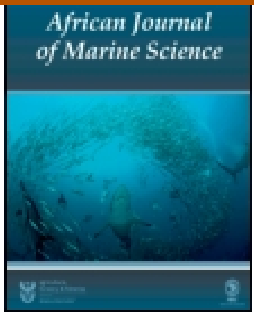

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Aspects of the biology and fisheries of an economically important sparid *Dentex macrophthalmus* (Bloch 1791) in the Namibe province, Angola

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The sparid *Dentex macrophthalmus* is a widespread, important fishery species along most of the West African coast from southern Namibia to the Mediterranean. In southern Angola it is an important artisanal species targeted predominantly by handline fishers. A biological and fisheries study was conducted on this species in southern Angola between June 2008 and July 2009. It was the dominant species in the artisanal fishery, accounting for 99% of the sparids captured and 67% (by mass) of the total catch. The life history of *D. macrophthalmus* was characterised by slow growth (females: $L_t = 309[1 - e^{-0.06(t + 5.43)}]$, males: $L_t = 248[1 - e^{-0.16(t - 1.77)}]$), advanced age at maturity (females: 7.4 years, males: 6.0 years) and high longevity (females: 36 years, males: 38 years). The sex ratio was 1:1 male:female. The length- and age-frequency distributions and macroscopic observations suggested that the species is a late gonochorist. Males and females reached 50% maturity at 151 and 166 mm fork length respectively. Although individuals with ripe gonads were found during most of the year, the peak spawning period appeared to be in December and January. Despite a life history that renders *D. macrophthalmus* vulnerable to overexploitation, only 38% of artisanal fishers noticed a decline in the catches of this species. Potential reasons for this include: technology creep; limited pressure on the juvenile portion of the stock as a result of late recruitment (above the length of 50% maturity); the 'basin affect', whereby depleted areas are reseeded by areas (e.g. deeper water) inaccessible to the linefishery; and a deep-water reserve of large individuals. It is recommended that precautionary management strategies be implemented until the age estimates are revised by the countries in which this species forms significant fisheries.

Keywords: growth, large-eye dentex, management, mortality, reproduction, Sparidae

Introduction

Dentex macrophthalmus is a small, commercially important sparid fish that is abundant in the deeper waters (range 50–500 m) of the Mediterranean Sea (Trunov 1970), the North-West African shelf (Goode and Bean 1896, Fowler 1936), including the Cape Verde and Canary Islands, and the south-eastern Atlantic from the Equator to just south of Lüderitz (27°40′ S) (Trunov 1970). Because of its high abundance, it is of considerable economic importance and is captured in large numbers in both artisanal and commercial fisheries in many countries. Although it is the most important artisanal species along the entire Angolan coast, it is most abundant in the southern region (Kilongo et al. 2007). Despite its economic importance in Angola and elsewhere, relatively little is known on its abundance, fisheries and biology.

The available knowledge on the abundance of *D. macrophthalmus* in Angola is limited to information from non-species-specific demersal acoustic surveys. Between 1986 and 1992, the biomass of seabream (Sparidae) in the demersal zone of Angola was estimated at between 35 000 and 84 000 t. Results of trawl surveys conducted along the Angolan coast indicated that *D. macrophthalmus* is by far the dominant sparid between the Cunene and Tômbua (Figure 1), while the red pandora *Pagellus bellottii* is the most abundant species (~50%) between Benguela and Luanda, followed by roughly equal proportions of *D. macrophthalmus* and *D. angolensis* (~15%) (Duarte et al. 2005). Between Luanda and Cabinda, the red pandora remain dominant (~30%), whereas *D. macrophthalmus* is one of the minor seabream species (~2%) in that region (Duarte et al. 2005).

Small sparids account for approximately 18% of the catch in the Angolan artisanal fishery (Duarte et al. 2005). Unfortunately, there is little resolution in terms of the species composition as fishers and fisheries personnel

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Figure 1: Map of the southern Angolan coastline showing the study area and sites mentioned in the text

generally refer to small, pink sparids (<40 cm total length [TL] of any species) as 'cachuchu' and larger fish as 'pargo'. Nevertheless, *D. macrophthalmus* was identified to be one of the main artisanal species in six of the seven coastal provinces (Duarte et al. 2005).

Whole otoliths, scales and length frequency analysis were used by Domanevskiy et al. (1970), Nguyen and Wojciechowski (1972), Trunov (1972), Mennes (1985) and Domanevskaya 1987 to age *D. macrophthalmus*. Those authors described it as being relatively fast-growing, reaching maturity at approximately 1 year and having a maximum age of between 6 and 13 years. Although there is little published information specifically on their reproduction, the species has been described as a late gonochorist (Alexseev 1975, cited in Heese 1985), with males and females maturing at a relatively small size (13–24 cm TL; Druzhinin 1976, Bauchot and Hureau 1986, Magnusson and Magnusson 1987). Their spawning season appears to be fairly protracted, being reported in all months of the year in Namibian waters (Druzhinin 1976). It has been described as an opportunistic carnivore (Domanevskaya and Patonika 1985, Kilongo et al. 2007).

Despite its dominance in the catch of artisanal fisheries and its obvious importance to the livelihoods of coastal communities, there is no management directed towards *D. macrophthalmus* in Angola. This is in part due to that government's policies, which rely on the artisanal fishery being the major food provider, while the government focuses on repairing infrastructure after the war (1975–2002), and to the misguided belief that management strategies should only be implemented once the total catch in the artisanal fishery exceeds 150 000 t per annum (Duarte et al. 2005).

Although often neglected by coastal states, rigorous scientific assessment should underpin the development of fisheries management strategies (Mora et al. 2009). Here, we describe aspects of the fishery for *D. macrophthalmus,* the perspectives of artisanal fishers, as well as the life history of the species, including age, growth, size- and age-at-sexual-maturity, and reproductive seasonality. Management options for the species in the Angolan fishery are identified and discussed.

Material and methods

Study area

The Namibe province is dominated by the dry Namib Desert and is characterised by a low population density that is concentrated in three major coastal towns, Tômbua, Namibe and Lucira (Figure 1). With a lack of industry and agricultural opportunities, the fishery, and most specifically the artisanal fishery, is critical for the livelihoods of the coastal communities in the region.

Fishery information

Catches in the artisanal boat-based hook-and-line fishery were inspected during a two-week period in June 2008, October 2008, January 2009 and May 2009. Inspection sites were situated at artisanal landing sites in the towns of Tômbua, Namibe and Lucira (Figure 1). Fishers in this sector use an average of four handlines per vessel, with small hooks ranging in size from 10 to 14 with a mode of 10 (gape width = 9.3 mm). Artisanal fishers use motorised vessels, 'chatas' (<8 m) and 'catrongas' (>8 m), and primarily target reef-associated species such as *D. macrophthalmus* and geelbek (known locally as corvina) *Atractoscion aequidens* at depths between 100 and 250 m. Besides identifying and weighing the fish in the catches, fishers were formally interviewed using a questionnaire to determine their perceptions of the fishery, including their perceived status of important artisanal species.

