



Different environmental drivers influence the reproduction of a tropical sponge (*Tedania ignis*) along a latitudinal gradient

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ABSTRACT: The life history of marine invertebrates is intrinsically related to the environmental conditions of their habitats. However, the effect of environmental factors on life history traits, e.g. reproduction, is poorly understood due to difficulties in cultivating these animals in controlled conditions. Natural experiments, using latitudinal gradients, provide an alternative to better understand this relationship. We investigated the effect of environmental factors on some aspects of the reproduction of *Tedania ignis* (Porifera, Demospongiae) along a latitudinal gradient in the Western Atlantic Ocean (WAO). We assessed the predicted trade-off between size and fecundity and biogeographical patterns in some of the life history traits of this sponge species. Except for the southernmost population, all populations of *T. ignis* reproduced aperiodically, but their reproductive dynamics were modulated by different sets of environmental factors. Therefore, this trait seems to be a physiological adaptation to local conditions. Nonetheless, the species reproduced mainly when the temperature was above 21°C, which could be a factor limiting its distribution along the tropical WAO. We did not detect any trade-off between size and quantity of oocytes and larvae in this species. A possible explanation is that the species invests low energy in offspring in a given period, resulting in a low but continuous reproductive effort, independently of the environmental conditions. These findings will be important to support management plans, as this species is a potential target for obtaining biotechnological natural products.

KEY WORDS: Trade-off · Temperature · Western Atlantic Ocean · Thorson's rule · Demospongiae · Porifera

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1. INTRODUCTION

Life histories of marine invertebrates are intrinsically related to the environment they inhabit. Changes

in physicochemical and biological aspects of an organism's surroundings will influence its phenology and several physiological activities (Stearns 1976, Mercier & Hamel 2009). Therefore, to better comprehend the

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impact that a changing world will have on populations of marine invertebrates, studies focussing on how the environment regulates different aspects of their life history are important. Investigations on the effect of environmental factors (e.g. seawater temperature, rainfall, photoperiod, etc.) on a given life history trait require refined experimental designs to control the variable(s) being examined. Although some advances have been made in the last decades (e.g. Fell et al. 1989, Smart et al. 2012, Ramsby et al. 2018), most invertebrates occurring in the oceans are difficult to maintain in laboratory conditions, and developments in this area still rely on field observations or experimentation (Underwood et al. 2000, Scrosati & Ellrich 2016, Lanna et al. 2018). Examples of natural experiments include investigations into long-term data series, in which some environmental factor is related with the biological aspect being examined (e.g. Ben-David-Zaslow et al. 1999, Scrosati & Ellrich 2016, Ramsby et al. 2017). Additionally, shorter investigations across wider spatial distributions, especially across different locations that present distinct climate conditions, are also important to understand the effect of the environment on the life history of marine invertebrates. This could be exemplified in investigations along latitudinal gradients with species presenting wide distributions (e.g. Lardies & Castilla 2001, O'Connor 2002, Wakefield et al. 2015, Baldanzi et al. 2018, Oyarzún et al. 2018). This type of study can provide strong evidence, for example, for the minimal temperature for the onset of reproduction, how temperature influences aperiodic vs. episodic reproductive patterns, and on the reproductive output (fecundity) of the population (e.g. O'Connor 2002, Baldanzi et al. 2018).

Sponges (Porifera) are among the groups of marine invertebrates that are difficult to maintain in tanks (Osinga et al. 1999). They are one of the most abundant and important groups of the benthos. Sponges can play many ecological roles; for example, they couple benthic–pelagic resources, participate in nutrient cycles, filter bacteria and many other small particles, are food sources, and provide refuge to different organisms (Wulff 2006, Becerro 2008, de Goeij et al. 2013). In addition, they are relevant from a biotechnological point of view, as they provide several natural products that have potential to be used in pharmacology and other areas (Evans-Illidge et al. 2013). As these animals lack organs (and thus no endogenous system controls their activities), the majority of their physiological activities are usually associated with fluctuations in the environment (Maldonado & Riesgo 2008, Riesgo & Maldonado 2008, Lanna et al. 2015,

2018). Therefore, to better predict sponge population dynamics and their adaptations to the environment, it is important to understand how poriferans control their reproduction. Understanding this central life history trait is particularly key in planning conservation agendas or to plan better extraction protocols to obtain sponge extracts for natural products. For instance, this knowledge is important to define periods of no-take in natural populations during the reproductive cycle of the species, as is usually used in sustainable fisheries (e.g. Walker 2005).

The reproduction of few species of sponges has been investigated across a wide geographical range. Fell (1974, 1976) investigated the reproduction of *Chalinula loosanoffi* (Hartman, 1958) in different locations along the south coast of the USA and observed that water temperature plays an important role in controlling reproduction of that species. Similar findings were observed for *Halichondria panicea* (Pallas, 1766) in the North Sea. Populations investigated in 3 different locations ranging over 4.5° of latitude presented higher reproductive activity in warmer months, while different salinities in those locations had no effect on its reproduction (Witte et al. 1994). The reproduction of *Paraleucilla magna* Klautau, Monteiro & Borojevic, 2004 was studied in Rio de Janeiro (Brazil) and on the southern Italian coast (ranging more than 63° of latitude) (Longo et al. 2012, Lanna et al. 2015). In this case, instead of determining when the sponges should start reproducing, temperature could be modulating the fecundity of the species (Lanna et al. 2015). However, none of these studies was carried out investigating different populations at the same time and/or using the same methodology. Therefore, a study applying the same methodology to collect, process, and obtain data about the reproduction of a species with broad distribution, and applying the same statistical treatment, will be valuable to better comprehend the effect of the environmental factors on the life history traits of sponges.

The poecilosclerid demosponge *Tedania ignis* (Duchassaing & Michelotti, 1864) has a wide distribution along the coast of the Western Atlantic Ocean, being found in shallow waters from Bermuda (ca. 33.3° N) to Santa Catarina State (Brazil, ca. 27.6° S), more than 8000 km apart (Muricy et al. 2011). This species is known as the fire-sponge, as it can harm the skin when touched, causing dermatitis in humans. The chemical causing such rashes is still unknown, but it is probably related to tedanolide, a potent cytotoxic molecule (Costantino et al. 2009). This species has been targeted for several studies about its chemistry, microbiology, and pharmacology along the

Brazilian coast and the Caribbean (e.g. Costantino et al. 2009, Muricy et al. 2011). Several studies have investigated different aspects of the ecology of *T. ignis* (e.g. Bingham & Young 1991, Leite et al. 2016, Oliveira & Lanna 2018). Moreover, some aspects of the reproduction of *T. ignis*, such as its mode of reproduction, ultrastructure of spermatogenesis, and the larvae, were also investigated previously (Jaeckle 1995, Lanna et al. 2018, Vasconcellos et al. 2019). Maldonado & Young (1996) investigated the presence of embryos/larvae in the tissue, the larval behaviour, settlement, and survival of *T. ignis* at Fort Pierce Inlet (Florida, USA; 27.0° N). The Florida population brood embryos and spawn larvae asynchronously from April to late August, especially when the water temperature is higher than 25°C. The population of Salvador (Bahia, Brazil; 13.0° S) was constantly reproductively active, with embryos being found at low densities and low frequencies in the population during the whole year. In Salvador, different combinations of environmental factors seem to control the dynamics of gametes and embryos of *T. ignis* (Lanna et al. 2018). Therefore, as this species has a wide geographical distribution, and information about its biology is already available, it provides a good model to investigate ecological and evolutionary aspects of the life history of sponges.

