

MATURITY, FECUNDITY, AND REPRODUCTIVE CYCLE OF *CONODON NOBILIS* (ACTINOPTERYGII: PERCIFORMES: HAEMULIDAE) IN TROPICAL WATERS OF THE ATLANTIC OCEAN

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Background. Reproductive aspects of fishes are very useful in the development of management and conservation strategies of stocks. The information available on this subject, however, is very limited for tropical species, especially for those with low economic value, such as the barred grunt, *Conodon nobilis* (Linnaeus, 1758). This species is a common member of the family Haemulidae off the coasts of Brazil and it plays an important ecological role in coastal areas acting as a biological vector of organic matter. Thus, this study was intended to provide data on the reproductive parameters of *C. nobilis* to fill the gap in the existing knowledge.

Material and methods. Reproductive traits of *C. nobilis* were estimated from 410 fish collected in the coast of Alagoas, during fishery surveys carried out between December 2009 and June 2012. Length–weight relations (LWRs) for males and females were calculated from the observed length and weight by regression analysis. Data on the maturity status were used to estimate the size at first maturity for females, males, and pooled sexes. The fecundity was assessed by the volumetric method, and information on the reproductive period was retrieved from the gonadosomatic and the reproductive activity indices.

Results. Sex ratio differed between sexes with mature females being more abundant than males. Although no evidence of sexual dimorphism was found in the length distribution, LWRs showed that males have a negative asymptotic growth and females present a positive asymptotic growth. The first sexual maturity for females, males, and pooled sexes was attained at 20.78, 20.57, and 20.72 cm of the total length (TL), respectively. Gonadosomatic and reproductive activity indices indicated that *C. nobilis* may be capable of spawning all year round with a more intense activity occurring between the rainy season in the region studied. The batch fecundity fluctuated between 1640 and 105 471 oocytes with a mean of $45\,384 \pm 16\,737$ eggs per female and was positively correlated to female size.

Conclusions. Overall, *C. nobilis* showed an intermediate fecundity rate with reproductive activity throughout all year round. No evidence of sexual dimorphism in maturity and size distribution was found for the species. We hope that our findings may be helpful for fishery biologists in the design of effective management strategies for this ecologically important species.

Keywords: barred grunt, first maturation, reproduction, spawning type

INTRODUCTION

The Haemulidae is a diverse and widespread family, represented by about 145 species distributed worldwide (Tavera et al. 2012). Commonly known as grunts, fishes in this family are usually associated with coral reef ecosystems, but many genera (i.e., *Conodon* and *Orthopristis*) are more typical of brackish waters and sandy bottoms (Menezes and Figueiredo 1980). Regardless of playing an important role in the transfer of nutrients and

organic matter across habitat boundaries during feeding migrations (Appeldoorn et al. 2009), little is known about the biological parameters of the majority of grunts, with the bulk of available information for this family restricted to few species only (Appeldoorn et al. 2009, Shinozaki-Mendes et al. 2013).

In Atlantic waters, for example, the barred grunt, *Conodon nobilis* (Linnaeus, 1758), has no data on its reproductive biology, despite being one of the most

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abundant haemulid species in the region (Pinheiro and Martins 2009, da Silva et al. 2013, Souza et al. 2018). *Conodon nobilis* is usually found along sandy shores and over shallow muddy bottoms, using coral reefs mostly as shelters (Brotto and Zalmon 2008). Even though it is not targeted by local fisheries (Menezes and Figueiredo 1980, Rangely et al. 2010), the barred grunt plays an important ecological role by acting as a biotic vector of organic matter from reef environments to adjacent areas, or vice versa, due to its low dependence on rock substrate and relatively wide diet range, such as mysids, amphipods, and fish fragments (Brotto and Zalmon 2008, Appeldoorn et al. 2009, Pombo et al. 2014).

As this fish is commonly caught as bycatch in different types of harvesting activities along the Atlantic coast (Freire et al. 2009), the correct estimation of its population parameters is an important factor for its conservation, especially since *C. nobilis* has been characterized as highly susceptible to stock collapse due to low population numbers (Pinsky et al. 2011). In this context, the presently reported study was intended to contribute to the current knowledge on the reproductive biology of *Conodon nobilis* in tropical Atlantic waters by providing data on this species' size at first maturation, fecundity, and monthly variation of gonadal maturation stages.

MATERIALS AND METHODS

Fish sampling and data collection. Specimens were monthly sampled from December 2009 to June 2012, during fishery surveys in the coast of Alagoas, north-eastern Brazil (09°38'S, 035°39'W to 09°59'S, 035°55'W). The area is characterized by a narrow continental shelf (50 km) and a tropical semi-humid climate with two well-defined seasons—dry and rainy (Oliveira and Kjerfve 1993). The fish were sampled in depth zones that ranged from 13 to 35 m, using different fishing gears (i.e., beach seine, gillnets, and trawls) to collect a wider size range of individuals (Froese 2006). The presently reported study has been carried out in accordance with Brazilian regulations (Federal Scientific Fish Sampling Licence 1837810).

Upon capture, fishes were stored on ice to aid preservation until further analysis. In the laboratory, each individual was identified to species level following Menezes and Figueiredo (1980), measured to the nearest 1 cm (total length), weighted (total and somatic weight; in grams), and sexed. Specimens were then assigned to a maturity stage using macroscopic gonadal examination following (Menezes and Paiva 1966): 1 (immature), 2 (maturing), 3 (mature), 4 (resting). Whenever necessary, the maturity status was confirmed by histological analyses of gonads' morphology, organization and development (Vazzoler 1996).

