

Population structure and physiological plasticity of *Favia gravida* with differences in terrestrial influence

Cristiano M. Pereira^{1,2*}, Emiliano N. Calderon^{2,3}, Débora O. Pires^{2,4},
Clovis B. Castro^{2,4}

¹ Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brazil

² Instituto Coral Vivo, Rua dos Coqueiros, 87, 45807-000, Santa Cruz Cabralia, BA, Brazil

³ Programa de Pós-Graduação em Ciências Ambientais e Conservação, Instituto de Biodiversidade e Sustentabilidade NUPEM, Universidade Federal do Rio de Janeiro, Avenida São José do Barreto, 794, 27965-045, Macaé, RJ, Brazil

⁴ Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brazil

*Corresponding author: cristianomp@gmail.com

ABSTRACT

Terrestrial runoff is a source of sediments and nutrients to coral reefs. Due to runoff, Brazilian reefs are typically turbid, and have coral species that are naturally turbidity-resistant. This study investigated how terrestrial input influences population and physiology for the coral *Favia gravida* on two reefs with differences in river mouth proximity in eastern Brazil. The population structure and physiological traits of *F. gravida* colonies were assessed on both reefs, then some colonies selected for a subsequent transplantation experiment. The reef less impacted by terrestrial influence showed higher population density and lower recruitment. At this site, the coral colonies displayed higher calcification and larger larvae. The reproductive effort between coral populations at the two sites showed no significant difference. The transplantation experiment confirmed the high physiological plasticity of *F. gravida* colonies at the more turbid reef site. Despite being regarded as a more challenging environment, where *F. gravida* has a lower population density, the reef closer to the river mouth appears to secure more nutrients, which may heterotrophically compensate its coral colonies.

Descriptors: Estuaries, heterotrophy, larvae production, nutrients, tolerance, turbid reef.

INTRODUCTION

Rivers are the primary source of terrigenous sediments and nutrients to coastal coral reefs (van Dam *et al.*, 2011). Terrestrial runoff reduces coral calcification and may inhibit fertilization and larval development (Fabricius, 2005). Turbidity also reduces settlement rates, larval survival, and gametogenesis (Tomascik and Sander, 1987; Wittenberg and Hunte, 1992; Gilmour, 1999). Nevertheless, some coral species

may be well-adapted to naturally turbid reefs (Sofonia and Anthony, 2008), which seems to be related to the heterotrophic capacity of these stress-tolerant species (Anthony, 2000). Furthermore, smaller coral colonies with internal larval development (brooding corals) and multiple reproductive cycles per year are advantageous in less favorable habitats due to the greater recruitment rate (Szmant, 1986). However, it is unclear how terrestrial runoff influences specific coral species both in populational and physiological aspects.

Skewness measures the asymmetry of a frequency distribution, using the long or extended tails on either side of the data distribution (Crawley, 2013). For example, negative skewness means a long left

Submitted on: 7/October/2019

Approved on: 21/September/2020

Editor: Rubens M. Lopes



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tail. Coral populations on impacted reefs generally have negative skewness. Impacted reefs are mainly composed of large coral colonies, with few small or medium-sized colonies (Meesters *et al.*, 2001). Therefore, the frequency of colony sizes is a suitable indicator of declining coral reefs for environmental assessment and monitoring programs (Bak and Meesters, 1998).

Brazilian coral reefs are the only true coral reefs in the South Atlantic, extending for approximately 2,600km along the Brazilian coast (Castro and Pires, 2001). They are naturally exposed to high sedimentation levels from river discharges (Dutra, Kikuchi, and Leão, 2006; Segal and Castro, 2011; Castro *et al.*, 2012). Therefore, these reefs exist under conditions typically detrimental for corals that thrive in oligotrophic waters, favoring stress-resistant species (Laborel, 1970; Leão, Kikuchi, and Testa, 2003; Vasconcelos, Leão, and Kikuchi, 2018). Compared to the Caribbean and Indo-Pacific reefs, Brazilian reefs have higher endemism of coral species, despite their lower diversity (Castro and Pires, 2001; Castro and Zilberberg, 2016). These reefs are negatively impacted by unregulated tourism, overfishing, coastal pollution, invasive species, and climate change (Tedesco *et al.*, 2017). However, experimental *in situ* studies on Brazilian reefs are scarce (Mantelatto, Cruz, and Creed, 2018).

Favia gravida (Verrill, 1868) is a coral species endemic to the South Atlantic (Zibrowius *et al.*, 2017). It populates a variety of habitats, from low to high hydrodynamic conditions, ranging from close to estuaries to oceanic islands, but is most commonly found in well-lit shallow habitats near oceanic islands and on turbid reef surfaces. Their wide ecological range explains their resilience to environmental variations in temperature, salinity, and turbidity (Laborel, 1969). *F. gravida* has a semi-spherical shape, and its diameter is usually less than 10 cm (Hetzl and Castro, 1994). Their colonies are hermaphroditic, with internal fertilization and a monthly planulae release (Calderon, Castro, and Pires, 2000; Conceição *et al.*, 2006).

It is essential to understand how terrestrial discharges influence coral species, both in terms of population and physiology. In this study, we evaluated the effects of terrestrial influence from the Buranhém River (Eastern Brazil) on the population structures

of *F. gravida* on reefs at varying distances from the river mouth. Emphasis was given to the colonies' population densities and their size frequencies. We also evaluated how the river influence affects the growth, health, and settlement success of *F. gravida*.

MATERIALS AND METHODS

To assess how terrestrial influence affects coral species at the population level, we sampled *F. gravida* colonies from reefs at two distances from the Buranhém River's mouth (Porto Seguro, Eastern Brazil). The colonies were counted and measured within quadrats at both sites. To assess terrestrial influences on physiology, we evaluated the calcification rate and reproductive effort. Then, a coral transplantation experiment was conducted between the sampled sites to assess if the physiological differences are due to the species' physiological plasticity or environmental variation.