Biological data collection

Biological sampling for *D. macrophthalmus* was conducted between June 2008 and May 2009. Samples were purchased monthly (except November) from the artisanal fisheries in the towns of Namibe and Tômbua. Every effort was made to purchase fish from as wide a size range as possible each month. Once purchased, fish were stored on ice or frozen until they could be processed. In the laboratory, fish were measured to the nearest mm (fork length [FL] and total length), dissected and sexed. The gonads were categorised macroscopically according to five developmental stages (Table 1) and weighed to the nearest 0.1 g. Saggital otoliths were removed from each fish and stored in labelled manila envelopes.

Table 1: Macroscopic criteria used to stage gonad development for *D. macrophthalmus* in southern Angola

Stage	Development	Macroscopic appearance
I	Juvenile	Not possible to visibly distinguish sex Gonad appears as a translucent, gelatinous strip
II	Immature	Ovaries translucent orange tubes. Oocytes are not macroscopically distinguishable Testes are discernible as thin, flat, white bands
III	Resting	Ovaries slightly larger. Oocytes visible as tiny yellow granules in gelatinous orange matrix Testes noticeably broader and appears as a flat, broad, white band
IV	Developing	Ovaries larger in diameter and orange/yellow in colour Oocytes readily visible and occupying the entire ovary Testes broadened, distended and mottled and creamy-beige in colour
V	Ripe	Ovaries large in diameter and orange. Oocytes dark orange, large (>90 mm diameter) and hydrated Testes swollen to maximum size. Cream in colour due to considerable quantities of sperm. Sperm extruded when pressure is applied to the abdomen
VI	Spent	Ovaries pinky-red, flaccid and sac-like with few vitellogenic oocytes visible Testes shrivelled, reduced in size and grey in colour

Laboratory analysis

Otoliths were embedded in clear polyester casting resin and sectioned (0.4 mm) transversely through the nucleus with a double-bladed, diamond-edged saw. The sections were mounted onto glass slides with DPX mountant, and examined for opaque growth zones on three occasions under transmitted light at a magnification of between 20× and 50×. The median of the three readings was accepted as the age estimate, but the otolith was rejected if all three readings differed. The periodicity of opaque zone formation was validated using a marginal zone analysis. The outer margin of the otolith was examined and the optical appearance was categorised as either opaque or hyaline and expressed as a fraction of the monthly sample.

Data analysis

The precision of the aging process was measured using the index of average percentage error (APE) (Beamish and Fournier 1981) and the mean coefficient of variation (CV) (Chang 1982). The monthly proportions of otoliths with a hyaline edge were fitted to a periodic logistic regression using the methods described in Winker et al. (in press). A log-likelihood ratio test was used to test the null hypothesis that the annual hyaline ring deposition was unimodal (rejected if $p < 0.05$).

A three-parameter von Bertalanffy (Ricker 1975) growth model was fitted to the observed length-at-age data using a downhill simplex search (Nelder and Mead 1965), which is a non-linear minimisation routine to obtain model parameter estimates. Model fits were obtained by minimising the negative normal log-likelihood of the observed and predicted lengths-at-age. To compare the model fits, a non-parametric, one-sample runs test for residual randomness and the Bartlett's test for their homoscedascity were applied. In addition, variance estimates were calculated using the (conditioned) parametric bootstrap resampling method (Efron 1982) with 1 000 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). A likelihood ratio test (Cerrato 1990) was used to compare the male and female fitted growth model parameters.

The length- and age-at-50% sexual maturity was determined using macroscopic staging information (Table 1). All fish in stages I, II and III were considered immature and those in stages IV, V and VI mature. Fish were separated into 50 mm length classes and one-year age classes, and the proportion of sexually mature fish in each length and age class was fitted with a logistic ogive of the form:

$$PM_i = 1/1 + e^{-(l_i - l_{50})/\delta}$$

where PM_i is the proportion of mature fish in the ith length class, l_i is the midpoint of the ith length (or age) class, l_{50} is the mean length (or age)-at-50% maturity and δ is the width of the logistic ogive (this describes the rate at which the population changes from 0% to 100% mature). Maximum likelihood estimates of the parameters were obtained by minimising a binomial likelihood.

The age-at-50% sexual maturity could not be estimated in the same way as the length-at-50% sexual maturity because the low number of fish in each age class reduced the validity of the model. To overcome this, a simple conversion of the length-at-50% maturity to age-at-50% maturity using the von Bertalanffy growth model equation

$$t = t_0 - \frac{1}{K}\ln(1 - \frac{L_t}{L_\infty})$$

was considered logical. However, this method only provides an age-at-50% maturity estimate without an indication of the rate of maturation (or the 'steepness' of the ogive). Using the steepness of the length-at-50% maturity ogive as the age-based equivalent is negatively biased (as fish tend to take longer to grow to larger lengths).

It should be noted that the steepness parameter

$$\delta_L = \frac{L_{75} - L_{50}}{\ln(3)}$$

where L_{75} and L_{50} are the lengths corresponding to when 75% and 50% of the population are mature due to a reparameterisation of the logistic ogive, such that

$$P(L)=\left[1+\exp\left(-\frac{(L-L_{50})}{\delta_L}\right)\right]^{-1}=\left[1+\exp\left(-\ln(3)\frac{(L-L_{50})}{(L_{75}-L_{50})}\right)\right]^{-1}$$

The age-based estimates of maturity were therefore calculated using the method proposed by Booth and Weyl (2004):

$$P(t)=\left[1+\exp\left(-\frac{(t-t_{50})}{\delta_t}\right)\right]^{-1}$$

where $\delta_t=\frac{1}{K}\ln\left(1-\frac{L_\infty-\delta_L}{\sigma_L\ln(3)}\right)$ and $t_{50}=t_0-\frac{1}{K}\ln(1-\frac{L_{50}}{L_\infty})$.

Results

Fishery information

In all, 155 boat inspections and interviews were conducted. *Dentex macrophthalmus* was the dominant species (67% by mass) in the catch of the Namibe, Tômbua and Lucira artisanal fisheries, followed by *A. aequidens* (22%) and horse mackerel *Trachurus trecae* (7%). There were no other sparid species important in the artisanal catch. The monthly catch rate remained high throughout the year (average = 6.7 kg boat h^{-1} (SD 4.7); range = 3.4–8.6 kg boat h^{-1}) with no apparent seasonal fluctuations. Recruitment into the fishery appeared to occur at approximately 160 mm FL as the smallest *D. macrophthalmus* observed in the catch was 156 mm FL.

Almost all (89%) of the 155 interviewed fishers felt that artisanal fishing effort had increased in the past five years. Whereas 88% of the fishers had noticed reductions in the size and abundance of all fish in the fishery, only 38% noticed a decrease in the catches and/or size of *D. macrophthalmus.*

Biological information

A total of 444 *D. macrophthalmus*, ranging in size from 156 mm FL (60 g) to 331 mm FL (708 g) with a mean length of 227 FL mm and weight of 230 g (Figure 2), was examined. The relationship between FL and TL was described by the linear relationship: TL = 1.08 × FL + 2.17, whereas the relationship between FL and mass (*M*) was best described by a power function: $M = 0.00002 \times FL^{2.98}$.

