	1.63
(mm^2)	σ	0.10	0.02	0.03	0.02	0.06	0.02	0.21	0.09
perimeter	a	1.19	1.20	1.10	1.23	0.51	1.44	1.23	1.47
sulcus	b	0.89	0.88	0.91	0.87	1.15	0.83	0.87	0.82
(mm)	σ	0.05	0.04	0.01	0.04	0.01	0.04	0.10	0.03
weight	a	0.05	0.10	0.03	0.03	0.01	0.11	0.07	0.14
sagitta	b	2.18	1.97	2.32	2.32	2.59	1.87	2.01	1.86
(mg)	σ	0.06	0.02	0.06	0.06	0.02	0.02	0.18	0.10

bles showed the first component accumulating 79.5% of the system inertia. The ordination obtained can be explained according to interspecific size differences (Fig. 4). The species with the largest otoliths (*M. merluccius*) was found to be associated with the most positive values; species with smaller otoliths (*M. paradoxus* and *M. productus*) were associated with the most negative values. *M. bilinearis, M. capensis* and *M. gayi* have intermediate otolith sizes and were placed in the intermediate values. The second axis (with 10.7% of the inertia) separates *M. bilinearis* from the rest of the species (Fig. 3). We interpret this second axis as resulting from the height/length otolith relationship, since the otoliths of *M. bilinearis* are longer than those of other species of the genus *Merluccius*. The other four species appear in mixed clusters. No clear structure can be seen in this mixture, either among species or between different geographical populations of the same species (e.g. *M. gayi* and *M. productus*).

Table 4. a and b parameters for equation $Y= aX^b$, and standard error of b (σ). x= preanal length of the individual in cm and y each of the biometric variables of the otoliths for the following species of *Coelorhynchus:* CCO *C. coelorhynchus,* CFA *C. fasciatus,* COC *C. occa,* CPA *C. parallelus,* CSP *Coelorhynchus* sp.

		CCO	CFA	COC	CPA	CSP
Sample size		10	41	10	38	10
length	a	2.00	2.48	2.33	2.62	2.27
sagitta	b	0.75	0.71	0.60	0.58	0.60
(mm)	σ	0.16	0.03	0.08	0.04	0.04
height	a	1.49	1.67	1.44	1.43	1.42
sagitta	b	0.68	0.59	0.61	0.64	0.61
(mm)	σ	0.12	0.02	0.06	0.05	0.04
area	a	1.60	2.84	2.19	2.61	2.15
sagitta	b	1.57	1.32	1.24	1.23	1.21
(mm^2)	σ	0.28	0.05	0.10	0.08	0.09
perimeter	a	6.11	6.55	3.8.69	6.14	
sagitta	b	0.71	0.73	0.91	0.63	0.63
(mm)	σ	0.14	0.04	0.19	0.04	0.05
area	a	0.20	0.46	0.51	0.63	0.37
sulcus	b	1.93	1.50	1.13	1.10	1.36
(mm^2)	σ	0.35	0.07	0.20	0.10	0.14
perimeter	a	3.39	3.99	3.72	4.33	2.27
sulcus	b	0.82	0.58	0.67	0.63	0.60
(mg)	σ	0.15	0.03	0.11	0.07	0.05
weight	a	1.14	2.35	0.23	2.88	0.16
sagitta	b	2.26	1.87	0.94	1.58	1.12
	σ	0.34	0.07	0.18	0.07	0.05

In both analyses (*Coelorhynchus* and *Merluccius*) the individuals (otoliths) were separated first according to relative size. Relative sizes can be interpreted as particular characteristics of these species.

Relationship between relative weight and temperature

The relationship between the standardized weight of otoliths and temperature for *Coelorhynchus* showed a significant relationship (Fig. 5a) (r^2= 0.63; a= −9.50± 16.47; b= 13.47± 1.01). The relative weight increased with temperature. *C. coelorhynchus,* which lives in the warmest waters, has the greatest relative size of otoliths, and *Coelorhynchus* sp., which lives in the coldest waters has the smallest otoliths. Similar relationships were observed in *Merluccius capensis* and *M. paradoxus* from Namibia (Fig. 5b) (r^2= 0.64; a= 41.45± 13.89; b= 9.15± 1.37).

