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Age and growth of forkbeard, *Phycis phycis*, in Portuguese continental waters

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The forkbeard, Phycis phycis, *is an important commercial species in Portugal; however, little information is available on its biology. Age and growth of the forkbeard from Portuguese continental waters were studied using 687 otoliths from specimens caught between May 2011 and December 2012. Otoliths were transversally sectioned, and assigned ages were validated by marginal increment analysis and edge analysis, and indices of precision were also calculated to corroborate ageing within and between readers. Validation techniques showed that an annual growth increment is formed every year, corresponding to the succession of an opaque and a translucent growth zone. Specimens ranged from 15.5 to 67.1 cm total length (TL), and their estimated ages ranged between 0 and 18 years. The forkbeard is a relatively slow growing, long lived species, that does not show sexual dimorphism in growth. The von Bertalanffy growth parameters estimated for forkbeard from the Portuguese continental waters were* $L_\infty = 75.14$ *cm TL,* $k = 0.10\ yr^{-1}$ *and* $t_o = -2.09$ *yr.*

Keywords: age, growth, validation, indices of precision, sectioned otoliths, *Phycis phycis*, forkbeard

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INTRODUCTION

Information on the age of individual fish significantly enhances the quality of studies of population characteristics such as growth, recruitment, mortality and reproduction, and it is often a prerequisite for more detailed studies of life history strategies and ecology (Labropoulou & Papaconstantinou, 2000). Most of the studies on age and growth of fish involve the determination of age of specimens by counting of growth increments in hard body parts, usually otoliths. The mechanism that regulates the cyclic deposition of these growth increments in otoliths is not well understood (Beckman & Wilson, 1995), but it is commonly assumed to be related to seasonal variation in somatic growth, spawning, environmental factors and food availability (Boehlert, 1985; Campana, 1999; Morales-Nin & Panfili, 2005).

Interpreting otolith structure and counting annual growth increments underlies the method used for age assignment (e.g. Bagenal, 1974; Pentilla & Dery, 1988; Fowler, 1995). To ensure that the age estimates are accurate, ages assigned to specimens need to be validated (Beamish, 1992; Campana, 2001), since non-validated ages commonly result in seriously biased age estimates (Beamish & McFarlane, 1983, 1995; Lai & Gunderson, 1987). Since growth parameters constitute key input to stock assessment models used to analyse population dynamics in relation to exploitation and management measures (Cailliet *et al.*, 2001; Stewart & Hughes, 2007), biased ageing could lead to less effective fishery management policies (Beamish and McFarlane, 1983; Campana, 2001; Cailliet & Andrews, 2008).

Recent analyses suggest that most fished stocks are fully or over-exploited (Botsford *et al.*, 1997). The most dramatic results of intensive fishing have been the economic collapse of some commercially important stocks such as cod, *Gadus morhua* Linnaeus, 1758, and herring, *Clupea harengus* Linnaeus, 1758 (Beverton, 1990; Myers *et al.*, 1997). One of the challenges for fisheries scientists is the provision of management advice for developing fisheries and for species for which there are limited biological data.

The forkbeard, *Phycis phycis* (Linnaeus, 1766) lies in the category of a developing fishery species, but is already one of the most important gadiform species commercially exploited by the Portuguese fleet in southern north-east Atlantic, together with European hake, *Merluccius merluccius* Linnaeus, 1758, pouting, *Trisopterus luscus* Linnaeus, 1758 and blue whiting, *Micromesistius poutassou* Risso, 1827 (INE, 2013). In Portuguese waters, forkbeard is mainly caught by a longline fishery, with trawl, trammel net and trap fisheries contributing a small percentage of the landings. The fisheries range from coastal waters to offshore seamounts off the mainland and also in the Azores and Madeira archipelagos, reaching a total of 800 t landed per year (INE, 2013). Forkbeard has already attained an important acceptance by final consumers, with its commercial price reaching approximately €9/kg. Although this species has a wide distribution, from the Bay of Biscay to Morocco, south to Cape Verde and also in the Mediterranean Sea (Cohen *et al.*, 1990), little information exists on its biology. In fact, only data from Azorean and Mediterranean waters are available. With regard to age and growth, data obtained from burned sectioned otoliths from fish caught off the Azores showed

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forkbeard to be a relatively slow growing, long lived species (maximum age of 18 years for specimens of 71 cm total length (TL)), with no sexual dimorphism in growth (Abecasis *et al*., 2009). Matić-Skoko *et al.* (2011), using ground otoliths from fishes collected in the south-eastern Adriatic Sea, estimated maximum ages of 5 years for fish of 45.8 cm TL, and these authors stated that forkbeard showed sexual dimorphism in growth, with males reaching a larger size and growing more slowly than females.

The present study investigated age and growth of forkbeard from Portuguese continental waters, the first study on this subject for this area, where forkbeard is an important commercial species. The main goals were (1) to understand the deposition pattern of growth increments in sectioned otoliths of the forkbeard, (2) to validate the assignment of age and (3) to model the growth of the species.

