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Struggling with fish age, a comparison of otolith preparation techniques to unravel age and growth of boarfish, *Capros aper* (Linnaeus, 1758)

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Fish age and growth data are crucial for understanding vital species' traits and their populations. Boarfish is a pelagic species widely distributed in the Northeast Atlantic that is one of the most discarded non-commercial species on the Portuguese coast. Due to its potential valorisation as a new fishery in the Northeast Atlantic, boarfish has become object of interest in several published studies. However, since no age standard protocol has been implemented for boarfish, studies have used a variety of different otolith preparation techniques to estimate age, leading to contradicting and discrepant results. This research aims to consolidate biological insights into boarfish age and growth, lay the foundation for a standardized ageing protocol and serve as a benchmark study for the Portuguese west coast before commercial exploitation. Through the comparison of two otolith ageing methodologies, this study recommends using whole otoliths as the best method, revealing a maximum age of 15 years. The growth pattern estimated, indicated a biphasic growth pattern, with a faster initial growth rate that slows down at 2.4 years, the moment of change, when energy is allocated for sexual maturation. This finding was corroborated by a maturity ogive and analysis of fish size and otolith length relationship.

Keywords Bayesian inference, Life-history traits, Biphasic growth, Length at first maturity, Portuguese coast

Data on fish age and growth are essential for the understanding of vital traits of species and populations¹, however choosing which method to use is not the most straightforward and consensual step of the process. Most studies on age and growth of fish rely on the determination of individuals' age by counting growth increments in hard body parts, like otoliths, scales and even some parts of the fish's skeletons¹. Otoliths are considered the most reliable structures for age estimates, since it is assumed that they contain information on the entire growth history of the individual fish². Nevertheless, there are several methods to estimate age of individual fish, with some of the most common otolith preparation techniques including the examination of the whole structure, sectioned, broken or burnt. Each technique influences the structure's optical properties differently³ which consequently influences its interpretation as well as the process's accuracy and precision. Incorrect age estimates can lead to over- or underestimation of a species age and contribute to the mismanagement and assessment of a stock. Underestimation of fish age has proven to be problematic for some fish species since it usually leads to an overestimation of individual and population growth rates³. On the contrary, an overestimation of fish age can result in the underestimation of the individual and population's growth and overestimation of survival rates⁴.

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Both situations have major implications for the stock assessment and might ultimately lead to the implementation of flawed management actions. Moreover, estimating species age is not an exact science, and either over time, among or even within readers age estimates may drift or vary⁵. As such, it is vital to reach a consensus regarding standard ageing methodologies and preparation techniques to avoid errors and achieve consistent, valuable, and comparable results regarding species age. For some species, ageing protocols providing general guidelines for age estimation are already developed, implemented and well-known, however for many other species, this is yet to be unravelled.

Boarfish is a small pelagic shoaling fish distributed along the Northeast Atlantic, from Norway to Senegal, including the Mediterranean Sea, the Azores, the Canary Islands, Madeira, and the Great Meteor Seamount⁶. It is usually found between 40 and 600 m in shelf seas and slopes⁷, over rock, coral, and sand substrates^{6,8}. This species was considered rare in Northeast Atlantic, however since the second half of the twentieth century, various periodic increases in its abundance have been observed, which increased the commercial interest in the species. These sporadic population booms have been attributed to rising temperatures, periods of low predation, low fisheries exploitation and high availability of preys⁷. In most countries, boarfish is considered a nuisance bycatch usually present in mixed demersal fisheries of certain species like mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), occasionally blue whiting (*Micromesistius poutassou*) and crustacean trawl fisheries. Notwithstanding, in some countries like Ireland and Denmark, some targeted fisheries have been developed⁹. In Portugal boarfish is still an unexploited bycatch species, yet with its increasing abundance in the recent years, alongside the potential for generating income for fishermen by developing added-value food products¹⁰, with nutritious value¹¹, the species can represent a significant opportunity for a new fishery to be established.

During the last years, boarfish has become object of interest of several published studies. Although the increased interest on the species has contributed to the growing knowledge on the species age and growth, these studies present contradicting conclusions. White et al.⁸ provided the first age estimations from the south and west coast of Ireland, using sectioned otoliths, and estimated boarfish maximum age at 26 years, for individuals with less than 15 cm SL (standard length). Similar results were obtained for the south and west coast of Ireland and Brittany coast, but using whole otoliths, Hüsey et al.¹² and Coad et al.¹³ set the maximum age at 30 years old for individuals approximately with 17 cm TL (total length) and 13 cm TL, respectively. On the other hand, Yapıcı and Filiz¹⁴ sampled individuals from the southeast Aegean Sea and, using only sectioned otoliths, concluded that this species reached a maximum age of 4 years, for fish with an approximated mean TL of 9 cm. Vagenas et al.¹⁵, using the sBCB technique (the standardized burn-crack-burn technique), estimated maximum ages of 12 years at 10.5 cm TL for the Aegean Sea, and 17 years at 10 cm TL for the Ionian Sea. More recently, Castro-Gutiérrez et al.¹⁶, using whole otoliths that were first immersed in a glycerol-alcohol solution, estimated maximum age at 5 years for individuals with less than 10.7 cm TL. For other areas of the species' distribution, such as the Portuguese coast, there is no information available. Ultimately, no consensus has been reached regarding boarfish age, with maximum age estimates ranging from 4 up to 30 years, depending on the used otolith preparation, observation techniques and the geographic region sampled, due to the absence of a standard protocol for age estimation for this species.

Therefore, the main objective of this work is to study age and growth of boarfish, in the Portuguese coast, in particular we want to (1) determine the best otolith preparation technique and establish a growth pattern criterion to unravel the discrepancies surrounding boarfish age, (2) validate estimated ages using two semi-direct methods, the marginal increment analysis (MIA) and otolith edge analysis, (3) model the species' growth using different approaches to the von Bertalanffy growth model, and finally, (4) estimate species growth parameters for the Portuguese coast based on the best growth model approach, serving as benchmark before boarfish commercial exploitation initiates in this area. To the best of our knowledge this is the first study on this subject for this area.

Material and methods

Study area and sampling

This study was conducted along the western Portuguese coast, in the Iberian Peninsula (Fig. 1). Located on a biogeographic transition zone, between temperate and tropical waters¹⁷, this area is also influenced by both the North Atlantic Oscillation and persistent upwelling-type circulations leading to high primary productivity in the area^{18,19}. The seasonal mean sea surface temperature registered along this area has been increasing since 1973, with values ranging from 14.08 °C, in winter, up to 20.38 °C, in summer²⁰.

A total of 463 boarfish individuals (177 males and 286 females) were collected monthly as bycatch onboard fish and crustacean bottom-trawlers operating at depths between 120 and 984 m, on rocky, sandy, and muddy bottoms along the western Portuguese coast, between September 2011 and October 2012 (excluding April 2012 due to bad weather conditions). Samples were collected, by an on-board observer, from fishing vessels registered at the Peniche fishing port within the VALOREJET project. In the laboratory, TL (in cm with a 0.1 mm resolution), total and gutted weight (in g with 0.1 g resolution), and gonad weight (in g with 0.01 g resolution) were recorded on fresh fish. Total length ranged between 4.3 and 17.0 cm, with male maximum TL being 16.2 cm and female maximum TL 17.0 cm. Sagitta otoliths (hereafter referred to as otoliths) were removed, rinsed with water, air-dried, and stored in labelled vials for further analysis. Sex and maturity phases were assigned by histological examination following the standardized terminology suggested by Brown-Peterson et al.²¹. The same dataset was used in an earlier article²², which explains further details about the sex and maturity analysis.

