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Spawning ecology of the Saint Paul's Gregory *Stegastes sanctipauli*, a damselfish endemic to the remote St Peter and St Paul's Archipelago

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Abstract

We studied the spawning ecology of *Stegastes sanctipauli*, a damselfish endemic to the small and remote St Peter and St Paul's Archipelago (Brazil), aiming to determine the main correlates of reproductive success, as inferred from rates of egg losses along a spawning season. New clutches appeared mostly in the last quarter moon, when egg predation intensified. Predation by heterospecifics, particularly *Halichoeres radiatus* (Linnaeus, 1758), accounted for most egg losses, while filial cannibalism showed negligible influence. Predation pressure was highest for larger nests with higher initial density of eggs. Hatching of eggs occurred close to the new moon (*i.e.*, ~5 days after spawning). Most nests occur in shallow reefs (<16 m depth), where main food resources for adults (turf algae) are concentrated, but abundance of egg predators, particularly *H. radiatus*, is also highest. This latter result suggests that the spawning activity of *S. sanctipauli* is influenced by the trade-offs between food accessibility by adults and egg predation risk. The patterns recorded here are similar to those known for other tropical damselfish species and may reflect strategies for attenuating predation pressure over new fry and eggs.

KEYWORDS
agonistic interaction, egg predation, moon phase, oceanic island, reproductive behaviour

1 | INTRODUCTION

Reproductive patterns of marine fish vary strongly in space and time according to environmental (*e.g.*, tidal amplitude, moon phase, temperature, depth) and biotic (*e.g.*, food availability, competition and predation risk) conditions (Randall, 1961; Robertson *et al.*, 1990; Wilson & Harrison, 2003; Yamahira, 2001). Many reef fish show lunar/tidal periodicities in reproduction, with spawning activity generally peaking close to full and/or new moons, when tidal amplitude is higher (Doherty, 1983; Foster, 1987; Robertson *et al.*, 1990). This lunar/tidal pattern has been recorded for many reef fish families, such as Epinephelidae, Labridae, Pomacentridae and Siganidae (*e.g.*, Colin *et al.*, 1987; Foster, 1987; Ross, 1983; Takemura *et al.*, 2004; Zabala *et al.*, 1997).

Territorial damselfishes (Pomacentridae) are widely used as models in studies about reef fish ecology (Ceccarelli, 2007; Hixon, 2011; Sikkel & Petersen, 1995). During the spawning season, female damselfish lay benthic adhesive eggs within nests that are previously prepared by males (Asoh, 2003; Francini-Filho *et al.*, 2012; Kohda, 1988; Thresher, 1984). Females may choose nests based on traits of the guardian male (*e.g.*, body size; Schmale, 1981, Petersen, 1995) and/or nest quality, such as accessibility to predators and predominant benthic cover (Goldschmidt *et al.*, 1993; Jones, 1981; Sikkel, 1995a; Unger & Sargent, 1988). Eggs are externally fertilized by the guardian male soon after oviposition (Asoh, 2003; Petersen, 1995; Sikkel, 1995a). Multiple clutches, from a single or multiple females, may occur simultaneously within the same given nest that is permanently protected by the

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guarding male until hatching (Knapp & Warner, 1991). For tropical species, egg development may last from 3 to 5 days (Gladstone, 2007; Thresher, 1984) and egg susceptibility to predation may be influenced by the quality of parental care, quality of nests and/or abundance of predators (Esmlie & Jones, 2001).

Although there is a significant body of literature on damselfish reproductive ecology (Sikkel & Petersen, 1995; DeMartini & Sikkel, 2006) and the influence of geographic isolation on their dispersal and connectivity patterns (Hogan *et al*., 2012; Tenggardjaja *et al*., 2016), no studies to date have examined intraspecific variations in damselfish reproductive traits as a function of the degree of geographic isolation by comparing multiple sites. This is because data for damselfish populations endemic to small and isolated oceanic islands are scarce (*e.g*., Asoh, 2003; Tyler III & Stanton, 1995). Such information has important implications for understanding population persistence, as greater geographical isolation may promote the selection of reproductive traits that favour self-recruitment (Robertson, 2001; Swearer *et al*., 1999, 2002).

Many studies report on the influence of the lunar cycle on the reproductive activity of damselfish (*e.g*., Foster, 1987; Mizushima *et al*., 2000). Explanations on the adaptive value of lunar synchronicity include (1) decreased offspring predation due to low light levels in the new moon, (2) increased chance of meeting a reproductively active mate with which to breed during collective spawning triggered by moon phase, (3) increased protection against predators due to crowding effects and (4) greater dispersal potential after hatching due to relatively large tidal amplitude (Gladstone, 2007; Robertson *et al*., 1990).

Predation appears to play a key role in the spawning of damselfishes. For example, male courtship behaviour may be diminished in the presence of piscivores and egg predators (Figueira & Lyman, 2007). In addition, males protecting nests with eggs spend more time in agonistic interactions than nonguardian males, particularly when intruders are egg predators (Haley & Muller, 2002; Itzkowitz, 1990). Finally, levels of aggressiveness may increase according to the number of egg predators attempting to enter the territory and the number of clutches within a nest (Itzkowitz, 1990; but see Haley & Muller, 2002).