The smallest mature female and male were 168 mm FL (91 g) and 160 mm FL (81 g) respectively. Length-at-50% maturity for all fish was 160 mm FL, with males maturing at a smaller size (151 mm FL) than females (166 mm FL). The pattern of maturation for the species was described by the logistic curves presented in Figure 3. Although the population sex ratio was 1:1, males dominated the small and females the large size classes (Figure 4).

Females with ripe gonads were present throughout most of the year, but the greatest proportion of ripe female fish was found in December and January (Figure 5a). Almost all females were in a developing phase from February, with an increasing proportion of fish with ripe gonads each month thereafter (Figure 5a). Female gonadosomatic index (GSI) gradually increased from June and peak between October and January (Figure 6a). Males with ripe gonads were present throughout most of the year, suggesting no clear seasonal pattern of reproductive development. However, as the gonads of all male fish were in a resting phase in February, it appears that the primary spawning time was in

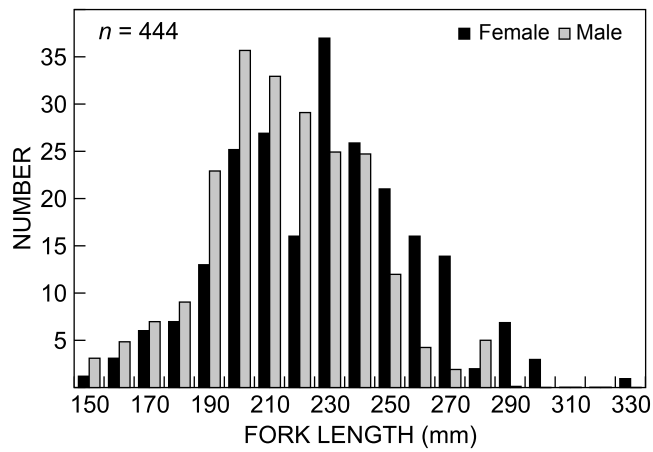

Figure 2: Length frequency of *D. macrophthalmus* captured in the artisanal fishery in southern Angola between June 2008 and May 2009

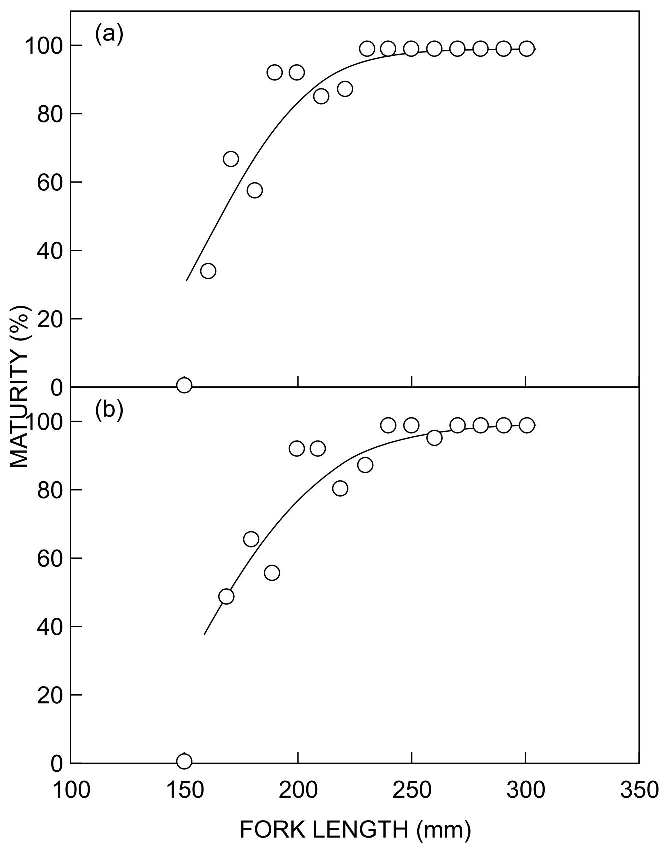

Figure 3: Pattern of sexual maturation by length of (a) female and (b) male *D. macrophthalmus* in southern Angola between June 2008 and May 2009

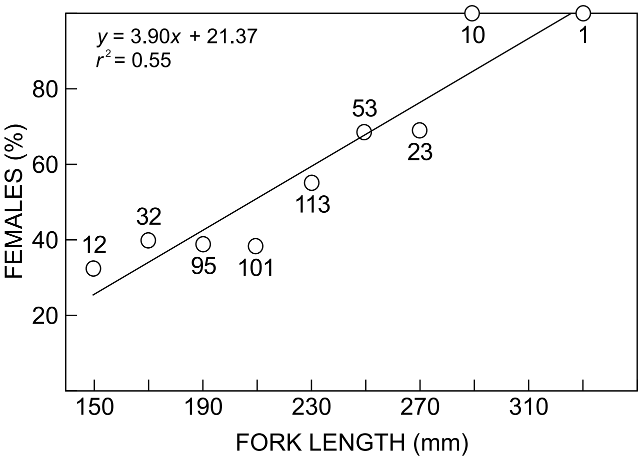

Figure 4: Relationship between the proportion of females and the fork length of *D. macrophthalmus* in southern Angola between June 2008 and May 2009. The number of fish in each size class is shown

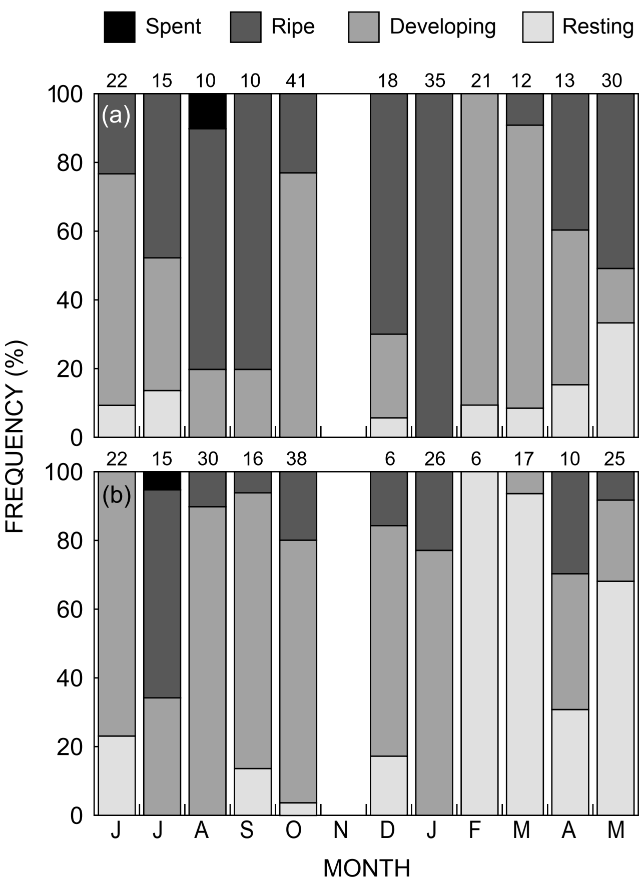

Figure 5: Seasonal macroscopic categorisation of the gonads of (a) mature female and (b) male *D. macrophthalmus* in southern Angola between June 2005 and December 2006. Numbers denote the number of individuals examined

January (Figure 5b). The male GSI fluctuated throughout the year, with peaks in July, October and January (Figure 6b).