Total length and otolith radius relationship

The relationship between fish total length (TL in cm) and otolith radius (OR in mm) (n = 463) was evaluated using both a segmented linear (TL = aOR + b) and power function (TL = aOR^b) models, with the former only

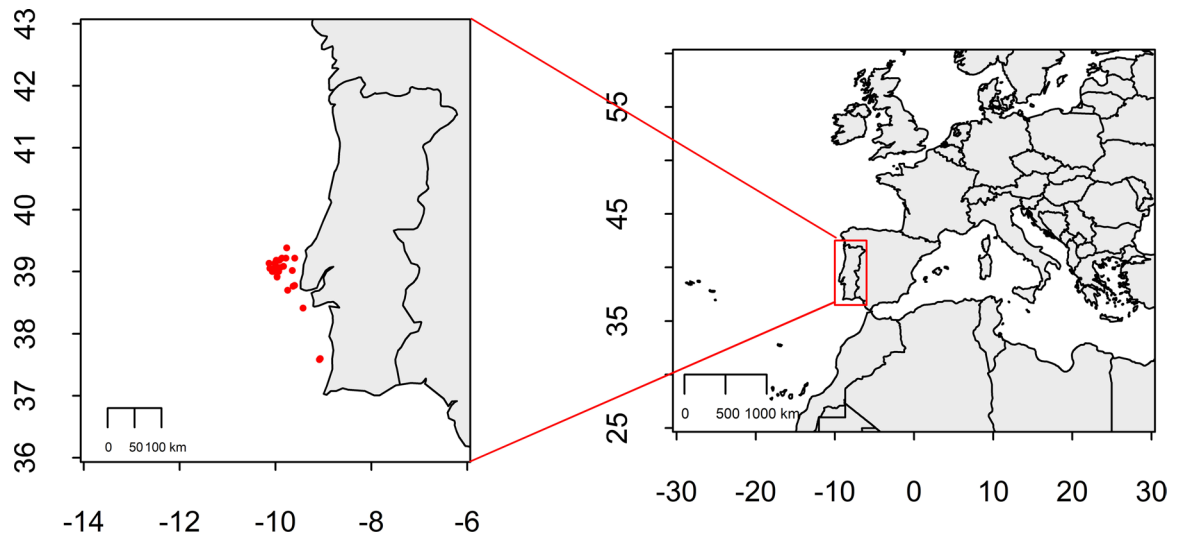


Fig. 1. Map of sampling sites' location of boarfish individuals on the western Portuguese coast. Red circles indicate each sampling site. Produced with R Statistical Software (version 4.3.0—<https://www.R-project.org/>).

being used to detect if and when a change in the growth pattern was present. These models were implemented in R (version 4.3.0) using the `stats`²³ and `segmented`²⁴ packages.

Ageing methodologies comparison and precision

In a representative subsample ($n = 92$, 52 males and 40 females) covering all the lengths in the total sample (4.3–17.0 cm TL), two different otolith preparation techniques (whole and sectioned otoliths) were applied for each pair of sagitta otoliths.

Whole left otoliths were placed with the *sulcus acusticus* downwards and observed immersed in water under a stereomicroscope (Nikon SMZ74ST) using reflected light, 5 \times magnification and a dark background. Right sagitta otoliths were transversally sectioned through the nucleus²⁵ and along the longest otolith radius, with a diamond-tipped saw blade (PRESI Mecatome T330 High Capacity Cutting Machine) rotating at 3700 rpm, by technicians from IPMA (Portuguese Institute for Sea and Atmosphere). Slides of 0.5 mm thick were mounted in a glass slide with translucent glue, brushed with a natural oil, to enhance increment visualization, and observed under a stereomicroscope with transmitted light and a 5 \times magnification. The distances from the otolith's nucleus to each successive translucent increment were measured using ObjectJ 1.05j (a plugin for ImageJ software 1.53e) along an axis in the dorsal region on the external face of whole otoliths, and in both dorsal or ventral depending on the section's condition.

To determine the best method for boarfish's age estimation, precision among age readings, the Mann–Whitney U-test, Bowker's symmetry test, and bias evaluation (based on age bias plots) were used.

Precision of age estimations (and their reproducibility) was evaluated within the same reader (reader 1, R1) and between two different readers (R1 and reader 2, R2), for both whole and sectioned otoliths. For that, blind interpretation of the subsample (where the otoliths used had no information on biological variables, with the exception of the month to allow accurate assessment of edge type) was executed twice by R1 with a lag of 3 months, and by both readers. Comparisons between readings in whole and sectioned techniques made for both R1 and R2, between R1's first and second readings for whole and sectioned otoliths, and between R1 and R2's whole and sectioned otoliths readings were made. The average percentage error (APE)²⁶, the coefficient of variation (CV)²⁷, and the percentage of agreement were used to compare assigned ages within and between readers. The nonparametric Mann–Whitney U-test was used to detect the existence of significant differences between age estimations, and the Bowker's symmetry test^{28,29} to investigate if the differences found were systematic or not (a 0.05 significance level was used). Age bias plots³⁰ were used to evaluate bias between readers and readings, allowing visualizing deviation of the age readings from the 1:1 equivalence line.

Age validation

Marginal increment analysis (MIA) and otolith edge analysis, both semi-direct validation methods, were used to validate the increments deposition pattern and check the periodicity of growth increment formation in all otoliths (that were read using the best otolith preparation technique). The marginal increment ratio (MIR)³¹ was calculated as a proportional state of completion, ranging from near zero, when an increment is just beginning to form, to one, when a complete increment has formed (as well as all values in between)³². The edge of each otolith was classified as opaque (more dense, light increments) or translucent (less dense, dark increments)³³. MIR calculation is only implemented for individuals with at least 2 visible growth increments³². Coincidentally, age 2 separates juvenile and adult individuals and, as such, mean MIR and standard deviation, and otolith edge type were plotted for all adult individuals ($n = 422$).

Growth modelling

Initially, the von Bertalanffy growth model (VBGM)³⁴ was fitted to each sex separately and the likelihood ratio test³⁵ was used to detect and evaluate the significance of differences on the growth parameters between sexes. Since no significant differences in growth between sexes were detected ($\chi^2 = 1.13$, $df = 3$, p -value = 0.770), all subsequent analyses were applied to both sexes together.

To model the boarfish growth, two growth functions following different approaches were used. Firstly, following a frequentist approach, the conventional von Bertalanffy growth model (Freq VBGM 3p Eq. (1)), was fitted to the length-at-age data using the FSA³⁶ and stats²³ packages in R.

$$L_t = L_\infty \times (1 - e^{-k \times (t-t_0)}) \quad (1)$$

Secondly, a Bayesian inference approach (Bayes VBGM 3p) was used to estimate the parameters associated with the same model previously mentioned, Eq. (1). The Bayes VBGM 3p fitted to the total sample used 3 MCMC (Markov chain Monte Carlo) chains with 100,000 simulations, a burn-in period of 5000 simulations and thinning of 15. Normally distributed informative priors were set for L_∞ , k and t_0 parameters. The value of each prior's precision (inverse of variance) was initially defined as 10% of the mean value set for each parameter but, depending on the need to improve the growth model fitting, its value was reduced or increased accordingly³⁷. In this model, the prior for the L_∞ parameter had a mean, μ , defined with a value higher than the maximum length of fish found in the dataset (17.0 cm TL) and a precision, τ , of 0.5, that represents a variance of 10% of the mean value. The prior distribution for k was centred around 0.5 and had a precision, τ , of 2. The prior distribution for t_0 had a mean μ of -2 and a precision τ of 2. Thirdly, a 5-parameter biphasic growth model (Bayes VBGM 5p, Eq. (2))³⁸ was also fitted, following only a Bayesian approach (the algorithm used to estimate the 5-parameter biphasic growth model did not converge using the frequentist approach).