The Saint Paul's Gregory, *Stegastes sanctipauli* Lubbock & Edwards 1981, is a damselfish endemic to the remote St Peter and St Paul's Archipelago (SPSPA), Mid Atlantic Ridge, Brazil (Pinheiro *et al*., 2018, 2020). Despite the genetic similarities between *S. sanctipauli* and *Stegastes rocasensis* (Emery, 1972) (Souza *et al*., 2017), the geographic specificity and colour differences between them still warrants their discrimination (Pinheiro *et al*., 2018, 2020). Both male and female *S. sanctipauli* are territorial and females lay benthic adhesive eggs that are defended by the guardian male until hatching (pers. obs.). *Stegastes sanctipauli* is amongst the most abundant reef fish species in the SPSPA (Luiz *et al*., 2015; Rosa *et al*., 2016), feeding mostly on turf algae, but also opportunistically preying on benthic invertebrates and plankton (Feitoza *et al*., 2003) and acting as a cleaner when juvenile (Gasparini *et al*., 2008).

Our main goal here was to determine the main correlates of reproductive success of *S. sanctipauli* in the SPSPA, using daily rates of egg losses during a spawning season as a proxy. We specifically evaluated (1) the biotic and abiotic correlates of the spatial distribution of nests and the number of clutches within nests, (2) the relative contribution of different attributes of the guardian males and nests on egg predation risk, (3) the identity of egg predators and (4) the main correlates of egg loss during a spawning season. Based on studies of other damselfish species with similar social structure, we expected a strong synchronicity in spawning, which can enhance components of fitness of both adult and larval fish (Doherty, 1983; Gladstone, 2007; Robertson *et al*., 1990). We also expected that nests located in areas with higher predation risk for both adults and eggs, due to higher abundance of predators and lower benthic complexity, will experience greater egg losses. While larger nests may be more attractive to females and thus harbour more clutches, they may also be more attractive to egg predators. To mitigate egg predation risk, guardian males may become more aggressive towards intruders, at the cost of decreased foraging rates. Finally, larger males may harbour greater numbers of clutches within their nests and experience lower rates of egg loss. Our results offer insights into the ecological processes influencing the spawning success of a damselfish endemic to one of the smallest and most isolated tropical oceanic reef systems of the world, where local reproductive success and self-recruitment may be critical for population persistence (Macedo-Soares *et al*., 2012; Robertson, 2001; Swearer *et al*., 1999).

2 | MATERIALS AND METHODS

The study procedures complied with Brazilian animal welfare laws, guidelines and policies as approved by permit SISBIO 41583–1.

2.1 | Study area

The SPSPA is a small group of five islets and rocky points (total emerged area ~15,000 m^2) located in the central equatorial Atlantic Ocean, along the Mid Atlantic Ridge and about 1000 km off the north-east Brazilian coast (Edwards & Lubbock, 1983). The SPSPA is located in a tectonically active region and was formed by uplift of the oceanic mantle (Campos *et al*., 2010). The islets of Belmonte, St Peter, St Paul and Barão de Teffe are separated by narrow channels, forming a bay with depths <30 m (Edwards & Lubbock, 1983; Magalhães *et al*., 2015) (Figure 1). Sampling was performed in the bay using SCUBA in depths ranging from 0 to 30 m during 45 days of fieldwork (September 2010, May/June 2011 and August 2011).

2.2 | Data collection

Fish abundance, including potential damselfish and egg predators, was estimated using nested stationary visual censuses (cf. Minte-Vera *et al*., 2008). A total of 35 samples were obtained along the 0–30 m depth gradient between 09:00 and 16:00 h. Abundance of nests was

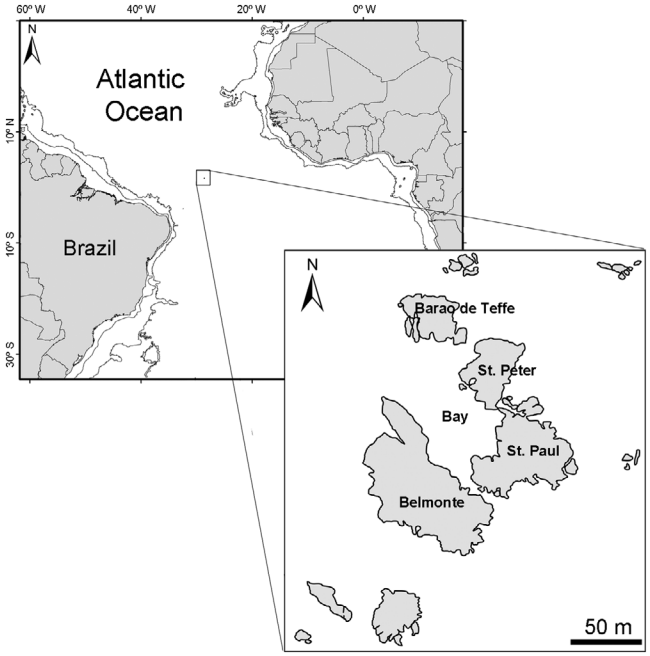

FIGURE 1 Location of the St Peter and St Paul's Archipelago in the Central Atlantic Ocean and insert showing the study area (bay)

simultaneously estimated with fish counts through intensive search within the 4 m radius for 5 min soon after the end of the fish counts. Three piscivorous species (*Caranx lugubris* Poey, 1860, *Muraena pavonina* Richardson, 1845 and *Rypticus saponaceus* Bloch & Schneider, 1801) were classified as potential predators of *S. sanctipauli* adults based on literature data (Almany, 2004; Luiz *et al*., 2015) and personal observations. Egg predators were identified by the experimental exposition of eggs to predators through the translocation of individual clutches laid in small unattached rocks away from the guardian male territory ($n = 5$ clutches exposed for 10 min at ~10 and 20 m depth).