The aim of the present work was to investigate a set of reproductive traits of *T. ignis* along a latitudinal gradient ranging from 8° to 28° S along the Brazilian coast covering 2 distinct biogeographical provinces (Tropical Southwestern Atlantic and Warm Temperate Southwestern Atlantic, Spalding et al. 2007). In addition, we are using this large data set to answer questions related to life history strategies along a gradient of latitude, as many life history traits are expected to covary with this gradient (Marshall & Burgess 2015, Barneche et al. 2018, Reed et al. 2021). We investigated the trade-offs between quantity and size of the propagules (a proxy for the quality of oocytes and larvae, Moran & McAlister 2009) of the species. We also investigated if the life history traits presented patterns related to biogeography along a latitudinal gradient, i.e. is there a minimal temperature for the reproduction of the species that could delimit its distribution? Are Rass's and Thorson's Rules, which predict larger eggs (Rass 1941) and larvae (Thorson 1950), respectively, at higher latitudes true for the species?

Put together, our findings will help us understand if the phenotypic life history traits investigated here are phylogenetically constrained resulting from natural selection over time or are physiological adaptations of the population to the current environment

(Stearns 1976). Therefore, our working hypotheses were (1) the reproductive dynamics of the species are not the same in different locations; (2) the variation in the same environmental factors will modulate the dynamics of the reproductive traits of the species; (3) reproduction will be continuous (aperiodic) in the tropical populations, while it will be periodic in warm temperate populations; (4) there is a minimum temperature for reproduction; (5) there is a trade-off between quantity and quality of the reproductive propagules; and (6) the size of the propagules will increase, while their number will decrease with latitude (as expected by Rass's and Thorson's Rules).

2. MATERIALS AND METHODS

2.1. Sampling design and study sites

We collected 10 specimens of *Tedania ignis* every month from September 2014 to February 2016 in 4 different locations along the Brazilian coast: Ponta de Pedras (PPE) in Pernambuco State, Salvador (SSA) in Bahia State, Angra dos Reis (ANG) in Rio de Janeiro State, and Florianópolis (FLN) in Santa Catarina State (Fig. 1; for more details of each locality, see Text S1 in Supplement 1 at www.int-res.com/articles/suppl/m667p025_supp1.pdf). The distance between the northernmost and southernmost sampling locations was approximately 3700 km (Fig. 1). Fragments of individuals, haphazardly chosen, were collected monthly from the shallow sublittoral level (<1 m depth) on rocky shores. Parts of the data collected from the SSA population (from September 2014 to July 2015) were previously used by Lanna et al. (2018).

Samples were collected for the most part during the period of the month when the tides were the lowest in each locality. Unfortunately, due to bad climate conditions, especially in Florianópolis, or due to operational reasons, we missed collections in some months (PPE: November and December 2014; SSA: December 2015; ANG: February 2016; and FLN: June to August and December 2015, and January 2016). All specimens were fixed in saline 4% formalin for 24 h and subsequently transferred to 70% ethanol until being processed to obtain histological preparations.

2.2. Histology and reproductive output quantification

All histological procedures were performed in the same laboratory to avoid procedure biases due to

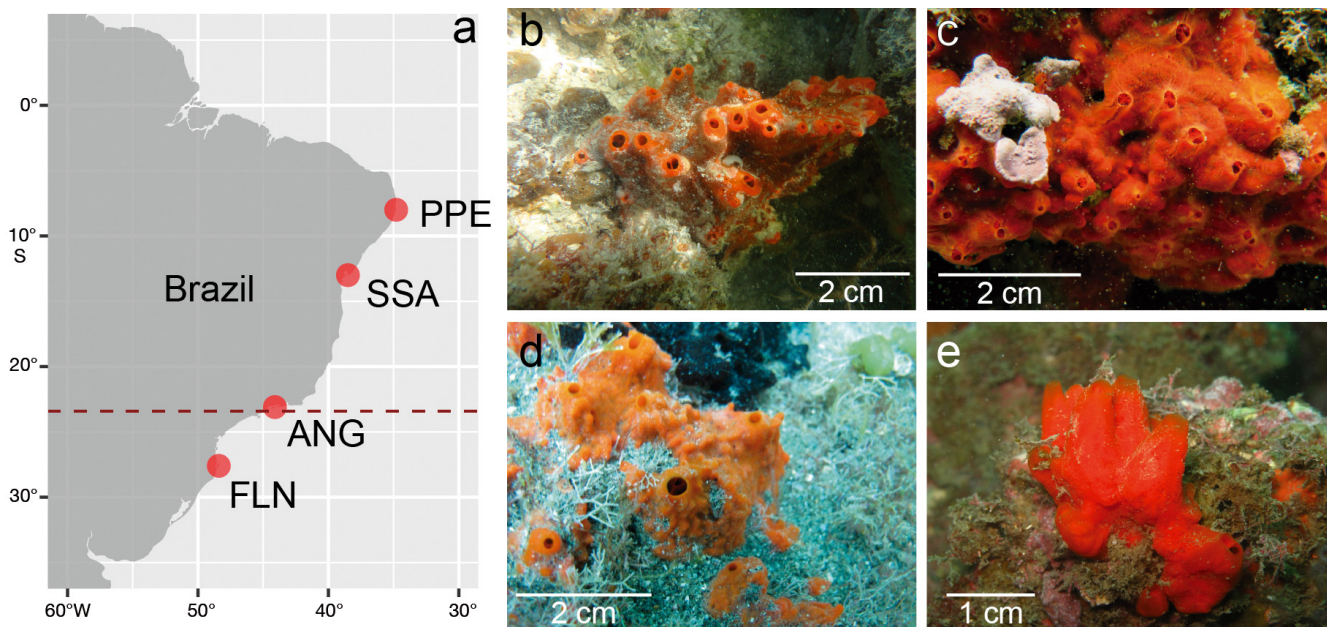


Fig. 1. (a) Sampling sites of *Tedania ignis* along the Brazilian coast. Dashed line indicates the Tropic of Capricorn. Also shown are *in situ* photographs of *T. ignis* collected in (b) Ponta de Pedras (PPE); (c) Salvador (SSA); (d) Angra dos Reis (ANG); and (e) Florianópolis (FLN)

different techniques. The spicules of the samples were removed by immersing the sponge tissue in 5% hydrofluoric acid for 6 h at room temperature. After that, the fragments were processed using standard histological techniques to stain 5 μm sections with haematoxylin and eosin (see Lanna et al. 2018 for more details). We produced 2 slides per specimen and analysed them using a light microscope to verify the reproductive status of the specimen and to quantify their reproductive effort. If any reproductive elements (gametes, embryos, and larvae) were present, the sponge was considered to be reproductively active. When estimating the percentage of the population engaged in gametogenesis, we counted the number of individuals with either male or female gametes in their choanosome. We estimated the percentage of individuals carrying out embryogenesis when the specimens were brooding embryos or larvae in the choanosome. To estimate the density of gametes (oocytes or spermatic cysts), embryos, and larvae, we took 5 non-overlapping pictures haphazardly (final magnification 100 \times in a Nikon Eclipse CI) of each specimen. The pictures were analysed using the software ImageJ (Rasband 2018) to quantify the reproductive elements in the image. We also measured the area occupied by the sponge tissue in each photograph to estimate the density (in mm^2) of the reproductive

elements in each photograph. Next, we calculated the average density ($\pm\text{SD}$) per mm^2 for each specimen. Last, to estimate the density of the reproductive elements per month, we calculated the average of the mean densities of all specimens in that month for each locality (Lanna et al. 2015, 2018).