STUDY AREA

The region between Buranhém River's mouth and the Recife de Fora Marine Protected Area (RFMPA; no-take zone) harbors a reef complex with approximately equidistant reefs (≈ 2 km). The two reef sites were chosen due to their differences in seawater physicochemical parameters and differing distances from the Buranhém River mouth. They were labeled station two (S2; Carapindaúba Reef – 16°25'43.0"S, 039°01'29.9"W) and station four (S4; Labirinto Reef – 16°25'06.1"S, 038°59'27.0"W), located approximately 4 and 8km away from the river mouth, respectively (Fig. 1; Leite *et al.*, 2018; Marques *et al.*, 2019). We maintained their previously designated nomenclatures to facilitate comparisons with published studies (Leite *et al.*, 2018; Marques *et al.*, 2019). The reef near the river mouth, S2, has a higher concentration of metals (especially Cu, Zn, and Cd) and sterols compared to the farther reef, S4 (Marques *et al.*, 2019), suggesting the presence of differences in terrestrial and anthropogenic influences between the two sites. The potential influence from terrestrial sources by site was also detected through increased ecological complexity of the microbial core of the coral *Mussismilia hispida* and the reduction of Enterobacteriaceae in tandem with increasing distance from the Buranhém River mouth (Leite *et al.*, 2018). Reefs farthest from the river mouth

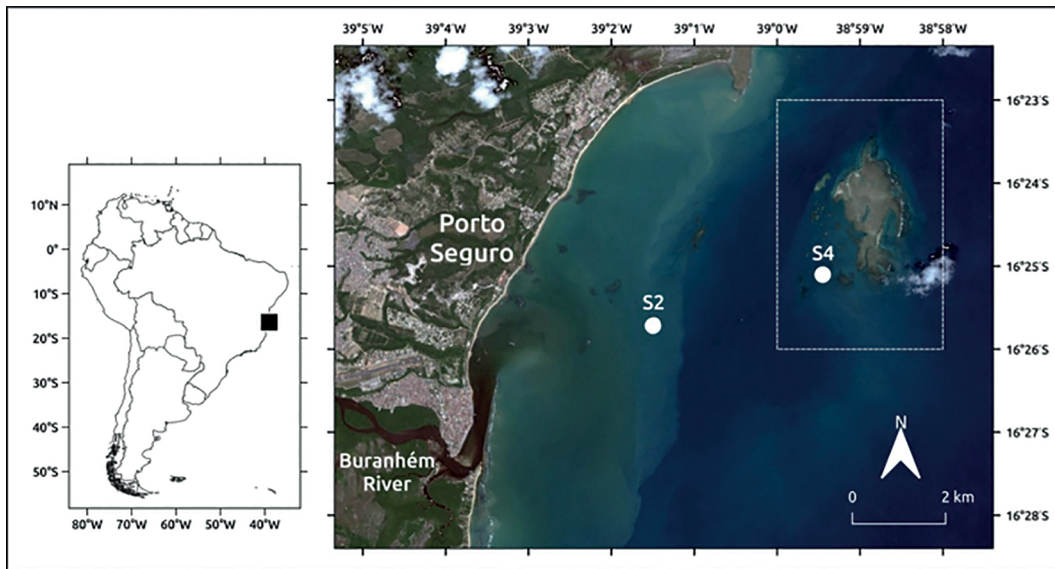


Figure 1. Sample sites at Porto Seguro (Eastern Brazil) used to assess *Favia gravida* population and physiological parameters at different distances from the Buranhém river mouth. Dashed square indicates Recife de Fora Marine Protected Area, **S2** Carapindaúba Reef (4km away from the Buranhém River mouth), **S4** Labirinto Reef (8km away from the Buranhém River mouth).

were also observed to have greater coral population densities and lower sponge population density than reefs near the mouth (Abrantes, 2018).

POPULATION STRUCTURE ASSESSMENT

We sampled four 10m-long transects along reef surfaces at each site. Four quadrats, 1m² per transect, were chosen at random to estimate the population density of *F. gravida* (totaling 16 quadrats per site). Colonies found in those quadrats were measured to estimate the population structure using colony surface area. We used a caliper to measure the maximum diameter across the base (D) and minimum diameter (d) of each colony. These measurements were used to estimate the surface area of each colony using the standard formula for the surface area (A) of an hemisphere where $A=2\pi(D/2.d/2)$. If fewer than 100 colonies were found and sampled along the transect at each site, additional quadrats were randomly placed next to the transect until 100 colonies were sampled to ensure an adequate analysis of the population structure (Lins de Barros and Pires, 2006).

Additionally, to assess distribution patterns, we used the T-square distance sampling method. We selected thirty points at random in each transect and measured the distance to the nearest *F. gravida* colony, and from this colony to its nearest neighbor

(Ludwig and Reynolds, 1988). With these two measurements, we calculated a Spatial Pattern Index (C-Index). A Dispersion Index (I-Index), which uses the distance from a random point to the nearest colony, was also calculated (Ludwig and Reynolds, 1988). It is possible to infer if a population has a random, uniform, or clumped distribution pattern by comparing the two indices in a standard normal probability distribution (Ludwig and Reynolds, 1988; Carlon and Olson, 1993). A maximum distance of 150cm was considered here (including values greater than 150cm) to meet logistical requirements. Data acquisition was performed following the Brazilian Environmental Agency's regulations (IBAMA/SISBIO permit 61794-1).