Substrate complexity was estimated using a 40 cm long stick that was rotated following all contours of the substrate through a linear distance of 4 m within each stationary visual census plot (based on the methodology outlined by Wilding *et al*., 2007). The absolute number of rotations was used as a measure of complexity, with increased number of rotations indicating greater complexity.

A total of 34 nests between 4 and 27 m depth were marked with numbered plastic tags fixed to the nearby substrate and monitored along the lunar cycle. Sampling included sequential digital planar photographs of clutches to estimate egg density, and observational sessions of 5 min to evaluate the time spent in different activities by the guardian male (see below). Each nest was photographed at least three times on different days along a spawning season with the use of an adjacent ruler for scale. Total nest area was estimated using eCognition Developer software. Nests of *S. sanctipauli* are prepared by the guardian male by cleaning the substrate (*i.e*., removing bryozoans and macroalgae) and are composed mostly by red epilithic algae, crustose calcareous algae and/or bare rock (Figure 2a). Based on authors' observations of egg colour, individual clutches were classified as new (white egg, generally 1 day old), intermediate (grey eggs, 2–3 days old) or old (semi-transparent eggs, 4–5 days old) (Figure 2a).

Preliminary observations indicated differences in egg density between central and peripheric portions of the clutches. Thus, egg density was estimated in the digital images by counting all eggs in four 1 cm^2 squares projected within each clutch, two of them allocated in the clutches' centre and two in the periphery (*i.e*., at least 1 cm away from the clutches' edges; adapted from Esmlie & Jones, 2001). Sequential images (three to five images taken along 4–5 days) obtained from spawning to hatchling for the 34 clutches allowed us to calculate daily rates of egg loss.

The 5 min observation sessions ($n = 121$) focused on the behaviours performed by males guarding the same nests for which egg density/loss were estimated. Samples were obtained in three periods of the day: dawn (05–07 h, $n = 33$), midday (08–16, $n = 51$) and dusk (17–18 h, $n = 37$). The following information was recorded: (1) maximum distance travelled from the nest by the male, (2) number of bites given by the male on the nearby substrate, on its own nests and/or on planktonic items, (3) number of intra- and interspecific agonistic interactions and (4) level of nest access to potential predators (low, medium and high) and nest inclination (in degrees). Nest access and inclination were visually estimated. Nests characterized by low access were less exposed to predators (*e.g*., within crevices), while nests with high access were more exposed (*e.g*., planar surfaces with low complexity).

We used raw data from photo-quadrats collected by R.B.F.F. and previously published (Magalhães *et al*., 2015) for evaluating the bathymetric distribution in turf algae abundance.

2.3 | Data analysis

Boosted regression trees (BRT) (Buston & Elith, 2011; Elith *et al*., 2008) were used for evaluating the relative effect of the independent variables (see Table 1 for details) on the abundance of nests, number of clutches per nest, frequency of agonistic interactions and daily rates of egg loss. The BRT approach is based on the combination of a large number of simple regression trees (in which predictions are based on recursive binary splits) using the boosting technique for improving model accuracy. A new tree is fitted for the residuals from the previous model at each step, aiming to reduce the loss function. Only a subset of the original data, set at random, is used at each step. The most important attributes of BRT models are (1) bag fraction (proportion of data selected to fit a tree at each step), (2) learning rate (contribution of each tree to the overall model explanation) and (3) tree complexity (number of nodes of each tree) (Elith *et al*., 2008). Optimal BRT models, that is, the ones with lowest values of cross-validation (CV) deviance and standard error, were selected by examining all possible combinations of values for bag fraction = 0.5 and 0.75, learning rate = 0.001, 0.005, 0.01 and 0.05, and tree complexity = 1 to 5 (cf. Elith *et al*., 2008). Only the five most important variables for each model were considered as they represented

