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Life-history traits of a common Caribbean coral-excavating sponge, *Cliona tenuis* (Porifera: Hadromerida)

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Clionoids are important competitors and bio-eroding agents on coral reefs; however, little is known of their biology. We studied aspects of life history of *Cliona tenuis*, in particular its sexual reproduction and growth. Temporal variations in these traits were studied over a year, in correlation with water temperature as a proxy for seasonality. Growth and sexual reproduction occurred at separate times and followed intra-annual variations in temperature. Growth increased during the warmest months of the year, reaching an average rate of 29.9 ± 6.7 mm during 286 days. *Cliona tenuis* is oviparous, and the results suggest gonochorism. Gametogenesis occurred between the coldest months and the period when temperature was increasing. Recruitment was constant throughout the year, possibly associated with post-settlement processes. Juvenile-size individuals were represented in the studied population, suggesting that processes like competition and mortality may control the population, whose size structure may be sustained by high recruitment rates.

Keywords: Porifera; *Cliona*; bio-erosion; reproduction; life cycle; recruitment; growth; Glover's Atoll; Belize

Introduction

The simple structural organization of sponges, their great evolutionary persistence, and their symbiotic associations with a wide range of organisms are attributes that have enabled sponges to occupy a wide range of niches on coral reefs (Wulff 2006; Bell 2008). Among the key roles of sponges, bio-erosion and competition for space are perhaps the most studied sponge-driven processes on coral reefs, because these activities make a large relative contribution to the functioning of these ecosystems (Díaz and Rützler 2001; Bell 2008).

Sponges contribute as much as 95% of the internal erosion of the reef carbonate matrix (Scoffin et al. 1980; Pari et al. 2002), varying among reef substrates (Calcinai

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et al. 2007). The three-dimensional structure of this matrix is the result of a balance between erosion and accretion forces, which is critical for the maintenance of coral reefs (Glynn 1997). In addition to their eroding activities, some dominant bio-eroding and dinoflagellate-associated sponges of the family Clionaidae are highly competitive with corals and other reef organisms (Schönberg and Wilkinson 2001; Rützler 2002; López-Victoria et al. 2006), and potentially have a high tolerance of environmental stressors including elevated temperature (Vicente 1990; Schönberg et al. 2008), storms (López-Victoria and Zea 2004) and sedimentation (Carballo 2006).

Despite the ecological and geological importance of these sponges, we lack basic knowledge of their biology and population dynamics. Clionaid species for which we have data on reproduction are oviparous, which is a characteristic reproductive strategy of the majority of species in the order Hadromerida (Ereskovsky 2010). In the absence of parental brooding, clionaid individuals allocate much energy to mass production of eggs (Mariani et al. 2001; Piscitelli et al. 2011); this attribute combined with a high growth rate can facilitate the successful widespread colonization of space becoming newly available after reef perturbation. The majority of studies of clionoids have stemmed from temperate systems, and studied the reproductive strategies and phenology; respective knowledge for tropical representatives of this family is scarce, particularly those in the Caribbean region.

We investigated the growth and reproduction of *Cliona tenuis* Zea and Weil 2003 in the Caribbean. We describe the reproductive cycle, fecundity, recruitment and temporal changes in growth rate of this species. Our results provide insights into the reproductive strategies and role of reproduction in maintaining the population of this species over time.

Material and methods

Study site

The study was conducted at Glover's Reef Atoll Marine Reserve, Belize, located approximately 30 km from the mainland and 15 km east from the Mesoamerican Barrier Reef. Two study sites were established on the windward side of the Atoll, at about 1 km from each other, on a fringing reef dominated by *Montastraea annularis* Ellis and Solander, 1786, at depths of 8–10 m: Long Caye Wall (LCW; 16.730° N, 87.786° W) and Middle Caye Wall (MCW; 16.753° N, 87.787° W). The study was carried out over 12 months, from January to December 2009. *Cliona tenuis* dominates the brown clionoids at the study sites (personal observation). Taxonomic analysis confirmed the identity of the species in juvenile and adult samples (*sensu* Zea and Weil 2003). However, newly recruited individuals were not sampled for taxonomic analysis, assuming that morphological characteristics were not yet sufficiently developed to distinguish between closely related species (i.e. *Cliona caribbaea* and *Cliona aprica*).

Cliona tenuis is a common excavating sponge in this area (personal observation) and has recently been classified as belonging to the brown species of the *Cliona viridis* complex (Schönberg 2002), some of which may be associated with a thermally tolerant clade (G) of zooxanthellae (Granados et al. 2008; Schönberg et al. 2008). *Cliona tenuis* is among the fastest growing species of brown clionoids in the Caribbean, and frequently out-competes corals (López-Victoria et al. 2006). The species typically has an encrusting growth form (β), and although rare, papillar growth (α) has been observed on the edge of adult colonies (Zea and Weil 2003). The tissues of the sponge penetrate

up to 2 cm into the dead coral skeleton and laterally expand as a thin tissue veneer using the excavating filaments (Zea and Weil 2003).

Reproduction

To describe the reproductive biology and quantify the reproductive effort of *C. tenuis*, samples were collected monthly (3–12 per month; total 72) at LCW from haphazardly selected individuals ranging in size from 200 to 500 cm², and separated by a minimum distance of 5 m. For each sponge approximately 1 cm³ was haphazardly sampled by chipping the coral matrix in which the sponge was growing to a depth of 1 cm. Following collection, the samples were fixed in FACCS gonad fixative solution (10 ml 40% formaldehyde solution, 5 ml glacial acetic acid, 1.3 g calcium carbonate dihydrate and 85 ml water; Fromont et al. 2005) and preserved in 70% ethanol in preparation for histology. Water temperature was measured *in situ* during the study period using HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA), which took measurements every 30 min throughout the year.

Decalcification and histology

To remove any residual calcium carbonate before histology the sponge samples were decalcified in formic acid (1%) under constant agitation for 48 h. The decalcification process was monitored constantly, and at completion the samples were again stored in 70% ethanol. To visualize reproductive propagules the samples were processed using standard histological techniques (Fromont and Bergquist 1994; Whalan et al. 2007). Tissue preparation was automated (Thermo Scientific tissue processor; Thermo Scientific, Waltham, MA, USA), using a graduated ethanol dehydration and xylene clearing system followed by paraffin impregnation in a vacuum oven (Thermo Scientific, Waltham, MA, USA). Following processing the tissue samples were embedded in paraffin blocks, and 5-μm sections were cut (Shandon microtome, Thermo Scientific, Waltham, MA, USA). To facilitate cutting the blocks were placed on ice for 10–15 min before sectioning. The sections were then stained with Harris haematoxylin (nucleic acids) and aqueous eosin Y (cytoplasm counterstain; Thermoshandon, Pittsburgh, PA, USA).