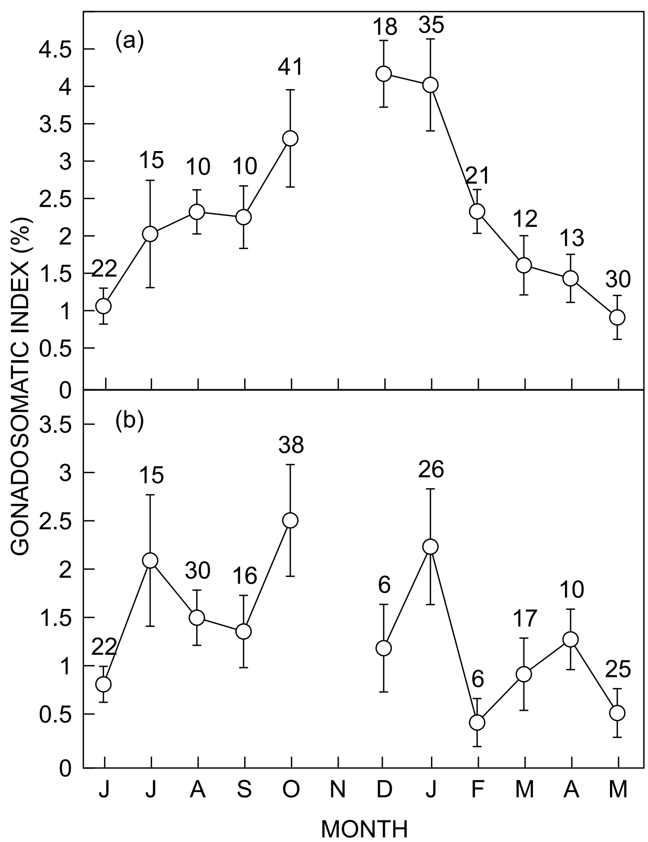

Figure 6: Monthly gonadosomatic index values for (a) mature female and (b) male *D. macrophthalmus* in southern Angola between June 2005 and December 2006. Numbers denote the number of individuals examined

Of the 444 otoliths examined for age determination, 75 were rejected because the number of opaque rings observed during all three readings differed. The APE was 5.5% and the CV was 7.1%. Although the margins of most of the otoliths were opaque during most months, the proportion of otoliths with hyaline zones decreased from a distinct peak in July to the lowest levels the following May (Figure 7). The periodic regression estimated a period of 12.1 months for the formation of one opaque and one hyaline zone, so the hypothesis that one opaque zone was formed per annum was accepted (p = 0.97).

The oldest female was 36 years and in males 38 years, and the mean individual age was 15.9 years. The three-parameter von Bertalanffy growth model appeared to fit the observed length-at-age data for each sex, with realistic estimates of L_∞ and residuals that were both random and homoscedastic. A comparison of the female and male von Bertalanffy growth parameters showed no significant difference in the Brody coefficient (k) (p = 0.07) or in the theoretical length at age zero (t_0) (p = 0.09). However, the calculated asymptotic length (L_∞) (p = 0.04) and whole model (p = 0.01) for male and female fish was significantly different, suggesting that females grow significantly faster than males (Figure 8). Female and male growth (in mm) was described

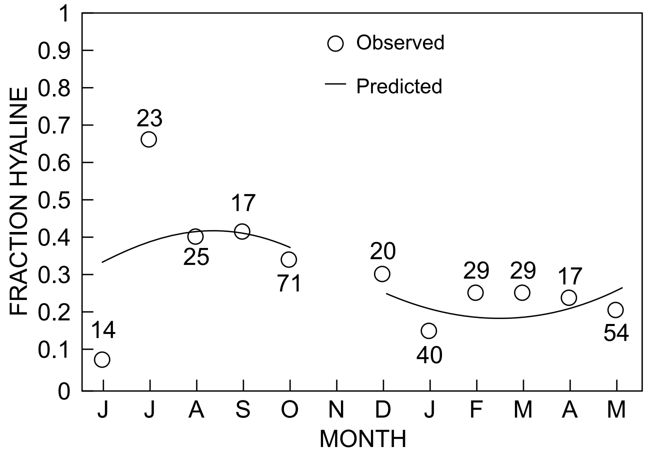

Figure 7: Periodic regression fitted to the marginal zone analysis of *D. macrophthalmus* captured between June 2008 and May 2009. Numbers denote the number of individuals examined

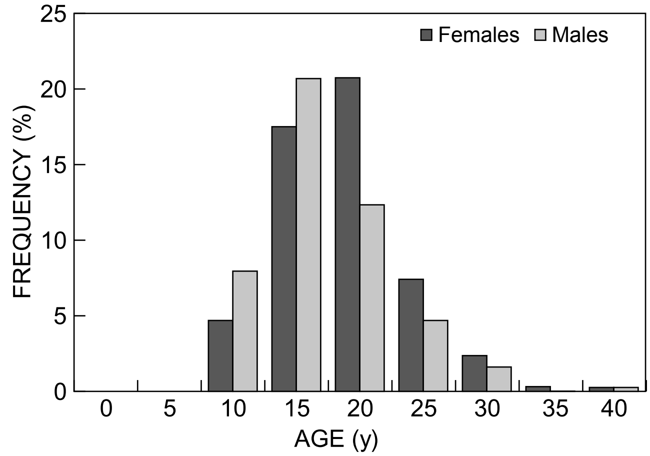

Figure 9: Age frequency of *D. macrophthalmus* sampled in southern Angola between June 2008 and May 2009

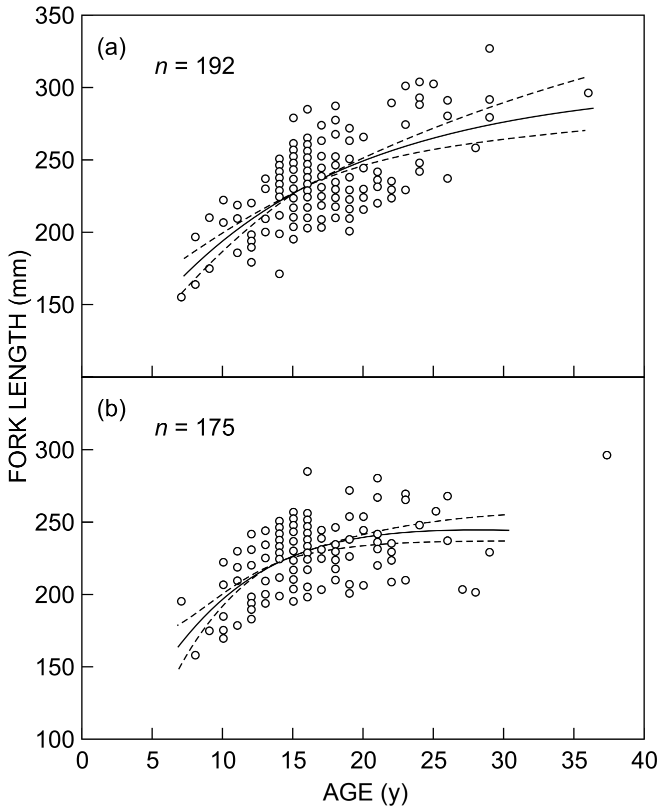

Figure 8: Growth of (a) female and (b) male *D. macrophthalmus* collected between June 2008 and May 2009 in southern Angola. Dashed lines denote 95% confidence intervals from the bootstrapped predicted lengths at age.