Discussion

The decrease in relative otolith size with increasing body size appears to be common within the order Gadiformes, to which *Merluccius* and *Coelorhynchus* belong (Saetersdal 1953, Beamish 1979, Frost & Lowry 1981, Wilson 1985, Lombarte & Morales-Nin 1989, Lombarte 1992). Campana (1990) suggests that the decrease in otolith growth rate is related to the decrease in body growth rate with in-

Table 5. Sample size and accumulated percentages in the first, second and third axes of the CPAs.

	Sample size	Axis 1	Axis 2	Axis 3
Merluccius	75	79.48	90.18	95.06
Coelorhynchus	49	85.39	92.23	95.94

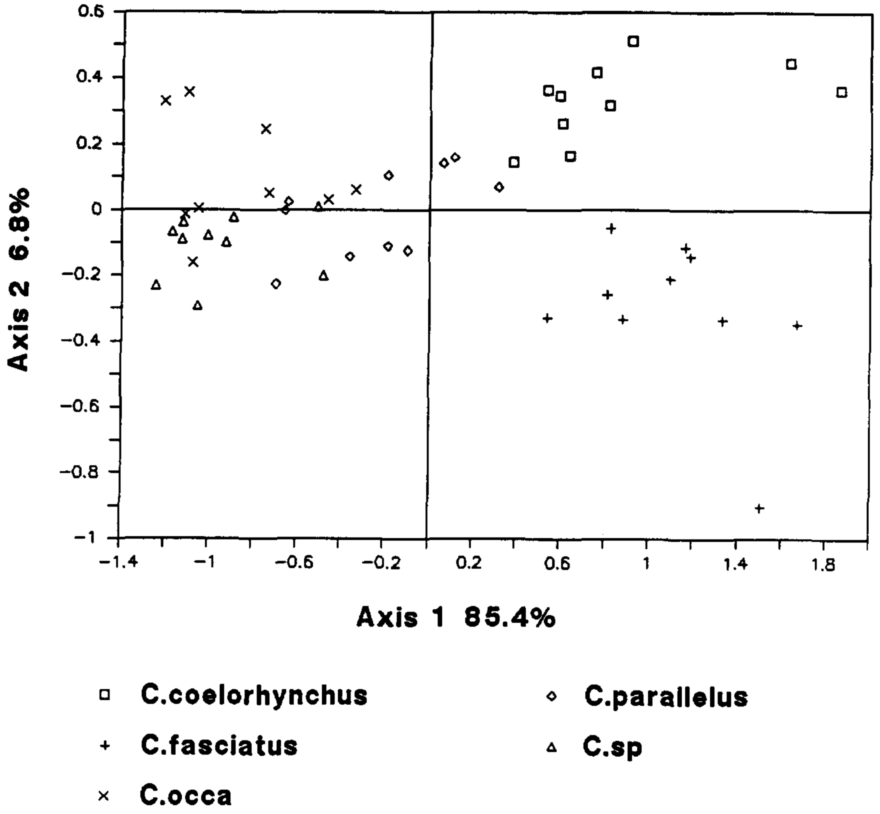

Fig. 3. Representation of the variability of 49 sagittae of *Coelorhynchus* from Namibia, in the first two principal components.

creasing age, but it is unlikely that growth rate is the only variable which can influence relative otolith size. Since larger fish of these genera live in deeper water than smaller ones (Macpherson & Duarte 1991), there may be environmental influences on otolith growth rate. Thus, *M. merluccius* from the Mediterranean Sea (the only species studied herein with an otolith growth rates near to isometry in relation with body growth), mainly inhabits depths of between 100 and 400 m, where temperatures remain fairly constant between 13° C–14° C (Salat & Font 1987).

A decrease of otolith relative size with increasing depth of capture, as seen in individuals within a given species (intraspecific variability), can also be observed between species (interspecific variability). The distribution of otolith sizes in the species of *Coelorhynchus* in the first component showed interspecific variability of size that followed the depth distribution (Fig. 3, Table 2). Relationships between depth and specific otolith size were also found in abyssal macrourids (Wilson 1985).

The decrease of temperature with increasing habitat depth seems to be an important factor regulating the growth of otoliths (Wilson 1985). Additionally, the otolith growth rates continue to increase above the temperatures of maximum somatic growth (Mosegaard et al. 1988). Gauldie (1991) also found a linear relationship between average microscopic growth increment width and temperature. Our results corroborate the relationship between otolith growth and temperature. In the SE Atlantic the relative size of the otoliths of *Coelorhynchus* and *Merluccius* increased with increasing bottom water temperature.