Statistical analyses. A chi-square test (χ^2) was performed to identify whether the operational sex ratio of mature female and male individuals differed from the expected 1 ÷ 1 proportion (Zar 2010). As total length (TL) data did not meet the assumptions of normality and homoscedasticity even after several transformations, differences in size

distribution between sexes were assessed by the non-parametric Kruskal–Wallis test.

Length–weight relations for females, males, and the whole population (pooled sexes and individuals that could not be sexed) were estimated by fitting a linear model of length against weight. Prior to analysis, length and weight data were plotted for visual inspection and removal of outliers (da Silva et al. 2017). Parameters a and b were then estimated by linear regressions using the equation

$$\log W = \log a + b \log TL$$

where W is the body weight, TL is the total length, a is the intercept, and b is the slope (Le Cren 1951, Froese 2006).

Length at first maturity (L_{50}) and maximum maturity size (L_{99}) were estimated by fitting a logistic model using the logarithm percentage of mature individuals (Y) per 1 cm size class (X) following King (2007)

$$Y = \frac{1}{1 + e^{-(a+bX)}}$$

The values of L_{50} for females, males and the pooled sexes were assessed by the ratio between estimated constants

$$L_{50} = -a \cdot b^{-1}$$

Subsequently, sexual size dimorphism in LWR parameters, L_{50} and L_{99} were tested by analysis of covariance (ANCOVA).

Gonadosomatic index (GSI) was calculated for females of *C. nobilis* as an indicator of seasonal variability of reproductive status

$$GSI = 100W_G \cdot W_T^{-1}$$

where W_G is the gonad weight and W_T is the total body weight (Shinozaki-Mendes et al. 2013). We also estimate reproductive activity by using the index of reproductive activity (IRA) per month following Dei Tos et al. (2002)

$$IRA = \frac{\ln N_i \left(\frac{n_i}{\sum n_i} + \frac{n_i}{N_i} \right) \times \frac{GSI_i}{GSI_e}}{\ln N_m \left(\frac{n_m}{\sum n_i} + 1 \right)} \times 100$$

where N_i is the total number of females in a month i , n_i is the number of mature females in the sample unit i , N_m is the number of females in the largest sample unit, n_m is the number of mature females in the sample unit with the largest n , GSI_i is the mean gonadosomatic index of mature females for a month i , GSI_e is the largest female value of GSI. Subsequently, differences in the monthly GSI were tested with the non-parametric Kruskal–Wallis test and IRA values were evaluated to estimate spawning period.

The fecundity was determined by the volumetric method described in Vazzoler (1996). In this analysis, 30 ovaries of mature females (stage 3) were kept in vials with Gilson's solution for 24 h to promote dissociation of oocytes from stromal tissue and ovarian follicles. During this time, vials were periodically shaken to help the detachment process and the volume necessary to promote complete dissociation (S) was measured in mL using a pipette. A subsample of this suspension (1 mL) was taken and then photographed under a microscopic in a petri dish against a black background to assist in counting oocytes. Total number of oocytes was extrapolated by using the formula

$$N = S \times \frac{n_o}{s}$$

where n_o is the total number of oocytes counted in a sample of a volume s (1 mL) from the total volume necessary to promote complete dissociation (S).

A subsample of 100 oocytes was randomly selected from each sample and measured (μm) using an ocular micrometre (at $\times 10$ magnification). Mature oocytes were only considered to be those greater than or equal to the size of the last mode of the distribution (Souza et al. 2015). Batch fecundity was then estimated as

$$F = o' \times N$$

where o' is the proportion of mature oocytes estimated within each ovary, and N is the total number of oocytes (Vazzoler 1996). Moreover, the relation between batch fecundity and total length and somatic weight was tested by regression analyses in order to test variability in fecundity according to female size.

All statistical analyses were performed in the software R statistics at a significance level of $P < 0.05$. Length at first maturity (L_{50}) and maximum maturity size (L_{99}) were estimated using the package FSA*.

RESULTS

A total of 410 specimens (including mature and immature individuals) were caught during the period studied, and although *Conodon nobilis* was found in almost all samples, no specimens were captured during samplings carried out in January. Out of all individuals, 179 were females, 127 males, and 104 could not be sexed. The total length ranged from 2.8 to 35.4 cm, and the largest individual was female (Fig. 1). No evidence of sexual dimorphism was found in the size distribution ($P < 0.05$), however, the length–weight relation was significantly different between sexes ($P < 0.05$). LWR data and related statistic for *C. nobilis* are summarized in Table 1.

Mature individuals were found in almost all samples, with the smallest specimen being a male of 17.2 cm and the largest a female of 35.4 cm. Mature females were typically more numerous than males, resulting in an operational sex ratio of $1 \div 0.5$ ($F \div M$, $P < 0.05$). The first maturity (L_{50})

for females, males, and pooled sexes was attained at the TL of 20.78, 20.57, and 20.72 cm, respectively, whereas the estimated length where all individuals are mature (L_{99}) was 29.8, 25.45, and 27.99 cm for females, males, and pooled sexes (Table 2, Fig. 2). The gonadosomatic index (GSI) of females varied significantly between months, with the lowest values recorded in February, steadily increasing in subsequent months, and reaching its peak in June (Fig. 3, $P < 0.05$). Meanwhile, the reproductive activity (IRA) started in March, and was more intense in May (Fig. 4).