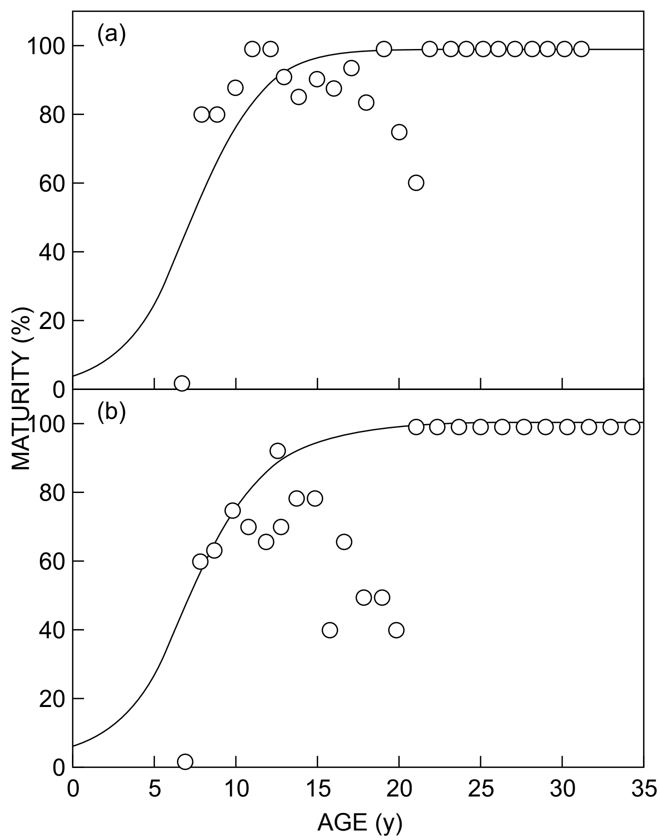

Figure 10: Pattern of sexual maturation by age of (a) female and (b) male *D. macrophthalmus* in southern Angola between June 2008 and May 2009

by the von Bertalanffy growth equations: $L_t = 309(1 - e^{-0.06(t + 5.43)})$ and $L_t = 248(1 - e^{-0.16(t - 1.77)})$ respectively (Figure 8). Male fish were dominant up to the age of 20 years, after which females dominated the population (Figure 9).

The age-at-50% maturity was 7.7 years and 7.5 years for males and females respectively. The pattern of maturation for the species was described by the logistic curves presented in Figure 10.

Discussion

Comparing historical studies on *D. macrophthalmus* to the present study, it is clear that, while the size at maturity and reproductive seasonality are similar, the age, growth and age at maturity estimates differ considerably (Table 2). This may be on account of smaller and larger individuals not being well represented in our study. Although the maximum size for this species is 608 mm FL (650 mm TL) (Bauchot 1987), no individuals near that size were observed during various surveys in southern Angola between 2005 and 2010. In fact, the maximum size reported from previous studies on this species off the West African coast is 355 mm FL (390 mm TL) (Heese 1985). Because trawl data were not used in our study, the small size classes (<150 mm FL) were under-represented. However, in a feeding study of *D. macrophthalmus* in Angolan and Namibian waters, Kilongo et al. (2007) found few specimens (n = 9) <150 mm FL in trawl samples. It is likely that large *D. macrophthalmus* were well represented in our study, but that small individuals were under-represented. This bias could be rectified by incorporating extensive trawl surveys in the sampling programme, but the cost of this would be prohibitive.

With no discernible differences found in the size range of *D. macrophthalmus* examined during the current study and those in previous age and growth studies, the differences in the growth rates may be a consequence of the less robust ageing techniques used in the past. The comparatively low maximum ages and fast growth rates estimated in some previous studies can be attributable to the aging techniques used. The use of scales (Trunov 1972) and whole otoliths (Domanevskiy et al. 1970, Nguyen and Wojciechowski 1972) have been shown to significantly underestimate the age of older sparids (Buxton and Clarke 1989, 1991, Francis et al. 1992, Brouwer and Griffiths 2004) and other fish (Beamish and McFarlane 1987, Hyndes et al. 1992, Horn and Sutton 1996). The species under study was no exception, because an initial analysis of the otoliths showed that age estimates were underestimated when the whole otoliths were read (Figure 11). The use of length frequency analysis for aging *D. macrophthalmus* (Mennes 1985) is considered unsuitable as there are no clearly discernible modal length classes in longer-lived species (Morales-Nin 1989), and the modal age and length classes frequently do not correspond (Campana 2001). Furthermore, the use of one length frequency sample pooled over three years (Mennes 1985) is not considered a robust ageing method as the modal length progressions cannot be followed (Campana 2001). Besides the questionable accuracy of the aging techniques, the age validation in the previous studies must be considered. Domanevskiy et al. (1970) and Trunov (1972) used a marginal zone analysis on scales and whole otoliths and validated the formation of two seasonal rings annually. Whereas studies that validated the annuli of whole otoliths using a marginal increment analysis were accepted for other long-lived species such as redfish (*Sebastes* spp.), subsequent studies have demonstrated that whole otoliths grossly underestimate age in older fish (Campana et al. 1990). Brouwer and Griffiths (2004) supported this finding when they concluded that sectioned otoliths are an improved technique for aging sparid fish.

Table 2: A comparison of the aging methods, validation results and selected life-history characteristics of *D. macrophthalmus*

Country/region	Aging method	Validation (rings y^{-1})	A_{max}	L_∞	k	t_0	Phi prime (Φ)	Omega (ω)	L_{50}	A_{50}	Source
South-West Africa (now Namibia)	WO/SC	2	6								Trunov (1972)
Mauritania	WO	None	13	37.5	0.16	−1.32	5.4	6.0			Nguyen and Wojciechowski (1972)
Cape Verde	WO	None	13	39.0	0.16	−0.88	5.5	6.24			Nguyen and Wojciechowski (1972)
Morocco	LF	None		57.0	0.25		6.7	14.25			Mennes (1985)
Mauritania and Cape Verde		None	13	40.5	0.20	−1.06	5.8	8.1	16	1	Domanevskaya (1987)
Mauritania	WO	2	6						13–14		Domanevskiy et al. (1970)
Bojador, Morocco	NI	NI		34.3	0.19	−0.16	5.4	6.5			Anon. (1987)
Ajadir, Morocco	NI	NI		52.7	0.09	−1.54	5.5	4.7			Anon. (1987)
Mauritania									15–17		Stepkina (1970)
Cape Verde									18–21		Magnusson and Magnusson (1987)
Mediterranean									24	2	Bauchot and Hureau (1986)
Angola (females)	SO	1	37	30.9	0.06	−5.43	4.0	1.9	15	6	This study
Angola (males)	SO	1	36	24.8	0.16	1.77	4.6	4.0	17	7	This study