MATERIAL AND METHODS

Sampling

A total of 687 samples of the forkbeard were collected monthly between May 2011 and December 2012 from commercial vessels operating off mainland Portugal (Peniche), using longline (at depths between 220 and 275 m), trawl (up to 310 m depth), trammel net and traps (at 55–90 m depth). TL (to the nearest 0.1 cm), total weight (TW, to the nearest 0.01 g) and sex of each fish were recorded, and the *sagitta* otoliths were removed, rinsed with water, air dried and stored in labelled plastic tubes.

Length-weight relationship

Length–weight relationships are important in fisheries science, notably to raise length–frequency samples to total catch, or to estimate biomass from landings length composition (Morato *et al*., 2001).

The relationship between TL (cm) and TW (g) was calculated using a power function:

$$TW = aTL^b.$$

The Student's *t*-test was used to verify the existence of significant differences between sexes and to test the allometry in growth (Zar, 1996).

Ageing methodology and validation

Right *sagitta* otoliths were transversally sectioned (Bedford, 1983; McCurdy, 1985) with a diamond-tipped saw blade (Labcut 230 Cutting Machine) rotating at 3700 rpm. Slides 0.5 mm thick were mounted in a glass slide with translucent glue, brushed with a 1:1 glycerin-alcohol solution and observed under a stereomicroscope under transmitted light with a 12× magnification. The distances from the nucleus to each successive translucent increment (hereafter referred as nucleus-to-increment distances) and to the otolith edge were measured on the same axis of the ventral face of the sectioned otoliths, using a micrometer eyepiece. The ventral face was chosen since this area showed a larger radius and, thus, a better individualization of the growth increments.

Marginal increment ratio (MIR) (Samamé, 1977) and edge analysis (N = 687) were used to examine the periodicity of growth increment formation and therefore semi-directly validate the frequency of growth increments formation (Panfili and Morales-Nin, 2002). The nucleus-to-increment distances were used to calculate the marginal increment. The edge of the otoliths was classified as opaque (highly calcified, light increments) or translucent (less calcified, dark increments). Mean MIR and standard deviation, and edge type were plotted by month and for both younger (0–4 years) and mature older specimens (5–18 years) to verify periodic trends in growth increment formation. Age at first maturity was used as the criterion for the separation of younger and older specimens (A.R. Vieira, personal observatiom).

Precision

Precision of age assignments (and their reproducibility) within and between readers was evaluated. For this purpose, a random sample of 306 otoliths, covering the length range of the total sample, were read twice, with a lag of four months, by two readers (reader 1, R1, and reader 2, R2).

The average percentage error (APE) (Beamish & Fournier, 1981), the coefficient of variation (CV) (Chang, 1982) and the index of precision (D) (Chang, 1982) were used to compare age readings within and between readers. APE and CV produce similar values (Chang, 1982), but the latter is statistically more rigorous and thus is more flexible (Campana *et al*., 1995). Bias evaluation was based on age bias plots (Campana *et al*., 1995) which allows visualizing deviation of the age readings from the 1:1 equivalence line.

The nonparametric Mann–Whitney U-test (since data did not meet the assumption of normality and homogeneity of variance) was used to compare age assignments within and between readers. The Bowker-type test for symmetry (Bowker, 1948) was applied to investigate the existence of systematic differences on the ages assigned between readers (Hoenig *et al*., 1995).

Growth model

To model the growth of forkbeard, sex-specific length-at-age data were fitted to the von Bertalanffy growth model (von Bertalanffy, 1938). Akaike's information criterion (AIC; Shono, 2000) was used to evaluate the models' adequacy to the model assumptions and the goodness-of-fit. The likelihood ratio tests (Kimura, 1980) were used to evaluate the significance of differences on growth parameters between sexes (Venables & Ripley, 2002). The von Bertalanffy growth model was estimated in R software v.2.15.1.

RESULTS

Length–weight relationship

A total of 687 specimens were sampled: 369 females (53.7%) and 318 males (46.3%). The sex-ratio did not differ significantly from unity ($\chi^2 = 3.64$; df = 1; $P = 0.06$), and total length and total weight were not significantly different between sexes (paired *t*-test, TL: *t*-test = 1.35; df = 685; $P = 0.178$; TW: *t*-test = 1.61; df = 685; $P = 0.109$).

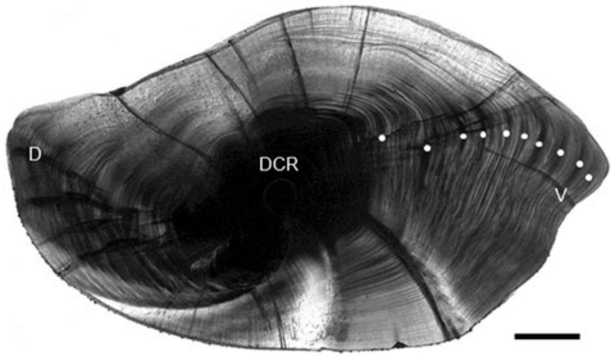

Fig. 1. Right sectioned *sagitta* otolith of a 10 years old forkbeard, *Phycis phycis*, from the Portuguese continental waters, with 52.8 cm TL. Inside the nucleus, the demersal check ring (DCR) is shown. White dots represent the growth increments. D, dorsal face; V, ventral face. Scale bar = 1 mm.