Fecund females were sampled within the size range of 18.8–35.4 cm. The total number of oocytes varied between 3038 and 195 316 per ovary, and batch fecundity fluctuated between 1640 and 105 471 oocytes per female with a mean of $45\,384 \pm 16\,737$ eggs. The fecundity was

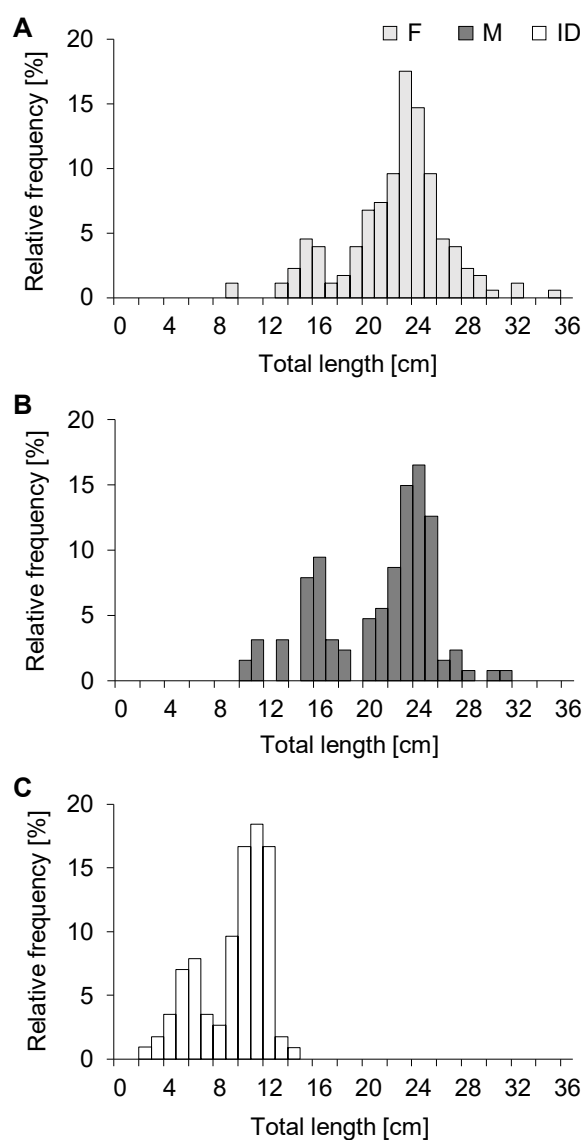


Fig. 1. Length frequency distribution of mature and immature females (A), males (B), and individuals that could not be sexed (C) of *Conodon nobilis* sampled in tropical waters of the Atlantic Ocean

* Ogle D.H. 2019. Package 'FSA': Simple Fisheries Stock Assessment Methods. <https://cran.r-project.org/web/packages/FSA/FSA.pdf>

Table 1

Descriptive statistics and estimated parameters of length–weight relations for females, males, and the whole population (pooled sexes and individuals that could not be sexed) of *Conodon nobilis* sampled from 2009 to 2012 in tropical waters of the Atlantic Ocean

Sex	Length [cm]	Weight [g]	$a \pm CI$	$b \pm CI$	r^2	P -value
Females	9.2–35.4	11.01–649.6	0.014 ± 0.002	3.01 ± 0.05	0.98	0.01
Males	10.8–31.2	17.24–411.2	0.020 ± 0.003	2.89 ± 0.06	0.98	0.01
Population	2.8–35.4	0.09–649.6	0.007 ± 0.001	3.20 ± 0.01	0.99	0.01

a = regression intercept, b = the slope of the regression coefficient; a and b values are given with their confidence intervals; r^2 = correlation coefficient, P is the P -value.

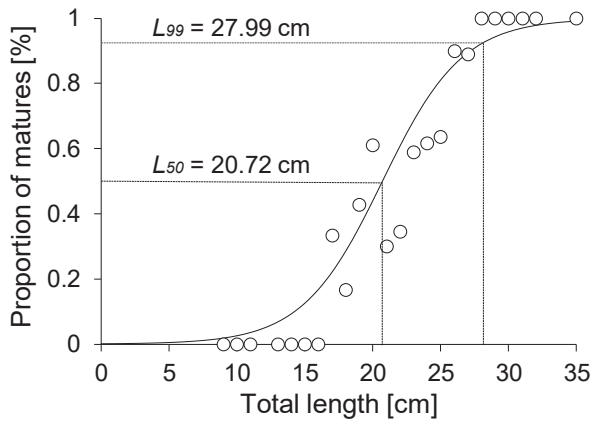


Fig. 2. Size at first maturity (L_{50}) and size where all individuals are mature (L_{99}) of *Conodon nobilis* sampled in tropical waters of the Atlantic Ocean

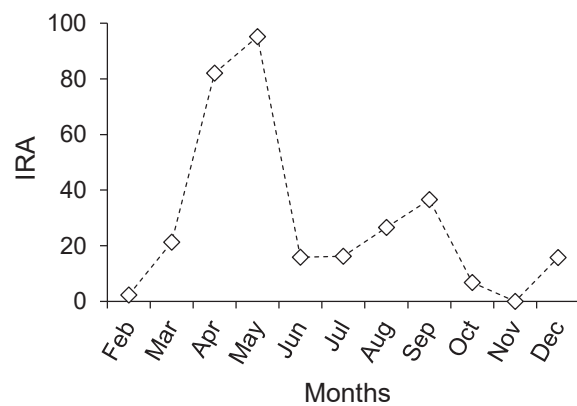


Fig. 4. Monthly variation of the index of reproductive activity (IRA) for females of *Conodon nobilis* sampled in tropical waters of the Atlantic Ocean

