Fisheries Research 220 (2019) 105351

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Short communication

The visual quality of annual growth increments in fish otoliths increases with latitude

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ARTICLE INFO

Handled by B. Morales-Nin

Keywords:
Otolith growth increments
Seasonality
Ageing

ABSTRACT

This study evaluated the latitudinal influence on otolith readability through average percent error (APE) assessments and contrast ratios evaluations of the opaque and translucent incremental zones in *Micropogonias furnieri* otoliths (n = 83) sampled along the Southwestern Atlantic Ocean. Otolith images show well-structured increments in high latitudes. Contrast ratios increased and APE decreased significantly with latitude, respectively, therefore suggesting that *M. furnieri* otolith visual quality and growth increment readability increase with latitude.

1. Introduction

Otolith increment analysis is the most frequently applied technique to estimate the age and growth of teleosts today. Since their discovery in 1899 (Reibish, 1899), the existence of annual growth otolith increments has been validated for numerous fish species worldwide (Campana, 2001). Annual growth increments are bipartite structures formed by an opaque and protein-rich zone followed by a translucent and protein-poor zone alternately deposited onto otoliths. These otolith zones are induced by the effect of seasonality on fish growth rates throughout the year (Secor et al., 1991; Fowler, 2009). The visual quality of growth increments depends on the visual contrast between the opaque and translucent zones and deeply affects the ability of scientists to conduct reliable age determinations in bony fish. As temperature influences fish growth rates, and its seasonal range decreases towards low latitudes, the visual quality of growth increments has been suggested to decrease towards the tropics (Fowler, 1995; Lalli and Parsons, 1997). Although this idea is currently well accepted among fisheries scientists, the influence of latitude on the visual quality of otolith growth increments has not yet been objectively examined.

The whitemouth croaker *Micropogonias furnieri* (Desmarest, 1823) is a highly abundant demersal Sciaenid that occurs along the Western Atlantic, from the Gulf of Mexico down to Argentina. It supports important fisheries in Argentinean, Uruguayan and Brazilian coastal waters (Vasconcelos and Haimovici, 2006; Carozza, 2010) and is, therefore, easily sampleable along the southwestern Atlantic Ocean. This species is perhaps the most studied fishery resource in the South America and many otolith studies have previously examined stock differentiation (Haimovici et al., 2016), growth and validation (Albuquerque et al., 2009; Borthagaray et al., 2011), otolith morphometry (Santos et al., 2017), and life history (Albuquerque et al., 2010, 2012).

In this context, the present study used adult *M. furnieri* otoliths sampled along the southwestern Atlantic Ocean as a model to test the hypothesis that the visual quality of growth increments in otoliths increases with latitude.

2. Material and methods

Micropogonias furnieri otoliths were sampled by bottom trawling boats operating in Argentina (38 °S 57 °W, n = 15), Uruguay (35 °S 56 °W, n = 15), and Brazil (32 °S 51 °W to 05 °S 35 °W, n = 53), thus encompassing a 33° latitudinal range along the southwestern Atlantic Ocean (Fig. 1). Once in the lab, the otoliths were embedded in epoxy resin, sliced to the core using a low speed diamond saw and glued onto glass slides. Section surfaces were sanded with silicon carbide papers (4000–8000 grit) and photographed using a stereomicroscope (10 – 20x) under transmitted light.

The visual quality of the growth increments was evaluated by applying two objective approaches. First, growth increments were

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https://doi.org/10.1016/j.fishres.2019.105351
Received 27 May 2019; Received in revised form 19 August 2019; Accepted 22 August 2019
Available online 06 September 2019
0165-7836/

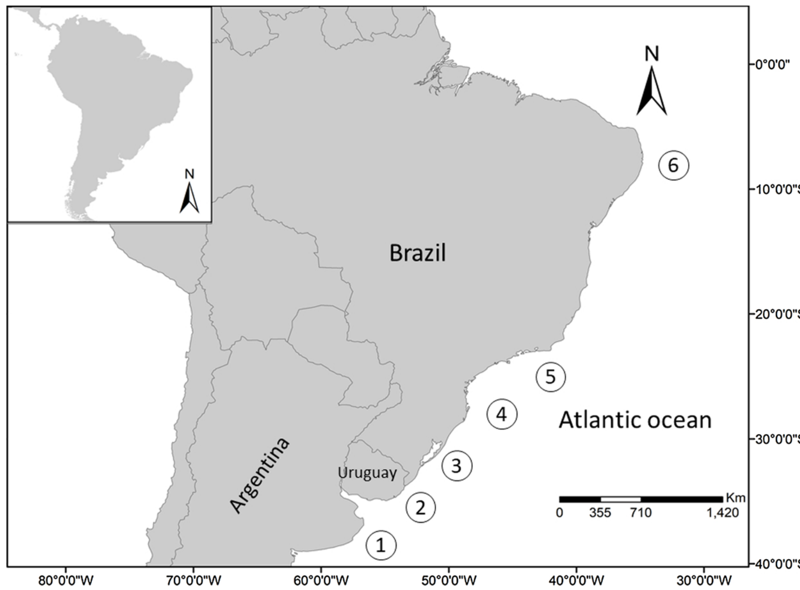

Fig. 1. Sampling region along the Southwestern Atlantic Ocean. Each number represents a sampling site: 1 – Argentina; 2 – Uruguay; 3, 4, 5 and 6 – Brazil.