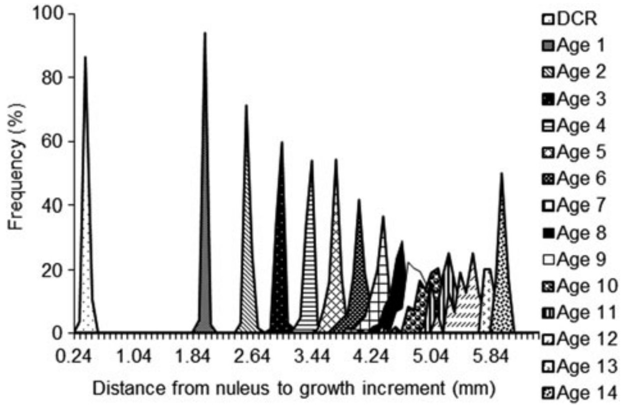

Fig. 2. Frequency distributions of the distances from the nucleus to growth increments of the ages assigned in ventral face of sectioned otoliths of forkbeard, *Phycis phycis*, from the Portuguese continental waters.

The equations that express the length–weight relationship for the forkbeard were:

$$TW = 0.0049TL^{3.2286}(R^2 = 0.98) \text{ for females}$$

and

$$TW = 0.0042TL^{3.2524}(R^2 = 0.99) \text{ for males.}$$

Both females and males of forkbeard showed positive allometric growth (paired *t*-test, females: *t*-test = 6.27; df = 368; $P < 0.001$; males: *t*-test = 6.90; df = 317; $P < 0.001$).

Ageing methodology and validation

In sectioned otoliths of the forkbeard (N = 687, 369 females and 318 males), a regular pattern was visible, with alternate opaque and translucent concentric growth increments deposited around a large opaque nucleus. Inside the nucleus structure, a strongly marked check ring was always evident and appeared, in the ventral face, at 0.41 + 0.03 mm (mean + SD) from the nucleus. The deposition pattern of growth increments varied as the otolith grows: in the region closer to the nucleus, growth increments were wide (typically the first four increments) and afterwards they became thinner and closer together (Figure 1). The first growth increment corresponds to the first well-marked increment visible after the