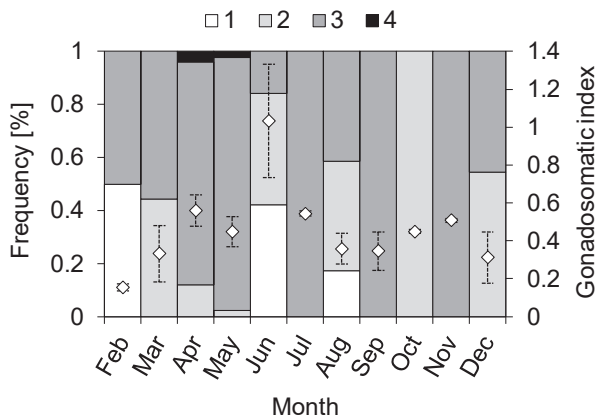


Fig. 3. Monthly distribution of gonadal maturation stages in percentage (1 = immature, 2 = maturing, 3 = mature, 4 = spawning) and gonadosomatic index (mean \pm standard error of the mean) of females of *Conodon nobilis* sampled in tropical waters of the Atlantic Ocean

Table 2

Length at first maturity (L_{50}) and maximum maturity size (L_{99}) of *Conodon nobilis* sampled in tropical waters of the Atlantic Ocean

Sex	n	$L_{50} \pm CI$ [cm]	$L_{99} \pm CI$ [cm]
Female	179	20.78 ± 1.11	29.80 ± 2.02
Male	127	20.57 ± 0.85	25.45 ± 2.87
Pooled sexes	306	20.72 ± 0.60	27.99 ± 1.42

positively related to the fish length and somatic weight, with higher fecundity rates found in individuals of greater sizes ($P < 0.05$, Fig. 5). However, the coefficients of determination (r^2) for both relations were 0.55 and 0.62 for length and weight, respectively, which indicates that only about 50% of the variation in the fecundity can be explained by these variables.

DISCUSSION

Mature females of *C. nobilis* were more numerous than mature males in almost all samples and operational sex ratio differed from the expected 1 \div 1 proportion. Higher proportions of adult females in natural populations may be associated with many factors, such as the birth rate, growth characteristics, mortality, and fish behaviour (Dala-Corte and Azevedo 2010). This predominance of one sex in fish populations, however, may also be an indicator of stress caused by natural and anthropogenic activities (Vasconcelos et al. 2011). Specifically, when faced with high predation rates and/or overexploitation, a species may display differences in the sex ratio as a compensatory response to the quickly increasing population size (S  arez et al. 2017). In the particular case of *C. nobilis*, this species is often caught as bycatch throughout the Atlantic coast, which typically affects fish populations by removing a huge number of juveniles (da Silva et al. 2013, Duarte et al. 2013). Therefore, the greater number of females found in our study may indicate that the burred grunt is highly

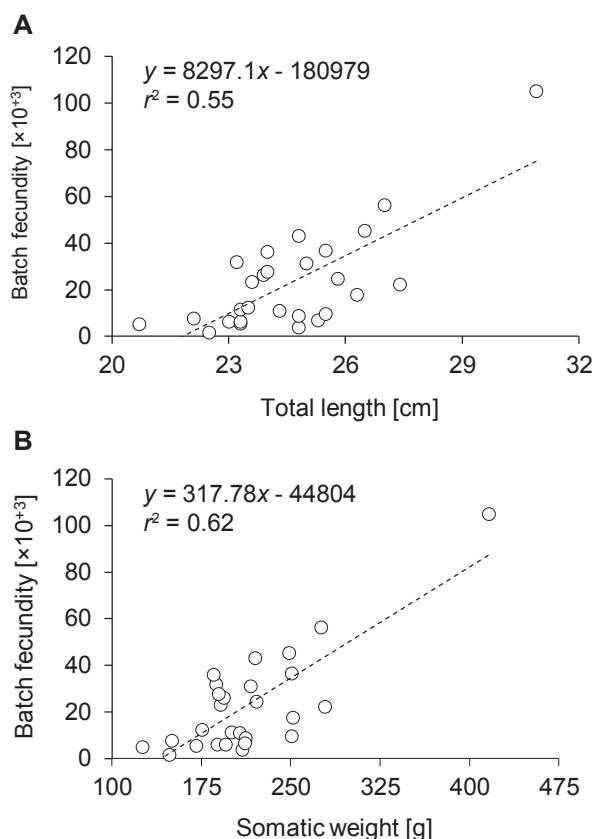


Fig. 5. A relation between batch fecundity and total length (A) and somatic weight (B) for females of *Conodon nobilis* sampled in tropical waters of the Atlantic Ocean

vulnerable to fishing pressure and the sex ratio of the adult population may be associated with sex-specific mortality in juveniles (Olsen et al. 2006). Nonetheless, we have to take in account the great number of individuals who could not be sexed due to limitations of macroscopic analysis (Klibansky and Scharf 2015), thus, the information herein should be treated with caution.

With respect to the size structure of the studied population, the length range recorded in our study for *C. nobilis* (2.8 to 35.4 cm) differed from the one reported for Pombo et al. (2014) in the south-eastern Brazil (4.9 to 18 cm) and for Passos et al. (2012) in the southern Brazil (4.6 to 15.2 cm), with a new maximum total length of 35.4 recorded for the species. Differences in the size structure of *C. nobilis* between different locations may result from a variety of factors, such as, latitudinal variation, environmental conditions, and food availability (Jeppesen et al. 2010, de Queiroz et al. 2018), but especially from the applied sampling methods (Le Cren 1947, Beamesderfer and Rieman 1988). For instance, in both studies cited earlier (Passos et al. 2012, Pombo et al. 2014), specimens were sampled using only trawl nets, whereas in our study a variety of fishing gears were used (i.e., beach seine, gillnets, and trawls) for sampling individuals from a broader size range.