Reproductive effort

Light microscopy was used to identify the reproductive cells (oocytes and spermatoocytes) or structures containing reproductive cells (spermatic cysts), hereafter collectively termed reproductive propagules. The sexual development of these propagules in tissue was monitored monthly from January to December 2009. Three tissue-section fields of 1.4 mm² were haphazardly selected per sample, and images of each were captured using a SCION microscope camera (Scion Corp., Frederick, MD, USA). Reproductive propagules in each image were identified as oocytes or spermatic cysts and counted. The area of each propagule and the total tissue area were measured using IMAGE J software (Rasband 2011). From these data the reproductive effort (RE) of *C. tenuis* was calculated as the sum of the propagule areas divided by the total tissue area multiplied by 100 (Corriero et al. 1998; Whalan et al. 2007). The RE is a measure of fecundity, estimated as the percentage tissue area occupied by sexual propagules.

The propagule density (number of reproductive propagules per mm² of tissue) and area (μm²) were also estimated from the tissue slides as further descriptors of the development of reproductive propagules over time.

Growth

The growth of *C. tenuis* was determined by measuring the linear extension (hereafter “growth”) of sponges tagged in January 2009 at both sites. The growth was estimated as the change in position of the same edge of the sponge between consecutive dates. The initial position of the growth edge was tagged using a galvanized nail driven into the adjacent dead coral substrate, and the subsequent measurements from the nail to the new growth edge of the sponge were made using callipers (± 0.01 mm). Growth was measured three times: at 68, 222 and 286 days from the start of the experiment, resulting in growth rates estimated in three periods through the year: (1) January–April, (2) April–August and (3) August–November. A total of 253 sponges was initially tagged, however as competition compromises the growth of excavating sponges (López-Victoria et al. 2006), the resulting dataset was filtered to include only those measurements where the sponge was in direct contact only with short turf algae ($n = 46$) throughout the year. Short turf algae offer the least competitive resistance to sponges (López-Victoria et al. 2006, González-Rivero et al. 2012). Removal of data derived from situations where the sponge was in contact with highly competitive organisms eliminated confounding competition factors that may have affected the interpretation of sponge growth (refer to Appendix section for details). In addition, the estimation of growth as a linear extension avoided the confounding effect of size on growth estimations, as these two parameters are not significantly correlated (linear regression, response variable: log-transformed linear growth, explanatory variable: size (cm²), estimated: -0.0001 , standard error 0.0002 , $t = -0.581$, $DF = 28$, $p = 0.566$).

The growth of clionoids associated with autotrophic symbionts is given by the lateral extension of tissue into the adjacent substrate, because individuals only vertically penetrate the substrate by up to two centimetres, possibly as a result of light limitation in the autotrophic symbionts (Bergman 1983; Acker and Risk 1985). These observations were confirmed for *C. tenuis* by measuring the maximum depth of substrate penetrated by sponge samples for histology, and this did not vary significantly among individuals (1.2 ± 0.1 cm, mean $\pm 95\%$ CI, $n = 26$) (see also Zea and Weil 2003; Lopez-Victoria et al. 2004).

Recruitment and size structure

Six recruitment plots (5×1 m²) were established at each site and separated by a minimum distance of 5 m to guarantee incorporating the spatial variability of recruitment at each site. In May 2009, the initial location of each sponge in each plot was mapped, and the sponges were identified. At intervals of approximately three months, new individuals recruited into the plots were detected by comparison with previous maps, and recorded in the dataset. Newly recruited individuals had an average diameter of 0.5 cm. The presence of new and dead individuals was updated in the maps following every survey to enable the identification of new individuals in the plot at each subsequent survey. Although rare, *C. tenuis* can show papillae as the excavating filamentous growth into the dead coral skeleton (Zea and Weil 2003; Lopez-Victoria et al. 2004). These papillae can reassemble newly recruited individuals. Therefore, new individuals were recognized when observed at more than 10 cm from adult sponges.

The size structure of the population was estimated from video images of all the sponges along 10 belt-transects ($10 \times 1 \text{ m}^2$) laid randomly at each site. The video images were processed using the VIDANA software for area estimations (Hedley 2006).

Data analysis

Changes in the RE of *C. tenuis* during the reproductive period January–June 2009 were evaluated by comparing the RE, and the area and density of oocytes during the reproductive months using a Kruskal–Wallis (K-W) non-parametric analysis of variance. To describe the development of RE in female sponges as a function of temperature, a general linear model (GLM) was fitted to the data using a cubic linear regression function (Eq. 1) and a least square fitting approach (R software, version 2.15.0). Average monthly RE data were arcsine square root transformed to satisfy normality and homoscedasticity assumptions of the model.

$$RE = \alpha T^3 + \beta T^2 + \gamma T + C \quad (1)$$

Where RE represents the reproductive effort of female individuals, T is seawater temperature, and, α , β , γ and C (constant) are the coefficients of the cubic polynomial regression.

The daily growth rate was compared among the three sampling periods using a K-W non-parametric analysis of variance. Temperature was assessed as a possible factor controlling the growth cycle of *C. tenuis* by correlating growth to intra-annual variations in temperature. Hence, a general linear mixed model (GLMM) was fitted for growth as a function of temperature, and fixing the individual ID as a random effect to account for the repeated measurements on the same individuals over time. A quadratic polynomial regression (Eq. 2) was used as the function describing the relationship between growth and temperature. Growth was natural log-transformed to satisfy the homoscedasticity of residuals.

$$G = \alpha T^2 + \beta T + C \quad (2)$$

Where G represents the growth of *Cliona tenuis* individuals, T is seawater temperature; α , β and C (constant) are the coefficients that define the quadratic polynomial regression.

Recruitment rates as a function of time and site were compared independently using a K-W non-parametric analysis of variance. The size structure distribution was compared between sites using a Kolmogorov–Smirnov (K-S) test.

Results

Reproduction

Gametogenesis

The proportion of reproductive individuals reached its maximum in February for females, and individuals with male gametes were only observed in June (Figure 1A). The spermatocysts of *Cliona tenuis* were spherical with a diameter of $55.6 \pm 9.8 \text{ }\mu\text{m}$ and an area of $1278.9 \pm 85.5 \text{ }\mu\text{m}^2$ (mean $\pm$ SE; Figure 1A). The spermatocysts were scattered throughout the choanosome, but were most abundant in central and basal