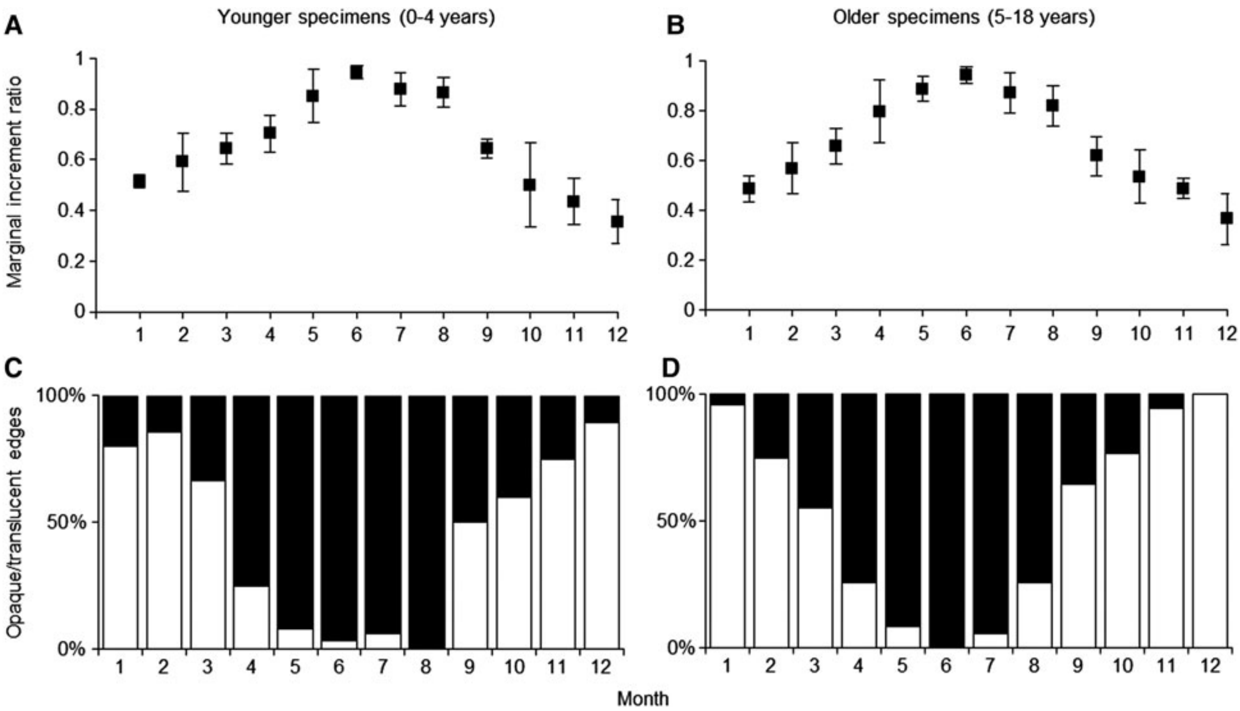

Fig. 3. Monthly evolution of marginal increment ratio in sectioned otoliths of (A) younger (0–4 years) and (B) older (5–18 years) specimens of forkbeard, *Phycis phycis*, from the Portuguese continental waters. Dots are the mean values and whiskers are ± standard deviation. Annual variation pattern of the percentage of opaque and translucent edges in sectioned otoliths of (C) younger (0–4 years) and (D) older (5–18 years) specimens. Black bars are opaque edges and white bars are translucent ones.

otolith nucleus and appeared, in the ventral face, at 2.00 ±0.02 mm (mean ±SD) from the nucleus. Figure 2 shows the level of overlapping of increment deposition range of the first 14 years at the ventral face of sectioned otoliths. The growth increments corresponding to ages 1, 2 and 3 years were completely separated from each other; thereafter the overlap of growth increments increased with fish age.

Marginal increment ratio and proportion of opaque and translucent edges of younger (0–4 years; N = 149) and older specimens (5–18 years; N = 538) are shown in Figure 3. An identical pattern throughout the year could be seen. MIR presented a clear annual pattern of growth increment formation for both younger and older specimens, with the marginal increment showing an increasing trend from January to June and a decreasing trend after June (Figure 3A, B). The highest values of MIR occurred between May and August and the lowest between October and January for both younger and older specimens (Figure 3A, B), an indication that new increments are formed during this period. For both younger and older specimens, opaque edges were more frequent in spring and summer months (April–August), while translucent edges dominated during autumn and winter (October–March) (Figure 3C, D).

Based on the previous results, the assumptions for age assignment of the forkbeard were: (1) an annual growth increment corresponds to the succession of an opaque and a translucent growth zone (validated by MIR and edge type), so age can be assigned by counting translucent zones; and (2) first January is considered to be the birth date since the spawning season of the species occurs in the last quarter of the year (A.R. Vieira, personal observation).

Precision

Both readers aged twice 306 forkbeard otoliths. Indices of precision for age readings within and between readers are presented in Table 1, and the age-bias plots are in Figure 4. For R1, the estimates of APE, CV and D were 1.51%, 1.30% and 0.92%, respectively, reflecting high precision of the age readings. R1 comparative readings showed a total agreement of 81%. Ages assigned by R1 showed non-significant differences between the 1st and 2nd readings (Mann–Whitney U test: $U = 234947$; $P = 0.815$). For R2 the APE, CV and D indices were 2.77%, 2.52% and 1.96%, respectively. The comparative readings of this reader showed a total agreement of 86%. Ages assigned by R2 showed non-significant differences

Table 1. Indices of precision for age readings of forkbeard, *Phycis phycis*, from the Portuguese continental waters, within and between readers. R1 = reader 1; R2 = reader 2.

Index	Comparison		
	Within reader		Between readers
	R1	R2	
APE (%)	1.51	2.77	1.80
CV (%)	1.30	2.52	1.65
D (%)	0.92	1.96	1.17
Total agreement (%)	81	86	82
Agreement (0 ± 1) (%)	100	99	100