The beginning of sexual maturity is a crucial part of the population's dynamics and it influences species'

survival, growth and fitness (S arez et al. 2017). Although a few females showed greater sizes than males, both sexes attained maturity at similar lengths, showing no evidence of sexual dimorphism in gonadal maturation ($L_{50} = 20.72$ cm for pooled sexes). This absence of sexual size dimorphism appears to be a common pattern among Haemulidae species (Palaz n-Fern ndez 2007, Pitt et al. 2009, Shinozaki-Mendes et al. 2013, Eduardo et al. 2018), and it can be related to many variables, such as environmental conditions, growth characteristics, fishing pressure and predation rate (Estlander et al. 2017).

Monthly distribution of gonadal maturation stages combined with gonadosomatic index values (GSI) and the index of reproductive activity (IRA) indicate that *C. nobilis* may be capable of spawning all year round with a more intense activity occurring between May and September, during the rainy season of studied region (da Silva et al. 2018). Relations between spawning period and rainfall rates have been reported for many tropical fish species (Khan et al. 1990, Muchlisin et al. 2010, Freitas et al. 2011, P rez et al. 2012). Such relation is usually related to increases in productivity levels and changes in environmental variables caused by rainfall (Robins et al. 2005), which provides better feeding condition for species and improves the quality of spawning habitats (Bergenius et al. 2005, Robins et al. 2005).

In comparison to other haemulid species, such as *Haemulon plumierii* (Lacep de, 1801) ($197\,704 \pm 16\,145$ eggs) and *Pomadasys jubelini* (Cuvier, 1830) ($35\,744 \pm 626$ eggs), *C. nobilis* ($45\,384 \pm 16\,737$ eggs) showed an intermediate fecundity with great variability (Palaz n-Fern ndez 2007, Falahatimravast et al. 2012). Changes in the fecundity rate among species in the same family may occur due to many factors, such as distinct reproductive behaviours (Vazzoler 1996) and differences in environmental conditions (Cowen and Sponaugle 1997). In addition, body length and weight were both positively correlated to batch fecundity, indicating that larger individuals produce more eggs. Although the great variability in egg production (3038–195 316 eggs per ovary) found for *C. nobilis* may be partly explained by these relations (r^2 for both models only explained about 50% of variance), other factors can be related to this variability, such as constant changes in primary and secondary productivity levels (McBride et al. 2015). Indeed, many studies have shown that intraspecific changes in the fecundity depend mainly on local food availability (Rideout and Morgan 2010, Somarakis et al. 2012). The area studied, for instance, is characterized by continuous changes in the productivity due to its narrow shelf and intense estuarization process (Passos et al. 2016), thereby, it appears that there is a strong relation between the available food, fish condition, and the reproductive potential for *C. nobilis*.

This study represents the first north-eastern Brazilian report of reproductive aspects of *Conodon nobilis*, a common species often caught as bycatch throughout the Brazilian coast. Overall, *C. nobilis* showed an intermediate fecundity rate with reproductive activity throughout all

year-round. Mature females were more predominant in the studied population, and no evidence of size sexual dimorphism in maturity and size distribution was found for the species. As samples encompassed different years and seasons, we hope that information herein may be useful for this species management and conservation.

