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Reproduction of the Blue Jack Mackerel, *Trachurus picturatus*, in Western Portugal: Microscopic Gonad Analysis Reveals Indeterminate Fecundity and Skipped Spawning Patterns

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Blue jack mackerel, *Trachurus picturatus*, is the fifth most landed fish species in mainland Portugal, but information on its reproductive biology is scarce. From September 2018 to August 2019, 626 specimens were collected from commercial vessels to clarify the reproductive strategy of the *T. picturatus* population off the west coast of Portugal. The proportion and length range of males and females were similar. Only three of the specimens collected were categorized as immature, indicating that the fish caught in the fishery are primarily mature. The spawning season lasted from late January until the end of March, with gonadosomatic indices being similar for males and females. Fecundity was indeterminate, and estimated batch fecundity ranged between 6,798 (at 25.4 cm TL) and 302,358 oocytes (at 33.8 cm TL). The low number of females showing direct evidence of imminent or recent spawning suggests a low number of spawning events. In addition, 12.7% of females were considered non-reproductive due to ovary abnormalities including parasitic infection by *Kudoa* species, atretic structures and skipped spawning events. This study highlights the importance of accounting for skipped spawning events and ovary abnormalities in the management of species fisheries.

Key words: Carangidae, Low-valued fish, Skipped spawning, Fecundity, Portugal.

BACKGROUND

Portugal has one of the largest exclusive economic zones (EEZs) in the European Union and a socially and culturally important fishing sector. Many coastal communities depend almost exclusively on fisheries

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and related activities. The fishing industry is dominated by small fishing vessels that operate near the coast, use diverse fishing gear, and target multiple species. Purse seine and trawling account for about 61% of the total volume of catches (DGRM 2019). However, only a small proportion of species population units have been scientifically assessed, and some management actions are defined for groups of related species rather than for individual species. For example, the horse mackerel, *Trachurus trachurus*, in ICES Division IXa has been assessed, but the Total Allowable Catch (TAC) was established for *Trachurus* spp. in general (*i.e.*, horse mackerel; blue jack mackerel, *T. picturatus*; and Mediterranean horse mackerel, *T. mediterraneus*) (ICES 2019a). This strategy of managing groups of species under combined TAC may lead to the overexploitation of individual species (ICES 2019b).

Regarding reproductive strategy, most teleost marine commercial species are iteroparous and gonochoric, possess no sexual dimorphism, exhibit external fertilisation, and release many pelagic eggs (Murua and Saborido-Rey 2003). All organisms' life histories are a life-long trade-off between reproduction, growth, and survival driven by the allocation of resources among growth, egg production, and energy storage (Jørgensen et al. 2006). In terms of fecundity and depending on the energy allocated to egg production, fishes are usually classified as having a determinate fecundity type, in which all oocytes that will spawn in a reproductive cycle are recruited from primary growth to secondary growth prior to the beginning of the spawning period, or having an indeterminate fecundity type where oocytes continue to be recruited to secondary growth throughout the spawning season (Ganias et al. 2015).

However, atypical scenarios can be found. "Skipped spawning" occurs when individual fish that are potentially capable of spawning do not spawn because they present low levels of stored energy (individual condition is poor) or there are unsuitable environmental conditions to forego egg production until the subsequent year (Rideout et al. 2000; Rideout and Tomkiewicz 2011). Skipped spawning individuals do not conform to the normal reproductive development schedule and are thus considered abnormal in relation to other individuals or populations (Rideout and Tomkiewicz 2011). Other abnormalities that affect the normal reproductive potential by reducing it are, for example, the presence of follicular cysts (Tomkiewicz et al. 2003) or parasitic infections that interfere with gamete production (Ruehl-Fehlert et al. 2005), leading to yolk fragmentation and complete degradation of the oocyte (Neves et al. 2020). Among the fish parasites, the Myxozoans are the most common. However, its phylum classification has a long history since its discovery. They were originally included in Sporozoa (protozoan), but more recently they were transferred to Metazoa (Lom and Dyková 2006). Their simply body form is viewed as the result of large-scale reduction due to adaptation to parasitism. In Metazoa, there is no consensus among authors regarding their systematic position, with some authors considering the group as belonging to the phylum Myxozoa (*e.g.*, Videira et al. 2020) and others including them in the phylum Cnidaria (*e.g.*, Giulietti et al. 2020). Their life cycle typically involves a tubificid oligochaete or a polychaete and a fish. *Kudoa* species, with over 100 species described, are among the most common species of Myxozoans that infect marine and estuarine fish species worldwide (Giulietti et al. 2019); they mainly affect the skeletal musculature, but can also occur in the brain, heart, gills, kidney, ovary and intestines (Eiras et al. 2014).

The blue jack mackerel is widespread in the Eastern Atlantic, from the southern Bay of Biscay to southern Morocco, including the Macaronesia archipelagos, Tristan de Cunha and Gough Islands, and in the Western Mediterranean Sea and the Black Sea. This oceanic pelagic fish inhabits the neritic zones of islands shelves, banks and seamounts (Smith-Vaniz 1986). In 2019, it was the sixth most landed fish in mainland Portugal, reaching 3472 tons (INE 2021). In the last 15 years, species landings have displayed strong fluctuations that appear to reflect not only fishing effort, but changes in abundance and availability (ICES 2019a). Therefore, we must better understand the life-history of blue jack mackerel in the Portuguese coast to shed light on these fluctuations.

Recent studies on the blue jack mackerel populations in the Atlantic based on geometric morphometrics, otolith shape analysis and parasites show different populations units in Madeira, Canaries and mainland Portugal (Costa et al. 2012 2013; Hermida et al. 2016; Vasconcelos et al. 2017a). In addition, studies on otolith elemental and isotopic signatures revealed four different population units in the Azores, Madeira, the Canary Islands, and mainland Portugal (Moreira et al. 2018). These populations show similar spawning seasons (Costa 2019; Garcia et al. 2015; Jesus 1992; Jurado-Ruzafa and Santamaría 2013 2018; Vasconcelos et al. 2017b), but age at first maturity varies between individuals from Azores, Madeira and the Canary Islands (Garcia et al. 2015; Jesus 1992; Jurado-Ruzafa and Santamaría 2013). Little is known about species life history in mainland Portugal, with available information being limited to spawning season estimated by macroscopic gonad observation (Costa 2019).

Macroscopic observation of fish gonads (external appearance of the ovary) was the most widely used approach since it is the simplest and most rapid method, but its accuracy is uncertain, and it may be too subjective (Kjesbu 2009). Microscopic observation based on a histological approach, on the other hand, is the most accurate technique (Brown-Peterson et al. 2011). This approach is fundamental for determining several features of each species' reproductive strategy like the presence (and quantification) of atresia, the type of oocyte development, the type of ovary organisation, the recruitment of oocytes and the spawning pattern (Murua and Saborido-Rey 2003). Microscopic analysis through histological techniques is also essential for detecting the presence of parasitic infection of the gonads like the one described by Neves et al. (2020) in *T. picturatus* from the Portuguese coast. This parasite, *Kudoa* sp., had already been found in *T. trachurus* from the northeast Atlantic (Campbell 2005; MacKenzie et al. 2008) and the Mediterranean (Mansour et al. 2013), but never in *T. picturatus*. This parasite infects and destroys the large vitellogenic ovaries, causing a strong decrease in reproductive potential (Neves et al. 2020). It can also decrease fish muscles, harming the fish and significantly decreasing its fecundity Adlerstein and Dorn (1998).

