



## REVIEWS

# Sectioned or whole otoliths? A global review of hard structure preparation techniques used in ageing sparid fishes

Alexander Claus Winkler  · Murray Ian Duncan · Matthew William Farthing · Warren Mason Potts

Received: 24 October 2018 / Accepted: 1 June 2019  
© Springer Nature Switzerland AG 2019

**Abstract** While otoliths are considered the most reliable structure to accurately age fish, a variety of otolith preparation techniques are available, which have consequences on the otolith's optical properties and therefore interpretation of growth bands. Recently, numerous studies from a variety of authors have criticised the use of whole otoliths in ageing sparids with sectioned otoliths subsequently acknowledged as the most reliable preparation technique. Despite this criticism; ageing data is still being generated from whole otoliths and other unreliable structures such as scales. In an attempt to understand the severity of this issue we conducted a global literature review of otolith preparation protocols used for sparids. We identified global spatial inconsistencies in otolith preparation techniques with some regions predominately using methods other than sectioned otoliths to age sparids. The review

highlights the need for a standardisation of otolith preparation methods and a move towards the use of sectioned otoliths, or at least valid support where alternative structures or preparation techniques are used. Given that large numbers of studies have been conducted on whole otoliths in certain regions, it may be necessary to reevaluate the existing growth parameters to ensure that accurate information is incorporated into management structures.

**Keywords** Age and growth · Fisheries management · Sclerochronology · Sparidae

## Introduction

Accurate fish ageing is critical for the estimation of individual and population growth rates, age-at-maturity, and other related indices (de Pontual et al. 2002). Otoliths (usually Sagitta) are considered the most reliable hard structures for ageing fish, due to their metabolically-inert formation, which hinders re-absorption, unlike other structures, such as scales (Simkiss 1974). The Lapillus otolith is less commonly used, due to its small size in most species with the exception of fish from the Cyprinidae family, in which it is larger than the Sagitta and more reliable for ageing purposes (Vilizzi 2018). Most reviews on fish ageing correctly scrutinize the effects of poor age validation techniques and specifically address the timing and

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s11160-019-09571-1>) contains supplementary material, which is available to authorized users.

---

A. C. Winkler (✉) · M. I. Duncan ·  
M. W. Farthing · W. M. Potts  
Department of Ichthyology and Fisheries Science, Rhodes  
University, Grahamstown 6140, South Africa  
e-mail: alexwinkrsa@gmail.com

M. I. Duncan  
South African Institute of Aquatic Biodiversity,  
Grahamstown 6139, South Africa

periodicity of increment formation (Beamish and McFarlane 1983; Horn and Sutton 1996; Campana 2001). While this is an important consideration, the preparation technique used before examining the otoliths should also be taken into account. Currently, fish otoliths are either examined whole, sectioned, broken, or ground-and-polished and in certain instances heat treated or chemically stained to make interpretation of growth increments easier (McCurdy et al. 2002). Sectioned otoliths are usually mounted on a microscope slide using a clear adhesive such as DPX mountant or Canada Balsam. While whole and broken otoliths are read under an immersion medium such as water, glycerol or methyl salicylate to elucidate growth bands (McCurdy et al. 2002). The different techniques influence the optical properties of the otoliths and potentially ageing accuracy and precision.

The most accepted otolith preparation technique for fishes is sectioning, which has been shown to be more reliable (Buxton and Clarke 1989, 1991; Hyndes et al. 1992; Horn and Sutton 1996; Brouwer and Griffiths 2004; Abecasis et al. 2006; Potts et al. 2010; Baudouin et al. 2016; Farthing et al. 2018) but also more time consuming (Hyndes et al. 1992). Whole otoliths are usually used in the ageing of fast growing fish, or in fish with small otoliths that are hard to section and have distinct central rings (Morales-Nin and Panfili 2002). The use of whole otoliths for the ageing of slow-growing fish, or fish with thick otoliths, has been discouraged due to the difficulty of observing growth bands in the central thickened opaque structure of large otoliths, which can cause age underestimation and therefore the mismanagement of fisheries (Hilborn and Walters 2013).

The underestimation of fish age is problematic as it results in an over estimation of individual and population growth rates. This has major implications for the stock assessments of economically-important species, where incorrect analysis can lead to overexploitation (Tyler et al. 1989; Hilborn and Walters 2013). In the case of under-ageing, this occurs when mortality indices are calculated (often based on maximum age) and this is exacerbated when using yield per recruit models, when maximum age is also used to calculate the maximum sustainable yield of a fishery (Beverton and Holt 2012).