CALCIFICATION RATE AND REPRODUCTIVE EFFORT ASSESSMENTS

Ten mature adult *F. gravida* colonies (4 to 7cm in diameter) were collected at each site (totaling 20 colonies) by SCUBA divers and transported to the Coral Vivo Project's laboratory (12km away from the sites). The live colonies were incubated for three hours at 25°C in acrylic chambers for instant calcification analysis, based on the protocol used by Marangoni *et al.* (2017). After incubation, the colonies were fixed in a 10% formalin seawater solution, decalcified in a 10% formic acid and 5% formalin solution, rinsed in

running tap water for 24 hours, and preserved in a 10% formalin solution. Each preserved coral colony's surface area was measured using ImageJ software (Rasband, 2016) by analyzing overhead photos taken with a Sony DSC WX100 camera. We assume that for each mole of CaCO_3 produced, the total alkalinity decreases by two moles in incubation seawater (Smith and Key, 1975). Calcification was defined as the ratio between CaCO_3 difference, colony area, and incubation length (Riebesell *et al.*, 2010), and used here as a proxy for growth.

Studies suggest that the reproductive cycle of *F. gravida* is regulated by a lunar rhythm, starting after the new moon (Pires *et al.*, 2016). Therefore, colonies were collected a few days before the new moon to avoid differences in larval release due to lunar periodicity (Szmant-Froelich, Reutter, and Riggs, 1985). The days chosen for colony collection were February 23rd and 24th, 2017 (three and two days before the new moon, respectively). A standard-sized tissue sample (1.450cm²) of each preserved colony was collected to quantify the number of planula larvae. The tissue samples were collected within the central colony area to avoid infertile zones (Chornesky and Peters, 1987) and corresponded to approximately five polyps per colony. The mesenteries were not included in the quantification to avoid egg counting. The reproductive effort was calculated from the ratio between the number of larvae in the coelenteron and the tissue area sampled, then used as a proxy for health (Van Moorsel, 1983; Szmant, 1986; de Putron and Smith, 2011; Pires, Segal, and Caparelli, 2011). Larvae sizes were estimated using ImageJ software by analyzing overhead photos taken with a Sony E2343 camera coupled with a Leica S6 D stereo microscope. For larval size, we calculated the area of each larva rather than volume; this parameter was used as a proxy for settlement success (de Putron *et al.*, 2017).

TRANSPLANTATION EXPERIMENT

Along with collection for calcification rate and reproductive effort assessments, an additional ten *F. gravida* colonies per site were collected and transplanted to the other site (i.e., transplantation of corals from S2 to S4, and vice-versa). On January 15th, 16th, and 17th, 2018 (two and one days before and during the new moon, respectively), 11 months after the transplantation, we collected and transported

the transplanted colonies to the laboratory. We also collected native colonies (ten per site). The physiological assessments (for calcification rate and reproductive effort) were repeated for the acquired colonies. Collections for the physiological assessments and transplantation experiments were performed under the Porto Seguro Environment Secretary's approval (SMMA/Porto Seguro permit 01/17) and the Brazilian Environmental Agency's regulations (IBAMA/SISBIO permit 57898-1).

STATISTICAL ANALYSES

All statistical analyses were performed using R software (v. 3.5.2; R Core Team, 2018). The estimated surface area (A) of the colonies was logarithmically transformed to improve normality (Meesters *et al.*, 2001; Lins de Barros and Pires, 2006). The transformed size data were compared between sites using a generalized linear model (GLM). The population structure of each site was analyzed for mean size and standard deviation (sd), coefficient of variation, largest colony observed, 95th percentile of colony surface area, and skewness (*moments* package). The spatial pattern indices (*nn* package) were compared between sites using a GLM. The coral population density was compared between sites with a negative binomial distribution (*MASS* package) to avoid overdispersion.

Each parameter – calcification, reproductive effort, and larval size – was compared between sites using a GLM analysis. The groups analyzed for the transplantation experiment were as follows: native colonies from S2 (S2-N); native colonies from S4 (S4-N); colonies transplanted from S2 to S4 (S2-S4); and colonies transplanted from S4 to S2 (S4-S2). Pairwise differences between groups were tested with post-hoc multiple comparisons of means (Tukey HSD test; *multcomp* package).

RESULTS

Colonies presented larger size (mean area) on the reef farthest from the river mouth (S4; GLM ANOVA, $F_{1,198} = 4.517$, $p = 0.035$). Colonies from the site closer to the river mouth (S2) had larger maximum sizes, 95th percentile, skewness, standard deviation, and coefficient of variation. The *F. gravida* population at S2 thus had fewer small to intermediate colonies and a greater number of large colonies compared to S4's

population (Figs. S1 and S2). The C-Index indicated a clumped distribution pattern for both sites (S2: 0.664, $p < 0.001$; S4: 0.676, $p < 0.001$). However, for the I-Index, the population at S2 was distributed uniformly (1.697, $p = 0.089$) while the population at S4 had a clumped distribution (2.469, $p = 0.009$; Table 1). Furthermore, between the two sites, there were no significant differences in the C-Index (GLM ANOVA, $F_{1,6} = 0.080$, $p = 0.786$) or I-Index (GLM ANOVA, $F_{1,6} = 2.562$, $p = 0.161$). There was, however, a significant increase in the colonies' population density at S4 (Table S1 and Fig. S3).

Colonies closer to the river mouth presented the highest calcification rates (GLM ANOVA, $F_{1,14} = 22.955$, $p < 0.001$; Fig. 2A). The reproductive effort did not differ between sites (GLM ANOVA, $F_{1,14} = 0.078$, $p = 0.784$; Fig. 3A). However, the colonies at S2 had larger larvae than at S4 (GLM ANOVA, $F_{1,14} = 4.804$, $p = 0.046$; Fig. 4A).

Of the 20 colonies transplanted, seven colonies from S2-S4 and eight colonies from S4-S2 showed no signs of competition, predation, or disease and were used in the analyses. The remaining colonies struggled to survive (two from S2-S4 and one from S4-S2) or did not survive at all (one from each site). Calcification was significantly different between the groups (GLM ANOVA, $F_{3,24} = 13.727$, $p < 0.001$). The post-hoc test indicated that S2-N colonies had the highest calcification, followed by S4-N colonies. Colonies from S4-S2 had the third highest calcification, but there were no significant differences between S2-S4's colonies and S4-N's or S4-S2's colonies (Fig. 2B).