$$L_t = \begin{cases} L_\infty \times (1 - e^{-k_0 \times (t-t_0)}), & t < t_1 \\ L_\infty \times (1 - e^{-k_0 \times (t_1-t_0) - k_1 \times (t-t_1)}), & t \geq t_1 \end{cases} \quad (2)$$

With the rjags package³⁹, the Bayes VBGM 5p used 3 MCMC chains with 1,000,000 iterations, a burn-in period of 5000 simulations and thinning of 100. Normally distributed informative priors were set for L_∞ , k_0 , k_1 , t_0 and t_1 parameters, based on expert opinion and available literature for the species, as stated by Doll and Jacquemin⁴⁰. L_∞ prior had a μ defined with a value of 20, slightly higher than the fish's maximum TL found in the data set³⁷, and a τ of 0.5, that represents a variance of 10% of the mean value. The prior distributions for k_0 , k_1 were centred around 0.3 and 0.15, respectively and both set with a τ of 1. Parameter τ for these two growth coefficient's parameters was increased to allow the convergence of the model. For t_0 and t_1 the prior distributions had a mean of -2 and 3, respectively, and a precision of 0.5 (equal to all the other parameters). The Bayesian approach models were checked for convergence and autocorrelation with diagnostic plots implemented within the rjags package³⁹. To compare each model's performance, within the Bayesian approach, the deviance information criterion (DIC) was used, where a smaller value of DIC corresponds to a better fit⁴¹ and was calculated using the same rjags package above.

Sexual maturity

Based on the maturity phases histologically assigned, each individual was classified as immature or mature. Consequently, using the fraction of mature individuals per length class in the total sample, a maturity ogive (both sexes combined) was estimated by adjusting a logistic model proposed by Figueiredo et al.⁴². While not a widely adopted practice, combined-sex maturity ogives remain relevant in stock assessment⁴³. Length at first maturity (L_{50}) and length at which majority of the population is mature (hereafter designated as " L_{100} ") were determined.

Results

Total length and otolith radius relationship

The relationship between TL and OR changed at a certain point during fish's life. Fitting a power function model (Fig. 2A), TL and OR demonstrated a negative allometric relation ($TL = 0.75 \times OR^{0.70}$, $R^2 = 0.77$) and using the segmented linear model (Fig. 2B) showed a change in the relationship at 1.50 mm in otolith radius, which corresponds to an approximate fish total length of 11.98 cm. This model had an associated R^2 value of 0.75.

Ageing methodologies comparison and precision

Boarfish sagitta otoliths are characterized by their hourglass shape and asymmetric dorsal and ventral regions, where a diffuse pattern of concentric and alternate opaque and translucent increments could be identified.

In whole otoliths, increments were more easily distinguished, and a regular pattern was visible, with alternated opaque and translucent concentric increments around the otolith's nucleus (Fig. 3A). This method was also faster to apply and easier to replicate, since it required no preparation.

In sectioned otoliths, numerous marks were visible, making it difficult to distinguish between true and false increments (Fig. 3B). This preparation technique produced a considerable percentage of otoliths rendered unusable and unreadable (broken, poorly mounted on the glass slides or sections that did not include the best section plane) and comparing it with the percentage of interpretable/viable otoliths, the success rate of this technique was only 37%.

The precision indices between techniques for the same reader and between readers, the Mann–Whitney and Bowker's symmetry test, and the age bias plots results are presented in Table 1 and Fig. 4.

For the comparison between whole and sectioned techniques for R1, high values for the precision indexes and low agreement percentages were obtained. The Mann–Whitney U-test showed significant differences in

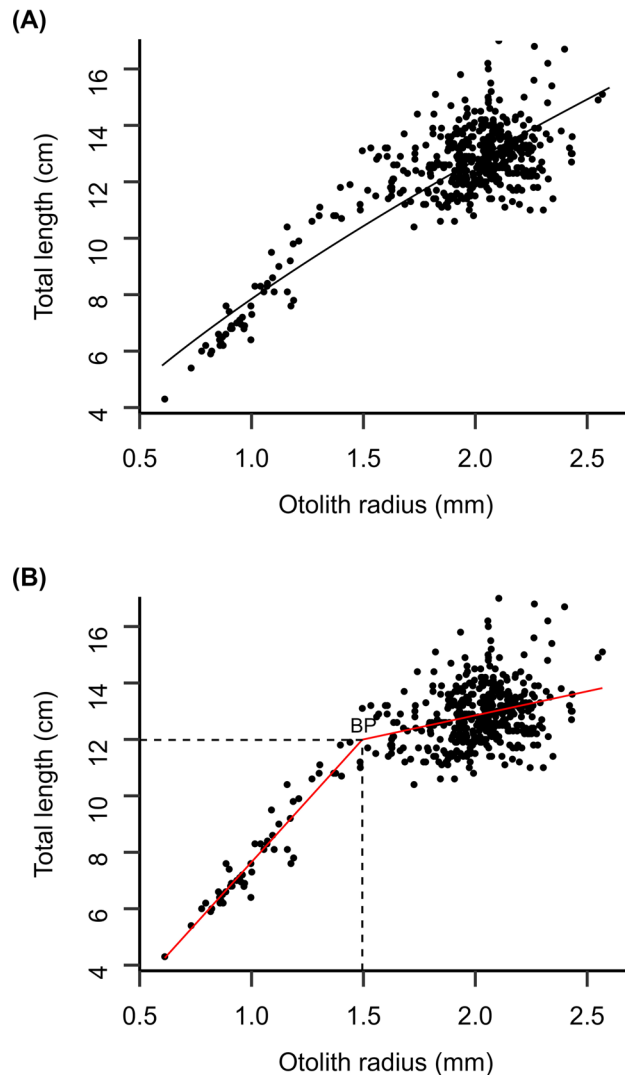


Fig. 2. Relationship between fish total length (in cm) and otolith radius (in mm) for boarfish from the Portuguese continental coast, fitted with (A) a power function model, and (B) a segmented linear regression model. BP—breaking point, in which a change in the relationship between the variables occurs.

the ages assigned with each technique, which were not considered systematic by the Bowker's symmetry test. The age bias plots (Fig. 4A) showed a low coincidence of the ages assigned by both techniques, demonstrating that the same otolith could be assigned with two different ages. The comparison between techniques for R2 also demonstrated high values for the precision indices, but the Mann–Whitney test revealed non-significant differences that were not considered systematic by the Bowker's symmetry test. The age bias plots (Fig. 4B) showed low coincidence of assigned ages with the equivalence line. For the two readings in whole otoliths performed by R1, low values of precision indices were obtained and the Mann–Whitney U-test showed non-significant differences, which were not systematically different. Total agreement and differences of ± 1 corresponded to 100%. A high coincidence with the equivalence line, in the age bias plots, was observed for this comparison (Fig. 4C). For R1 age readings in sectioned otoliths, the values of precision indices were higher than the previous comparison and the total agreement together with differences of ± 1 corresponded to 90%. The Mann–Whitney U-test did not show significant differences that were not considered systematic by the Bowker's symmetry test. When analysing the age bias plots (Fig. 4D), the two readings performed by R1 were less consistent compared to the whole otoliths' technique. Between readers, the whole otoliths' technique demonstrated relatively low precision indices values and the total agreement together with differences of ± 1 allocated to this comparison was 100%. The Mann–Whitney U-test showed non-significant differences, that were not considered systematic. Additionally, the age bias plot demonstrated high coincidence of the assigned ages with the equivalence line (Fig. 4E). For the sectioned otoliths technique between the two readers, precision indices obtained were higher than the previous comparison, total agreement percentage was only 47%, and differences of up to 6 years between readings were attained. Regarding age bias plots, there was low coincidence of the assigned ages with the equivalence line, with