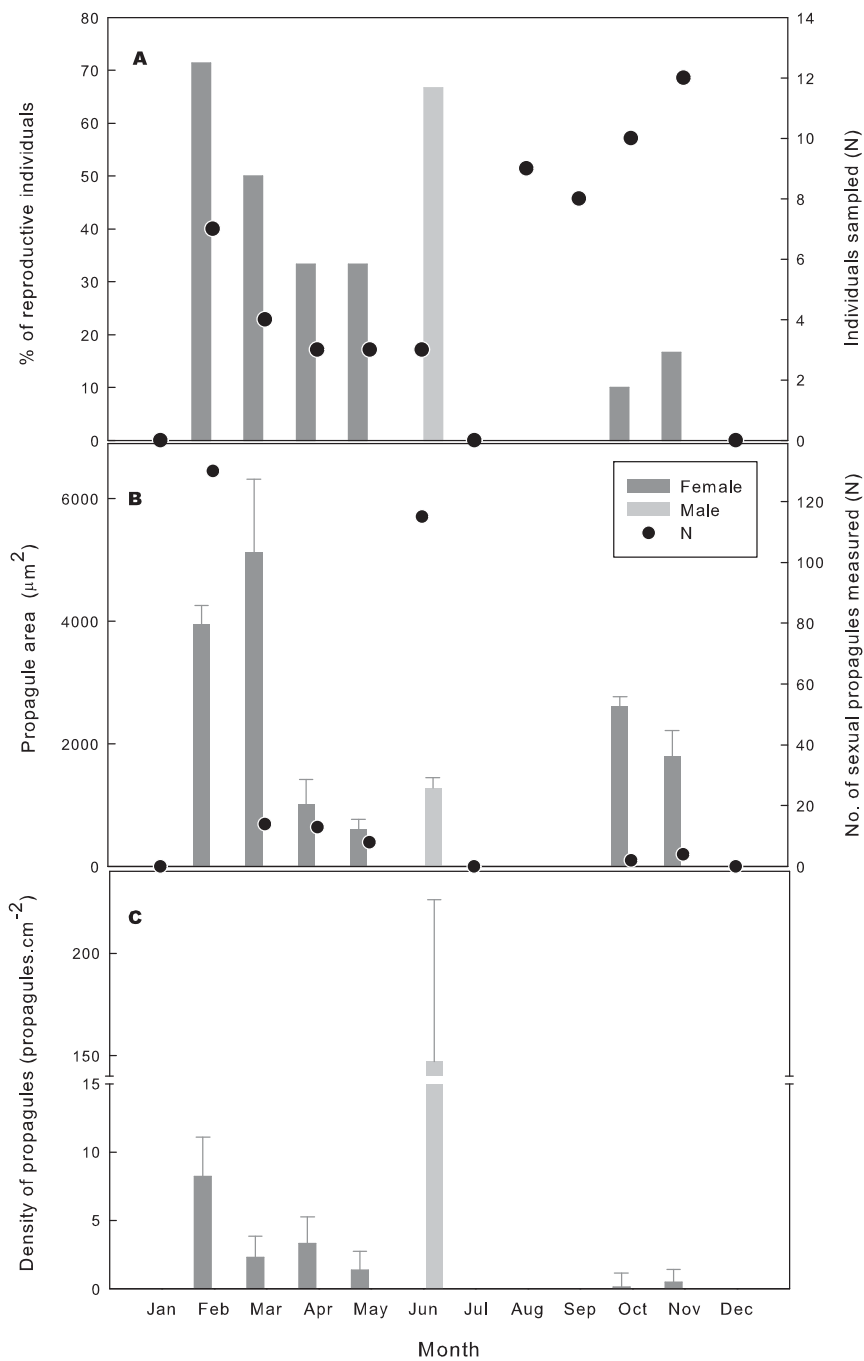


Figure 1. Temporal variation of attributes describing the reproductive cycle in *Cliona tenuis*. (A) Proportion of reproductive sponges (bars) and the total number of individuals sampled (circles); (B) mean propagule size over time; the circles show the number of propagules measured; (C) density of propagules over time. Error bars depict standard error.

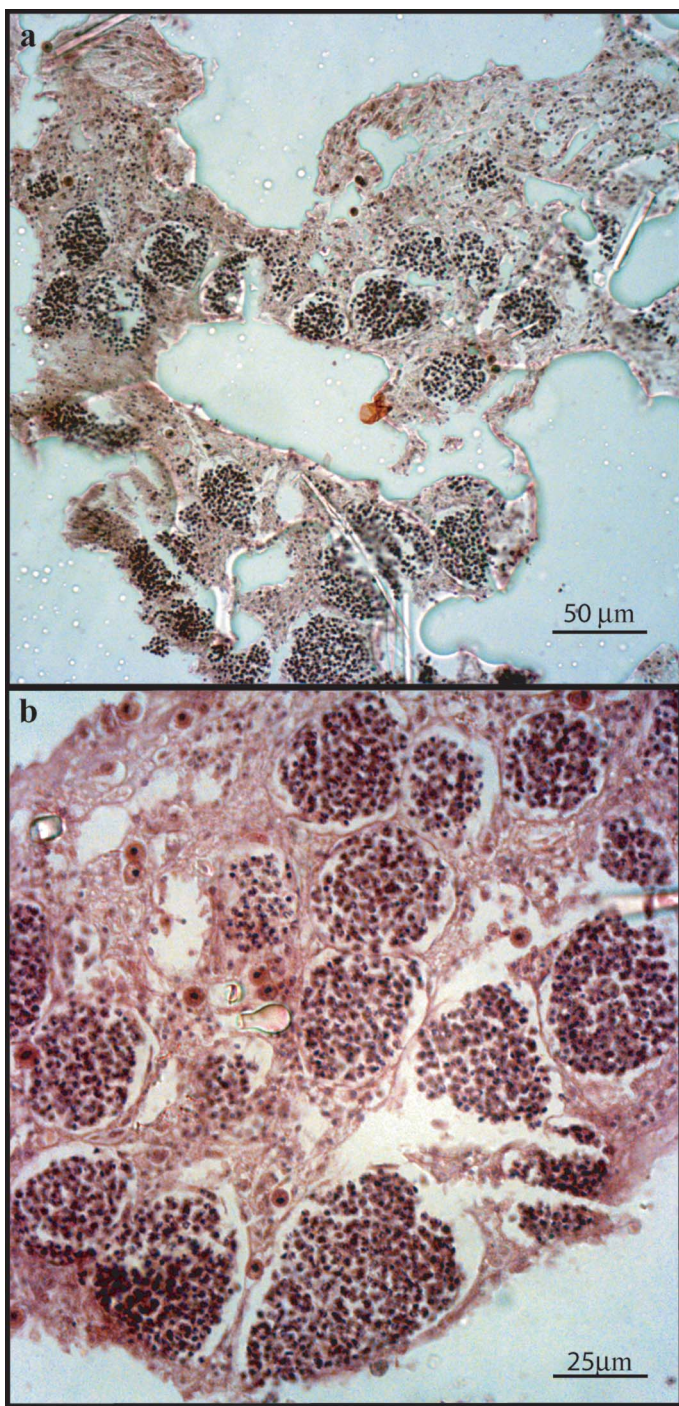


Figure 2. Spermatic cysts of *Cliona tenuis*. (A) Distribution of sexual propagules in the tissue; (B) high magnification view of the spermatic cysts containing spermatocysts at the second stage of development.