For the reproductive effort assessment, the total number of planula larvae acquired at each site was

82 (from S2) and 112 (S4). For the transplantation experiment, the total number of planula larvae acquired was 252 (S2-N), 113 (S4-N), 94 (S2-S4), and 71 (S4-S2). The acquired larvae were used for both reproductive effort and larval size analyses. The reproductive effort was not significantly different between groups (GLM ANOVA, $F_{3,24} = 1.932$, $p = 0.151$; Fig. 3B). However, larval size differed significantly between groups (GLM ANOVA, $F_{3,24} = 0.174$, $p = 0.020$). The post-hoc test indicated that the S4-S2 colonies had the largest larvae, while S2-S4 colonies had the smallest. Additionally, S2-N and S4-N colonies had intermediate larvae sizes that did not differ significantly from S2-S4 or S4-S2 colonies (Fig. 4B).

DISCUSSION

The analyzed *F. gravida* displayed negative skewness in colony size frequencies in both sites, which indicates that the majority of the observations were below the mean. However, S4's skewness was -0.7, *i.e.*, more skewed than S2's (Fig. S1). This asymmetry to the left was also observed in other corals on Brazilian (Lins de Barros and Pires, 2006) and Caribbean reefs (Johnson, 1992a; Meesters *et al.*, 2001). Meesters *et al.* (2001) studied 11 coral species in the Caribbean and pointed to two situations associated with the skewness of coral colony-size frequency distributions. First, the populations of larger species tended to skew to the left (negative skewness), while small-sized species were skewed to the right (positive skewness). Second, the species in degraded areas tended to show increased negative skewness. However, while the *F. gravida* colonies

Table 1. *Favia gravida* population structure data for two reefs in an estuarine influence gradient. **S2** Carapindaúba Reef (4km away from the Buranhém River mouth), **S4** Labirinto Reef (8km away from the Buranhém River mouth, inside the Recife de Fora Marine Protected Area), **SD** standard deviance, **CV** coefficient of variation, **C-Index** Index of Spatial Pattern, **I-Index** Index of Dispersion.

| Population parameter | S2 | S4 |
|---|-------------|-------------|
| Size - mean (mm ²) | 482.09 | 631.60 |
| Size - SD (mm ²) | 2.71 | 2.20 |
| Size - CV (mm ²) | 1.45 | 1.32 |
| Size - maximum (mm ²) | 3455.75 | 2557.26 |
| Size - 95 th percentile (mm ²) | 2748.74 | 2113.35 |
| Skewness | -0.3437 | -0.7625 |
| C-Index (mean±SD) | 0.663±0.080 | 0.676±0.031 |
| I-Index (mean±SD) | 1.770±0.311 | 2.125±0.317 |
| Density - individual.m ⁻² (mean±SD) | 4.75±4.75 | 10.75±5.13 |

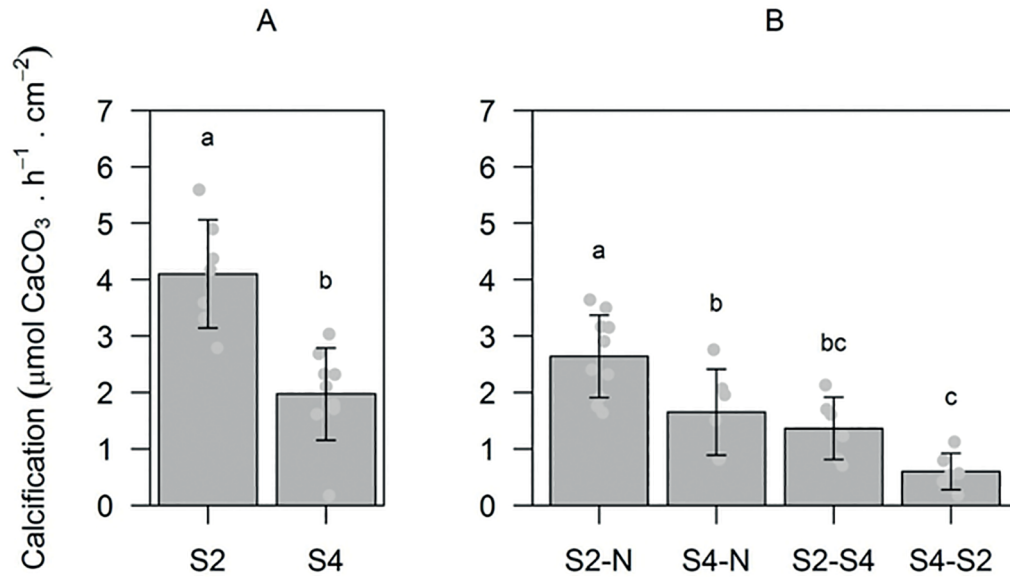


Figure 2. Calcification rate in *Favia gravida* from two reef sites in a gradient of estuarine influence (A, left panel) and after a transplantation experiment of 11 moths between such sites (B, right panel). **S2** corresponds to colonies from Carapindaúba Reef (4km away from the Buranhém River mouth), whereas **S4** are colonies from Labirinto Reef (8km away from the Buranhém River mouth, inside the Recife de Fora Marine Protected Area). **S2-N** and **S4-N** correspond to native colonies from S2 and S4, respectively, whereas **S2-S4** and **S4-S2** are S2 colonies transplanted to S4 and vice-versa ($6 \leq n \leq 10$). Data are mean \pm standard deviation. Light gray dots show single observations. Different letters indicate significant differences between sites (A) or experimental groups (B) ($p < 0.05$).