In addition to counting the number of reproductive elements, we measured the longest length of the oocytes (usually oval and in the vitellogenic stage, see Fig. S1 in Supplement 1). Although oocyte measurements should be made preferentially when the nucleus and nucleolus are visible in the histological section to avoid measurements of the smaller top slice or edge of the oocyte, which hampers a more accurate estimate of its size, we measured oocytes irrespectively of the presence of the nucleus. This method was chosen because the oocytes in Poecilosclerida usually have a very granular cytoplasm hiding the nucleus and nucleolus. We observed few oocytes during the study, and most of them were in the vitellogenic stage with granular cytoplasm (see Fig. S1). To avoid measuring different sections of the same oocyte, we measured the longest length of the eggs in a section and then measured other oocytes after 5 sections (ca. 25 μm) of the serial histological slide. For larvae, we measured their longest length in the tissue using the same approach used for the oocytes.

2.3. Data analysis

All data sets were tested for normality and homoscedasticity prior to analysis. To examine the null hypothesis of joint variation amongst populations and to test if the reproductive output varied along the latitudinal gradient, considering the seasons and the interaction between populations and seasons, we used a generalized linear model with a Tweedie compound Poisson–gamma distribution error (Brooks et al. 2017). The Tweedie distribution best resembles the distribution of reproductive variables, since they include many zeros, and the remaining values are distributed in a compound Poisson–gamma fashion. We included as predictor variables the month and location (or population) with an interaction term. To investigate whether there is a trade-off between quantity (density) and the diameter of the propagules, we carried out linear regressions crossing these traits (density and diameter) in the same month for each population (small scale) and for the Brazilian coast as a whole (large scale). We also carried out a cross-correlation analysis to check possible delays in these relationships. In this last case, we used only the large-scale data set (i.e. all populations pooled together, ‘Brazilian coast’). We applied a generalized linear mixed model (GLMM) to test whether the environmental factors were significantly different amongst locations and seasons. Month was used as a random effect. Environmental variables were transformed to create a normal distribution and scaled before all analyses (using the package ‘normalizer’ available at <https://github.com/BrunoVilela/normalizer>).

We evaluated the effect of 5 different environmental factors on the reproduction of *T. ignis* along the latitudinal gradient: photoperiod (in min), rainfall (as mm accumulated in a month), superficial seawater temperature (hereafter referred to simply as ‘temperature’, in °C), diurnal low tides (referred to as ‘low tides’, in m), and chlorophyll *a* concentration (referred to as ‘chl *a*’, in mg m⁻³). Except for temperature, which was obtained *in situ* using an Ibutton® datalogger in PPE, SSA, and ANG, most of the data were obtained through online databases. The methodology to obtain these data and their respective results are shown in Texts S1 & S2 and Fig. S2 in Supplement 1). We choose these environmental factors as predictors of the reproduction of *T. ignis* because they are expected to influence the reproduction of shallow-water marine invertebrates (see Leite-Castro et al. 2016, Lanna et al. 2018).

The effect of the environmental factors on the reproduction of *T. ignis* was investigated at both large

(Brazilian coast) and small (local) scales. To test the effects of environmental variables on reproductive outputs along the Brazilian coast, we used a GLMM with a Tweedie compound Poisson–gamma distribution error (Brooks et al. 2017). The temporal autocorrelation structure was accounted for in the model’s covariance structure using an autoregressive model considering the sequence of months in each location. We applied the model to all environmental variables and seasons as predictors. We created a model for variables measured simultaneously with the reproductive outputs and 1, 2, and 3 mo before (the lags are represented by –1, –2, and –3 written after the name of the environmental factor). To check whether there was a difference in the factors influencing the reproductive output of each region, we also used a GLMM with a Tweedie compound Poisson–gamma distribution error. However, to reduce the number of variables, for each time lag (0, 1, 2, and 3 mo before), we selected the combination of variables that generated the model with the lowest Akaike’s information criterion (AIC). The reason to test this lag is that sponges may take a while to respond to environmental changes occurring during the year, as evidenced in previous studies by graphical analysis (Mariani et al. 2005, Ettinger-Epstein et al. 2007, Riesgo & Maldonado 2008) or statistically (Lanna et al. 2018, Calazans & Lanna 2019).

Finally, we applied a quantile regression test to investigate whether temperature limits reproduction in this species (Planque & Buffaz 2008). The quantile regression consists of adjusting regressions on different parts of the distribution (quantiles, or ‘ τ ’). This approach allows an approximation of the ecological concept of a limiting factor (Planque & Buffaz 2008). We carried out this test only for the large-scale dataset using the ‘quantreg’ package in R (Koenker 2018). All statistical analyses were carried out in the R environment (version 3.5.1, R Core Team 2018).

3. RESULTS

3.1. Population engagement in gametogenesis and reproduction

The populations of *Tedania ignis* from PPE, SSA, and ANG were reproductively active throughout the year, with gametes and embryos found in most months (peaks were not observed specifically in any season) (Fig. 2). The FLN population, however, reproduced mainly during the austral spring–summer period of the year (Fig. 2d,h,l,p). On average, the per-