The present study aims to clarify the range of reproductive strategies of blue jack mackerel off the west coast of Portugal. This is a coastal and more northern boundary population than the other oceanic and southern populations living in island shelves and sea mounts from the Macaronesia archipelagos populations, which are characterised by warmer and more stable sea temperature. The occurrence of skip spawning females and fecundity estimates are also reported for this species for the first time.

MATERIALS AND METHODS

Samples of blue jack mackerel were acquired from small-scale fishing vessels operating off the west coast of Portugal (Peniche, Fig. 1) in 2018 and 2019, every fortnight throughout the reproductive season and monthly outside of this period. Fish were kept on ice until being processed in the lab (half a day). Each fish was analysed for total length (TL, to the nearest 0.1 cm), eviscerated weight (EW, to the nearest 0.01 g), gonad and liver weights (GW and LW, respectively, to the nearest 0.01 g), and sex. Gonads were fixed in 4% buffered formalin for histological analysis.

Histological analysis

Maturity stage was confirmed histologically in five individuals from each group and each sampling day with macroscopically similar gonads. Furthermore, all females sampled during the spawning season were histologically analysed. For each individual, a cross section from the middle of the right gonad about 0.5 cm^3 was dehydrated in ethanol, embedded in methacrylate, sectioned at 3 μm and stained with toluidine blue.

Oogenesis and spermatogenesis stages were classified based on Wallace and Selman (1981) and Grier and Uribe-Aranzábal (2009), respectively. Maturity phases were assigned according to Brown-Peterson et al. (2011): immature (I), developing (D), spawning capable (SC), with actively spawning subphase (AS), regressing (RS), and regenerating (RN).

The thresholds for secondary growth (SG) and advanced vitellogenic oocytes (AVTG) were determined from the mean diameter of about 100 oocytes of each stage with visible nucleus. The maximum and minimum diameters were used to minimize the error from the loss of spherical shape associated with histological processing. Measurements were made using the software package ImageJ (http://imagej.nih.gov/ij/).

Sexual cycle and length at first maturity

The sex ratio was estimated as the ratio of sampled females to males and evaluated for deviations from 1:1 with the Pearson's *Chi*-squared test (Agresti 2007). The spawning season was defined by the occurrence of more than 50% SC females and corroborated from the monthly variation in gonadosomatic index (GSI = 100 × GW/EW) in mature females and males. Fish condition was evaluated with two bioenergetic indices—the hepatosomatic index (HIS = 100 × LW/EW) and the relative condition (Kn)—calculated as the ratio of the observed EW over the predicted EW (Le Cren 1951). The predicted EW was estimated using length-weight equations ($EW = a \times TL^b$) for each sex calculated from all individuals sampled (300 females: $EW = 0.0047 \times TL^{3.16}$; 326 males: $EW = 0.0055 \times TL^{3.11}$).

Monthly variation in the three indices was tested using the Kruskal-Wallis rank sum test and post hoc Dunn's test for pairwise comparisons (Dunn 1964). Correlation between GSI and sea surface temperature (SST) was evaluated with Spearman rank coefficient. SST mean values for the sampled months in the west coast of Portugal were obtained using COBE SST data provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, from their website at https://psl.noaa.gov/.

Fecundity type

Homogeneous distribution of oocytes was checked on samples from the posterior, middle and anterior zones of the right ovary lobe and middle zone of the left ovary lobe. Following Ganias et al. (2014), direct gravimetric measurements of oocyte size frequency distribution (OSFD) were made for two SC females. Frequency distributions of oocytes above 125 µm in each zone and lobe at 50-µm intervals were compared with a beta regression model for proportions (Ferrari and Cribari-Neto 2004). Because no significant differences were found between zones ($p > 0.94$) and lobes ($p = 0.65$), random samples from the right ovary lobe were used in subsequent analyses.

Fecundity type was assessed based on (i) the presence of a hiatus in the OSFD between pre-vitellogenic and vitellogenic oocytes, (ii) the trend in the stock of SG oocytes during the spawning period, (iii) the trend in mean oocyte diameter (OD) of the AVTG, and (iv) the prevalence of ovarian atresia throughout the spawning period (Hunter et al. 1992; Greer-Walker et al. 1994; Murua et al. 2003).

The first three criteria were assessed from counts and diameters of oocytes from 27 SC females sampled during the spawning season, determined using the gravimetric method. Trends and differences among sampling dates in oocyte number and diameter were investigated with linear regression and Kruskal-Wallis rank sum test, respectively. The prevalence of atresia by month, defined as the percentage of ovaries showing atresia, was determined by examining histological ovary preparations of all SC females sampled during the spawning season.

Fecundity estimation

Only 18% of the females showed advanced mature or hydrated oocytes during the spawning season,