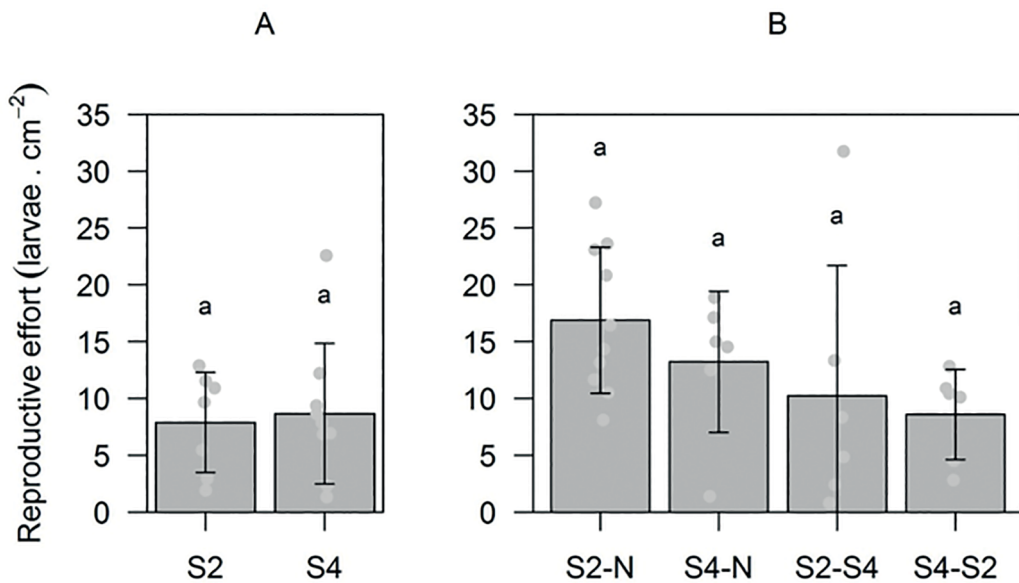


Figure 3. Reproductive effort in *Favia gravida* from two reef sites in a gradient of estuarine influence (A, left panel) and after a transplantation experiment of 11 moths between such sites (B, right panel). **S2** corresponds to colonies from Carapindaúba Reef (4km away from the Buranhém River mouth), whereas **S4** are colonies from Labirinto Reef (8km away from the Buranhém River mouth, inside the Recife de Fora Marine Protected Area). **S2-N** and **S4-N** correspond to native colonies from S2 and S4, respectively, whereas **S2-S4** and **S4-S2** are S2 colonies transplanted to S4 and vice-versa ($6 \leq n \leq 10$). Data are mean \pm standard deviation. Light gray dots show single observations. Different letters indicate significant differences between sites (A) or experimental groups (B) ($p < 0.05$).

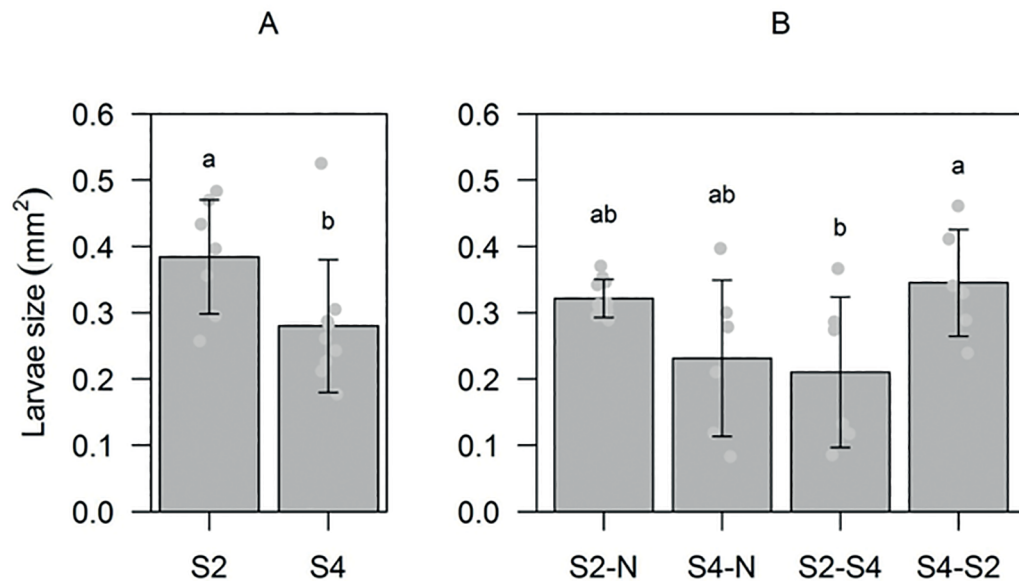


Figure 4. Larvae size in *Favia gravigida* from two reef sites in a gradient of estuarine influence (A, left panel) and after a transplantation experiment of 11 moths between such sites (B, right panel). **S2** corresponds to colonies from Carapindaúba Reef (4km away from the Buranhém River mouth), whereas **S4** are colonies from Labirinto Reef (8km away from the Buranhém River mouth, inside the Recife de Fora Marine Protected Area). **S2-N** and **S4-N** correspond to native colonies from S2 and S4, respectively, whereas **S2-S4** and **S4-S2** are S2 colonies transplanted to S4 and vice-versa ($6 \leq n \leq 10$). Data are mean \pm standard deviation. Light gray dots show single observations. Different letters indicate significant differences between sites (A) or experimental groups (B) ($p < 0.05$).

analyzed in our study were small, the populations were mostly negative skewness. Additionally, S2 was presumably more impacted by the river discharges than S4 (Leite *et al.*, 2018; Marques *et al.*, 2019) and, therefore, had lesser negative skewness. It appears that the *F. gravigida* populations sampled in this study did not behave as expected. Similar cases have been reported for other corals, such as *Orbicella faveolata* (formerly *Montastrea faveolata*; family Merulinidae) and *Eusmilia fastigiata* (family Meandrinidae; Meesters *et al.*, 2001). These characteristics may explain the success of *F. gravigida* in coping with extreme environments, such as high turbidity (Segal and Castro, 2011).

