Reproductive biology of *Haemulon plumierii* in the
south-western Atlantic Ocean’s most extensive reefs:
implications for fisheries management

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The reproductive biology of the white grunt *Haemulon plumierii* was studied from 360 individuals
obtained from artisanal fisheries landings in the Abrolhos Bank, Brazil, between August 2010 and
March 2012. The overall sex-ratio did not differ significantly from 1:1, although males predominated
in larger size classes. β-Binomial modelling of historical sex-ratio data indicated that the catch rate of
females has increased in recent years. Females reached maturity at a smaller total length (*L*<sub>T</sub>; 214 mm)
than males (235 mm *L*<sub>T</sub>) and the *L*<sub>T</sub> at which 50% of all individuals are mature (*L*<sub>50</sub>) was 220 mm,
corresponding to 41.5% of the maximum recorded *L*<sub>T</sub>. Variation in the gonado-somatic index and in the
relative frequency of reproductive stages indicates that reproduction occurs year round, with increased
activity during the austral spring and summer. Fecundity was not size dependent. The reproductive
parameters provided here can support management measures focussed on seasonal closures during
spawning peaks (September to November and February to March) and minimum sizes (>*L*<sub>50</sub>) for the
capture of this important artisanal fisheries resource in Abrolhos, the region with the largest and most
biodiverse coraline reefs in the South Atlantic Ocean.

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Key words: Abrolhos Bank; batch fecundity; marine protected areas; small-scale fisheries; spawning;
white grunt.

INTRODUCTION

More than half of the world’s fish stocks are already fully fished and an additional 30%
are at biologically unsustainable exploitation levels (FAO, 2016). Apart from overfish-
ing, small-scale tropical fisheries are being heavily impaired by the global decline of
coral reefs due to pollution, habitat destruction and climate change (Pandolfi et al., 2013). Reef fisheries supply food for hundreds of millions of people in tropical developing nations, where they are often the most important income source for coastal communities (Munro, 1996; Jackson et al., 2001). Despite their importance, databases focused on reef fisheries are scarce and constrained by the multispecies and multi-gear nature of reef fisheries, as well as by their scattered landings, unreported subsistence uses and local informal commerce (Johnson et al., 2013; Teh et al., 2013). In addition to such overall data deficiency, management is further hindered by the endemic poverty and fragile socio-political context of most tropical countries (Johnson et al., 2013). Although management strategies should incorporate socio-economic objectives and consider such challenging governance regimes, life-history parameters of target species remain as core components to balance harvest with natural replenishment rates (Johnson et al., 2013).

The Brazilian coast has a latitudinal range of >4000 km, with coralline reefs and rhodolith beds distributed from 3° N to 20° S and rocky reefs southwards to 32° S. Reef fisheries are exploited mostly by local and small-scale fleets on the tropical northern and north-eastern coasts (Costa et al., 2003; Moura et al., 2013), with less activity on subtropical rocky reefs (Begossi & Figueiredo, 1995). In the Abrolhos Bank, the region with the largest and richest coralline reefs in the South Atlantic Ocean (Moura et al., 2013), Haemulidae comprise up to 10% of total fish biomass recorded on in situ surveys (Francini-Filho & Moura, 2008). Together with Scarinae, Carangidae, Epinephelidae and Lutjanidae, haemulids comprise the most important fisheries resource in this region (Costa et al., 2003; Olavo et al., 2005; Freitas et al., 2011). Family Haemulidae comprises 133 species in 19 genera (Nelson et al., 2016), several of which are important fisheries resources in tropical and subtropical regions of the North Atlantic, Indian and Pacific Oceans (Meyer & Schultz, 1985; Lindeman & Toxey, 2002).