WO = whole otoliths
SC = scales
LF = length frequency
NI = not indicated

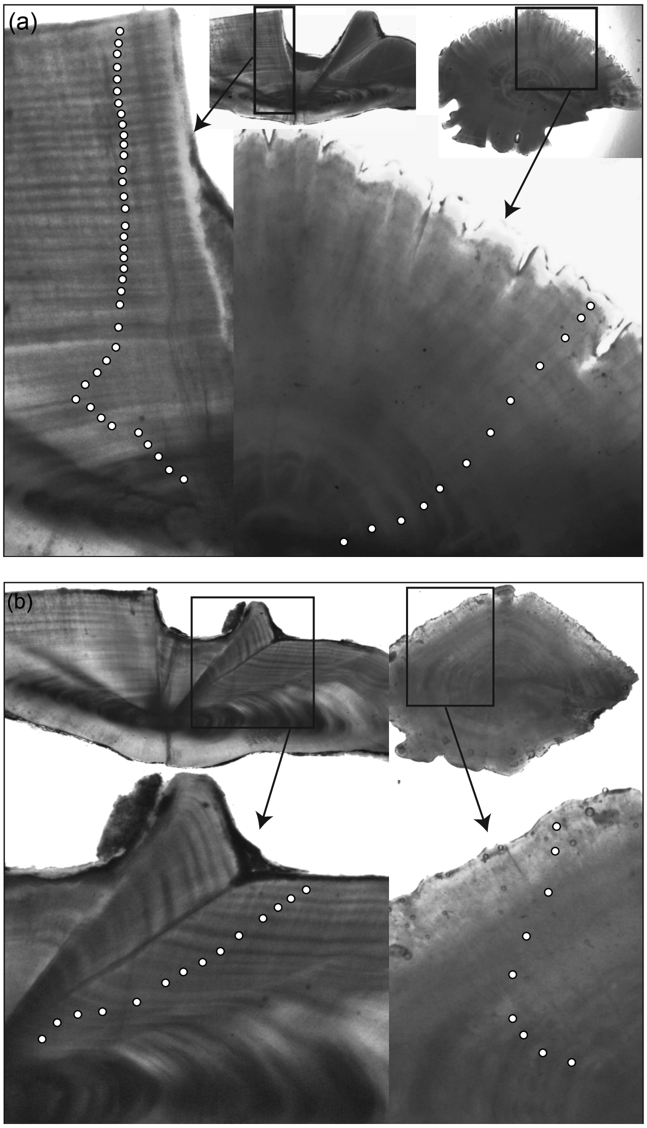

Figure 11: Comparison of the number of opaque zones (white dots) visible on a sectioned (left) and a whole (right) otolith from (a) a 38-year-old and (b) a 13-year-old *D. macrophthalmus* from southern Angola

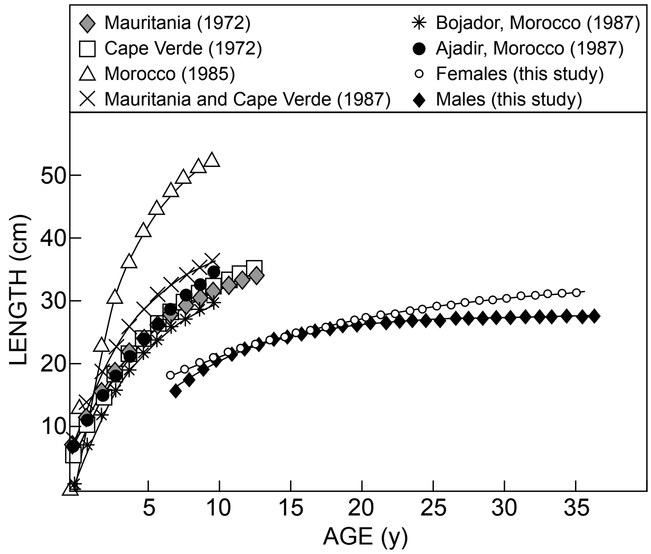

Figure 12: Comparison of the growth curves estimated for *D. macrophthalmus* at various locations in West Africa (refer to Table 2 for sources of these data)

Marginal zone analysis of the sectioned otoliths in our study confirmed the deposition of only one opaque and hyaline ring per annum. Although it is recognised that a marginal zone analysis is one of the least robust techniques for age validation (Campana 2001), the deep habitat occupied by these fish precluded the use of more appropriate techniques, such as chemical marking. Other techniques such as radiocarbon analysis, which is particularly suitable for long-lived fish (Campana 2001), was not considered due to costs considerations.

Having accepted the validation of one opaque and hyaline zone per year, the current growth estimates of *D. macrophthalmus* are appreciably slower, and the maximum age higher, than was previously thought (Figure 12). It is well documented that sparids are generally slow-growing and long-lived species, and reports of ages in excess of 20 years are not uncommon, even for smaller species such as carpenter *Argyrozona argyrozona* (Brouwer and Griffiths 2004), blacktail seabream *Diplodus capensis* and zebra seabream *Diplodus hottentotus* (Mann and Buxton 1997). Furthermore, the low temperature, low energy and low productivity conditions generally found in deep water (Clark 2001) are not suited for fast growth in fish. Compared with some other deep-water species, such as orange roughy *Hoplostethus atlanticus* and redfish *Sebastes mentella*, with validated maximum ages of 149 years (Fenton et al. 2001) and 75 years (Campana et al. 1990) respectively, *D. macrophthalmus* is a relatively short-lived, deep-water species.

The dominance of males in the smaller and females in the larger length classes (Figures 2, 4) suggests protandrous hermaphroditism in *D. macrophthalmus*. However, the similar age frequency distribution (Figure 9) indicates that the slower growth rate exhibited by males (Figure 8) causes the dominance of females in the larger size classes. In addition, no macroscopic evidence of hermaphroditism (intersex individuals) was observed during our study, supporting Alexeev's (1975; cited in Heese 1985) conclusion that the species is a late gonochorist.

According to the guidelines proposed by the Fish and Agriculture Organization (FAO 2001), which use life-history traits to classify finfish species by productivity, its slow growth, late sexual maturity and old maximum age place *D. macrophthalmus* in the low-productivity category. Fish in this category are expected to only sustain low levels of fishing effort. The slow growth and old age of this species has significant consequences for the management of its fisheries. It is therefore recommended that countries with significant fisheries for this species apply a precautionary approach while re-evaluating their stock assessments, beginning with updating their age and growth estimates using sectioned otoliths.

Despite the low productivity of *D. macrophthalmus* and increasing fishing pressure, only 38% of artisanal fishers perceived reductions in the catch of this species in Angola. The response of the fishers to the questionnaire may have been influenced by the inability of fishers to recall their historical catch rates (recall bias), misunderstanding or misinterpreting the question (response error), or intentional deception, whereby fishers report consistent catches for fear of management intervention (Pollock et al. 1994). Although these biases may have influenced the results, the suggestion by the same fishers interviewed that other fishery species such as *A. aequidens* had declined severely gives some confidence in the reliability of the results.