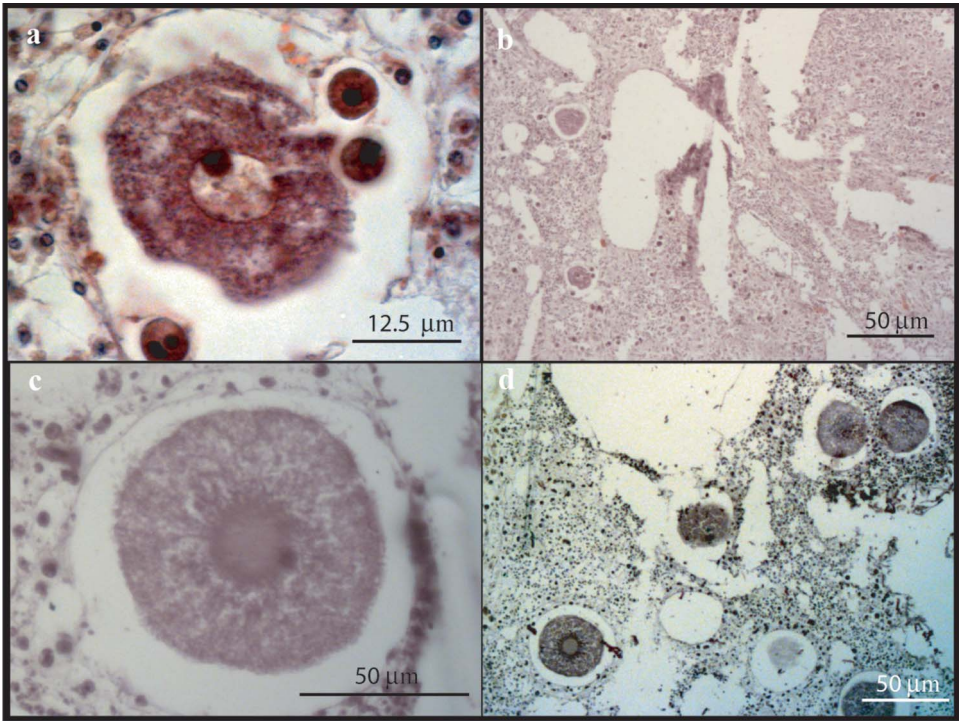


Figure 3. Female reproductive elements in *Cliona tenuis*. (A) Immature oocyte in April 2009; (B) sparse distribution of immature oocytes in the tissue; (C) mature oocyte showing a distinctive nucleolus and nucleus, and the absence of nurse cells; (D) oocyte distribution and abundance in February 2009.

areas of the male sponges (Figure 2A and 2B). A mean density of spermatocysts of 147 ± 79 individuals. mm^{-2} (mean $\pm$ SE) was observed in June (Figure 1C). In each male sponge in the study population the development of gametes was synchronous within each spermatocyst.

The oocytes were irregular or oval-shaped with a homogeneous cytoplasm containing rare small inclusions, a homogeneous nucleus and a prominent nucleolus (Figure 3A, B). The youngest oocytes were $26\text{--}36\text{ }\mu\text{m}$ in diameter, $849.5 \pm 140.8\text{ }\mu\text{m}^2$ (mean $\pm$ SE; Figure 1B) in area, and had nuclei of $9\text{--}12\text{ }\mu\text{m}$ diameter. Mature oocytes had a spherical or slightly oval shape (Figure 3C, D), were $68\text{--}76\text{ }\mu\text{m}$ in diameter and $4375 \pm 198\text{ }\mu\text{m}^2$ in area (Figure 1B), and reached a maximum density of 8 individuals. mm^{-2} in February (Figure 1C). Vitellogenesis intensified significantly in April, and during this process the oocytes gradually became surrounded by a single layer of flat pinacocyte-like cells. Neither aggregates of amoeboid cells nor specialized nurse cells were evident during oogenesis (Figure 3C). The cycle was characterized by significant changes over time in the size (K-W; $p < 0.05$) and density (K-W; $p < 0.05$) of oocytes (Figure 1B, C).

Reproductive effort and temperature

Female sexual reproduction in *C. tenuis* occurred during the northern winter (maturation) and spring (release). Consistent patterns that followed the seasonal trend of

Table 1. Statistical analysis of polynomial regression coefficients fitted to describe the reproductive effort of female individuals of *Cliona tenuis* as function of intra-annual variations of temperature during 2009 [see Equation (1)].

Coefficient	Estimate	Standard error	Degrees of freedom	<i>t</i> -value	<i>p</i> -value
C	0.043	0.005	6	7.974	<0.001
A	− 0.164	0.017	6	− 9.757	<0.001
B	0.075	0.017	6	4.442	<0.004
Γ	− 0.030	0.017	6	− 1.765	0.128

p-values in bold represent the statistically significant coefficients based on $\alpha < 0.05$. $R^2 = 0.93$, $p < 0.001$.

water temperature were observed in the occurrence and size of oocytes among female individuals (GLM, $R^2 = 0.93$, $p < 0.001$, Table 1). Oocyte formation commenced in October, when the water temperature dropped to $29.5^\circ\text{C} \pm 0.01^\circ\text{C}$ (mean $\pm$ SE). Consequently, female reproductive development occurred concomitant with a gradual seasonal decline in temperature, and reached maximum output ($3.7 \pm 1.4\%$; mean $\pm$ SE) in February, when the water temperature was coldest ($26.0^\circ\text{C} \pm 0.01^\circ\text{C}$; mean $\pm$ SE; Figure 4). The reproductive output declined significantly to $0.3 \pm 0.1\%$ (K-W; $p < 0.05$) in April, as the water temperature began to increase to its summer maximum (Figure 5).

Oogenesis took approximately 6 months, but spermatogenesis was a comparatively brief process, with fertile males only evident in June, when the water temperature reached $29.2^\circ\text{C} \pm 0.01^\circ\text{C}$ (mean $\pm$ SE). During this month the RE in male sponges was three-fold the maximum reproductive output observed in female sponges, and occupied $10.8 \pm 7.1\%$ of the mesohyl (mean $\pm$ SE; Figure 4). It is assumed that fertilization occurred immediately after spermatogenesis, completing the reproductive cycle.

Growth

Growth and reproduction were separated in time, with growth reaching its maximum at the end of the active male reproduction period. In the absence of significant spatial competition the growth of *C. tenuis* correlated with variations in water temperature (GLMM; $p < 0.001$, Table 2). The maximum daily growth rate ($0.5 \pm 0.1 \text{ mm.day}^{-1}$) occurred during the third observation period (to 286 days), between September and November 2009 concurrent with peak temperatures (Figure 6A), and was significantly higher than in the earlier measuring periods, when the water was cooler (K-W; $p < 0.001$). This coincides with the observed positive correlation of growth with water temperature (GLMM, $p < 0.001$, Table 2). Over the 286 days of observation *C. tenuis* increased in growth by $29.9 \pm 6.7 \text{ mm}$ (mean $\pm$ 95% CI; Figure 6).

