THE ECOLOGY OF BIOERODING SPONGES ON CARIBBEAN CORAL REEFS

Submitted by ***Manuel Alejandro González Rivero*** to the University of Exeter
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature:

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others, to jointly-authored works, statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis.

Statement of Contributions by Others to the Thesis as a Whole

Peter J. Mumby provided supervision, support and funding for the project. Christine Schönberg supervised and supported discussions over the progress in Chapters 2,3 and 5.

Renata Ferrari provided funding and support over fieldwork and contributed to the discussions of Chapters 2, 3 and 5.

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Laith Yacob, contributed, as a jointed author in Chapter 4, with analytical model development and discussions.

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ABSTRACT

Sponges contribute to large number of functions in coral reef ecosystems. Among these, bioerosion is perhaps one of the most widely studied, largely due to the important contribution of excavating sponges to the carbonate budget on coral reefs (up to 95 % of the total internal bioerosion). Despite our current knowledge, much of the literature is centred on individual-based observations, and little is known about their ecological role and interactions with other reef taxa in complex coral reef systems. The aim of this thesis was to quantify the ecological interactions of bioeroding sponges with major reef taxa by scaling up individual observations to population and ecosystem-based approaches. A cosmopolitan, abundant and highly competitive bioeroding sponge from Glover's Atoll, Belize (*Cliona tenuis*) was used as model species. Monitoring of *C. tenuis* populations throughout 2009 indicated a trade-off between reproduction and growth, with the highest growth rates (31.4 ± 5.6 mm.y–1) occurring in summer, and a peak in reproductive output during winter. Populations typically show strong left-skewed size frequency distributions, mostly represented by juvenile-size individuals (46%), suggesting that regulating mechanisms (e.g. competition and predation) may be acting in constraining the transition of juveniles to adult sizes. Long-term in situ manipulations showed no effect of predation, yet competition with macroalgae significantly reduced the size of the sponge by 38% ± 11% (SE). While *C. tenuis* exhibit high growth and recruitment rates that could theoretically result in rapid population growth, the likelihood of sponges forming an alternative stable state as reefs sustain greater levels of disturbance is unclear. An analytical modelling approach of the interplay between macroalgae, coral and sponge was used to explore the likelihood of alternate stable states. The results show that irrespective of successful sponge invasion, inclusion of this third antagonist (in the interplay between coral and macroalgae) can qualitatively affect the likelihood of alternative stable state. The model exhibits emergent properties suggestive of intransitivity between the three competing taxa. Despite the potential of *C. tenuis* to benefit from disturbance, there are few cases in the literature reporting increases in bioeroding sponge abundance followed disturbance. Therefore, regulating mechanisms such as competition with other taxa, recruitment limitation or mortality are expected to exert demographic control on the populations of bioeroding sponges when space limitation is relaxed due to coral mortality. To determine processes regulating sponge populations, an individual-based spatial modelling approach was used to simulate the population dynamics of *C. tenuis* in a dynamic ecosystem environment. Using an orthogonal hypothesis testing approach, it was found that competition, and to a lesser extend partial mortality of the sponge tissue, largely regulate the population structure of *C. tenuis*. While reductions in coral cover may temporarily favour the rapid colonization by sponges, the competitive superiority of macroalgae may steal the opportunity from the opportunists.

Keywords: Porifera, *Cliona tenuis*, coral reefs, Caribbean, ecology

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CONTENT

FIGURES

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GENERAL INTRODUCTION

Caribbean coral reef ecology: an overview

The Wider Caribbean region contains coral reefs supporting extremely high biodiversity. However, Caribbean reefs are changing as coastal habitats sustain greater levels of disturbance, which add to the global statistics of coral reef degradation (Pandolfi et al. 2003, Bellwood et al. 2004, Wilson et al. 2006). Approximately three decades ago a series of stressors led to profound changes in the health of Caribbean reefs (Gardner et al. 2003). On particular, pandemic episodes of mortality in 1) the major reef-complexity builder coral species, *Acropora* spp (Gladfelter 1982, Aronson and Precht 2001), and 2) one the most important herbivores in reefs, the sea urchin *Diadema antillarum* (Lessios et al. 1984, Lessios 1988) led to significant reef degradation (Hughes 1994, Bellwood et al. 2004, Mumby et al. 2006). The increasing effects of local and global stressors continue to degrade Caribbean coral reefs (Hughes 1994, Wilkinson 1999, Pandolfi et al. 2003, Bellwood et al. 2004).

This increasing effect of local and global stressors such as, nutrients, fishing, sediments, climate change and cyclones is driving important changes in the state of current coral reef ecosystems. The scientific literature contains many examples of situations where anthropogenic disturbance has altered the dynamics of these ecosystems during the past two decades (Nyström et al. 2000, Nyström and Folke 2001). Temporal patterns of reef benthic communities typically show that disturbance drives coral cover down while macroalgal cover increases to the point where reinforcing feedbacks favour their dominance over corals (Mumby 2009). However, the inherent complexity of coral reefs makes it difficult to accurately predict the putative trajectories of the system. Thus it is problematic to understand the response of many common reefs dwelling taxa, such as sponges, a group that remains largely understudied despite their potential role in determining ecosystem trajectories (Norström et al. 2009, González-Rivero et al. 2011).

Coral reef sponges and their role in ecosystem dynamics

Sponges are a functionally important component of coral reefs. Their simple structure, the ability of their cells to change form and function as needed, and their strong associations with a wide diversity of other organisms have remained largely unchanged since the Late Cambrian period (Hooper and van Soest 2002). These attributes have allowed the group to occupy a wide range of niches on coral reefs and contribute to the complex functioning of these systems (Díaz and Rützler 2001, Bell 2008). As recently reviewed by Bell (2008), the role of sponges in reef ecosystem processes can be divided in three main categories: (a) impacts on the substrate, including bioerosion (Rützler 1975, Díaz and Rützler 2001, Rützler 2002, 2004), reef accretion and substrate stabilization, consolidation and regeneration (Wulff and Buss 1979), (b) bentho-pelagic coupling (Lesser 2006) including carbon cycling (de Goeij et al. 2008), silicon cycling, oxygen depletion and nitrogen cycling (Díaz and Ward 1997, Richter et al. 2001, Scheffers et al. 2004, Southwell et al. 2008); and (c) associations with other organisms such as the facilitation of primary (Wilkinson 1983, 1987), and secondary production (Meylan 1988, 1990, Cheshire and Wilkinson 1991, Cleary et al. 2008), the provision of microhabitats (Villamizar and Laughlin 1991, Ribeiro et al. 2003, Wulff 2006a) and as agents of biological disturbance (Vicente 1990a, Aerts 1998, Rützler 2002).

The role of sponges in the face of coral reef disturbance

Despite the known contribution of sponges to ecosystem function, their role may change as coastal systems sustain greater levels of disturbance. In the past decades a long list of anthropogenic stressors have increased in frequency and intensity, and are predicted to continuously rise through time (IPCC 2007, Hoegh-Guldberg 2011). As a common response to disturbances, the space released by coral mortality provides favourable conditions for the successful colonization and space pre-emption of fast-growing and highly reproductive species (McManus and Polsenberg 2004, Mumby 2009, Norström et al. 2009, Fung et al. 2011). Typically in Caribbean reefs, these conditions strongly favour the successful colonization and dominance of macroalgae, to the point that the system has the capacity to flip to macroalgae-dominated alternative stable states as a function of disturbance intensity and frequency (Petraitis and Dudgeon 2004, Mumby et al. 2007). While macroalgae-dominated states are widely observed on Caribbean reefs, certain conditions can induce alternative trajectories of the system following disturbance, facilitating the rapid colonization of poorly studied, but highly competitive species (Norström et al. 2009). Among them, sponges are noted for their environmental plasticity, strong competitive abilities, functional contribution to the ecosystem and wide diversification of niches exploited; qualities suggesting the response of this group could have profound effects on the ecosystem (Rützler 2004, Wulff 2006a).

A number of studies have reported changes in the species composition and abundance of sponges over the past two decades. In the Caribbean, Wulff (2001, 2006b) showed a rapid decline in species abundance (42.6% in volume) and richness (51.3% of the total number of species) within 11 years in San Blas, Panama. A possible cause of this trend was disease, which increased in three common species between 1994 and 1998 at San Blas (Wulff 2007). On the other hand, some studies have also shown that certain sponge species can benefit from or be unaffected by disturbance such as hurricanes (Wulff 1995, 2006c), sedimentation and human settlement (de Voogd et al. 2006), nutrient enrichment (Ward-Paige et al. 2005, Chiappone et al. 2007), disease (Wulff 2006d); and bleaching-induced mortality (Vicente 1978). At Chanel cays, Belize, an encrusting and highly competitive sponge (*Chondrila nucula*) increased in cover from ~15 to 43%, after a significant bleaching-induced coral mortality event in 1998 (Aronson et al. 2002). In the same line, bioeroding sponges are perhaps one the most successful group of sponges in the face of disturbance owed to their rapid growth, strong competitive abilities and high tolerance to environmental stressors (Rützler 2002, Schönberg and Ortiz 2008, Chadwick and Morrow 2011; further discussed in Chapter two).

Bioeroding sponges: putatively benefiting from disturbance

On coral reefs, the various activities that erode the $CaCO_3$ reef matrix are coined as bioerosion (Glynn 1997). Bioeroding or excavating sponges, mostly exclusive members of the family Clionaidae, often dominate shallow reefs (Rützler 1970, 1975). Their activities account for as a much as 95% of the total bioerosion, substantially contributing to the carbonate budget of this systems (Scoffin et al. 1980). This group of sponges erode as they grow into the skeleton by physical and chemical mechanisms (Schönberg 2008). Within this group, a conspicuous subgroup of sponges associated with zooxanthellae, is known as the *Cliona-viridis* complex (Sammarco et al. 1987, Schönberg 2002). Although they penetrate into the coral skeleton 1-2cm, this group of sponges can laterally expand as fast as 19cm/yr (Rützler 2002). Most of our current understanding on the biology of this group is provided by studies on temperate congeners. They reproduce on a yearly basis and fertilization of female propagules occurs externally in a protective egg mass. After hatching, larvae have weak swimming abilities, and therefore lack a planktonic stage, showing a crawling behaviour instead (Mariani et al. 2005). Hence, the strong relationship observed between the local abundance of adults and larvae (Mariani et al. 2000). As a common characteristic of excavating sponges, this group of sponges are strong competitors for space, frequently outcompeting corals by undermining their polyps, and avoiding their defence mechanisms (Rützler 1975, Rützler 2002, Chaves-Fonnegra and Zea 2007).

In coral reefs confronting increased disturbance regimes, bioeroding sponges may benefit. They are highly resistant to thermal- and light-induced mortality (Vicente 1990b, Schönberg and Loh 2005), withstand heavy sedimentation rates (Carballo 2006), and have a cryptic habitat allowing them to tolerate high levels of mechanical stress from waves (Wulff 2006c). Also, hurricanes can increase colonization of bioeroding sponges though fragment dispersal (López-Victoria and Zea 2004). Once these sponges disperse, they readily colonize due to their strong competitive abilities for space (Rützler 2004, López-Victoria et al. 2006, Chaves-Fonnegra and Zea 2011). Furthermore, certain disturbances can facilitate the colonization of bioeroding sponges, such as nutrient enrichment (Holmes 2000, Ward-Paige et al. 2005, Schönberg and Ortiz 2008). In addition, these sponges exhibit low background mortality rates and are capable to reach sizes in the orders of square meters per individual (Rützler 2002, Lopez-Victoria and Zea 2005). However, other common taxa on coral reefs, such as algae and octocorals are also strong competitors for space and can restrain the fast expansion of clionaids (Cebrian and Uriz 2006, López-Victoria et al. 2006), and little to nothing is yet known about down regulating mechanisms that may control these populations when conditions favour their outbreaks (i.e., Cebrian 2010).

The thesis scope

Despite the expected numerical response of clionaids on reefs confronting disturbance, few studies have demonstrated a numerical increase in the abundance of these species following disturbance (Rose and Risk 1985, Ward-Paige et al. 2005, Chiappone et al. 2007, Schönberg and Ortiz 2008), and to date only one study has investigated their population structure (Lopez-Victoria and Zea 2005). Although their performance in confrontation with corals has been extensively studied (Rützler 1974, Rützler 1975, Schönberg and Wilkinson 2001, Rützler 2002, Chaves-Fonnegra and Zea 2007, Chaves-Fonnegra et al. 2008, Chaves-Fonnegra and Zea 2011), and more recently extended to macroalgal interactions (Cebrian and Uriz 2006, López-Victoria et al. 2006, Cebrian 2010, Chaves-Fonnegra and Zea 2011), our current understanding of the dynamics of these populations in the context of changing ecosystems is poorly understood. In addition, fundamental aspects of clionaid life history traits, such as reproduction, mortality and longevity, their interactions with other taxa remains to be investigated. These knowledge gaps hinder our understanding of the role excavating sponges could play in perturbed systems, such as Caribbean coral reefs. The science presented here is aimed to fulfil these fundamental knowledge gaps by exploring aspects of the biology and ecology of a common and abundant excavating sponge in Caribbean reefs, *Cliona tenuis*. For this general aim, different organizational levels (individual, population and ecosystems) and approaches (theoretical and empirical) are employed to systematically increase our understanding of the population dynamics of these sponges confronting reef degradation.

Outline of research chapters

1.5.1. **CHAPTER TWO - Life-history traits of a common Caribbean coral-excavating sponge, *Cliona tenuis* (Porifera: Hadromerida).** Aspects of the life history of the demosponge *Cliona tenuis* are here studied, in particular its sexual reproduction and growth. Temporal variations in reproduction and growth rate were studied over a nearly one-year period in correlation with water temperature as a proxy for seasonality. This chapter describe for the first time the reproduction development, the phenology of reproduction and growth, as well as recruitment rate for *C. tenuis*. Interestingly, this species exhibits a phonological trade-off between growth and reproduction, putatively governed by seasonal changes in water temperature.

1.5.2. **CHAPTER THREE- Impacts of macroalgal competition and parrotfish predation on the growth of a common bioeroding sponge.** This study examined the relative effect of predation and macroalgal competition on the growth of *Cliona tenuis*. A field experiment was designed to isolate the importance of each factor and their interactions, by means of exclusion cages for fish predators and algal transplantation for competition (*Lobophora variegata*). To obtain complementary data on the net outcome of predation and competition *in situ*, predation intensity and the competitive effects of *Cliona* against five different competitors were monitored in the field.

1.5.3. **CHAPTER FOUR - The role of sponge competition on coral reef alternative steady states.** This chapter builds on the knowledge gained in chapters two and four, to understand the qualitative response of ecosystem dynamics when sponges are included in the equation. The study explores the interplay among coral, algae and the sponge, using an analytical model, described by a system of ordinary differential equations representing multi species competition and predation in the reef. Emergent properties arise from our simple model of this complex system, and these include a special case in which heightened competitive ability of macroalgae versus coral may counter-intuitively prove to be advantageous to the persistence of corals. Importantly, the results show that even under scenarios whereby sponges fail to invade the system, inclusion of this third antagonist can qualitatively affect the likelihood of alternative stable states – generally in favour of macroalgal dominance. Ultimately, the necessity of identifying the extent by which this process takes place in tropical systems is highlighted in order to improve projections of alternative stable states for Caribbean coral reefs

1.5.4. **CHAPTER FIVE – When the beneficiaries of disturbance don't benefit: The role of competition with other opportunists in regulating excavating sponge populations.** Merging the knowledge gained on *Cliona tenuis,* this chapter explores and quantifies the relative role of regulating mechanisms on the sponge populations. Using a spatial simulation model, the population dynamics of *C. tenuis* are simulated in the framework of a dynamic neighbourhood environment. Regulating mechanisms are explored using an orthogonal hypothesis testing approach where each of the proposed mechanisms is individually incorporated into the model, and validated against an independent dataset of field observations. This holistic approach supports the emerging concept in benthic ecology of community-level density dependence mechanisms of regulation, and highlight the needs of incorporating the complexity of interactions among reef dwelling taxa to accurately predict the response of the ecosystem in the face of increasing levels of disturbance.

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~ II ~

LIFE-HISTORY TRAITS OF A COMMON CARIBBEAN CORAL-EXCAVATING SPONGE, *CLIONA TENUIS* (PORIFERA: HADROMERIDA)

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Abstract

Clionaids are important space competitors and bioeroding agents on coral reefs. Despite their ecological role little is known of the biology and population dynamics of tropical bioeroding sponges. We studied aspects of life history of the demosponge *Cliona tenuis* at Glover's Atoll, Belize, in particular its sexual reproduction and growth, and suggest likely population dynamic strategies. Temporal variations in reproduction and growth rate were studied over a nearly one-year period in correlation to water temperature as a proxy for seasonality. Growth and sexual reproduction occurred at separate times and followed seasonal variations in temperature. The results suggested a trade-off occurs between reproduction and growth, which may be related to energy costs, disruption of physiological processes, and seasonal availability of resources. Lateral growth increased significantly during the warmest months of the year, reaching an average rate of 31.4 ± 5.6 $\text{mm}\cdot\text{y}^{-1}$. *C. tenuis* is oviparous, and the separate occurrence of female and male propagules in sampled individuals suggests gonochorism. Gametogenesis occurred in the coldest months (females) and the period when temperature was increasing (males). Onset of development of male and female propagates was therefore temporally separated, but both reached a maximum output during the first six months of the year (February-June). Despite the discrete occurrence in time of sexual development in *C. tenuis*, recruitment was observed constant throughout the year, possibly associated to post-settlement processes. Juvenile-size individuals mostly represented the studied population (46%), suggesting that processes like competition and mortality may control the population, whose size structure may be sustained by the observed high sexual recruitment rates.

Keywords: Porifera, *Cliona*, bioerosion, 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, bioerosion 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, Stearn et al. 1980; Pari, Peyrot-Clausade et al. 2002). 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 bioeroding dinoflagellate-associated sponges of the family Clionaidae are highly competitive with corals and other reef organisms (Schönberg and Wilkinson 2001; Rützler 2002; López-Victoria, Zea et al. 2006), and potentially have a high tolerance to environmental stressors including elevated temperature (Vicente 1990; Schönberg, Suwa et al. 2008) and sedimentation (Carballo 2006).

Despite the ecological and geological importance of these sponges, we still lack basic knowledge of their biology and population dynamics. Clionaid species of 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, Piscitelli et al. 2001; Piscitelli, Corriero et al. 2011); this attribute combined with a high growth rate can facilitate the successful wide-spread colonization of space becoming newly available after reef perturbation. The majority of studies of clionaids have stemmed from temperate systems, *sensu* the reproductive strategies and phenology, and 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. This species is a common excavating sponge in this area (pers. obs.) 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, Camargo et al. 2008; Schönberg, Suwa et al. 2008). *C. tenuis* is among the fastest growing species of brown clionaids in the Caribbean, and frequently outcompetes corals (López-Victoria, Zea et al. 2006). 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.