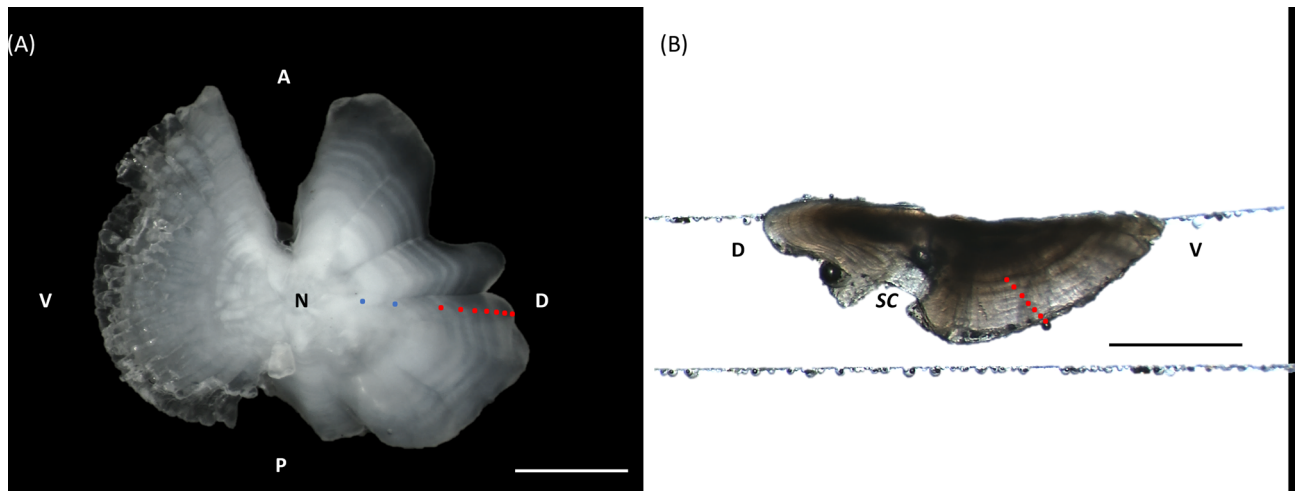


Fig. 3. (A) Whole left otolith of a 7-year-old boarfish, with 15.2 cm TL. (B) Sectioned right otolith of a 7-year-old boarfish, with 13.9 cm TL, both from the Portuguese coast. Red dots represent the growth increments and blue dots represent false increments; N—nucleus; V—ventral face; P—posterior face; D—dorsal face; A—anterior face; SC—sulcus acusticus; Scale bars = 1 mm.

Indices/statistical test	Between techniques		Within reader 1		Between readers	
	R1	R2	Whole otoliths	Sectioned otoliths	Whole otoliths	Sectioned otoliths
APE (%)	10.34	9.43	0.67	3.93	1.41	7.41
CV (%)	14.63	13.34	0.94	5.57	2.00	10.48
Total agreement (%)	32	36	91	68	80	47
Agreement (0, ±1) (%)	62	64	100	90	100	77
Mann–Whitney U-test	0.033*	0.884	0.991	0.803	0.892	0.015*
Bowker symmetry	0.136	0.733	0.423	0.654	0.540	0.093

Table 1. Precision indices for age readings of boarfish caught off the Portuguese continental coast. Values are presented for comparisons between techniques, within Reader 1 and between readers (R1, reader 1; R2, reader 2). Mann–Whitney U-test and Bowker symmetry p-values for each comparison are also given; * indicates values with statistical significance (p-value < 0.05).

R2 constantly assigning higher ages (Fig. 4F). The Mann–Whitney U-test and for the Bowker's symmetry test confirmed significant and systematic differences between the two readers for this technique.

Whole otoliths showed lower values for the precision indices, higher agreement percentages and non-significant differences both within and between readers, they also favoured the identification of the increment deposition pattern, making this technique the most appropriate for age estimates in boarfish.

Growth pattern and validation

The general growth pattern of boarfish whole otoliths consisted in a relatively clear pattern of concentric and alternate opaque and translucent increments, in the external face, around the otolith's nucleus that was more evident in the dorsal and less ornate region (Supplementary Fig. S.1). After the nucleus, in the central part of the otolith, two false increments were identified (Fig. 3A). These two marks were clearly visible in 86% of the samples and, when present, usually appeared at very consistent distances from the nucleus, at 0.525 ± 0.059 mm and 0.827 ± 0.071 mm, respectively (Fig. 5). The first true increment corresponded to the first clear and well-defined mark in the otolith, after the two false increments described above, that could be identified consistently at around 1.045 ± 0.07 mm from the nucleus (Fig. 5). The deposition of true increments changed with the otolith growth, with the first three increments being larger and more spaced in between and the remaining increments being thinner and closer together. The maximum observed age was 15 years (TL = 13.2 cm) for a female.

MIA and otolith edge analysis graphical representations are shown in Fig. 6. MIR evolution throughout the sampled months (Fig. 6A) displayed a pattern with clearly increasing values starting in May, reaching its peak in August and September, and decreasing values from September until December. Accordingly, and regarding the otolith edge type evolution (Fig. 6B), opaque edges were more frequent during the spring and summer months (from May to October) and translucent edges were more prevalent in the late autumn and winter months. These results support the existence of a cyclical one-year pattern growth for boarfish, with new increments being formed from December to March (when MIR values were the lowest and translucent edges prevailed).