Recruitment and size structure

A continuous rate of recruitment of new individuals was observed in the study area during the evaluation period (Figure 7), despite the observed alternating efforts for growth and reproduction. The average recruitment rate was

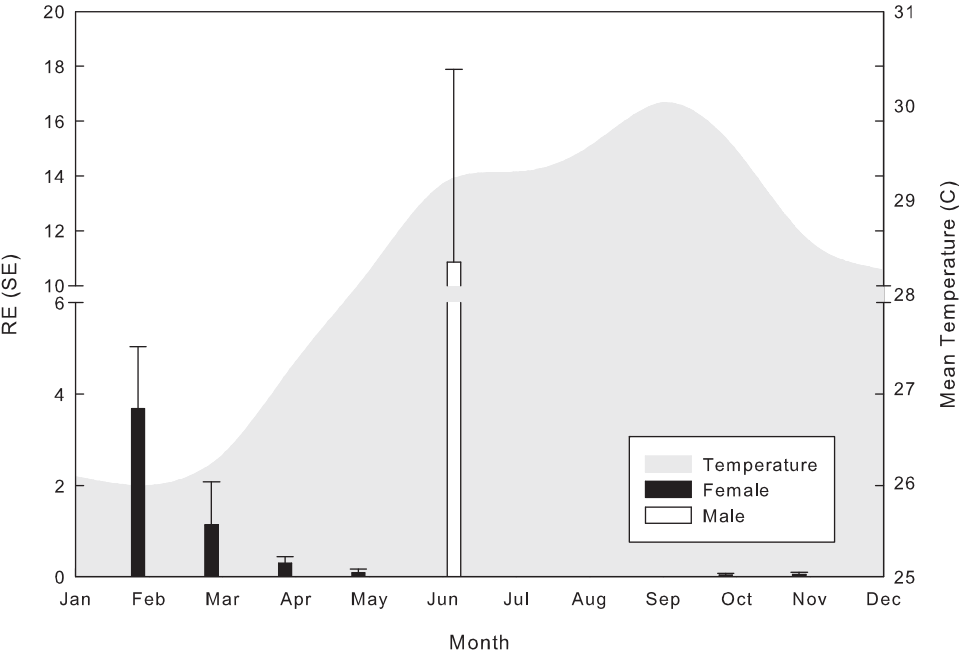


Figure 4. Annual variation in the reproductive output of *Cliona tenuis*, and water temperature at Glover's Atoll, Belize. Vertical lines depict standard error.

2.5 ± 0.8 recruits.m⁻².year⁻¹ (mean $\pm$ 95% CI), which did not vary between the studied populations or over time (between populations $p > 0.5$; among time periods in LCW, $p > 0.5$; and MCW, $p > 0.5$; K-W).

At both study sites the size structure of *C. tenuis* displayed a left-skewed distribution, with 46.1% of the populations comprising juvenile-size sponges (10 cm²; approximately 1 year old according to the fitted logistic growth function). The occurrence of sponges larger than 200 cm² was rare and the maximum sponge size observed on any transect was 8162 cm², at MCW (Figure 8A, B). No significant difference was found in the size distribution of the population among sites (K-S; $p > 0.10$).

Discussion

Our data on the life history of *C. tenuis* at Glover's Reef Atoll are mostly consistent with previous reports of growth and reproduction for other clionoids (see Lopez-Victoria et al. 2004, 2006; Piscitelli et al. 2011), but generate unexpected results in terms of reproduction, which are partly explained here. A more complete understanding is hindered by the limitations of seasonal replication and sampling effort. The present results indicate that *C. tenuis* is an iteroparous sponge that putatively produces offspring in successive (probably annual) cycles. *Cliona tenuis* appears to be gonochoric, as are other clionoid species (Piscitelli et al. 2011). Growth rate increase with water temperature, reaching a maximum in summer, as described in *C. tenuis* (reported as *Cliona caribbaea*, Rützler 2002; Zea and Weil 2003) and conspecific individuals of *Cliona celata* (Carver et al. 2010), while reproductive development occurs

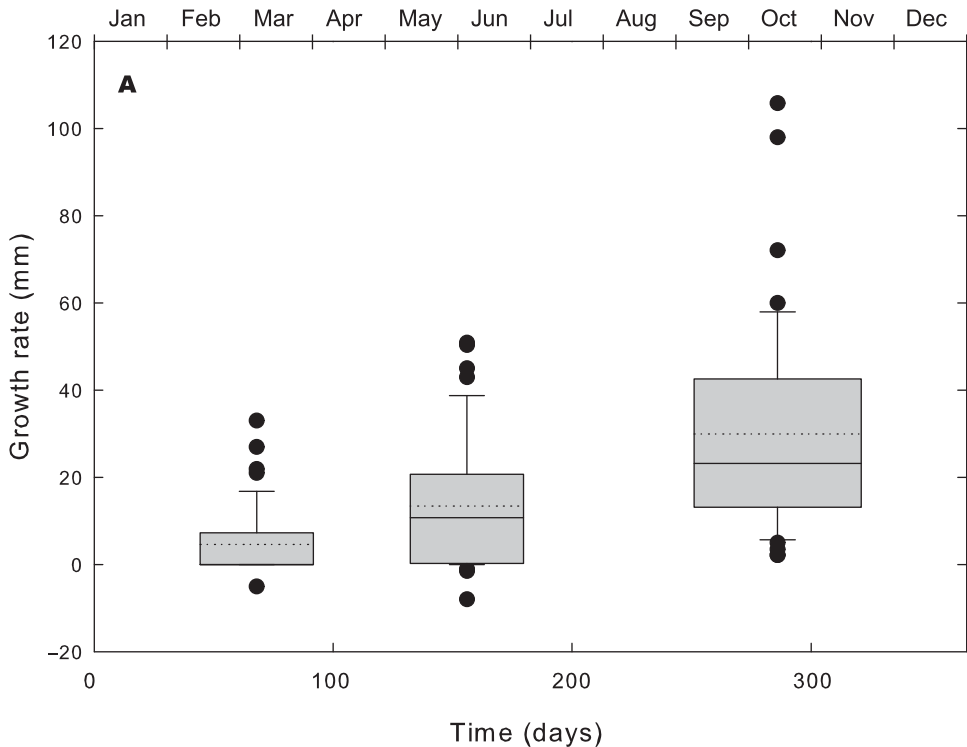


Figure 5. Linear growth of *Cliona tenuis* measured during the studied period. The timeline is represented as ordinal dates in days of the year. Data points out of the 5th and 95th confidence intervals (bars) are represented by dots, and box indicates the interquartile range. The solid line inside the box represents the median, whereas the dotted line represents the mean.

during winter and reaches its maximum during the warming period from February to June. Spermatogenesis occurred ephemerally within one month in temporary structures (spermatic cysts) that were differentiated from choanocyte chambers and within which sperm development was almost synchronous. In contrast, oogenesis was a long process (six months), as described for other hadromerid and clionaid species (Pomponi and Meritt 1990; Rosell 1993; Piscitelli et al. 2011). Both oocytes and spermatic cysts, however, reached a smaller average size than other reported values for clionoids (Bautista-Guerrero et al. 2010; Piscitelli et al. 2011). It is assumed that water currents carried the mature eggs through the oscula to the environment, where fertilization occurred (see Mariani et al. 2001).