Materials 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, distanced by about 1 km, on a fringing reef dominated by *Montastraea annularis* Ellis and Solander, 1786, at depths of 8 to 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 clionaids at the study sites (pers. obs.). Taxonomic analysis confirmed the identity of the species in juvenile and adult samples (sensu 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 cm^2 to 500 cm^2, and separated by a minimum distance of 5 meters. For each sponge approximately 1 cm^3 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, Craig 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, USA), which took measurements every 30 min throughout the year.

Decalcification and histology

To remove any residual calcium carbonate prior to 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, Battershill et al. 2007). Tissue preparation was automated (Thermo Scientific tissue processor, USA), using an ethanol dehydration and xylene clearing system followed by paraffin impregnation in a vacuum oven (Thermo Scientific, USA). Following processing the tissue samples were embedded in paraffin blocks, and 5 μm sections were cut (Shandon microtome, USA). To facilitate cutting the blocks were placed on ice for 10−15 min prior to sectioning. The sections were then stained with Harris haematoxylin (nucleic acids) and aqueous eosin Y (cytoplasm counterstain; Thermoshandon, Pittsburg, USA).

Reproductive effort (RE)

Light microscopy was used to identify the reproductive propagules and monitor sexual development in the specimens. Three tissue section fields of 1.4 mm^2 were haphazardly selected per sample, and images of each were captured using a SCION microscope camera (Maryland, 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, Scalera Liaci et al. 1998; Whalan, Battershill 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 mm^2 of tissue) and area (μm^2) were also estimated from the tissue slides as further descriptors of the development of reproductive propagules over time.

Growth

The growth rate 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 at three points in time: 68, 222 and 286 days from the start of the experiment, resulting in growth rates estimated in three periods through the year: 1) Jan-April, 2) April-August and 3) August-November. A total of 253 sponges were initially tagged, however as competition compromises the growth of excavating sponges (López-Victoria, Zea 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, Zea et al. 2006). 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. 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, p-value = 0.566).

The growth of clionaids 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 due to light limitation in the autotrophic symbionts (Bergman 1983, Acker and Risk 1985). These observations were confirmed for *Cliona 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 ± $CI_{95\%}$, n= 26).

Recruitment and size structure

Six recruitment plots (5 × 1 m^2) were established at each site and separated by a minimum distance of 5m to guarantee incorporating the spatial variability of recruitment at each site. In January 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.

The size structure of the population was estimated from video images of all the sponges along 10 belt-transects (10 x 1 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. A linear fixed effect model was fitted to evaluate monthly changes in the RE of female sponges, using temperature as a proxy for seasonal changes.

The growth of *C. tenuis* was evaluated over the year by fitting multiple models to the data. The fitted models were exponential and logistic functions using a robust non-linear least squares method with bi-square weights. Functions were compared in terms of the best fitting and biologically meaningful description of growth. Temperature was assessed as a possible seasonal factor controlling the growth cycle of *C. tenuis* by correlating growth to seasonal variations in temperature. Thus, a mixed effect model (MEM) was fitted for growth as a function of temperature, accounting for repeated measurements on the same individuals over time. Growth was natural log-transformed to de-trend non-linear relationships with temperature and to normalize residuals. The daily growth rate was also compared amongst the three sampling periods using a K-W non-parametric analysis of variance.

Recruitment rates as a function of time and site were compared independently using a K-W non-parametric analysis of variance. The size structure was compared between sites using a Kolmogorov-Smirnoff (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 II-1a). The spermatic cysts of *Cliona tenuis* were spherical with a diameter of 19−21 µm and an area of 1278.9 ± 85.5 μm^2 (mean ± SE; Figure II-1b). The spermatocysts were scattered throughout the choanosome, but were most abundant in central and basal areas of the male sponges (Figure II-2a and II-2b). A mean density of spermatocysts of 147 ± 79 $ind \cdot mm^{-2}$ (mean ± SE) was observed in June (Figure II-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 homogenous cytoplasm containing rare small inclusions, a homogeneous nucleus and a prominent nucleolus (Figure II-3a and II-3b). The youngest oocytes were 26−36 µm in diameter, 849.5 ± 140.8 μm^2 (mean ± SE; Figure II-1b) in area, and had nuclei of 9−12 µm diameter. Mature oocytes had a spherical or slightly oval shape (Figure II-3c and II-3d), were 68−76 µm in diameter and 4375 ± 198 μm^2 in area (Figure II-1b), and reached a maximum density of 8 $ind \cdot mm^{-2}$ in February (Figure II-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 II-3c). The cycle was characterized by significant changes over time in the size (K-W; $p < 0.05$) and density of oocytes (K-W; $p < 0.05$; Figure II- 1b and II-1c).

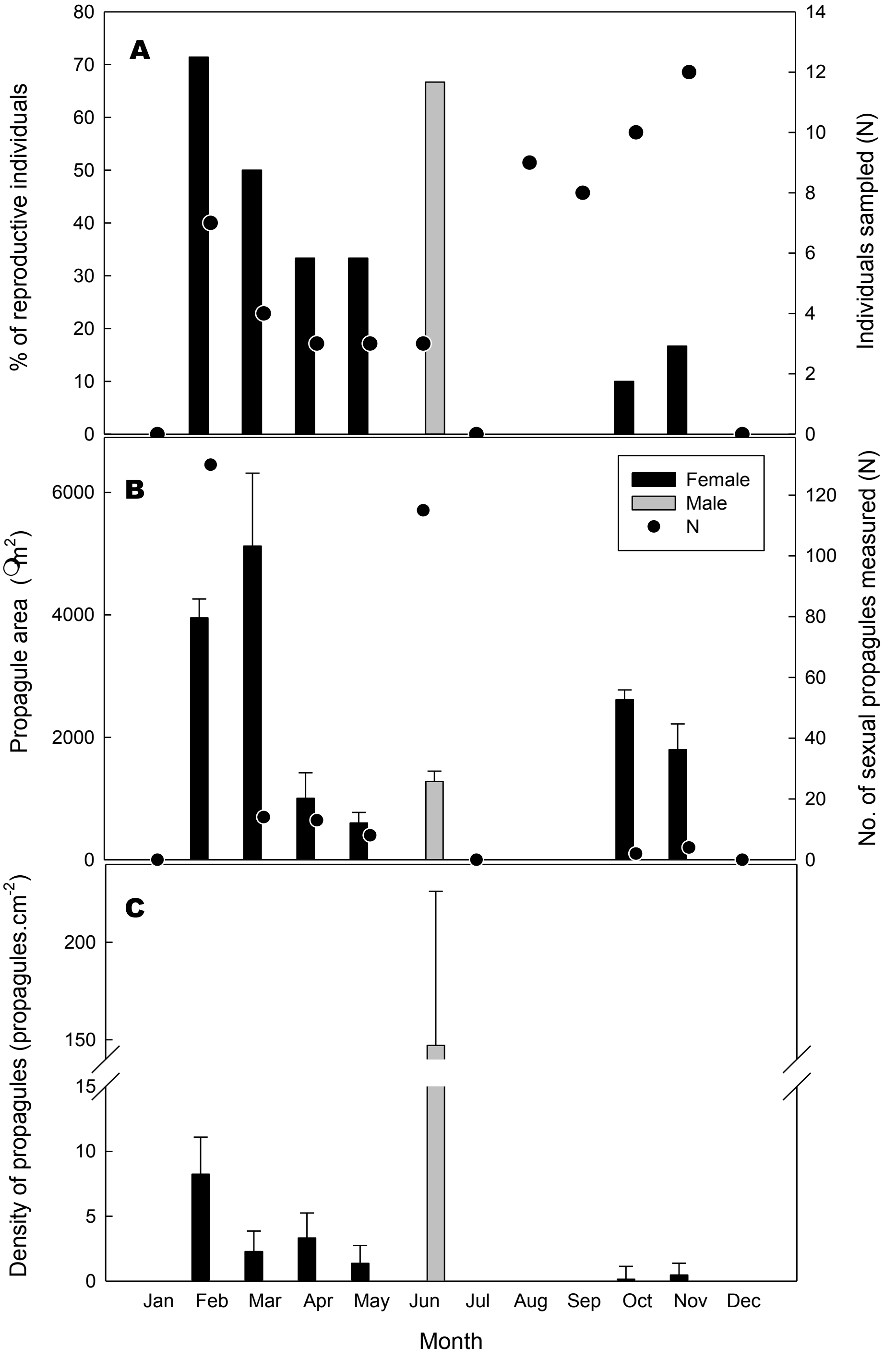

Figure II-1. Temporal variation of attributes describing the reproductive cycle in *Cliona tenuis*. A) Proportion of reproductive sponges (bars) and the total number of individuals sampled (circles); B) Mean propagule size over time; the circles show the number of propagules measured; C) Density of propagules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

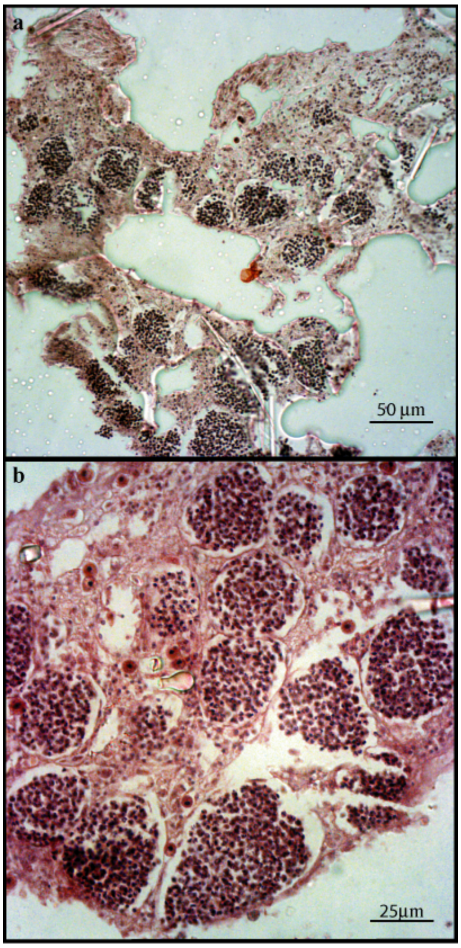

Figure II-2. Spermatic cysts of *Cliona tenuis*. A. Distribution of sexual propagules in the tissue. B. High magnification view of the spermatic cysts containing spermatocysts at the second stage of development.

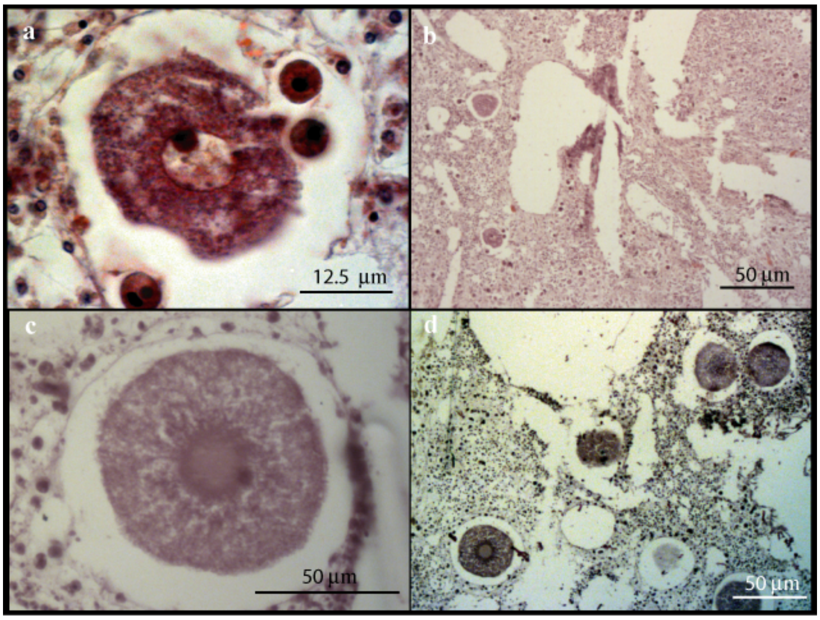

Figure II-3. Female reproductive structures in *Cliona tenuis*. A. Immature oocyte in April 2009. B. Sparse distribution of immature oocytes in the tissue. C. Mature oocyte showing a distinctive nucleolus and nucleus, and the absence of nurse cells. D. Oocyte distribution and abundance in February 2009.

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 water temperature were observed in the occurrence and size of oocytes among female individuals (Figure II-4). Oocyte formation commenced in October, when the water temperature dropped to 29.5 °C ± 0.01 °C (mean ± SE). Consequently, female reproductive development occurred concomitant with a gradual seasonal decline in temperature, and reached maximum output (3.7 ± 1.4%; mean ± SE) in February, when the water temperature was coldest (26.0 °C ± 0.01 °C; mean ± SE; Figure II-4). The reproductive output declined significantly to 0.3 ± 0.1% (K-W; $p < 0.05$) in April, as the water temperature began to increase to its summer maximum.

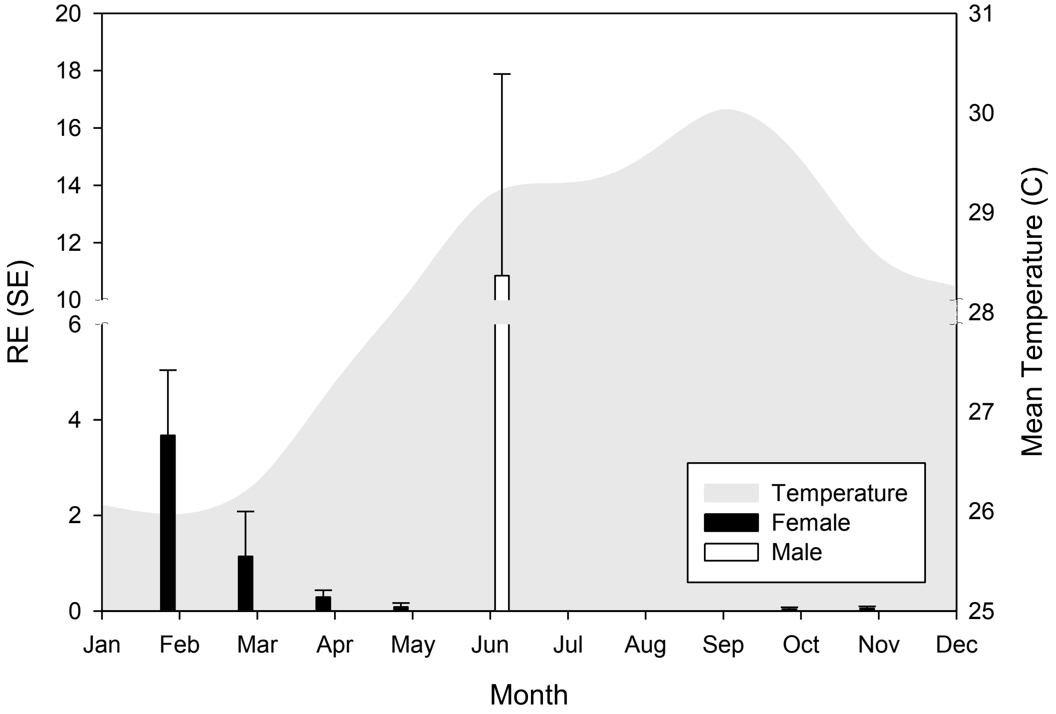

Figure II-4. Annual variation in the reproductive output of *Cliona tenuis*, and water temperature at Glover's Atoll, Belize. Vertical lines show the standard error.

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 °C ± 0.01 °C (mean ± SE). During this month the RE in male sponges was three-fold the maximum reproductive output observed in female sponges, and occupied 10.8 ± 7.1% of the mesohyl (mean ± SE; Figure II-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 (MEM; $p < 0.001$). The maximum daily growth rate (0.5 ± 0.1 mm·day$_{-}{}^{1}$) occurred during the third observation period (to 286 days), between September and November 2009 concurrent with peak temperatures (Figure II-5A), and was significantly higher than in the previous measurement periods when the water was cooler (K-W; $p < 0.001$). We therefore assume that the growth rate increased with increasing temperature. Over the 286 days of observation *C. tenuis* increased in growth by 29.9 mm ± 6.7 mm (mean ± $CI_{95\%}$; Figure II-5a), and extrapolations from the fitted exponential curve suggest that the annual growth *C. tenuis* could have been as much as 46.2 ± 15.5 mm·y$_{-}{}^{1}$ (estimate ± $CI_{95\%}$, R^2-adjusted = 0.84). However, if growth follows seasonal patterns of temperature, a decrease in the rate would be expected towards the coldest time of the year. This pattern is better described by a logistic function (Eq. 1), which behaves similarly to an exponential function during the growth phase (Figure II-5b), after which the growth rate declined during the reproductive phase (Figure 6). Given this scenario and using a logistic function, the predicted growth of *C. tenuis* is 31.4 mm·yr^{-1} ± 5.6 mm·yr^{-1} (estimated ± $CI_{95\%}$; R^2-adjusted = 0.78).

$$G(t) = \frac{22.64\, e^{0.0143(t)}}{50+0.45(e^{0.0143(t)}-1)} \qquad \text{Eq (1)}$$

where, *G(t)* is the growth rate as a function of time '*t*'.

Recruitment and size structure

A continuous rate of recruitment of new individuals was observed in the study area during the evaluation period (Figure II-7), despite the observed alternating efforts for growth and reproduction. The average recruitment rate was 2.5 ± 0.8 recruits$\cdot m^{-2}\cdot y^{-1}$ (mean ± $CI_{95\%}$), 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 cm^2; approximately one year-old according to the fitted logistic growth function). The occurrence of sponges larger than 200 cm^2 was rare and the maximum sponge size observed on any transect was 8162 cm^2, at MCW (Figure II-8a and II-8b). No significant difference was found in the size distribution of the population among sites (K-S; $p > 0.10$).