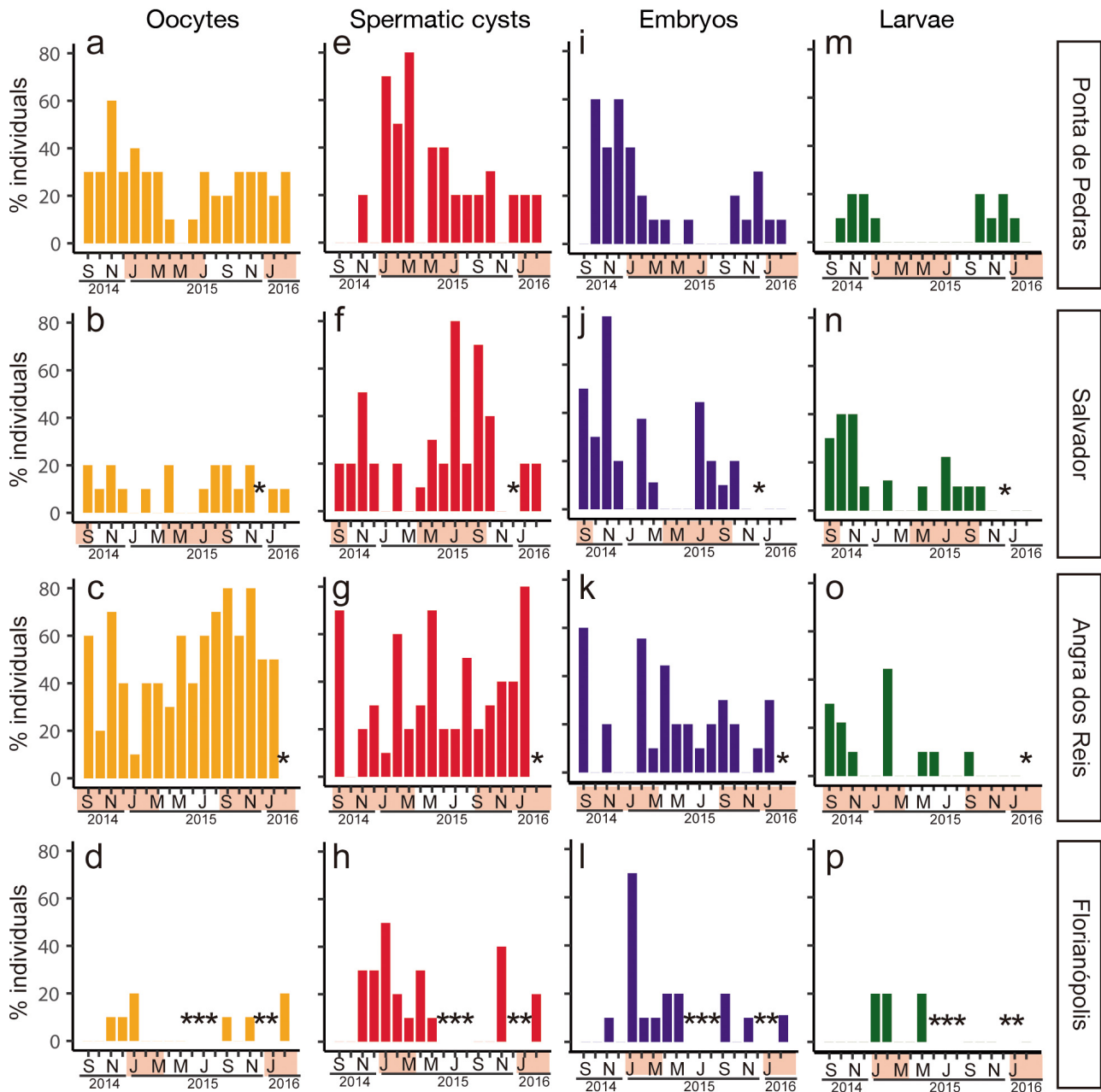


Fig. 2. Percentage of *Tedania ignis* (a–d) engaged in oogenesis, (e–h) engaged in spermatogenesis, (i–l) brooding embryos, and (m–p) with larvae across sites. Shaded boxes on x-axes indicate the rainy period in each location and asterisks indicate no sampling in that month. (Note that part of the data for the Salvador population from September 2014 to July 2015 overlaps with Lanna et al. 2018)

centage of individuals producing oocytes was higher in ANG than in all other locations (4× higher than in FLN; Fig. 2a–d; Fig. S3a in Supplement 1). The percentage of the population engaged in spermatogenesis was also, on average, higher in ANG than in the other locations (2× higher than in FLN, Fig. 2e–h; Fig. S3d). The dynamics of the percentage of individuals brooding embryos (Fig. 2i–l; Fig. S3g) and/or lar-

vae (Fig. 2m–p; Fig. S3j) was similar to those engaged in gametogenesis. Other descriptors of the population engagement in reproduction (i.e. maximum percentage of individuals engaged in gametogenesis/embryogenesis in a given month, and the number of months when more than 50% of the population was engaged in the production of the reproductive element) did not follow a latitudinal gradient (Fig. S3).

3.2. Dynamics of reproductive elements

The dynamics of the density of the reproductive elements were not concordant among the investigated populations, as evidenced by the significant effect of the interaction term between time (months) and space (localities): oocytes ($F = 2.695$, $p < 0.0001$), spermatogenic cysts ($F = 2.536$, $p < 0.0001$), embryos ($F = 2.576$, $p < 0.0001$), and larvae ($F = 1.968$, $p = 0.0004$) (Tables S1–S4 in Supplement 1). In all populations, spermatogenic cysts were more frequently observed than any other reproductive elements, while larvae were less frequent (Fig. 3). On average, oocytes were almost 8× more abundant in the northernmost population (PPE) compared to the southernmost (FLN) (Fig. 4a). How-

ever, the SSA population presented similar values to FLN (Fig. 3a,e,i,m), indicating an absence of latitudinal pattern for this trait. The absence of latitudinal pattern could be observed when the maximum density observed during the study and the annual production of oocytes were compared amongst populations (Fig. 4b,c). We measured a total of 349 oocytes and found that their diameter varied from 5.8 to 125 μm , but on average ($\pm\text{SD}$), the diameter of the oocytes measured $26.1 \pm 14.9 \mu\text{m}$ along the Brazilian coast. Most oocytes observed in all 4 populations were in the vitellogenic stage with granular cytoplasm (Fig. S1). Oocyte diameter was larger in the central locations (SSA, ANG) than in the north and south extremes, varying significantly in time and space ($F =$

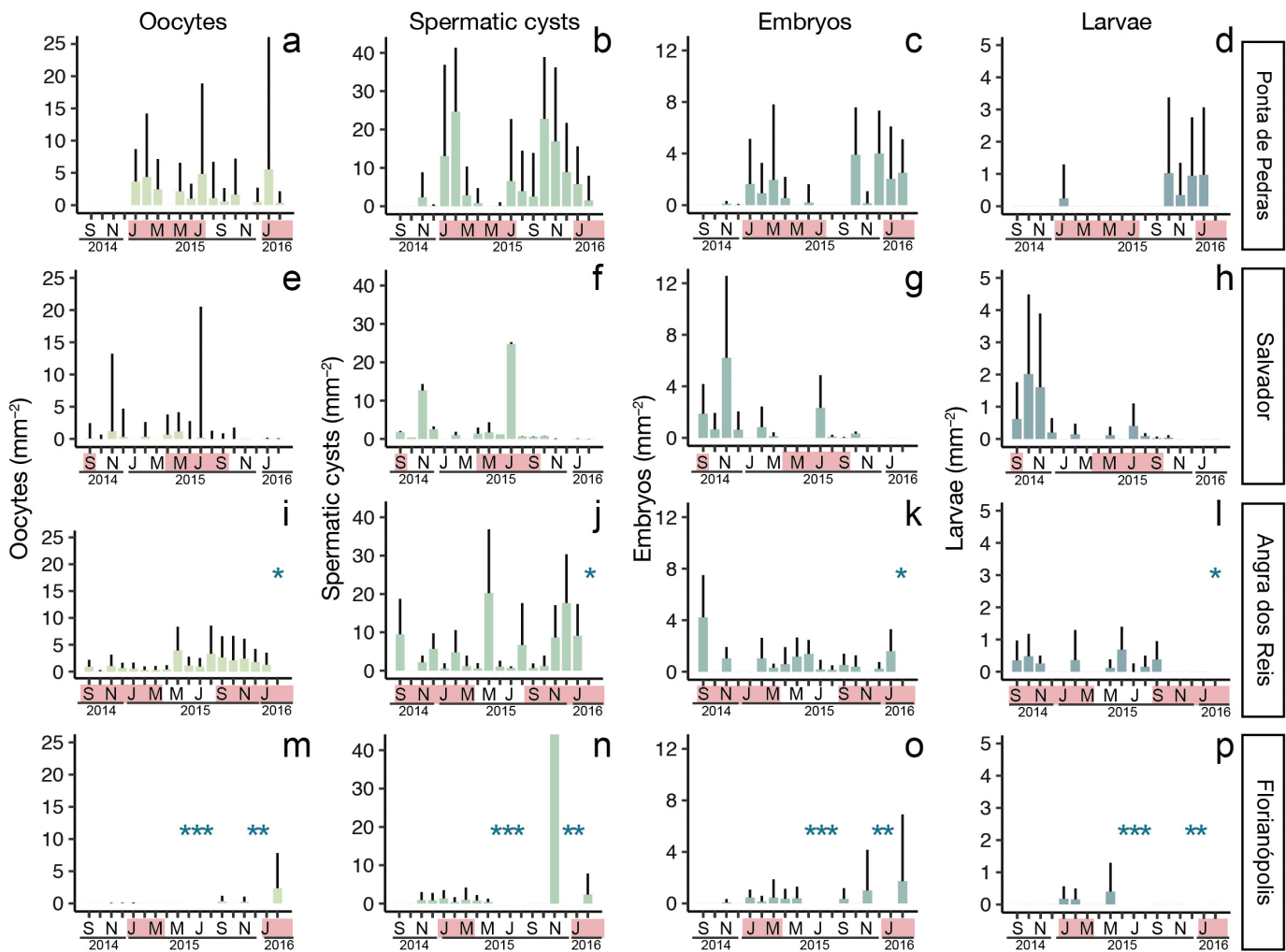


Fig. 3. Temporal dynamics of the density of the reproductive elements of *Tedania ignis* along a gradient of latitude: (a–d) Ponta de Pedras (PPE); (e–h) Salvador (SSA); (i–l) Angra dos Reis (ANG); and (m–p) Florianópolis (FLN). The monthly average of oocytes (a,e,i,m), spermatogenic cysts (b,f,j,n), embryos (c,g,k,o), and larvae (d,h,l,p) are presented as bars, and the lines indicate standard deviation. (Shaded boxes on x-axes indicate the rainy period at each location, and asterisks indicate no sampling in that month). Note that the y-axes are not on the same scale and that part of the data for the SSA population overlaps with Lanna et al. (2018) (from September 2014 to July 2015)