Our data deviate from other studies in that oogenesis did not appear to develop with rising temperatures towards mature eggs to be synchronized with fertile sperm (see Ereskovsky 2010). In temperate species, such as *C. celata*, *C. viridis* and *Pione vas-tifica*, oogenesis and fertilization occur during calendar spring–summer (Nassonow 1883; Bergquist and Sinclair 1973; Mariani et al. 2000; Rosell and Uriz 2002; Piscitelli et al. 2011), whereas *C. tenuis* reproduce during the calendar winter–spring, as observed in some individuals of the sister species *C. caribbaea* (Rützler 1974). Where other data are available, gamete release is achieved by oviparity in clionoids, leading to

Table 2. Coefficients of the General Linear Mixed effect Model fitted to describe the growth of *Cliona tenuis* as a quadratic function of intra-annual variations of temperature during 2009 (see Equation (2)).

Coefficient	Estimate	Standard error	Degrees of freedom	t-value	p-value
C	4.704	0.018	72	265.8	<0.001
α	0.639	0.122	72	5.227	<0.001
β	0.103	0.122	72	0.842	0.407

p-values in bold represent the statistically significant coefficients based on $\alpha < 0.05$.

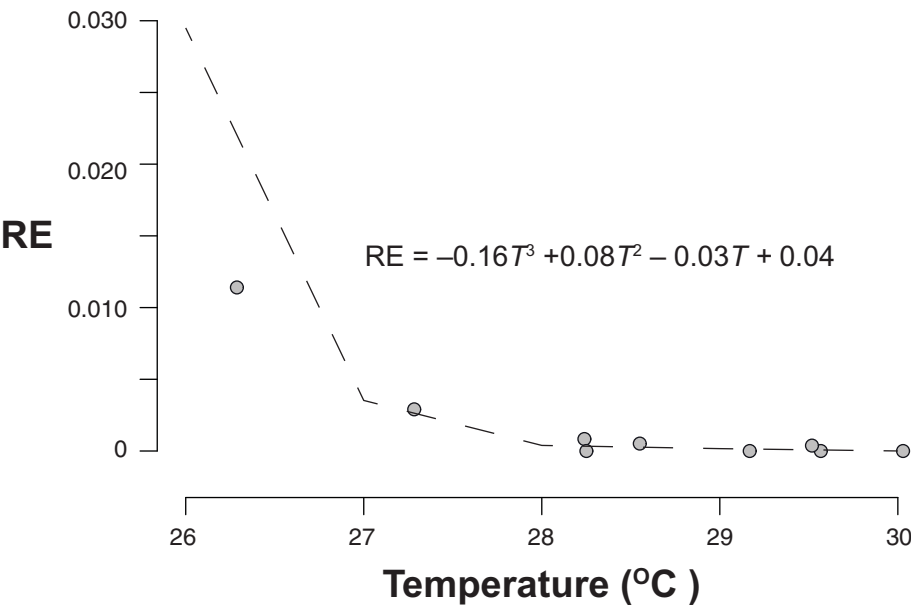


Figure 6. Decline of the reproductive effort of female individuals of *Cliona tenuis* as temperature increases across the surveyed year. Dots represent the estimated reproductive effort analysed from histological sections. Dashed line represents the predicted reproductive effort as a function of temperature using a cubic polynomial regression (see Table 1).

quick larval development and settlement, a process that usually takes no longer than a few days (Warburton 1966; Mariani et al. 2001). Although eggs can be transferred to the sponge surface in a protective gelatinous mass (Mariani et al. 2001), the 4-month time lag between the occurrence of mature eggs and sperm here observed would render survivorship and fertilization of the eggs impossible. We therefore hypothesize that *C. tenuis* may be reproducing as a semi-continuous iteroparous organism, a reproductive strategy whereby the release of gametes reoccurs at several intervals during the reproductive period (October–July) as has been described for other sponges and invertebrates where reproductive seasons are broad (Bell 1976; Olive and Clark 1978; Reiswig 1983). Additionally, *C. tenuis* may show a more extended spermatogenesis, the onset of which we missed because sampling effort and frequency were low. In any case,

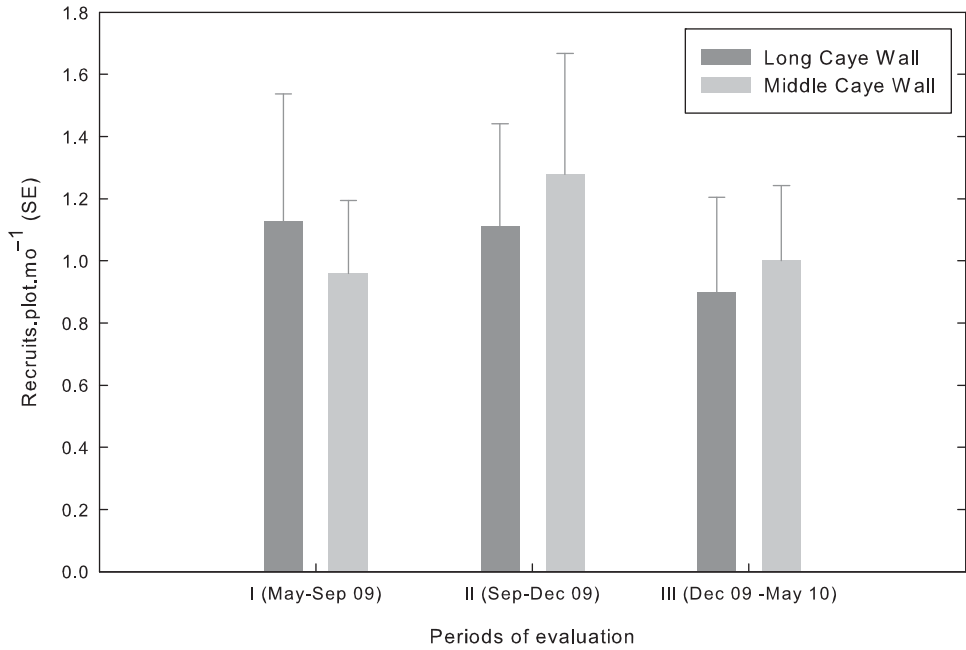


Figure 7. Temporal variation in recruitment (individuals.plot⁻¹) among periods of evaluation and between study sites. Vertical bars depict standard error.