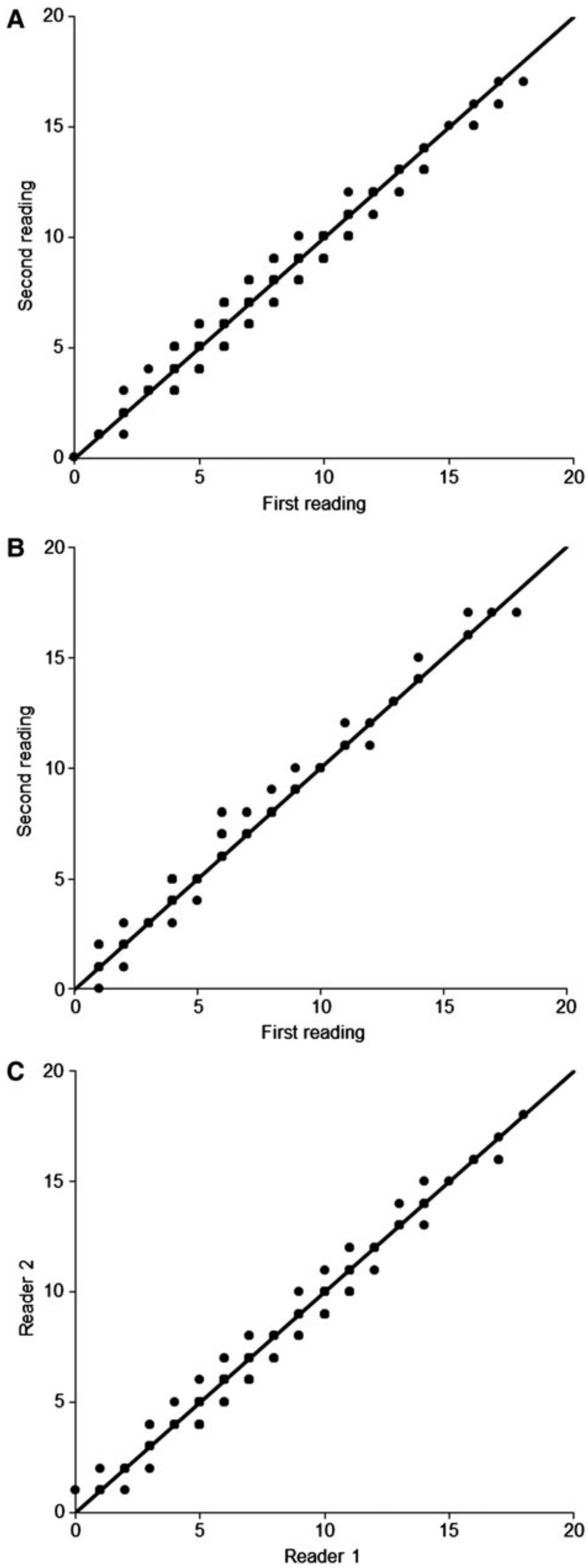

Fig. 4. Age bias plots for the readings comparisons within readers: (A) reader 1, (B) reader 2 and (C) between readers, for forkbeard, *Phycis phycis*, from Portuguese continental waters. The 45° line represents 100% agreement.

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Table 2. Age–length key for the forkbeard, *Phycis phycis*, from the Portuguese continental waters for the period 2011–2012. n, number of fish; TL, mean, mean total length; SD, standard deviation.

Length class (cm)	Age (yr)																			Total
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
15	1																			1
17		1																		1
19		2																		2
21		4	2																	6
23		1	5																	6
25			14	2																16
27			3	15																18
29			2	13	1															16
31				13	7															20
33				2	22															24
35					29	5														34
37					10	36														46
39					1	38	7	1												47
41						16	38													54
43							48	22												70
45						1	10	40	6											57
47							1	26	24											51
49								6	14	30	7									57
51									2	9	24	4								39
53										4	20	21	1							46
55										1	7	22	1							31
57											1	1	8							10
59													2	9	4					15
61														6	5					11
63															2					2
65																	3	3		6
67																			1	1
n	1	8	26	45	70	96	104	95	46	44	59	48	12	15	11	–	3	3	1	687
TL mean	15.5	21.5	25.9	29.8	35.1	39.3	43.1	46.2	48.5	51.0	53.1	54.8	57.4	60.6	61.6	–	65.9	65.7	67.1	–
SD	0.00	1.87	1.78	2.04	1.80	1.80	1.50	1.63	1.43	1.39	1.67	1.34	1.43	1.10	1.25	–	0.46	0.81	0.00	–

Table 3. Summary of the von Bertalanffy growth parameters estimated for forkbeard, *Phycis phycis*, from the Portuguese continental waters. Standard error of parameters is given in parentheses. L_∞, asymptotic length; k, growth rate; t_0, hypothetical age when L = 0.

	L_∞ (cm)	k (yr^{-1})	t_0 (yr)	n	R^2	AIC
All data	75.14 (1.11)	0.10 (0.00)	−2.09 (0.11)	687	0.94	2688.90
Females	75.56 (1.74)	0.10 (0.00)	−2.19 (0.18)	369	0.93	1473.35
Males	74.84 (1.44)	0.10 (0.00)	−2.00 (0.14)	318	0.95	1219.60

between age readings (Mann–Whitney U test: $U = 11041$; $P = 0.781$).

The indices of precision between readers were 1.80%, 1.65% and 1.17% for APE, CV and D, respectively, reflecting a high precision. A total agreement of 82% was allocated. Only one difference between readers higher than ±1 year was assigned (Figure 4C). The Mann–Whitney test proved that there were non-significant differences between ages assigned by R1 and R2 (Mann–Whitney U test: $U = 46158.5$; $P = 0.763$). There was also no evidence of systematic disagreement for ages assigned between R1 and R2 (test of symmetry; $\chi^2 = 24.20$, df = 16, $P = 0.085$).

Ages assigned by R1 were used to fit the von Bertalanffy growth model to the length-at-age data of forkbeard due to the higher precision obtained and previous experience in ageing gadiform species (see Vieira *et al.*, 2013).

Growth model

For ageing estimate all 687 otoliths were used. Forkbeard females caught off the Portuguese continental coast ranged between 18.8 and 66.6 cm TL and were aged by sectioned otoliths from 1 to 17 years. Males ranged from 15.5 to 67.1 cm TL and were aged from 0 to 18 years. The age–length key is shown in Table 2. The estimated von Bertalanffy growth parameters for forkbeard from the Portuguese continental waters are presented in Table 3. No significant differences between males and females growth parameters were found (Likelihood ratio test: $\chi^2 = 2.71$, df = 3, $P = 0.439$) and the von Bertalanffy growth curve is presented in Figure 5. It is worthwhile to mention that 50% of the maximum observed total length is attained at age 4 years.