In other taxa, such as foraminifera, brachiopods, shelled molluscs and echinoderms, a similar relationship between temperature and growth in calcium structures exists. Species which live in cold waters have smaller, thinner and less sculptured shells

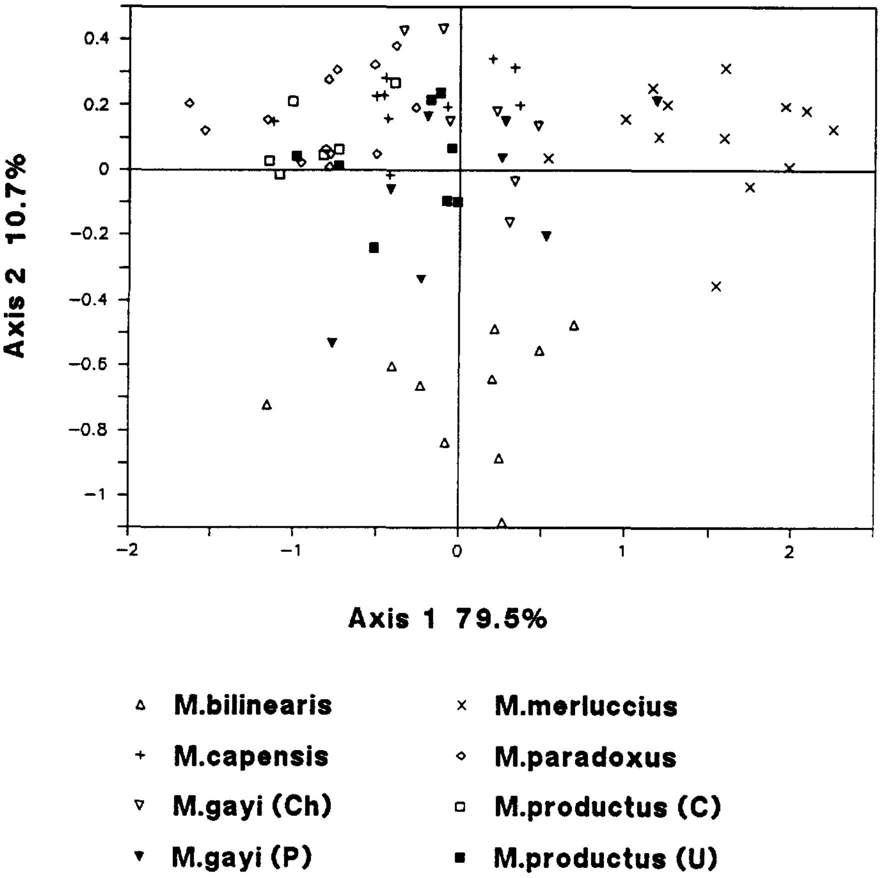

Fig. 4. Representation of the variability of 75 sagittae of *Merluccius*, in the first two principal components.

than warmer water species (Arnaud 1974, Vermeij 1978).

Otolith growth has a different response to environmental factors than somatic growth. The deposition of material in the otolith is an extracellular process which is under different physiological control than somatic cellular growth (Simkiss 1974). The chemical processes involved in otolith growth are more directly affected by temperature than the metabolic processes involved in body growth (Casselman 1990).

For fish inhabiting carbonate-saturated levels, like *Merluccius* and *Coelorhynchus* (e.g. in the North Atlantic), the depth of the undersaturation level was roughly at 2000m (Milliman 1974). The most plausible explanation for the decrease of otlith relative size with increasing depth is a slowing down of the chemical and metabolic processes involved in the incorporation of calcium carbonate. This slowing was produced by the reduction of water temperature (Vermeij 1978). An increase in the proportion of carbonates and trace elements is found in otoliths as temperature increases (Woodhead 1968, Gauldie et al. 1980, Radtke & Targett 1984, Morales-Nin 1987, Kalish 1989). A similar relation between temperature and the concentration of organic constituents of otoliths found in blood has been reported (Mugiya 1964).

