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Reproductive biology of the mackerel scad *Decapterus macarellus* from Cabo Verde and the implications for its fishery management

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The mackerel scad *Decapterus macarellus* is of great social and economic importance to Cabo Verde citizens; however, in recent years catches have shown an unexplained decline. The harvest is regulated by way of a minimum legal size and a seasonal closure, with both measures based on the results of reproductive studies that did not consider the microscopic characteristics of the gonads. This study aimed to analyse the gonads microscopically in order to classify the sexual development stage of individuals and to estimate the size at first maturity and the reproductive season. This information was then used to analyse the match between the reproductive parameters and the management measures. The samples comprised 284 females (20–36 cm fork length [FL]) and 85 males (21–35 cm FL). The annual variation in gonadosomatic index and the monthly frequencies of mature phases suggest that the reproductive season occurs from March to October, with two spawning peaks, one in March and another from July to October. The current seasonal closure (from July to September) covers the main reproductive period. However, the species has a long spawning period and the timing of peaks can vary between years; hence, a reassessment of this management measure is recommended. The sizes at first maturity were estimated at 24.1 cm FL for females, and 26.6 cm FL for males. These values are higher than the minimum legal size (20 cm FL) currently established for management of the species at Cabo Verde; thus, we strongly recommend an increase in the minimum legal size in an attempt to reduce catches of immature individuals.

Keywords: eastern Atlantic, gonad histology, minimum legal size, pelagic fish, seasonal closure, size at first maturity, spawning period

Introduction

Fishes of the family Carangidae, including the genus *Decapterus*, are economically important resources in tropical and subtropical waters (Jaiswar et al. 2001; Ohshimo et al. 2006; Shiraishi et al. 2010). In Cabo Verde, in the eastern Atlantic Ocean, the mackerel scad *Decapterus macarellus* (Cuvier, 1833) is of great social and economic importance, since it is the most-consumed pelagic fish. Given that 70% of the animal protein consumed by the Cabo Verde population comprises fish, the species is also important in terms of food security (Belhabib et al. 2015). *Decapterus macarellus* is also used as bait in tuna fisheries in the region. At Cabo Verde, the species is caught using gillnets, purse-seine, and handlines (Stobberup and Erzini 2006).

Despite its economic and social importance, little is known about the reproductive biology of the species in the Cabo Verde Archipelago. *Decapterus macarellus* is gonochoristic and presents iteroparity with synchronous group development of the oocytes (Shiraishi et al. 2010). In the archipelago, Almada (1997) observed higher gonadosomatic indices (GSI; defined below) in April and from June until August, which coincide with the higher water temperatures during the boreal summer, whereas Almada and Lopes (1998) observed mature ovaries throughout the year.

Knowledge of life history is fundamental to the development of any fishery management measure (Dowling et al. 2015). Some measures, including minimum landing sizes and closed fishing seasons, rely upon the reproductive biology of fish stocks (Morgan 2008), which is the case for the D. macarellus stock in Cabo Verde (Cabo Verde 2016). However, reproductive studies for the species have not included microscopic analysis of the gonads. Microscopic techniques are more reliable than macroscopic ones for purposes of describing the developmental stages of ovaries and testes and provide detailed information on the spawning model and spawning season, as well as the number of individuals in each maturity stage (Mackie and Lewis 2001; Duarte et al. 2007; Thulasitha and Sivashanthini 2013). Accurate information on this number is crucial for the estimation of sizes and ages at first maturity. An increase in the reliability of such information leads to increased effectiveness of management measures.

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The stock of *D. macarellus* from Cabo Verde has been assessed several times (e.g. Almada 1997; Carvalho and Caramelo 1999; Jardim 1999) and the most recent assessment considered the stock to be healthy (Stobberup and Erzini 2006). Between 1989 and 2013 annual catches

ranged between 1 000 and 3 000 t, with an average of 2 000 t (INDP 1989–2013). In 2009, two management measures were established: a seasonal closure from 1 August to 30 September, and a minimum legal size of 18 cm fork length (FL) (Cabo Verde 2009). Five years later, in 2014 and 2015, the catches declined abruptly, to 150 t and 643 t, respectively, which led to an adjustment of the management measures in 2016; the seasonal closure was changed to 15 July–14 September, and the minimum legal size was increased to 20 cm FL (Cabo Verde 2016). However, neither of these changes were based on new studies on the reproductive biology of the species.

Thus, the objective of this study was to describe the ovarian and testicular development of *D. macarellus* from Cabo Verde, using microscopy of the gonads to estimate the reproductive season and the size at first maturity, in order to review the suitability of the current management measures as they relate to the reproductive characteristics of the species.