The I-Index of *F. gravigida* resembled that observed for *Favia fragum* (Carlson and Olson, 1993). This index is affected by the coefficient of variation (ratio of the dispersion of the data around the mean), but not by the average distance between colonies. The population at S2 presented a lower I-Index than the population at S4 because, despite having greater average distance (lower density), the coefficient of variation for S2 was lower than for S4. However, the I-Index for the population at S2 was not significantly

different from a uniform distribution (as highlighted previously). The C-Index is mainly affected by the ratio of the distances (random point to the nearest colony, and nearest colony to its nearest neighbor). The clumped distribution pattern of *F. gravigida* was also found for *F. fragum* and other brooding species (Lewis, 1970). Such a distribution pattern was reported for other coral species across a 10,000km gradient (Karlson, Cornell, and Hughes, 2007). Although further data are scarce, this distribution pattern may be common for hermaphroditic brooder species (Lewis, 1970). As fertilization is internal, aggregated colonies could favor sperm exchange. For example, the sperm of *Isopora palifera* (formerly *Acropora palifera*) has a dispersal potential over tens of meters (Ayre and Miller, 2006). However, brooding corals can also exhibit self-fertilization under limited sperm conditions (*e.g.*, low populational densities; Sherman, 2008). This may explain the broad geographical distribution of *F. gravigida* and its extensive genetic differentiation (Nunes, Norris, and Knowlton, 2011).

The density of *F. fragum* (3 colonies m⁻² at the reef surface) was lower than that of *F. gravigida* (Carlson, 2002). However, Carlson (2002) did not consider

colonies smaller than 1cm in diameter. When we excluded these colonies (approximately 157mm² of the total surveyed area), *F. gravida* colony density was 3.81 ± 3.92 colonies m⁻² (mean \pm sd) for S2 and 8.75 ± 3.42 colonies m⁻² for S4. Consequently, the *F. gravida* colony density was similar to *F. fragum*'s at S2 but much higher at S4.

The S2 site showed lower recruitment (lower population density and less significant negative skewness) than S4 (higher population density and more significant negative skewness). It is not clear if the lower recruitment results from lower larval arrival, higher mortality of the larvae that try to settle, or higher mortality of the newly settled larvae. However, the colonies at S2 appear to possess some adaptive advantage, given that colonies at S2 have larger surface areas and have a higher 95th percentile of surface area than the colonies at S4.

The calcification rate of sampled *F. gravida* corals was 20 times greater than that of *Stylophora pistillata* (similar size and brooder; Gutner-Hoch *et al.*, 2017), four times greater than broadcast spawners such as *Acropora eurystoma* (similar size; Schneider and Erez, 2006), and two times smaller than *Orbicella faveolata* (bigger colony; Colombo-Pallotta, Rodríguez-Román, and Iglesias-Prieto, 2010). This rate is influenced by dissolved inorganic matter (nitrogen and phosphorus), particulate organic matter, and sedimentation (Fabricius, 2005). As the regions of the studies regarding these four species (Brazil, the Red Sea, and the Caribbean) appear to have similar nitrogen and phosphorus concentrations (Costa Jr., Attrill, and Nimmo, 2006), particulate organic matter and characteristics particular to each species may justify the differences observed.

Hartmann, Marhaver, and Vermeij (2018) reported a lower reproductive effort for brooding and broadcast spawning corals on reefs with high anthropogenic impact. Our results showed no significant difference in the reproductive effort among reefs with apparent dissimilarities in environmental conditions and anthropogenic impacts (Leite *et al.*, 2018; Marques *et al.*, 2019). Hence, the reproductive effort seems to be regulated by the species' intrinsic characteristics, which may vary according to environmental characteristics. Alternatively, the environmental variation between sampled sites did not alter *F. gravida*'s reproductive effort.

Larvae size of *F. gravida* (estimated using the largest diameter of the circular cross-section) was similar to other brooding species such as *S. pistillata* (Rinkevich and Loya, 1979) and *F. fragum* (Hartmann, Marhaver, and Vermeij, 2018). However, larvae were larger compared to *Scolymia wellsii* (Pires, Castro, and Ratto, 2000) and *Manicina areolata* (Johnson, 1992b). All the species cited above belong to the same clade of *F. gravida* (family Mussidae) except for *S. pistillata* (Budd *et al.*, 2012). However, colonies at S2 had larger larvae than those of at S4. Although not analyzed experimentally, larger larvae may have higher lipid content, as observed in *Porites astreoides* larvae (de Putron *et al.*, 2017). The larger larval size may increase settlement success (de Putron *et al.*, 2017) and represent an adaptive advantage for the colonies at S2.

Reefs closer to Porto Seguro's coast had concentrations ten times greater for chlorophyll *a* and two times greater for suspended solids than RFMPA's offshore reef (Costa Jr *et al.*, 2002). These additional nourishment sources could explain the higher rates of calcification and larvae size observed at S2, which may be associated with a greater ability of some coral species to feed on suspended sediments. *Acropora millepora* and *Pocillopora damicornis* (both hermaphroditic broadcast spawner species) have a capacity that is two to three times greater for feeding on suspended sediments on nearshore turbid reefs than on offshore clear-water reefs (Anthony, 2000). This higher heterotrophic capacity may increase protein and lipid concentrations and increase skeletal growth in corals (Houlbrèque and Ferrier-Pagès, 2009). This feature remains unverified for *F. gravida*, but its relatively large colonies indicate that it may be an effective heterotroph (Anthony and Fabricius, 2000). Also, larger larvae at S2 may have occurred due to higher nutrient intake and heterotrophy developed by parental colonies on the coastal reef, increasing the S2 colonies' fitness.

