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Demography of the black grouper, *Mycteroperca bonaci* (Poey, 1860) (Teleostei: Epinephelidae) from the North Brazil Shelf

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Abstract

Mycteroperca bonaci (black grouper) is one of the most sought species of grouper along its entire distribution, being a prime target for demersal line fisheries because of its high commercial value. Nonetheless, because of population declines the species is considered near threatened according to the IUCN red list. The present study aimed to determine the population parameters of *M. bonaci*, including growth, reproduction and mortality, and thus contributes to measures towards its conservation and management in the southwestern Atlantic. The sampling area is in the North Brazil Shelf, off Maranhão State, an area of intense fisheries development and yet poorly known. The large continental shelf harbours unique coral reef formations and has been declared an ecologically or biologically significant marine area (EBSA). Sampling on landing sites was carried out monthly between May 2017 and January 2019. A total of 137 black grouper specimens were sampled from commercial landings of artisanal fisheries. The size of the specimens ranged from 44 to 157 cm, and the weight varied from 0.976 to 54 kg. The length–weight was established: $\log(TW) = -11.26 + 3.01\log(TL)$. Histological analysis of the gonads confirmed only the presence of female individuals, and the occurrence of individuals in the sexual transition was not recorded. Higher GSI values and higher frequency of spawning capable staged individuals occurred during the months of June to August, indicating spawning peaks. The estimated age of sexual maturity A50 for females was 4.62 years ($\underline{x}$ 93 cm–TL). The growth parameters for the Von Bertalanffy model were TL_∞ (cm): 185.5, *k*: 0.04, t_0 (year): −4.75 (t_0 not fixed) and TL_∞ (cm): 141, *k*: 0.11 ($t_0 = 0$ fixed). The total estimated mortality rate (*Z*) according to catch length presented a *Z* value = 0.11, and the natural mortality was $M = 0.04\ year^{-1}$. This is the first study on the age and growth of *M. bonaci* in the SWA, a region where the species is considered as endangered according to Brazil's red list regional assessment. Only females were present in the samples, results that suggest either differential capturability of sexes because of distinct patterns of behaviour or distribution or an effect of selective mortality upon larger and older individuals, as the species is described as a protogynous hermaphrodite. This indicates the need to closely manage this population to avoid collapses. Recovery plans that have been planned by the Brazilian government but not yet implemented for the species must be put into practice to avoid progressive decline as fisheries target more remote areas.

KEYWORDS
demersal line fishery, female individuals, management, North Brazil Shelf, recovery plan, vulnerable species

1 | INTRODUCTION

The black grouper *Mycteroperca bonaci* (Poey, 1860) is a widely distributed western Atlantic grouper occurring from Massachusetts in the U.S.A. to southern Brazil, including Bermuda, the southern Gulf of Mexico, Florida Keys, the Bahamas, Cuba and the Caribbean (Craig *et al*., 2011; Heemstra & Randall, 1993). It is the second-largest grouper in the western Atlantic and has historically been a primary target of fisheries (Padovani-Ferreira *et al*., 2018).

Along the southwestern Atlantic coast, black grouper is an important component of demersal fisheries caught by handline, longline and spearfishing in reef environments off the continental shelf and/or oceanic banks (Lessa & Nóbrega, 2000; Nóbrega *et al*., 2009). At that time this species represented *c*. 8% of the total weight of demersal fish commercially exploited (Ibama., 1999a; Ibama., 1999b; Lessa *et al*., 2004). The present level of capture is uncertain due to a lack of official statistics since 2008 (Freire *et al*., 2021). Reconstruction of catches, however, indicates that Brazilian catches still account for the majority of reported and reconstructed catches in the western Atlantic (Freire *et al*., 2021), although declines of 30%–50% have been reported on landings, interviews (Teixeira *et al*., 2004; Bender *et al*., 2014; Giglio *et al*., 2014) and catch per unit effort data from Brazil over the past three generation lengths (Padovani-Ferreira *et al*., 2018), prompting an evaluation of its national status as vulnerable according to the Brazilian red list (Icmbio, Instituto Chico Mendes DE Conservação DA Biodiversidade, 2018).

The inherent characteristics of the Epinephelid family (*e.g*., reproduction mode and behaviour) make them more susceptible to stock collapses when subjected to heavy unmanaged fisheries. Some of them are protogynous hermaphrodites, so selective size fishing mortality may remove males from the population (Crabtree & Bullock, 1998; Padovani-Ferreira *et al*., 2018). In addition, the species is known to aggregate both to spawn and in periodic runs (Eklund & Schull, 2001; Parrish, 2005; Teixeira *et al*., 2004).

Although this species has been studied in most of its area of occurrence, such as the northern Atlantic and Caribbean (Brulé *et al*., 2003; Crabtree & Bullock, 1998; Manooch & Mason, 1987; Rénan *et al*., 2013), and in the southwestern Atlantic (Freitas *et al*., 2011, 2018; Teixeira *et al*., 2004), there is a lack of studies on this species in the North Brazil Shelf or Amazonian ecoregion, where the species occurs mainly offshore Maranhão State.

Furthermore, studies in Brazil refer to reproductive aspects (Freitas, 2014; Freitas *et al*., 2011; Freitas *et al*., 2018; Teixeira *et al*., 2004), ethnoichthyology (Gerhardinger *et al*., 2007; Begossi and Figueiredo, 1995), feeding ecology (Freitas *et al*., 2017) and fisheries (Paiva and Andrade-Turbino, 1998; Costa *et al*., 2003), with a lack of studies reporting on the age and growth of *M. bonaci*.

Therefore, the present study aimed to determine the population parameters of *M. bonaci* covering the growth, reproduction and mortality of the species for an important part of its distribution, the North Brazil Shelf. To this end, data on growth parameters, age structure, age at maturity, size, sexual transition, sexual composition and natural and total mortality were established so that it is possible to design planning measures and practices that ensure sustainable exploitation of this resource.

2 | MATERIALS AND METHODS

2.1 | Sampling site

The black grouper samples came from commercial landings sold daily at the fish market in Fortaleza, capital of the state of Ceará, northeastern Brazil. The fish are brought to the market by middlemen who buy them at the port of the city of Camocim, an important landing place for Ceará fishing, located in the far west of Ceará.

The black groupers were captured by the artisanal fishing fleet from Ceará using motorized wooden vessels, which operate on the coast of the state of Maranhão, northeast Brazil, capturing demersal species with handlines and longlines. The coast of the state of Maranhão, Brazil, has a large continental platform and shallow coastal waters that are influenced by large river basins (Kjerfve *et al*., 2002). The fishing areas of the study are composed of estuary bars, islands and marine state park located on the inner and middle continental shelf as well as the slope (Figure 1). The marine park, known as Parcel Manuel Luiz, covers a large coral reef area located on the continental shelf, 86 km from the coast, and has been declared both a state marine park and an ecologically or biologically significant marine area (EBSA) (CBD, 2014). After landing, the catch is packed in trucks and transported to the capital Fortaleza for sale in the fish market.

2.2 | Collecting and processing the samples

Sampling was performed monthly from May 2017 to January 2019 in fishmongers located at the fish market in Fortaleza. The fishery occurs throughout the year.

In the fishmonger (Figure 2), the total length TL (0.1 cm), weight of the whole fish TW (0.01 kg) and gonad GW (0.01 g) and pairs of *sagittae* otoliths were obtained. For this purpose, a tape measure, a commercial scale and a precision scale (0.001 g) were used. As many fish were gutted before landing (68% of the total samples), it was not possible to sample gonads from all individuals.