Besides issues with stock assessments, the use of different ageing techniques undermines the ability for comparative research across bioregions. This hampers

our understanding of ecological patterns across geographical and temporal scales. One of the fundamental goals of fish life history research is to compare the findings of one study with those of other populations to detangle the allopatric and environmental effects impacting fish growth. Without standardised ageing protocols, growth comparisons are nearly impossible to conduct and therefore limit our ability to understand the allopatric effects on fish life histories.

The Sparidae belong to the order Perciformes and are commonly known as sea breams or porgies (Hanel and Tsigenopoulos 2011). These are found in the temperate and tropical coastal seas around the world where they are important in many subsistence (Richardson et al. 2011), artisanal (Gómez et al. 2006), recreational (Morales-Nin et al. 2005) and commercial (Griffiths 2002) fisheries throughout their distribution. They are known to be slow growing and long-lived (Hanel and Tsigenopoulos 2011) fauna that can be susceptible to over-exploitation (Comeros-Raynal et al. 2016). Sparid fishes generally have relatively large sagittal otoliths (Lapillus are too small to be used in ageing studies), and despite a wealth of literature denouncing the use of whole otoliths in growth studies on Sparid fishes (Buxton and Clarke 1989, 1991; Brouwer and Griffiths 2004; Potts et al. 2010; Baudouin et al. 2016; Farthing et al. 2018) and scales (Baudouin et al. 2016; Abecasis et al. 2008), these techniques are still commonly used. The aim of this study is to conduct a global review to identify the spatiotemporal patterns of the hard structure and otolith preparation methods used for aging the Sparidae. This information will be used to understand the evolving patterns of Sparid ageing research and to identify regions of concern, where suboptimal methods which may have negative consequences for the management and sustainability of Sparid fisheries, are still being used.

## Materials and methods

### Literature review

An online literature review was conducted using both Google Scholar (scholar.google.com) and The Web of Science (webofknowledge.com) online search engines until September 2018 therefore only reviewing papers published before this date. Identical search terms were

used in both search engines, and included key words: “age”, “growth”, “sparid”, “Sparidae”, “porgy” and “seabream”. Search results were manually filtered and only included in the data set if they presented any ageing, age-growth or age-dependent information for a sparid, and explicitly stated which age-determination method was used. Age-determination methods included the use of sectioned otoliths, whole otoliths, other otolith techniques (broken, baked, burnt, ground or polished otoliths) and other structures (scales and vertebrae).

### Data analysis

Data from the literature review were sorted into respective FAO fisheries geographical management areas (see Table 1) and year of publication. A binary (1,0) dataset was generated from the literature review based on whether a study used sectioned (1) or other methods (whole, broken, baked, burnt, ground or polished otoliths and other structures) (0) to age fish. The probability of either otolith method being employed per region over time (year of publication) was estimated using a logistic regression using the R statistical software environment (R Core Team 2018). We applied a generalised linear model (GLM) with a binomial distribution and a logit link function to the data with FAO area (categorical) and year of publication (continuous) as explanatory variables. The trained GLM was used to predict the hypothetical probability of a study being published in each region over time, from the time the first sparidae age and growth study was published until the time the review was completed. In order to understand the global trend