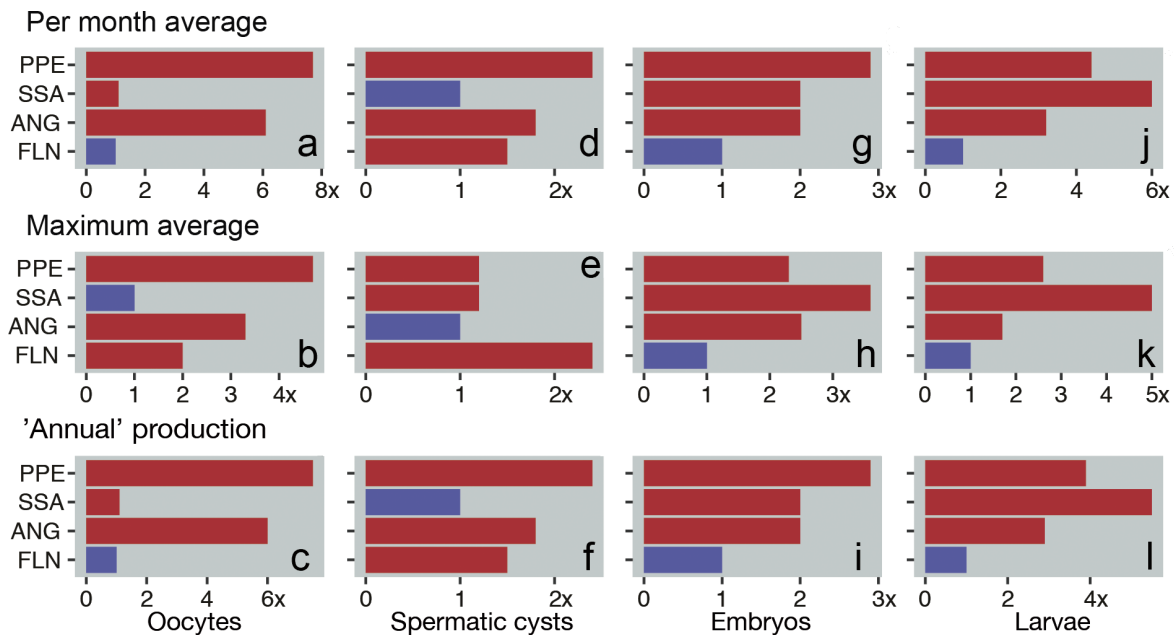


Fig. 4. Relative values of some aspects of the density of reproductive elements of *Tedania ignis* on a latitudinal gradient: (a–c) oocytes, (d–f) spermatic cysts, (g–i) embryos, and (j–l) larvae. Per month average of reproductive elements during the study (a,d,g,j) (calculated by averaging all monthly averages during the study); maximum monthly average attained by the population during the study (b,e,h,k); and the annual production (i.e. sum of the average of all months of the study) are compared based on the lowest value observed in one of the locations (in blue) during the study. The x-axis represents the relative variation (folds) on the density of the reproductive elements. PPE: Ponta de Pedras; SSA: Salvador; ANG: Angra dos Reis; FLN: Florianópolis

7.196, $p = 0.0001$). However, clear seasonal patterns of maturation of the oocytes could not be observed in any of the studied populations, as small and large oocytes were constantly present in the sponges at all locations (Fig. S4 in Supplement 1). Spermatic cysts were also more abundant in PPE than in other locations, circa 2× for average and annual production (Figs. 3b,f,j,n & 4d,f). However, when the maximum value observed was compared, FLN (48.12 spermatic cysts mm^{-2} in November 2015) was 2.5× higher than other locations (Fig. 4e). Embryos were found constantly in the mesohyl of *T. ignis* at all 4 locations, but in low densities (Fig. 3c,g,k,o). Following the trend observed for gametes, the average density of embryos was highest in PPE (Fig. 4g). The same was observed for the annual production (Fig. 4i), but the maximum average was more than 3× higher in SSA (6.21 embryos mm^{-2}) than in FLN (1.72 embryos mm^{-2}) (Figs. 3g,o & 4h). Larvae were more abundant and frequent in SSA (Fig. 3d,h,l,p), but it was noticeable that the density of larvae was more stable in ANG over the studied period. On average, the density of larvae was 6× higher in SSA than FLN (the southernmost population presenting the lowest densities of this reproductive element) (Fig. 4j). A similar trend was also observed for the maximum value and the

annual production of larvae (Fig. 4k,l). The diameter of larvae ranged from 138.0 to 598.0 μm , with an average $363.7 \pm 88.6 \mu\text{m}$ ($n = 124$) along the Brazilian coast during the investigated period. Larval diameter varied significantly among the locations, being larger in PPE ($F = 0.0164$; $p = 0.0164$). However, we did not observe any effect of the interaction between locations and months ($F = 0.065$; $p = 0.5815$).

3.3. Trade-off between quantity and quality of propagules

The diameter of the oocytes was not significantly related to the density of this gamete, either regionally or at the large scale (Fig. S5b,e in Supplement 1), even when different time lags were considered (Fig. S5f). On the other hand, larval diameter was positively and significantly related to its correspondent density in the same month (Fig. S5d,e). Although the methodology used here to measure the oocytes is not the most appropriate, and some variability is likely present in our dataset, these results might indicate that a trade-off between quantity and quality of these propagules, at least in the same month, is unlikely. However, cross-correlation analyses indicated that the density