2.2.1 | Age and growth

The sagittae pairs of otoliths were removed by the operculum at the data collection site while the fish were gutted. As the specimens were

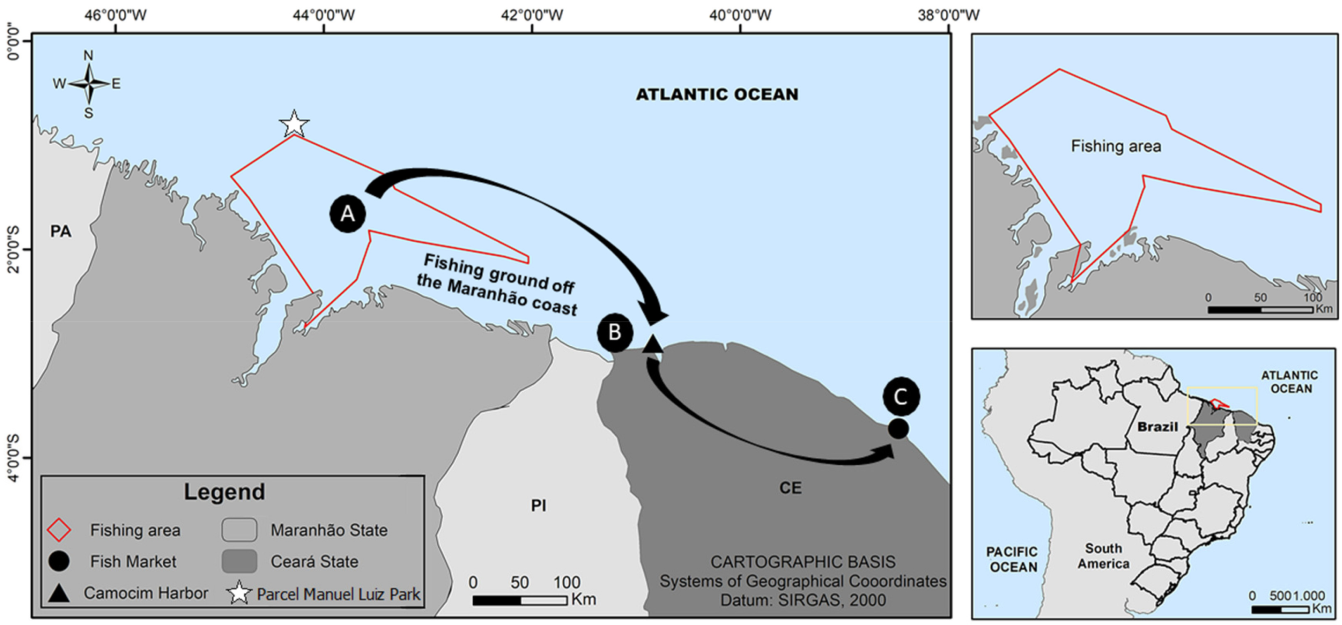

FIGURE 1 Map of the fishing region with highlights of the sea (A to B) and land (B to C) routes of *Mycteroperca bonaci* captured off the coast of Maranhão. Assumed fishing area as reported by fisher's personal communication

FIGURE 2 Arrival of catches of *Mycteroperca bonaci* in fishmongers containing specimens of various sizes captured on the coast of Maranhão (a, b, c) and biometrics being carried out before sale (d)

not bought, this technique was preferred as it maintains the appearance of the animal and does not affect its sale. In the Population Dynamics and Ecology of Marine Fishes laboratory (DIPEMAR) from Federal University of Ceará, the otoliths were cleaned and rinsed, dried, weighed on a precision scale (0.001 g) and stored in a properly labelled Eppendorf-type container. The left otoliths were selected for readings. The otoliths were then embedded in epoxy resin and cross-sectioned in a low-speed Buehler-Isomet diamond blade saw in 350 μm sections in the Ocean and Reef Ecosystems laboratory from Federal University of Pernambuco.

The slices were mounted on glass slides using Entellan, and when necessary, they were further ground and polished using sandpaper 2000. Age marks were examined in a reflected-light magnifier with a camera attached (Leica S9D), and the opaque zones were counted and considered for age determination (Green *et al*., 2009a; Hoedt, 1992; Volpedo & Vaz-Dos-Santos, 2015).

Two independent readings were performed without prior knowledge of the animal length. A single axis of reading established from the nucleus to the ventral region was standardized (Figure 3). The mean error percentage index (MEI) was calculated to estimate the accuracy of the two readings (rings) (Beamish & Fournier, 1981). If the index of average percentage error (IAPE) values were equal to or greater than 10%, a third reading was triggered.

To verify whether the otolith is a suitable structure for the study of age and growth, dispersion diagrams were plotted, and significance was established through Pearson's correlation between the data: length of the radius of the otolith – total length of the fish and length of the otolith – the weight of the otolith, and regression between the variables ($P < 0.05$).

Based on previous studies, it was assumed that for the black grouper each pair of bands (opaque and translucent) is formed/deposited annually (Crabtree & Bullock, 1998; Rénan *et al*., 2013). Indeed, almost all tropical groupers studied lay increments annually (Choat *et al*., 2009), as observed for *Epinephelus morio* (Valenciennes 1828), *Epinephelus adscensionis* (Osbeck, 1765; Marques & Ferreira, 2018), *Alphestes afer* (Bloch, 1793; Marques & Ferreira, 2016) and *Cephalopholis fulva* (Linnaeus 1758) (Burgos *et al*., 2007; Reñones *et al*., 2007; Araujo & Martins, 2006, Lombardi-Carlson *et al*., 2008), including the black grouper *M. bonaci* (Crabtree & Bullock, 1998; Manooch & Mason, 1987 and Rénan *et al*., 2013).

The growth in length was modelled using the von Bertalanffy growth function (VBGF, Beverton & Holt, 1956), where the expected size for a given age is obtained by the equation: $L_T = L\infty\{1-e[-K(t-t_0)]\}$. The calculated parameters were the maximum asymptotic mean total length (TL∞); the growth coefficient (k) and the theoretical age at the time the length equals zero (t_0). The growth curve was adjusted using the R package nlstools and FSA (Fish Stock Assessment) (Baty *et al*., 2015). To compare growth curves, the growth performance [$\Phi' = \log(K) + 2\log(L\infty)$] (Moureau *et al*., 1986) was calculated using the growth parameters obtained through the VBGF. The Φ' was calculated for this study and previous ones (Table 1).

Linear regression analysis was used to determine the simple relationship between otolith weight and fish age (Ferreira & Russ, 1994). Student's *t*-test was used to evaluate the slope of the linear weight–length relationship, where the null hypothesis $b = 1$ means no changes in fish condition.

2.2.2 | Reproduction

The gonads were fixed in 10% formalin for 24 h and stored in 70% alcohol diluted in sea water. Later, the median fraction of each gonad was submitted to the histological routine established by Vazzoler (1996) for sex confirmation and determination of maturation stages. The sections obtained had a thickness of 6 μm. Staining was performed using Harris haematoxylin and eosin.

The gonadal development phases were described according to the histological criteria of Brown-Peterson *et al*. (2011) which correspond to Immature (never spawned), Developing (beginning to develop, but not ready to spawn), Spawning capable (able to spawn), Regressing (cessation of spawning) and Regenerating (sexually mature but reproductively inactive), this later corresponding to resting stage in other terminologies (Teixeira *et al*., 2004). To this classification was added Transition phase (at the time fish begin to change sex), to accommodate alternative reproductive strategies, such as hermaphrodites (Brown-Peterson *et al*., 2011).