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REFERENCES

- Appeldoorn R.S., Aguilar-Perera A., Bouwmeester B.L.K., Dennis G.D., Hill R.L., Merten W., Recksiek C.W., Williams S.J.** 2009. Movement of fishes (grunts: Haemulidae) across the coral reef seascape: A review of scales, patterns and processes. *Caribbean Journal of Science* **45** (2–3): 304–316. DOI: [10.18475/cjos.v45i2.a16](https://doi.org/10.18475/cjos.v45i2.a16)
- Beamesderfer R.C., Rieman B.E.** 1988. Size selectivity and bias in estimates of population statistics of smallmouth bass, walleye, and northern squawfish in a Columbia River reservoir. *North American Journal of Fisheries Management* **8** (1): 505–510. DOI: [10.1577/1548-8675\(1988\)008<0505:SSABIE>2.3.CO;2](https://doi.org/10.1577/1548-8675(1988)008<0505:SSABIE>2.3.CO;2)
- Bergenius M.A.J., McCormick M.I., Meekan M.G., Robertson D.R.** 2005. Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish. *Marine Biology* **147** (2): 291–300. DOI: [10.1007/s00227-005-1575-z](https://doi.org/10.1007/s00227-005-1575-z)
- Brotto D.S., Zalmon I.R.** 2008. Structural complexity of substrata and antifouling paint effects on spatial distribution of *Conodon nobilis* Linnaeus, 1758 (Teleostei, Actinopterygii). *Brazilian Journal of Oceanography* **56** (2): 133–137. DOI: [10.1590/S1679-87592008000200005](https://doi.org/10.1590/S1679-87592008000200005)
- Cowen R.K., Sponaugle S.** 1997. [Chapter fifteen] Relationships between early life history traits and recruitment among coral reef fishes. Pp. 423–449. DOI: [10.1007/978-94-009-1439-1_15](https://doi.org/10.1007/978-94-009-1439-1_15) In: Chambers R.C., Trippel E.A. (eds.) *Early life history and recruitment in fish populations*. Chapman & Hall Fish and Fisheries Series, Vol. 21. Springer, Dordrecht, the Netherlands. DOI: [10.1007/978-94-009-1439-1](https://doi.org/10.1007/978-94-009-1439-1)
- da Silva C.A.B., de Araújo M.E., Feitosa C.V.** 2013. Sustainability of capture of fish bycatch in the prawn trawling in northeastern Brazil. *Neotropical Ichthyology* **11** (1): 133–142. DOI: [10.1590/S1679-62252013000100016](https://doi.org/10.1590/S1679-62252013000100016)
- da Silva V.E.L., Teixeira E.C., Batista V.S., Fabr e N.N.** 2017. Length–weight relationships of two mugilid species from tropical estuarine systems in Alagoas, northeastern coast of Brazil. *Journal of Applied Ichthyology* **33** (3): 631–632. DOI: [10.1111/jai.13325](https://doi.org/10.1111/jai.13325)
- da Silva V.E.L., Teixeira E.C., Batista V.S., Fabr e N.N.** 2018. Spatial distribution of juvenile fish species in nursery grounds of a tropical coastal area of the southwestern Atlantic. *Acta Ichthyologica et Piscatoria* **48** (1): 9–18. DOI: [10.3750/AIEP/02299](https://doi.org/10.3750/AIEP/02299)
- Dala-Corte R.B., Azevedo M.A.** 2010. Biologia reprodutiva de *Astyanax henseli* (Teleostei, Characidae) do curso superior do Rio dos Sinos, RS, Brasil. [Reproductive biology of *Astyanax henseli* (Teleostei, Characidae) in the upper Rio dos Sinos, RS, Brazil.] *Iheringia. S rie Zoologia* **100** (3): 259–266. [In Portuguese.] DOI: [10.1590/S0073-47212010000300012](https://doi.org/10.1590/S0073-47212010000300012)
- de Queiroz J.D.G.R., Salvador N.L.A., Sousa M.F., Da Silva V.E.L., Fabr e N.N., Batista V.S.** 2018. Life-history traits of *Chloroscombrus chrysurus* (Actinopterygii: Perciformes: Carangidae) in tropical waters of the Atlantic Ocean. *Acta Ichthyologica et Piscatoria* **48** (1): 1–8. DOI: [10.3750/AIEP/02315](https://doi.org/10.3750/AIEP/02315)
- Dei Tos C., Barbieri G., Agostinho A.A., Gomes L.C., Suzuki H.I.** 2002. Ecology of *Pimelodus maculatus* (Siluriformes) in the Corumb  Reservoir, Brazil. *Cybiurn* **26** (4): 275–282.
- Duarte L.O., D az-Vesga R., Cuello F., Manjarr s L.** 2013. Cambio estacional de la fauna acompa ante de la pesquer a artesanal de arrastre de camar n del Golfo de Salamanca, Mar Caribe de Colombia. [Seasonal shift of bycatch in the artisanal shrimp trawl fishery of the Gulf of Salamanca, Caribbean Sea of Colombia.] *Acta Biol gica Colombiana* **18** (2): 319–328.
- Eduardo L.N., Lira A.S., Fr dou T., Fr dou F.L.** 2018. Population structure and reproductive biology of *Haemulopsis corvinaeformis* (Perciformes, Haemulidae) in the south coast of Pernambuco, northeastern Brazil. *Iheringia. S rie Zoologia* **108**: e2018007. DOI: [10.1590/1678-4766e2018007](https://doi.org/10.1590/1678-4766e2018007)
- Estlander S., Kahilainen K.K., Horppila J., Olin M., Rask M., Kube ka J., Peterka J., R ha M., Huuskonen H., Nurminen L.** 2017. Latitudinal variation in sexual dimorphism in life-history traits of a freshwater fish. *Ecology and Evolution* **7** (2): 665–673. DOI: [10.1002/ece3.2658](https://doi.org/10.1002/ece3.2658)
- Falahatimarvast A., Poorbagher H., Lokman P.M.** 2012. The reproductive biology of *Pomadasyss kaakan* (Osteichthyes: Haemulidae) in the northern Persian Gulf. *Cahiers de Biologie Marine* **53** (1): 25–34. DOI: [10.21411/CBM.A.433EABDB](https://doi.org/10.21411/CBM.A.433EABDB)
- Freire K.M.F., Rocha G.R.A., Souza I.L.** 2009. Length–weight relationships for fishes caught by shrimp trawl in southern Bahia, Brazil. *Journal of Applied Ichthyology* **25** (3): 356–357. DOI: [10.1111/j.1439-0426.2009.01220.x](https://doi.org/10.1111/j.1439-0426.2009.01220.x)
- Freitas M.O., de Moura R.L., Francini-Filho R.B., Minte-Vera C.V.** 2011. Spawning patterns of commercially important reef fish (Lutjanidae and Serranidae) in the tropical western South Atlantic. *Scientia Marina* **75** (1): 135–146. DOI: [10.3989/scimar.2011.75n1135](https://doi.org/10.3989/scimar.2011.75n1135)
- Froese R.** 2006. Cube law, condition factor and weight–length relationships: History, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22** (4): 241–253. DOI: [10.1111/j.1439-0426.2006.00805.x](https://doi.org/10.1111/j.1439-0426.2006.00805.x)