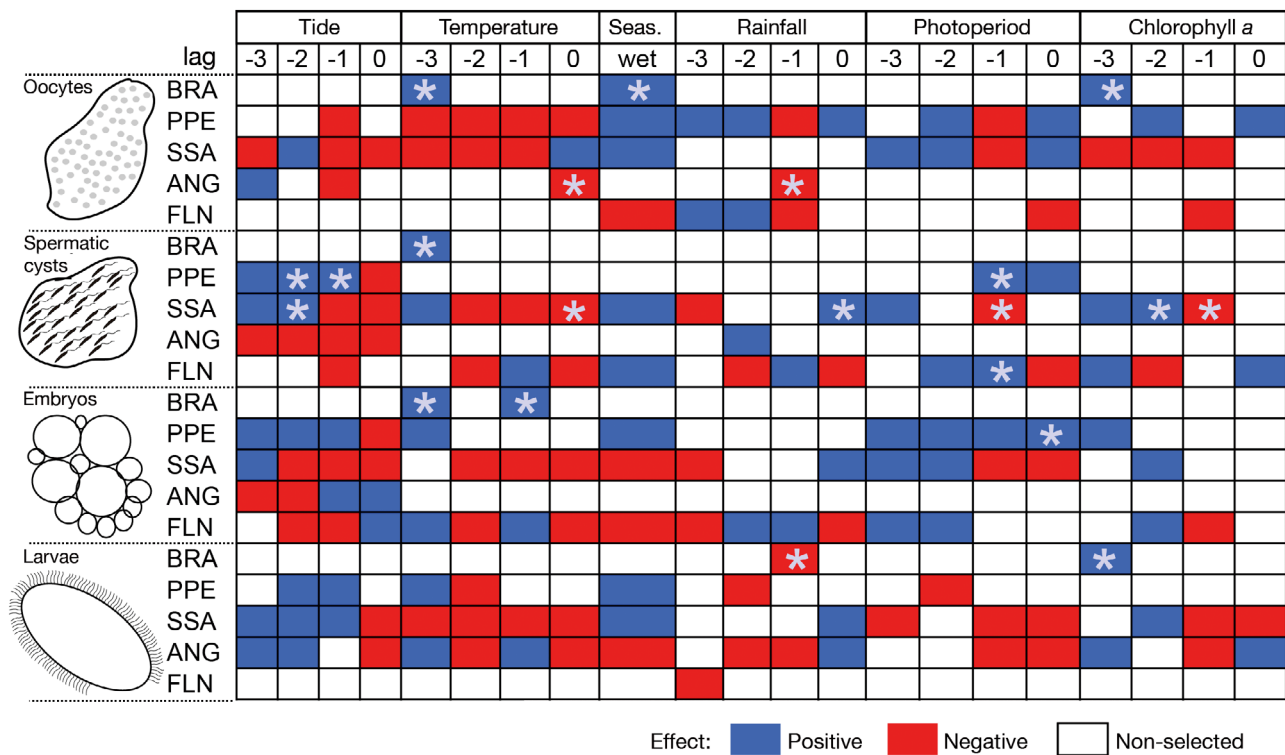


Fig. 5. Summary of the effect of the environmental factors and their respective lags (3, 2, 1, or 0 mo) in the reproductive elements of *Tedania ignis* along the latitudinal gradient on the Brazilian coast. Site abbreviations as in Fig. 4. Asterisks (*) indicate factors that were significant in the models

of oocytes can be related to the density of larvae several months later (see Text S3, Fig. S5f–i).

3.4. Effect of the environmental variables on the reproduction of *T. ignis*

The dynamics of the environmental variables used in this study to investigate the exogenous factors influencing the reproduction of *T. ignis* are described in Supplement 1 (Text S2, Fig. S2). Only rainfall was related with the seasons defined in this study (rainy/dry). The photoperiod regime was related to the classical seasons (winter/summer).

On a large scale (Brazil), the dynamics of oocyte density were positively influenced by temperature(-3) (standard coefficient $\beta = 0.68 \pm 0.20$ [SE]; $p < 0.001$) and chl *a*(-3) ($\beta = 0.47 \pm 0.18$; $p = 0.011$) and season ($\beta = 0.85 \pm 0.30$; $p = 0.005$) (Fig. 5, Table 1). However, different combinations of environmental factors in each locality influenced this trait; most of them were not concordant either among the localities, or with the large scale (Fig. 5; Table S5 in Supplement 1). Spermatic cysts were only influenced (positively) by tem-

Table 1. Generalized linear mixed model coefficients and p-values for the relationships of the environmental factors and the reproductive elements of *Tedania ignis* along the Brazilian coast. Lags represent 0, 1, 2, or 3 mo. Estimates represent the standard coefficient. Chl *a*: chlorophyll *a*; temp: temperature; photo: photoperiod. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

	Estimate	SE	z	Pr(> z)
Oocytes				
Lag (0)				
(Intercept)	2.3267	0.43513	-5.347	<0.0001***
Temp	-0.2931	0.25697	-1.141	0.2539
Photo	0.0254	0.19227	0.133	0.8946
Tide	-0.0175	0.38423	-0.046	0.9635
Chl <i>a</i>	0.0472	0.15496	0.305	0.7603
Rainfall	0.0285	0.13902	0.206	0.8371
Season	0.8811	0.34776	2.534	0.0113***
Lag (-1)				
(Intercept)	-2.2582	0.39092	-5.777	<0.0001***
Temp	-0.0684	0.25665	-0.267	0.7898
Photo	-0.0398	0.18246	-0.219	0.8270
Tide	0.0102	0.35666	0.029	0.9771
Chl <i>a</i>	-0.0140	0.17051	-0.082	0.9345
Rainfall	-0.2473	0.14483	-1.708	0.0877
Season	0.8741	0.33027	2.647	0.0081***

Table continued on next page

perature(-3) ($\beta = 0.38 \pm 0.16$; $p = 0.021$) considering the large dataset (Brazil; Table 1). As for oocytes, the dynamics of these gametes were also influenced by combinations of different environmental factors in each locality (Fig. 5; Table S5). Embryos were significantly and positively related to temperature(-1) ($\beta = 0.48 \pm 0.24$; $p = 0.045$) and temperature(-3) ($\beta = 0.56 \pm 0.24$; $p = 0.019$) at the large scale (Fig. 5, Table 1). The larvae were influenced negatively by rainfall(-1) ($\beta = -0.58 \pm 0.25$; $p = 0.021$) and positively by chl *a*(-3) ($\beta = 1.11 \pm 0.39$; $p = 0.004$) in Brazil (Fig. 5, Table 1). As for the gametes, we found that the combinations of environmental factors influencing the density of embryos and larvae were not concordant among the locations (Fig. 5; Table S5).

Although we were not able to find among-location concordant models for any of the reproductive traits, apparently *T. ignis* seldom reproduced at temperatures below 21°C (Fig. 6). The slopes of the quantile regressions between the reproductive elements of *T. ignis* and temperature at the large scale increased with the quantiles (Fig. 6a,c,e,g). Slope values for lower quantiles were usually close to zero and increased towards the upper quantiles (Fig. 6b,d,f,h). The quantile regression coefficients were significant only at the higher quantiles ($\tau > 0.8$, Table 2), indicating that higher reproductive efforts were never observed at low temperature levels, especially below 21°C.

4. DISCUSSION

4.1. Most populations reproduced aperiodically, but with different drivers

Studies investigating latitudinal variation in life history traits of sponges have rarely included the broad latitudinal range covered in this work. Therefore, our findings offer new insight into the ecology and evolution of this central biological aspect of sponges. Species adapt to climatic variations along latitudinal gradients by adjusting their reproductive strategies to the condition of the environment where they are found (Stearns 1976, van de Kerk et al. 2016). Therefore, although our results support hypothesis 1 (i.e. that each population of *Tedania ignis* would present different reproductive dynamic), the modulation of the dynamics of the reproductive elements by environmental

factors was usually not concordant among the locations and at the large-scale, challenging our hypothesis 2. Hypothesis 2 was based on the speculation that individuals of *T. ignis* should have evolved to respond to the environmental stimuli within a determined range and, although some variation was predicted, all populations were expected to be controlled by the same factors. Lanna et al. (2018) proposed a combination of environmental factors contributing to control the reproduction of *T. ignis* in one of the current investigated populations (i.e. SSA). However, most of the factors controlling reproduction in this species found in that study were not linked to any of the reproductive elements in SSA, or in any other location. It should be noted that the data investigated here might have other complex interactions that were not captured by the methodology applied to the current study (and/or due to limitations in sample size and sampling during certain months). We did not observe concordance in the environmental factors controlling the dynamics of each reproductive element among the populations. This finding led us to hypothesize that the response of the sponges to environmental regimes is not a characteristic phylogenetically defined for the species (as it varies from population to population), but is likely an adaptation to the local conditions.