S2 colonies appear to possess higher physiological plasticity, because the calcification rate of colonies transplanted to S4 (S2-S4) equaled that of native colonies at S4 (S4-N). In contrast, S4's colonies appear to be more restrictive compared to S2 colonies. S4 colonies transplanted to S2 (S4-S2) had lower calcification rate than native colonies at S2 (S2-N), and colonies that remained at S4 (S4-N);

Fig. 3B). Similar results were observed for *Pocillopora grandis* (formerly *Pocillopora eydouxi*; hermaphroditic broadcast spawner with larger colonies). However, no difference was observed for *Porites lobata* (gonochoric broadcast spawners with larger colonies; Smith *et al.*, 2008). Therefore, the conclusions drawn are that (1) S2 is a more challenging environment, and (2) colonies that live at S2 present more notable fitness. This may be due to the considerable annual variation in the sedimentation rates and the highest nutrient availability on this coastal reef (Abrantes, 2018; Costa Jr. *et al.*, 2002). Furthermore, lesser fitness for S4 colonies transplanted to S2 is particularly remarkable, given they had calcification rates significantly lower than both S2 and S4 colonies in native conditions. Additionally, the time from transplantation to collection appears to have been sufficient, as the transplanted S2 colonies (S2-S4) entered physiological homeostasis, similar to the native S4 colonies. Once again, we emphasize that no signs of competition, predation, or disease were found in the majority of the transplanted colonies, results similar to those found by Carlon (2002) with *F. fragum*.

The S2 site appears to have contributed to the increased fitness of *F. gravida* colonies as the larval size of the S4-S2 colonies was higher than that of S2-S4 colonies. These results corroborate the hypothesis of more significant fitness of colonies at S2 (due to heterotrophy) and the plasticity of *F. gravida*. It is noteworthy that there was no significant difference in reproductive effort between native or transplanted colonies. These results support that *F. gravida* is a species resistant to environmental variations (Laborel, 1969), so much so that reproduction, one of the final processes in energy allocation (Leuzinger, Willis, and Anthony, 2012), was unaltered. Moreover, *F. gravida* exhibits high phenotypic plasticity in other characteristics as well. There are variations observed in its skeleton (corallite, septa, and meander) among and within locations along the Brazilian coast (Amaral and Ramos, 2007). Therefore, *F. gravida* seems to be a resilient coral, adapting to high turbidity rates and benefiting from it. In an era of climate change, this may be crucial for this species' survival (Morgan *et al.*, 2017; Teixeira *et al.*, 2019).

CONCLUSION

Our results indicate that terrestrial or estuarine conditions influence some aspects of *F. gravida*'s biology. For reefs farther from the river mouth, colony density was greater and smaller coral colonies occurred with higher frequency, indicating increased recruitment success. While the calcification rate and larval size were greater for colonies on the reef near the river mouth, the reproductive effort between these two locations did not vary. These results suggest that *F. gravida* colonies possess high physiological plasticity, enabling it to adapt to highly turbid environments and possibly benefit from it. Our conclusions may help understand the populational and physiological responses of corals inhabiting naturally turbid environments in Brazil and worldwide.

ACKNOWLEDGMENTS

The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES - Programa Ciências do Mar, Brasília, DF, Brazil; grant #1984/2014) provided the financial support for this study. The Projeto Coral Vivo and its sponsors Petrobras, through the Programa Petrobras Socioambiental, and Arraial d'Ajuda Eco Parque, provided support during field research and access to laboratory facilities. CAPES (grant #001) also provided fellowship funding to CMP and ENC. The authors would like to extend their gratitude to Carla Zilberberg, for her valuable advice, and Miguel Mies for his aid in the manuscript's earlier revision. We also would like to acknowledge the comments suggested by anonymous reviewers, which improved our manuscript.

AUTHOR CONTRIBUTIONS

C.M.P.: Conceptualization; Investigation; Formal analysis; Writing - original draft;

E.N.C.: Conceptualization; Investigation; Writing - review & editing;

D.O.P.: Conceptualization; Writing - review & editing;

C.B.C.: Conceptualization; Writing - review & editing;

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SUPPLEMENTARY MATERIAL

Table S1. Parameters of *Favia gravida* density estimated in a GLM with a negative binomial distribution (log-link function) with the site as a response variable. **DF** degrees of freedom, **Dev** deviance, **Rs DF** residual degrees of freedom, **Rs Dev** residual deviance, **Pr(>Chi)** probability.

| Effect | DF | Dev | Rs DF | Rs Dev | Pr(>Chi) |
|--------|----|-------|-------|--------|----------|
| Null | | | 31 | 48.394 | |
| Site | 1 | 11.22 | 30 | 37.713 | < 0,001 |