Materials and methods

Specimens of *Decapterus macarellus* were obtained between 2012 and 2018 from landings of the industrial fishery in the northernmost islands of Cabo Verde (i.e. São Vicente, Santo Antão, Santa Luzia, Sal, and Ilheu Branco). The FL was measured in centimetres, rounded down, and the total weight (Wt, g) and gonad weight (Wg, g) were recorded. The gonads were classified according to the maturation scale of Brown-Peterson et al. (2011) and individuals that were classified at the stage 'spawning capable' and onwards were considered mature.

The gonads were sectioned (1 cm^2) and preserved in 10% formaldehyde solution. After fixation, the tissues were kept in 70% alcohol until histological processing, when they were dehydrated in ethyl alcohol (through a gradient of concentrations), diaphanised with xylol, impregnated, and embedded in paraffin (Kiernan 2015). Tissue sections of thickness 3–5 µm were stained with haematoxylin-eosin.

A binocular optical microscope with magnification of ×40 to ×1 000 was used for the observation and analysis of the slides and for taking the microphotographs.

The reproductive cycle was determined by analysing changes in the monthly mean gonadosomatic index (GSI) of mature individuals, calculated as GSI = 100 × (Wg/Wt) (Wootton 1998). The fork length at first maturity (FL₅₀) was calculated using a Bayesian approach to the logistic model (Kinas and Andrade 2010; Cardoso and Haimovici 2014). The total number (n_i) and the total number of mature individuals (y_i) were calculated for both sexes for each length class of 1-cm interval. The probability that an individual of a determined length class *i* is sexually mature is expressed as θ_i . It was assumed that this probability follows a binomial distribution, Bin (n_i , θ_i).

The data were adjusted to a logistic model defined by the logit-link function, which transforms the parameter θ_i , restricted to the interval [0,1], into a binomial distribution in m, defined between $-\infty$ and $+\infty$ (Kinas and Andrade 2010). The logistic model was defined as:

$$m_i = f(\theta_i) = \log(\theta_i / 1 - \theta_i)$$
$$m_i = \beta_0 + \beta_1 x_i$$

where *f* is the logit-link function, and m_i is the probability of maturity of each x_i , where x_i is a length class. From this model, the length at first maturity is defined as:

$$FL_{50} = -\beta_0/\beta_1$$

The posterior distributions of the parameters were obtained using the stochastic process of the Monte Carlo Markov Chains (MCMC) method, which enables visual comparison of the posterior probability distributions of the resulting parameters. The *a priori* distributions of β_0 and β_1 were considered to be normal, with an average of zero and wide variance (1 000). In a single chain, 31 000 iterations were generated with burn-in of the first 10 000 values,

		Tatal							
Month	2012	2015		2017		2018		Total	
-	F	F	М	F	М	F	М	F	Μ
1									

Table 1: The number of *Decapterus macarellus* individuals sampled at Cabo Verde, by sex, year and month; no data were collected in December and January. F = females; M = males

	F	F	М	F	М	F	М	F	Μ
1									
2	5					5	8	10	8
3	5			58	5			63	5
4	5			80	10	5	10	90	20
5				6	7			6	7
6	9			9	6			18	6
7	5	62	24					67	24
8		3						3	
9				10	5			10	5
10				10	5		1	10	6
11				7	4			7	4
12									

then every second value was retained from the remaining 21 000, resulting in a final sample with 10 500 values in the posterior distribution of each parameter (Kinas and Andrade 2010). All statistical analyses were performed using R 3.3.1 (R Core Team 2016), and the OpenBUGS package with the libraries R2WinBUGS (Sturtz et al. 2005) and BRugs (Thomas et al. 2006).

Results

The samples comprised 284 females (20–36 cm FL) and 85 males (21–35 cm FL). The individuals were obtained between February and November from 2012 to 2018 (Table 1).

The synchronous development of various cohorts of oocytes during the reproductive period suggests several spawning events per individual, which characterises *D. macarellus* from Cabo Verde as a multiple spawner (Figure 1). Macroscopically, male and female gonads were distinguishable by their colour and texture. The mature ovaries were enlarged, yellowish, and had visible oocytes.

The ovaries were classified into the five stages of maturity on the maturation scale proposed by Brown-Peterson et al. (2011), based on the development of the most-advanced oocytes and their histological characteristics:

- Immature stage (Figure 2): mean GSI 0.04 (SD 0.05). Immature ovaries were found in individuals between 23 and 24 cm FL.
- Developing stage: mean GSI 1.33 (SD 0.63), found in individuals 28–29 cm FL.