There are a number of fishery and ecological explanations for the perceived 'stable' catch rate of *D. macrophthalmus*. One is technology creep. The Angolan government has recently upgraded its artisanal fisheries (Duarte et al. 2005), in many cases converting artisanal vessels to small-scale commercial fishing vessels. Besides the government vessels with inboard diesel motors, sophisticated GPS systems and depth finders, some commercial fishery enterprises have purchased new outboard engines for artisanal fishers, and fishing cooperatives have facilitated microcredit for the purchase of upgraded equipment by fishers. With better vessels and motors, fishers have extended their fishing grounds and increased their fishing time, resulting in possible increase in catches. The Angolan government policies, which promote artisanal fisheries by improving technology, will compound this issue further as catch rates are likely to remain high, even under a situation of declining biomass. This suggests that the relationship between catch rates and technological improvements should be monitored closely in the Angolan artisanal fishery.

A possible second explanation for a perceived consistent catch rate is that the stock may be in a healthy condition. The selectivity of the fishing gear may play an important contributory role to the health of the fishery. At present, recruitment into the fishery occurs at approximately 160 mm FL, which corresponds closely with the length-at-50% maturity of the species. This provides inherent protection for the fish, because it allows at least half of the individuals the opportunity to reproduce at least once. While a reserve of small reproductively active fish will provide a buffer to the effects of overfishing, the low fecundity of recently matured fish and the relatively low survival of their offspring, when compared with large adult fish (Palumbi 2004), suggests that even a small increase in fishing effort or change in environmental conditions may result in a decrease in the catch rate. The obvious fishery response to a reduced catch rate is a reduction in the hook size by artisanal fishers, or an increase in effort by the non-selective demersal trawl fishery. Presently, a reduction in the hook size of the artisanal fishery is unlikely as the capture of small fish is not economically viable. However, if the catch rates in the artisanal fishery begin to fall, it is likely that the hook size will be reduced. This will remove the buffer of the small reproductively active fish and have serious consequences for the *D. macrophthalmus* fishery.

A third explanation may be the 'basin effect', whereby a reserve of fish from areas inaccessible to handline fishers (e.g. in deep water of 300–500 m depth) are reseeding the shallower-water fishing grounds. This situation would be characterised by a fairly consistent catch rate for some period until the deep-water reserves are depleted, after which the fishery is likely to decline rapidly or collapse. The misconception that stable catches indicate fisheries sustainability has been well documented (reviewed by Mullon et al. 2005) and must be recognised in the context of artisanal fisheries management in Angola.

Further, a reserve of older (larger) fish in the deeper waters is another possible explanation. Historical information suggests that larger *D. macrophthalmus* are found at greater depths (>250 m) (Domanevskiy et al. 1970, Domanevskiy and Stepkina 1971). Handline fishers in the Namibe province generally do not fish deeper than 250 m, so a proportion of the adult fish may be underexploited. These areas are considered critical to the sustainability of the *D. macrophthalmus* fishery because large and old adult female fish are highly fecund (Marteinsdottir and Steinarsson 1998, Palumbi 2004) and produce fast-growing larvae with improved survival (Longhurst 2002, Berkeley et al. 2004). This situation has been documented in the Mediterranean Sea, where the catch rate and recruitment of Mediterranean hake *Merluccius merluccius smiridus* remained high in the 1980s compared with that in the North Sea, despite similar high levels of fishing pressure (Caddy 1999). It is thought that the deep-water shelf habitat present in the Mediterranean Sea provides a refugium for the large adult fish as they were out of range of the demersal trawls (Caddy 1999). The large, adult *D. macrophthalmus* in deeper waters may therefore provide regular pulses of recruitment to this fishery and their protection is considered critical for the sustainability of this fishery.

The dominance of *D. macrophthalmus* in the catches of the southern Angolan and indeed the whole country's artisanal fishery (Duarte et al. 2005) demonstrates the importance of this species both in terms of the economy and livelihoods of fishers, their families and their communities. To prevent the humanitarian crisis that would be caused by the collapse of this fishery, it is recommended that the Angolan government review their current policy of not actively managing the artisanal fishery (until the total annual catch is greater than 150 000 t), because this approach is certain to lead to the overexploitation of the more vulnerable fishery species. To this end, it is imperative that a well-designed artisanal fishery monitoring protocol is initiated in order to develop simple fishery indicators. In terms of the fishery information, the distribution of effort, types of vessels and gear, and the total effort and catch, should be monitored. The collection of biological indicators such as size structure, age structure and reproductive biology parameters would be useful for the most abundant species. Whereas length or age-based stock assessments can be considered, the expense of this undertaking should be weighed against the value of the species under consideration. Ultimately, simpler, more cost-effective indicator methods such as a 'Traffic Light System' management framework (Potts et al. 2008) may be the most appropriate method in the long term.

Fishery regulations that may be beneficial to the *D. macrophthalmus* stock in southern Angola would be input controls, which could include limiting the number of artisanal fishing permits, as well as technical measures, which could include hook size restrictions, and a closed season that corresponds with the peak spawning season (December and/or January). The establishment of marine protected areas, which (if effectively policed) are considered effective management measures for sustaining fish stocks in instances where catch and effort is not easily restricted, is also strongly recommended. In the case of *D. macrophthalmus*, areas that support populations of large, fecund adult females should ideally be protected.

The stock identification of *D. macrophthalmus* is critical for national and regional management strategies. There is evidence to suggest that the population size structure of this species may differ between the southern, central and northern parts of Angola (Kilongo et al. 2007). Whereas these differences may reflect the level of exploitation, it is possible that there are separate stocks of this species. Ideally, different stocks should be identified, assessed and managed as independent units. To this end, it is recommended that future research on *D. macrophthalmus* should initially focus on stock identification, which would include a national or regional, molecular (mitochondrial and nuclear DNA), otolith microchemistry, meristic and morphometric study.

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References

Anon. 1987. Report of the first *ad hoc* working group on seabream (Sparidae) stocks in the Northern CECAF Zone. CECAF/ECAF Series: 86/38. Rome: Food and Agricultural Organization.

Bauchot M-L. 1987 Poissons osseux. In: Fischer W, Bauchot ML, Schneider M (eds), *Fiches FAO d'identification pour les besoins de la pêche. Méditerranée et mer Noire. Zone de pêche* 37. Vol. II. Rome: Commission des Communautés Européennes and FAO. pp 891–1421.

Bauchot ML, Hureau JC. 1986. Sparidae. In: Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, Tortonese E (eds), *Fishes of the north-eastern Atlantic and the Mediterranean.* 2. Paris: UNESCO. pp 883–907.

Beamish RJ, Fournier DA. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 982–983.

Beamish RJ, McFarlane GA. 1987. Current trends in age determination methodology. In: Summerfelt RC, Hall GH (eds), *Age and growth of fish.* Ames, Iowa: Iowa State University Press. pp 15–42.

Berkeley SA, Chapman C, Sogard SM. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops. Ecology* 85: 1258–1264.

Booth AJ, Weyl OLF. 2004. Investigations into a potential directed fishery for *Labeo cylindricus* in Lake Chicamba, Mozambique. *African Zoology* 39: 77–90.

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. *Fisheries Research* 67: 1–12.

Buckland ST. 1984. Monte Carlo confidence intervals. *Biometrics* 40: 811–817.

Buxton CD, Clarke JR. 1989. The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. *South African Journal of Marine Science* 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. *South African Journal of Marine Science* 10: 285–296.