counted on the screen by three experienced readers and their agreement was assessed through an Average Percent Error (APE, equation below) calculation following Campana (2001), which indicates the degree of error between readers.

$$APE = 100\frac{1}{R}\sum_{i=j}^{R}\frac{|x_{ij} - x_j|}{x_j}$$

Where x_{ij} is the i_{th} age determination of the j_{th} fish, x_j is the mean age estimate of the j fish and R is the number of times that each fish was aged.

Low APE values stand for good visual quality of growth increments. Second, the contrast between growth bands was determined using the ImageJ free software (University of Winsconsin, USA). The contrast ratio was calculated as the ratio between (1) the mean grey level measured in the three translucent bands (high grey values) closest to the otolith edge and (2) the mean grey level measured in their respective opaque bands (low grey values). Therefore, greater contrast ratio values imply better visual quality of growth increments. Latitudinal trends in the visual quality of the growth increments were examined through a correlation analysis, by regressing APE and contrast ratios against sampling latitude. As temperature range plays an important role in fish growth, minimum and maximum sea surface temperatures (SST, Fig. 2A) were obtained from the scientific literature (Lentini et al., 2001; Santiago et al., 2005) and were also plotted against latitude data.

3. Results

Total length and ages of the sampled fish (n = 83) ranged from 360 to 710 mm and from 3 to 43 yr, respectively. Opaque and translucent growth bands in *M. furnieri* otoliths were reasonably discernible, resulting in adequate precision during the otolith reading process regarding the whole sample (APE = 6.7%). However, APE increased significantly towards low latitudes when sampling locations were examined individually (Fig. 2B, r = 0.609; $p < 0.0001$), with the lowest values observed for Uruguay (APE = 2.3%) and the highest for northeastern Brazil (APE = 16.8%). Similarly, contrast ratios between opaque and translucent bands decreased significantly towards lower latitudes (Fig. 2C, r= -0.428; $p < 0.0001$), with the best and worse contrasts observed for Argentinean and northeastern Brazilian otoliths, respectively. Fish from southeastern Brazil presented intermediate contrast ratios. Both APE and the contrast analysis are consistent when visually compared to annual SST ranges, which decreased from about 15 °C off the Argentinean coast to about 4 °C off the northeastern coast of Brazil (Fig. 2A).

The findings reported herein point to a general pattern where the visual quality of growth increments increases with latitude, as also observed in otolith sections along the sampled region (Fig. 3). Otolith increments were clearly visible at temperate and highly seasonal regions such as latitude 40 °S, (Fig. 3A) resulting in adequate agreement between readers. As the seasonal thermal amplitude decreases towards northeastern Brazil (Fig. 2A), the increments become quite hard to see (Fig.3B), with no possible visual separation between opaque and translucent bands in some cases (Fig. 3C).

4. Discussion

This study objectively demonstrated for the first time that the visual quality of annual growth increments in otoliths consistently increases with latitude. The findings corroborate the general understanding that age-based studies from tropical fish otoliths are sometimes untrustworthy and quite hard to develop (Choat and Robertson, 2001; Smith and Deguara, 2003), while the clear incremental structure in temperate fish otoliths allow for reliable growth and mortality evaluations. Accurate information concerning these parameters are