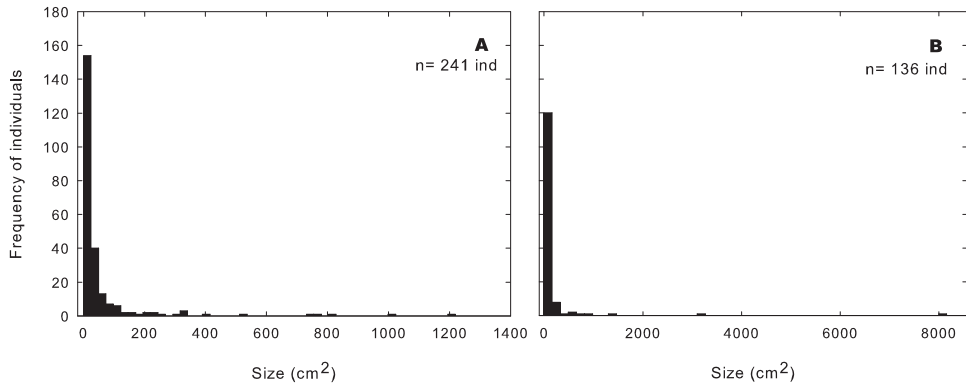


Figure 8. Size structure of *Cliona tenuis* populations at: (A) Long Caye Wall and (B) Middle Caye Wall.

further studies on *C. tenuis* and other *Cliona* spp. are needed to clarify this particular issue.

Little is known about seasonal changes in the growth of tropical clionoids, although some temperate clionoids undergo a cold-induced diapause with arrested growth and tissue regression (Cobb 1975; Pomponi and Meritt 1990; Carver et al. 2010). Observations of *C. tenuis* in Belize (reported as *C. caribbaea*, Rützler, 2002) suggested that temperature plays a role in growth differences that occurred between

two measurement periods. At Glover's Atoll changes in the growth rate of *C. tenuis* throughout the year paralleled seasonal changes of temperature, and our estimates of growth rate (29.9 ± 6.7 mm in 286 days) are similar to values previously reported for *C. tenuis* individuals in contact with dead substrate or with algal turf in Colombia (24.0 ± 8.0 mm.year⁻¹, López-Victoria et al. 2006, 0.5 mm.day⁻¹ as *Cliona* sp. in Lopez-Victoria et al. 2004). In addition, the daily growth rate of *C. tenuis* was higher than the average growth rate reported for the same species in the Mesoamerican Barrier Reef (reported as *C. caribbaea*, Rützler, 2002). This may be a consequence of the effects of competition of *C. tenuis* with other organisms, such as macroalgae (please refer to Appendix and González-Rivero et al. 2012 for details).

The maximum growth of *C. tenuis* during the period September–November corresponded with the period when post-reproductive restorative morphogenesis of the parent sponge tissue was completed and a new round of gametogenesis had not yet begun or was incipient. Such an inter-reproductive period typically corresponds to somatic growth phases in iteroparous organisms, which produce offspring in successive cycles, such as annual or seasonal (Ereskovsky 2010). This alternated cycle of growth versus reproduction has not been reported from any other clonoid. However, in *Pione trutti* sexual reproduction and asexual reproduction with gemmules follow a similar cycle (Pomponi and Meritt 1990). Sexual reproduction is a costly exercise at the expense of energy and the life-history strategy of a species is determined by trade-offs that are the result of selection for optimal energy allocation (Reznick 1983; Ramirez Llodra 2002). Although growth of *C. tenuis* occurred throughout the year it increased significantly following reproduction and coincided with increasing water temperature. Therefore, physiological disruption, allocation of metabolic energy to gamete formation (Rosell 1993), additional occurrence of asexual reproduction and seasonal availability of resources are likely to control the reproductive and growth processes, patterns of which differ between species (e.g., Pomponi and Meritt 1990: asexual and sexual reproduction trade-off, Leong and Pawlik 2010: growth and chemical defence trade-offs). These observations support the logistic behaviour of growth rate throughout the year, as observed in *C. celata* (Carver et al. 2010).

The life cycles of marine sponges are often controlled by seasonal patterns that are governed by temperature variation (i.e. Ettinger-Epstein et al. 2007; Riesgo and Maldonado 2008; Bautista-Guerrero et al. 2010; Di Camillo et al. 2012; Ereskovsky et al. 2013), lunar cycles/tides (Usher et al. 2004) or salinity (Roberts et al. 2006). Variation in water temperature and its correlation with our observations on *C. tenuis* suggest that life-history traits such as growth and reproduction follow a temperature-related pattern, as is true for other clonoids (Mariani et al. 2001; Rützler 2002; Fromont et al. 2005; Piscitelli et al. 2011). Although this study lacks seasonal replication, assumed patterns can be supported by comparing the average temperature at the study site over the previous 24 years with the average temperature reported for 2009 (source: AVHRR pathfinder, NOAA. See Kilpatrick et al. 2001). This comparison showed that temperatures in 2009 followed the long-term seasonal behaviour of temperature for the site (Figure 9). However, it is important to highlight that seasonal replication should be further studied to formally address the effects of environmental seasonality on the life-history traits studied here.

Despite the within-year temporal variation in the sexual reproduction of *C. tenuis*, the levels of recruitment did not show significant differences over time. Therefore it is expected that recruitment might be regulated by a process other than larval supply.

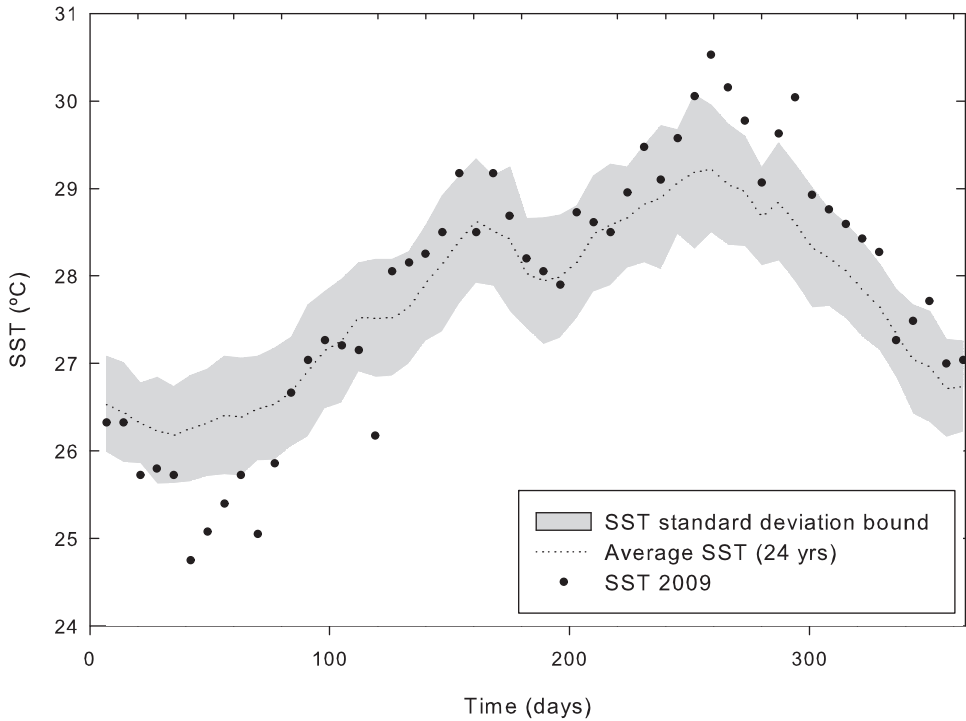


Figure 9. Seasonal change in sea surface temperature (SST) at the study site over time (ordinal date in days of the year): average temperature over 24 years (grey band) and during the 2009 study year (filled dots). Source: AVHRR pathfinder, NOAA.