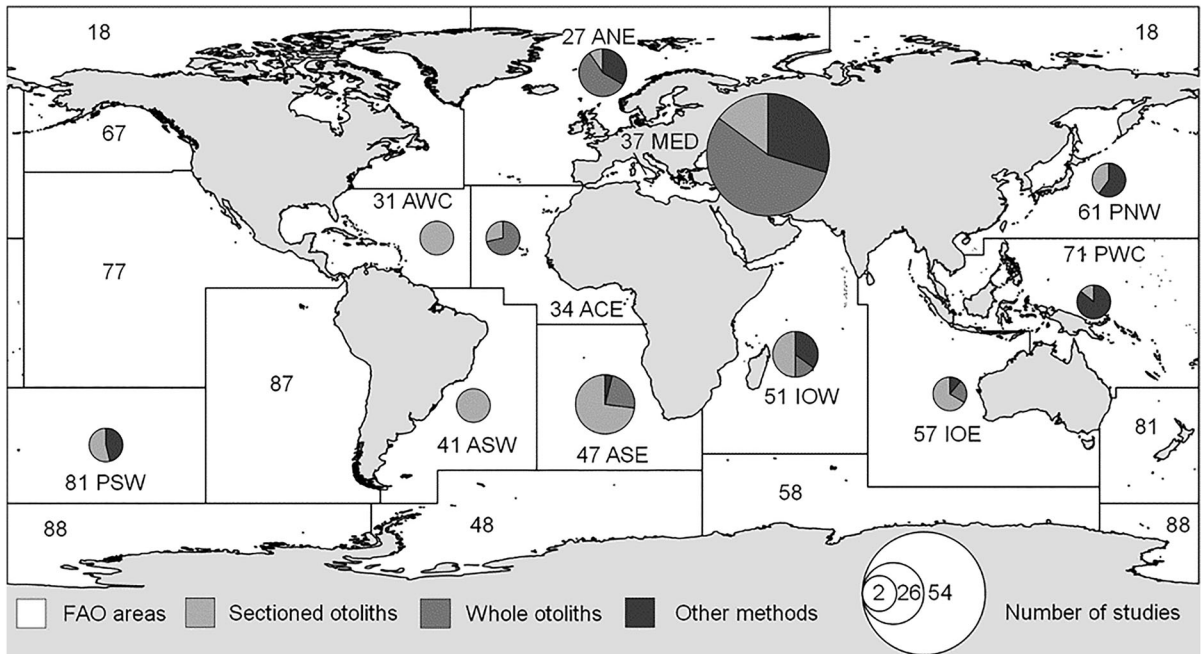
in the probability of sectioned otolith use another GLM was trained with year being the only explanatory variable used. The resultant predicted probability data was plotted using ggplot2 (Wickham and Chang 2016).

### Results

A total of 148 sparidae ageing studies were found based on the literature review’s search criteria (see online Table A1). Based on these results sparidae ageing studies have been conducted in 11 different FAO fisheries regions globally, encompassing the entire geographic range of sparids (Fig. 1). The highest number of sparid ageing studies have been conducted within the MED (FAO 37), followed by the ASE (FAO 47), WIO (FAO 51), AEC (FAO 34), ANE (FAO 27), where 48, 24, 15, 14 and 13 studies were conducted respectively (Fig. 1). Within the six other regions  $\leq 10$  ageing studies have been conducted on sparids (Fig. 1). The AWC (FAO 31) and ASW (FAO 41) regions have only ever published sparid ageing data derived from sectioned otoliths, while areas ASE (FAO 47), WIO (FAO 51), EIO (FAO 57) and PSW (FAO 81) have predominantly published ageing studies using sectioned otoliths ( $> 50\%$  use of sectioned otoliths) (Fig. 1). In contrast, the ANE (FAO 27), AEC (FAO 34), and MED (FAO 37) regions have predominantly utilised whole otoliths ( $> 50\%$  use of whole otoliths) while areas PNW (FAO 61) and PWC (FAO 71) have primarily used structures ( $> 50\%$  use of other structures) other than otoliths for ageing (Fig. 1).

**Table 1** List of FAO fisheries management areas and their associated acronyms in which Sparid fishes are captured and therefore used in this study

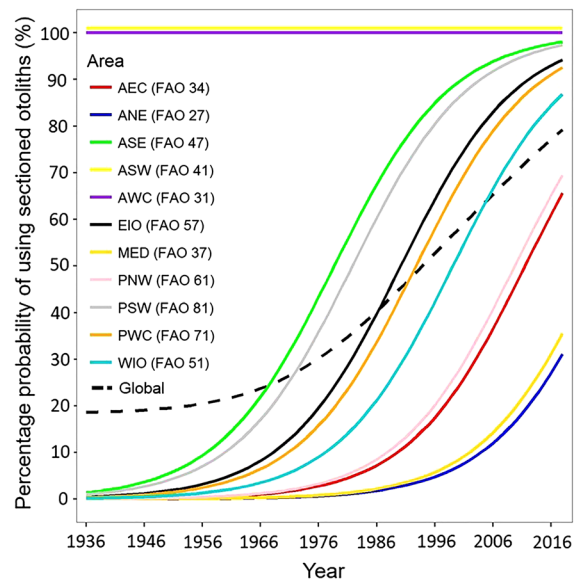
FAO area	Acronym
FAO area 27, Atlantic Ocean, Northeast	ANE (FAO 27)
FAO area 31, Atlantic Ocean, Western Central	AWC (FAO 31)
FAO area 34, Atlantic Ocean, Eastern Central	AEC (FAO 34)
FAO area 37, Mediterranean and Black Sea	MED (FAO 37)
FAO area 41, Atlantic Ocean, Southwest	ASW (FAO 41)
FAO area 47, Atlantic Ocean, Southeast	ASE (FAO 47)
FAO area 51, Indian Ocean, Western	WIO (FAO 51)
FAO area 57, Indian Ocean, Eastern	EIO (FAO 57)
FAO area 61, Pacific Ocean, Northwest	PNW (FAO 61)
FAO area 71, Pacific Ocean, Western Central	PWC (FAO 71)
FAO area 81, Pacific Ocean, Southwest	PSW (FAO 81)