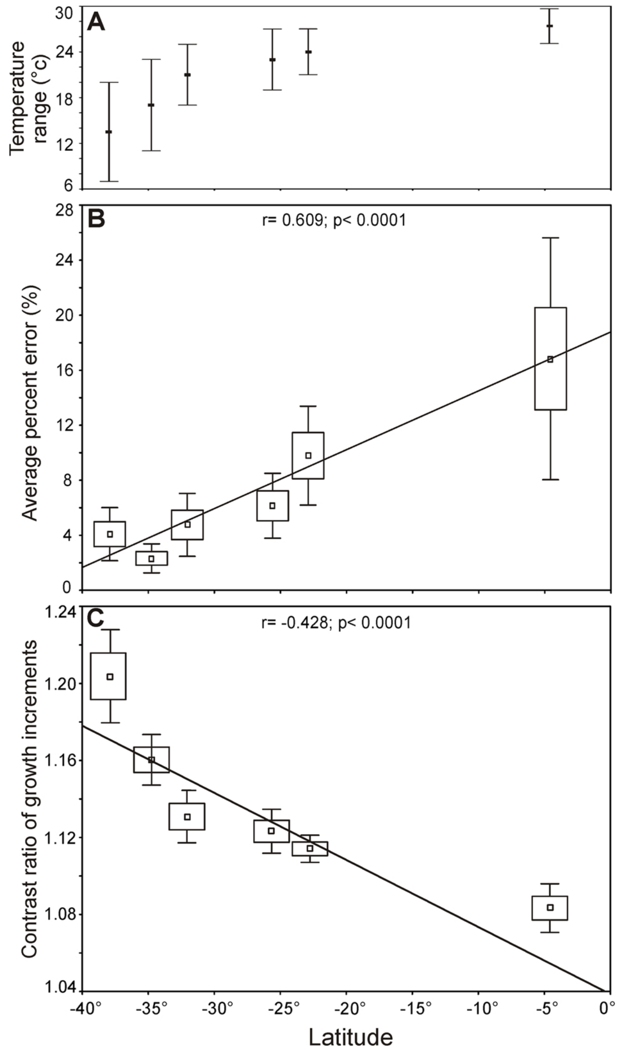

Fig. 2. Sea surface temperature (A), average percent error (B) and contrast ratios of growth increments (C) for *M. furnieri* otoliths plotted against sampling latitudes. Error bars in fig. A represent the means and maximum and minimum values. Boxplots in fig. B and C represent the means, standard errors and 95% confidence intervals. Sea surface temperature data were obtained from Lentini et al. (2001) and Santiago et al. (2005).

mandatory for stock assessments and for the effective management of exploited fish populations (King, 2007).

The growth increments studied here are considered annual (Borthagaray et al., 2011; Santos et al., 2017), and may be classified as type B (Katayama, 2018). However, there is no consensus on the timing of opaque and translucent band formation, as both summer (Santos et al., 2017) and winter (Borthagaray et al., 2011) have been suggested to induce the formation of opaque bands in *M. furnieri* otoliths. The physiological processes underlying otolith biomineralization are not completely understood, but the formation of opaque and translucent zones is generally believed to result from differential fish growth along annual seasons (Høie et al., 2009). Water temperature directly influences fish growth (Brown et al., 2004; Sander et al., 2019), and is perhaps the most important seasonal factor inducing otolith growth increment formation. Following this rationale, fish from temperate regions are suggested to form opaque bands mostly during warm seasons (Aldanondo et al., 2016) as a result of fast growth. However, opaque and translucent zones would not be strictly related to specific annual temperatures, but to a complex interplay between temperature and food availability (Høie et al., 2008; Fablet et al., 2011).

While the processes behind otolith seasonal growth cannot yet be fully explained, the findings reported herein suggest a close relationship between temperature range and visual quality of growth increments in *M. furnieri* otoliths, although they do not yet allow for the establishment of a causal relationship. Therefore, this study aids in increasing the perception that temperature annual range plays an important role on the patterns of growth increment deposition in fish otoliths.

5. Conclusions

This study accepted the hypothesis that the visual quality of growth increments in otoliths increases with latitude, as objectively evaluated by APE and a contrast analysis. The annual temperature range was also higher towards high latitudes, therefore indicating a close relationship between annual seasonality and the visual quality of growth increments in *M. furnieri* otoliths along the Southwestern Atlantic Ocean.

Acknowledgments

MVC acknowledge fellowship support from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES -88882.31316871/2019-01). LCSL would like to thank UFERSA for a PICI undergraduate fellowship (Project number PI1618A-316).

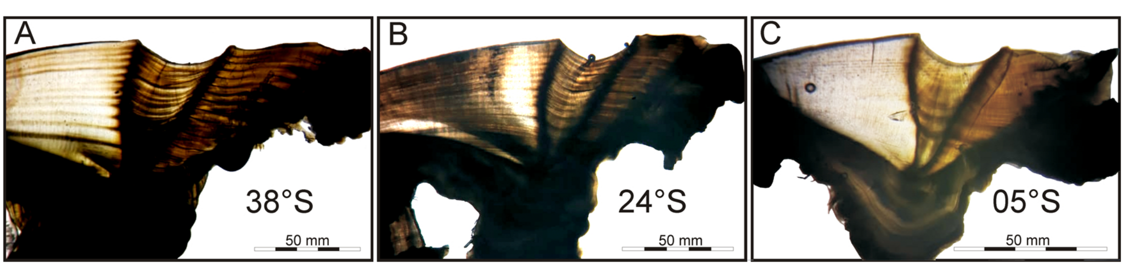

Fig. 3. Photomicrography of 0.5 mm thick *M. furnieri* otolith sections sampled in Argentina (A, latitude 38 °S) and Brazil (B, latitude 24 °S; C, latitude 05 °S). Images were obtained using a stereomicroscope under transmitted light.

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