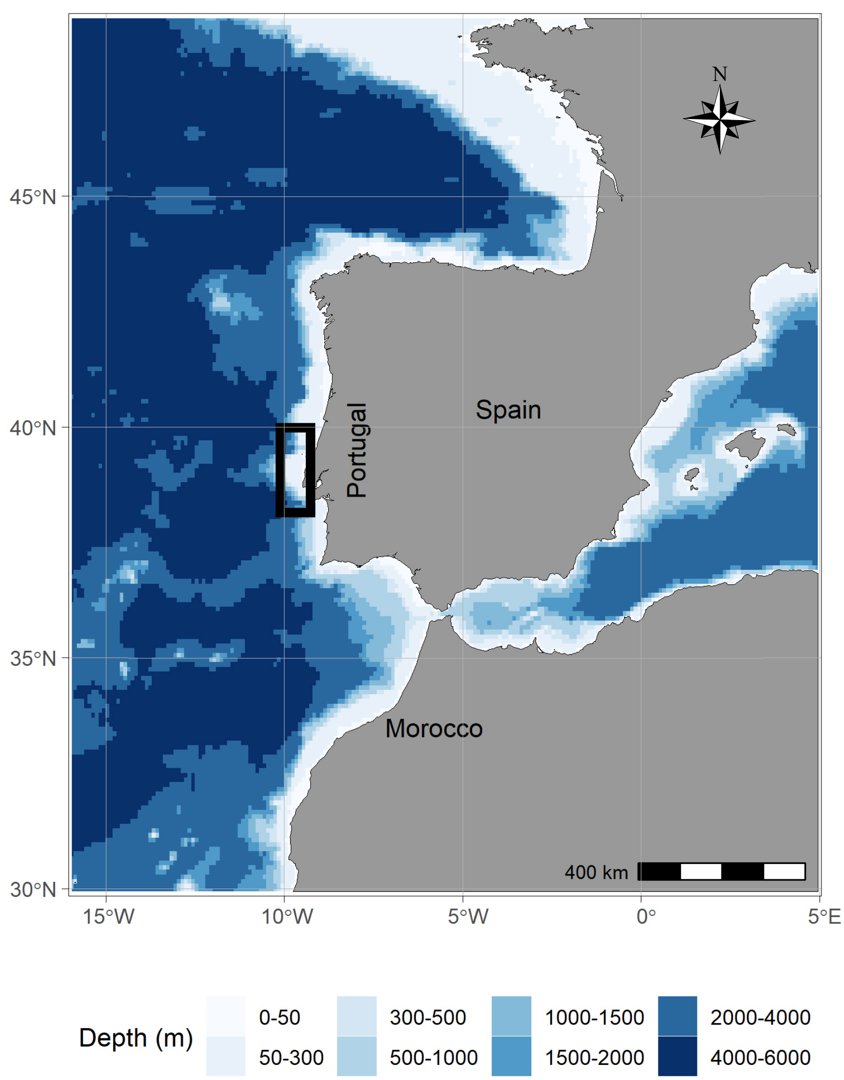

Fig. 1. Map of Portugal showing the continental slope: the surveys were conducted along the coast at 20–300 m deep (represented by the rectangle in the figure).

so the "hydrated oocyte method" (Ganias et al. 2014) could not be used for batch fecundity (BF) estimation. Therefore, batch measurements were based on the "most advanced mode of oocytes" (Ganias et al. 2014). The least and most advanced modes were determined for 48 females (24.3–38.2 cm TL, 111.30–477.50 g EW) using the Bhattacharya's based Modal Progression Analysis (MPA) with the routine in FAOICLARM Fisheries Assessment Tools (FiSAT II version 1.2.2) software (Gayanilo et al. 2005). Batch estimates were obtained using a combination of the Bhattacharya's method and the NORMSEP module in FiSAT II software (Plaza et al. 2002). The relationships between BF and TL and between BF and EW were investigated with exponential regression models.

Statistical analyses and graphics were done in R studio version 1.3.1093 (RStudio Team 2020) using the R packages PMCMR (Pohlert 2014), betareg version 3.1-0 (Cribari-Neto and Zeileis 2010), ggOceanMaps version 1.2.6 (Vihtakari 2022) and ggplot2 version 2.2.1 (Wickham 2016). Significance of statistical testing was assessed at p-value < 0.05.

RESULTS

In total, 626 blue jack mackerel individuals were sampled, including 300 females (TL: 31.7 ± 5.4 cm; 23.4–46.4 cm; EW: 287.12 ± 161.07 g; 94.5–871.10 g) and 326 males (TL: 31.7 ± 5.9 cm; 21.0–47.5 cm; EW: 287.49 ± 171.94 g; 73.94–931.30 g). The overall sex ratio was 1:1.09, and no deviations from 1:1 were found in individuals in the 5 cm length classes ($\chi^2 = 7.3$, $d.f. = 5$, p-value = 0.1989).

Only two immature males and one immature female were sampled, precluding the estimation of mean length at 50% maturity. The smallest male (21.0 cm) was caught in December and was immature while the smallest female (23.4 cm) was caught in February and was in the SC phase. The only immature female (26.7 cm) was also caught in February.

Reproductive cycle

Most males were already spawning capable in December, whereas more than 50% of the females were ready to spawn in late January (Fig. 2). In February and March, all males and 80% of females were SC/AS, while 11% of the females captured between April and July were reproductively active. Developing females occurred all year round except in September and the second half of March.

Variation in the gonadosomatic index was similar between sexes (Kruskal-Wallis *Chi*-squared = 0.87, *d.f.* = 1, *p*-value = 0.3718) and supported the maturity frequency distributions (Fig. 3), ranging from 0.10 in November to 9.87 in the first half of February for females and from 0.01 in October to 8.64 in the first half of February for males. Females attained higher GSI from the second half of January to the end of March (Kruskal-Wallis *Chi*-squared = 123.08, *d.f.* = 14, *p*-value < 0.0001), while males showed higher GSI from the beginning of January to the end of March (Kruskal-Wallis *Chi*-squared = 256.46, *d.f.* = 14, *p*-value < 0.0001). GSI was highly negatively correlated with SST, rho = -0.88 (*p*-value < 0.0001) for both sexes.

Significant differences between sexes were found for HSI (Kruskal-Wallis *Chi*-squared = 27.07, *d.f.* = 1, *p*-value < 0.001) but not for Kn (Kruskal-Wallis *Chi*-squared = 0.41, *d.f.* = 1, *p*-value = 0.519). Nevertheless, both bioenergetic indices varied significantly over the months, with the HSI showing higher values from March to July (F: Kruskal-Wallis *Chi*-squared = 146.23, *d.f.* = 14, *p*-value < 0.0001; M: Kruskal-Wallis *Chi*-squared = 157.27, *d.f.* = 14, *p*-value < 0.0001) and Kn peaking by the end of March through July (F: Kruskal-Wallis *Chi*-squared = 126.26, *d.f.* = 14, *p*-value < 0.0001: M: Kruskal-Wallis *Chi*-squared = 109.61, *d.f.* = 14, *p*-value < 0.0001).

Multiple ovary abnormalities were found over the sampling period. During the spawning period, 4% of females showed atretic structures, with only PG and early SG viable oocytes (Fig. 4a, b) and no structures suggesting reproductive events; these individuals were considered non-reproductive. In the second half of February, two females presented mass atresia, but still some AVTG remained (Fig. 4c) and were considered to have skipped at least one spawning event. In total, 7.2% of females showed a *Kudoa* spp. infection in the ovary, which led to total degradation of AVTG and prevented reproduction (Fig. 4d).

These abnormalities were not detectable from macroscopic examination of the gonads, but they were associated with lower somatic indices in all cases except those with *Kudoa* spp. infection. The reproductively inactive ovaries with cystic structures and the spawning capable individuals with massive atresia showed lower somatic indices, while *Kudoa* spp.- infected ovaries appeared at all levels as actively spawning individuals and could only be diagnosed from histological analyses (Fig. 5).

Fecundity

Estimated mean diameter was 146 ± 28 µm for CA oocytes, 267 ± 66 µm for EVTG oocytes and 475 ± 101 µm AVTG oocytes. Histological preparations from AS females showed oocytes at different stages, denoting an asynchronous development (Fig. 4e). No hiatus between pre-vitellogenic and vitellogenic oocytes nor a progressing dominant cohort was seen in OSFD during the spawning season (Fig. 6a). One advance cohort, around 600 μm OD, was observed all along the entire spawning season (Fig. 6a). The numbers of early developing oocytes (CA and EVTG) and AVTG (Fig. 6b) showed no linear trends (r^2 = 0.08, *p*-value = 0.0792 and r^2 = 0.02, *p*-value = 0.2478, respectively) or significant variations among sampling dates (Kruskal-Wallis *Chi*-squared = 6.19, *d.f.* = 4, *p*-value = 0.1856 and Kruskal-Wallis *Chi*-squared = 1.17, *d.f.* = 4, *p*-value = 0.8838, respectively). Likewise, AVTG OD showed neither significant trends (r^2 = 0.02, *p*-value = 0.2283) nor differences throughout the spawning season (Kruskal-Wallis *Chi*-squared = 8.65, *d.f.* = 4, *p*-value = 0.0704, Fig. 6c). The prevalence of atresia varied between 23% in January and 70% in the second half of February, with a mean of 45% over the spawning season. Mass atresia occurred at the end of the spawning season, in April (Fig. 4f).