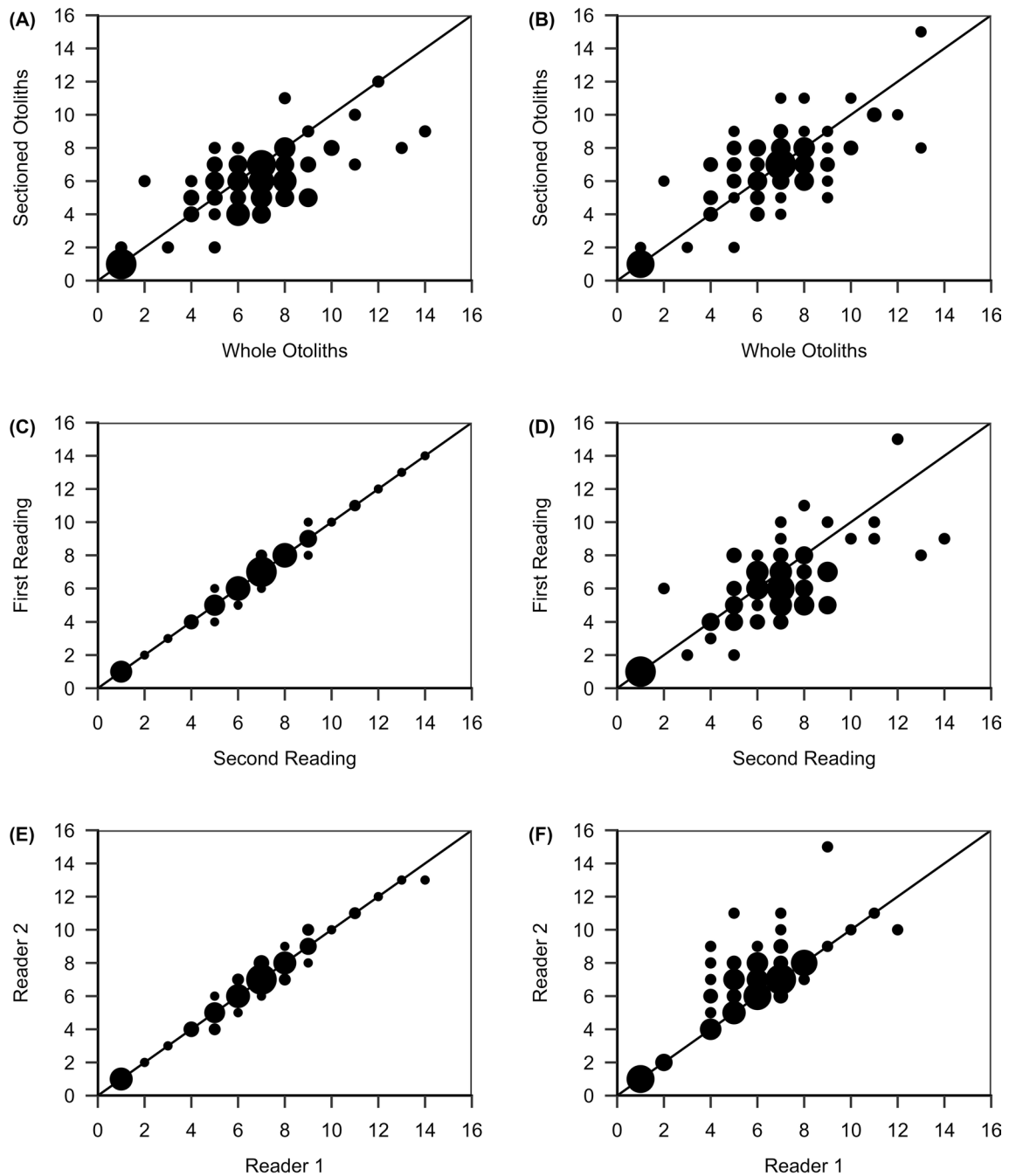


Fig. 4. Age bias plots for the readings comparisons: (A) between whole and sectioned techniques for reader 1 and (B) for reader 2, (C) between reader 1's first and second readings for whole otoliths and (D) for sectioned otoliths; (E) between reader 1 and reader 2's readings of whole otoliths and (F) sectioned otoliths. The 45° equivalence line represents 100% agreement.

Based on these results, ageing assumptions for the boarfish for the Portuguese coast are: (1) the first growth increment is the first clear and well-defined increments, after two false increments, marked at 1.045 ± 0.07 mm; (2) only one growth increment is deposited each year, as validated by MIR and otolith edge type analysis; (3) an annual growth increment corresponds to the succession of a translucent and an opaque increments, and as such, age can be assigned by counting translucent ones; (4) 1st January is considered to be the species birth date (rule accepted for the North Hemisphere^{1,44}). These assumptions were crucial for the age estimates performed for the total sample and used in the growth modelling.

Growth modelling

For growth modelling, a total of 463 individuals (177 males and 286 females) ranging from 4.3 to 17.0 cm TL were used. Fish were aged from 0 (average TL of 6.5 cm) to 15 years (average TL of 13.2 cm), although most individuals

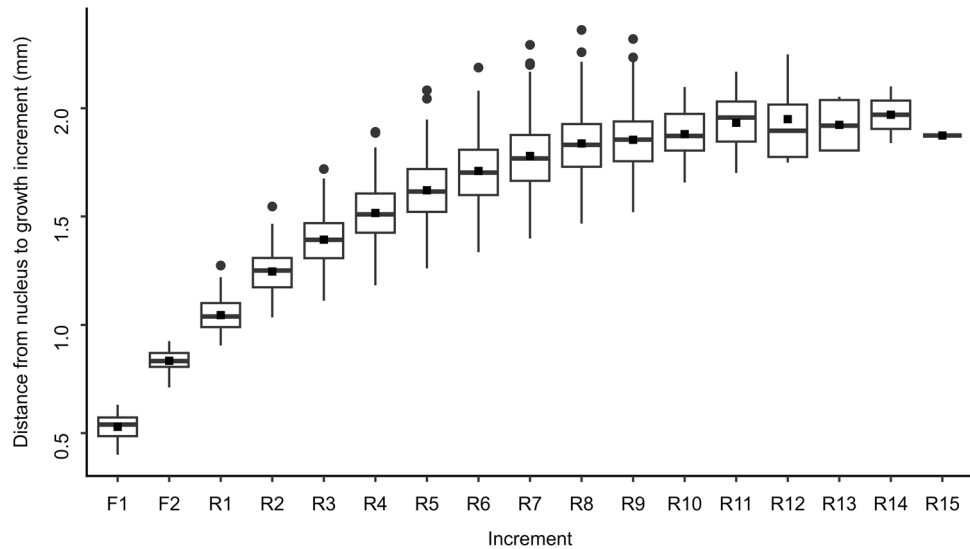


Fig. 5. Box and whiskers plot of the distance from the nucleus to each growth increment (in mm) measured in whole otoliths ($n = 463$) of boarfish from the Portuguese continental coast. F refers to false increments and R to growth increments. Black square is the mean value, black horizontal line is the median value, each box represents 75% of distances registered and black vertical lines (whiskers) are the maximum and minimum extreme values for each increment.

were 5–7 years old. The age-length key is presented in Supplementary Table S.1 in Supplementary material. All models applied to the dataset are represented in Fig. 7 and their respective parameters estimates and 95% credible intervals, expressed in Table 2. Both the frequentist and the Bayesian inference approach to the regular VBGM (Freq VBGM 3p and Bayes VBGM 3p, respectively) provided very similar results (summary statistics for the Bayes VBGM 3p are available in Supplementary Table S.2 and Fig. S.2). Both approaches provided L_{∞} values lower than the maximum total length observed in the sample: frequentist $L_{\infty} = 13.92$ cm; Bayesian $L_{\infty} = 14.01$ cm. Additionally, estimates for coefficient k were also close: (frequentist $k = 0.30$ year $^{-1}$; Bayesian $k = 0.29$ year $^{-1}$). For the Bayes VBGM 5p, the estimated L_{∞} was 19.68 cm and the k_0 coefficient estimate 0.19 year $^{-1}$ (summary statistics for the Bayes VBGM 5p are available in Supplementary Table S.3 and Fig. S.3). Additionally, this model also computed an estimate for a second growth coefficient that is considerably lower, $k_1 = 0.05$ year $^{-1}$, revealing a decrease of the individual's growth after age 2.4 years (t_1). The age at which the difference in the coefficient k is detected (t_1), corresponds to individuals with an average TL of 11.54 cm. Comparing between the two models performed with a Bayesian inference approach (Bayes VBGM 3p and Bayes VBGM 5p), the lower DIC value associated to the 5-parameter Bayesian VBGM model (DIC value for Bayes VBGM 5p = 1202) indicated that this was the best model to describe the boarfish growth.

Sexual maturity

The graphical representation of the maturity ogive, using all individuals, is represented in Fig. 8. The logistic model ($R^2 = 0.99$) allowed for the estimation of the length at which half of the population is mature (L_{50}) at 9.35 cm TL, and the length at which the majority of the population is mature (" L_{100} ") at 11.81 cm TL.

Discussion

Age and growth information of fish species, obtained through calcified structures, is a key tool to evaluate fish stocks status, contributing to the effectiveness of fisheries assessment and management. This essential information is usually obtained as result of a dynamic process of age estimation that includes various steps, where each one has a myriad of options and methodologies to choose from¹. However, it is important when evaluating a specific species, to reach a consensus regarding these steps so that consistent, valuable, and comparable results are obtained. This dynamic process starts with the choice of the calcified structure's preparation technique, followed by the definition of the structure's interpretation and general pattern/criteria and only then are the precision and accuracy procedures applied. These steps collectively summarise the development of a species-specific protocol for age estimation⁵, which for some species are already well-known and put into practice, while for others, like boarfish, it is yet to be unravelled.