- 3. Spawning-capable stage (Figure 1): mean GSI 4.64 (SD 2.18), found in individuals 27–34 cm FL.
- 4. Regressing stage (Figure 3): mean GSI 0.56 (SD 0.41), found in individuals 25–29 cm FL.
- 5. Regenerating stage: mean GSI 0.42 (SD 0.22), found in individuals 25–29 cm FL.

Mature testes produced sperm when pressure was applied, and spermatozoa were present in the testicular lobes when analysed microscopically (Figure 4).

The average values of GSI by month are presented in Figure 5. The highest values were observed during two periods for both sexes, the first in March and April and the second from July to October. Concurrently, high frequencies of females capable of spawning were observed in March and April and from June until October (Figure 6). These results suggest that *D. macarellus* from Cabo Verde might spawn twice a year, with one peak in March and the other from July to October. Fish of post-spawning stages were found at higher frequencies during November and February (i.e. subsequent to the proposed spawning season). However, no data were collected in December or January.

A significant relationship between length and sexual maturity was observed for both sexes since the posterior distributions of β_1 did not include zero (Table 2). The length at first maturity (FL₅₀) did not differ between the sexes, as can be observed by the overlapping posterior distributions of the estimated parameters (Table 2). FL₅₀ was estimated to be 24.1 cm for females, and 26.6 cm for males (Table 2;



Figure 1: Photomicrograph of ovarian histology of *Decapterus macarellus* from Cabo Verde, showing an ovary at the spawning-capable stage. CA = oocyte I cortical alveoli; PG = oocytes of primary growth; Vtg1 = vitellogenic oocytes 1; Vtg2 = vitellogenic oocytes 2; Vtg3 = vitellogenic oocytes 3



Figure 2: Photomicrograph of ovarian histology of *Decapterus macarellus*, showing an immature ovary. OL = ovarian lamella; OW = ovarian wall; PG = oocytes of primary growth



Figure 3: Photomicrograph of ovarian histology of *Decapterus macarellus*, showing a regressing ovary. BV = prominent blood vessel; CA = cortical alveoli oocyte; PG = oocytes of primary growth



Figure 4: Photomicrograph of testicular histology of *Decapterus macarellus*, showing a mature testis. Spermatozoa (Sz) were present in the lobes of the testes (LT)



Figure 5: Monthly changes in the mean gonadosomatic index of mature *Decapterus macarellus* from Cabo Verde. Vertical bars represent 95% confidence intervals

Figure 7). The length at 95% of maturity (FL₉₅) was 27.8 cm FL for females, and 35 cm FL for males (Table 2).

Discussion

The synchronous development of several oocyte stages (Figure 1) during the reproductive period of

Decapterus macarellus from Cabo Verde suggests multiple spawning events per individual. According to the annual variation in GSI observed in the present study and by Almada (1997), in Cabo Verde the species might have two spawning periods a year, from March until April and from July until October. In Japan, the species reproduces once a year, from April until July (Shiraishi et al. 2010). The longer spawning season for the species at Cabo Verde is consistent with the general pattern of spawning by teleost fishes from tropical waters (Potts and Wootton 1989). Furthermore, our determination of this protracted spawning period is in agreement with studies on species of the same family in other places at lower latitudes, such as the Philippines (Tiews 1958; Tiews et al. 1975) and the Java Sea (Delsman 1926). However, although the individuals sampled in the present study were obtained over several years, interannual variations in spawning events might not be apparent in the available data.

The histological analysis of ovaries and testes provided precise identification of the maturation stage of each individual fish, which resulted in robust estimations of the size at maturity. Furthermore, the estimated size at maturity of 24.1 cm FL for females is in agreement with the sizes reported by Shiraishi et al. (2010) for *D. macarellus* females from Japanese waters (25.8 cm), by Clarke and Privitera (1995) from Hawaiian waters (24.5 cm), and by Hariati (2004, as cited by Tetelepta [2018]) from Indonesian waters



Figure 6: Monthly frequencies of the maturity stages of female *Decapterus macarellus* from Cabo Verde. The number of sampled individuals is provided above each column

Table 2: Mean and credibility intervals (CrI, $\alpha = 0.05$) for the model parameters (β_0 and β_1) and estimated length at first maturity (FL₅₀) and length at 95% of maturity (FL₅₀) for *Decapterus macarellus* in Cabo Verde

Demonsterne		Females		Males			
Parameters	Mean	Crl _{2.5%}	Crl _{97.5%}	Mean	Crl _{2.5%}	Crl _{97.5%}	
β1	0.81	0.57	1.12	0.38	0.19	0.58	
βο	-19.6	-27.8	-13.3	-10.3	-15.8	-4.9	
FL ₅₀	24.1	22.8	25.1	26.6	24.6	28.1	
FL ₉₅	27.8	26.9	28.8	35.0	31.9	41.1	

(24.9 cm). However, the sizes at first maturity estimated in this study were larger than the minimum legal size currently used by the fisheries' management system in Cabo Verde, which is 20 cm FL (Cabo Verde 2016). Given that the estimated sizes at 95% of maturity were 27.8 cm FL for females and 35 cm FL for males, and given the current decline in the catches, we strongly recommend that the minimum legal size for *D. macarellus* from Cabo Verde be changed to a length larger than 26 cm FL.