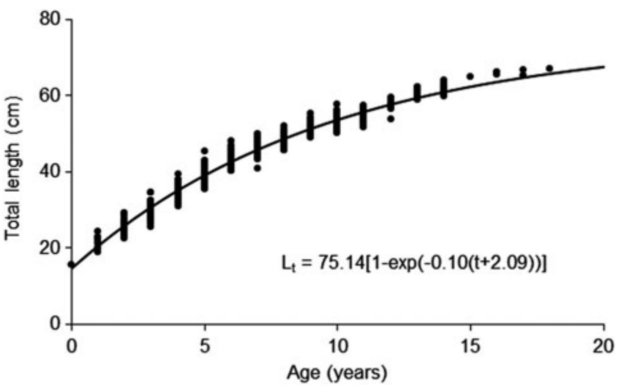

Fig. 5. The von Bertalanffy growth model for the entire sample ($n = 687$) of forkbeard, *Phycis phycis*, from the Portuguese continental waters, for the period 2011–2012.

DISCUSSION

Age estimation in gadiform fish has been known to present some difficulties due to otolith thickness, which in most species requires special processing methods so that growth increments become visible (Morales-Nin *et al.*, 1998; Deree, 1999). Sectioning has been considered a suitable technique for dense gadiform otoliths, allowing faster and better otolith analysis (e.g. Morales-Nin *et al.*, 1998; Deree, 1999; Casas & Piñeiro, 2000; Vieira *et al.*, 2013). Regarding the forkbeard, this study shows that sectioned otoliths are a precise method for age estimation, since the values of precision indices obtained both within and between readers were very low; much lower than those adopted in the literature (CV < 7.6% and APE = 5.5%) (Campana, 2001). Other studies were published recently on age and growth of forkbeard from Azorean waters (Abecasis *et al.*, 2009) and the Adriatic Sea (Matić-Skoko *et al.*, 2011). Burning and sectioning otoliths was considered a precise procedure for age estimation of this species from Azorean waters by Abecasis *et al.* (2009); however, with this technique, the authors obtained 9.5% of unreadable otoliths. Matić-Skoko *et al.* (2011) used both otolith grinding and morphometric otolith parameters (length, width and weight) to estimate age of forkbeard from the Adriatic Sea, and they suggested that the most precise age estimator was the otolith weight linear model, instead of otolith growth increment counting. These otolith weight models are cheaper and quicker than otolith analysis (Cardinale *et al.*, 2000). However, they still require ageing techniques to achieve an appropriate regression between age estimated by otolith analysis and otolith weight (to reduce any bias that could modify the estimated age-structure and affect the analysis) (Lai & Gunderson, 1987; Bradford, 1991) and a recalibration for each new fish sample (Cardinale *et al.*, 2000; Francis & Campana, 2004). For these reasons, these models can be advantageous for ageing species with high commercial interest and with a large sample (thousands) of otoliths for analysis (e.g. Atlantic cod, *Gadus morhua*, Cardinale *et al.*, 2000), but seem to be less effective for analysing a smaller sample (hundreds) of fish.

Age validation is crucial in age and growth studies. It is common to underestimate ages of long-lived species and thus overestimate growth rates and reproductive potential. This may, in turn, lead to too-optimistic stock assessments and harvesting strategies (Beamish & McFarlane, 1983; Campana, 2001; Cailliet & Andrews, 2008). Regarding this issue, MIR and edge analysis support the hypothesis that a single set of translucent and opaque increments is formed every year in the forkbeard off the Portuguese continental coast. Translucent increments are deposited during autumn and winter and opaque increments are laid down in the spring and summer. The same results have been obtained by Abecasis *et al.* (2009) for forkbeard from Azorean waters, and by Matić-Skoko *et al.* (2011) for forkbeard caught in the Adriatic Sea, who found that opaque increments were laid down during spring and summer months.

The von Bertalanffy growth parameters estimated for the forkbeard show that it is a relatively slow growing and long lived species. Similar results were obtained in Azorean waters (Abecasis *et al.*, 2009). Although the maximum TL recorded in the present study was 67.1 cm, the historical record of 74 cm TL (Pinho, 2003) is close to the estimated L_∞ of 75.1 cm TL. The present study showed no sexual