In this study, whole and sectioned otoliths preparation techniques were compared, and a growth pattern criterion was described, contributing to unravel the discrepancies surrounding boarfish age estimation using otoliths.

Accomplishing its first objective, this study concluded that, for the western Portuguese coast, whole sagitta otoliths seem to be the most accurate method for age estimation of boarfish. Whole otoliths consisted in a cost and time efficient method that also originated consensual results between different readers and within the same reader, resulting in a higher precision than those suggested as references³² and when compared to the sectioned otoliths' associated precision. It also allowed for a general growth pattern criterion that was easily reproducible

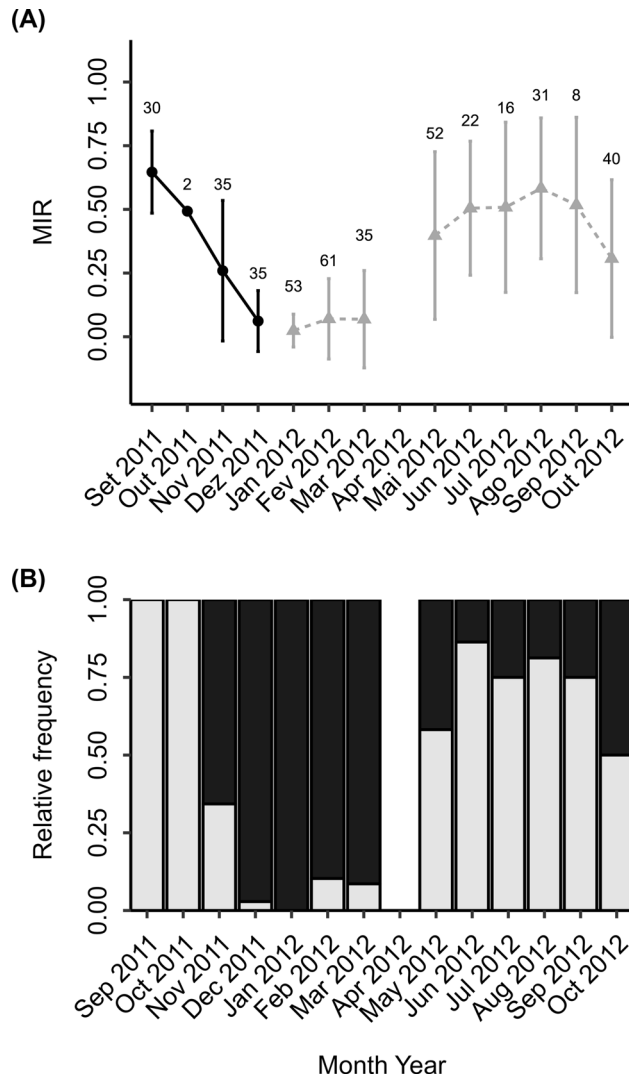


Fig. 6. (A) Monthly evolution of marginal increment ratio in whole otoliths of boarfish from the Portuguese continental waters. Black dots are the mean values for MIR observed in 2011 and grey dots are the mean values for MIR observed in 2012. Black and grey vertical lines (whiskers) are \pm standard deviation. Back solid line and grey dashed line represent the MIR evolution between months for 2011 and 2012, respectively. Numbers plotted above symbols are the sample size for each month (B) Annual variation pattern of the percentage of opaque and translucent edges in whole otoliths. Black bars are translucent edges and grey bars are opaque ones.

for other readers and through time, to be established, supporting this as the most appropriate choice for our study area. On the other hand, the sectioning method, was very time consuming, had a low precision associated, suggesting a low agreement between readers and readings, and produced a high percentage of unreadable otoliths (63%) according to both experienced readers. The maximum age registered in the present study (15 years), using whole otoliths, contrasts with the values of other already published studies (Table 3). While Yapıcı and Filiz¹⁴ suggest a maximum age of 4 years (TL of 9 cm), for the Mediterranean region using sectioned otoliths, Hüseyin et al.¹² indicates that maximum age surpasses 30 years (TL of 17 cm), for the Northeast Atlantic region using whole otoliths. It is unlikely that either environmental factors, like temperature, or intrinsic factors to the species are the sole root cause of differences of such magnitude. Instead, the described age discrepancies across regions are most likely due to the different techniques and differing criteria of the general growth pattern used in existing studies^{8,12-14,16}.

For some species, particularly those that grow slowly or have thick otoliths, the sectioned otoliths technique seems to be more appropriate and produces better results (e.g. *Mora moro*⁴⁵, *Pachymetopon blochiibefore*⁴⁶, *Coryphaenoides rupestris*⁵). On the other hand, for species that grow rapidly and have distinct growth increments or small and difficult-to-section otoliths, whole otoliths are usually the preferred approach (e.g. *Trachurus picturatus*^{37,47}, *Scomber colias*⁴⁸ and *Sardina pilchardus*⁴⁹) However, there are also some documented instances that show the use of different techniques of the same calcified structure and different criteria resulting in diverse age estimations for the same species from different geographical areas⁵⁰⁻⁵².

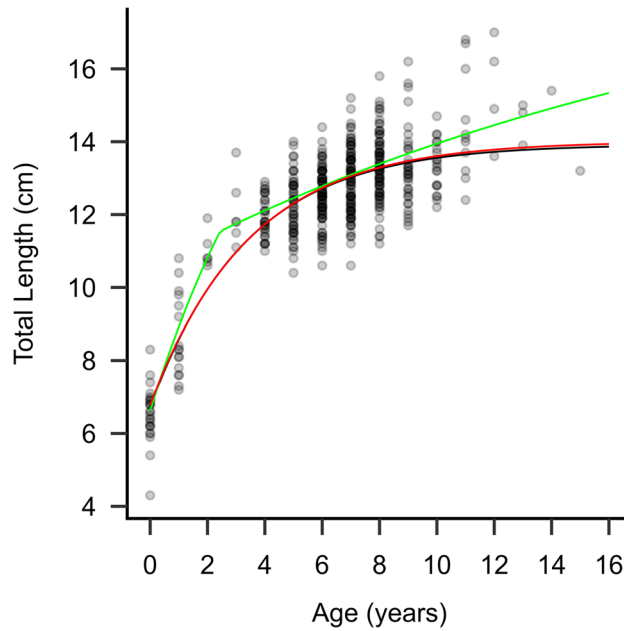


Fig. 7. The von Bertalanffy growth functions from the three approaches adjusted to age-at-length data of boarfish from the Portuguese continental coast. Black line—Frequentist von Bertalanffy growth model with 3 parameters approach (Freq VBGM 3p); red line—Bayesian von Bertalanffy growth model with 3 parameters approach (Bayes VBGM 3p); green line—Bayesian von Bertalanffy growth model with 5 parameters (Bayes VBGM 5p).