4.2. Aperiodic vs. periodic reproduction: the importance of temperature

We predicted that reproduction should be continuous/aperiodic in the tropical populations (PPE, SSA, and ANG), but periodic in the warm temperate FLN (hypothesis 3). This proposal was based on the assumption that tropical marine invertebrates, due to the more homogeneous environmental conditions throughout the year, are more inclined to reproduce

Table 2. Quantile regression summary for relationships between temperature and the density of reproductive elements of *Tedania ignis* at the large scale (Brazil). Significant p-values ($p < 0.05$) are shown in **bold**; Coef: coefficients; Temp: temperature

Quantile (%)	Temp (°C)	Oocytes		Spermatic cysts		Embryos		Larvae	
		Coef	p	Coef	p	Coef	p	Coef	p
15	21.1	0.000	1.000	0.003	0.986	0.000	1.000	0.000	1.000
25	23.3	0.001	0.975	0.035	0.869	0.000	1.000	0.000	1.000
50	26.3	0.026	0.653	0.110	0.655	-0.013	0.792	0.000	1.000
75	27.9	0.118	0.088	0.357	0.086	0.055	0.180	0.013	0.214
80	28.1	0.141	0.050	0.461	0.220	0.124	0.043	0.000	0.975
90	29.0	0.254	0.004	1.117	0.013	0.183	0.007	0.064	0.013

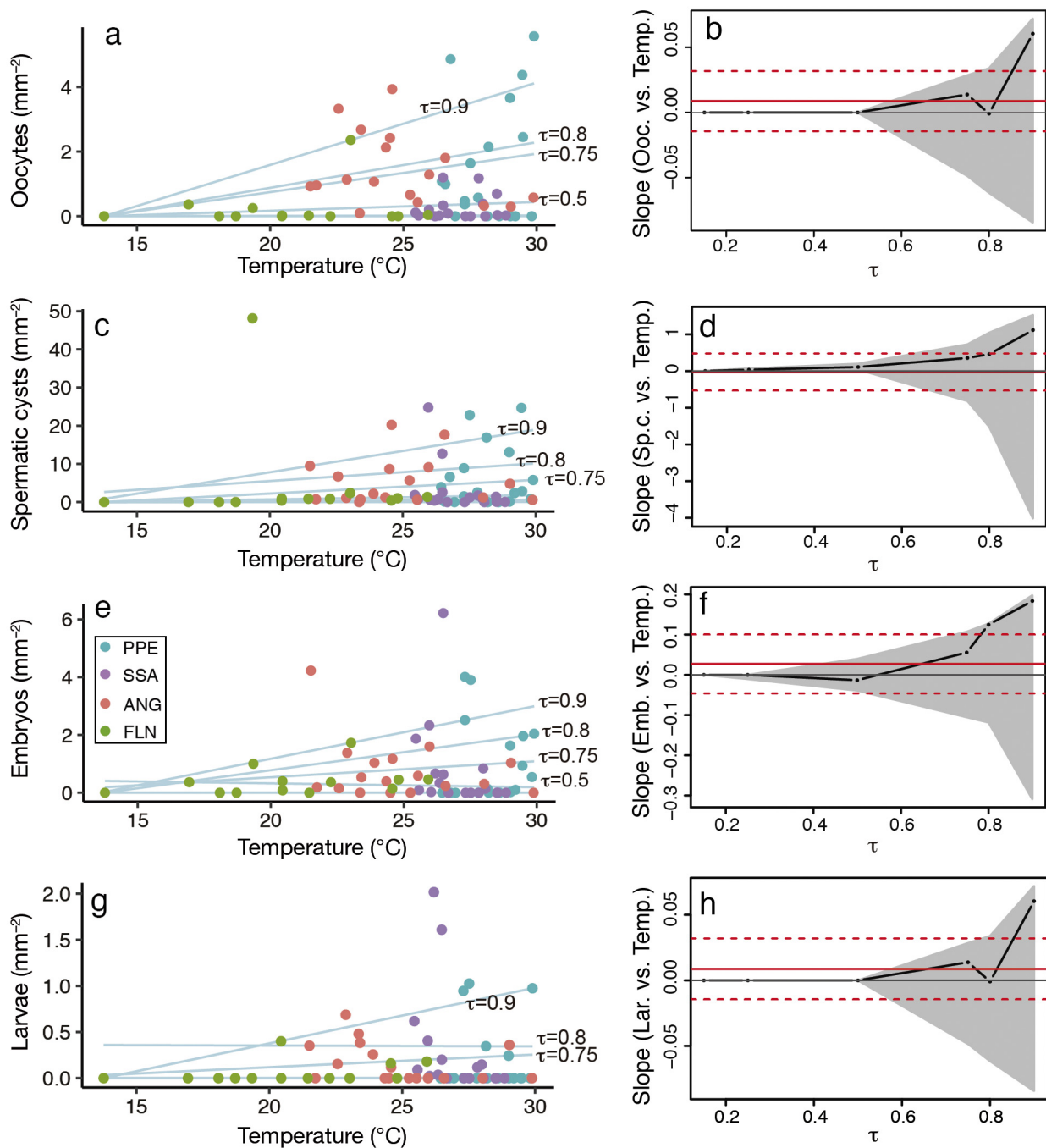


Fig. 6. Relationships between temperature and the density of the reproductive elements of *Tedania ignis* along the Brazilian coast (large scale): (a,b) oocytes, (c,d) spermatocysts, (e,f) embryos, (g,h) larvae. In the left-hand panels, the lines indicate the regression quantiles for different values of τ . The right-hand panels show the slope of the quantile regression as a function of τ (0.1–0.9): shaded area indicates the envelope of 95% of the slopes under the null hypothesis (i.e. no relationship between temperature and reproductive elements) and the dashed lines indicate the confidence interval

aperiodically, while those in subtropical/temperate environments should reproduce seasonally (van de Kerk et al. 2016, reviewed by Lanna et al. 2018). We observed that the PPE, SSA, and ANG populations were reproductively active, carrying out both game-

togenesis and brooding embryos and larvae, during the entire investigated period, while the FLN population reproduced mainly in warmer months (austral spring–summer). In the Caribbean, Maldonado & Young (1996) found larvae in the choanosome of a

large percentage of individuals of *T. ignis* during most of the investigated period. They suggested that the reproduction of *T. ignis* in Florida (27°N) was long and asynchronous in the population, characteristics that were corroborated in all 4 populations investigated here. Together, these findings suggest that a long reproductive season is an intrinsic characteristic of the species. However, we observed that temperature seems to be a limiting factor for reproduction in this species. Apparently, a minimum temperature (ca. 21°C) must be attained for the onset of reproduction in this sponge, as the specimens seldom reproduced below this temperature (Fig. 6), corroborating our hypothesis 4.

Decapods, copepods, oysters, other invertebrates, and even fishes investigated across latitudinal gradients present a similar characteristic of a minimum temperature to start reproduction independently of latitude (e.g. Lardies & Castilla 2001, Lardies & Wehrmann 2001, O'Connor 2002, Castilho et al. 2007). Orton (1920) proposed that the distribution of marine organisms would be directly related to the relationship between their reproduction and the temperature in their habitats and predicted that with an increase in water temperature, 'tropical' organisms would probably expand their distribution to previously colder regions. The current geographic distribution of *T. ignis* ranges from Florida, USA, to Santa Catarina (FLN), Brazil (Muricy et al. 2011). The average temperature moving northwards from Florida or southwards from Santa Catarina will continuously decrease from 21°C, which could be one of the possible explanations for the distribution of the species in the Western Atlantic Ocean (other conditions, e.g. suitable habitats, food supply, etc., also likely contribute to this distribution). The minimal temperature observed for the reproduction of *T. ignis* could also be an important variable regulating its bathymetric distribution. Specimens of this species are found from intertidal regions to a maximum of 31 m depth, but usually they are found shallower than 13 m (Muricy et al. 2011). We can foresee that the increase in the superficial seawater temperature predicted for the next decades will influence the latitudinal and bathymetric distribution of *T. ignis*, as this will allow it to reproduce in these previously colder waters.