Newly recruited individuals were observed at a size of 0.5 cm in diameter, by which time they had already attempted to settle and had experienced early post-settlement mortality. There are at least five possible mechanisms that might account for the observation of constant recruitment. First, larvae may settle at different times and therefore develop asynchronously. Alternatively, but less likely, growth rates might vary among individual settlers such that the total number reaching observable size is fairly constant (i.e. the fastest growing individuals are incorporated in early censuses and slower growing individuals are incorporated in later censuses). Second, while we quantified the spawning time for the local clonoid population, it is possible that other, connected populations spawn asynchronously. In this way, larval dispersal may be maintained throughout the year through different source populations reproducing at different times. Hughes (1990) suggested an identical mechanism to account for the lack of relation between fecundity and recruitment of the bryozoan *Cellepora pumicosa* in Ireland. Third, as mentioned above, it is possible that our sampling of reproduction missed some spawning events, which might partly account for the continuous recruitment observed. Fourth, despite the dominance of adults of *C. tenuis* at the study site, species identification at recruit level may be inaccurate. Therefore, if the reproduction of the closely related species, *C. caribbaea* or *C. aprica*, peaks at a different time, the misidentification of the observed recruits could be a confounding factor in this analysis. Lastly, all of the putative mechanisms mentioned here might be subjected to

density-dependent growth and mortality, which may further regulate the abundance of recruits (Caley et al. 1996; Lopez-Victoria and Zea 2005).

The skewed size distribution of *C. tenuis* indicates that the population is dominated by juveniles, which implies that mortality in larger size classes may be creating a bottle-neck effect on the population (i.e. Muko et al. 2001; Mumby et al. 2006). The observed size distribution differs from other demographic studies on this species (Lopez-Victoria and Zea 2005), suggesting that local processes may control the observed patterns in this study. Possible causal mechanisms include high mortality of adults, caused by predation, disease, hurricanes, etc (Loh and Pawlik 2009). On the other hand, severe competition with other taxa, nutrient limitation and availability of well-lit substrate (given by topological complexity) may constrain the potential of individuals to transition to larger size classes (Lopez-Victoria and Zea 2005; Cebrian and Uriz 2006; González-Rivero et al. 2012). Therefore, given the high growth and recruitment rates observed in bio-eroding sponges, with increasing concerns about reef accretion (Hoegh-Guldberg et al. 2007), and in view of the potential of bio-eroding sponges to alter the transition trend of perturbed reefs (González-Rivero et al. 2011), understanding the factors controlling their population dynamics is becoming increasingly urgent. Here, we conclude that there appears to be a trade-off between reproduction and growth, that growth is strongly positively related to sea temperature, that recruitment appears to be fairly constant over time, and that a bottleneck may occur in small sizes of the population. Reproduction remains somewhat unclear; there may be a single annual spawning event. Future studies will increase the sampling frequency (particularly during the reproductive season) and seek evidence of asynchrony among neighbouring populations.

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Appendix

Effects of competition on seasonal variations of growth rate observed in Cliona tenuis

In this manuscript, the growth rate of *Cliona tenuis* has been standardized to minimal competition effects by only selecting individuals constantly in contact with short turf algae throughout the year (see González-Rivero et al. 2012 for details). In this Appendix section, we extended observations to the whole data set including various competitors with different competitive strength against *C. tenuis* (Figure A1, previously described in González-Rivero et al. 2012). As demonstrated by González-Rivero et al. 2012, the growth rate of *C. tenuis* is strongly constrained by competitive interactions, in particular with macroalgae. In addition, the seasonal increase in *C. tenuis* growth rate in competition with short turf is also observed, but to a lesser extent, when it is competing with mild competitors such as corals. However, stronger competitors such as the macroalgae *Lobophora variegata* and *Dictyota pulchella*, strongly overpower the seasonal variations in growth rate of *C. tenuis*. Please refer to González-Rivero et al. 2012 for more details.

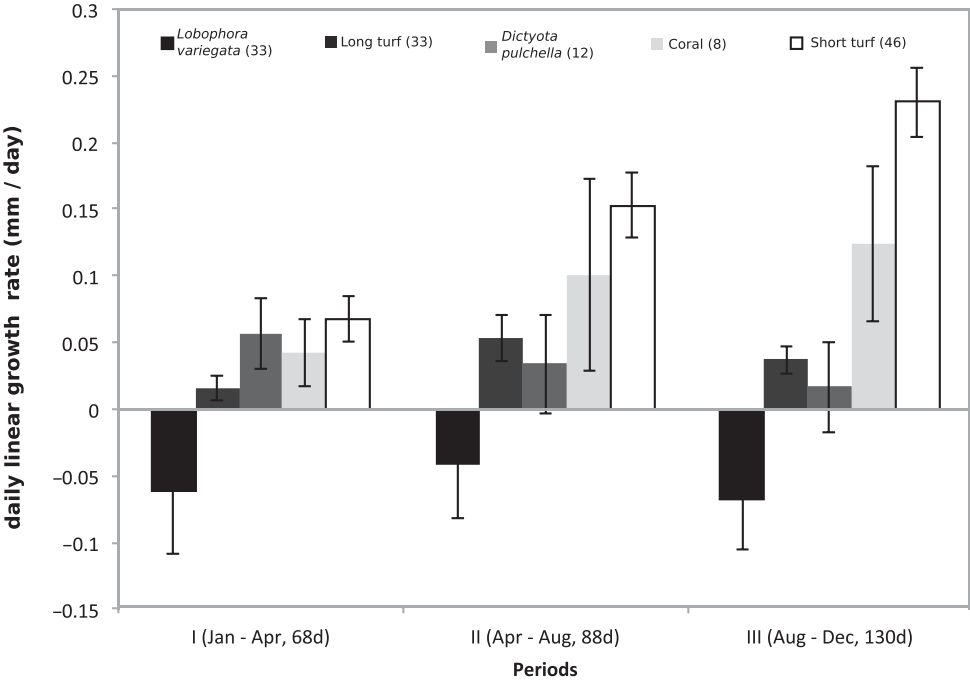


Figure A1. Daily growth rate (linear extension) of *Cliona tenuis* during the three observational periods described in this manuscript and under constant competition with *Lobophora variegata*, *Dictyota pulchella*, coral, and short and long turf algae (more details of the methodology are explained in the methods section of this manuscript and in González-Rivero et al. 2012). Error bars depict standard error.