The white grunt Haemulon plumieri (Lacépède 1801) is an invertebrate feeder that occurs in coastal waters from Chesapeake Bay, U.S.A. (36° N), to southern Brazil (Froese & Pauly, 2016) and may be a locally important commercial and recreational resource (Darcy, 1983; Palazón-Fernández, 2007). They form heterotypic schools that often numerically dominate shallow reef fish communities, from the shoreline to 30 m (Darcy, 1983; Pereira et al., 2010, 2011). For H. plumieri, there are studies from across its north-western Atlantic Ocean range in Florida (Murie & Parkyn, 2005), Puerto Rico (D. S. Erdman, unpubl. data), Cuba (García-Cagide, 1987), Jamaica (Gaut & Munro, 1983) and Venezuela (Palazón-Fernández, 2007), with later contributions urging the protection of spawning areas (Grüss et al., 2014) and seasonal fishery closures (Armstrong et al., 2013). Conversely, there are no specific management measures for H. plumieri in the South Atlantic Ocean and reproductive data from this entire region is restricted to two studies carried out in Ceará State, on the northern Brazilian coast (Alves & Aragão, 1973; Shinozaki-Mendes et al., 2013). Reproductive data (e.g. sex ratio, maturation frequency, length at maturity and batch fecundity) may be used to implement simple management measures such as minimum or maximum sizes and closures, and may also contribute to determining productivity and resiliency to exploitation (Jackobsen et al., 2009; Wootton & Smith, 2015).

The present study was undertaken in order to provide new biological information on H. plumieri in the South Atlantic Oceans’s largest reef complex, allowing for contrasts with data from northern Brazil and the Caribbean. The results, together with information already available in the literature, may be a foundation for stock assessment for
**H. plumieri** in the Abrolhos. In addition, simple management measures are proposed that could be readily presented to stakeholders and further implemented, reducing the long-standing gaps in management, scientific and local knowledge (Freitas et al., 2011, 2014; Previero et al., 2011, 2013; Giglio & Freitas, 2013; Moura et al., 2013).

**MATERIALS AND METHODS**

**STUDY SITE**

The Abrolhos Bank (16° 40′–19° 40′ S; 39° 10′–37° 20′ W) is a 46 000 km² enlargement of the eastern Brazilian continental shelf (Fig. 1) and is the most biodiverse region in the South Atlantic Ocean (Dutra et al., 2005). This extensive shallow water (<70 m) region comprises three main benthic mega-habitats: rhodolith beds (43% of the area), unconsolidated sediments (39%) and coralline reefs (18%) (Moura et al., 2013). The region is under the synergistic effects of climatic and local anthropogenic stressors (Bruce et al., 2012; Francini-Filho et al., 2013), with overfishing a major concern (Francini-Filho & Moura, 2008; Freitas et al., 2011). Abrolhos is Brazil’s main reef fishing grounds and has the country’s first national marine park (910 km², established 1983) and two community-based extractive reserves (ER), Cassurubá ER (1010 km², established 2009) and Corumbau ER (815 km², established 2000).

**SAMPLE COLLECTION AND DATA ANALYSES**

Specimens (n = 360) were obtained from a fisheries monitoring programme of commercially important reef fishes (Freitas et al., 2011; Moura et al., 2013) focused on the hook-and-line and gillnet landings in the municipalities of Alcobaça (offshore reef fisheries) and Caravelas (coastal reef fisheries) (Fig. 1). Sampling was carried out monthly between August 2010 and March 2012. Total length (L_T) and mass (M_T) were determined to the nearest 1 mm and 10 g, respectively. Gonads were removed and immediately fixed in 10% formalin for 24 h and subsequently stored in 70% ethanol before histological preparation.

For each gonad, maturity was initially determined macroscopically, based on gonad size, consistency, colour, vascularization, presence of lateral sperm sinuses, ovarian cavity, ovarian lamellae and identifiable oocytes (García-Cagide et al., 2001; Sadovy de Mitcheson & Colín, 2012). Histological sections were further examined and categorized into the five developmental phases described by Brown-Peterson et al. (2011): immature (IM), developing (D), spawning capable (SC), regressing (RS) and regenerating (RN).

Sex ratio was calculated monthly and also for each 20 mm L_T class, with significant differences determined by a χ²-test (χ² < 3.840, d.f. = 1, P < 0.05). Overall sex ratio was compared with published data through a Bayesian method, using the total numbers of females (f) and the number of females plus males (n). A conjugate β-binomial model was utilized to estimate the proportion of females with uninformative β (1,1) as a prior distribution and β (f + 1, n − f + 1) as posterior distribution (Gelman et al., 2004).