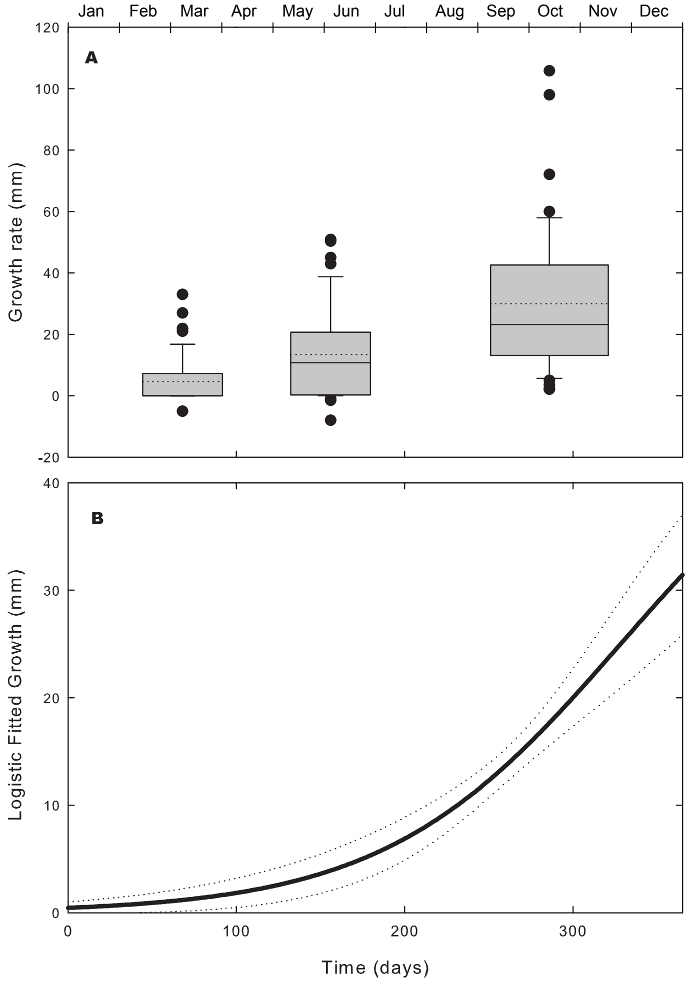

Figure II-5. Linear growth of *Cliona tenuis* A) measured during the studied period, and B) fitted into a continuous logistic function. The timeline is represented as ordinal dates in days of the year. A: Data points out of the 5th and 95th confidence intervals (bars) are represented by dots, and box indicates the inter-quartile range. The solid line inside the box represents the median, whereas the dotted line represents the mean. B: Dotted lines show the predicted 95% confidence intervals for the fitted function.

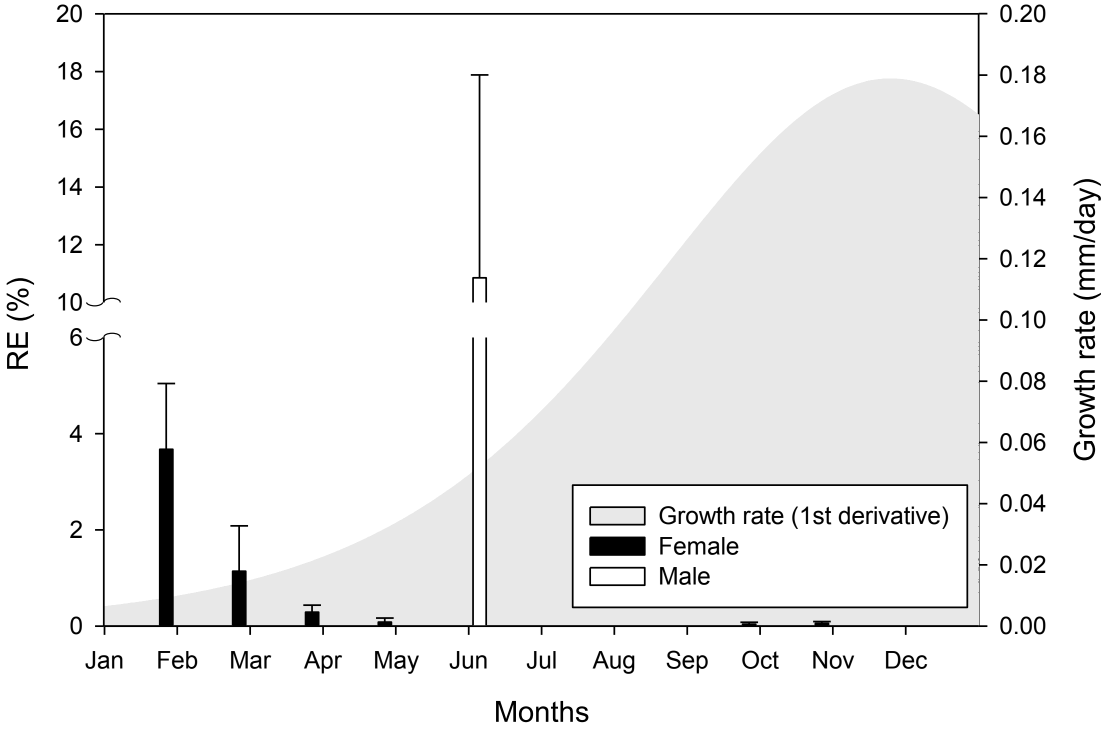

Figure II-6. Temporal variations in the daily growth rate and fecundity (RE) of *Cliona tenuis* during the study period. Vertical lines show the SE of RE.

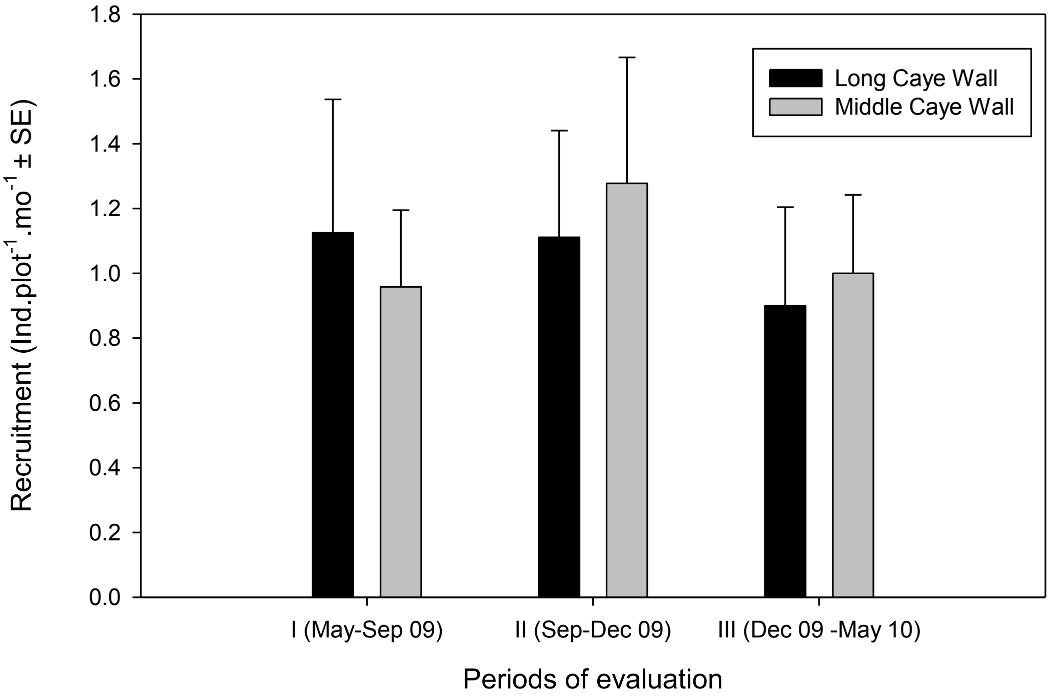

Figure II-7. Temporal variation in recruitment (ind.plot^{-1}) among periods of evaluation and between study sites. Vertical bars depict the standard error.

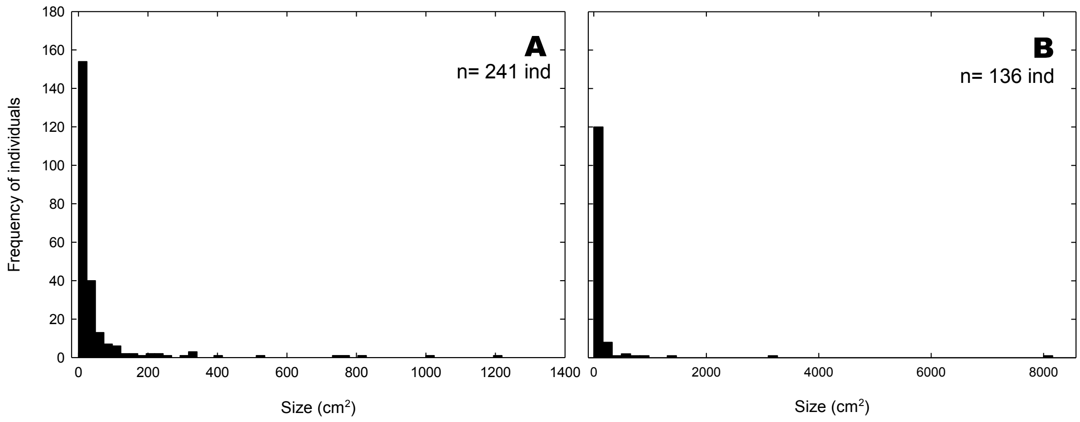

Figure II-8. Size structure of *Cliona tenuis* populations at: A. Long Caye Wall and B. Middle Caye Wall.

Discussion

Our data on the life history of *Cliona tenuis* at Glover's Reef Atoll is mostly consistent with previous reports of growth and reproduction for other clionaids (see López-Victoria, Zea et al. 2006; Carver, Theriault et al. 2010; Piscitelli, Corriero et al. 2011), and generate unexpected results in terms of reproduction, which are partly explained here. A more complete understanding is hindered by 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. *C. tenuis* appears to be gonochoric, as are other clionaid species (Piscitelli, Corriero et al. 2011). The sponge appears to trade-off growth and reproduction with seasonal variations in temperature during the year. Growth rate increase with water temperature, reaching a maximum in summer, as described in conspecific individuals of *Cliona caribbaea* and *Cliona celata* (Rützler 2002; Carver, Theriault et al. 2010), while the reproductive development occurs during winter and reaches its maximum during the warming up period from February to June. Spermatogenesis occurred ephemerally within 1 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 (6 months), as described for other Hadromerida and clionaid species (Pomponi and Meritt 1990; Rosell 1993; Piscitelli, Corriero et al. 2011). It is assumed that water currents carried the mature eggs through the oscula to the environment, where fertilization occurred (see Mariani, Piscitelli 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 vastifica*, oogenesis and fertilization occurs during calendar spring-summer (Nassonow 1883; Bergquist and Sinclair 1973; Mariani, Uriz et al. 2000; Rosell and Uriz 2002; Piscitelli, Corriero et al. 2011), while *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 clionaids, leading to a quick larval development and settlement, a process that usually takes no longer than few days (Warburton 1966; Mariani, Piscitelli et al. 2001). Although eggs can be transferred to the sponge surface in a protective gelatinous mass (Mariani, Piscitelli et al. 2001), the four-month time lag between the occurrence of mature eggs and sperm here observed would render survivorship and fertilization of the eggs impossible. We thus hypothesize that *C. tenuis* may be reproducing as a semi-continuous iteroparous organisms, 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 due to sampling effort and frequency was low. In any case, 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 clionaids, although some temperate clionaids undergo a cold-induced diapause with arrested growth and tissue regression (Cobb 1975; Pomponi and Meritt 1990; Carver, Theriault et al. 2010). Observations of *C. caribbaea* in Belize (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 the annual growth rate (31.4 ± 5.6 mm·yr^{-1}) are similar to values previously reported for *C. tenuis* individuals in contact dead substrate with algal turf in Colombia (24.0 ± 8.0 mm.yr–1, López-Victoria, Zea et al. 2006). In addition, the daily growth rate of *C. tenuis* was higher than the average growth rate reported for *C. caribbaea* in the Mesoamerican Barrier Reef (Rützler 2002). This may be a consequence of the effects of competition of *C. caribbaea* with other species, and because *C. tenuis* is thought to have a faster growth rate than other brown clionaids in the Caribbean (López-Victoria, Zea et al. 2006).

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 it 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 vs. reproduction has not been reported from any other clionaid. However, in *Pione truitti* sexual 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, which patterns differ between species (e.g., Pomponi and Meritt 1990: asexual and sexual rerpoduction trade-off; Leong and Pawlik 2010: growth and chemical defense trade-offs). Using data from a study comparing the competitive effects on growth rate (González-Rivero et al 2012), the seasonal increase of growth rate is also observed while *C. tenuis* is confronting by other organisms, such as corals. These observations support the logistic behaviour of growth rate throughout the year, as observed in *C. celata* (Carver, Theriault et al. 2010). However, it is important to highlight that seasonal replication is required to fully confirm our observations and that stronger competitors, such as macroalgae, dampen the observed seasonal effect (See appendix).

The life cycles of marine sponges are often controlled by seasonal patterns that are governed by temperature variation (i.e., Ettinger-Epstein, Whalan et al. 2007; Riesgo and Maldonado 2008; Bautista-Guerrero, Carballo et al. 2010), lunar cycles/tides (Usher, Sutton et al. 2004) or salinity (Roberts, Davis 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 clionaids (Mariani, Piscitelli et al. 2001; Rützler 2002; Fromont, Craig et al. 2005; Piscitelli, Corriero 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, Podesta et al. 2001). This comparison showed that temperatures in 2009 followed the long-term seasonal behaviour of temperature for the site (Figure II-9). Given, therefore, the potential implications of environmental factors driving changes in reproduction and growth of the sponge, it may also be expected in populations subjected to different environmental regimes (i.e., wave exposure, temperature, and salinity).

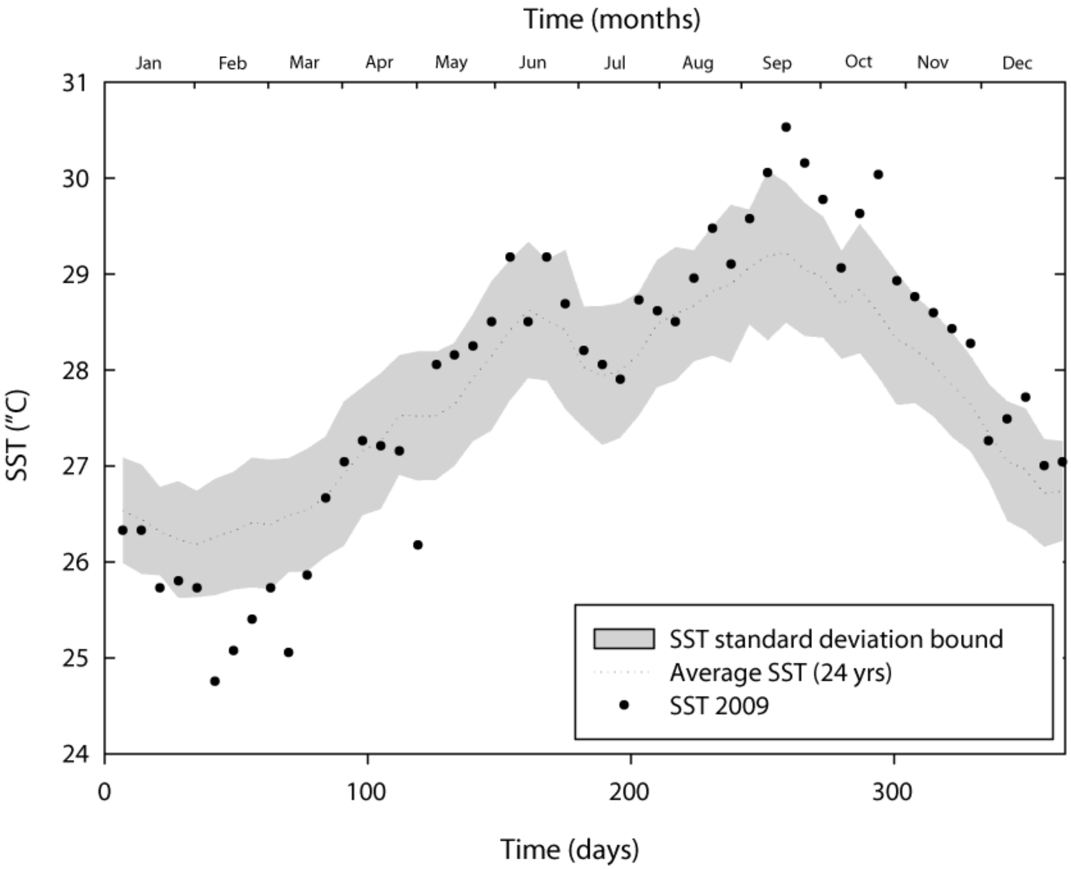

Figure II-9. Seasonal change in sea surface temperature (SST) at the study site over time (ordinal date in days of the year): average temperature over 24 years (grey band) and during the 2009 study year (filled dots). Source: AVHRR pathfinder, NOAA.

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 process other than larval supply. Newly recruited individuals were observed at a size of 0.5cm 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 asynchronically. 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 clionaid 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, *Cliona viridis*, peaks at 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, Carr et al. 1996).

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 bottleneck effect on the population (i.e., Muko, Sakai et al. 2001; Mumby, Hedley et al. 2006). Possible causal mechanisms include high mortality of adults, because predation, disease, hurricanes, etc (Loh and Pawlik 2009). On the other hand, severe competition with other taxa and nutrient limitation may constrain the potential of individuals to transition to larger size classes (Cebrian and Uriz 2006). Therefore, given the high growth and recruitment rates observed in bioeroding sponges, with increasing concerns about reef accretion (Hoegh-Guldberg, Mumby et al. 2007), and in view of the potential of bioeroding sponges to alter the transition trend of perturbed reefs (González-Rivero, Yakob 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 I, 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, by comparing different competitors the seasonal increase in growth rate in the period between August and December discussed in this manuscript when in competition with short turf is also observed, but to a lesser extend, when the sponge is in competition with mild competitors such as corals. However, stronger competitors such as the macroalgae *Lobophora variegata* and *Dictyota pulchella*, strongly over power the seasonal variations in growth rate of *C. tenuis*. Please refer to González-Rivero et al 2012 for more details.