Batch fecundity ranged between 6,798 and 302,358 oocytes for females with 25.4 cm TL and 33.8 cm TL, respectively. Mean relative fecundity was 221.92 ± 167.63 oocytes per gram of EW, ranging between 51.16 and 856.20 oocytes per gram of EW. The number of females with hydrated oocytes or recent POFs was low (< 5%), precluding the estimation of spawning frequency and, therefore, of annual fecundity. Poor relationships were found between BF and TL (r^2 = 0.25) and EW (r^2 = 0.25) (Fig. 7).

DISCUSSION

Sustainable management of fisheries requires knowledge of species' life histories, and particularly of their reproductive biology. However, much of this information has been based on macroscopic identification of the maturity stages, leading to erroneous characterisations of fish spawning conditions. In fact, in a previous study on a related species, *Trachurus trachurus*, Costa (2009) reported that macroscopic analysis misclassified maturity stages

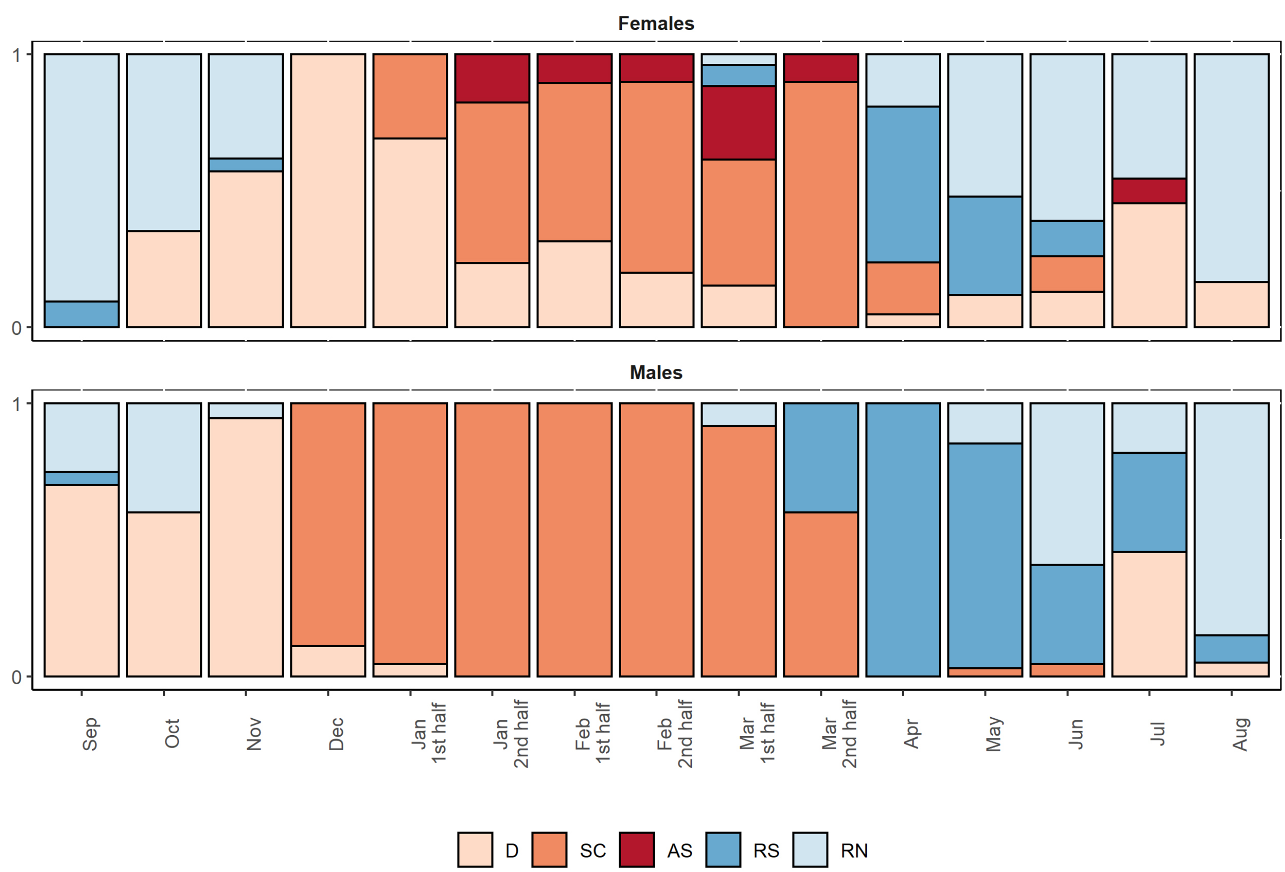

Fig. 2. Maturity phase frequency by sampling date for blue jack mackerel (*Trachurus picturatus*) females and males caught off the western coast of Portugal. D, developing; SC, spawning capable; AS, actively spawning; RS, regressing; RN, regenerating. 1st half, month first fortnight; 2nd half, month second fortnight.

59% more than did microscopic identification. Also, Vitale et al. (2006) showed that macroscopic analysis consistently overestimates the proportion of mature females for all age classes of cod. These two studies (among many others) show that erroneous macroscopic identification of maturity stages has clear consequences for fishery management. The present study is the first to analyse the reproductive strategy of *T. picturatus* based on microscopic analysis with the aim of supporting its fisheries in mainland Portugal. Histology techniques revealed that this species shows indeterminate fecundity and may face a possible reduction in reproductive potential due to ovary abnormalities.

Trachurus picturatus seems to have similar and balanced proportions of males and females across their populations (Jurado-Ruzafa and Santamaría 2013; Garcia et al. 2015; Costa 2019; the present study). However, the species shows marked differences in mean length at 50% maturity (L50), which range from 23 cm in the Canary Islands (Jurado-Ruzafa and Santamaría 2013) to 28 cm in Azores (Garcia et al. 2015; Table 1). The lack of immature individuals precluded the estimation of L50 off the west coast of Portugal, but almost 200 mature individuals between 23–27 cm TL were sampled, suggesting that local L50 is probably closer and even lower than that for the Canary Islands. However, the estimation of the length at first maturity in the Macaronesia archipelagos was based on the macroscopic analysis of the gonads, which may yield a degree of uncertainty. For example, Garcia et al. (2015) reported the presence of very large but still immature fish (above 40 cm fork length, Table 1), which is uncommon.