**Fig. 1** Spatial representation of literature review grouped by FAO region where the size of the pie charts represents the total number of ageing studies conducted on sparids and shaded pie

chart segments represent the proportion of studies using either sectioned, whole or other structures (such as scales, opercula and spines) for ageing

Overall, there was an increase in the probability of using sectioned otoliths in Sparid ageing studies from 18.6% in 1936 to 79.3% in 2018 based on the global models' predictions (Fig. 2). The AWC (FAO 31) and ASW (FAO 41) regions had a continuous 100% probability of publishing sparid ageing data using sectioned otoliths regardless of year, while there was a > 80% probability of data using sectioned otoliths by 2018 in the ASE (FAO 47), PSW (FAO 81), PWC (FAO 71), EIO (FAO 57) and WIO (FAO 51) regions of (Fig. 2). In contrast, there was a < 80% probability of publishing data from sectioned otoliths in the AEC (FAO 34) and ANE (FAO 27) regions and < 40% probability in the MED (FAO 37) and PNW (FAO 61) regions by 2018 (Fig. 2).



**Fig. 2** The predicted probability of each FAO region and a combined global region publishing sparid ageing studies using sectioned otoliths as a function of year from when the first study was conducted in 1936 until 2018

**Discussion**

The findings of this review suggest that there are large spatiotemporal discrepancies between the otolith preparation methods used in the ageing of sparids. While there appears to be an increase in the use of sectioned otoliths over time, the probability of certain

regions using this technique remains comparatively low. Areas of particular concern are the ANE (FAO

27) and MED (FAO 37), where the probability of these regions publishing sparid ageing data using sectioned otoliths is well below 50% by 2018 (Fig. 2).

While these results may suggest that there are fundamental problems with the age estimates of Sparid fishes in some regions, it is important to recognise that whole otoliths can, however, remain valid method for estimating the age of short-lived fast growing species (Winker et al. 2011). Fast growth rates are rare in sparids, but certain species do exhibit these features and may therefore be suitable for ageing using whole otoliths (e.g. *Boops boops*) (Massaro and Pajuelo 2018).

Unfortunately, the vast majority of sparids are slow growing, and thus whole otoliths are unsuitable for their ageing. For example, Brouwer and Griffiths (2004) in a comprehensive study, validated the age and growth of *Argyrozona argyrozona*, found that the use of whole otoliths for their ageing was valid up until an age of 10 years. However, due to the thickening of the central region of the otolith (and reductions in its clarity) it was not possible to distinguish the early growth increments of individuals older than 10 years. To evaluate the potential bias of the thickening of the otolith in studies where whole otoliths are used it is recommended that a subset of otoliths from fish of a wide range of sizes are examined whole and sectioned and an age bias plot is produced (Campana et al. 1995; Taylor and Weyl 2012; Baudouin et al. 2016). This approach was used by James et al. (2003) in their study on *Acanthopagrus berda* and the findings provided support for the use of whole otoliths in ageing this species. A pilot study that assesses the validity of using whole otoliths may be an appropriate way forward, as the use of sectioned otoliths may still be a preferable technique which offers more consistency in the optical properties of the increments than whole otoliths (Baudouin et al. 2016). This is critical as there may be considerable intraspecies variation in the clarity of otolith increments (Farley et al. 2006) which would reduce the comparability of studies using whole otoliths.