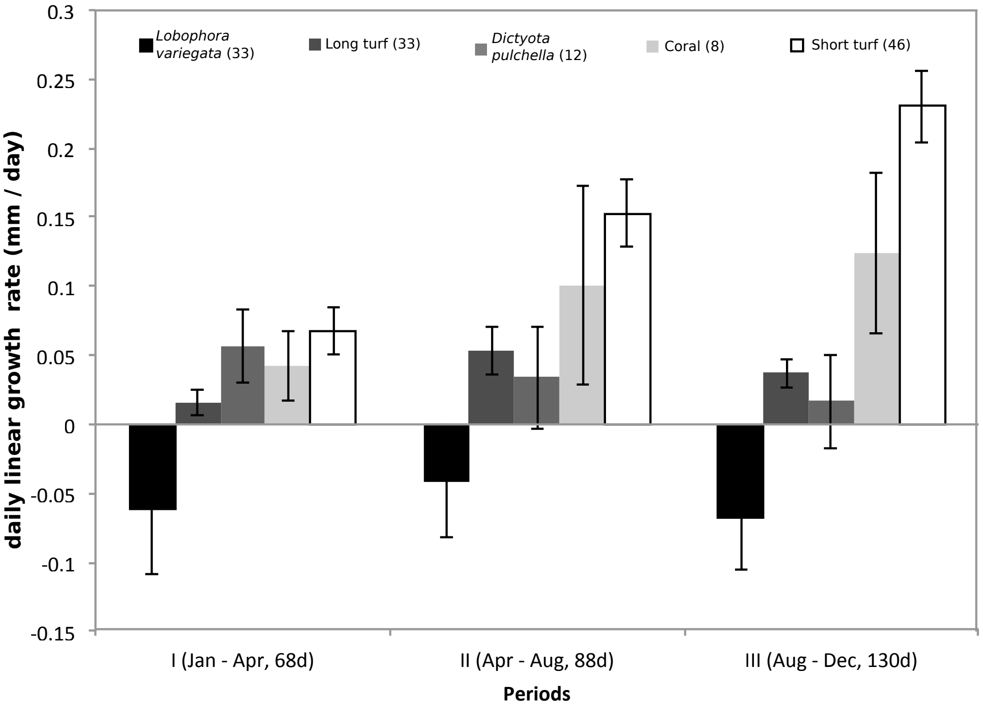

Figure I. Daily growth rate (linear extension) on *C. tenuis* along the three observational periods described in this manuscript and under constant competition with *Lobophora variegata*, *Dictyota pulchella*, Coral, short and long turf algae (more details of the methodology are explained in the methods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

~ III ~

IMPACTS OF MACROALGAL COMPETITION AND PARROTFISH PREDATION ON THE GROWTH OF A COMMON BIOERODING SPONGE

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Abstract

Clionaids, an abundant group of bioeroding sponges, are important competitors of corals, but their interactions with other major taxa are poorly understood. This study examined the relative effect of predation and macroalgal competition on the growth of *Cliona tenuis* at Glover's Reef Atoll, Belize. A field experiment was designed to isolate the importance of each factor and their interactions, by means of exclusion cages for fish predators and algal transplantation for competition (*Lobophora variegata*), during 286 days. To obtain complementary data on the net outcome of predation and competition *in situ*, predation intensity and the competitive effects of *Cliona* against five different competitors were monitored in the field. Competition with macroalgae significantly reduced the size of the sponge by 38% ± 11% (SE). Despite a high predation rate (1 bite $\cdot$ 100 $cm^{-2} \cdot h^{-1}$), no effect of the interaction with macroalgal competition was detected. The *in situ* observations found that *L. variegata* was the strongest competitor, limiting the growth of *Cliona*. Overgrowth of corals by clionaids and macroalgae continues to be a matter of concern, but our results suggest that the antagonistic competition between sponges and algae might weaken their potential combined effect on corals.

Key words: Porifera · *Cliona tenuis* · *Lobophora variegata* · Competition · Predation ·Caribbean · coral reefs

Introduction

Sponges are abundant and functionally important components of coral reef ecosystems (e.g., Díaz & Rützler 2001), because they act in a number of processes that support ecosystem functions (Díaz & Rützler 2001, Rützler 2004, Bell 2008). Bioerosion and competition are perhaps the most widely studied ways in which sponges contribute to the dynamics of coral reefs (Rützler 1975, López-Victoria et al. 2006, Bell 2008). Bioeroding sponges, mainly represented by clionaids and the genus *Aka* are often the dominant internal borer organisms on shallow coral reefs (Rützler 1975, Sammarco et al. 1987, Glynn 1997), and can cause as much as 95% of the total internal bioerosion (Scoffin et al. 1980, Pari et al. 2002). Clionaids members can develop into large colonies spreading over several square metres (Rützler 2002, Lopez-Victoria & Zea 2005). They are strong competitors for space, often overgrowing corals (Schönberg & Wilkinson 2001, Rützler 2002, Chaves-Fonnegra & Zea 2007).

Given the interactions between excavating sponges and corals, and their great resistance to environmental stress (Rose & Risk 1985, Vicente 1990b, Holmes 2000, Rützler 2002, Ward-Paige et al. 2005, Carballo 2006, Schönberg 2006), the ecosystem-level role of such sponges is expected to change as corals sustain greater levels of perturbation (Nyström et al. 2000, Rützler 2002, Ward-Paige et al. 2005): sponge abundance is expected to increase following coral reef disturbance (Ward-Paige et al. 2005, Schönberg & Ortiz 2009). However, few studies have examined the response of *Cliona* to rapid coral mortality, which is one of the most striking outcomes of disturbance on reefs (Rützler 2002, Ward-Paige et al. 2005, Schönberg & Ortiz 2009). Surprisingly, while increases in sponge density were found in the Florida reef tract, little change was found in the total cover of *Cliona delitrix* (Ward-Paige et al. 2005). This result implies that factors other than competition with living corals, such as competition with other taxa (i.e., algae), predation or sexual reproduction, may be constraining populations of *Cliona* on reefs.

To date, several studies have examined the role of predation (e.g., Dunlap & Pawlik 1996, Wulff 1997, Pawlik 1998, Pawlik et al. 2002, Wulff 2005) and competition (Vicente 1990a, Aerts & van Soest 1997, Aerts 1998) on non-clionaid massive sponges. Predation appears to be a major driver of the distribution of non-excavating sponge species on reefs (Wulff 2005, 2006). However, little is known about the effect of predation on *Cliona*. Moreover, even though many excavating sponges are competitively superior to corals (Schönberg & Wilkinson 2001, Rützler 2002, López-Victoria & Zea 2004, López-Victoria et al. 2006), their interactions with other benthic taxa are little understood (López-Victoria et al. 2006). Studies in the temperate Mediterranean and on the Australian Great Barrier Reef were undertaken to show that macrophytes may reduce the growth of *Cliona* spp., although the individual competitor species were not identified (Cebrian & Uriz 2006, Cebrian 2010). Similarly, monitoring of symbiotic clionaids in the Caribbean revealed that their growth can be reduced through competitive interactions with macrophytes, though, once again, the importance of individual competitors remains unclear (López-Victoria et al. 2006, Chaves-Fonnegra & Zea 2011).

This study investigated the effect of macroalgal competition and fish predation on the growth of a common excavating sponge in the Caribbean, *Cliona tenuis* Zea & Weil 2003. The study was comprised of three parts: I) a factorial experiment to distinguish the effects and interaction of (a) competition by the common fleshy alga *Lobophora variegata* Lamouroux 1809, hereafter referred to as *Lobophora*, and (b) fish predation on the growth of *C. tenuis*; II) monitoring of *in situ* and non-manipulated interactions between *C. tenuis* and other benthic taxa to compare the Study I to the competitive outcomes with a wider range of (non-manipulated) species; and III) *in situ* estimates of predation intensity to better understand the composition of species involved and quantify the rate of the process.

Materials and methods

This study was conducted at Glover's Reef Atoll Marine Reserve, Belize (Figure III-1), located approximately 30 km off the Central American mainland and 15 km east from the Mesoamerican Barrier Reef. Studies were conducted between February and November 2009 (~41 weeks) on the windward side of Glovers Atoll on a *Montastraea* dominated fringing reef (16.753° N; 87.779° W).

Study I. Manipulation of predation and competition

72 Individuals of *Cliona tenuis* were haphazardly chosen on SCUBA by swimming along a depth contour of 8 m. The mean size of sponges used in this study was 53 cm^2 ± 10 cm^2 (± SE), i.e. they had an approximate diameter of 8 cm. All sponges were tagged and mapped to allow repeated measurements. Specimens were chosen in the field, based on the morphological descriptions for *C. tenuis* (Zea & Weil 2003), and species identification was corroborated *a posteriori* in the laboratory, using a subsample of ten sponges randomly chosen from previously tagged sponges. For these samples, tissue was digested in 70% nitric acid to obtain clean

spicules, tylostyles and spirasters. Permanent spicule slides were prepared for microscopic examination, mounted on Araldite (Huntsman UK). Total length and axis width were measured in 15 randomly chosen spirasters per sample under a light microscope (1250x in immersion oil) using the software Openlab (Improvision 2008). Spicule measurements and the external morphology of individuals were compared to the published descriptions of the three common species of brown Caribbean Clionaidae (Zea & Weil 2003), and our samples were identified as *C. tenuis*.

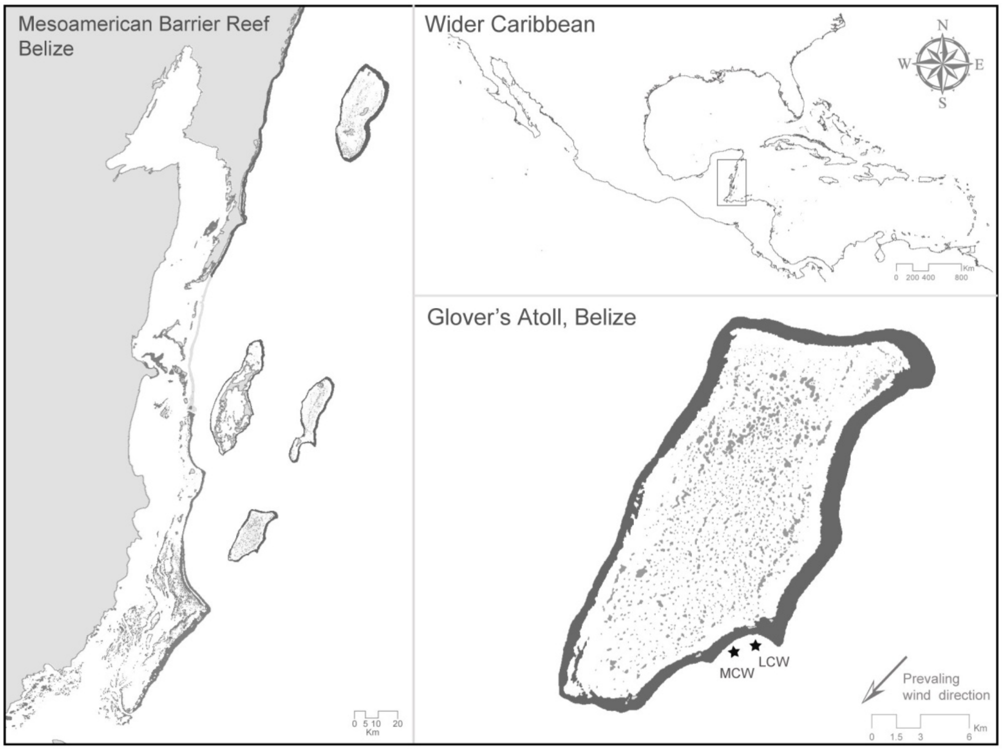

Figure III-1. Location of study site at Glover's Atoll in the Mesoamerican Barrier Reef (Belize), and the relative location of the atoll in the wider Caribbean region. Source data: Global Self-consistent, Hierarchical, High-resolution Shoreline database (GSHHS) and Millennium Coral Reef Mapping project (MCRM).

The effects of macroalgal competition and parrotfish predation on the growth of *Cliona* were tested using a fully orthogonal manipulative experiment over 286 days. The macroalgal effect was carried out for the one of the most abundant algal species, *Lobophora variegata*. Any pre-existing algal competition was eliminated by clearing a 10 cm belt around the periphery of all the sponges, using wire brushes. Polyvinyl chloride (PVC) exclusion cages of 40 x 40 x 50 cm and a 5 cm mesh width were used to control for the effects of predation and herbivory on algae.

Cage controls had two lateral panels removed and were used to measure the potential cage effects of attenuated water flow and suppressed light on the sponge growth, while allowing fish predation. Given that *Cliona tenuis* maintain a symbiotic relationship with zooxanthellae (Granados et al. 2008), Photosynthetic active radiation (PAR, 400-700 nm) was measured to evaluate the extend of attenuation of a potential resource for the individuals under study. Measurements were carried out every 30 min during the experimental period inside and outside the cages using underwater PAR loggers (Dataflow Systems 2008). Individuals of *C. tenuis* were randomly allocated to 6 treatments listed below (Figure III-2).

Treatment 1 - macroalgal competition (n=12)**:** Sponges were caged to control for the effect of predation on the sponge. Rubble pieces colonized by *Lobophora* were positioned next to sponges such that algal fronds were in direct contact with approximately 75% of the perimeter of the sponge. Stainless steel and galvanized nails were driven into the dead coral substrate 10 cm from the sponge perimeter and used to affix the rubble pieces using cable ties.

Treatment 2 - predation (n=12). Sponges were uncaged and exposed to predators. Potential algal competitors were regularly cleared.

Treatment 3 - combined effect of macroalgal competition and predation (n=13)**:** To understand interactive effects of both stressors, *Cliona tenuis* was uncaged and maintained in contact with *Lobophora* (as in treatment 1).

Treatment 4 - Sponge growth in absence of predation and competition (n=11)**:** Predation and competition effects were removed using cages and clearing each sponge periphery.

Treatments 5 & 6 - Cage effects (n=12x2)**:** Testing for experimental artefacts on caged sponges due to potentially reduced light attenuation and water flow (Rosell & Uriz 1992, Hill 1996, Schönberg 2006). Two treatments with partial cages were used: predation-only, no algal contact (T5) and the combined effect, predation and algal competition (T6). The caging effect was evaluated by comparing these treatments to the equivalent treatments that lacked cages, while both treatments allowed predators to feed on the sponge.

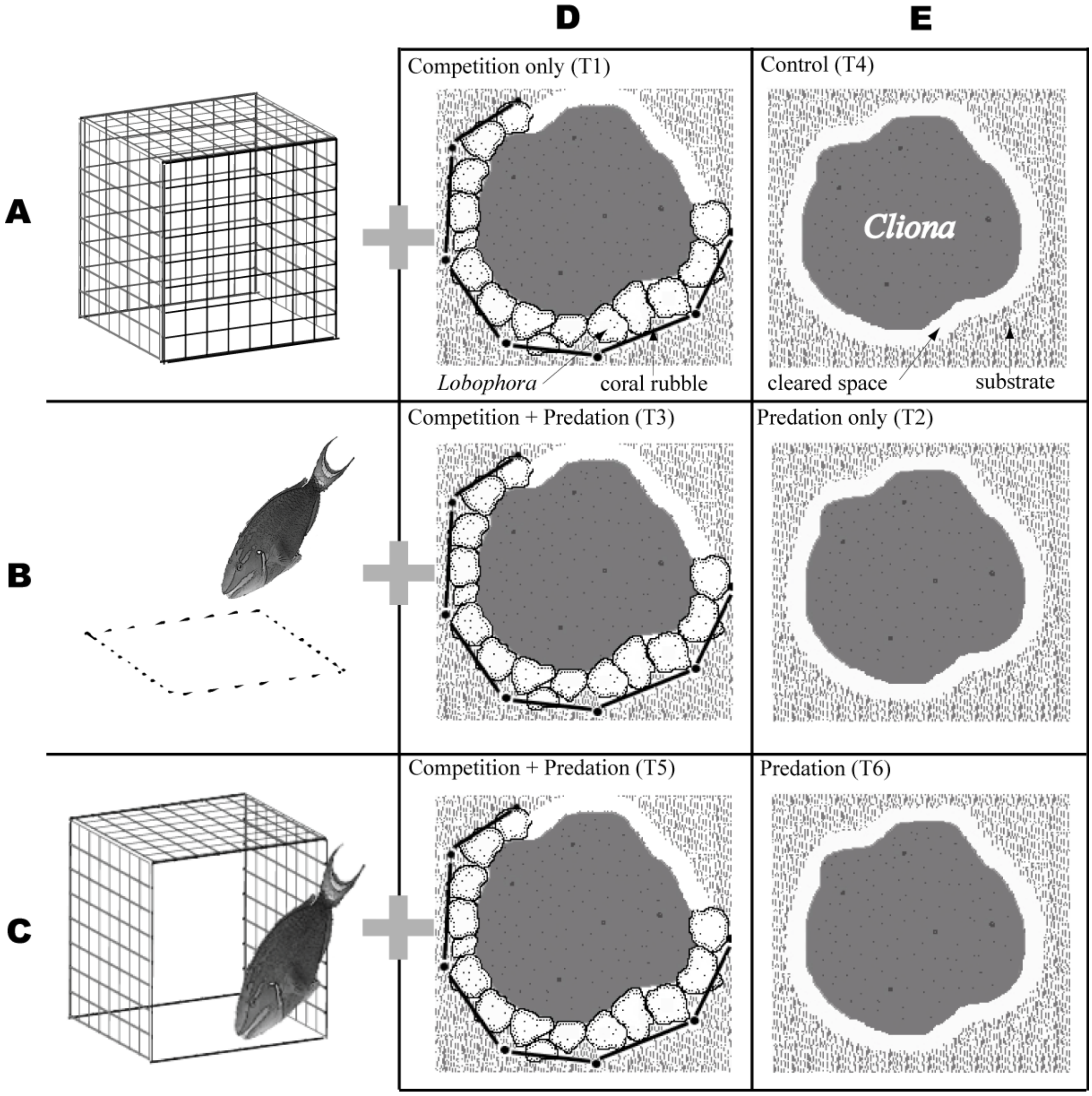

Figure III-10. Schematic diagram of the experimental design to evaluate the effects of macroalgal competition and predation of the growth of *Cliona*. Rows show the treatments under predation exposure: A) predation excluded (Treatments 1 and 4; n = 12 & 11 respectively), B) predation exposed (Treatments 2 and 3; n=12 & 13 respectively) and C) Predation exposed but simulating caging effects. Columns D and E , show those treatments in which *Cliona* was contact with *Lobophora* (D, Treatments 1, 3 and 5; n =12,13 & 12 respectively) or without algal competition (E, treatments 2, 4, 6; n = 12, 11 & 12 respectively).

Maintenance of treatment conditions was performed every three weeks, which included: cleaning cages, replacing algae (when needed to keep constant the amount of competition) and clearing the sponge perimeter in the appropriate treatments. Sponges were filmed every three months to determine sponge area, using the software VidAna (Hedley 2006). Photographic parallax error was avoided by using a frame whose area was previously known and which was placed in the same plane as the sponge. The depth of tissue penetration into the substrate for species of the *Cliona viridis* complex is limited to the first couple of centimetres, possibly due to the autotrophic association with zooxanthellae (Bergman 1983, Acker & Risk 1985, Lopez-

Victoria & Zea 2005). Therefore, for this experiment, individuals of *C. tenuis* were considered to be sheets of constant thickness, independently of the experimental treatment, and growth is directly proportional to their lateral expansion and reported as the difference in size between the same individual, at the beginning (t = 0 days) and end of the experiment (t= 286 days).

To assess the significance of competition and predation effects on sponge growth, a Generalized Least Squares approach to a two-factor Analysis of Covariance (ANCOVA GLS) was developed (method Restricted Maximum Likelihood). The included predicted variables were predation (T2 and T4) and competition (T1 and T4), as two-level factors (presence/ absence), which accounted for interactions (T3). Initial size of each individual (continuous) was included into the analysis as a covariate. The response variable used in the analysis was somatic growth (cm^2) after 286 d, which was log transformed (ln(Growth+100)) to satisfy assumptions. The variance of residuals was fitted to the model using a combination of the functions VarIdent, to account for heterogeneous variance within explanatory variables, and VarFixed to account for the over-dispersion of residuals with the covariate (Pinheiro & Bates 2000, Zuur et al. 2009).