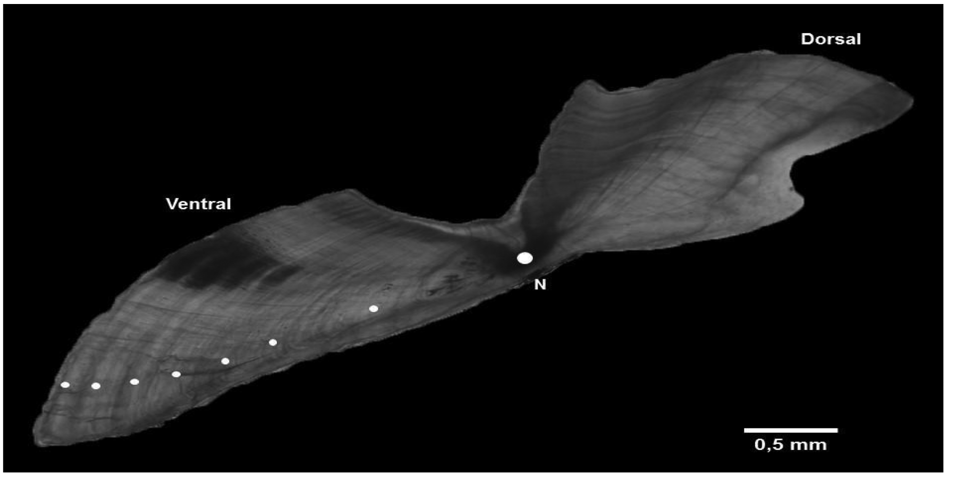

FIGURE 3 Otolith sectioned from a 71 cm long specimen of *Mycteroperca bonaci* captured from May 2017 to March 2019 on the coast of Maranhão, Brazil, showing the standardized reading axis (nucleus – ventral region). N: nucleus

TABLE 1 Von Bertalanffy parameters available in the literature and *growth performance* for black grouper with grouped sexes

Researches	TL_∞ (cm)	*K*	t_0 (year)	Φ'	Area
Crabtree and Bullock (1998)	130.6	0.169	−0.769	3.46	Florida
Rénan *et al.* (2013)	138.4	0.12	0.068	3.36	Golfo do México
Manooch and Mason (1987)	135.2	0.11	0.92	3.30	Southeast of United States
Present study	185.5	0.04	−4.75	3.14	Northeastern coast of Brazil
Present study ($t_0 = 0$)	141	0.11	0	3.34	Northeastern coast of Brazil

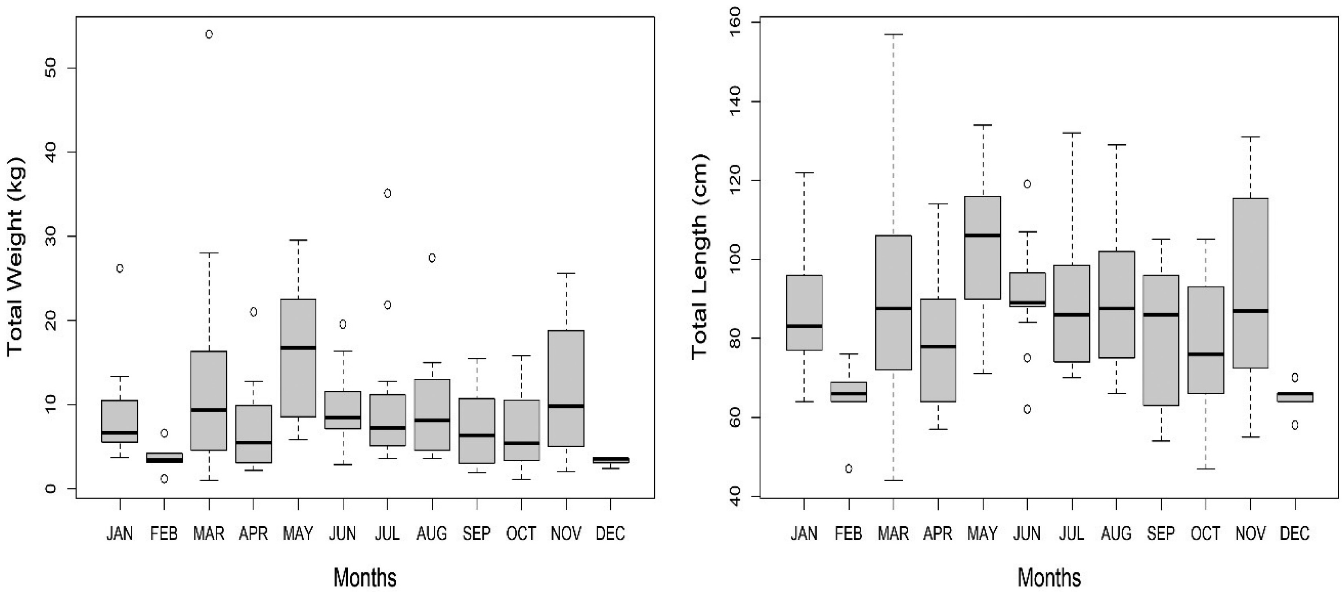

FIGURE 4 Boxplot of the total weight and total length of *Mycteroperca bonaci* specimens sampled from May 2017 to March 2019 from the coast of Maranhão, Brazil

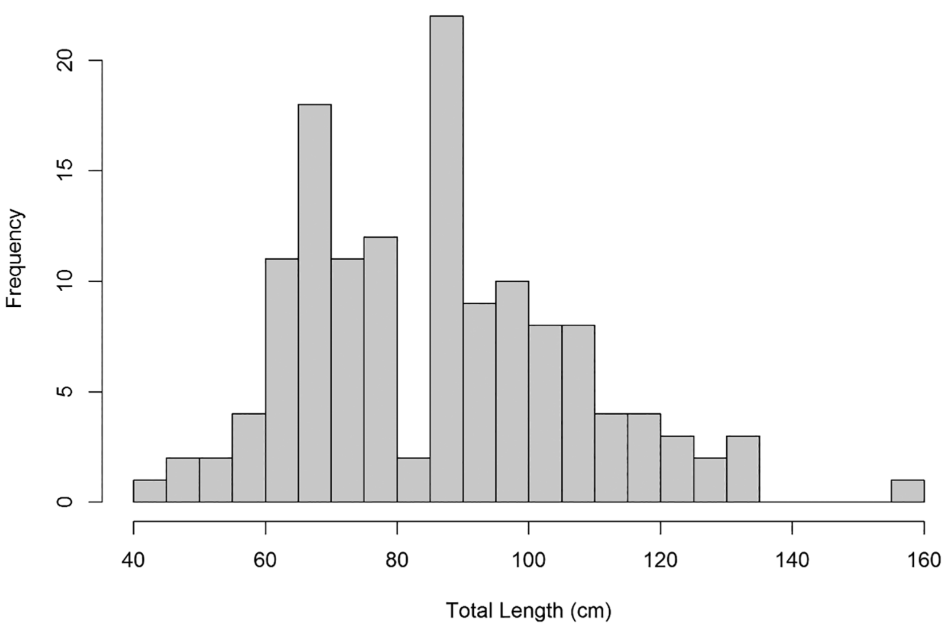

FIGURE 5 Frequency distribution by length classes of *Mycteroperca bonaci* specimens sampled from May 2017 to March 2019 from the coast of Maranhão

The monthly variation in the gonado-somatic index (GSI) covered all fish in the sample. The GSI was determined using the percentage ratio of gonad weight (GW) to fish body weight (TW) subtracted from the fish GW given by the relation GSI = [GW/(TW−GW)]*100 and was evaluated for the definition of spawning season (García-Díaz *et al.*, 1997) in conjunction with the