The small number of individuals available for the estimations of sizes at first maturity increases the uncertainties of the estimations. However, the similarity between the estimate for females in this study and the estimates from elsewhere (Clarke and Privitera 1995; Hariati 2004, as cited by Tetelepta [2018]; Shiraishi et al. 2010), coupled with the Bayesian approach used and the stochastic procedure, which estimates the uncertainty using a pre-defined probability distribution and non-informative priors, helps to overcome this problem (Kinas and Andrade 2010). Furthermore, the precision of the identification of immature and mature gonads provides greater robustness for the estimation of maturity parameters than in previous studies of the species in the Cabo Verde Archipelago (Almada

1997; Almada and Lopes 1998). To reduce the uncertainties present in the estimations made in this study we recommend further studies with larger sample sizes.

Currently, there is a seasonal closure of the fishery for *D. macarellus* in Cabo Verde from 15 July until 14 September, which covers one of the reproductive periods identified in this study but does not include the other. Since the species has a long spawning period that extends through most of the year and given that the peaks of spawning might vary interannually, it is necessary to revisit the timing of the closed season as a management measure. Even so, further studies on potential annual variation in the reproductive peaks are necessary because such peaks might not be constant and might be related to environmental drivers.

The management advice emanating from this study was prompted by the decline in catches of *D. macarellus* at Cabo Verde. However, this decline might not be related to fishing exploitation only, but might also be driven by global climate change. Lam et al. (2012) previously warned of the potential negative impacts of climate changes on fisheries in West Africa, since it is a region with a high probability of decline in the maximum catch potential according to the modelling study by Cheung et al. (2010).



Figure 7: Length-maturity ogives (solid lines) and the posterior distributions of the estimated size at first maturity (dashed lines) for females and males of *Decapterus macarellus* sampled at Cabo Verde

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References

- Almada EO. 1997. Life history of scad mackerel, *Decapterus macarellus* (Cuvier, 1833), in the waters off the Cape Verde Islands. MSc thesis, University of Reykjavik, Iceland.
- Almada E, Lopes JA. 1998. A diversidade biológica de Cabo Verde. Análise e hierarquização das pressões humanas sobre a DB marinha e identificação das prioridades para a sua conservação e utilização sustentável. Unpublished report. Praia, Cabo Verde: Direcção Geral do Ambiente, Praia.
- Belhabib D, Sumaila UR, Pauly D. 2015. Feeding the poor: contribution of West African fisheries to employment and food security. *Ocean and Coastal Management* 111: 72–81.
- Brown-Peterson N, Wyanski DM, Saborido-Rey F, Macewicz BJ, Lowerre-Barbieri SK. 2011. A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries* 3: 52–70.
- Cabo Verde. 2009. Resolução No. 10. Boletim Oficial da República de Cabo Verde, No. 18. Available at https://kiosk.incv. cv/1.1.18.225/ [accessed 27 February 2019].