Possible cage effects were also tested using two separate ANCOVA GLS analyses on comparable treatments under caged and partially caged conditions. For both analyses initial size was included as a covariate. The response variable was the log-transformed growth after 286. The first test compared the cage effect between treatments exposed to predation (uncaged: T2, partially caged: T6). The second test evaluated the effect between treatments exposed to the interaction of predation and competition (uncaged: T3 and partially caged: T5). For the second test, the model was fitted including a variance structure to allow a heterogeneous variance of residuals within explanatory variables and correlated to the covariate, which was not needed for the first test. This variance structure was adjusted to the model using the function VarIdent (Pinheiro & Bates 2000, Zuur et al. 2009). Homoscedasticity and normality of residuals in all analyses were tested graphically (McGuinness 2002, Zuur et al. 2009), and the graphs from the final models are shown in Appendix A. Analyses were performed using R, and the “nlme” package (Pinheiro et al. 2009, R Development 2010).

Study II. Un-manipulated interactions of Cliona tenuis *against other competitors.* Interactions between *Cliona tenuis* and five common competitor categories were evaluated by measuring the linear advance of each competitor over time. A total of 113 sponges were randomly selected and tagged in January 2009. Competitor categories were: 1) Coral (n = 7), involving the species: *Montastraea annularis, M. faveolata, Siderastrea siderea, Porites porites* and *Agaricia agaricites*; 2) Short algal turf (height < 10mm; n = 44); 3) Tall algal turf (height >10 mm; n = 33), which can trap sediment and forms a dense mat; 4) *Dictyota pulchella* (n = 12); and 5) *Lobophora variegata* (n = 13). The initial position of the sponge-competitor interface was tagged using a stainless steel and galvanized nail. Approximately every 90 days measurements of the distance from the nail to the edge of the interaction were taken using callipers (±0.01 mm). Because the growth of the sponge is not entirely symmetrical, the linear expansion was measured across an imaginary line directed to the centre on the sponge, and in a window of 1cm of the perimeter of the sponge to minimize sampling errors. Positive values represent a linear advance of the sponge over the competitor, and negative values indicate sponge retraction. We present the final outcome of the interaction, as linear growth, after 286 days of evaluation, which we term ‘linear advance’.

Competitive outcomes of sponge linear advance were evaluated by fitting a Linear Model using a generalized least squares approach (GLS, Estimation method: Restricted Maximum Likelihood). The response variable was sponge linear advance, log transformed (ln(‘linear advance’+100)), and the predictor variable was the species ID of each competitor (categorical, five levels). Because within-group heterogeneity of variance was observed, the structure of the variance was defined using the function varIdent to allow for different standard deviations of residuals among competitors (Pinheiro & Bates 2000, Zuur et al. 2009). Size and linear advance were not correlated (General Linear model, t-statistic = -0.569, df = 28, p = 0.574), therefore size was not included in the analysis. For these tests, we employed the package nlme (v3.1) using the software R v2.13.0 (Pinheiro et al. 2009, R Development 2010). The model was evaluated using graphical methods (see Appendix I, Figure I-4). Post-hoc comparisons among the effects of competitors on the linear advance were then evaluated using an Unequal N Tukey's HSD test (Software STATISTICA v6.0, StatSoft 2001).

Study III. Predation levels. Fish predation intensity was measured using static underwater video cameras, placed between 1-2 meters from the sponge, over periods of 1 h. A total of 12 h of High Definition footage was taken on 12 randomly selected sponges in November 2009. Approximate size of any evaluated sponges was 50 cm^2. Fish species was identified from the footage and for each individual the number of bites was counted. Data was pooled due to the low predation intensity, only considering those species that left bite marks on the sponge tissue, and therefore consumed the sponge. A species list the fishes observed biting on the sponge is presented. Predation intensity was estimated as the average number of bites per hour on each 100 cm^2 of the sponge (bites · 100 cm^{-2} · h^{-1}).

Results

Study I. Manipulation of predation and competition

In the absence of competition by *Lobophora* and predation by parrotfish *Cliona tenuis* grew an average of 24.8 cm^2 ± 23.1 cm^2 (mean ± CI_{95th}) after 286 days, which was significantly dependent on the initial size (ANCOVA GLS; df = 1, 38; F= 12.32; $p < 0.005$; Table 1; Figure III-3). *Lobophora* was found to overgrow sponge tissue, which appeared transparent before necrosis. Nearly 12 cm^2 sponge colony (11.98 cm^2 ± 11.2 cm^2; Figure III-3) was overgrown by *Lobophora* in 286 d (ANCOVA GLS; df = 1, 38; F = 5.33; $p < 0.05$; Table III-1). Sponges exposed to predation did not change size when compared to control treatments (ANCOVA GLS; df = 1, 38; F = 0.475; p = 0.495; Table III-1; Figure III-3). The combined effect of macroalgal competition and exposure to fishes did not interact significantly and prevented sponge growth causing a change in size of only 6.1 cm^2 ± 19.2 cm^2 (Mean ± CI_{95th}; ANCOVA GLS; df = 1, 38; F = 0.602; p = 0.443; Table III-1; Figure III-3). Most sponges exposed to predation received at least one bite mark in the period of 286 days, but the recovery of scars was fast, being indistinguishable from the rest of the sponge after approximately two weeks.

Table III-1. Effects of macroalgal competition and fish predation on growth (*G*) of *Cliona tenuis*. The table shows the summary outcome of a two factor ANCOVA GLS using initial size as a covariate. The degrees of freedom (df), Sum of Squares (SS), F statistic (F) and the significance (p) of each factor are shown. The asterisks mark those factors that showed a significant effect. The analysis was performed using the software R, v2.13.0 package nlme (Pinheiro et al. 2009, R Development 2010). Assumptions of the model were graphically evaluated and are shown in the Appendix I (Figure I-1).

Parameters	df	SS	F	p	
Competition (A)	1	0.5078	5.3369	**<0.05**	*
Predation (P)	1	0.0452	0.4749	0.495	
A : P Interaction (AP)	1	0.0573	0.6023	0.443	
***Size* (covariate)**	1	1.1730	12.323	**<0.005**	**
A : ***Size***	1	0.0227	0.2385	0.628	
P : ***Size***	1	0.0278	0.2924	0.592	
A : P : ***Size***	1	0.0749	0.7873	0.381	
Residuals	38	3.6615			

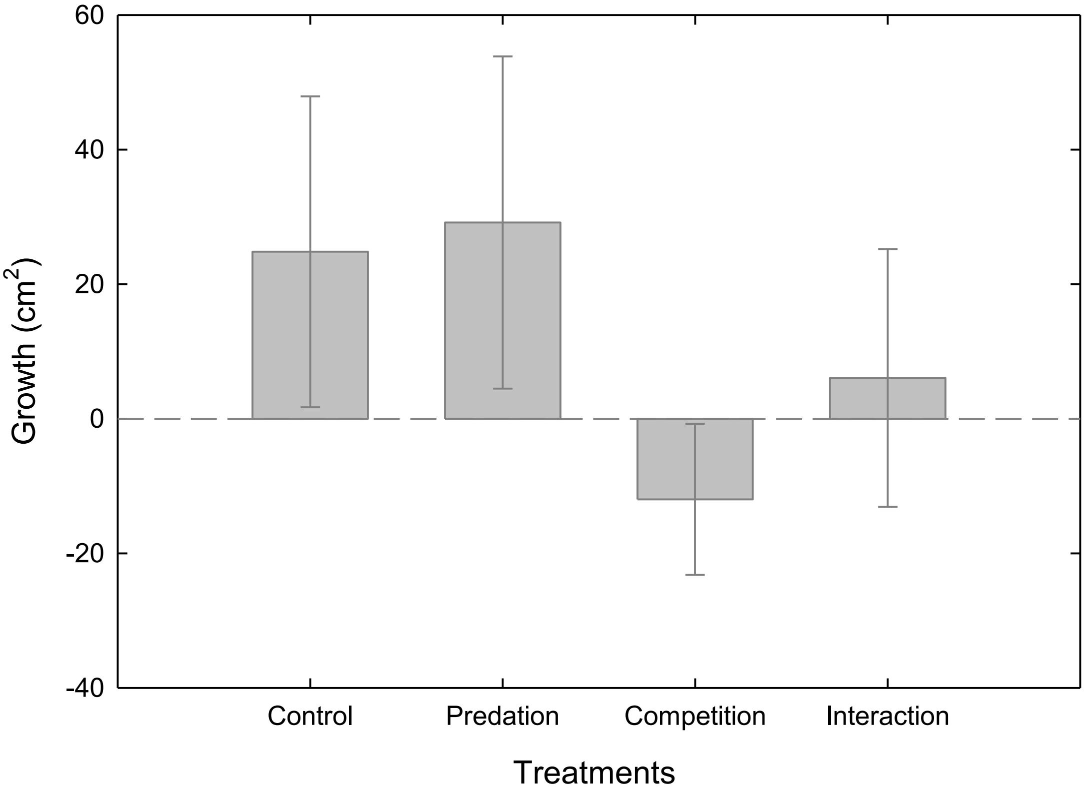

Figure III-11. Average growth (area) of *Cliona* under different treatment conditions after an experimental period of 286 days. Vertical bars are the Confidence of Intervals (α = 0.05) of the respective means, and the dashed line shows null growth. Please refer to Figure 2 for a detailed description of the treatments.

Cages significantly attenuated PAR by 18% ± 2% (SE) of ambient levels (one-tailed paired t-test, $p < 0.001$). This light attenuation only weakly reduced the growth of *Cliona tenuis* and was only associated with non-significant differences between comparable partially caged and uncaged treatments (Figure III-4): Predation (ANCOVA GLS; df = 1, 17; F = 0.661; p = 0.427; Figure III-4a) and predation + competition (ANCOVA GLS; df = 1, 18; F = 2.065; p = 0.168; Figure III-4b).

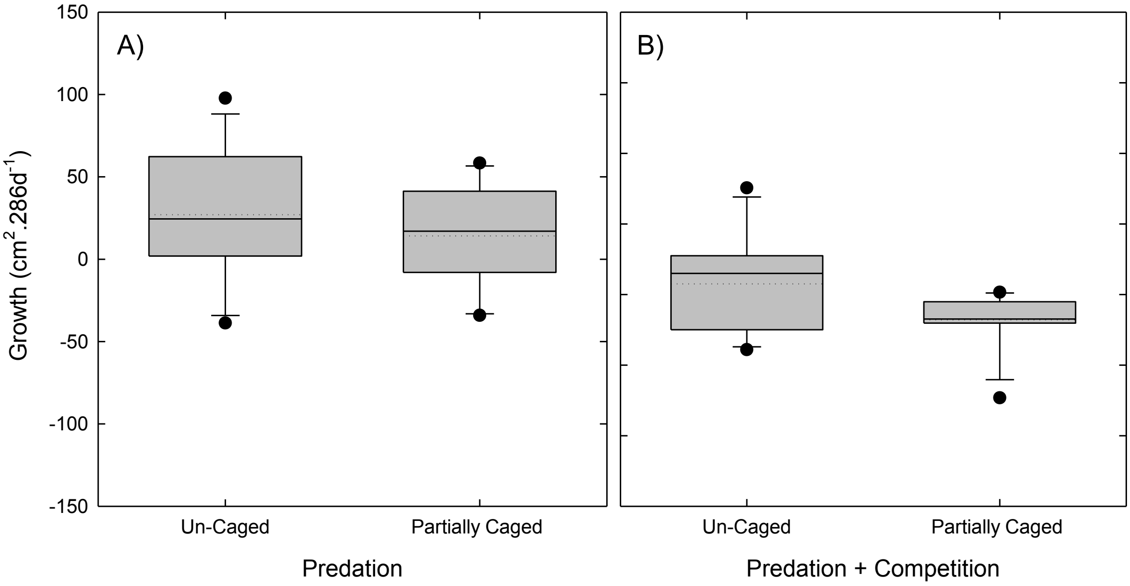

Figure III-12. Caging effects on sponge growth of sponges under comparable treatments, but exposed (partially caged) or not (uncaged) to cage effect over a period of 286 days. A) Only Predation effects (T2 vs. T5), and B) Combined effect of algal competition and predation (T3 vs. T6). No significant caging effect was observed in either of these comparisons (see Results section). The box plot compares the growth of sponges in treatments without caging influence (cage control) versus uncaged treatments. Data points out of the 5th and 95th confidence intervals (bars) are represented by dots, and box indicates the inter-quartile range. The solid line inside the box represents the median, whereas the dotted line represents the mean. Please refer to Figure 2 for a detailed description of the treatments and sample sizes.

Study II. Un-manipulated interactions of Cliona tenuis against other competitors

On average, the growth of *Cliona tenuis* significantly varied among competitors, where the sponge was able to grow linearly over all but one of the competitor categories, the exception being *Lobophora variegata* (GLS; df = 4, 104; F = 24.41; p < 0.0001). In the un-manipulated observations *Lobophora* overgrew *C. tenuis* by 12.7 mm ± 6.2 mm (mean ± $CI_{95\%}$; Tukey's HSD; p < 0.05; Figure III-5). Short turf offered the least resistance and was overgrown by *C. tenuis* at a rate of 26.7 ± 5.2 mm linear extension (mean ± $CI_{95\%}$; Tukey's HSD; p < 0.05; Figure III-5), followed by corals, which did not significantly differed from short turf (Table III-2). The other two competitors significantly reduced the linear extension rate of *C. tenuis*, but their relative impacts did not differ significantly from one another (see Table III-2 for details). No evidence of collateral damage by tagging nails was observed (Appendix B).

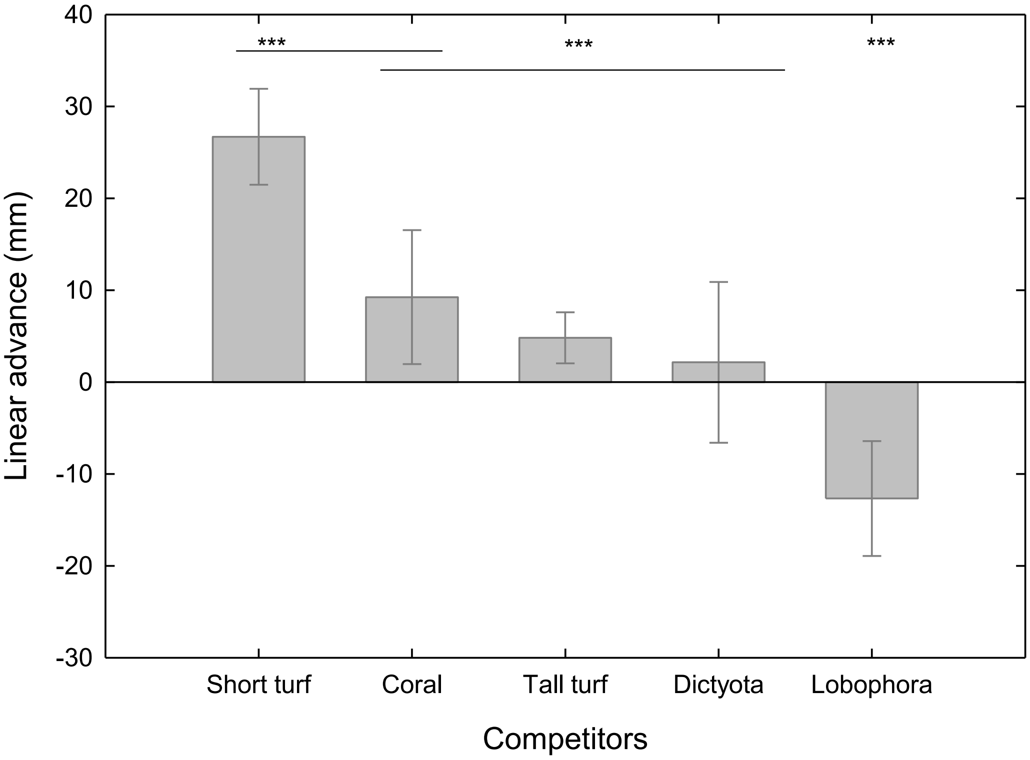

Figure III-13. Linear growth of *Cliona tenuis* neighbouring common competitors over 286 days. Vertical bars show the Confidence Intervals (α = 0.05). Significant differences were observed on the sponge growth according to the species in competition. Horizontal bars group the categories that did not show significant differences among them. Asterisks show the categories where significant differences were found using unequal N Tukey's HDS test for post-hoc comparisons. Please refer to Table III-2 for details.

Table III-2. Effects of the interaction with other competitors on the linear advance of the sponge after 286 days. The effect was evaluated fitting a Linear Model (Generalized least squares approach (GLS), accounting for heterogeneity of variance within the explanatory variable).The ID of competitors was included as the predictive variable to explain changes in the linear advance of the sponge (GLS; df = 4, 104; SS = 45.823; F = 24.41; $p < 0.0001$). The table shows the outcome of Unequal N HDS test, (Error: Between MS = .41606, df = 104) which includes the p-values of the pairwise comparisons among competitors. The analyses were performed using R (v2.13.0, The R Foundation for Statistical Computing 2011) and STATISTICA (v6.0, StatSoft 2001). Assumptions of the model were graphically evaluated and are shown in the Appendix I (Figure III-A-3).

Parameters	Short Turf	Coral	*Dictyota*	Tall turf	*Lobophora*
Short Turf		0.159	**<0.001**	**<0.001**	**<0.001**
Coral			0.828	0.972	**<0.050**
Dictyota				0.978	**<0.050**
Tall turf					**<0.005**
Lobophora					

Study III. Predation levels

Parrotfish were the most frequent predators observed biting *Cliona tenuis.* Although the data were pooled because of the low number of observations per species of fish, the following species were involved, from the most to the fewest bites: parrotfish *Scarus iserti*, *S. coelestinus*, *Sparisoma viride*, the damselfish *Stegastes planifrons*, *S. partitus*, and the surgeonfish *Acanthurus coeruleus*. *S. viride and S. coelestinus* bit more intensively and left obvious marks on *C. tenuis* compared to the other fishes (*S. iserti*, and *S. planifrons*, *S. partitus*, *A. coeruleus*), which left no visible impact of predation. The latter species were therefore excluded from the analysis, assuming that their activities did not significantly damage the sponge. Using the remaining two parrotfish species, the average predation intensity per sponge recorded was: 1.0 ± 0.6 bites · 100 cm^{-2} · h^{-1} (mean ± SE).