Total length at maturity (L_M, length at which 50% of the individuals were mature) was estimated in order to define sexual maturity and was estimated separately for females, males and both sexes combined. The following logistic regression model was used: p_M = 1[1 + e(α+βL)]−1, where p_M is the proportion of mature specimens in length class L, α is a constant and L_M = −α/β. For the L_M analysis, D, SC, RS and RN were considered sexually mature (adults). To predict the probability that an individual was mature at a given length, binary maturity observations (0 = immature, 1 = mature) and L_M were fitted to binary logistic models (logit function) to construct maturity ogives (maturity-at-length probability plots) based on logistic regression (Hazelton, 2007). A bootstrap method with 1000 interactions was applied to estimate 95% c.i.

For L_M comparisons with published data, a Bayesian method was implemented using the automatic differentiation model builder (ADMB) software (Fournier et al., 2012) and uninformative priors. Samples from the posterior distributions of the parameters were obtained using the Markov chain Monte-Carlo algorithm (Gelman et al., 2004) with a 10 million chain and samples saved once every 10 000 iterations.
The reproductive season of sexually mature males and females was determined through the use of the gonado-somatic index ($I_G$), obtained by expressing gonad mass ($M_G$) as a proportion of total mass ($M_T$): $I_G = \left[ \frac{M_G}{M_T - M_G} \right] 100$. Relative frequency of reproductive stages for each sex was calculated monthly. Total fertility was estimated from SC ovaries according to Murua et al. (2003). Batch fecundity was analysed for 30 female gonads ranging from 250 to 590 g and 255 to 330 mm $L_T$.

**RESULTS**

The samples included 173 (48%) females ($L_T$ range: 185–355 mm) and 187 (52%) males ($L_T$ range: 200–530 mm). The sex ratio did not differ significantly when all size classes were pooled ($\chi^2 = 0.55$, females:males = 0.93:1, $n = 360$). The proportion of females was higher than males only in the 185–205 ($\chi^2 = 7.36$), 246–265 ($\chi^2 = 3.93$) and 266–285 mm ($\chi^2 = 6.56$) $L_T$ classes, whereas males outnumbered females in all $L_T$ classes > 306 mm. Male predominance was observed in September ($\chi^2 = 4.76$) and October 2010 ($\chi^2 = 6.26$) and females in October 2011 ($\chi^2 = 4.76$) and February 2012.
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($\chi^2 = 4.26$). The Bayesian analysis found that the posterior distribution of the proportion of females declined in recent studies, including the present observations from Abrolhos Bank (Fig. 2).

Female $L_{50}$ was estimated at 214 mm and all females $>255$ mm $L_T$ were mature ($L_{95}$). The smallest and largest mature females were 185 and 355 mm $L_T$, respectively. For males, $L_{50}$ was estimated at 235 mm and all males $>269$ mm $L_T$ were mature (Fig. 3). The smallest and largest mature males were 225 and 530 mm $L_T$, respectively. Considering both sexes, $L_{50}$ and $L_{95}$ were estimated at 220 and 267 mm $L_T$, respectively. The 90% Bayesian credibility interval of the posterior distribution of size when 50% of the females were mature, estimated through the $\beta$-binomial model, was 214–230 mm $L_T$ (Fig. 4).

Histological examination of reproductively active ovaries ($n = 103$) revealed the simultaneous occurrence of oocytes in different developmental stages, indicating multiple spawning. Immature and developing females contained only primary growth oocytes (PG). Ovaries in the SC phase showed primary growth oocytes (Vtg1), cortical alveolar oocytes, oocytes in secondary (Vtg2) and tertiary (Vtg3) vitellogenic stages and germinal vesicle migration (GVM) [Fig. 5(a)]. 