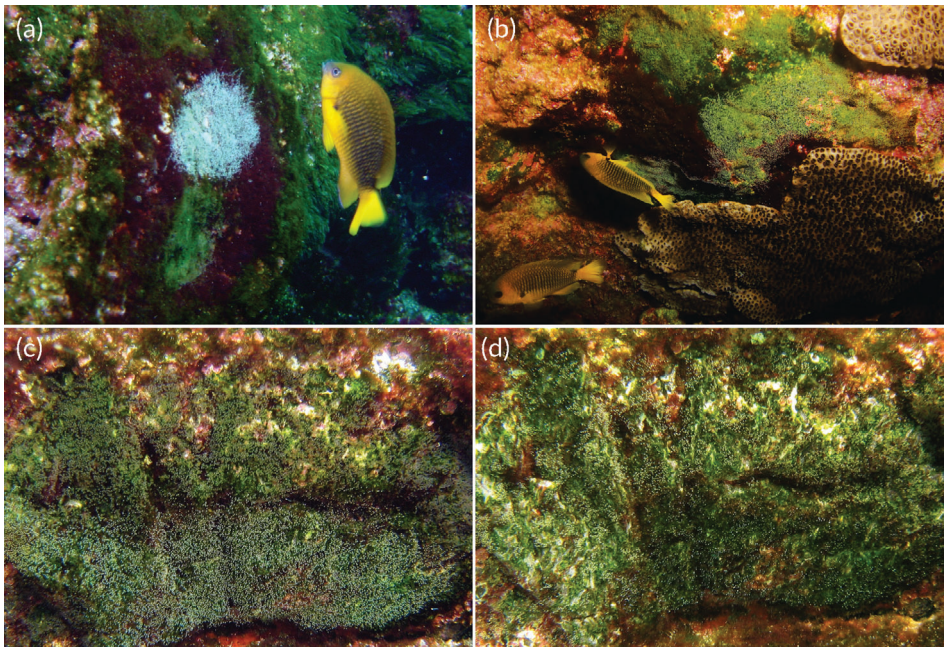

FIGURE 2 Images showing (a) a guardian male of *Stegastes sanctipauli* defending its nest (area dominated by red epilithic algae) with two clutches (a newer clutch with white eggs in the upper portion of the nest and an older one in the lower portion), (b) a female of *S. sanctipauli* laying its eggs in a nest at dawn (note guardian male in the left lower portion of the image), (c) a clutch with recently laid eggs and (d) the same clutch shown in (c) after predation, with bite scars typical of *Halichoeres radiatus*

TABLE 1 Predictors used in boosted regression trees models aimed at explaining abundance of *Stegastes sanctipauli* nests across a depth gradient (*N*), number of clutches per nest (NC), frequency of agonistic interactions between guardian males and egg predators and daily rates of egg loss (EL)

	Model			
Predictors (units)	**N**	**NC**	**AI**	**EL**
Environmental variables				
Depth (m)	x	x	x	x
Substrate complexity (dummy codded)	x			
Nest access (dummy codded)		x	x	x
Nest size (cm^2)		x	x	x
Nest slope (°)		x	x	x
Biotic variables				
Abundance of conspecifics ($individuals.m^{-2}$)	x			
Abundance of egg predator ($individuals.m^{-2}$)	x			
Abundance of damselfish predators ($individuals.m^{-2}$)	x			
Agonistic interaction ($number.5\ min^{-1}$)		x		x
Bites on plankton/substrate ($number.5\ min^{-1}$)		x	x	x
Bites on own eggs ($number.5\ min^{-1}$)		x	x	x
Mean distance travelled from nest ($cm.5\ min^{-1}$)		x	x	x
Fanning behaviour ($number.\ 5\ min^{-1}$)		x	x	x
Hiding behaviour ($number.\ 5\ min^{-1}$)		x	x	x
Initial egg density ($egg.cm^{-1}$)			x	x
Male body size (cm; total length)		x	x	x
Temporal variables				
Moon phase		x	x	x
Period of day			x	

Note: See text for more details.

85%–100% of the total models' explanation and the remaining variables showed weak to no patterns. All models were fitted based on a Gaussian distribution using the package gbm (version 1.5–7) in R version 3.5.1 (R Core Team, 2021).

3 | RESULTS

Guardian males of *S. sanctipauli* with nests within their territory were commonly observed during the entire sampling period. The size of the

TABLE 2 Optimal settings and predictive performance of boosted regression trees (BRTs) used for modelling nest abundance, number of clutches per nest, frequency of agonistic interactions and egg loss for *Stegastes sanctipauli*

	Optimal settings					
BRT model	***lr***	***bf***	***tc***	**Number of trees**	**CV deviance (±S.E.)**	**CV correlation (±S.E.)**
Nest abundance	0.005	0.8	4	1000	0.072 (0.012)	0.251 (0.188)
Number of clutches	0.01	0.5	3	1150	0.014 (0.003)	0.677 (0.047)
Agonistic interactions	0.005	0.25	4	1000	0.091 (0.006)	0.238 (0.086)
Egg loss.day^{-1}	0.5	0.8	3	500	0.092 (0.025)	0.887 (0.07)

Abbreviations: CV, cross-validation; S.E., standard error.

monitored males ranged between 7.3 and 10.6 cm total length (TL) and their nests occurred on flat and nearly vertical surfaces (mean inclination = 93.7 ± S.E. 1.85 degrees) and were mostly surrounded by turf algae and/or the zoantharian *Palythoa caribaeorum* Duchassaing & Michelotti, 1860 (Figure 2a,b).

All spawning events ($n = 29$) recorded during observation sessions occurred at dawn (05–07 h; Figure 2b). A single event of two females spawning simultaneously within the same nest was recorded. Females left the nests soon after spawning, while males remained protecting the eggs during the entire period of embryonic development. One to six clutches were recorded per nest (mean = 2.06 ± S.E. 0.1). Parental care included defending the nest against potential egg predators and fanning of eggs by beating pectoral fins close to the clutch surface. Egg hatching occurred 4–5 days after spawning.