- Cabo Verde. 2016. Resolução No. 29. Boletim Oficial da República de Cabo Verde, No. 16. Available at http://extwprlegs1.fao.org/ docs/pdf/cvi154189.pdf [accessed 27 February 2019].
- Cardoso LG, Haimovici M. 2014. Long-term changes in the sexual maturity and in the reproductive biomass of the southern king weakfish *Macrodon atricauda* (Günther, 1880) in southern Brazil. *Fisheries Research* 160: 120–128.
- Carvalho EM, Caramelo AM. 1999. Avaliação do estado da pescaria de Cavala preta e do chicharro em Cabo Verde. In: Carvalho EM, Morais J, Nascimento J (eds), *Investigação e gestão haliêutica em Cabo Verde*. Mindelo, Cabo Verde: Instituto Nacional de Desenvolvimento das Pescas. pp 142–152.
- Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Zeller D, Pauly D. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* 16: 24–35.
- Clarke TA, Privitera LA. 1995. Reproductive biology of two Hawaiian pelagic carangid fishes, the bigeye scad, *Selar crumenophthalmus*, and the round scad, *Decapturus macarellus*. *Bulletin of Marine Science* 56: 33–47.
- Delsman HC. 1926. Fish eggs and larvae from the Java Sea. 5. Caranx kurra, Decapterus macrosoma and Selar crumenophthalmus. Treubia 8: 199–211.
- Dowling NA, Dichmont CM, Haddon M, Smith DC, Smith ADM, Sainsbury K. 2015. Guidelines for developing formal harvest strategies for data-poor species and fisheries. *Fisheries Research* 171: 130–140.
- Duarte S, Araújo FG, Sales A, Bazzoli N. 2007. Morphology of gonads, maturity and spawning season of *Loricariichthys spixii* (Siluriformes, Loricariidae) in a subtropical reservoir. *Brazilian Archives of Biology and Technology* 50: 1019–1032.
- INDP (Instituto Nacional do Desenvolvimento das Pescas). 1989–2013. Boletins estatísticos: dados sobre pesca artesanal, pesca industrial, conservas e exportações. Mindelo – São Vicente, Cabo Verde: INDP.

- Jaiswar AK, Chakraborty SK, Swamy RP. 2001. Studies on the age, growth and mortality rates of Indian scad *Decapterus russelli* (Ruppell) from Mumbai waters. *Fisheries Research* 53: 303–308.
- Jardim J. 1995. Contribuição para o estudo da pescaria de cavala preta (*Decapterus macarellus*) no Arquipelago de Cabo Verde: relatório da disciplina de estágio. Faro, Portugal: Universidade Algarve.
- Kiernan JA. 2015. Histological and histochemical methods: theory and practice. London: Scion Publishing.
- Kinas PG, Andrade HA. 2010. Introdução à análise Bayesiana (com R). Porto Alegre, Brazil: Mais Qnada.
- Lam VW, Cheung WW, Swartz W, Sumaila UR. 2012. Climate change impacts on fisheries in West Africa: implications for economic, food and nutritional security. *African Journal of Marine Science* 34: 103–117.
- Mackie M, Lewis P. 2001. Assessment of gonad staging systems and other methods used in the study of the reproductive biology of narrow-barred Spanish mackerel, *Scomberomorus commerson*, in Western Australia. *Fisheries Research Report* No. 136. Perth, Australia: Department of Fisheries, Government of Western Australia.
- Morgan MJ. 2008. Integrating reproductive biology into scientific advice for fisheries management. *Journal of Northwest Atlantic Fishery Science* 41: 37–51.
- Ohshimo S, Yoda M, Itasaka N, Morinaga N, Ichimaru T. 2006. Age, growth and reproductive characteristics of round scad *Decapterus maruadsi* in the waters off west Kyushu, the East China Sea. *Fisheries Science* 72: 855–859.
- Potts GW, Wootton RJ. 1989. *Fish reproduction strategies and tactics* (3rd edn). London: Academic Press.

- R Core Team. 2016. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.
- Shiraishi T, Tanaka H, Ohshimo S, Ishida H, Morinaga N. 2010. Age, growth and reproduction of two species of scad, *Decapterus macrosoma* and *D. macarellus*, in the waters off southern Kyushu. *Japan Agricultural Research Quarterly* 44: 197–206.
- Stobberup KA, Erzini K. 2006. Assessing mackerel scad, Decapterus macarellus in Cape Verde: using a Bayesian approach to biomass dynamic modelling in a data-limited situation. Fisheries Research 82: 194–203.
- Sturtz S, Ligges U, Gelman A. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* 12: 1–16.
- Tetelepta JMS. 2018. Some biological aspects of mackerel scad (*Decapterus macarellus*) in Ambon Island waters, Indonesia. International Journal of Fisheries and Aquatic Studies 6: 171–175.
- Thomas A, O'Hara B, Ligges U, Sturtz S. 2006. Making BUGS Open. *R News* 6: 12–17.
- Thulasitha WS, Sivashanthini K. 2013. Microscopic staging system used in the identification of gonad developmental stages of *Scomberoides lysan. Journal of Fisheries and Aquatic Science* 8: 355–366.
- Tiews K. 1958. Report to the Government of the Philippines on marine fishery resources. *Philippine Journal of Fisheries* 6: 134–138.
- Tiews K, Ronquillo IA, Borja PC. 1975. On the biology of round scads (*Decapterus bleeker*) in Philippine waters. *Philippine Journal of Fisheries* 9: 45–71.
- Wootton RJ. 1998. The ecology of teleost fishes (2nd edn). Fish and Fisheries Series No. 24. Dordrecht, Netherlands: Kluwer.