Reproduction has been considered to occur from January to April/May (Jurado-Ruzafa and Santamaría 2013; Garcia et al. 2015; Vasconcelos et al. 2017b; Costa 2019), but the present study suggests that it is actually from mid-January to the end of March (Table 1). This slight difference in spawning season duration is most likely due to the criteria used for its definition,

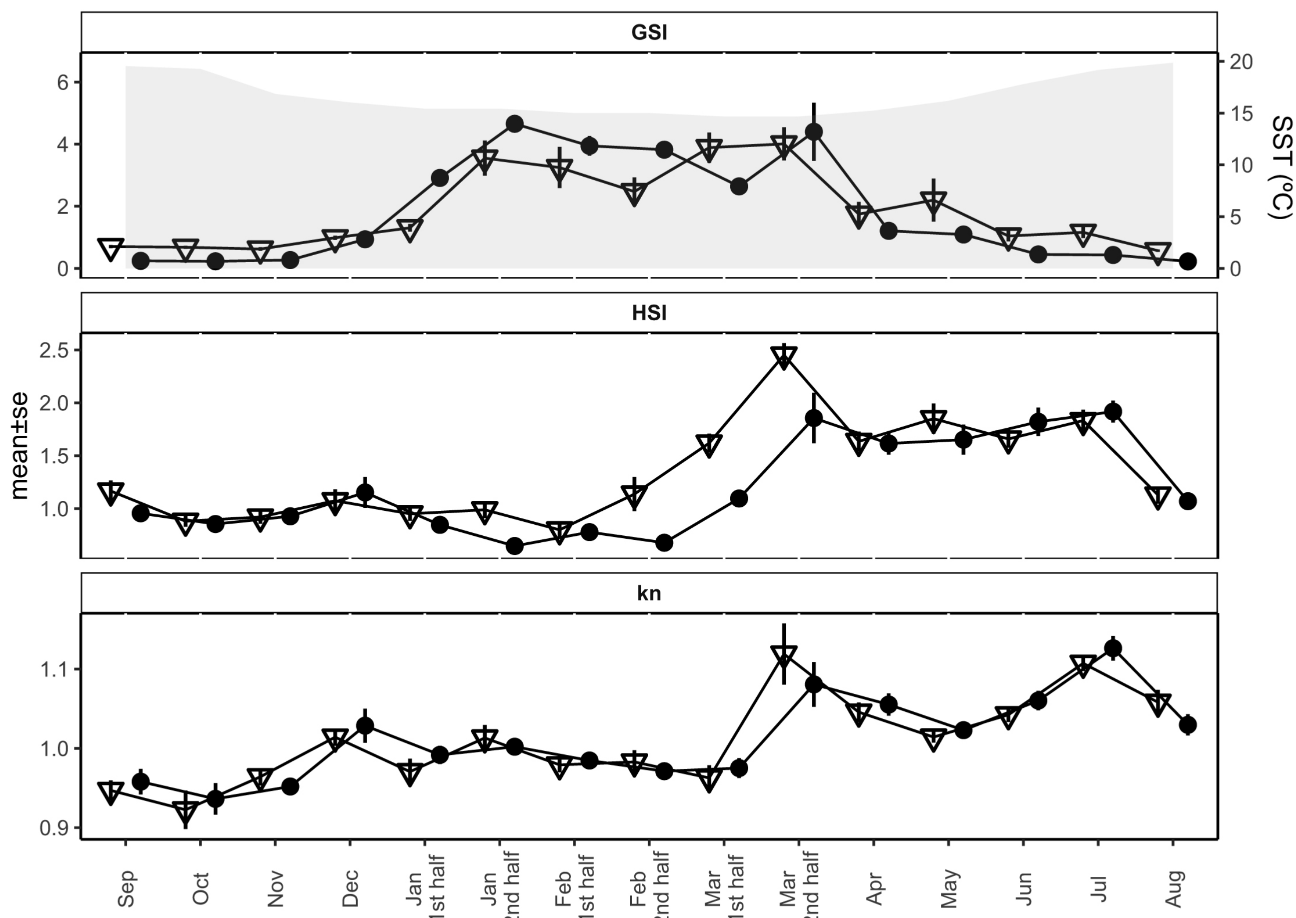

Fig. 3. Mean (± standard error) gonadosomatic index (GSI), hepatosomatic index (HSI), and relative condition (Kn) for blue jack mackerel (*Trachurus picturatus*) females (black dots) and males (open triangles) off the western coast of Portugal by sampling date. Sea surface temperature (SST, grey shadow). 1st half, month first fortnight; 2nd half, month second fortnight.