3.1 | Correlates of nest abundance and number of clutches per nest

Optimal settings and predictive performance of all BRT models are given in Table 2. Depth was by far the most important variable influencing nest abundance (49.7% of the model explanation), with nests concentrated in depths <16 m. A positive relationship between nest abundance and egg predator abundance was recorded (18.4% of the model explanation), indicating the spatial co-occurrence of nests and egg predators in shallow reefs. The other three variables (*S. sanctipauli* abundance, abundance of damselfish predators and benthic complexity) explained <2% of nest abundance (Figure 3a).

The number of clutches per nest peaked in the last quarter moon (17.4% of the model explanation) and was positively influenced by nest size (27.2%) and depth (11.8%), sharply increasing for nests >160 cm^2 and in depths >12 m. Surprisingly, the number of clutches decreased as male body size increased, particularly above 9.5 cm TL (Figure 3b).

3.2 | Correlates of agonistic interactions and identity of egg predators

During observation sessions, a total of 456 agonistic interactions between guardian males and other fish were recorded, including 14 species: *S. sanctipauli* ($n = 293$), *Azurina multilineata* (Guichenot, 1853) ($n = 69$), *Malacoctenus* sp. ($n = 34$), *Abudefduf saxatilis* (Linnaeus, 1758) ($n = 21$), *Halichoeres radiatus* ($n = 16$), *Ophioblennius trinitatis* Miranda-Ribeiro, 1919 ($n = 8$), *M. pavonina* ($n = 4$), *Melichthys niger* (Bloch, 1786) ($n = 3$), *Emblemariopsis* sp. ($n = 2$), *Myripritis jacobus* Cuvier, 1829 ($n = 2$), *Bodianus insularis* Gomon & Lubbock, 1980 ($n = 1$), *C. lugubris* ($n = 1$), *Chaetodon striatus* Linnaeus, 1758 ($n = 1$) and *Holacanthus ciliaris* (Linnaeus, 1758) ($n = 1$). Amongst the three kinds of agonistic behaviour recorded, chasing (87.5%) was the most common, followed by lateral display (10.5%) and bites (2%).

The frequency of agonistic interactions was mostly explained by nest size (26.1% of the model explanation), with a consistent increase in the number of interactions for nests larger than 100 cm^2. Moon phase was the second most important explanatory variable (23.1%), with higher rates of agonistic interactions in the last quarter and new moons. Foraging rates declined with increased frequency of agonistic interactions (19.9%) and slightly increased (12%) for males travelling farther from their nest (Figure 3c).

Four egg predators were identified in the clutch exposure experiment: *H. radiatus* ($n = 102$ bites), *C. striatus* ($n = 51$ bites), *M. niger* ($n = 43$ bites) and *H. ciliaris* ($n = 12$ bites). *H. radiatus* was the species that left most prominent scars, similar to those recorded during the photographic monitoring of clutches (Figure 2c,d). Although predation scars were prevalent and predation was clearly the most important process influencing egg loss, no successful event of egg predation was witnessed during the observation of nests.

3.3 | Spawning success and correlates of egg losses

Global daily rate of egg losses was estimated at 19.6 ± S.E. 5.6%, with no nest exhibiting 100% embryo survival until hatchling. Old semi-transparent eggs were the most frequently consumed. Moon phase was the most important predictor of egg losses (50.6% of the model explanation), with the highest rates of egg losses recorded in the last quarter (mean egg loss = 33.1%), followed by new moon (mean egg loss = 17.1%). Rates of egg losses increased according to the initial density of eggs (29.1% of the model explanation) and nest size (12%), with higher losses recorded for clutches >150 eggs cm^{-2} and for nests