Parameter	Freq. VBGM 3p	Bayes VBGM 3p		Bayes. VBGM 5p	
		Prior	Posterior	Prior	Posterior
L_{∞} (cm)	13.92 (13.62–14.30)	N (20, 0.5)	14.01 (13.69–14.39)	N (20, 0.5)	19.68 (17.06–22.42)
k/k_0 (year ⁻¹)	0.30 (0.25–0.34)	N (0.5, 2)	0.29 (0.25–0.34)	N(0.3, 0.5)	0.19 (0.14–0.26)
t_0 (year)	-2.22 (-2.65 to -1.86)	N (-2, 2)	-2.30 (-2.71 to -1.92)	N (-2, 0.5)	-2.12 (-2.64 to -1.68)
k_1 (year ⁻¹)	-	-	-	N (0.5, 0.5)	0.05 (0.03–0.07)
t_1 (year)	-	-	-	N (3, 0.5)	2.44 (1.95–3.00)
DIC	-	1233		1202	

Table 2. Summary of the von Bertalanffy growth parameters estimated for boarfish from the Portuguese continental coast. 95% credible intervals of each parameter for the Frequentist model and credible interval for the Bayesian model are given in brackets. L_{∞} is the asymptotic length; k is the growth coefficient from the von Bertalanffy growth model; k_0 is the first growth coefficient (before t_1); t_0 is the hypothetical age at length zero; k_1 is the second growth coefficient (after t_1); t_1 is the age/specific moment of change in the growth parameters; DIC is the deviance information criterion.

One example of this is the black scabbardfish (*Aphanopus carbo*). Using whole otoliths, Morales-Nin and Sena-Carvalho⁵³ estimated black scabbardfish' age to be between 8 and 12 years, while Kelly et al.⁵⁴ using sectioned otoliths estimated a maximum age of up to 32 years. Later on, Vieira et al.⁵⁵, by comparing both otolith preparation techniques as well as the ageing criteria used by the previous authors, suggested that sectioned otoliths were the most appropriate technique, since it better evidenced the growth increments and facilitated the ageing of larger specimens, with maximum ages attained being 12 (mainland Portugal) and 15 years (Madeira archipelago). For the bluemouth (*Helicolenus dactylopterus*), a benthic deep-water scorpionfish, the same issue was documented. Age and growth were described for several areas, using different techniques, resulting in an age range between 10⁵² and 43 years⁵¹. After comparing whole and sectioned otoliths, although the first and true growth increments were more easily identified in whole otoliths, Sequeira et al.⁵⁶ considered that both techniques can be used for ageing bluemouth and settled a maximum age of 30 years. Similarly, debates about European hake's (*Merluccius merluccius*) age and growth have been widely discussed since the 1930s. This species age estimation difficulties were not only due to the use of different techniques across different areas, but also due to differences in the criteria used to interpret the otolith's growth pattern. In this case, only after tagging experiments a consensus about the age and growth of this species was reached, with hake having a somatic growth twofold higher than the initially

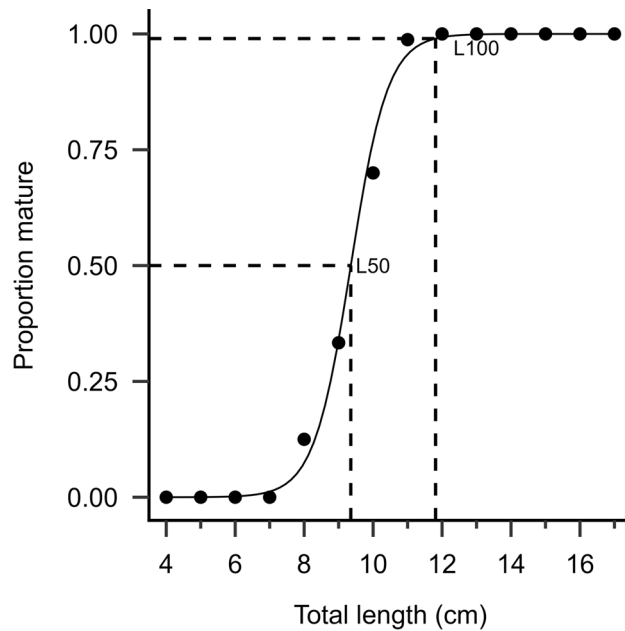


Fig. 8. Maturity ogive of boarfish from the Portuguese continental coast; L50—length at first maturity; “L100”—length at which approximately 100%/majority of the population is considered mature.

References	Study area	Size range (cm)	Preparation technique	Max. age (year)	von Bertalanffy parameters		
					L_{∞} (cm)	k (year ⁻¹)	t_0 (year)
White et al. ⁸	NE Atlantic	1.5–14.0 (SL)	Whole otoliths for individuals ≤ 2.3 cm SL and sectioned otoliths	26	13.00	0.186	–0.01
Hüssy et al. ¹²	NE Atlantic	8.0–13.0 (TL)	Whole otoliths	30	16.52	0.145	–2.897
Coad et al. ¹³	NE Atlantic	10.0–16.0 (TL)	Whole otoliths	29	15.77	0.167	–2.814
Yapıcı and Filiz ¹⁴	SE Aegean	3.5–10.5 (TL)	Sectioned otoliths	4	11.05	0.447	–0.57
Vagenas et al. ¹⁵	Central Aegean Central Ionian	3.3–11.2 (TL)	sBCB	12	11.19	0.270	–0.570
				17	10.43	0.210	–3.410
Castro-Gutiérrez et al. ¹⁶	Gulf of Cádiz	3.5–10.7 (TL)	Whole otoliths	5	11.80	0.21	–1.60

Table 3. Summary of the von Bertalanffy growth parameters for boarfish age estimated by previous studies, for other areas. With size range (in cm) and maximum age (in years). L_{∞} is the asymptotic length; k is the growth coefficient; t_0 is the hypothetical age at length zero. ¹von Bertalanffy parameters presented were estimated for females only.

thought^{50,57}. The tagging experiments clearly showed that there was overestimation of this species’ age, which underestimated its growth and led to incorrect assessments of the stocks for years.

Regarding the general growth pattern in boarfish whole otoliths, it was possible to identify two false increments very close to each other and at consistent distances from the nucleus (0.525 ± 0.059 mm and 0.827 ± 0.071 mm) before the deposition of the first growth increment at approximately 1.045 ± 0.07 mm from the centre, which presented as the first intense mark that could be followed all around the otolith’s nucleus. Marks in the otolith classified as false increments were not as intense and clear as the true ones and, although in younger individuals these false increments could be seen as very clear and sharp marks, they often presented as more faded marks in older individuals. Environmental conditions can induce changes in otoliths structure and increment patterns, and although only scarce information about the early life of this species (e.g. Rodriguez et al.⁵⁸) or about its life history is available, some authors demonstrated that boarfish shows a change in feeding activity that probably reflects an ontogenetic shift, as well as other changes in feeding regime, related with the environmental conditions⁵⁹. These same authors also reported ontogenetic shifts related to habitat, living the adult specimens in deeper water than the juveniles. The two false increments were hypothesised to reflect those changes in feeding activity and bathymetry shifts, as reported by Carpentieri et al.⁵⁹. To avoid misinterpretations of the false rings with the first annual increment, the radius of the first translucent increment was measured and used as a guideline to exclude the false rings in older individuals.

Identification of the first true growth increment is a crucial component of any age study, since without it, age determinations will be consistently wrong by a constant amount³². Age validation is also a pivotal part of age estimation, preventing under or overestimation of ages, that could lead to erroneous decisions regarding species assessment and management. As set in the second objective, MIR and otolith edge analysis supported the

assumption that a set of one translucent and one opaque increment corresponds to 1 year of growth in boarfish from the Portuguese coast. Opaque increments formed from May to October, when MIR values were higher, while the translucent increments were deposited from December until March, when MIR values were lower, an indication that new increments are formed during this period.