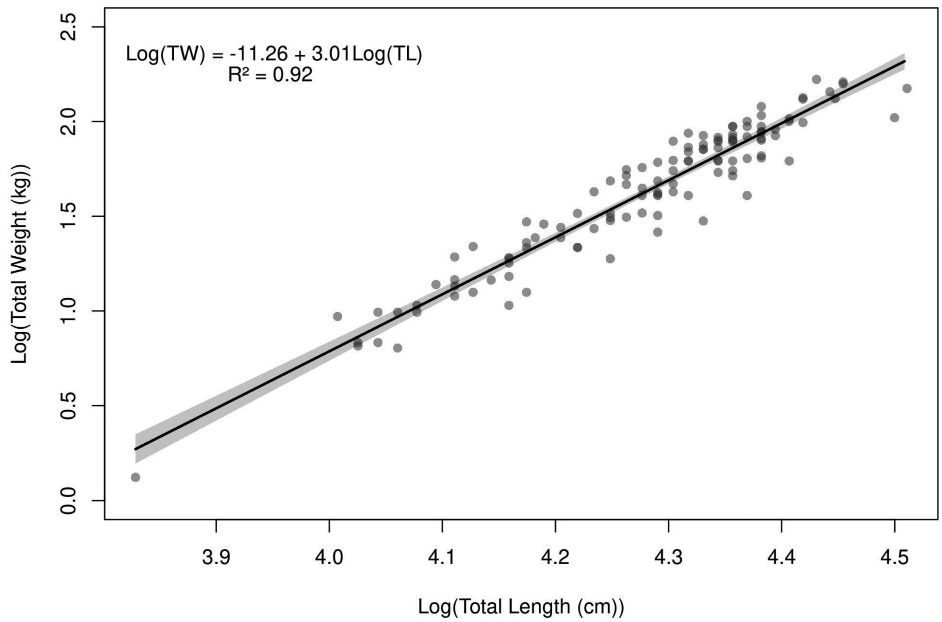

FIGURE 6 Length–weight relationship of black grouper *Mycteroperca bonaci* captured from May 2017 to March 2019 on the coast of Maranhão, Brazil

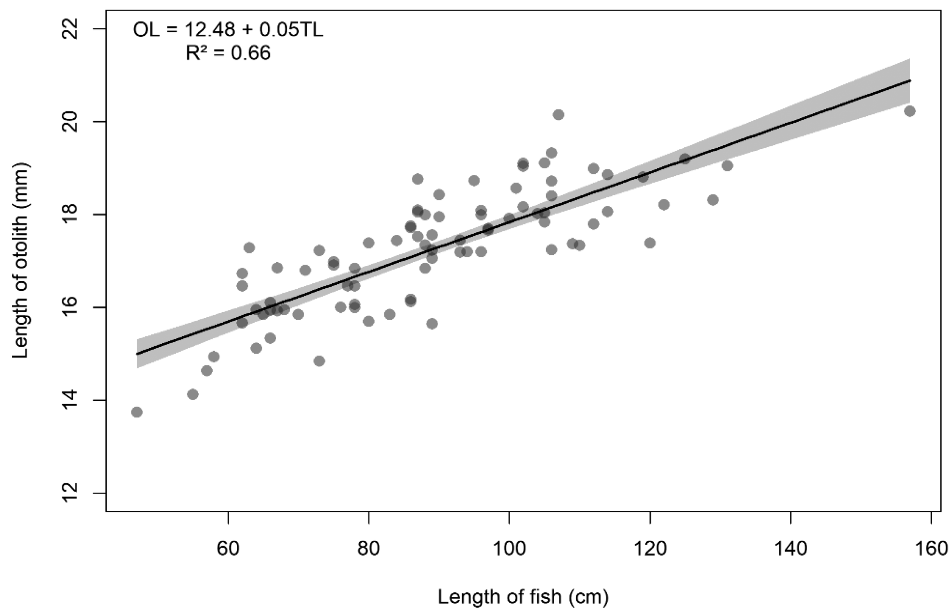

FIGURE 7 Relationship between total length of fish (cm) and length of otoliths (mm) of black grouper *Mycteroperca bonaci* captured from May 2017 to March 2019 on the coast of Maranhão, Brazil

temporal variation in the frequency of the gonadal stages. The Kruskal–Wallis (K–W) test was used to determine monthly differences in GSI values. The Nemeyi test was considered a *post hoc* test. The significance level for all analyses was set at two-tailed $P < 0.05$. The A50 was calculated from the inverse equation of VBGF ($t(L) = t_0 - 1/k*\ln(1 - L/L\infty)$).

2.2.3 | Mortality

The total mortality rate (*Z*) was estimated using the linearized catch curve method, and the estimated value of natural mortality (*M*) was calculated using the Pauly empirical formula (1990) $\text{Log } M = -0.0066 - 0.279 \text{ Log } L\infty + 0.654 \text{ Log } k + 0.4534 \text{ Log } T$, where *k* is the growth coefficient per year, $L\infty$ is the maximum asymptotic mean total length in centimetres, as well as the mean sea surface temperature (SST) (28.3°C). The annual average temperature in the Amazon coast of the Brazilian Northeast was calculated using the SST data for the fishing area obtained from the AQUA SENSOR MODIS satellite.

2.2.4 | Ethical statement

This research was not submitted to local or national permitting authority because the samples were obtained from animals caught in artisanal fisheries. At the time of sample removal, the animals were already dead.

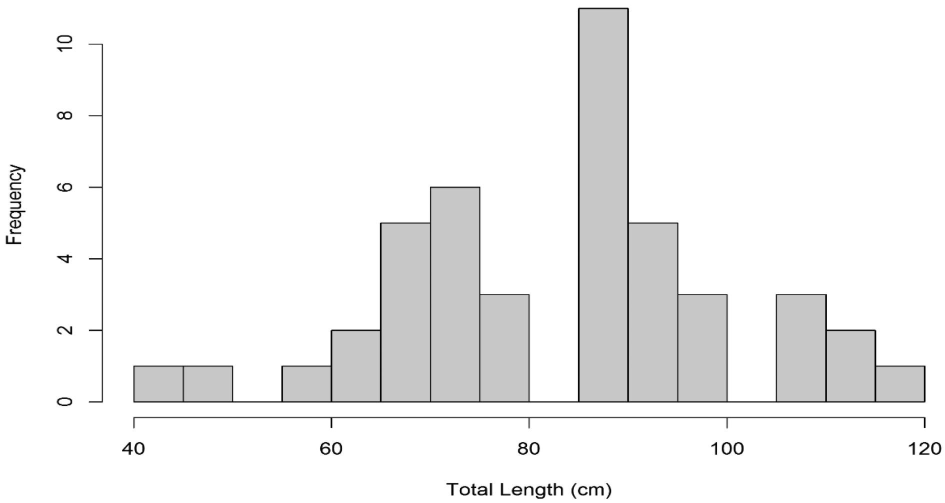

FIGURE 8 Frequency distribution by length classes of *Mycteroperca bonaci* specimens with gonads sampled from May 2017 to March 2019 from the coast of Maranhão, Brazil