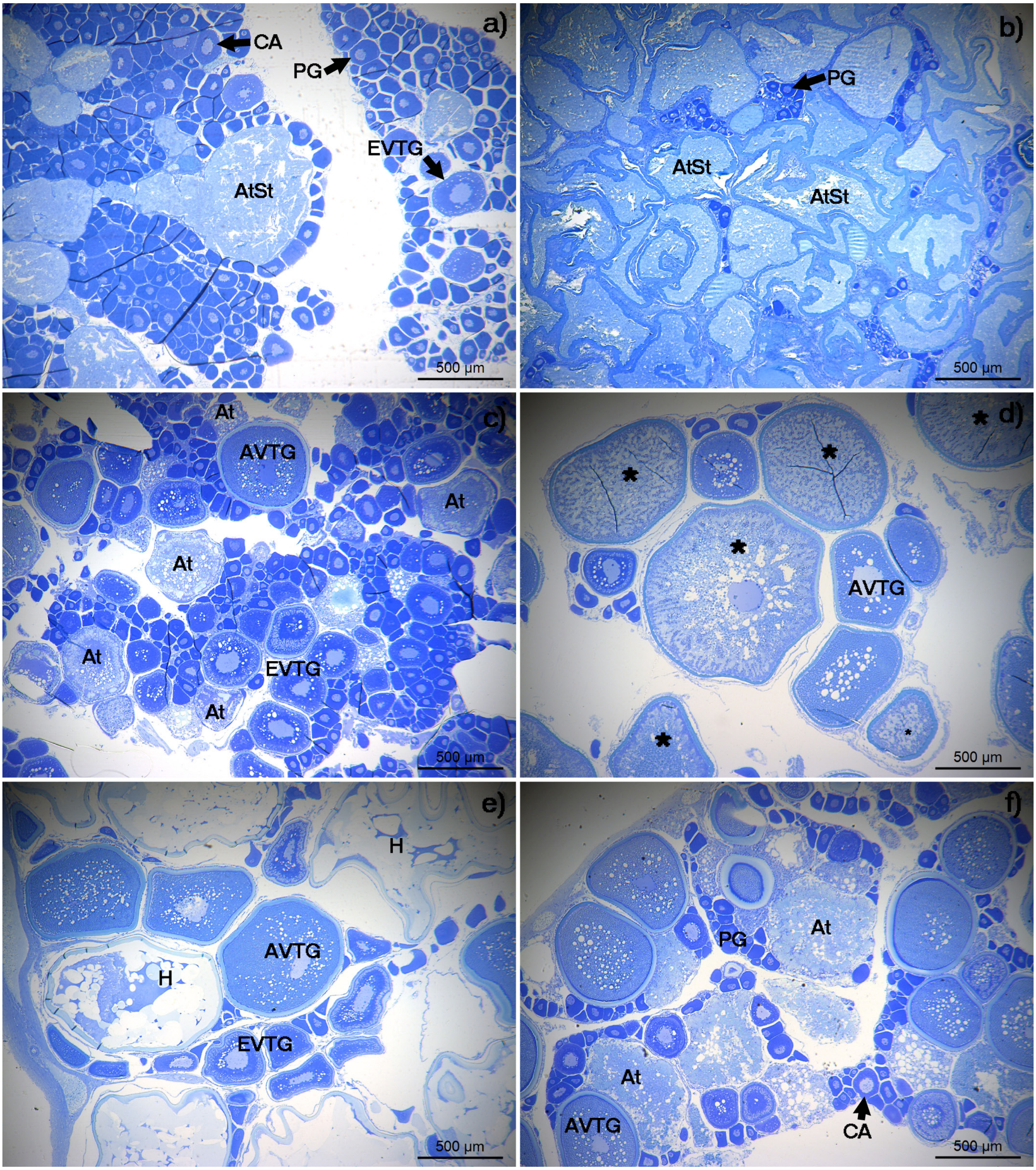

Fig. 4. Histological sections of ovaries of blue jack mackerel (*Trachurus picturatus*) with abnormalities: a) reproductive inactive ovaries with cystic structures with only PG and early SG oocytes (female with 38.1 cm TL, caught in the first half of January); b) reproductive inactive ovaries with massive cystic structures with only a few PG oocytes remaining (female with 26.2 cm TL, caught in the first half of March); c) spawning capable individuals with massive atresia (female with 25.8 cm TL, caught in second half of February); d) *Kudoa* spp.-infected ovary (female with 25.5 cm TL, caught on the first half of March); e) actively spawning (female with 31.1 cm TL, caught on the second half of March); f) regressing female with massive atresia (female with 27.3 cm TL, caught in April). *, *Kudoa* spp. infection; AVTG, advance vitellogenic oocytes; At, atresia; AtSt, atretic structures; CA, cortical alveoli oocytes; EVTG, early vitellogenic oocytes; H, hydrated oocytes; PG, primary growth oocytes.

where only the period when more than 50% of females are spawning capable was considered. However, a few (~11%) spawning females were caught from April to July, indicating some variability in spawning timing within the population. The highly negative relationship between SST and GSI found in this study can justify the shortener spawning season observed because water temperature is known to be a key factor for the reproductive stimuli (Pankhurst and Porter 2003), and, in the case of *T. picturatus*, this appears to cease when SST begins to rise. The more stable environmental conditions in the different seamounts associated with the Macaronesia archipelagos may also contribute to such differences.

Bioenergetic indices showed a synchronous pattern over the year, with low values at the beginning of the spawning season that started to increase near the end and remained high in the following months. No depletion in feeding activity was observed during the spawning season, as was also previous reported by Battaglia et al. (2020), indicating concurrent intake for reproduction as found in income breeders (McBride et al. 2015). However, multiple-spawning fishes often supplement egg production with stored energy (McBride et al. 2015). *Trachurus picturatus* apparently supports spawning energy from direct feeding, storing energy by the end of the spawning season, as reflected by higher values of HSI and Kn during this time.

A decrease in energy reserves can lead to spawning failure, a phenomenon known as skipped spawning (Rideout et al. 2005). Skipped spawning has been described for a variety of fish species with determinate fecundity, but it is difficult to identify in species with indeterminate fecundity (Rideout and Tomkiewicz 2011). Some blue jack mackerel females caught off the west coast of Portugal showed gonads with evidence of interruption in oocyte development prior to vitellogenesis completion, and reabsorption

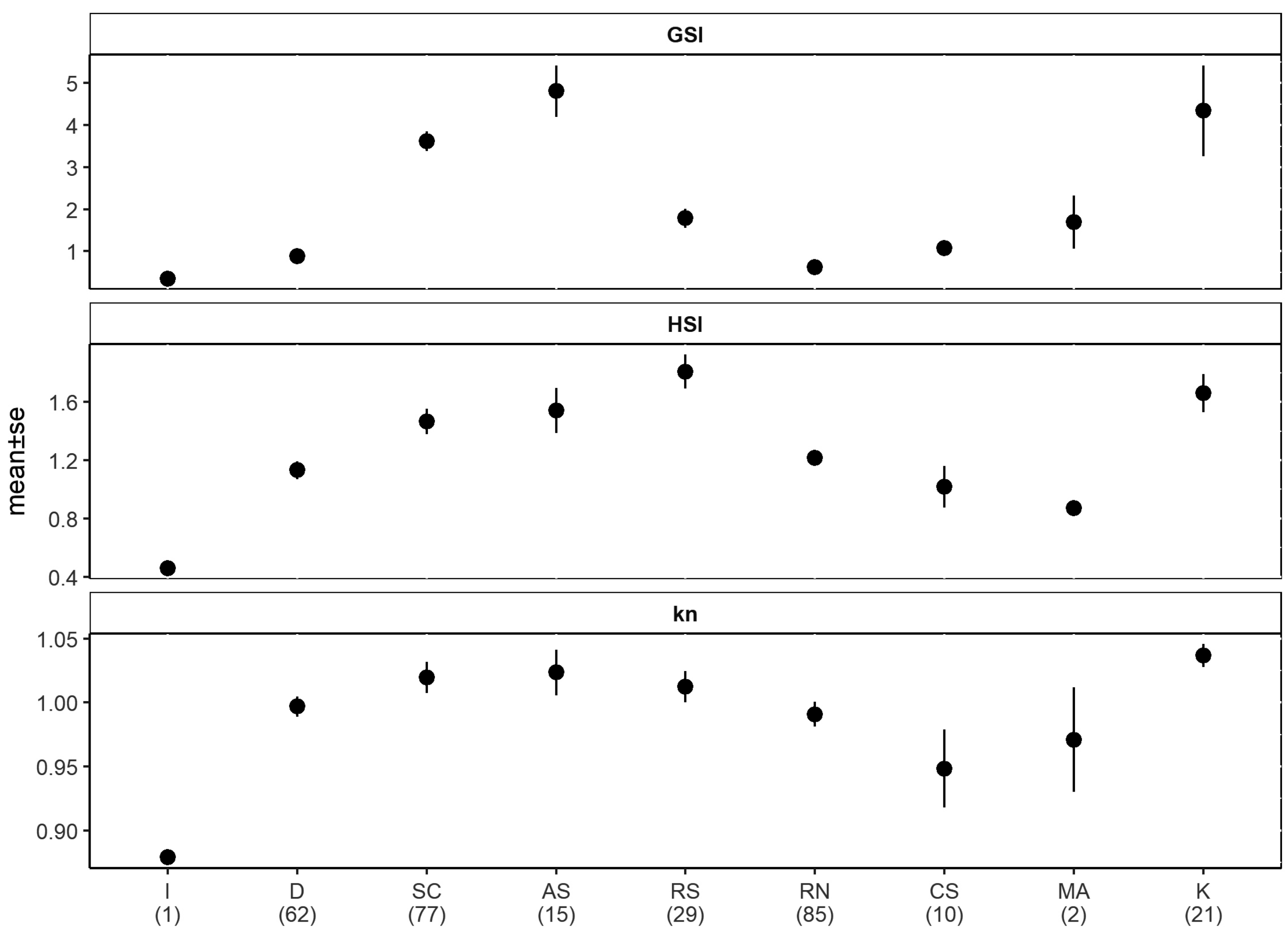

Fig. 5. Mean (± standard error) gonadosomatic index (GSI), hepatosomatic index (HSI), and relative condition (Kn) for blue jack mackerel (*Trachurus picturatus*) females off the western coast of Portugal by maturation phase and abnormal condition. I, immature; D, developing; SC, spawning capable; AS, actively spawning; RS, regressing; RN, regenerating; CS, reproductive inactive ovaries with cystic structures; MA, spawning capable individuals with massive atresia; K, *Kudoa* spp.-infected ovaries. Sample size for each group is given between brackets in the x-axis.

of AVTG and mature oocytes. These females showed lower bioenergetic indices than reproductive females, which is common in skipped spawning events (Skjæraasena et al. 2020). This is consistent with results of experiments with *T. trachurus* in captivity, indicating that, without proper environmental stimuli, individuals that have completed vitellogenesis fail to undergo oocyte maturation and spawning (Ndjaula et al. 2009).