Growth patterns are commonly assumed to be constant or subject to negligible changes during the species' lifespan⁶⁰ and therefore are usually described as a single curve. However, it has been recognized that directing investments toward reproductive strategies can lead to different growth stages during fish species lifetime⁶¹. For boarfish, the biphasic model that best described this species growth was proposed by Alós et al.³⁸, followed a Bayesian approach and proved to be crucial in achieving the final objectives. This model was not previously suggested for this species, however other more general and common models, like the conventional von Bertalanffy model, could not return realistic estimates, even when using individuals from all life stages and as young as 0 years of age. This model's characteristics improved its overall fitness and estimated, with more accuracy, the mean value of each parameter, as demonstrated by this model's lowest DIC value. With its 5 parameters, the model accommodated a faster growth rate in the initial years of life ($k_0 = 0.19 \text{ year}^{-1}$), that decreases quite abruptly to a much slower growth rate ($k_1 = 0.05 \text{ year}^{-1}$), when individuals reach 2–3 years of age ($t_1 = 2.4$ years, approximately 11.54 cm TL). Although many events can motivate and justify a change in the growth rates, like diet, ontogenetic or habitat shifts, this change seems to be motivated by investments in reproduction, as underpinned by the maturity ogive, adjusted for all individuals. Boarfish length of first maturity was estimated at 9.35 cm TL and around 100% of the population's individuals were mature at 11.81 cm TL, corresponding to 2–3 years of age, and coinciding with the breaking point between the fish and otolith size relationship (BP = 1.50 mm OR, approximately 11.98 cm TL) and the age of change in the growth coefficients from the biphasic growth model. The initiation of reproduction implies an energetic investment, that would be zero before the age of first reproduction and corresponds to some fraction of body mass afterwards⁶². Furthermore, the difference between the two growth coefficients found for the Portuguese coast is quite accentuated (Δ growth coefficients = 0.14 years^{-1}), which can be related to the high investment needed to maintain the year-long spawning period of the species in this area²². In relation to the energy acquisition and allocation to reproduction, boarfish is considered an income breeder²². This means that throughout the prolonged spawning season, the species allocates energy directly to reproduction, being dependent of factors such as the adults' daily foraging opportunities⁶³. Income breeders can recover the energy when good feeding conditions are re-established but can draw on the stored energy in the absence of these conditions. This could justify the change in growth found in boarfish.

The relationship between otolith radius and fish total length, which demonstrated an unusual trend, seeming to follow an almost isometric relationship up until a certain fish length, after which it disperses transitioning to an irregular pattern. This pattern translated into a weakly fitting power function model, with relatively low R^2 value. Using a segmented linear model, it was possible to detect a change in the relationship between the two variables, when otolith radius reached approximately 1.50 mm, corresponding to a fish total length of 11.98 cm and around 2–3 years of age. These results further corroborate the estimates obtained both with the biphasic growth model and the maturity ogive, supporting the existence of an event that induces a change in boarfish growth.

For boarfish from the Portuguese coast, the biphasic growth framework provided a more biologically realistic and significant estimate of the growth parameters than uniphasic models and allowed for the additional estimation/inference of another life-history trait (age-at-maturity) using only growth-related data. The conventional VBGM with 3 parameters, with both the frequentist and Bayesian approach, seemed to underestimate boarfish's asymptotic length (L_∞ frequentist = 13.92 cm; L_∞ Bayesian = 14.01 cm), since both estimated values were lower than the maximum TL registered in the present study and those available in literature⁶⁴. Additionally, these growth models' functions assume that the growth coefficient (k frequentist = 0.30 year^{-1} ; k Bayesian = 0.29 year^{-1}) is high and constant throughout the individual's life, which does not seem to be the case for boarfish from the Portuguese coast. Bayesian inference allowed the improvement of this species growth knowledge in comparison to the frequentist approach, since it was possible to incorporate prior information and allow a better estimation of the growth parameters, producing probability values and intervals that have a more intuitive interpretation. Specifically, within the biphasic growth model, the construction of priors, allowed for the "specification" of each growth coefficient and asymptotic growth, based on expert opinion and literature available. Even though some critics argue that the use of prior information based on expert opinion is highly subjective, its value cannot be discounted. The process of inclusion of priors for each parameter was duly explained and transparent in each model, and as mentioned by Doll and Jacquemin⁶⁵, in most situations, researchers already have some degree of prior information about the topic that would be beneficial to their results if included into their analysis.

Final remarks

In conclusion, whole otoliths were considered the best technique for boarfish age estimation from the western Portuguese coast, with maximum age estimated at 15 years. Considering that there is not a standard protocol for age reading for this species, and the existing inconsistencies regarding the technique and maximum age estimated between different laboratories, an interlab exchange event should be considered. The growth pattern showed that two false increments are laid before the first growth increment at 1.045 ± 0.07 mm, and that one growth increment corresponds the alternation between a transparent and opaque increment, with an annual deposition rate. This species growth was best described by a biphasic growth model, where a faster growth in the first years of life (before t_1), that slows down drastically after the maturation, was identified.

It is important that growth parameters, as well as other biology related information, are established during the early stages of a fishery development since their absence can lead to an uncontrolled exploitation. Information gathered early in the fishery development can provide initial estimates of stock distribution, size, and productivity⁶⁶. This study could become the benchmark for boarfish population, for the Portuguese western coast,

before its commercial exploitation initiates with growth parameters estimated from the 5-parameter biphasic model.

Data availability

The script for present Bayesian models is available in the Supplementary material. The data underlying this article will be shared on reasonable request to the corresponding author.

Received: 19 March 2024; Accepted: 26 August 2024

Published online: 31 August 2024

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Acknowledgements

We would like to thank Professor Tiago Marques (University of St. Andrews) for his expertise in statistical modelling and efforts in fostering connections with other esteemed experts in the field, broadening the impact of our research.

Author contributions

MIS conceptualised the idea, analysed data, prepared figures and tables and wrote the main manuscript text. RM contributed to the data analysis. VS and CAA participated in the sample collection. DS performed otolith sections. IF reviewed and edited the manuscript. LSG conceptualised the idea and acquired funding and resources. ARV conceptualised the idea, wrote the main manuscript text, acquired funding and resources, and supervised. All authors reviewed and edited the manuscript.

Funding

This study was partially supported by the European Maritime and Fisheries Fund MAR2020 through the Grant MAR-01.03.01-FEAMP-0003 (“VALOREJET: Valorização de espécies rejeitadas e de baixo valor comercial”), and by Fundação para a Ciência e a Tecnologia (FCT, Portugal) through strategic projects attributed to MARE (ref. UIDB/04292/2020, <https://doi.org/https://doi.org/10.54499/UIDB/04292/2020>; ref. UIDP/04292/2020, <https://doi.org/https://doi.org/10.54499/UIDP/04292/2020>) and ARNET (ref. LA/P/0069/2020, <https://doi.org/https://doi.org/10.54499/LA/P/0069/2020>) and research contracts attributed to Ana Rita Vieira (ref. CEEC-IND/01528/2017, <https://doi.org/https://doi.org/10.54499/CEECIND/01528/2017/CP1387/CT0040>) and Vera Sequeira (ref. CEECIND/02705/2017, <https://doi.org/https://doi.org/10.54499/CEECIND/02705/2017/CP1387/CT0042>).

Competing interests

The authors declare no competing interests.

Ethics statement

Sampling for the present study focused on the boarfish from the western Portuguese coast. Dead specimens were acquired in the commercial port of Peniche and no animals were killed specifically for this study. Ethical or government approval, specific permissions or licenses for sample collection were not required for this study, as all specimens were collected as part of routine fishing procedures by fishermen of commercial fleet. Considering the depth at which this species lives, fish are killed during the hauling of fishing gear due to differences in atmospheric pressure. The experiments were conducted on dead animals, hence, no animal welfare or animal use permits were required for this study. *C. aper* is not an endangered or protected species.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-71209-5>.

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