Application of multivariate analysis to characteristics such as length, height, perimeter or area makes it possible to interpret differences in relation to the size of an object, but not in relation to its form because there is not a clear relation between measure and shape (Lefebvre 1976). The results of the PCA of *Merluccius* otoliths (Fig. 3) showed a similar relationship between size and temperature as seen in *Coelorhynchus*. *M. merluccius* from the Northwestern Mediterranean, whose otoliths have

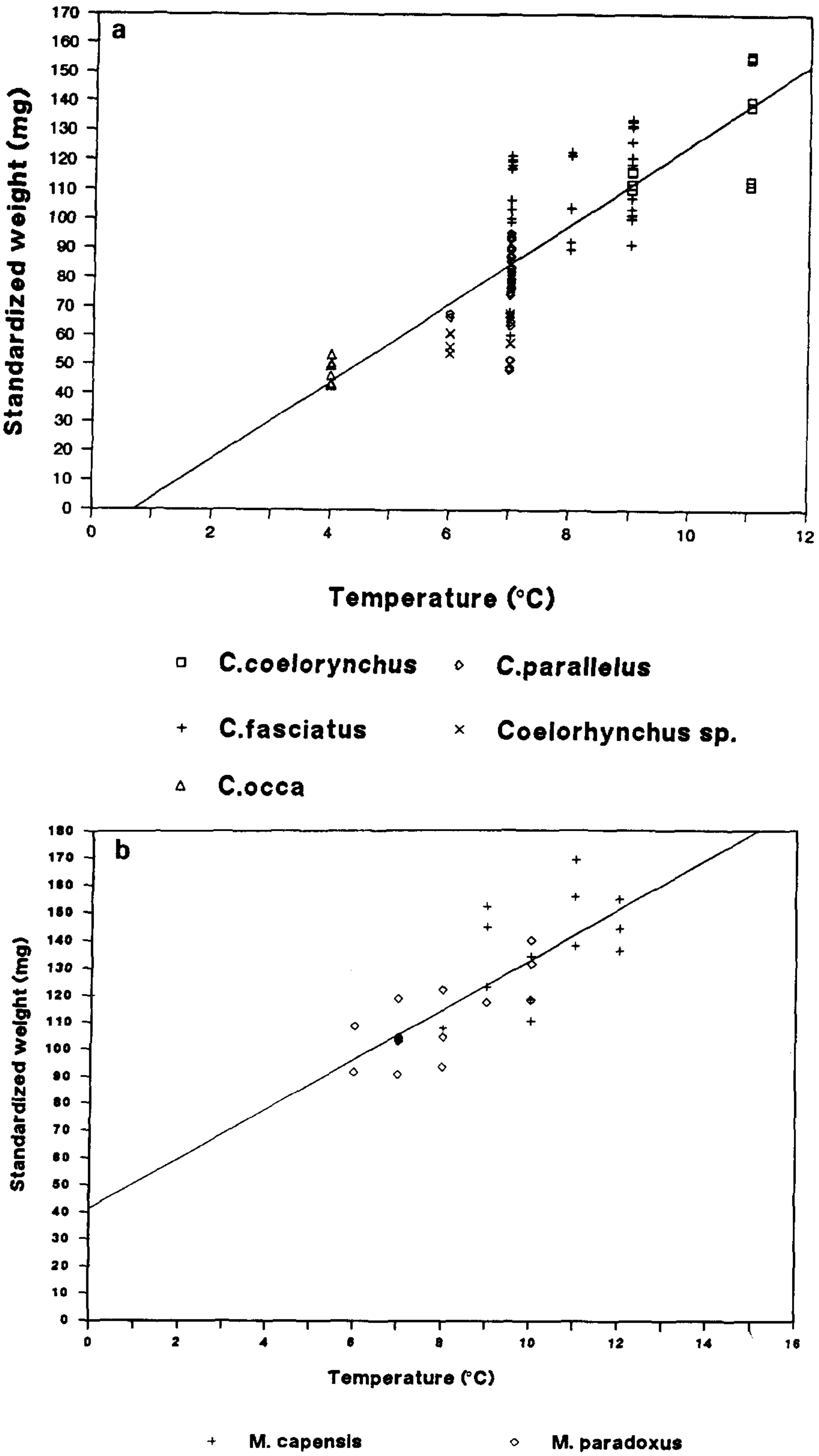

Fig. 5. Relationship between the standardized weight of the sagittal otolith (OW, mg) and temperature (T°C) in SE Atlantic: a – in *Coelorhynchus* (OW = –9.5+ T13.47), b – in *Merluccius* (OW = 41.45+ T9.15).

the largest relative size, live in the warmest waters (13 to 14° C) (Salat & Font 1987). *M. gayi, M. bilinearis* and *M. capensis* species with intermediate otolith relative sizes live in waters with temperatures of 7° C–12° C. *M. paradoxus* and *M. productus*, which live in the coldest waters (4°–10° C) (Botha 1971, Inada 1981) have the smallest otoliths. Similar relationships between geographical variations of temperature and otolith sizes have been found in other teleosts (Yefanov & Khorevin 1979, Dawson 1991). Present results dealing with otolith relative size do not show any strong relationship between otolith size and interspecific genetic distance. Thus, *M. productus* and *M. paradoxus*, which have the smallest relative size, belong to two differentiated phylogenetic lines within the genus *Merluccius* (Inada 1981, Ho 1990).