Discussion

Cliona tenuis and closely related species have been found to be important competitors for space (Schönberg & Wilkinson 2001, Rützler 2002, López-Victoria et al. 2006), being one of the fastest growing species among congeners (López-Victoria et al. 2006). However, the factors controlling the growth of *C. tenuis* populations after coral decline are unclear. Our study reveals that macroalgal competition can significantly compromise the growth of individual sponges, while the effects of predation on growth appear to be undetectable. This conclusion adds to an emerging view that sponges and algae compete (Cebrian & Uriz 2006, López-Victoria et al. 2006, Chaves-Fonnegra & Zea 2011) but also highlights the species-specific nature of such interactions. Here, the encrusting macroalga *Lobophora variegata* is shown to be the strongest competitor. Indeed, *Lobophora* appears to be an important competitor, most notably with corals (i.e., Steveninck van et al. 1988, Nugues & Bak 2006, Box & Mumby 2007, Foster et al. 2008, Diaz-Pulido et al. 2010).

While *Cliona tenuis* was often observed to be competitively superior to other taxa, such as corals and macroalgae (except *Lobophora*), competition still slowed down the lateral growth rate of the sponge. Previous studies have examined the mechanisms of sponge-coral interaction (López-Victoria et al. 2006, Chaves-Fonnegra & Zea 2007, Chaves-Fonnegra et al. 2008) and found that clionaids can avoid the mechanisms of coral defence by undermining their polyps (López-Victoria et al. 2006, Chaves-Fonnegra & Zea 2007). Although this is a physical interaction, polyp mortality might be achieved by chemical toxicity once the sponge is in contact with corals (Chaves-Fonnegra et al. 2008). In the case of confrontations between clionaids and macrophytes, however, much remains to be investigated.

Previous studies of coral-algal interactions might provide a framework for exploring algae-sponge interactions. These studies show that algae can affect their competitors through several mechanisms: (1) shading and asphyxiation, (2) compromising, by shading, the contribution of symbionts to the energy budget, (3) reduced access to food resources by compromising filtering/up-taking efficiency, (4) allelopathic interaction and (5) mechanical abrasion, where allelopathy and shading effects can play a large role (see McCook et al. 2001). Among the algal species, *Lobophora variegata* and *Dictyota bartayresiana* were shown to be strongly allelophatic when interacting with corals, causing bleaching and mortality of the coral tissue when they are in contact with the algae (Rasher & Hay 2010). Shading was also implicated as a major cause of stunted coral growth during interactions with macroalgae, in particular by *Lobophora* because of its morphological structure (Box & Mumby 2007).

The above mentioned mechanisms of macroalgal competition will be of particular concern for the group of brown clionaids, as they are characterized by their symbiotic association with zooxantellae (Granados et al. 2008), and the lack of light has been shown to reduce the growth rate of symbiotic clionaids when they are shaded to 3-5% of ambient levels (Hill 1996, Schönberg 2001). This suggests that the mechanisms by which *Lobophora* is competitively superior to *Cliona tenuis* are may be due to allelochemical interaction and/or its shading effects on the sponge. Similar mechanisms might apply to the interactions of the sponge with *Dictyota* spp. Other competitors, such as long turf may compete by offering physical resistance to the sponge expansion by trapping sediments and forming a thick mat acting as a barrier (see Purcell 2000, Birrell et al. 2005). Although the competition of *C. tenuis* over corals may itself rely on chemical components present in the sponge (Chaves-Fonnegra et al. 2008), allelochemical assays are needed to address the potential effects of algal toxic compounds on the sponge tissue or *vice versa*.

We found no direct effect of predation on the growth of *Cliona tenuis,* supported by previous observations in other congeneric excavating sponges, *C. varians and C. delitrix* (Hill 1998, Chaves-Fonnegra & Zea 2011). In contrast, studies on free-living or semi-cryptic sponges have clearly shown strong negative impacts of predation upon their growth and survival (i.e., Wulff 1997, Pawlik 1998, Loh & Pawlik 2009), which suggests that predation is an important driver of the abundance and distribution of coral reef sponges, at list is the case in fleshy species (Wulff 2005). Whether our observations arise because of relatively low predation rates or the conciliation of potential predation effects by exceptionally rapid healing of lesions of clionaids is not yet clear (see Guida 1976, Chaves-Fonnegra & Zea 2011). On the other hand, parrotfish have been identified as opportunistic predators of sponges in the Caribbean (Dunlap & Pawlik 1996, Wulff 1997, Dunlap & Pawlik 1998). Therefore, parrotfish limited impact on *C. tenuis* might simply reflect a relatively low preference for such sponges, possibly because of low palatability, low abundance, or a relative paucity of convex surfaces that parrotfish prefer to feed on. It should be noted that a low abundance of predators is unlikely to be a factor in our study because parrotfish biomass at our study site is among the highest levels in the Caribbean (Mumby 2006). We also point out that while fish predation might not strongly influence the dynamics of adult *C. tenuis* in our study, predation might be a more important problem at other stages of ontogeny, such as recruits and juveniles.

Although predation did not interact with macroalgal competition, a positive growth of sponges under the interaction treatment (treatment 3) was observed. This can be explained by the effects of herbivory on the transplanted algae, which may compromise the rate of advance of *Lobophora* even when the proportion of competition was maintained constant over the experimental time, as well as during the observational study (Study II). Therefore the growth rate of sponge may be expected to change along with changes in grazing intensity, highlighting the importance of herbivory mediating interactions among major benthic components of coral reefs (Coyer et al. 1993, Cebrian & Uriz 2006, Calderon et al. 2007, Mumby et al. 2007). Further, rapid increase of the encrusting sponge, *Chondrilla nucula*, after post-bleaching coral mortality in Belize might be explained by the depletion of macroalgal competition in an overgrazed system (Aronson et al. 2002).

A more complete understanding of the roles of herbivory, competition and predation on the dynamics of clionaids requires expansion to include a wider range of body sizes and other demographic processes such as fecundity and survival, as well as seasonal changes in the intensity of these interactions given the phenology of clionaids. In addition, while competition can mediate vital rates of benthic invertebrates, the role of other attributes, such as the physical environmental or alternative interaction pathways among benthic individuals, such as food resource leaking, should also be considered (Preciado & Maldonado 2005, van Duyl et al. 2011). With such information, individual-based observations of ecological processes can be scaled up to estimate responses at the population scale. Recent theoretical explorations of the competitive traits among sponges, corals and macroalgae showed that competitive abilities, and the diversion of herbivory into predation by excavating sponges are relevant on predicting the trajectory of the ecosystem into alternative stable states (González-Rivero et al. 2011). Further, with concerns rising about the future of reef accretion (Hoegh-Guldberg et al. 2007), achieving greater predictive power for the response of bioeroding sponges to changes in community structure is becoming increasingly urgent.

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Appendices

Appendix A. Graphical evaluation of fitted models

The following figures show the evaluation of residuals from the fitted models in each study. Please refer to the Materials and Methods section for details. This evaluation was done using graphical methods for normality and homoscedasticity, as detailed in Rutherford (2004), McGuinness (2002) and Zuur et al. (2009).

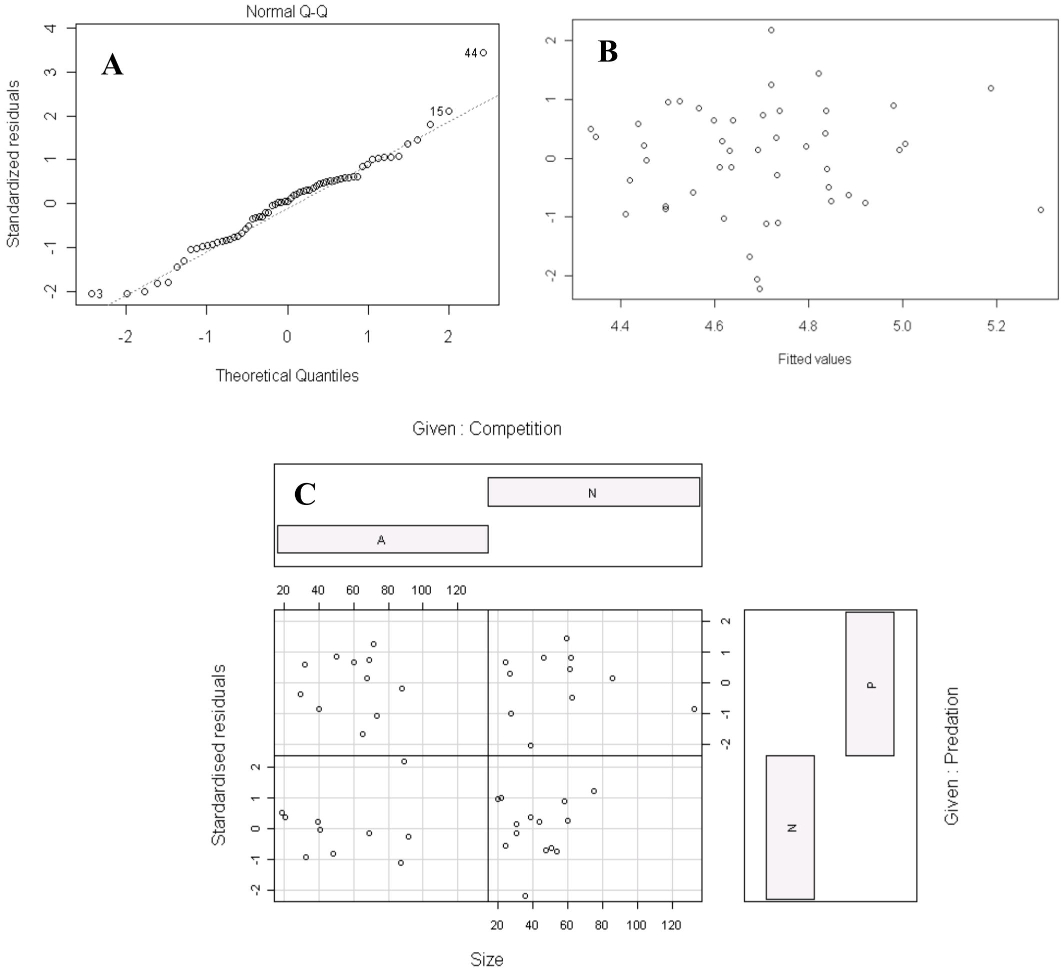

Figure III-A 1. Graphical evaluation of Normality and Homoscedasticity of residuals after fitting the Analysis of Covariance to test the effect of competition and predation on the growth of *Cliona tenuis*. Please refer to the section Study I in Methods for details. Panel **A** show a Q-Q plot of the standardized residuals against the theoretical Quantiles in a normal distribution. The dashed line shows the expected normal distribution of residuals and the open circles, the observed distribution. This plot shows a similar distribution of residuals when compared to the expected normal distribution. Panel **B** show the distribution residuals across the fitted space, where no dispersion is observed. Panel **C** show a combined plot of the standardised residuals within the levels of the explanatory variables Predation (P) and Competition (A), accounting for their interaction with the covariate. The graphs show a homogeneous distribution of results across the parameter space.

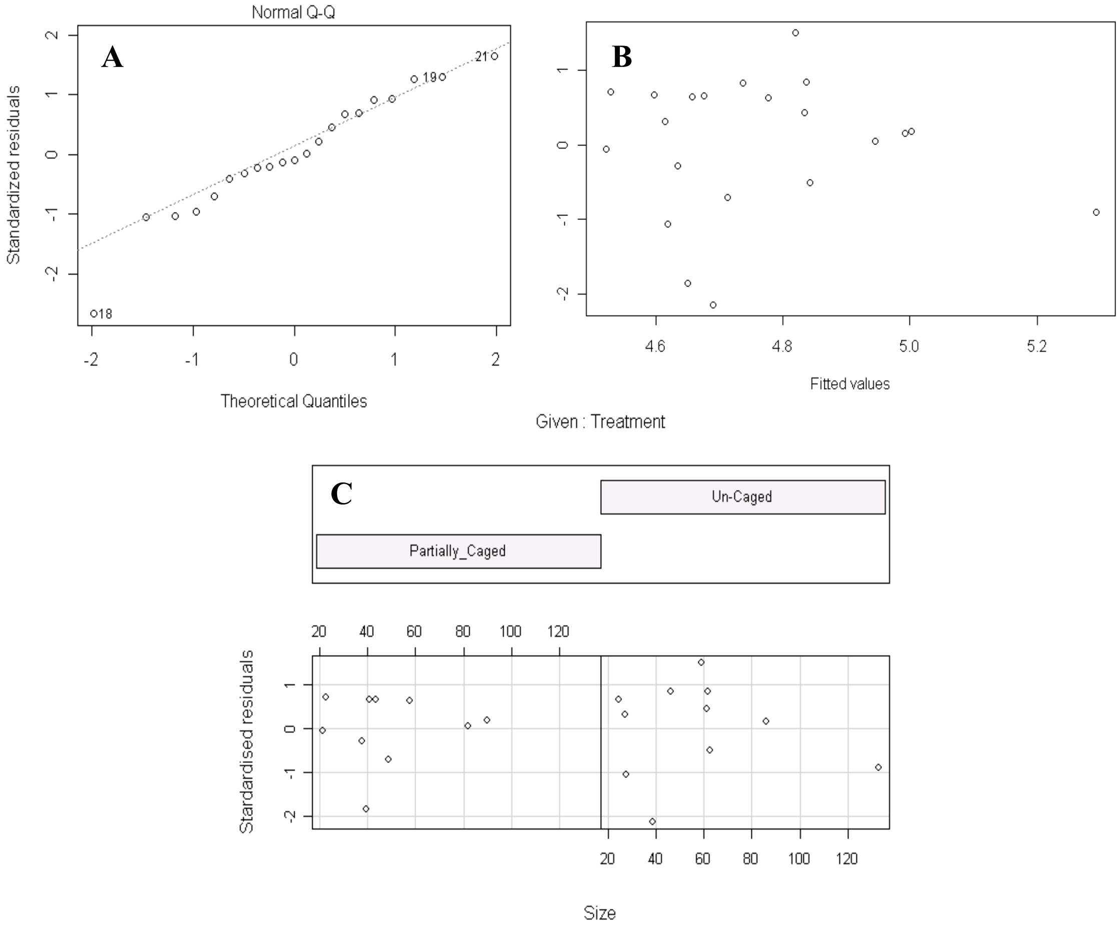

Figure III-A2. Graphical evaluation of residuals after fitting the Analysis of Covariance to test the effect of caging on the growth of *Cliona tenuis,* for Predation treatments (T2 & T6). Please refer to the section Study I in Methods for details. Panel **A** show a Q-Q plot of the standardized residuals against the theoretical quantiles in a normal distribution. The dashed line shows the expected normal distribution of residuals and the open circles, the observed distribution. This plot shows a similar distribution of residuals when compared to the expected normal distribution. Panel **B** show the distribution residuals across the fitted space. No overall trend is observed, indicating lack of dispersion. Panel **C** show a combined plot of the standardised residuals within the levels of the explanatory variable (Treatment), accounting for the interaction with the covariate (Size). The graphs show a homogeneous distribution of results across the parameter space.

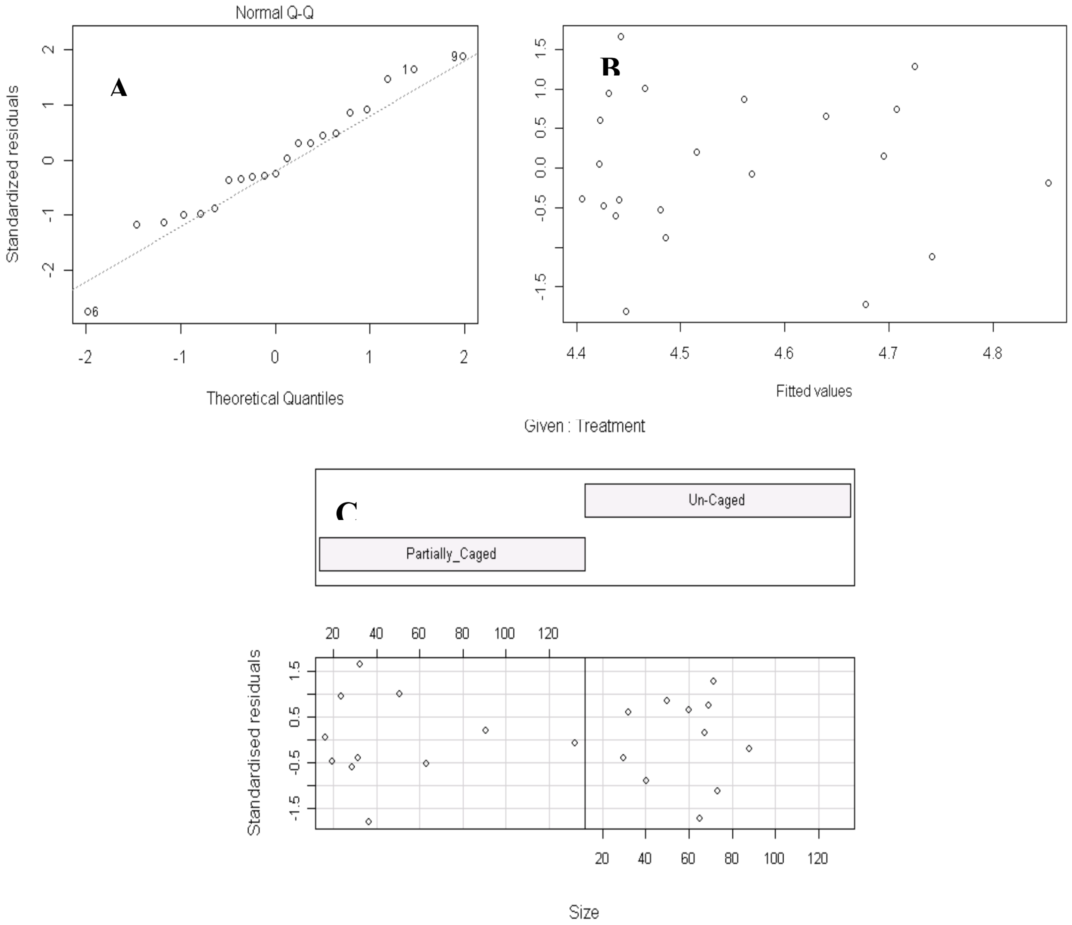

Figure III-A3. Graphical evaluation of residuals after fitting the Analysis of Covariance to test the effect of caging on the growth of *Cliona tenuis,* for Interaction treatments (T2 & T6). Please refer to the section Study I in Methods for details. Panel **A** show a Q-Q plot of the standardized residuals against the theoretical quantiles in a normal distribution. The dashed line shows the expected normal distribution of residuals and the open circles, the observed distribution. This plot shows a similar distribution of residuals when compared to the expected normal distribution. Panel **B** show the distribution residuals across the fitted space. No overall trend is observed, indicating lack of dispersion. Panel **C** show a combined plot of the standardised residuals within the levels of the explanatory variable (Treatment), accounting for the interaction with the covariate (Size). The graphs show a homogeneous distribution of results across the parameter space.