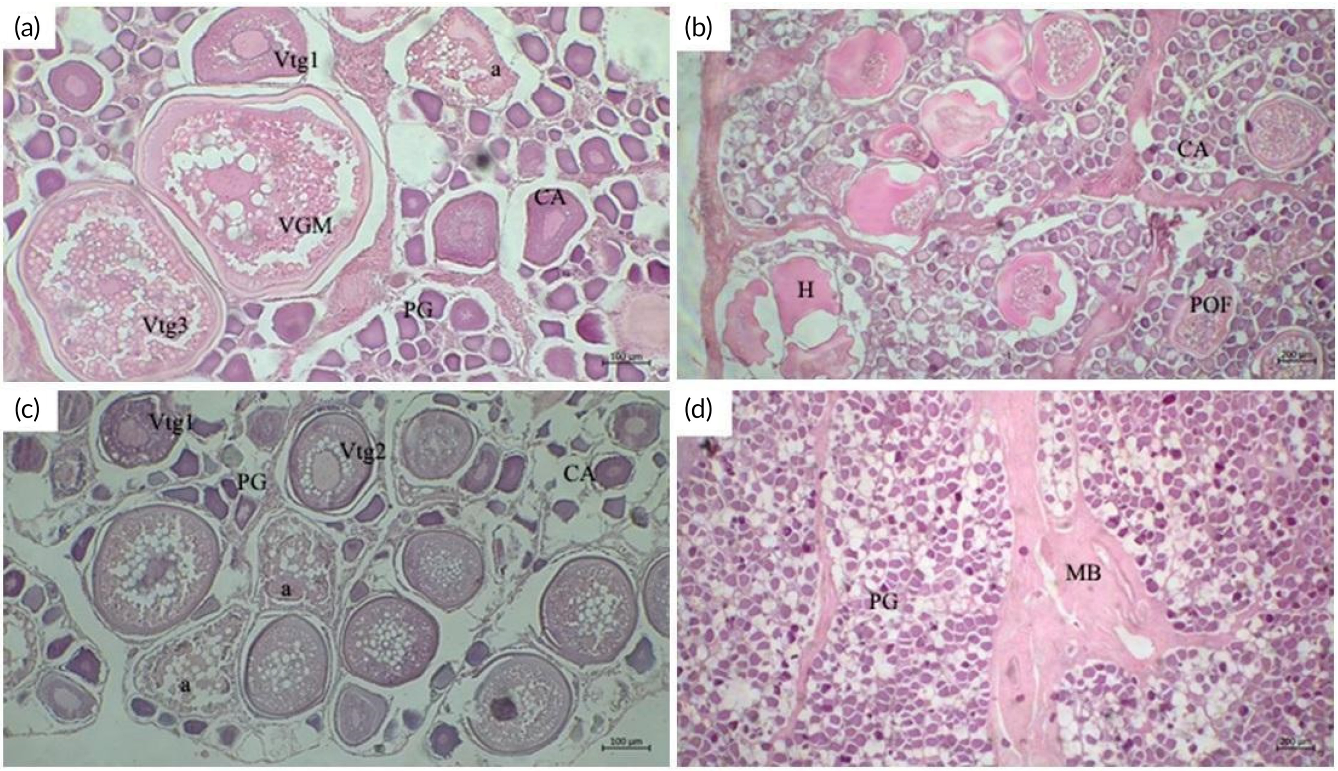

FIGURE 9 Photomicrographs of gonads of *Mycteroperca bonaci* sampled on the coast of Maranhão, Brazil. A: Female spawning capable, evidenced by the presence of oocytes with migration of germinal vesicle (VGM), vitellogenic oocytes stages (Vtg1 and Vtg3), primary growth (PG), cortical alveolar (CA) and atresia (a). B: Female classified as regressing, characterized by the presence of postovulatory follicles (POF), hydrated oocytes (H) and some CA. C: Female developing reproductive phase featuring atresia (a), PG, CA and Vtg1 and Vtg2 oocytes. D: Female regenerating phase exhibiting only PG and muscle bundles (MB)

3 | RESULTS

A total of 137 black grouper specimens from commercial landings of artisanal fisheries were sampled. Of these, 100 pairs of *sagittal* otoliths and 44 gonads were collected. The size and weight of the specimens varied from 44 to 157 cm and from 0.976 to 54 kg (Figure 4). The length class mode was 85–90 cm, which corresponds to 16% of the captures (Figure 5).

The distribution was normal ($W = 0.9767$). A single individual of 157 cm was observed and aged 34 years representing the largest reported individual in the sample. The linear length–weight relationship was expressed by this equation: log(TW) = −11.26 + 3.01log (TL) (Figure 6), where TW and TL refer to total weight and total length, respectively. Student's *t*-test showed changes in body becoming more elongated ($b > 1$), *t*-value = 23.78, *df* = 116 and *P*-value <0.0001.

The linear regression between fish length (TL) and otolith length was significant, where the parameters of the straight line obtained were $a = 12.48$, $b = 0.05$, F-statistic: 163.8, $df = 89$, $P = 2.2e^{-16}$, with a moderate correlation coefficient $r^2 = 0.6$ (Figure 7). A significant linear relationship between the age and weight of the otoliths was confirmed and is expressed by the following equation log (OW) = −3.50 + 0.74 log (Age), where OW refers to otolith weight. The correlation coefficient was $r^2 = 0.82$.

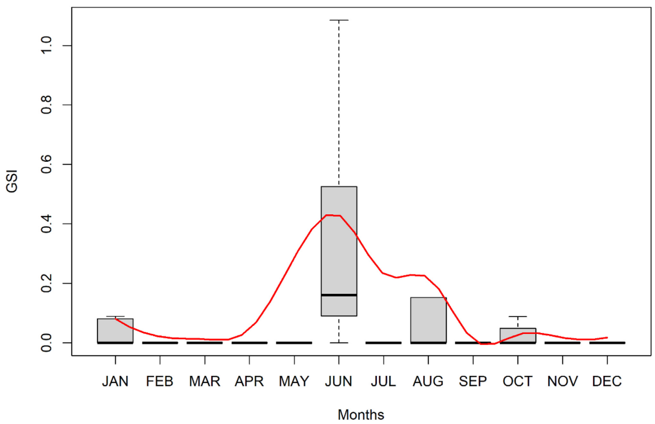

FIGURE 10 Monthly variation in the gonado-somatic index (GSI) analysis of the females of *Mycteroperca bonaci* during the period May 2017 to March 2019. Red line: polynomial fit, where there is a higher concentration of points

3.1 | Reproduction

Histologically sectioned gonads were obtained for 40 individuals (min and max sizes 58–119 cm, normality test confirmed by Shapiro–Wilk, $W = 0.980$, $P = 0.636$) (Figure 8). Only mature females were present in the samples, as confirmed by analysis of histological sections (Figure 9a–d).

During the entire sampling period (17 May to 19 March), the mean GSI presented by females was $\underline{x} = 0.44$. The largest GSI, accompanied by the spawning capable stage, was found in the months of June to August, indicating spawning peaks. Significant differences in GSI were identified (K–W = 39.761, *df* = 11, *P* = 3.93e-05). The month of June was responsible for the significant difference in GSI, where it differed from the months of March (*P* = 0.044), July (*P* = 0.0462), September (*P* = 0.0046) and November (*P* = 0.0136).

A single female with hydrated oocytes (85 cm−TL) and high GSI (2.5) presented in July (Figure 10). The months of September to May showed a predominance of the "regeneration" stage (75%), presenting only oogonia and primary growth (PG) oocytes. The developing stage (2.3%) was found in June, and the regressing stage (2.3%) was found in July (Figure 11). The largest female in the mature reproductive stage was 114 cm (TL) and in the spawned stage, and the smallest mature female was 58 cm (TL) and in the resting/regenerating stage. The A50 was 4.62 years (93 cm−TL).