Skipped spawning events together with parasitic ovary infection will negatively affect the reproductive potential of *T. picturatus*. These phenomena may also influence species recruitment and contribute to the strong fluctuations in landings that have been attributed to changes in the species' abundance/availability (ICES 2019b). Both skipped spawning and parasitic infection could only be detected by histology (Neves et al. 2020), confirming the importance of microscopic analysis to correctly perceive and interpret processes occurring in the gonads and avoid bias in estimating biological parameters (Vitale et al. 2006; Midway and Scharf 2012).

During the spawning season, there was no hiatus or trend in the AVTG number or OD; the mass atresia at the end of the spawning season suggests that *T. picturatus* displays indeterminate fecundity off the west coast of Portugal, similar to what has been suggested by Vasconcelos et al. (2017b) for the Madeiran population. This strategy is commonly reported for warm-water stocks (Ganias et al. 2015), but recent studies have shown that fecundity type is not species specific, as previously thought, since they were unclear if fecundity type is genetically predefined or modulated by habitat and environmental characteristics as an ecophenotypic response (Serrat et al. 2019). However, indeterminate fecundity is commonly reported in warmer waters, and different species from mainland Portugal occurring in different habitats have shown determinate fecundity, like the deep-water black scabbardfish (Neves et al. 2009), the demersal up to 700 m deep forkbeard (Vieira et al. 2016) and the coastal piper gurnard (Neves et al. 2021). Several techniques using parasites (Hermida et al. 2016**)**, geometric morphometrics and otolith shape analysis (Vasconcelos et al. 2018) and otolith elemental and isotopic signatures (Moreira et al. 2018) highlight

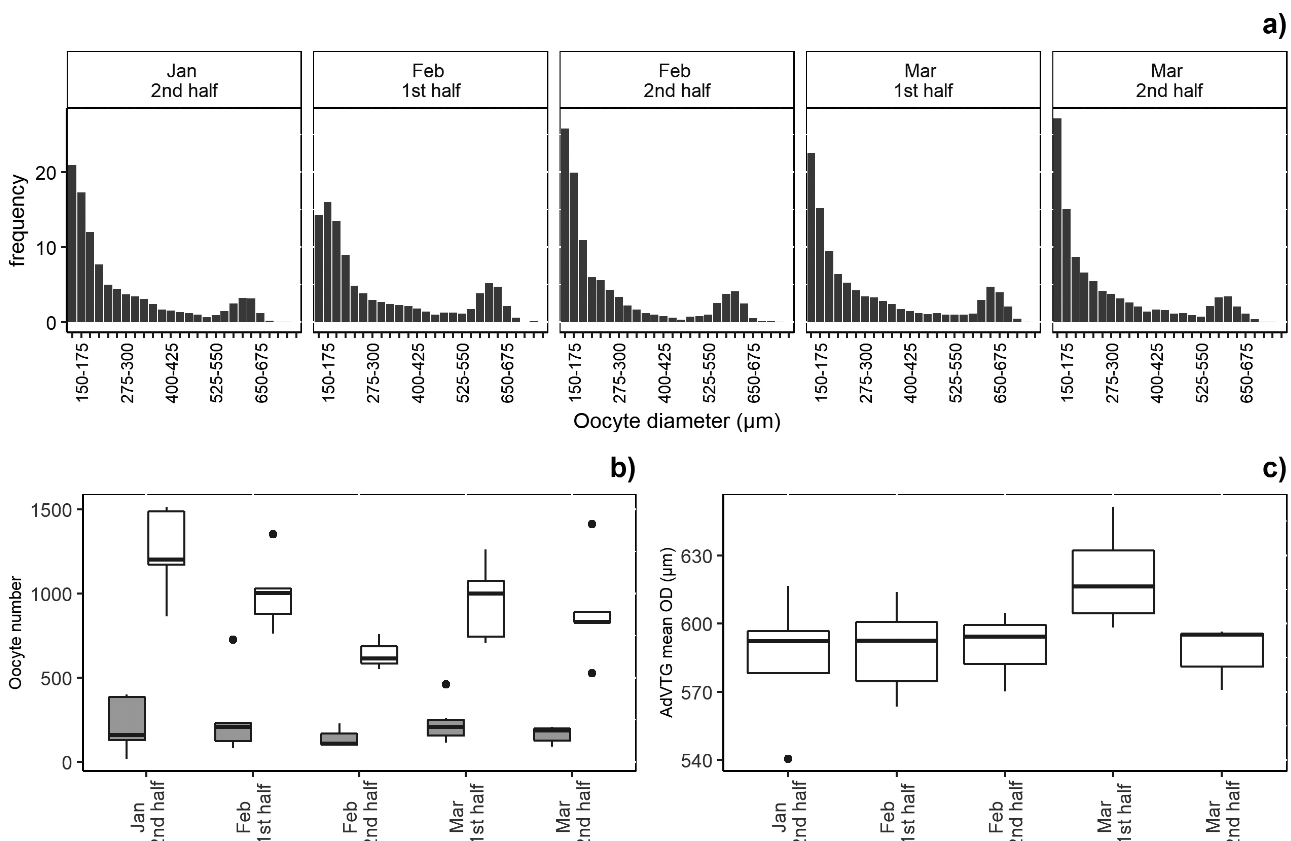

Fig. 6. Fecundity type of blue jack mackerel (*Trachurus picturatus*) off the western coast of Portugal, assessed from the variation throughout the spawning season of a) oocyte size frequency distribution; b) abundance of early developing oocytes (white) and advanced vitellogenic oocytes (grey); c) mean oocyte diameter (OD) of the advanced vitellogenic oocytes. Boxplot represents median, first and third quartiles, whiskers represent 1.5 × interquartile range and dots are possible outliers. 1st half, month first fortnight; 2nd half, month second fortnight.