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dimorphism in growth, although differences in growth between sexes are a common feature among related gadiforms, such as the greater forkbeard, *Phycis blennoides* (Casas & Piñeiro, 2000). This study showed that this species can attain a maximum age of 18 years. A strongly marked check ring—that appears in other species from genus *Phycis*, was always evident in the otolith nucleus (Matarrese *et al.*, 1998; Casas & Piñeiro, 2000). The maximum age observed in this study is very different from the one reported for the Adriatic Sea, where a maximum age of 5 years was reported. Contrarily to the results obtained for Portugal (mainland and Azores), forkbeard from the Adriatic Sea showed a sexual dimorphism in growth, with males reaching a larger size and growing more slowly than females (Matić-Skoko *et al.*, 2011). These differences in minimum and maximum ages and estimated von Bertalanffy growth parameters are probably related to the sizes of the specimens obtained in the different areas, which could be due to the sampling gear used: trammel nets in the Adriatic, longline in the Azores and longline, trawl and traps in mainland Portugal. Depending on mesh size, trammel nets may not be effective at sampling larger specimens (maximum 45.8 cm TL in the Adriatic study) whilst longlines do not capture smaller individuals (few specimens under 30 cm TL were used in the Azorean study). The use of different fishing gears in the present study allowed sampling of both smaller and larger specimens. Nevertheless, the possibility of different population size structures (or even different fishing pressure) in the north-east Atlantic and in the Mediterranean Sea cannot be discarded. The growth parameters obtained for the forkbeard from Azorean waters (Abecasis *et al.*, 2009) and the Adriatic Sea (Matić-Skoko *et al.*, 2011) were not statistically compared with those from mainland Portugal due to the absence of age–length keys.

Improved biological and fishery data for developing fisheries are essential to allow more robust assessments in the future (Hilborn & Waters, 1992). In this context, age and growth studies are fundamental, since it is most important to know the relative abundance of specimens of different ages in order to be able to evaluate population age structure in relation to fishing. The results of this study, associated with the improved knowledge of other biological aspects of the forkbeard, will provide important data to allow for improved assessments and management in the future.

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REFERENCES

Abecasis A.R.C., Canha A., Reis D., Pinho M.R. and Gil-Pereira J. (2009) Age and growth of the forkbeard *Phycis phycis* (Gadidae) from the Azorean archipelago, North Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 89, 629–633.

Bagenal T.B. (1974) *The ageing of fish: Proceedings of an International Symposium.* Woking: Unwin Brothers Ltd.

Beamish R.J. (1992) The importance of accurate ages in fisheries science. In Hancock D.A. (ed.) *Proceedings of the Australian Society for Fish Biology workshop on the measurement of age and growth in fish and shellfish.* Canberra: Bureau of Rural Resources, Australian Government Publishing Service, pp. 8–22.

Beamish R.J. and Fournier D.A. (1981) A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 982–983.

Beamish R.J. and McFarlane G.A. (1983) The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* 112, 735–743.

Beamish R.J. and McFarlane G.A. (1995) A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. In Secor D.H., Dean J.M. and Campana S.E. (eds) *Recent developments in fish otolith research.* Columbia, SC: University of South Carolina Press, pp. 545–565.

Beckman D.W. and Wilson C.A. (1995) Seasonal timing of opaque zone formation in fish otoliths. In Secor D.H., Dean J.M. and Campana S.E. (eds) *Recent developments in fish otolith research.* Columbia, SC: University of South Carolina Press, pp. 27–43.

Bedford B.C. (1983) A method for preparing sections of large numbers of otoliths embedded in black polyester resin. *ICES Journal of Marine Science* 41, 4–12.

Beverton R.J.H. (1990) Small marine pelagic fish and the threat of fishing; are they endangered? *Journal of Fish Biology* 37(A), 5–16.

Boehlert G.W. (1985) Using objective criteria and multiple regression models for age determination in fishes. *Fishery Bulletin* 83, 103–117.

Botsford L.W., Castilla J.C. and Peterson C.H. (1997) The management of fisheries and marine ecosystems. *Science* 277, 509–515.

Bowker A.H. (1948) A test for symmetry in contin gency tables. *Journal of the American Statistical Association* 43, 572–574.

Bradford M.J. (1991) Effects of ageing errors on recruitment time series estimates from sequential population analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 555–558.

Cailliet G.M. and Andrews A.H. (2008) Age-validated longevity of fishes: its importance for sustainable fisheries. In Tsukamoto K., Kawamura T., Takeuchi T., Beard T.D. Jr and Kaiser M.J. (eds) *Fisheries for Global Welfare and Environment, 5th World Fisheries Congress 2008.* Tokyo: TERRAPUB, pp. 103–120.

Cailliet G.M., Andrews A.H., Burton E.J. Watters D.L., Kline D.E. and Ferry-Graham L.A. (2001) Age determination and validation studies of marine fishes: do deep-dwellers live longer? *Experimental Gerontology* 36, 739–764.

Campana S.E. (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* 188, 263–297.

Campana S.E. (2001) Accuracy, precision and quality control in age determination including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59, 197–242.

Campana S.E., Annand M.C. and McMillan J.I. (1995) Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* 124, 131–138.

Cardinale M., Arrhenius F. and Johnsson B. (2000) Potential use of otolith weight for the determination of age-structure of Baltic cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*). *Fisheries Research* 45, 239–252.

Casas J.M. and Piñeiro C. (2000) Growth and age estimation of greater forkbeard (*Phycis blennoides* Brunnich, 1768) in the north and north-west of the Iberian Peninsula (ICES Division VIIIc and IXa). *Fisheries Research* 47, 19–25.

Chang W.Y.B. (1982) A statistical method for evaluating the re-producibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39, 1208–1210.