4.3. Internal trade-offs: fecundity vs. quality of the propagules

The density of oocytes in *T. ignis* was not related to the diameter of these gametes. Meanwhile, the den-

sity of the larvae was positively related to the diameter of this propagule. The diameter of reproductive elements is considered a proxy for their 'quality', as it is expected that more nutritive reserves (yolk) are present within the egg or in the embryo/larvae, especially in lecithotrophic species like *T. ignis* (Moran & McAlister 2009). Egg size and quantity (i.e. fecundity) are intimately linked with the life history strategy of the species, as they constitute the maternal investment in the offspring (Clarke 1993, Johnston & Leggett 2002, Ramirez Llodra 2002). Due to the restriction of the energetic budget of the organism, it is expected that the evolution of the life history will optimize the quantity of eggs in relation to their size. Therefore, although a trade-off between these 2 characteristics is expected (McGinley et al. 1987, Ramirez Llodra 2002), it was not observed here. A plausible explanation is related to the developmental mode of *T. ignis*. Oocytes are produced in the choanosome of the sponge, where they are fertilized and start their development. Embryogenesis occurs inside the parent and a mature larva is spawned whenever it is ripe (Maldonado & Young 1996), characterizing *T. ignis* as a viviparous species. Oocytes were always less abundant than embryos in the choanosome of *T. ignis*, indicating that fertilization is likely highly successful (indeed, our cross-correlation analysis suggests that the embryos may take 3 mo to develop inside the parental sponge choanosome; see Fig. S5h). We suggest that the absence of a trade-off between quantity and quality of oocytes in this species is mainly related to the high success in fertilization and the viviparous developmental mode. This suggestion is based on the fact that, independently of the quality of the eggs, they will be fertilized and the nutritional reserve for the larvae will be provided during embryogenesis (Ostrovsky et al. 2016). In this case, the sponge would maximize its energetic expenditure in a propagule that will have a larger chance of survival (large lecithotrophic larva). Thus, one would expect a possible trade-off not in the eggs, but in the larvae of the species (Clarke 1993, Ramirez Llodra 2002). Contrary to expectations, the size and the quantity of larvae of *T. ignis* were positively related to each other, indicating an absence of trade-off in this trait as well. We propose that the absence of this trade-off is related to a low number of propagules being incubated by the sponge at any time in comparison to their putative actual reproductive potential. We speculate that this is a life history trait fixed in the species, rather than a variable characteristic depending on the region where the sponge is found. This speculation is based on the observation that inde-

pendent of the environment where the species was investigated, it was almost always reproducing and showed a low reproductive effort, compared to other sponges (Maldonado & Young 1996, Lanna et al. 2018). Moreover, we reinforce the idea that this type of trade-off (quality vs. quantity) will be more easily observed in marine invertebrates that have 'periodic' reproductive periods (pulse strategies, van de Kerk et al. 2016) or are semelparous. In those species, the investment in the next generation must be done at once (Clarke 1993), thus gametes and larvae should be produced in synchronicity. On the other hand, as observed here, the aperiodic production of gametes/larvae would mask any possible trade-off, at least in quantitative terms.

4.4. Latitudinal trends in fecundity and propagule quality

While life history theory predicts that fecundity will be adapted to maximize the size of propagules, it is expected that the environment where the organism is living will define their quality (Johnston & Leggett 2002 and references therein). It is expected that the number of propagules (fecundity) is inversely proportional to latitude, while the size of the propagules would increase towards the poles (Rass 1941, Thorson 1950, Lardies & Castilla 2001, Lardies & Wehrmann 2001, Barneche et al. 2018). We found that the egg and larval densities were higher in the northern population (PPE) and lower in the southern ones (ANG and FLN). However, the SSA population presented lower densities of oocytes and higher densities of larvae when compared to the other locations. Moreover, the size of the oocytes and larvae did not show any latitudinal gradient. Therefore, with the current data, we can only partially fulfill Rass's and Thorson's Rules for *T. ignis* (our hypothesis 6). These rules associate the size of the propagules and the fecundity of the species to the stability of the area. In theory, the parental sponge would invest more energy in larger, but fewer, propagules towards the poles, because the environmental conditions are less stable over time. In this sense, larger propagules would have a better chance to settle, metamorphose, and start growing during the short window of time that better fits the species requirements (Rass 1941, Thorson 1950, Lardies & Castilla 2001, Lardies & Wehrmann 2001, Barneche et al. 2018, Ibáñez et al. 2018). Taking into consideration the temperature and the chl *a* of the investigated areas (these factors are the ones usually investigated in studies of latitudinal

gradient patterns in the life history of marine invertebrates and fishes; Marshall & Burgess 2015, Barneche et al. 2018, Ibáñez et al. 2018), SSA was the more stable region among the locations in our study, especially for chl *a* (a factor significantly related to spermatocyst density in this location). Therefore, it is surprising that the SSA population showed opposite trends to the general patterns observed previously for marine ectotherms (e.g. Marshall & Burgess 2015, Barneche et al. 2018, Ibáñez et al. 2018). Stochastic events during population establishment processes, like founder effects, diversification, and even recent colonization events, may have influenced the size and quantity of these propagules (Ibáñez et al. 2018), but other ecological conditions (e.g. population size, competition, predation, sedimentation, hydrodynamics, etc.) may also be affecting these life history traits of *T. ignis* in SSA (Moran & McAlister 2009). As mentioned by Marshall & Burgess (2015), it is important to observe that marine invertebrates exhibit significant phenotypic plasticity regarding offspring size and that the environment will interact with phenotypic plasticity in complex ways. Consequently, the way in which parental sponges cope with local conditions and modify their offspring will vary across the continua of the environments where they are found. Interestingly, previous studies that were able to identify clear latitudinal patterns for the reproduction of ectothermal marine animals usually did not focus on a single species along broad latitudinal gradients, but, rather, accessed the pattern using different species of a given higher taxon (i.e. genus or family; e.g. Marshall & Burgess 2015, Barneche et al. 2018, Ibáñez et al. 2018). Perhaps if latitudinal trends in size and fecundity of different species of sponges are accessed through a meta-analysis, the same pattern observed in classical studies (Rass 1941, Thorson 1950) and in more recent ones (e.g. Marshall & Burgess 2015, Barneche et al. 2018, Ibáñez et al. 2018) may emerge for Porifera.

In addition to the influence of the environmental factors investigated here, other biological factors might be contributing to the fecundity of the populations of *T. ignis*: competitive and predator pressures, body size of the sponge, and even the production of chemical products of the sponge (tedanolide). Another source of noise for the current analysis might be the influence of asexual reproduction (as this type of reproduction will compete in the energetic budget with sexual reproduction) for population maintenance (as observed for some species of corals, see Baird et al. 2002, Ramirez Llodra 2002). Body size and growth rates are life history traits of any organ-

isms that usually covary with latitude (Sainte-Marie 1991, Ramirez Llodra 2002, Marshall & Burgess 2015, Barneche et al. 2018, Reed et al. 2021). It is important to understand the direct relationship of an individual's characteristics (e.g. chemical concentration, growth rate, body size, competition, etc.) and its reproductive outputs to understand how fecundity is modulated in this and other species of sponges, as it has been observed in several marine ectotherms (cnidarians, copepods, molluscs, etc.).

In conclusion, we observed that there was no general pattern in the influence of the studied environmental factors on any of the reproductive traits of *T. ignis* along a latitudinal gradient. Although other exogenous variables could be acting to control the reproduction of the species in these different locations, it is more likely that the factors modulating its reproductive activity are related to adaptations to the local environment (i.e. proximate causation). We found that the onset of reproduction in *T. ignis* is limited by a minimum temperature and that above this temperature, the species would reproduce continuously with aperiodic peaks. However, below this minimal temperature (21°C), the species will seldom reproduce. Finally, we have demonstrated that there was no trade-off between size and fecundity in the sponge reproductive propagules. We also observed that oocytes and larvae of the species did not correspond to the expected latitudinal 'rules' for fecundity and size. These new findings reinforce the importance of *T. ignis* as a model to understand the ecology and evolution of Porifera and indicates that if it is to be exploited in the future, managers should consider that the species reproduces aperiodically, but with a low reproductive effort.

Data availability. Original data used for statistical analyses are available in Supplement 2 at www.int-res.com/articles/suppl/m667p025_supp2.xlsx.

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