While we acknowledge the findings of previous studies that utilised whole otoliths in the ageing of sparids, they most likely underestimated age and therefore growth rates for species that grow to older ages (> 10 years). When data from these studies has been incorporated into stock assessment models, the consequences of this bias can be significant. As age is underestimated, growth and natural mortality is

overestimated and this will most likely result in optimistic assessments and potential overharvest (Hilborn and Walters 2013). It is therefore critical that the sparids stocks that are managed based on age and growth information derived from whole otoliths be reassessed using sectioned otoliths. Fortunately, many otolith collections are probably still available as reading whole otoliths does not damage the structure of the otolith, allowing them to be sectioned in the future. For example, the ageing of *Pachymetopon blochii* was recently reconsidered by Farthing et al. (2018) using sectioned otoliths. They found an older maximum age (19 years) when compared with the historical study on the same species (12 years) by Pulfrich and Griffiths (1988). Likewise, Baudouin et al. (2016) aged *Dentex dentex* to 37 years while previous studies estimated a maximum age of 28 years using whole otoliths.

Although this study focused on the use of either whole or sectioned otoliths, other structures (including scales, opercula and spines) were also used for ageing sparids. In particular, > 25% of the ageing studies in as the PWC (FAO 71), PSW (FAO 81) and the MED (FAO 37) regions used these structures for ageing. Indeed, scales, opercula and spines have been recommended above otoliths for the ageing of several species e.g. Spines; *Lopius spp.* (Maartens et al. 1999), Scales; *cypinus carpio*, (Vilizzi 2018) and opercula bones; *Eumegistus illustris* (Mahe et al. 2016). However, a major drawback of the use of these structures is that unlike otoliths, they are metabolically active and prone to reabsorption, damage or removal (in the case of spines and scales) and subsequent regrowth (Simkiss 1974). While these structures may result in under-ageing, they have still been recommended for species whose otoliths do not provide reliable ageing information (e.g., *Lophius vomerinus*, Maartens et al. 1999), or in cases where species are extremely rare and non-lethal sampling methods are preferred (e.g. *Micopterus catatactae*, Long et al. 2018). However, otoliths have been shown to provide reliable ageing information in sparid fishes, a poor conservation status should be the primary factor used to motivate the use of scales or spines in the family. Presently, there are two Sparid species (*Chrysoblephus cristiceps*, *Polysteganus undulosus*) that have been categorised by the IUCN as critically endangered and four (*Chrysoblephus gibbiceps*, *Evynnis cardinalis*, *Lithognathus lithognathus*, *Petrus rupestris*) as

endangered (IUCN redlist) and these may be considered appropriate for ageing with scales or spines.

The broad variation in techniques used for ageing Sparid fishes around the world has limited the comparability of the life history traits between taxonomically similar species. This hampers our understanding of larger biogeographical and ecological patterns in the family. For example, the *Diplodus cervinus* species complex is distributed in the temperate waters of the Mediterranean, Eastern Atlantic, Southern Africa and Oman with numerous biogeographic barriers genetically isolating populations (Gwilliam et al. 2018). While ageing studies have been conducted in the, Eastern Atlantic (Pajuelo et al. 2003), South Africa (Mann and Buxton 1997) and Angola (Winkler 2014) the comparability and understanding of the patterns driving growth in this species complex is questionable as the fastest growing population (*D. c. cervinus*) in the Eastern Atlantic was aged using whole otoliths. Thus to improve the comparability of ageing research on Sparid fishes we recommend that researchers aim to standardise their techniques. Based on the dominant use of otoliths for ageing sparid fishes, we recommend that these structures are used for future age and growth studies in the family. In cases where the species has a poor conservation status, non-lethal sampling methods and the use of spines or scales can be considered. However, this should ideally be done in conjunction with some form of validation with otolith data (e.g. age-bias plots, Campana et al. 1995) to examine the likely error in age estimates for the larger (older) individuals. Due to the general increase in the use of sectioned otoliths (Fig. 2) and their largely accepted accuracy for fishes (Campana 2001) sectioned otoliths are recommended above whole otoliths for the ageing of sparid species.

Finally, the intention of this study is not to denounce previous work, but to highlight a potential bias in the life history assessment and management of sparid fishes. It is hoped that these findings will provide motivation for the reanalysis of ageing data where necessary and a standardised approach for scientists examining the age and growth patterns of fishes in this family. While this study only focused on one family of long-lived fishes, there may be similar concerns for fishes belonging to other families with similar life history characteristics, such as the Serranidae and Sebastes.