- Jeppesen E., Meerhoff M., Holmgren K., González-Bergonzoni I., Teixeira-de Mello F., Declerck S.A.J., De Meester L., Søndergaard M., Lauridsen T.L., Bjerring R., Conde-Porcuna J.M., Mazzeo N., Iglesias C., Reizenstein M., Malmquist H.J., Liu Z., Balayla D., Lazzaro X. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia* **646** (1): 73–90. DOI: [10.1007/s10750-010-0171-5](https://doi.org/10.1007/s10750-010-0171-5)
- Khan M.S., Ambak M.A., Ang K.J., Mohsin A.K.M. 1990. Reproductive biology of a tropical catfish, *Mystus nemurus* Cuvier et Valenciennes, in Chenderoh Reservoir, Malaysia. *Aquaculture Research* **21** (2): 173–180. DOI: [10.1111/j.1365-2109.1990.tb00454.x](https://doi.org/10.1111/j.1365-2109.1990.tb00454.x)
- King M. 2007. Fisheries biology, assessment and management. 2nd edn. Blackwell Publishing, Oxford, UK.
- Klibansky N., Scharf F.S. 2015. Success and failure assessing gonad maturity in sequentially hermaphroditic fishes: Comparisons between macroscopic and microscopic methods. *Journal of Fish Biology* **87** (4): 930–957. DOI: [10.1111/jfb.12765](https://doi.org/10.1111/jfb.12765)
- Le Cren E.D. 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. *Journal of Animal Ecology* **16** (2): 188–204. DOI: [10.2307/1494](https://doi.org/10.2307/1494)
- Le Cren E.D. 1951. The length–weight relationship and seasonal cycle in gonad weight and conditions in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* **20** (2): 201–219. DOI: [10.2307/1540](https://doi.org/10.2307/1540)
- McBride R.S., Somarakis S., Fitzhugh G.R., Albert A., Yaragina N.A., Wuenschel M.J., Alonso-Fernández A., Basilone G. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries* **16** (1): 23–57. DOI: [10.1111/faf.12043](https://doi.org/10.1111/faf.12043)
- Menezes M.F., Paiva M.P. 1966. Notes of the biology of tarpon, *Tarpon atlanticus* (Cuvier et Valenciennes), from coastal waters of Ceará State, Brazil. *Arquivo da Estação de Biologia Marinha da Universidade Federal do Ceará* **6** (1): 83–98.
- Menezes N., Figueiredo J.L. 1980. Manual de peixes marinhos do sudeste do Brasil. IV. Teleostei (3). [Manual of marine fishes of south-eastern Brazil. IV. Teleostei (3).] Museu de Zoologia, Universidade de São Paulo: São Paulo. [In Portuguese.]
- Muchlisin Z.A., Musman M., Azizah M.N.S. 2010. Spawning seasons of *Rasbora tawarensis* (Pisces: Cyprinidae) in Lake Laut Tawar, Aceh Province, Indonesia. *Reproductive Biology and Endocrinology* **8**: e48. DOI: [10.1186/1477-7827-8-49](https://doi.org/10.1186/1477-7827-8-49)
- Oliveira A.M., Kjerfve B. 1993. Environmental responses of a tropical coastal lagoon system to hydrological variability: Mundaú-Manguaba, Brazil. *Estuarine, Coastal and Shelf Science* **37** (6): 575–591. DOI: [10.1006/ecss.1993.1074](https://doi.org/10.1006/ecss.1993.1074)
- Olsen J.B., Miller S.J., Harper K., Nagler J.J., Wenburg J.K. 2006. Contrasting sex ratios in juvenile and adult chinook salmon *Oncorhynchus tshawytscha* (Walbaum) from south-west Alaska: Sex reversal or differential survival? *Journal of Fish Biology* **69** (sa): 140–144. DOI: [10.1111/j.1095-8649.2006.01119.x](https://doi.org/10.1111/j.1095-8649.2006.01119.x)
- Palazón-Fernández J.L. 2007. Reproduction of the white grunt, *Haemulon plumieri* (Lacépède, 1802) (Pisces: Haemulidae) from Margarita Island, Venezuela. *Scientia Marina* **71** (3): 429–440. DOI: [10.3989/scimar.2007.71n3429](https://doi.org/10.3989/scimar.2007.71n3429)
- Passos A.C., Schwarz R.jr., Cartagena B.F.C., Garcia A.S., Spach H.L. 2012. Weight–length relationship of 63 demersal fishes on the shallow coast of Paraná, Brazil. *Journal of Applied Ichthyology* **28** (5): 845–847. DOI: [10.1111/j.1439-0426.2012.01973.x](https://doi.org/10.1111/j.1439-0426.2012.01973.x)
- Passos C.V.B., Fabrè N.N., Malhado A.C.M., Batista V.S., Ladle R.J. 2016. Estuarization increases functional diversity of demersal fish assemblages in tropical coastal ecosystems. *Journal of Fish Biology* **89** (1): 847–862. DOI: [10.1111/jfb.13029](https://doi.org/10.1111/jfb.13029)
- Pérez A., Castillo O., Barbarino A., Fabrè N. 2012. Aspectos reproductivos del bagre rayado *Pseudoplatystoma tigrinum* (Siluriformes, Pimelodidae) en la Cuenca del río Apure, Venezuela. [Reproductive aspects of striped catfish *Pseudoplatystoma tigrinum* (Siluriformes, Pimelodidae) in the Apure River basin, Venezuela.] *Zootecnia Tropical* **30** (3): 251–262.
- Pinheiro H.T., Martins A.S. 2009. Estudo comparativo da captura artesanal do camarão sete-barbas e sua fauna acompanhante em duas áreas de pesca do litoral do estado do Espírito Santo, Brasil. [Comparative study of the artisanal catch of the Atlantic seabob and its bycatch in two coastal fishing areas of the state of Espírito Santo, Brazil.] *Boletim do Instituto de Pesca* **35** (2): 215–225. [In Portuguese.]
- Pinsky M.L., Jensen O.P., Ricard D., Palumbi S.R. 2011. Unexpected patterns of fisheries collapse in the world's oceans. *Proceedings of the National Academy of Sciences of the United States of America* **108** (20): 8317–8322. DOI: [10.1073/pnas.1015313108](https://doi.org/10.1073/pnas.1015313108)
- Pitt J.M., Trott T.M., Luckhurst B.E. 2009. Bluestriped grunt (*Haemulon sciurus*) in Bermuda: Age, growth, and reproduction studies. *Proceedings of the Gulf and Caribbean Fisheries Institute* **62**: 241–245.
- Pombo M., Denadai M.R., Bessa E., Santos F.B., de Faria V.H., Turra A. 2014. The barred grunt *Conodon nobilis* (Perciformes: Haemulidae) in shallow areas of a tropical bight: Spatial and temporal distribution, body growth and diet. *Helgoland Marine Research* **68** (2): 271–279. DOI: [10.1007/s10152-014-0387-2](https://doi.org/10.1007/s10152-014-0387-2)
- Rangely J., Fabrè N.N., Tiburtino C., Batista V.S. 2010. Estratégias de pesca artesanal no litoral marinho alagoano (Brasil). [Artisanal fishing strategies on the coast of Alagoas (Brazil).] *Boletim do Instituto de Pesca* **36** (4): 263–275. [In Portuguese.]
- Rideout R.M., Morgan M.J. 2010. Relationships between maternal body size, condition and potential fecundity of four north-west Atlantic demersal fishes. *Journal of Fish Biology* **76** (6): 1379–1395. DOI: [10.1111/j.1095-8649.2010.02570.x](https://doi.org/10.1111/j.1095-8649.2010.02570.x)