Cohen D.M., Inada T., Iwamoto T. and Scialabba N. (1990) FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. *FAO Fisheries Synopsis* 10, 1–442.

Deree H.L. (1999) Age and growth, dietary habits, and parasitism of the fourbeard rockling, *Enchelyopus cimbrius*, from the Gulf of Maine. *Fishery Bulletin* 97, 39–52.

Fowler A.J. (1995) Annulus formation in otoliths of coral reef fish–a review. In Secor D.H., Dean J.M. and Campana S.E. (eds) *Recent developments in fish otolith research*. Columbia, SC: University of South Carolina Press, pp. 45–63.

Francis R.I.C.C. and Campana S.E. (2004) Inferring age from otolith measurements: a review and a new approach. *Canadian Journal of Fisheries and Aquatic Sciences* 61, 1269–1284.

Hilborn R. and Waters C. (1992) *Quantitative Fisheries Stock Assessment: choice, dynamics and uncertainty*. New York: Chapman & Hall.

Hoenig J.M., Morgan M.J. and Brown C.A. (1995) Analysing differences between two age determination methods by tests of symmetry. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 364–368.

INE (2013) *Statistical data for fisheries 2001–2012*. Available at: http://www.ine.pt/xportal/xmain?xpid=INE&xpgid=ineindicadores&indOcorrCod=0001073&contexto=bd&selTab=tab2&exlang=en (accessed 28 May 2013).

Kimura D.K. (1980) Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77, 765–776.

Labropoulou M. and Papaconstantinou C. (2000) Comparison of otolith growth and somatic growth in two macrourid fishes. *Fisheries Research* 46, 177–188.

Lai H.L. and Gunderson D.R. (1987) Effects of ageing error on estimates growth, mortality, mortality and yield per recruit for wallaye pollock (*Theragra chalcogramma*). *Fisheries Research* 5, 287–302.

Matarrese A., D'Onghia G., Basanisi M. and Mastrototaro F. (1998) Spawning and recruitment of *Phycis blennoides* (Phycidae) from the north-western Ionian Sea (middle-eastern Mediterranean). *Italian Journal of Zoology* 65, 203–209.

Matić-Skoko S., Ferri J., Škeljo F., Bartulović V., Glavić K. and Glamuzina B. (2011) Age, growth and validation of otolith morphometrics as predictors of age in the forkbeard, *Phycis phycis* (Gadidae). *Fisheries Research* 112, 52–58.

McCurdy W.J. (1985) A low-speed alternative method for cutting otolith sections. *ICES Journal of Marine Science* 42, 186–187.

Morales-Nin B. and Panfili J. (2005) Seasonality in the deep-sea and tropics revisited: what can otoliths tell us? *Marine and Freshwater Research* 56, 585–598.

Morales-Nin B., Torres G.J., Lombarte A. and Recasens L. (1998) Otolith growth and age estimation in the European hake. *Journal of Fish Biology* 53, 1155–1168.

Morato T., Afonso P., Lourinho P., Barreiros J.P., Santos R.S. and Nash R.D.M. (2001) Length–weight relationships for 21 coastal fish species of the Azores, north-eastern Atlantic. *Fisheries Research* 50, 297–302.

Myers R.A., Hutchings J.A. and Barrowman N.J. (1997) Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* 7, 91–106.

Panfili J. and Morales-Nin B. (2002) Semi-direct validation. In Panfili J. and Pontual H. (eds) *Manual of fish sclerochronology*, Brest: Ifremer–IRD, pp. 129–134.

Pentilla J. and Dery L.M. (1988) Age determination methods for Northwest Atlantic species. *NOAA Technical Report NMFS* 72, 1–135.

Pinho M.R. (2003) *Abundance estimation and management of Azorean demersal species*. PhD thesis. University of the Azores, Horta, Portugal.

Samamé M. (1977) Determinación de la edad y crecimiento de la sardine *Sardinops sagax* (J). *Boletín–Instituto del Mar del Perú* 3, 95–112.

Shono H. (2000) Efficiency of the finite correction of Akaike's Information Criteria. *Fisheries Science* 66, 608–610.

Stewart J. and Hughes M. (2007) Age validation and growth of three commercially important hemiramphids in south-eastern Australia. *Journal of Fish Biology* 70, 65–82.

Venables W.N. and Ripley B.D. (2002) *Modern applied statistics with S*. 4th edn. New York: Springer.

Vieira A.R., Figueiredo I., Figueiredo C. and Menezes G.M. (2013) Age and growth of two deep-water fish species in the Azores Archipelago: *Mora moro* (Risso, 1810) and *Epigonus telescopus* (Risso, 1810). *Deep Sea Research II* (in press) http://dx.doi.org/10.1016/j.dsr2.2013.02.016.

von Bertalanffy L. (1938) A quantitative theory of organic growth (inquiries of growth laws II). *Human Biology* 10, 181–213.

and

Zar J.H. (1996) *Biostatistical analysis*. 3rd edn. Englewood Cliffs, NJ: Prentice-Hall.

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