When otoliths of the same species of *Merluccius* were analyzed using methods of classifying shapes (that do not depend on such measures, but rather on the outline of the object per se), the groupings obtained were different (Lombarte & Castellón 1991). The otoliths from individuals larger than 20 cm were classified into two geographic and phylogenetic groups: an Euro-African group (*M. merluccius, M. capensis* and *M. paradoxus*) with a caudal tip rounded, and an American group (*M. bilinearis, M. productus* and *M. gayi*) with an elongated caudal tip.

We suggest that otolith development occurs under dual regulation: genetic conditions regulate the form of the otolith, while environmental conditions, mainly temperature in carbonate-saturated waters, regulate the quantity of material deposited during the formation of the otolith.

Acknowledgements

We thank P. Abelló, B. Morales-Nin and M.P. Olivar for their valuable comments, J. Masoliver for help with digital analysis techniques, D.E. Garland, J.J. Hunt, G.A. McFarlane, J.L. Butler, and D. Flescher for donating the otoliths used in this study, and N. Mellen for improving the English version of the manuscript.

References cited

Aldrich, J.C. 1989. The world beyond the species, an argument for greater definition in experimental work. pp. 3–8. *In:* J.C. Aldrich (ed.) Phenotypic Responses and Individuality in Aquatic Ectotherms, Japaga, Ashford.

Arnaud, P.M. 1974. Contribution à la bionomie marine benthique des régions antarctiques et subantarctiques (Terre Adelie). Bull. Inst. Océanogr. Monaco 66: 3–24.

Beamish, R.J. 1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can. 36: 141–151.

Boehlert, G.W. 1985. Using objective criteria and multiple regression models for age determination in fishes. U.S. Fish. Bull. 83: 103–117.

Botha, L. 1971. Growth and otolith morphology of the Cape hakes *Merluccius capensis* Cast. and *Merluccius paradoxus* Franca. Invest. Rep. Div. Sea Fish. S. Afr. 97: 1–32.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47: 2219–2227.

Casselman, J.M. 1990. Growth and relative size of calcified structures of fish. Trans. Amer. Fish. Soc. 119: 673–688.

Dawson, W.A. 1991. Otolith measurements as a method of identifying factors affecting first-year growth and stock separation of mackerel (*Scomber scombrus* L.). J. Cons. int. Explor. Mer. 47: 303–317.

Frost, K.J. & U.F. Lowry. 1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationship. U.S. Fish. Bull. 79: 187–192.

Gaemers, P.A.M. 1976. New concepts in the evolution of the Gadidae (Vertebrata, Pisces), based on their otoliths. Mededelingen van de Werkgroep voor Tertiaire and Kwartaire Geologie 13: 3–22.

Gauldie, R.W. 1991. The morphology and periodic structures of the otolith of the chinook salmon (*Oncorhynchus tshawytscha*), and temperature-dependent variation in otolith microscopic growth increment width. Acta Zool. 72: 159–179.

Gauldie, R.W., E.J. Graynoth & J. Illingworth. 1980. The relationships of the iron content of some fish otoliths to temperature. Comp. Biochem. Physiol. A. 66: 19–24.

Ho, J. 1990. Phylogeny and biogeography of hakes (*Merluccius*; Teleostei): a cladistic analysis. U.S. Fish. Bull. 88: 95–104.

Inada, T. 1981. Studies on the merlucciid fishes. Bull. Far Seas Fisheries Research Laboratory 18: 1–172.

Kalish, J.M. 1989. Otoliths microchemistry: validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132: 151–178.

Lefebvre, J. 1976. Introduction aux analyses statistiques multidimensionelles. Masson, Paris. 259 pp.

Lombarte, A. 1992. Changes in otolith area: sensory area ratio with body size and depth. Env. Biol. Fish. 33: 405–410.

Lombarte, A. & A. Castellón. 1991. Inter and intraspecific otolith variability in the genus *Merluccius* as determined by image analysis. Can. J. Zool. 69: 2442–2449.