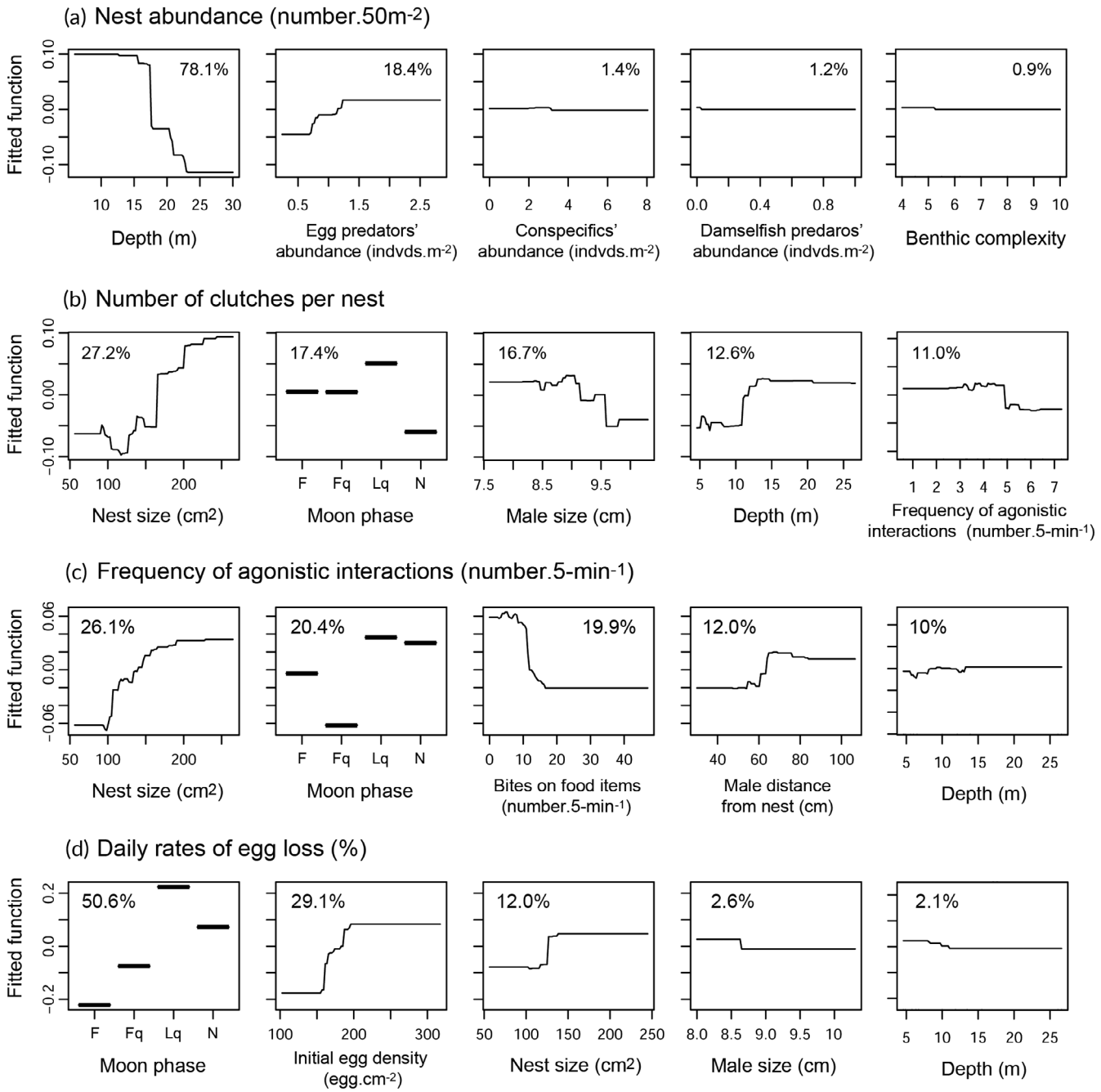

FIGURE 3 Partial dependence plots for the five most important variables for boosted regression tree models predicting (a) nest abundance, (b) number of clutches per nest, (c) frequency of agonistic interactions and (d) daily rates of egg loss. *y* axes are centred to have zero mean over the data distribution

>125 cm^2. Other explanatory variables showed negligible influences (Figure 3d).

Male *S. sanctipauli* were observed preying on their own eggs 646 times during the study (mean = 5.33 ± S.E. 0.61 bites per observational session). Some bites were directed to apparently dead eggs (generally concentrated in the edges of clutches), but most bites focused on apparently live eggs (*i.e.*, filial cannibalism). The presence of eggs in the gut contents of *S. sanctipauli* corroborates this result (M.B. Lucena et al., unpublished data). Filial cannibalism showed a small influence on daily rates of egg losses, with no clear pattern (<2% of the model explanation).

4 | DISCUSSION

The spawning activity of *S. sanctipauli* was concentrated in the last quarter moon and, after an embryonic development of about 5 days, hatching of eggs occurred close to the new moon. This is a period of

low light levels and high tidal amplitude. Our observations indicate that hatching occurred at night, a common pattern for most damselfishes (*e.g.*, Alcalay & Sikkel, 1994; Doherty, 1983; Foster, 1987) and corroborated by the predominance of *S. sanctipauli* larvae at night around the SPSPA (Macedo-Soares *et al.*, 2012). Hatching of eggs on dark nights may attenuate predation pressure by visually oriented planktivorous fish over *S. sanctipauli* fry (Alcalay & Sikkel, 1994; Johannes, 1978). In addition, *S. sanctipauli* is the most abundant species in the ichthyoplankton around the SPSPA, with larvae recorded as far as 2 km away from the archipelago (Macedo-Soares *et al.*, 2012). Larval dispersal away from reef predators may be facilitated by tidal currents close to the new moon and enhance larval survival in the first hours/days after hatching (Doherty, 1983; Foster, 1987; Johannes, 1978). It is important to note that planktivores dominate fish assemblages of the SPSPA (Luiz *et al.*, 2015), which may enhance the selective pressure over reproductive traits that maximize larval dispersal away from reef predators soon after hatching (Foster, 1987). Finally, higher tidal amplitude during new/full moons leads to higher nutrient concentrations in the waters of the SPSPA, possibly due to flushing of water from the surrounding emergent rocks saturated with guano from seabirds (Moreira *et al.*, 2015). This could be an additional energetic source increasing algal productivity and the nutritional condition of adult *S. sanctipauli*, thus potentially influencing spawning synchronicity. Similarly, a previous study showed that increased food abundance due to stream discharge triggered the spawning activity of *Abudefduf abdominalis* (Quoy & Gaimard, 1825) in Hawaii (Tyler III & Stanton, 1995).