- Robins J.B., Halliday A.I., Staunton-Smith J., Mayer G.D., Sellin J.M.** 2005. Freshwater-flow requirements of estuarine fisheries in tropical Australia: A review of the state of knowledge and application of a suggested approach. *Marine and Freshwater Research* **56** (3): 343–360. DOI: [10.1071/MF04087](https://doi.org/10.1071/MF04087)
- Shinozaki-Mendes R.A., Santander-Neto J., Silva J.R.F., Hazin F.H.V.** 2013. Reproductive biology of *Haemulon plumieri* (Teleostei: Haemulidae) in Ceará state, northeastern Brazil. *Brazilian Journal of Biology* **73** (2): 391–396. DOI: [10.1590/S1519-69842013000200020](https://doi.org/10.1590/S1519-69842013000200020)
- Somarakis S., Schismenou E., Siapatis A., Giannoulaki M., Kallianiotis A., Machias A.** 2012. High variability in the daily egg production method parameters of an eastern Mediterranean anchovy stock: Influence of environmental factors, fish condition and population density. *Fisheries Research*. **117–118**: 12–21. DOI: [10.1016/j.fishres.2010.11.027](https://doi.org/10.1016/j.fishres.2010.11.027)
- Souza C.D., Batista V.S., Fabr e N.N.** 2018. What are the main local drivers determining richness and fishery yields in tropical coastal fish assemblages? *Zoologia* **35**: e13047. DOI: [10.3897/zoologia.35.e12898](https://doi.org/10.3897/zoologia.35.e12898)
- Souza U.P., Ferreira F.C., Braga F.M.S., Winemiller K.O.** 2015. Feeding, body condition and reproductive investment of *Astyanax intermedius* (Characiformes, Characidae) in relation to rainfall and temperature in a Brazilian Atlantic Forest stream. *Ecology of Freshwater Fish* **24** (1): 123–132. DOI: [10.1111/eff.12131](https://doi.org/10.1111/eff.12131)
- S arez Y.R., Silva E.A., Viana L.F.** 2017. Reproductive biology of *Astyanax lacustris* (Characiformes: Characidae) in the southern Pantanal floodplain, upper Paraguay River basin, Brazil. *Environmental Biology of Fishes* **100** (7): 775–783. DOI: [10.1007/s10641-017-0604-3](https://doi.org/10.1007/s10641-017-0604-3)
- Tavera J.J., Acero P.A., Balart E.F., Bernardi G.** 2012. Molecular phylogeny of grunts (Teleostei, Haemulidae), with an emphasis on the ecology, evolution, and speciation history of New World species. *BMC Evolutionary Biology* **12** (1): 57. DOI: [10.1186/1471-2148-12-57](https://doi.org/10.1186/1471-2148-12-57)
- Vasconcelos L.P., S arez Y.R., Lima-Junior S.E.** 2011. Population aspects of *Bryconamericus stramineus* in streams of the upper Paran  River basin, Brazil. *Biota Neotropica* **11** (2): 55–62. DOI: [10.1590/S1676-06032011000200006](https://doi.org/10.1590/S1676-06032011000200006)
- Vazzoler A.E.A.M.** 1996. *Biologia da reprodu o de peixes tele steos: teoria e pr tica*. [Reproductive biology of teleost fish: Theory and practice.] EDUEM, Maring , Brazil. [In Portuguese.]
- Zar J.H.** 2010. *Biostatistical analysis*. 5th edn. Prentice Hall, Upper Saddle River, NJ, USA and Pearson Education Limited, Harlow, UK.

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