## References

- Abecasis D, Costa AR, Pereira JG, Pinho MR (2006) Age and growth of bluemouth, *Helicolenus dactylopterus* from the Azores. *Fish Res* 79:148–154
- Abecasis D, Bentes L, Coelho R, Correia C, Lino PG, Monteiro P, Gonçalves JMS, Ribeiro J, Erzini K (2008) Ageing seabreams: a comparative study between scales and otoliths. *Fish Res* 89:37–48
- Baudouin M, Marengo M, Pere A, Culioli JM, Santoni MC, Marchand B, Durieux ED (2016) Comparison of otolith and scale readings for age and growth estimation of common dentex *Dentex dentex*. *J Fish Biol* 88:760–766
- Beamish RJ, McFarlane GA (1983) The forgotten requirement for age validation in fisheries biology. *Trans Am Fish Soc* 112:735–743
- Beverton RJH, Holt SJ (2012) On the dynamics of exploited fish populations, vol 11. Springer, Berlin, pp 1–446
- Brouwer SL, Griffiths MH (2004) Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a marine protected area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark-recapture. *Fish Res* 67:1–12
- Buxton CD, Clarke JR (1989) The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. *Afr J Mar Sci* 8:57–65
- Buxton CD, Clarke JR (1991) The biology of the white musselcracker *Sparadon durbanensis* (Pisces: Sparidae) on the Eastern Cape coast, South Africa. *Afr. J. Mar. Sci* 10:285–296
- Campana SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J Fish Biol* 59:197–242
- Campana SE, Annand MC, McMillan JI (1995) Graphical and statistical methods for determining the consistency of age determinations. *Trans Am Fish Soc* 124:131–138
- Comeros-Raynal MT, Polidoro BA, Broatch J, Mann BQ, Gorman C, Buxton CD, Goodpaster AM, Iwatsuki Y, MacDonald TC, Pollard D, Russell B (2016) Key predictors of extinction risk in sea breams and porgies (Family: Sparidae). *Biol Conserv* 202:88–98
- de Pontual H, Panfili J, Wright PJ, Troadec H (2002) General introduction. In: Panfili J, de Potual H, Troadec H, Wright PJ (eds) *Manual of fish sclerochronology*. Ifremer-IRD coedition, Brest, pp 19–22
- Farley JH, Clear NP, Leroy B, Davis TL, McPherson G (2006) Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region. *Mar Freshw Res* 57:713–724
- Farthing MW, Winkler AC, Anderson K, Kerwath S, Wilke C, Potts WM (2018) The age and growth of hottentot seabream *Pachymetopon blochii* before and after the South African linefish state of emergency in 2000. *Afr J Mar Sci* 40:187–196
- Gómez S, Lloret J, Demestre M, Riera V (2006) The decline of the artisanal fisheries in Mediterranean coastal areas: the case of Cap de Creus (Cape Creus). *Coast Manage* 34:217–232
- Griffiths MH (2002) Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *Afr J Mar Sci* 22:81–110