Caddy JF. 1999. Fisheries management in the twenty-first century: will new paradigms apply? *Reviews in Fishery Biology and Fisheries* 9: 1–43.

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

Campana SE, Zwanenburg KCT, Smith JN. 1990. $^{210}Pb/^{226}Ra$ determination of longevity in redfish. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 163–165.

Cerrato RM. 1990. Interpretable tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1416–1426.

Chang WYB. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1208–1210.

Clark M. 2001. Are deepwater fisheries sustainable? — the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research* 51: 123–135.

Domanevskaya MV. 1987. Caracterisiques ecologiques et biologiques du dente aux gros yeux (*Dentex macrophthalmus* Bloch 1791) et du pageot argente (*Pegellus acarne* Risso 1926) de la region centre-est Atlantique. Report of the first *ad hoc* working group on seabream (Sparidae) stocks in the Northern CECAF Zone. CECAF/ECAF Series: 86/38 (Appendix 15). Rome: Food and Agricultural Organization.

Domanevskaya MV, Patonika FA. 1985. Feeding of the large-eyed dogtooth, *Dentex macrophthalmus*, and Spanish bream, *Pagellus acarne* (Sparidae), from the Central-Eastern Atlantic Ocean. *Journal of Ichthyology* 24: 107–112.

Domanevskiy LN, Stepkina MV. 1971. Features of the biology of *Dentex macrophthalmus* Bloch in the Central and Eastern Atlantic. *Journal of Ichthyology* 11: 346–353.

Domanevskiy LN, Stepkina MV, Tkatchenko VA. 1970. Some features of growth in *Dentex macrophthalmus* Bloch and *Sardinella aurita* Val. in the eastern Central Atlantic. *Journal of Ichthyology* 10: 861–869.

Druzhinin AD. 1976. *Sparid fishes of the world oceans*. Moscow: Pishchevaya Promyshlennost [translated from Russian].

Duarte A, Fielding P, Sowman M, Bergh M. 2005. Overview and analysis of socio-economic and fisheries information to promote the management of artisanal fisheries in the Benguela Current Large Marine Ecosystem (BCLME) region (Angola). Unpublished final report, Report No. LMR/AFSE/03/01/B. Cape Town: Environmental Evaluation Unit, University of Cape Town.

Efron B. 1982. *The jackknife, the bootstrap and other resampling plans*. Philadelphia: Society for Industrial and Applied Mathematics.

FAO. 2001. Second technical consultation on the suitability of the CITES criteria for listing commercially exploited aquatic species. FAO background document for the 2nd technical consultation on the suitability of CITES criteria for listing commercially exploited aquatic species. FAO Document FI:SLC2/2001/2.

Fenton GE, Short SA, Ritz DA. 1991 Age determination of orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae) using ^{210}Pb/^{226}Ra disequilibria. *Marine Biology* 109: 197–202.

Fowler HW. 1936. The marine fishes of West Africa. Based on the Collection of the American Museum Congo Expedition, 1909–1915. *Bulletin of the American Museum of Natural History* 70: 1–1493.

Francis RICC, Paul LJ, Mulligan KP. 1992. Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. *Australian Journal of Marine and Freshwater Research* 43: 1069–1089.

Goode GB, Bean TH. 1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers *Blake*, *Albatross*, and *Fish Hawk* in the northwestern Atlantic, with an atlas containing 417 figures. Special Bulletin, No. 2. Washington: United States National Museum.

Heese T. 1985. Morphological characteristics of *Dentex macrophthalmus* (Bloch, 1791) (Sparidae) from the Namibian shelf. *Acta Ichthyologica et Piscatoria* 15: 21–35.

Horn PL, Sutton CP. 1996. Validated ages, growth, and productivity parameters for silver warehou (*Seriolella punctata*) off the south and east coasts of South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 301–312.

Hyndes GA, Loneragan NR, Potter IC. 1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fisheries Bulletin* 90: 276–284.

Kilongo K, Barros P, Diehdiou M. 2007. Diet of large-eye dentex *Dentex macrophthalmus* (Pisces: Sparidae) off Angola and Namibia. *African Journal of Marine Science* 29: 49–54.

Longhurst A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fisheries Research* 56: 125–131.

Magnusson J, Magnusson JVV. 1987. ICEIDA/Cape Verde Islands Fisheries Project. Survey of demersal fish resources in the waters off Cape Verde Islands. IV. Report: summary of information on species. Icelandic International Development Agency/Marine Research Institute, Iceland.

Mann BQ, Buxton CD. 1997. Age and growth of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Sparidae) on the Tsitsikamma coast, South Africa. *Cybium* 21: 135–147.

Marteinsdottir G, Steinarsson A. 1998. Maternal influence on the size and viability of cod (*Gadus morhua* L.) eggs and larvae. *Journal of Fish Biology* 52: 1241–1258.

Mennes F. 1985. Multispecies assessment of fish stocks off the western Sahara region with emphasis on the family Sparidae. *Fishbyte* 3: 5–10.

Mora C, Myers RA, Coll M, Libralato S, Pitcher TJ, Sumaila RU, Zeller D, Watson R, Gaston KJ, Worm B. 2009. Management effectiveness of the worlds marine fisheries. *PLoS Biology* 7(6): e1000131. doi:10.1371/journal.pbio.1000131.

Morales-Nin B. 1989. Growth determination of tropical marine fishes by means of otolith interpretation and length frequency analysis. *Aquatic Living Resources* 2: 241–253.

Mullon C, Fréon P, Cury P. 2005. The dynamics of collapse in world fisheries. *Fish and Fisheries* 6: 111–120.

Nelder JA, Mead R. 1965. A simplex method for function minimization. *Computer Journal* 7: 308–313.

Nguyen XL, Wojciechowski J. 1972. Comparative biology of fish from genus *Dentex* (Sparidae) of North-West African coast. *Acta Ichthyologica et Piscatoria* 2(2): 77–94.

Palumbi SR. 2004. Why mothers matter. *Nature* 430: 621–622.

Pollock KH, Jones CM, Brown TL. 1994. Angler survey methods and their applications in fisheries management. *American Fisheries Society Special Publication* 25. Bethesda, Maryland: American Fisheries Society.

Potts WM, Childs AR, Sauer W, Duarte A. 2008. Collecting and using baseline biological and ecological information to design a 'traffic light stock status index' for the leerfish *Lichia amia* (Linnaeus 1758) in southern Angola. *African Journal of Marine Science* 30: 113–121.

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191: 1–382.

Stepkina MV. 1970 Sparidae of North-West African coast. *Fish Industry* 6: 8–10.

Trunov IA. 1970. On the morphological characteristics of *Dentex macrophthalmus* (Sparidae) from various regions of the eastern Atlantic. *Journal of Ichthyology* 10: 15–23.

Trunov IA. 1972. Determination of age in the large-eyed dentex (*Dentex macrophthalmus* (Bloch)) (Fam. Sparidae) from the Southeastern Atlantic. *Journal of Ichthyology* 12: 94–100.

Winker H, Ellender B, Weyl OLF, Booth AJ. In press. Validation of growth zone deposition in otoliths of two large endemic cyprinids in Lake Gariep, South Africa. *African Zoology* 45.