The lunar synchronicity in spawning may also confer advantages to adults by increasing their chances of finding a reproductively active mate with which to breed during collective spawning and by conferring increased protection against fish and egg predators due to crowding effects (Foster, 1987; Johannes, 1978; Robertson *et al.*, 1990). In fact, *S. sanctipauli* seems to form breeding colonies similar to those reported for other damselfishes, which are believed to maximize the adaptive advantages of collective spawning (*e.g.*, Foster, 1989; Gross & McMillan, 1981).

Spawning by *S. sanctipauli* occurred exclusively at dawn. A similar pattern has been recorded for many other damselfish species, such as *A. saxatilis* and *Microspathodon chrysurus* (Cuvier, 1830) the Caribbean (Foster, 1987; Sikkel & Kramer, 2006), *Abudefduf troschellii* (Gill, 1862) in the Pacific (Foster, 1987) and *Pomacentrus chrysurus* Cuvier, 1830 and *Pomacentrus wardi* Whitley, 1927 in the Indo-Pacific (Doherty, 1983). In addition, spawning activity of the damselfish *Amblyglyphidodon leucogaster* (Bleeker, 1847) occurs during the day, but peaks at dawn (Goulet, 1997, 1998). Territorial female damselfish may spawn at dawn as a strategy to reduce intrusion rates from diurnally active species searching for food inside their territories (Sikkel, 1995b, 1998). One alternative explanation is that spawning by dawn may decrease damselfish predation risk due to lower light levels (Albrecht, 1969; Doherty, 1983; Johannes, 1978). However, abundance of damselfish predators had no influence on the spatial distribution of *S. sanctipauli* nests (see Figure 3a), suggesting that factors other than adult predation risk may play a role in the daily timing of *S. sanctipauli* spawning.

New *S. sanctipauli* clutches appeared mostly in the last quarter moon, when egg predation intensity, as inferred by rates of agonistic interactions and egg losses, intensified. Our clutch exposure experiment suggests that the puddingwife wrasse *H. radiatus*, one of the most abundant reef fish species in the SPSPA (Luiz *et al.*, 2015), is the main predator of *S. sanctipauli* eggs. The other three egg predators identified during our experiments include *C. striatus*, *M. niger* and *H. ciliaris*. The former is relatively rare in the SPSPA (Luiz *et al.*, 2015), while *M. niger* and *H. ciliaris* are more abundant on deeper reefs (Rosa *et al.*, 2016; Figure 4). In addition, eggs are minor components in the *M. niger* diet and are absent from the *H. ciliaris* diet in the SPSPA (Mendes *et al.*, 2019; Reis *et al.*, 2013). In contrast, damselfish eggs are amongst the most frequent food items and are the most important items in terms of weight in the diet of *H. radiatus* in the SPSPA (Lucena *et al.*, 2022). Other wrasse species, such as *Thalassoma pavo* and *T. lunare*, are also major predators of damselfish eggs in the Mediterranean (Milazzo *et al.*, 2006) and Great Barrier Reef (Esmlie & Jones, 2001). Although no successful attempt of egg predation was witnessed during the behavioural observation sessions, clear and relatively big bite scars were frequently recorded in the photographic monitoring of clutches (see Figure 2d). Such scars were plausibly not caused by *S. sanctipauli* and were similar to those left by *H. radiatus* during the egg exposure experiments. In addition, according to our BRT model, filial cannibalism intensity had no influence on egg losses. These results corroborate previous studies showing that predation by invaders, and not filial cannibalism, is the main source of damselfish egg losses (Esmlie & Jones, 2001).

Egg predation may have occurred at late dusk, early dawn and/or night periods, when guardian males are still inactive and sheltered, and thus unable to defend their nests. Nocturnal/crepuscular damselfish egg losses due to unknown predators were previously recorded for *Stegastes dorsopunicans* (Poey, 1868) in the Caribbean (Petersen, 1990; Petersen & Hess, 1991). Considering that (1) *H. radiatus* is mostly active during the day (Lucena *et al.*, 2022), (2) predators of *S. sanctipauli* eggs apparently select nests with higher food availability based on chemical and/or visual cues (*i.e.*, larger nests with higher density of eggs) and (3) *S. sanctipauli* spawning occurs mostly on dark nights (few days before the new moon), we speculate that egg predation occurs mostly at late dusk/early dawn, when there is still some light, instead of the night period. Clearly, additional studies are needed to identify daily patterns and main sources of damselfish egg predation in the SPSPA and elsewhere.