3.2 | Age and growth

A total of 100 black grouper-sectioned otolith slides were analysed, with a size range of 44–157 cm TL and 88.11 ± 16.46 cm (mean ± S.D.). The Shapiro–Wilk test confirmed the normality of the age estimates

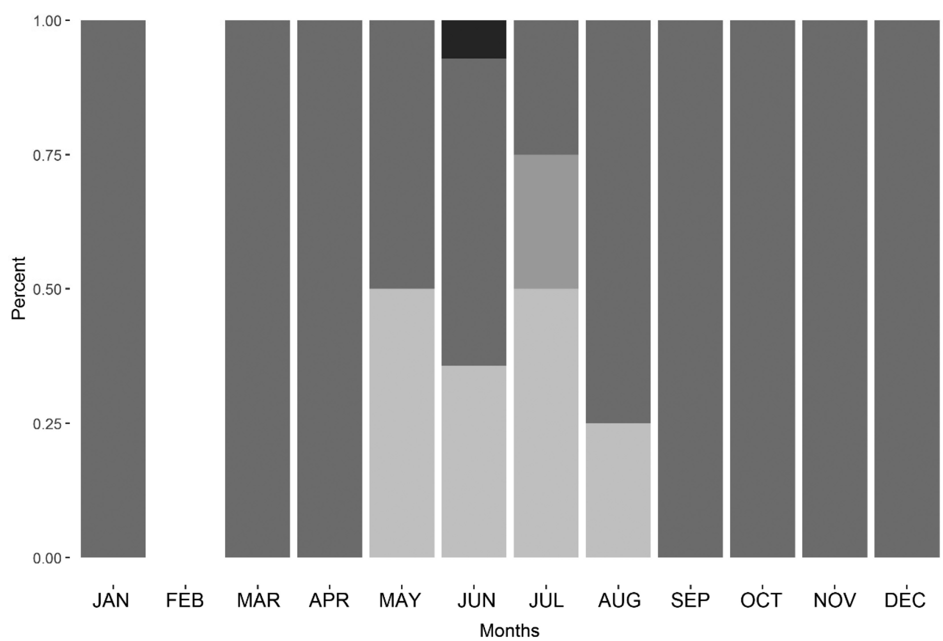

FIGURE 11 Relative frequency (%) of maturation stages for *Mycteroperca bonaci* females per month collected between May 2007 and March 2019 from Maranhão, Brazil. It was not possible to prepare a histological slide with the gonads collected in February. ■ Developing, ■ Regeneration, ■ Regressing, ■ Spawning

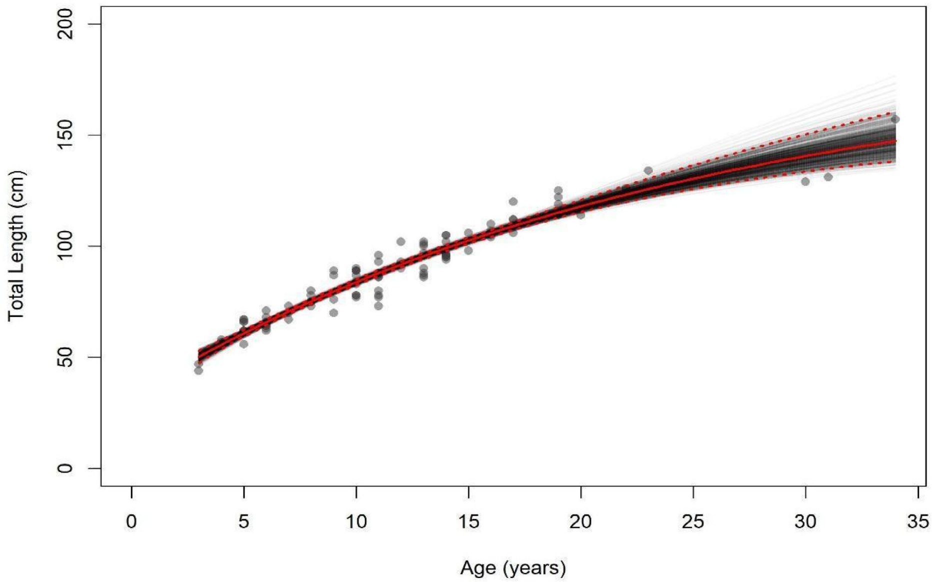

FIGURE 12 Von Bertalanffy growth curve with the parameter t_0 not fixed for black grouper *Mycteroperca bonaci* captured from May 2017 to March 2019 on the coast of Maranhão, Brazil

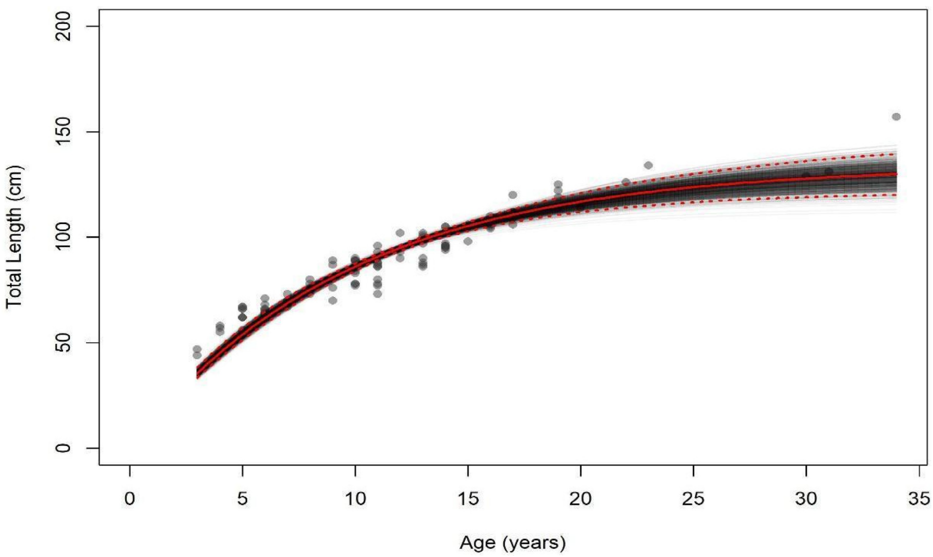

FIGURE 13 Von Bertalanffy growth curve with the parameter t_0 fixed at zero value for black grouper *Mycteroperca bonaci* captured from May 2017 to March 2019 on the coast of Maranhão, Brazil

($W = 0.982$, $P = 0.211$). The readers diverged in 26% of the slides, where the greatest difference was only two rings, resulting in an IAPE of 1.1%. As the IAPE was not higher than 10%, reading 1 was considered equal to reading 2. The first reading ranged from 3 to 34 rings, and the second reading ranged from 3 to 33 rings. Because periodicity of ring formation was established by previous studies (Crabtree & Bullock, 1998; Rénan *et al*., 2013), it was also assumed that each ring corresponded to a year class.

The most represented year classes among the specimens were 10 and 11 years, representing 22% of the sample, in which the total length ranged from 70 to 96 cm. The oldest individuals in the sample measured 129, 131 and 157 cm of TL and were aged 30, 31 and 34 years, respectively. The youngest individuals ($n = 5$) in the sample measured between 44 and 58 cm TL and were aged 3–4 years.

The growth parameters for the Von Bertalanffy model were calculated, and growth curves were fitted with t_0 not fixed (Figure 12) and $t_0 = 0$ fixed (Figure 13). One thousand resamples were performed by the bootstrap method from the original data set of age and length to determine new growth parameters and obtain estimates of standard errors.