Lombarte, A. & B. Morales-Nin. 1989. Crecimiento de *Nezumia aequalis* y *Coelorhynchus fasciatus* (Pisces: Macrouridae) en aguas de Namibia. Coll. scient. Pap. int. Commn SE. Atl. Fish. 16: 191–198.

Lombarte, A., J. Rucabado, J. Matallanas & D. Lloris. 1991. Taxonomia numerica de Notothenidae en base a la forma de los otolitos. Sci. Mar. 55: 413–418.

Macpherson, E. & C.M. Duarte. 1991. Bathymetric trends in demersal size: is there a general relationship? Mar. Ecol. Prog. Ser. 71: 103–112.

Masó, M. & M. Manríquez. 1987. Preliminary hydrological results of the 'Spanish Namibian Environmental Cruise' SNEC-II. Coll. scient. Pap. int. Commn SE. Atl. Fish. 14: 113–128.

Menon, M.O. 1950. The use of bones other than otoliths in determining the age and growth rate of fishes. J. Cons. Explor. Mer. 16: 311–335.

Messieh, S.N. 1972. Use otoliths in identifying herring stocks in the Southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Board Can. 29: 1113–1118.

Milliman, J.D. 1974. Marine carbonates. Springer Verlag, Berlin. 375pp.

Morales-Nin, B. 1987. The influence of environmental factors on microstructure of otoliths of three demersal fish species caught off Namibia. pp. 225–262. *In:* A.I.L. Payne, J.A. Gulland & K.H. Brink (ed.) The Benguela and Comparable Ecosystems, S. Afr. J. mar. Sci. 5.

Mosegaard, H., H. Svedang & K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45: 1514–1524.

Mugiya, Y. 1964. Calcification in fish and shell-fish. III. Seasonal occurrence of a prealbumin fraction, corresponding to the period of opaque zone formation in the otolith. Bull. Jap. Soc. Sci. Fish. 30: 955–967.

Nolf, D. & E. Steurbaut. 1989. Evidence from otoliths for establishing relationships within gadiforms. pp. 89–112. *In:* D.M. Cohen (ed.) Papers on the Systematics of Gadiform Fishes, Science Series, Natural History Museum of Los Angeles County 32.

Platt, C. & A.N. Popper. 1981. Fine structure and function of the ear. pp. 3–38. *In:* W.N. Tavolga, A.N. Popper & R.R. Fay (ed.) Hearing and Sound Communication in Fishes, Springer Verlag, New York.

Radtke, R.L. & T.E. Targett. 1984. Rhythmic structural and chemical patterns in otoliths of the Antarctic fish *Notothenia larseni:* their application to age determination. Polar Biol. 3: 203–210.

Saetersdal, G.S. 1953. The haddock in Norwegian waters. II. Methods in age and growth investigations. Rep. Norwegian Fish. Marine Invest. 10: 1–46.

Salat, J. & J. Font. 1987. Water mass structure near and offshore the Catalan coast during the winters of 1982 and 1983. Ann. Geophys. 198 (5B): 49–54.

Shannon, L.V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanogr. Mar. Biol. Ann. Rev. 23: 105–182.

Simkiss, K. 1974. Calcium metabolism of fish in relation to ageing. pp. 1–12. *In:* T.B. Bagenal (ed.) Ageing of Fish, Unwin Brothers, Old Woking.

Templeman, W. & H.J. Squire. 1956. Relationships of otolith lengths and weights in the haddock *Melanogrammus aeglefinus* (L.) to the rate of growth of the fish. J. Fish. Res. Board Can. 13: 467–487.

Turón, J.M., J. Rucabado, D. Lloris & E. Macpherson. 1986. Datos pesqueros de las expediciones realizadas en aguas de Namibia durante los años 1981 a 1984 (Benguela III a Benguela VII y Valdivia I). Datos Informativos Inst. Inv. Pesq. 17: 1–344.

Vermeij, G.J. 1978. Biogeography and adaptation patterns of marine life. Harvard University Press, Cambridge. 332pp.

Wilson Jr., R.R. 1985. Depth-related changes in sagitta morphology in six macrourid fishes of the Pacific and Atlantic oceans. Copeia 1985: 1011–1017.

Woodhead, P.M.S. 1968. Seasonal changes in the calcium content of the blood of arctic cod. J. mar. biol. U.K. 48: 81–91.

Yefanov, V.N. & L.O. Khorevin. 1979. Distinguishing populations of pink salmon *Oncorhynchus gorbuscha,* by the size of their otoliths. J. Ichthyol. 19: 142–145.