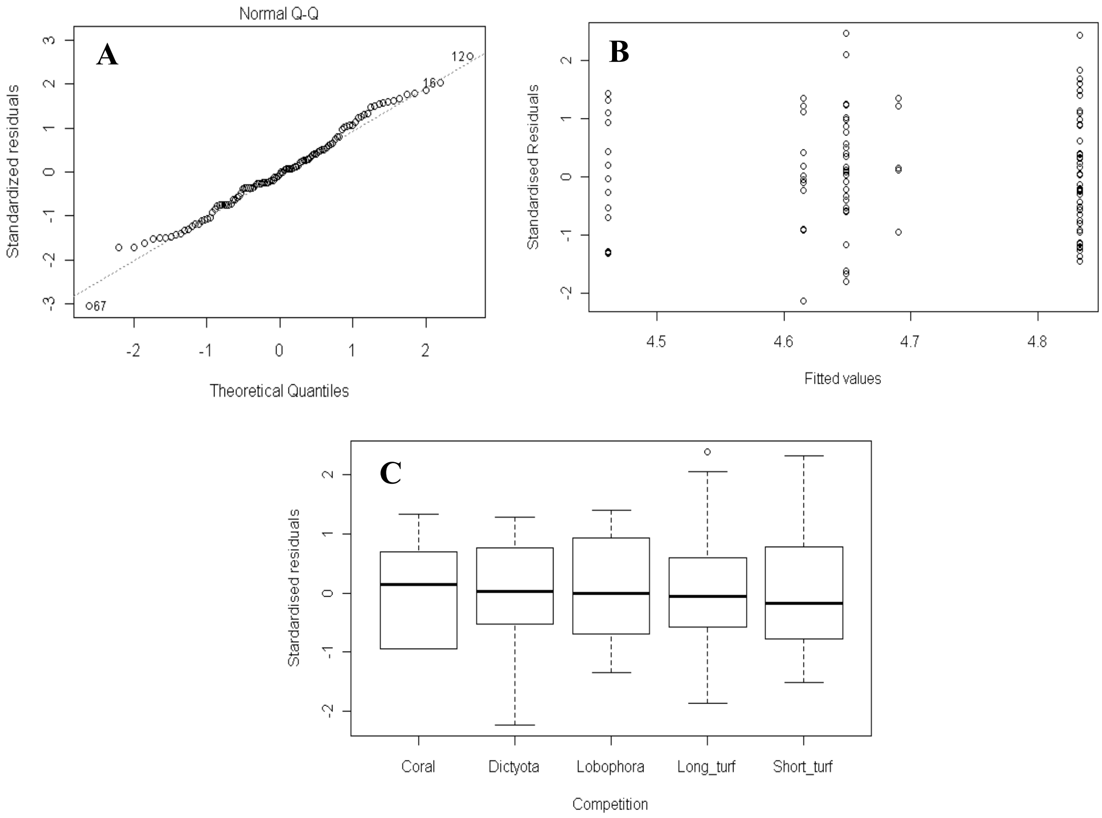

Figure III -A 4. Graphical evaluation of Normality and Homoscedasticity of residuals after fitting the General Linear Model to test the effect of different competitors on the linear extension of Cliona tenuis (please refer to the section Study II in Methods for details). Panel A show a Q-Q plot of the standardized residuals against the theoretical Quantiles in a normal distribution. The dashed line shows the expected normal distribution of residuals and the open circles, the observed distribution. This plot shows a similar distribution of residuals when compared to the expected normal distribution. Panel B shows the residuals of the model to evaluate the homogeneity of variance across the fitted space. The solid line shows no overall trend, implying Homoscedasticity. Four outlier samples were removed from the analysis and the average reported in the results section. The samples were removed because we were uncertain if they kept in competition over the evaluated time, which coincided with the outlying behaviour observed. Panel C show a boxplot of the residuals among the five levels of the explanatory variable. The graph demonstrates that the variability of residuals remains constant among levels of the explanatory variable. Data points out of the 5th and 95th confidence intervals (bars) are represented by dots, and box indicates the inter-quartile range. The solid line inside the box represents the median.

Appendix B. Evidence of no collateral damage on the sponge tissue during the observational study

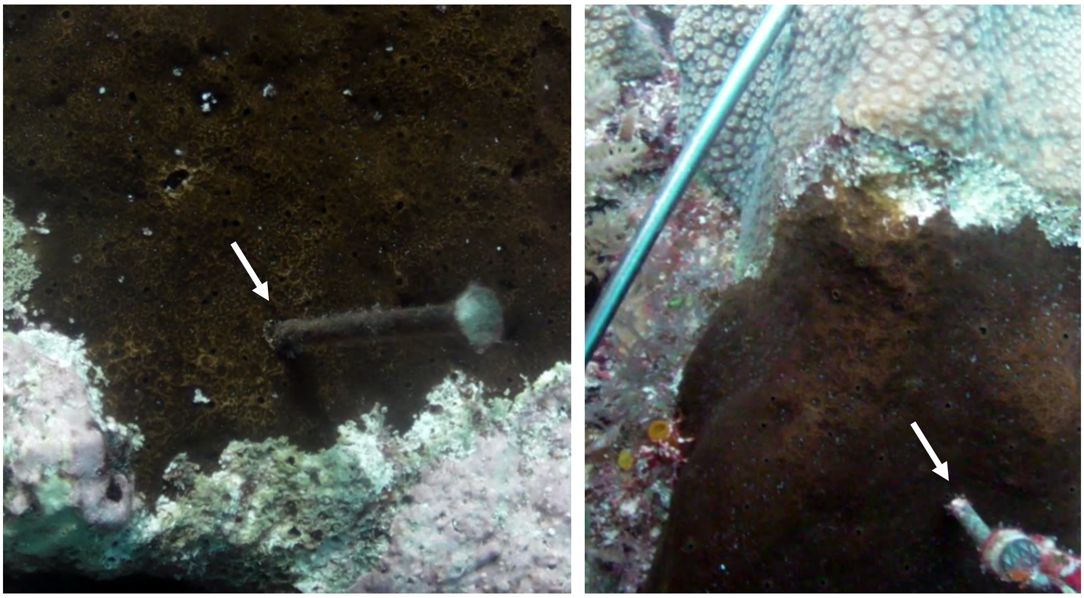

Figure III- B1. Individuals of *Cliona tenuis* evaluated during the Study II. For this study, sponges were tagged and followed during 286 days to compare the linear advance of the individuals under the constant competition against main benthic components in the reef. The pictures show the individuals at the end of the study where no damage can be seen as a consequence of driving the stainless steel nail (white arrows) on the edge of the individual at the beginning of the observational period.

~ IV ~

THE ROLE OF SPONGE COMPETITION ON CORAL REEF ALTERNATIVE STEADY STATES

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Abstract

Sponges constitute an abundant and functionally important component of coral reef systems. Given their demonstrated resistance to environmental stress, it might be expected that the role of sponges in reef systems under modern regimes of frequent and severe disturbance may become even more substantial. Disturbances have recently reshaped the community structure of many Caribbean coral reefs shifting them towards a state of persistent low coral cover and often a dominance of macroalgae. Using competition and growth rates recorded from Glover's Atoll in Belize, we parameterise a mathematical model used to simulate the three-way competition between sponges, macroalgae and coral. We use the model to determine the range of parameters in which each of the three species might be expected to dominate. Emergent properties arise from our simple model of this complex system, and these include a special case in which heightened competitive ability of macroalgae versus coral may counter-intuitively prove to be advantageous to the persistence of corals. Importantly, we show that even under scenarios whereby sponges fail to invade the system, inclusion of this third antagonist can qualitatively affect the likelihood of alternative stable states – generally in favour of macroalgal dominance. The interplay between multi-species competition and predation is complex, but our efforts highlight a key process that has, until now, remained unexplored: the extent to which sponges dissipate algal grazing pressure by providing generalist fish with an alternative food source. We highlight the necessity of identifying the extent by which this process takes place in tropical systems in order to improve projections of alternative stable states for Caribbean coral reefs.

Keywords: Porifera, *Cliona*, macroalgae, Grazing, coral reef, competition, community ecology.

Introduction

Sponges constitute an abundant and functionally important component of coral reef systems (Bell, 2008; Díaz and Rützler, 2001). They contribute to numerous ecosystem processes including substrate accretion (Wulff, 1984) and erosion (Rützler, 1975; Rützler, 2002; Scoffin et al., 1980), as well as nutrient and energy cycling (de Goeij et al., 2008; Díaz and Ward, 1997; Lesser, 2006). They also enhance biodiversity in these systems both directly, by their constituent number of species (Díaz and Rützler, 2001; Hooper and van Soest, 2002), and indirectly by the rich diversity of species that they host (Ribeiro et al., 2003; Villamizar and Laughlin, 1991). Importantly, they have been shown to compete with coral (López-Victoria et al., 2006; Suchanek et al., 1983; Vicente, 1990) and we explore the significance of this trait in the community context. Based on the observation of successful overgrowth events (Aerts, 1998; Suchanek et al., 1983; Vicente, 1978) sponges outcompete corals for space when the two taxa confront each other. A similar competitive interaction has been observed in bryozoans overgrowing coralline algae (Buss, 1980) and tunicates overgrowing bryozoans (Edwards and Schreiber, 2011) in rocky shore systems. Out of 128 sponge species found to be interacting with corals, 30 were engaged in coral overgrowth (Aerts, 1998). These include the excavating sponges - a group that is well known for its involvement in reef framework erosion (Rützler, 2002; Sammarco and Risk, 1990; Schönberg, 2002; Schönberg and Wilkinson, 2001; Scoffin et al., 1980). This group, mainly represented by clionaids, often dominates the composition of sponges in shallow coral reefs (Rützler, 2002) and accounts for as much as 95% of the total internal erosion of the coral skeleton (Pari et al., 2002; Scoffin et al., 1980). Their superior competitiveness for space coupled with their strong resistance to environmental stress (Carballo, 2006; i.e., Rützler, 2002; Schönberg, 2006) has resulted in an increasing abundance (cover and density) of these bioeroding sponges on reef systems that experience modern regimes of disturbance (Schönberg and Ortiz, 2009; Ward-Paige et al., 2005).

Combined effects of environmental and anthropogenic stressors have resulted in globally declining coral cover (i.e., Gardner et al., 2003; Paddack et al., 2009; Pandolfi et al., 2003) with many reef systems now dominated by other biological components, such as macroalgae and sponges (Norström et al., 2009; Nyström et al., 2000). Studies within the Caribbean basin have described a phase shift from coral dominance to macroalgal dominance during recent decades (Gardner et al., 2003; Hughes, 1994; McManus and Polsenberg, 2004). In theory, Caribbean reefs may exhibit two alternative stable states that are maintained by positive feedback processes (Mumby and Steneck, 2008). One state can be characterised by an ability of corals to exhibit recovery after disturbance whereas no recovery – in fact, net decline – occurs in the alternate state (Mumby, 2009). Understanding the mechanisms underlying the switch between alternative steady states is vital in order to facilitate conservation management and restoration projects (Schroder et al., 2005). Theoretical analyses, corroborated by field studies (Burkepile and Hay, 2006; Mumby and Harborne, 2010), have elucidated the fundamental role of herbivory in tempering reef dominance by competing species, even under conditions of elevated nutrient concentration (Mumby et al., 2007; Mumby et al., 2006). Mathematical models provide the conceptual framework of complex systems by defining critical underlying dynamics and interactions. Until now, however, theoretical studies of alternative steady states on coral reefs have only explored the statics and dynamics associated with competition between coral and macroalgae (Hastings, 1980; Mumby et al., 2007). Using field collected data, we extend the two-species analytical framework (Mumby et al., 2007) to perform a multispecies sponge invasion analysis and ascertain the resulting stability of the whole system. In doing so, we take this concept further by considering coral-macroalgae antagonism in the context of a more realistic system.

Methods

Study Site and Data Collection

Studies by Mumby and González-Rivero (unpublished, a summary of the data can be requested from the authors), which provided most of the data (Table IV-1), were carried out on the windward side of Glover’s Atoll in the Caribbean Sea (UTM 1,852,242; W 415,891N), during the years 2005 and 2009. Glover's Atoll is located approximately 30km from the mainland of Belize and 15km east from the Mesoamerican Barrier reef. Sites were located on *Montastraea* dominated fringing reef (Fig IV-1) and a combination of coral bleaching and three recent hurricane events has shifted the community structure towards macroalgal dominance (Mumby et al., 2005).

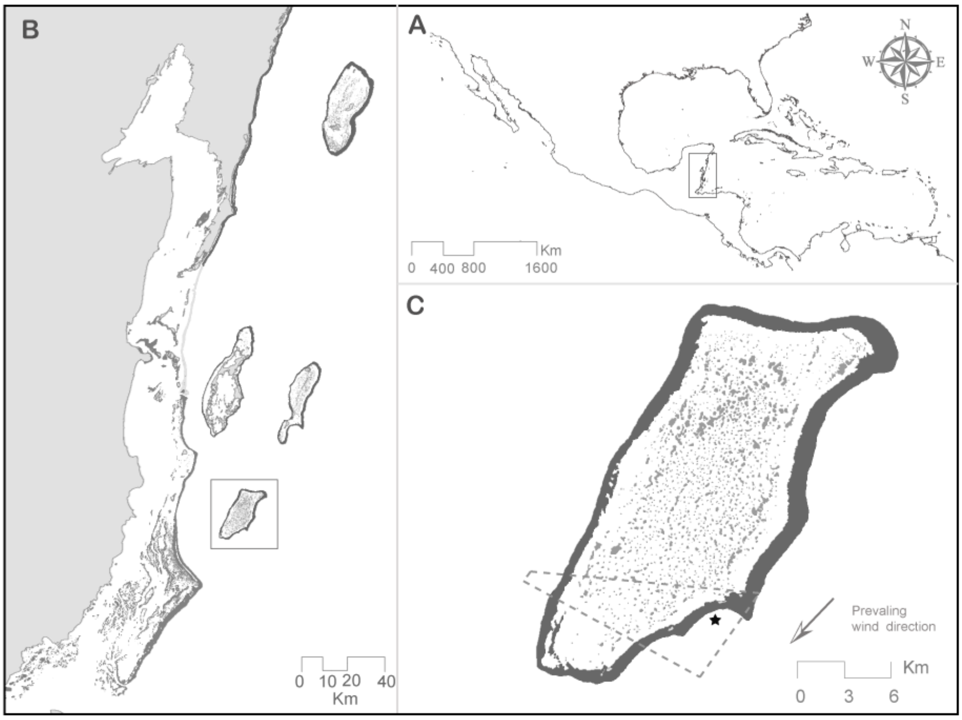

Figure IV-14. Map showing the area of study, relative to the location in the wider Caribbean (A), at Glover's atoll Belize (B) and on the seaward side of the atoll (C). Dashed line delimitate the boundaries of the Glover's Atoll Marine Protected Area.

Mathematical model

For the purposes of the mathematical analysis, representative species, or groups of species, have been chosen as models to describe the interactions among corals, macroalgae and sponges. Representatives were selected based on abundance and functional importance in Caribbean coral reefs. *Lobophora variegata* (*M*) is one of the most common macroalgal species on Caribbean reefs and is highly competitive with coral for space (Jompa and McCook, 2003; Nugues and Bak, 2006, 2008). Parameterisation for corals (*C*) was based on attributes of *Porites* *astreoides* and *P. porites* (see Table IV-1). *Cliona tenuis* (*S*)*,* a bioeroding sponge (Rützler, 2002; Zea and Weil, 2003), is both abundant and highly competitive (López-Victoria et al., 2006). In the particular case of Cliona, coral-sponge competition for space is mediated by physical contact (Chaves-Fonnegra and Zea, 2007; López-Victoria et al., 2006) and not directly by the release of allelochemical compounds into the water (Chaves-Fonnegra et al., 2008).

Table IV-3. Parameters of the model for mid-shelf Caribbean reefs.

Symbol	Parameter	*Details*	Value
γ	Macroalgae growth on turf	Following Mumby et al. (2007), the linear growth of *L. variegata* over dead coral or turf progresses at an annual rate of 25.32 cm yr^{-1}.	1
a_1	Macroalgae overgrowth on corals	*L. variegata* overgrow corals (*Agaricia* spp and *Porites* spp) at a rate of 1.14 cm yr^{-1} (Nugues and Bak, 2006).	0.05
a_2	Sponge overgrowth on corals	*Cliona tenuis* has been observed advancing over living coral at a rate of 1.6 cm yr^{-1} (González-Rivero, unpublished data). However, in the analysis, we considered the variability in sponge overgrowth rate as reported for Colombia (López-Victoria et al., 2006) and Belize (Rützler, 2002).	variable
z	Sponge growth on turf	López-Victoria et al. (2006) found that *C. tenuis* linearly advanced over turf algae at a rate of 2.4 cm yr^{-1} in Islas del Rosario Archipelago, Colombia. A similar rate was observed by González-Rivero (unpublished data) for Glover's Atoll, Belize (2.99 cm yr^{-1}).	0.09
a_3	Macroalgae overgrowth on sponges	González-Rivero (unpublished data) found that the average overgrowth rate of *C. tenuis* sponge by *Lobophora variegata* macroalgae is 1.45 cm yr^{-1}.	0.06
r	Coral growth on turf	Mumby et al. (2007) have reported the growth rate of *Porites astreoides* and *P. porites* to be 1cm yr^{-1}.	0.04
g	Grazing intensity	We test for shifts in system trajectory towards either coral dominance or macroalgal dominance across a wide range of grazing intensity.	variable
b	Grazing preference on sponges	The level of selectivity of herbivorous fish to graze on sponge rather than algae.	variable

Ultimately, space is the limiting resource of sponge (S), macroalgae (M), and coral (C), where turf (T) is assumed to be default cover, i.e. $T = 1 - (S+M+C)$. The following set of ordinary differential equations describes the continuous competition for space:

$$\frac{dC}{dt} = (rCT) - (a_1CM) - (a_2CS)$$

$$\frac{dM}{dt} = (a_1MC) + (a_3MS) + (\gamma MT) - \frac{gM}{M + T + (bS)}$$

$$\frac{dS}{dt} = (a_2SC) + (zST) - (a_3SM) - \frac{gbS}{M + T + (bS)}$$

Where r is coral growth rate, a_1 is the rate at which macroalgae overgrow coral, a_2 is the rate at which sponge overgrow coral, z is the rate at which sponge overgrow turf, a_3 is the rate at which macroalgae overgrow sponge, γ is the rate at which macroalgae overgrow turf and g is the grazing rate. Following empirical data, we assume that growth rates of the three competitors are constrained by $a_1, a_2 and\ a_3 < z < \gamma$. Previous studies have shown the relevance of herbivory in determining the bi-stability of coral reef systems (Mumby et al., 2007). Following studies in which herbivorous fish have been observed preying upon sponges (Pawlik, 1998; Wulff, 1997), we allow for a proportion of the grazing to be diverted away from macroalgae onto sponges $(0 \leq b \leq 1)$. The modelled species interactions are summarised in Figure IV-2. All growth and overgrowth rates are normalised to the exceptionally fast rate at which macroalgae grow from turf (Table IV-1).