The $I_G$ values were highly variable (Fig. 6), but higher values for both sexes tended to occur during the spring and summer of both years. Females in phases D or SC were found year round (Fig. 7). Females with germinal vesicle breakdown (GVBD) and hydrated oocytes were found in November 2010, January and February 2011 and also
Fig. 3. Mean ± 95% c.i. regression models for the estimated proportion of mature *Haemulon plumierii* relative to total length (L<sub>T</sub>) on the Abrolhos Bank. (a) Proportion of mature (p<sub>M</sub>) females: p<sub>M</sub> = 1 − exp(−18.564L<sub>T</sub><sup>0.005</sup>), 50% mature (●, L<sub>50</sub>) = 214 mm, 95% mature (●, L<sub>95</sub>) = 255 mm; (b) proportion of mature males: p<sub>M</sub> = 1 − exp(−17.779L<sub>T</sub><sup>5.734</sup>), L<sub>50</sub> = 235 mm, L<sub>95</sub> = 269 mm; (c) proportion of mature females + males: p<sub>M</sub> = 1 − exp(−20.104L<sub>T</sub><sup>5.416</sup>), L<sub>50</sub> = 220 mm, L<sub>95</sub> = 267 mm.

in July 2011. Females in the RS phase (with POFs) were recorded in January and from March to June 2011, with higher percentages in January and February. Regenerating females were observed year round, with the highest percentages in December (2010 and 2011).

The number of oocytes in SC females ranged from 34 450 to 1 229 785 (mean = 266 986) and was weakly correlated with the M<sub>T</sub> (r<sup>2</sup> = 0.327, P < 0.001) and L<sub>T</sub> (r<sup>2</sup> = 0.205, P < 0.01).

**DISCUSSION**

The *H. plumierii* is a gonochoric species with no evidence of external sexual dimorphism (Pajuelo *et al.*, 2003; Safi *et al.*, 2014). Akin to the pattern reported by Gaut & Munro (1983) and Palazón-Fernández (2007) from the north-western Atlantic Ocean, males also predominated in the largest size classes of the Abrolhos reef fishery landings. Females usually experience stronger energetic trade-off between growth and gamete production (Sadovy, 1996; Wootton & Smith, 2015), but the functional and
adaptive significance of the size-biased dimorphism observed here are unclear. Larger males in a given population can be associated with sexual selection (Berglund et al., 1986; Walker & McCormick, 2009), spawning modes (Jan, 2000), fecundity (Pélabon et al., 2003), growth rate (Choat et al., 2006) and patterns of parental investment (Barlow, 1981).

The overall sex ratio observed in the Abrolhos Bank, close to 1:1, was also found in other populations of *H. plumierii*, both in the south-western (Araújo & Martins, 2007; Shinozaki-Mendes et al., 2013) and north-western Atlantic Ocean (Palazón-Fernández, 2007). β-Binomial modelling of sex-ratio data showed a lower proportion of females in recent studies (Murie & Parkyn, 2005; Shinozaki-Mendes et al., 2013), including present observations (Fig. 2). Such intraspecific variation can be attributed to differential growth and longevity (Murie & Parkyn, 2005; Araújo & Martins, 2007), sex-biased mortality and catchability (Gaut & Munro, 1983; Zúñiga-Vega et al., 2012; Tamate, 2015) or even to spawning migrations (Sadovy, 1996).

Variation in $I_G$ in the two studied years, together with the consistent co-occurrence of different reproductive stages, indicates that *H. plumierii* is reproductively active year-round, with increased activity during the austral spring and summer, similar to the observations of Alves & Aragão (1973) and Shinozaki-Mendes et al. (2013) in northern Brazil. In the northern hemisphere, Silva & Murphy (2001) also observed reproductive activity of *H. plumierii* during the boreal spring (April to May). In Venezuela, Palazón-Fernández (2007) observed spawning capable females during the boreal winter (February to April) and summer–autumn (August to October). Spawning seasonality of most haemulids appears to follow this general trend of increased spring–summer activity (Gaut & Munro, 1983), including population-level contrasts in the spawning season of species that occur in different hemispheres (Freitas et al., 2011). As reported for several other reef-fish species in Abrolhos, peak captures tend to correlate with spawning periods (Freitas et al., 2011).