Territories and nests of *S. sanctipauli* were concentrated in the shallowest zone of the SPSPA (0–20 m depth), where abundances of the main food resources for adult *S. sanctipauli* (turf algae) and densities of *H. radiatus* were highest (Figure 4). This pattern suggests that the spawning activity of *S. sanctipauli* is governed by the trade-offs between food accessibility by adults and egg predation risk. The decline in male foraging rates with increased frequency of agonistic interactions corroborate this hypothesis and indicates that the necessity to defend a nest during the embryonic development could lead to detrimental effects on the nutritional condition of the guardian male. In this context, filial cannibalism may represent an important diet

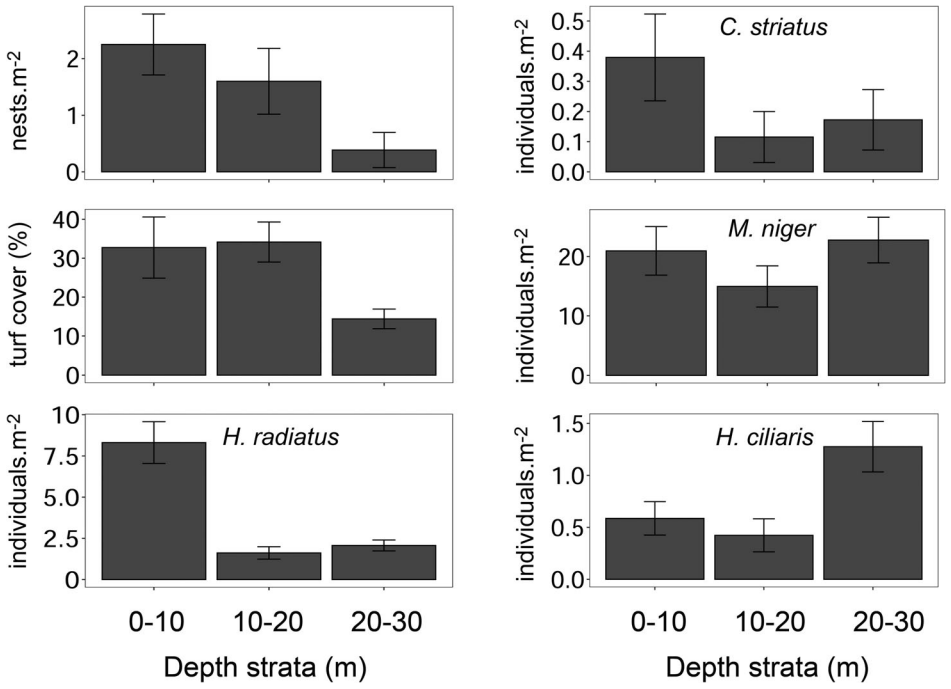

FIGURE 4 Nest abundance, turf algae cover and egg predator abundance across the depth gradient of the St Peter and St Paul's Archipelago

supplementation. In general, cannibalism in damselfish is focused on poor quality eggs, thus maximizing energy reallocation for future partners (Esmlie & Jones, 2001; Nematov & Clark, 1994; Petersen, 1990) and emptying space for new eggs to be laid (Sikkel, 1994). Filial cannibalism by *S. sanctipauli* was a relatively common ($n = 646$ event recorded during observation sessions; M.B. Lucena et al., unpublished data on *S. sanctipauli* stomach contents), suggesting that the burden of parental care may be compensated by an increase in filial cannibalism. It is worth noting that daily rates of egg losses were relatively high in our study system, with a global value of 19.6% and the highest value of 33.1% for the last quarter moon. The highest rates of egg mortality previously recorded for damselfish were for *Pomacentrus amboinensis* Bleeker 1868 in the Great Barrier Reefs (26%–69%), where predation by heterospecifics was identified as a major source of egg morality (Esmlie & Jones, 2001). Thus, for systems in which egg predators are prevalent, embryo mortality prior to hatching could be a major bottleneck in population persistence (Esmlie & Jones, 2001).

A larger number of clutches per nest was recorded for smaller *S. sanctipauli* males in the deeper zones (15–30 m) of the SPSPA, where the abundances of conspecifics and egg predators, as well as the frequency of agonistic interactions, were lower. Rates of egg losses were also slightly smaller for deeper reefs (see Figure 3b,c). Previous studies have shown that the spawning success of male damselfishes is unrelated to body size and mostly explained by high courtship rates. This pattern may be explained by the superior parental care provided by males with high courtship rates through unknown mechanisms (Knapp & Warner, 1991; Petersen, 1995). We hypothesize here that the smaller and less energy-demanding males of *S. sanctipauli* may counteract the intense competition for optimal food resources in shallow reefs by allocating territories in suboptimal microhabitats at deeper reefs (Pimentel *et al*., 2022). Such small males may be able to provide more efficient parental care due to less time spent defending their territory/eggs and thus be preferred by females.

We showed here that *S. sanctipauli* has evolved strategies to maximize offspring survival in a system where predation over eggs and fry is intense. This is particularly important when considering that reproductive success and self-recruitment may be critical for the local population persistence in the small and isolated SPSPA (Robertson, 2001; Swearer *et al*., 1999). Hatching of eggs in days close to the new moon may attenuate predation impacts over new fry due to reduced light levels and increased larval dispersal away from the reef by tidal currents. The spatial allocation of nests on shallow reefs, where main food resources for *S. sanctipauli* adults (turf algae) are concentrated, is accompanied by the trade-off of increased egg predation risk due to higher abundances of egg predators, particularly *H. radiatus*. Such increased egg predation risk is counteracted by increased aggression by the guardian males towards intruders, at the expense of decreased foraging rates. Finally, our study provides additional evidence for the key roles played by *S. sanctipauli* on the trophodynamics of the SPSPA through the transfer of biomass to higher trophic levels *via* intense egg and larval production (Lucena *et al*., 2022; Macedo-Soares *et al*., 2012).

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