The parameters available in the literature for the black grouper captured in the Gulf of Mexico, Florida, and in the south-east U.S.A. were used to calculate the Φ' for the purpose of comparing the growth curves (Table 1).

3.3 | Mortality

The total mortality rate was $Z = 0{,}11$ year^{-1} (Figure 14), and the natural mortality was $M = 0.04$ year^{-1}.

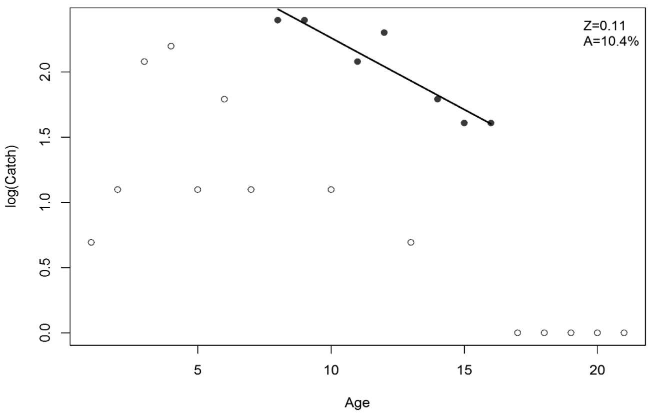

FIGURE 14 Catch curve based on observed age for black grouper *Mycteroperca bonaci* captured from May 2017 to March 2019 on the coast of Maranhão, Brazil. Ages 1–3 were excluded (outliers) because they were considered not fully recruited to the gear. A: annual survivorship; *Z*: total rate mortality. $F = 32.87$; $a = 3.48$; $b = -0.11$; $R^2 = 0.86$

4 | DISCUSSION

All previous studies reporting catches of *M. bonaci* are from landings observed along the East Brazil Shelf, from states of Ceará to Bahia (Lessa *et al*., 2004; Teixeira *et al*., 2004, REVIZZE, 2000; Revizee., 2006). Teixeira *et al*. (2004) compared size structures of black grouper from landings in the north and south areas along the north-east coast, east Brazil Large Marine Ecosystem (LME) and observed a significant difference, with smaller modal size (70 cm TL) and a distribution skewed to the left in the north area, contrasting with a larger modal size (90 cm TL) and normal distribution in the south. They concluded that although the fishery for *M. bonaci* in both areas showed similarities (*e.g.*, catch depth between 50 and 120 m and vessel types and fishing equipment), the number of vessels in northern area is four times larger than the southern area, and thus that higher fishing levels in the north had led to a reduction in the individuals' size. Fishing with a hook and line and hookah spearfishing are size selective, and therefore removed the largest individuals from the population (Ricker, 1975), an effect that could also explain the low frequency of males in Teixeira *et al*. (2004) and their absence in the present study.

In the present study, however, although landings were monitored in Ports of Ceará, northern part of the east Brazil LME, catches were from fishing grounds off the coast of Maranhão, North Brazil Shelf LME. Signs of overexploitation were observed in the early 2000s (Teixeira *et al*., 2004); therefore, it is believed that the fleet migrated further north in search of less exploited stocks.

Black grouper catches occurred throughout the inner and middle Maranhão continental shelf (isobaths of 40 and 60 m) encompassing Manoel Luís Marine State Park, as well as the slope (75 m) at depths of up to 180 m. The depth at the base of the continental slope is 2000 m (Castro *et al*., 2018). The Parcel Manuel Luís is one of the largest coral reefs in South America, formed by hard bottoms (*e.g.*, rocky, granite or diabase) and by a mobile biodetrital substratum (*e.g.*, calcareous algae, corals, spicules and microorganisms), being almost totally submerged (MMA, 2000; Palma, 1979). As a marine protected area, fishing within the limits of the park is prohibited; nonetheless, distance from the coast and poor enforcement hinder its effectiveness.

4.1 | Biological parameters

The relationship between the total weight and total length showed changes in fish condition with values similar to those of individuals in the southeastern U.S.A., $b = 3141$ (Manooch & Mason, 1987) and different from that found by Freitas *et al*. (2011) in waters of northeastern Brazil, in which the black grouper did not present changes in fish condition ($b = 2.98$). The variation among the growth patterns of this species in Brazilian waters probably occurred because of the size range between samples. In fish, the weight–length relationship, including juveniles and adults, may be affected by factors such as environmental conditions, gonadal maturity, sex, health condition, season, spatial, zonal and population variation (Froese, 2006; Macieira & Joyeux, 2009). In this study, no young/immature specimens were sampled, which influenced the recorded growth pattern. Furthermore, the changes in fish condition may also be related to the capture site of the specimen. Considering that the coast of Maranhão is characterized by mangroves, sandbars, sandy beaches, dunes and mainly estuaries (Moreira, 2000), it is worth noting that estuarine systems are the main suppliers of nutrients for other ecosystems on the continental shelf. Thus, the coefficient of allometry may also be associated with greater food availability (Ferraz & Giarrizzo, 2015).

Environmental factors also have a direct influence on the development of otoliths, such as growth (Mosegaard *et al*., 1988). Nonetheless, weight is not directly affected by this factor and therefore becomes a good variable to estimate the age of fish (Cardinale *et al*., 2004), with the same reliability of the sectioned otoliths counting rings (Green *et al*., 2009b). The average weight of an otolith increases continuously with age. The linear relationship suggests that relatively consistent amounts of otolith material (95%–97% calcium carbonate) (Campana, 1999; Campana *et al*., 1997) are added annually to the surface of the otolith (Craig *et al*., 1997; Lou *et al*., 2005; Newman, 2002). This relationship is confirmed in the current research (on the northeastern coast of Brazil; $r^2 = 0.83$), in the Gulf of Mexico ($r^2 = 69.80$; Rénan *et al*., 2013) and in Florida waters ($r^2 = 0.95$; Crabtree & Bullock, 1998); both studies were performed with black grouper otoliths.

The proportional growth of the *sagittae* otoliths in relation to the increase in the age of the fish was also confirmed. Nonetheless, for other species of grouper (*e.g.*, *Cephalopholis fulva*), there was asymmetry at a certain point in growth, where there was an inverse association between the growth of otolith *sagittae* and the TL of the fish as a result of ontogenetic changes (Araujo & Martins, 2006).

4.2 | Reproduction

Time patterns of spawning can be studied, analysed and confirmed, generating increasing knowledge about reproductive behaviours.

Nonetheless, the specifics of the time of each spawning have not yet been completely unveiled. It is believed that there is a direct influence of environmental variations (Sanchez *et al*., 2017). This result confirms a single spawning peak for the black grouper between June and August, consistent with patterns observed in other studies. Thus, it suggests the same spawning period for the southwestern Atlantic. Studies conducted with past oceanographic data obtained *in situ* and modelled from the Maranhão shelf suggest that a reduction in SST occurs and that a band of colder water appears in June in the oceanic region adjacent to the continental shelf (Silva *et al*., 2007), strong wind shear occurs from January to July (Geyer *et al*., 1996; Silva, 2006) and fresh water contributes hundreds of kilometres in an open sea direction (Ffield, 2007; Hellweger & Gordon, 2002).

In Abrolhos, northeast Brazil, Freitas *et al*. (2018) observed that the spawning peaks of black grouper *M. bonaci* occurred after reduction in SST and air temperatures associated with a higher incidence of winds. This fact was also observed in the Cuban shelf for this species, with spawning peaking at the colder months of the year, between November and April. The GSI values for females were similar to those of studies in regional waters as in Teixeira *et al*. (2004) (GSI $\underline{x}$ 1.4) and Freitas *et al*. (2018) (GSI $\underline{x}$ 2.3), in the Gulf of Mexico according to Brulé *et al*. (2003) (GSI $\underline{x}$ 2.2) and in Cuba by Garcia-Cagide & Garcia (1996) (GSI $\underline{x}$ 2.89).