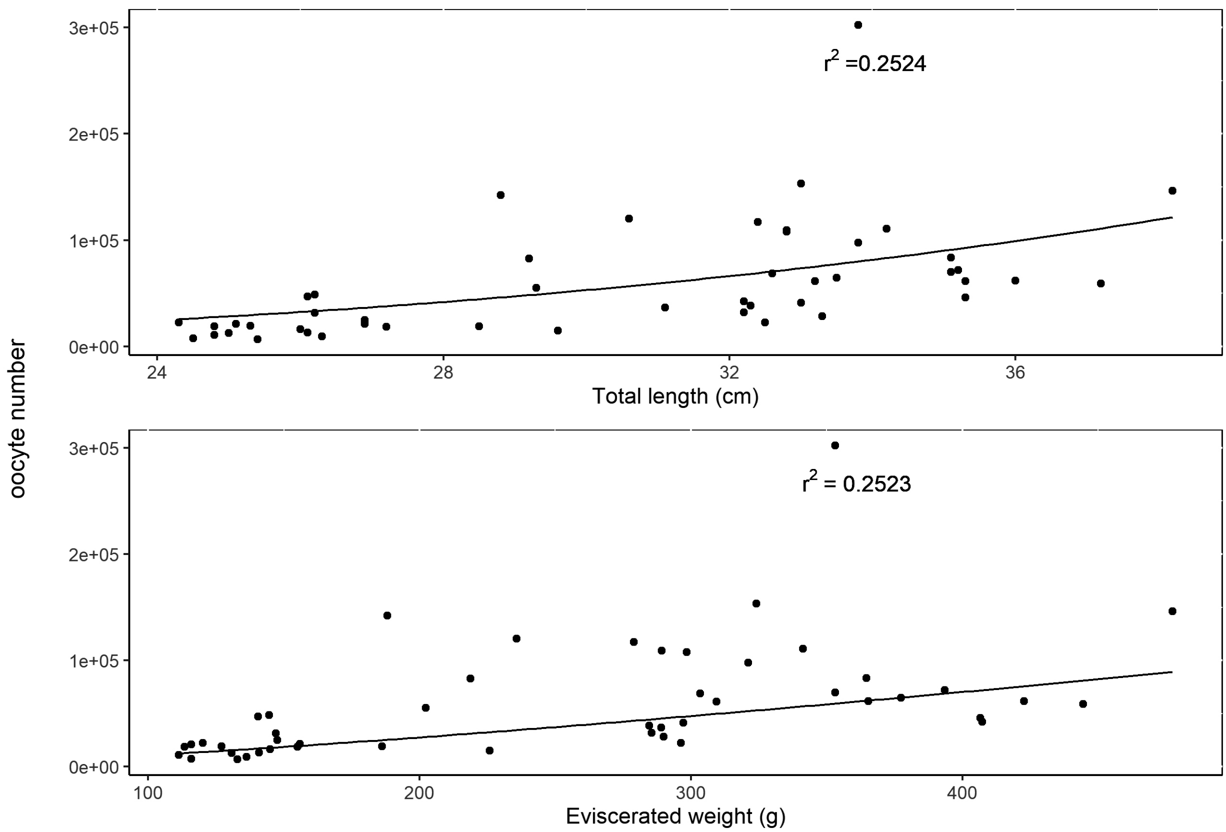

Fig. 7. Relationships between batch fecundity and total length (TL) and eviscerated weight (EW) for blue jack mackerel (*Trachurus picturatus*) females caught off the western coast of Portugal.

Table 1. Summary of the reproductive parameters estimated for *Trachurus picturatus* caught in Portuguese mainland and in the Macaronesia archipelagos

	TL range (cm)	Minimum mature TL (cm)	Maximum immature TL (cm)	L50 (cm)	Spawning season
Portugal mainland (this study)	21.0–47.5	21.0	26.7		Jan–Mar
Portugal mainland (Costa 2019)	17.8–44.3				Jan–May
Azores (Garcia et al. 2015)	9.8–54.2 FL	24.1 FL	45 FL	F: 27.7 M: 28.8	Dec–May
Madeira (Jesus 1992)	10–41	16	21	F: 17.7 M: 16.6	Nov–Apr
Madeira (Vasconcelos et al. 2017b)					Jan–Apr
Canary Islands (Jurado-Ruzafa and Santamaría 2013)	10.4–31.9	20		F: 23.1 M: 22.2	Jan–Apr

	Sex ratio (F:M)	Maturity stages evaluation	Fecundity type	Batch fecundity (ooc*g^{-1}EW)
Portugal mainland (this study)	1:1.09	microscopic	Indeterminate	221.92 ± 167.63
Portugal mainland (Costa 2019)	1.27:1	macroscopic		
Azores (Garcia et al. 2015)	1:1.11	macroscopic		
Madeira (Jesus 1992)	1.2:1	macroscopic		
Madeira (Vasconcelos et al. 2017b)			Indeterminate	
Canary Islands (Jurado-Ruzafa and Santamaría 2013)	1:1.36	macroscopic		

TL: total length; FL: fork length; L50: length at first maturity; F: females; M: males; ooc*g^{-1}EW: oocytes per gram of eviscerate weight.

the presence of separate populations of blue jack mackerel in the Atlantic, and possible differences in fecundity within those populations should be assessed for proper management.

The batch fecundity estimate for *T. picturatus* (221.92 oocytes per gram of EW female) was slightly higher than that for *T. trachurus* in the Iberian coast (~200, Gonçalves et al. 2009). There was also a high variance in the estimates of *T. picturatus* fecundity, but it is currently impossible to evaluate if this is characteristic of the species, given the lack of information on other populations.

Estimates of relative annual fecundity are essential for understanding the reproductive output of fish (Ganias 2018). In this study, it was not possible to estimate the fraction of spawning females in the population due the absence of individuals showing evidence of imminent (H) or just finished (POF) spawning. The capture of these females may have been hampered by aggregations occurring during spawning and by the relatively short duration of both H and POFs, as in the case of *T. trachurus* (Gonçalves et al. 2009). An estimate of *T. picturatus* annual fecundity would require a larger sampling effort. Nevertheless, the unusually low number of females with visible POFs, which last at least a few days in the ovary, suggests a large interval between spawning events, which may ultimately reduce the annual fecundity of the species.

CONCLUSIONS

Information gathered from the Portuguese mainland's coast indicates that *T. picturatus* is a winter, early spring spawner, similar to *T. trachurus*, which is caught in the same fishing areas. It is an indeterminate spawner that shows relatively high batch fecundity, but spawning frequency is probably low, which may reduce annual fecundity. Occurrence of mature non-reproductive females (skipped spawners and *Kudoa*-infected) was described for the first time and can also negatively affect reproductive potential and eventually lead to population fluctuations. Repeated measurements of fecundity are needed to get better insight into fluctuations in the reproductive output and population dynamics of *T. picturatus*.

List of abbreviations

AS, actively spawning.
AVTG, advanced vitellogenic oocytes.
BF, batch fecundity.
CA, cortical alveoli oocytes.
D, developing.
EVTG, early vitellogenic oocytes.
EW, eviscerated weight.
GSI, gonadosomatic index.
GW, gonad weight.
H, hydrated oocytes.
HSI, hepatosomatic index.
Kn, relative condition.
L50, length at 50% maturity.
LW, liver weight.
MLS, minimum legal size.
OD, oocyte diameter.
OSFD, oocyte size frequency distribution.
POF, postovulatory follicles.
SG, secondary growth.
SC, spawning capable.
TAC, total Allowable Catch.
TL, total length.

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