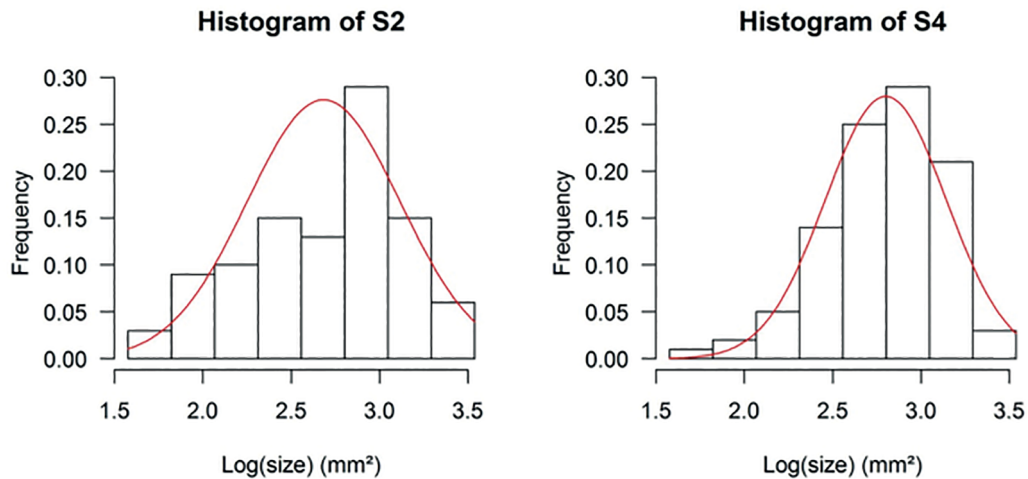


Figure S1. Histogram of colony size-frequency distribution of *Favia gravida* for two reef sites in a gradient of estuarine influence. Data are logarithm-transformed. **S2** corresponds to colonies from Carapindaúba Reef (4km away from the Buranhém River mouth), whereas **S4** are colonies from Labirinto Reef (8km away from the Buranhém River mouth, inside the Recife de Fora Marine Protected Area).

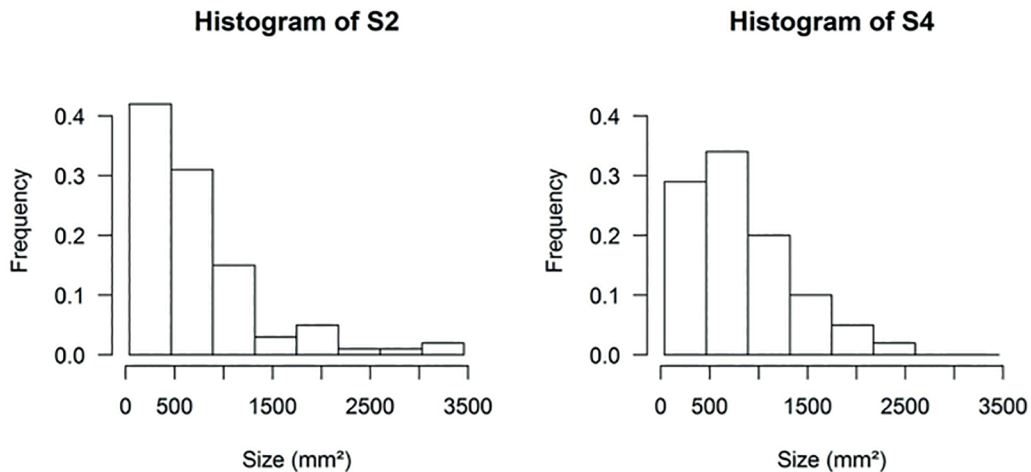


Figure S2. Histogram of colony size-frequency distribution of *Favia gravida* for two reef sites in a gradient of estuarine influence. **S2** corresponds to colonies from Carapindaúba Reef (4km away from the Buranhém River mouth), whereas **S4** are colonies from Labirinto Reef (8km away from the Buranhém River mouth, inside the Recife de Fora Marine Protected Area).

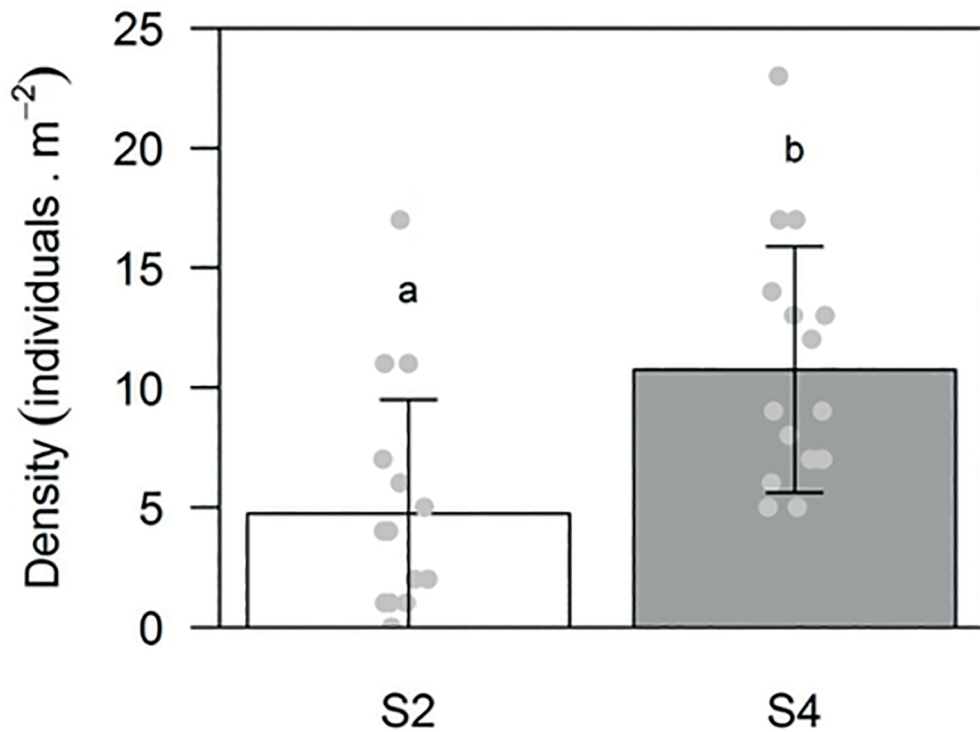


Figure S3. Colonies density of *Favia gravida* from two different reef sites in a gradient of estuarine influence. **S2** corresponds to colonies from Carapindaúba Reef (4 km from the Buranhém River mouth), whereas **S4** are colonies from Labirinto Reef (8 km from the river mouth, in Recife de Fora Marine Protected Area). Data are mean \pm standard deviation. Light gray dots show single observations. Different letters indicate significant differences between sites.