Although an increase in the number of oocytes associated with female body size (Hixon et al., 2014) was expected, no size dependency for fecundity was found, as observed by Palazón-Fernández (2007) for the *H. plumierii* in Venezuela. Several marine and freshwater fishes (Fitzhugh et al., 2012) do not have discernible increased

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Fig. 4. Posterior distribution of total length ($L_T$) when 50% of the females of *Haemulon plumierii* are mature ($L_{50}$) on the Abrolhos Bank (---), estimated through the β-binomial model. $L_{50}$ values from published data are shown for comparison: Alves & Aragão (1973); Palazón-Fernández (2007); Shinozaki-Mendes et al. (2013).
egg production with age or size, but other factors such as food availability and temperature may affect fecundity (Wootton & Smith, 2015). The present fecundity estimates for *H. plumierii* ranged from 34,450 to 1,229,785 eggs per female (mean = 266,986) and were consistent with those reported for other western Atlantic Ocean populations (García-Cagide, 1987; Palazón-Fernández, 2007).

Female *H. plumierii* from the Abrolhos Bank reached maturity at slightly smaller sizes than males (214 and 235 mm) and the $L_{50}$ at which 50% of all individuals are mature ($L_{50} = 220$ mm) corresponded to 41.5% of the maximum $L_T$ (530 mm). The present $L_{50}$ values are higher than those reported by Alves & Aragão (1973) and Shinozaki-Mendes et al. (2013) from northern Brazil, but lower than those reported by Palazón-Fernández (2007) from Venezuela. Such variability is not readily associated with any discernible geographic or temporal trends, but $L_{50}$ may be associated with environmental drivers (e.g. temperature) and local environmental conditions, as well as fisheries types and intensity (commercial vs. experimental) and gear selectivity (Mahon & Hunte, 2001; Patterson et al., 2012). These factors can interact and exert strong effects on population structure (Stergiou et al., 1996; Conover & Munch, 2002).

Traditionally, snappers (Lutjanidae) and groupers (Epinephelidae) comprise the most important coastal reef fishery resources in the tropical west Atlantic Ocean (Kawaguchi, 1974; Claro et al., 2001; Costa et al., 2003; Freitas et al., 2011) and they used to be the most heavily exploited reef fishes in Abrolhos (Olavo et al.,

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**Fig. 5.** Photomicrographs of histological sections from female and male *Haemulon plumierii* gonads collected from the Abrolhos Bank. (a) Spawning capable female, showing germinal vesicle migration (GVM) and germinal vesicle breakdown (GVBD). (b) Regressing female, showing postovulatory follicle (POF). (c) Late developing male, showing primary spermatocytes (Sc1), spermatid (St) and spermatozoa (Sz). (d) Section of regenerating male, showing spermatozoa (Sz).
Fig. 6. Monthly gonado-somatic index ($I_G$) of sexually mature (a) female ($n = 154$) and (b) male ($n = 154$) *Haemulon plumierii* from the Abrolhos Bank.

Fig. 7. Relative frequency of reproductive stages for (a) females and (b) male *Haemulon plumierii* from the Abrolhos Bank: ◆, developing; □, spawning capable; ■, regressing; ■, regenerating. Sample size ($n$) is shown at the top of each column.
2005; Freitas et al., 2011). As snapper–grouper catches declined sharply in the past three decades, however, fishers increasingly switched to alternative resources such as scarins, carangids and grunts. The medium-sized reef fish *H. plumierii*, formerly considered a subordinate fishery resource in Abrolhos, has become an important catch for the domestic fish market since 2010 (M. O. Freitas, unpubl. data). The biological information provided here can be readily used to support the ongoing efforts of the small-scale fisheries management inside multiple-use marine protected areas and in the buffer zones of no-take zones of the Abrolhos Bank (Giglio & Freitas, 2013). Simple measures such as seasonal closures during spawning peaks (September to November and February to March) and the establishment of a minimum size (>\(L_{50}\)) for *H. plumierii* captures can improve long-term sustainability of this important artisanal reef-fishery resource. Future directions for applied research include the identification of spawning grounds, essential habitat for recruitment and stock assessments. As such knowledge gaps may take decades to be filled, there is no reason to postpone immediate and well-informed simple decisions to control fishing effort over this and several other reef fishes in the Abrolhos Bank.

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where we should go and what we need to get there. *ICES Journal of Marine Science* **71**, 1515–1534. doi: 10.1093/icesjms/fsu038


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