In the present study, samples were obtained from commercial landings of bottom line fisheries and because of its selectivity for larger fishes, the smallest sized individual sampled was a 44 cm female. This seems to be the pattern in most bottom-line fisheries for species of the snapper-grouper complex because of gear selectivity (Teixeira *et al*., 2004), and thus the absence of immature individuals in the sample. Although the gear is expected to select larger and older individuals (Ricker, 1975), all sampled individuals were females, a pattern confirmed by histological analysis. The size of those females was mostly above the size at which this species initiates sex change in southwestern Atlantic, *e.g*., Teixeira *et al*., 2004 (64 cm TL), Garcia-Cagide & Garcia; 1996 (65 cm TL) and Freitas *et al*., 2011 (40 cm TL). The absence of male and individuals in sexual transition is therefore of concern, because it may suggest that fishing mortality is leading to their decline. Indeed, the vulnerability of larger and older protogynous hermaphrodites to fishing affects mainly male individuals, leading to lower reproductive potential (Shapiro, 1984).

Although it is possible that males are less susceptible than females to capture because of differential behaviour, the extirpation of larger individuals, where males would be better represented, is a well-described and expected consequence of fisheries pressure. For this reason, larger groupers are at higher risk of depletion and extinction throughout all their range of distribution (de Sadovy *et al*., 2012).

4.3 | Age and growth

The first age and growth study for *M. bonaci* was conducted by Manooch and Mason (1987) in the Florida Keys. The study obtained a good sample size $n = 183$ and determined the age range between 1–14 years. Consecutive surveys (Crabtree & Bullock, 1998; Rénan *et al*., 2013) reached the age range of 2–27 years and 3–33 years, respectively, with a sample size of $n > 700$ individuals. Although the present research obtained a low sample size ($n = 100$) when compared to previous studies, it acquired a good distribution of length classes. It recorded an age range 3–34 years, representing the oldest age ever found for the species.

The comparison of the growth parameters for the black grouper population in northeastern Brazil shows that the lowest growth rate was estimated in this research which determines a high $L\infty$, as they are inversely proportional parameters. Another assumption about the high $L\infty$ was that it may have been overestimated because of the high occurrence of large fish and/or the absence of smaller individuals in the study. Growth parameter estimates are known to be strongly associated with the presence and absence of individuals at the extremes of the curve (Campana, 2001). Therefore, to mitigate this effect the age and growth model was fitted by setting t_0 to zero. The growth parameters obtained here corroborate the characteristics pointed out by the literature, in which black grouper is a species with a long life cycle and slow growth. Similar data were found in the other three studies of age and growth for *M. bonaci*: Rénan *et al*. (2013); Crabtree and Bullock (1998) and Manooch and Mason (1987).

The growth rate (k) decreases with age (Volpedo & Vaz-Dos-Santos, 2015); thus, the older the specimen is, the smaller the ring spacing. This pattern was confirmed during the otolith age readings of black grouper. The older the age is, the more difficult it is to distinguish between the age rings. In addition, an entanglement of rings near the edge was observed, which made the readings more complex. Crabtree and Bullock (1998) also reported difficulty in older grouper as rings became more closely spaced.

4.4 | Mortality

Both mortality rates found $Z(0.10)$ and $M(0.04)$ were the lowest rates ever described for black groupers. Manooch and Mason (1987) calculated $Z(0.49)$ and $M(0.28)$. Other groupers, such *E. morio*, had rates of $Z(0.28)$ and $M(0.15)$ in South Florida (L. Lombardi-Carlson *et al*., 2008). The low total mortality rate can be explained by the assumption that *M. bonaci* sampling comes from a newly exploited population, where the exploitation should be sustainable, coupled with the occurrence of large fish in the sample (Sparre & Venema, 1997).

Although the low natural mortality coefficient of the research corroborates Ursin's (1967) statement that small species have higher natural mortality than large species, the value found remains far below. Nonetheless, the low value of the natural mortality coefficient matches the analogy made by Ximenes-Carvalho *et al*. (2012), in which they investigated the existence of a direct relationship between growth rates and natural mortality because of the lower chance of predation in large species, which may grow slowly and reach larger sizes. Therefore, the majority of grouper shows slow growth and low natural mortality rates (de Sadovy *et al*., 2012; Morato *et al*., 2006; Wakefield *et al*., 2013).

4.5 | Population status and conservation

In 2014, the Brazilian government established Ordinance No. 445 aimed at protecting and restoring fishing stocks that were under threat categories according to IUCN red list criteria, such as *M. bonaci*, considered as vulnerable (Icmbio, Instituto Chico Mendes DE Conservação DA Biodiversidade, 2014). A lengthy debate followed this decision, weakened by the lack of official landing statistics in the north-east and northern regions since 2008 (Gonçalves Neto *et al.*, 2021), and of clear directives and enforcement, increasing uncertainties regarding the ordinance (Previero & Gasalla, 2018).

Currently, a new Inter-Ministerial Ordinance No. 59-C/2018 defines rules for the sustainable use and recovery of some fishing stocks under a recovery plan, including a fishing closure during the spawning season and minimum sizes of capture for the black grouper *M. bonaci* and two more species of groupers (*Mycteroperca interstitialis and E. morio*). Lack of enforcement and of fisheries statistics, however, continue to hinder those efforts.

The size structure of fish sampled in the presented study showed size ranges similar (44–135, with a single individual of 157 cm TL) to those in previous studies conducted in Brazil, as observed in Bahia State by Freitas *et al.* (2011) and Freitas *et al.* (2018) (24.2–99 cm; 26–147 cm, respectively) and Ceará to Alagoas states by Teixeira *et al.* (2004) (55–135 cm). Modal sizes at 84–93 cm, however, were among the largest, comparable only to the ones found by Teixeira *et al.* (2004) for the south northeastern area almost 20 years ago, and larger than modal sizes observed by Freitas *et al.* (2011) and Freitas *et al.* (2018) (50 cm; 50–59 cm).

In the North Tropical Atlantic, the largest size range found was in the Gulf of Mexico by Rénan *et al.*, 2013 (25–160 cm), exceeding the range of this study, which also stands out in relation to data from Manooch and Mason (1987) (26–110 cm), Crabtree and Bullock (1998) (15.5–151.8 cm) and Brulé *et al.* (2003) (25.6–135 cm).

5 | CONCLUSION

The black grouper is a prime target for demersal line fisheries because of its high commercial value. Its life-history characteristics and aggregation behaviour make it susceptible to overfishing, particularly in the face of lack of adequate management. The present study represented the first study on age and growth of the species in the southwestern Atlantic. Moreover, this is the first one to report on fisheries occurring in the North Brazil Shelf, off Maranhão State. Although landings were monitored in Ports of Ceará, catches were from an area off the coast of Maranhão State, North Brazil Shelf LME, indicating that the fleet moved north, seeking less exploited stocks since the signs of overexploitation were already observed in the early 2000s (Teixeira *et al.*, 2004). Nevertheless, samples from the fishing activity comprised only females. This indicates the need to closely manage this population to avoid collapses. Recovery plans that have been planned but not implemented for the species must be put into practice to avoid progressive decline as fisheries target more remote areas.

CONFLICTS OF INTEREST

The authors have no conflict of interest that could influence the research result.

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