- Gwilliam MP, Winkler AC, Potts WM, Santos CV, Sauer WH, Shaw PW, McKeown NJ (2018) Integrated genetic and morphological data support eco-evolutionary divergence of Angolan and South African populations of *Diplodus hottentotus*. *J Fish Biol* 92:1163–1176
- Hanel R, Tsigonopoulos CS (2011) Phylogeny, evolution and taxonomy of sparids with some notes on their ecology and biology. In: Pavlidis MA, Mylonas CC (eds) Sparidae: biology and aquaculture of the gilthead sea bream and other species. Blackwell Publishing, Sussex, pp 51–74
- Hilborn R, Walters CJ (eds) (2013) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Springer, Berlin
- Horn PL, Sutton CP (1996) Validated ages, growth, and productivity parameters for silver warehou (*Seriotelella punctata*) off the south and east coasts of South Island, New Zealand. *N Z J Mar Fresh* 30:301–312
- Hyndes GA, Loneragan NR, Potter CI (1992) Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fish Bull* 90:276–284
- IUCN Redlist. [www.iucnredlist.org](http://www.iucnredlist.org). Accessed 15 Sept 2018
- James NC, Mann BQ, Beckley LE, Govender A (2003) Age and growth of the estuarine-dependent sparid *Acanthopagrus berda* in northern KwaZulu-Natal, South Africa. *Afr Zool* 38:265–271
- Long JM, Holley CT, Taylor AT (2018) Evaluation of ageing accuracy with complementary non-lethal methods for slow-growing, northern populations of shoal bass. *Fish Manag Ecol* 25:150–157
- Maartens L, Booth AJ, Hecht T (1999) The growth of monkfish *Lophius vomerinus* in Namibian waters, with a comparison of otolith and illicia methods of ageing. *Fish Res* 44:139–148
- Mahe K, Rabhi K, Bellamy E, Elleboode R, Aumond Y, Huet J, Roos D (2016) Comparison between the opercular bones, the scales and the otoliths to investigate the growth of the brilliant pomfret (*Eumegistus illustris*) off the coast of Reunion Island (SW Indian Ocean). *Int J Fish Aquat* 4:176–179
- Mann BQ, Buxton CD (1997) Age and growth of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Sparidae) on the Tsitsikamma coast, South Africa. *Cybiuim* 21:135–147
- Massaro A, Pajuelo JG (2018) Life-history traits of seabream *Boops boops* (Linnaeus, 1758) in the central eastern Atlantic Ocean (Canary Islands). *Afr J Mar Sci* 40(4):423–437
- McCurdy WJ, Panfili J, Meunier FJ, Geffen AJ, de Pontual H (2002) Preparation of calcified structures. In: Panfili J, de Pontual H, Troadec H, Wright PJ (eds) Manual of fish sclerochronology. Ifremer-IRD coedition, Brest, pp 331–355
- Morales-Nin B, Panfili J (2002) Observation. In: Panfili J, de Pontual H, Troadec H, Wright PJ (eds) Manual of fish sclerochronology. Ifremer-IRD coedition, Brest, pp 358–368
- Morales-Nin B, Moranta J, García C, Tugores MP, Grau AM, Riera F, Cerda M (2005) The recreational fishery off Majorca Island (western Mediterranean): some implications for coastal resource management. *ICES J Mar Sci* 62:727–739
- Pajuelo JG, Lorenzo JM, Domínguez-Seoane R (2003) Age estimation and growth of the zebra seabream *Diplodus cervinus cervinus* (Lowe, 1838) on the Canary Islands shelf (Central-east Atlantic). *Fish Res* 62:97–103
- Potts WM, Inácio LA, Santos CV, Richardson TJ, Sauer WH (2010) Aspects of the biology and fisheries of an economically important sparid *Dentex macrophthalmus* (Bloch 1791) in the Namibe Province, Angola. *Afr J Mar Sci* 32:601–611
- Pulfrich A, Griffiths CL (1988) Growth, sexual maturity and reproduction in the hottentot *Pachymetopon blochii* (Val.). *South Afr J Mar Sci* 7(1):25–36
- R core team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Richardson TJ, Potts WM, Santos CV, Sauer WH (2011) Comparison of the population structure and life-history parameters of *Diplodus capensis* (Sparidae) in exploited and unexploited areas of southern Angola. *Afr J Mar Sci* 33:191–201
- Simkiss K (1974) Calcium metabolism of fish in relation to ageing. In: Bengal TB (ed) The ageing of fish. Unwin Brothers Ltd, London, pp 1–12
- Taylor GC, Weyl OL (2012) Otoliths versus scales: evaluating the most suitable structure for ageing largemouth bass, *Micropterus salmoides*, in South Africa. *Afr Zool* 47:358–362
- Tyler AV, Beamish RJ, McFarlane GA (1989) Implications of age determination errors to yield estimates. *Can Spec Publ Fish Aquat Sci* 108:27–35
- Vilizzi L (2018) Age determination in common carp *Cyprinus carpio*: history, relative utility of ageing structures, precision and accuracy. *Rev Fish Biol Fish* 28:461–484
- Wickham, Chang (2016) ggplot: an implementation of the grammar of graphics in R. R package version 2
- Winker H, Weyl OL, Booth AJ, Ellender BR (2011) Life history and population dynamics of invasive common carp, *Cyprinus carpio*, within a large turbid African impoundment. *Mar Freshw Res* 62:1270–1280
- Winkler AC (2014) Taxonomy and life history of the zebra seabream, *Diplodus cervinus* (Perciformes: Sparidae), in southern Angola. M.Sc. Dissertation, Rhodes University. <http://hdl.handle.net/10962/d1012062>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.