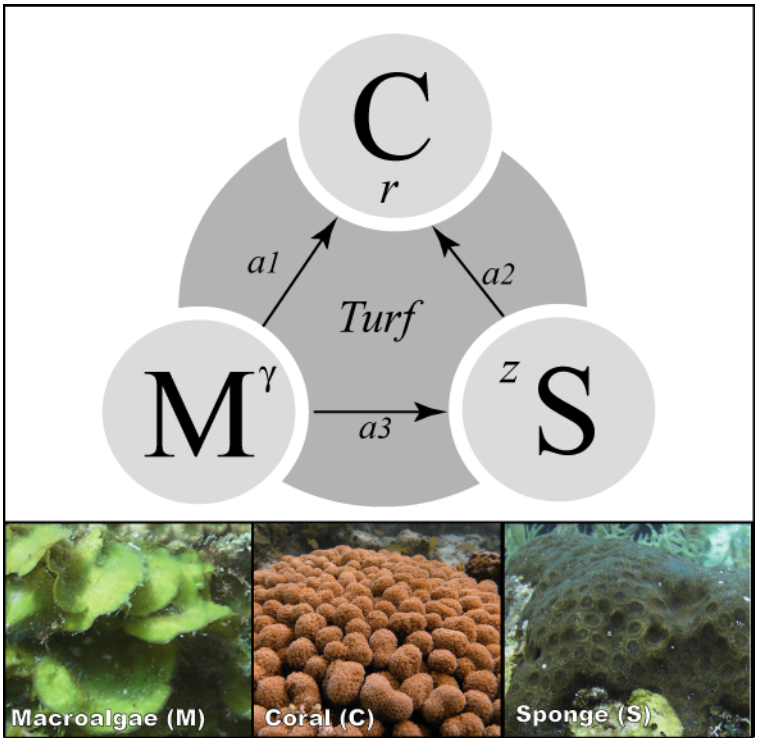

Figure IV-15. Diagram of the proposed competitive interactions among coral (C), macroalgae (M) and sponges (S). Intrinsic growth parameters are given by r, γ and z. Rates of competition are represented by the letters a_1, a_2 and a_3. See section 2.2 for more information.

Coral-macroalgal antagonism has been analysed previously (Mumby et al., 2007) and, using our data, collected from Glover's atoll, along with previously published data (Table 1), we initially test for multiple steady states of coral coverage as a function of grazing in the absence of sponge competition. Our next aim is to determine the significance of the inclusion of sponge dynamics, thereby allowing for the competition for space between three taxa (instead of just two taxa). Specifically, we want to identify conditions by which sponges can be expected to impact the health of coral reefs by instigating phase shifts in species dominance

Results

In the absence of sponges, alternative steady states arise in coral cover as a function of the macroalgal grazing rate (Figure IV-3). Results are generally in accordance with previous studies (Mumby et al., 2007) with two important exceptions. First, the range of grazing rates across which alternative stable states can emerge is much greater with our parameterisation (Figure IV-

3). Second, the level of grazing necessary to guarantee return trajectories to coral dominance (high coral cover) is notably higher than previous estimates (Figure IV-3). Meaning, following a major disturbance whereby coral coverage is substantially reduced, extremely high grazing rates (in the order of 0.55) are necessary to ensure coral recovery.

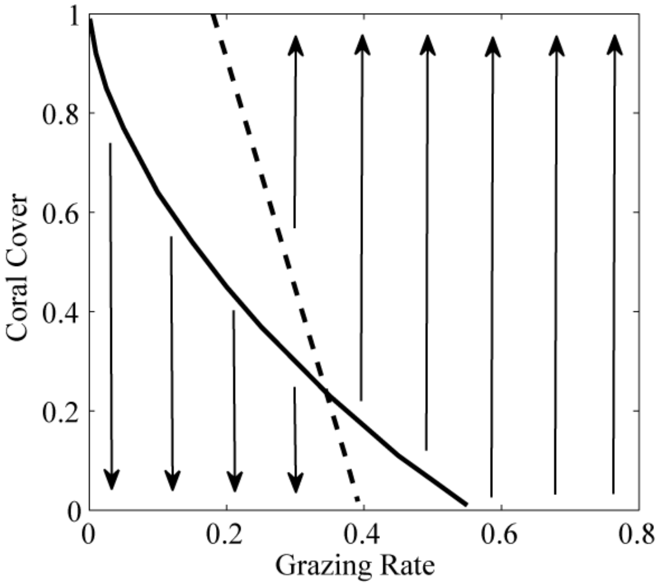

Figure IV-16. Alternative steady states of coral cover as a function of the macroalgae grazing rate. Our parameterisation from Glover's Atoll (solid line, Table 1) is compared with that of a previously published model (dotted line, (Mumby et al., 2007)).

Initiated at the unstable equilibrium of coral-macroalgal co-dominance, we examine the system perturbation following sponge introduction (Figure IV-4). The same qualitative pattern of dominance arises from all tested parameter ranges and combinations: 1) sponges successfully invade when they are able to overgrow coral provided that the rate at which they are preyed upon is low; 2) coral dominates when overgrowth by sponges is low-to-moderate and herbivores have intermediate grazing/predation preference for sponges; 3) macroalgae dominate when sponges divert some of the grazing and overgrow coral above a threshold rate (a_2>0.04 with the parameterisation used in Figure IV-4).

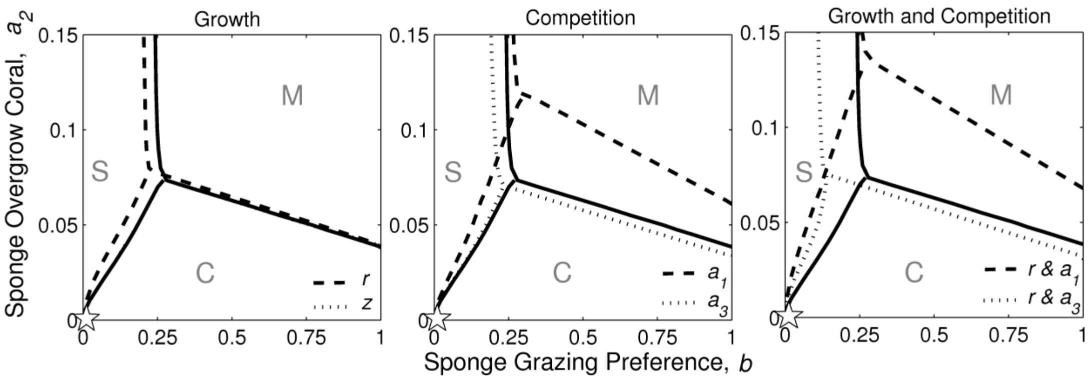

Figure IV-17. Stable equilibria following sponge invasion of a co-dominant (macroalgae-coral) system. Parameter spaces are dominated by sponges (S), coral (C) or macroalgae (M). Stable co-existence of coral and sponges can only occur when sponges are not grazed and do not overgrow coral (stars). The sensitivity of the model was tested to variability in parameters pertaining to growth and competition, both in isolation (first and second panel, respectively) and combined (third panel). Here the grazing rate is set to 0.3 (Mumby et al. 2007).

Species dominance is more sensitive to parameters governing competition than growth rates (Figure IV-4). The greatest model sensitivity arises from varying the rate at which macroalgae overgrow coral. Doubling the rate at which macroalgae overgrow corals counter intuitively results in greater parameter space (defined as the domain of the 2-dimenional surface produced across the ranges of two parameters) favouring coral dominance – largely at the cost of parameter space favouring macroalgal dominance. Simultaneous variations in growth and overgrowth rate give rise to synergistic effects whereby higher coral growth rate combined with an enhanced capacity of macroalgae to overgrow coral yields a yet greater coral-dominated parameter space. Figure IV-5 illustrates the unusual properties of this complex system: temporal dynamics exhibit transiently dominant competitors whereby the prevailing taxon has an unpredictable relationship with sponge growth rates.

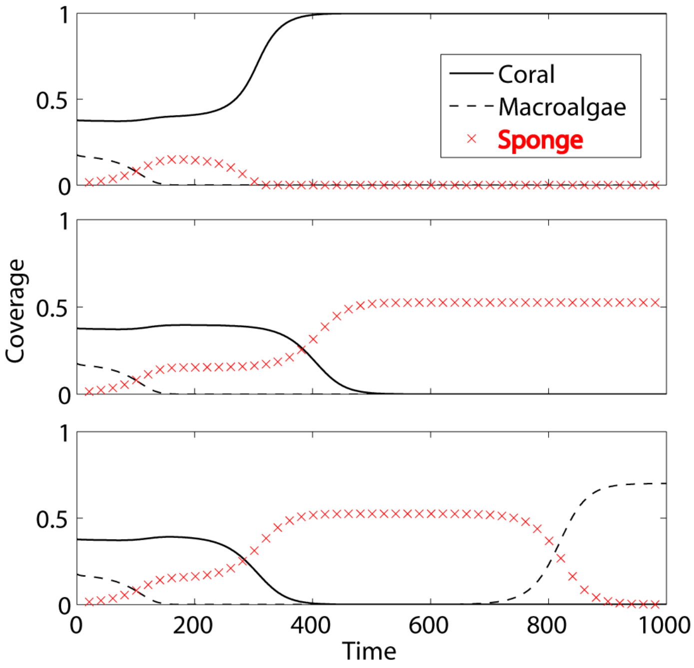

Figure IV-18. Temporal dynamics of a coral-macroalgae co-dominated reef system following sponge invasion. Rich transient dynamical behaviour eventually yields exclusive climax dominance for a single species. The prevailing species in this three-way competition can be quite unpredictable. For example, when the rate at which sponge overgrows coral (a_2) is 0.11720, coral dominates (top plot); a slightly higher value of 0.117235 yields sponge dominance (middle plot); and a still higher value of 0.11727 results in macroalgal dominance (bottom plot). All other parameters were standard values (Table 1).

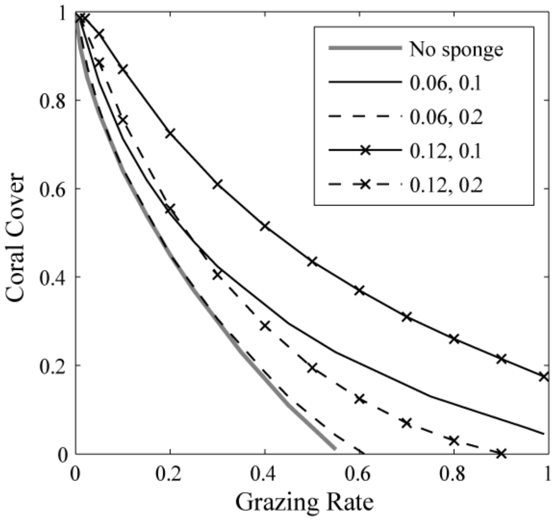

Figure IV-19. Inclusion of sponges can profoundly affect the balance between alternative stable states of coral coverage. Sponges tend to favour a low coral coverage stable state (compare grey with black lines). Hence, the least detrimental effect is experienced when sponge overgrowth of coral (a_2, first parameter value in key) is low and sponge predation (b, second parameter value in key) is high.

Finally, we address the impact of sponge inclusion on the balance between alternative stable states of coral coverage as a function of grazing (Figure IV-6). Overall, sponges tend to favour a low coral coverage stable state. Intuitively, the least detrimental effect to coral is experienced when sponge overgrowth of coral is low.

Discussion

Recent literature provides empirical support for alternative stable states in woodlands, lakes, marine communities and rivers (reviewed by Schroder et al., 2005). In coral reefs, several empirical studies have revealed phase shifts in the community structure that mostly favour large fleshy algae over coral (Gardner et al., 2003; Hughes, 1994; Maliao et al., 2008; McClanahan and Muthiga, 1998; McManus and Polsenberg, 2004). However, a minority of studies provide some evidence for the dominance of alternative space occupiers such as sponges (reviewed by Norström et al., 2009). Testing whether alternate phases of the community constitute alternate steady states is difficult because it requires demonstration of opposing trajectories of a state variable (e.g., coral cover) within the same environment (Petraitis and Dudgeon, 2004). Consequently, most experimental work to examine the presence of alternative stable states has been done under laboratory conditions rather than involving field manipulations (Schroder et al., 2005). While a field-validated demonstration of alternative stable states is lacking for coral reefs, simple analytic models and complex simulation models of Caribbean reefs support the view that Caribbean reefs slipped from having no alternate states before the early 1980s to possessing at least two alternate states thereafter (Mumby et al., 2007). The fulcrum between these switches in ecosystem behaviour was the region-wide disease-induced mortality of the urchin, *Diadema antillarum*, in 1983/4 (Lessios, 1988).

Here, using empirically derived data, we show how encrusting sponges – a group that has become increasingly abundant following recent disturbance regimes (Aronson et al., 2002; Ward-Paige et al., 2005) - can alter both the statics and the dynamics of a coral reef system. Our analysis highlights the conditions necessary for sponge invasion of a reef system. We show that even sponges with relatively low growth rates are able to dominate provided there is little-to-no predation. Although predation has been shown to be an important structuring process for non-excavating sponges (Dunlap and Pawlik, 1996; Loh and Pawlik, 2009; Pawlik, 1998; Schönberg and Ortiz, 2009; Wulff, 2005), data on predation of tropical excavating sponges are lacking. Observational studies of *Cliona celata*, a related excavator found in temperate regions, have demonstrated predation by both specialist and generalist consumers (Guida, 1976), and opportunistic predation by parrotfish has been recorded for other sponges (Dunlap and Pawlik, 1996; Wulff, 1997), and clionaids (González-Rivero et al 2012). However, despite high levels of predation, recent studies demonstrate the limited importance of predation on excavating sponges, thus reinforcing the need for further research to understand the main drivers that regulate sponge populations in coral reefs (González-Rivero et al 2012).

Unfortunately, the paucity of research on sponge ecology compared with other coral reef research, compromises our current knowledge on temporal and spatial trends of sponges. However, certain patterns observed in the Caribbean could be explained by our model. Such is the case of the Channel caye, Belize, where Aronson et al (2002) showed a disproportional increase in dominance of the sponge *Chondrilla nucula* coinciding with high coral mortality and a high level of macroalgal grazing by sea urchins.

Rich system behaviour is demonstrated by the temporal dynamics of this three-way competition for space, yielding unpredictable outcomes. Our model demonstrates emergent properties as defined by (Boccara, 2010):"large-scale effects of a system of locally interacting agents that are often surprising and hard to predict. The appearance of emergent properties is the essential feature of complex systems". We show unintuitive outcomes of species dominance as a function of the level of competitiveness of sponges with coral whereby an intermediate level resulted in sponge dominance, but a yet higher level resulted in macroalgal dominance. May and Leonard (1975) have described the concept of intransitive competition whereby the outcome of competition between multiple species is not always predictable in complex systems. Intransitive competition has received little attention in the field of ecology. It was previously believed to be the outcome of very specific conditions whereby there is a perfectly closed loop of competition. For example, species A outcompetes species B which outcompetes species C which, in turn, outcompetes species A. However, Edwards and Schreiber (2011) recently described a three-species model parameterised using a subtidal marine community in which intransitivity emerged as a function of competition, colonisation and space pre-emption tradeoffs. While several authors have highlighted greater opportunity for stable coexistence of multiple species in theoretical systems which demonstrate classic intransitivity (Gilpin, 1975; May and Leonard, 1975), Calcagno et al. (2006) have shown that, depending on the parameterisation, inclusion of pre-emption in a multispecies competition model can either enhance or deter coexistence. Our model describes a trade-off whereby coral and algae are competing for space and sponge is able to displace coral. Parameterised with data collected in Belize, we show that our coral-macroalgae-sponge model does not promote stable coexistence.

Depending on their competitive ability with corals, and the rate at which they are preyed upon, even sponges that fail to become dominant space occupiers can qualitatively shift the hysteresis between coral and macroalgae. In providing an alternative food source, sponges might divert herbivores away from macroalgal consumption. Therefore, previous calculations of threshold grazing rates to ensure that corals are able to exhibit recovery trajectories (Mumby et al., 2007) may be underestimated. The relationship between fishing, grazing rates and coral-macroalgal antagonism also becomes less clear-cut when sponges are introduced into the system. For example, how will preferentially fishing species that exclusively graze on macroalgae and turf differ from fishing species that also prey upon sponges?

Future analysis can incorporate additional complexity such as the inclusion of multiple coral/sponge species and competitiveness as a function of size structure (Riegl and Purkis, 2009). This model is parameterized from fast-growing coral species such as *Porites* spp. However, the inclusion of multiple functional species and their respective interaction rate with sponges will recreate a more complex, and thus realistic, scenario. More complete data and greater model complexity would facilitate predictive efforts under different scenarios. For example, nutrient enrichment positively alters the growth and competitive rate of sponges (Holmes, 2000; Ward-Paige et al., 2005) and potentially the competitive ability of macroalgae against sponges. While our non-spatial model shows inherent unpredictability of the system due to the presence of intransitive competition, it would be interesting to determine the robustness of this result following inclusion of explicit space (Laird and Schamp, 2008). Capturing all indirect and subtle ecological interactions of an ecosystem within a mathematical model is impossible. With this simple model, however, we demonstrate emergent properties of a complex reef system and highlight previously ignored processes that may prove to be integral in driving coral recovery or decline within Caribbean reefs.

Acknowledgements

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ASYMMETRICAL COMPETITION REGULATES FUGITIVE SPECIES OUTBREAKS FOLLOWING CORAL REEF DEGRADATION:

On the population dynamics of Caribbean excavating sponges

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Format: Ecology

Abstract

Given the increasing levels of disturbance in coral reef ecosystems, elevated abundances of competitive, fast-growing and disturbance-tolerant sponges may be expected to occur as space becomes available. Nonetheless, the temporal patterns of sponge abundance following coral degradation are variable. Whereby, the increase of sponge abundance has only been reported in few studies, yet the reasons for the lack of a general response remain elusive. To gain insight into the mechanisms regulating sponge populations, we use an individual-based spatial model to simulate the population dynamics of *Cliona tenuis*, a common reef-boring sponge in the Caribbean. The performance of the model was validated against an 11-year dataset (1998-2009) of field observations from Glover's Atoll, Belize. During this period, coral cover decreased by 74%, yet the sponge population did not exhibit significant changes in cover, density or size-frequency distribution. An orthogonal hypothesis testing approach was used, with each of four putative mechanisms: competition, stock-recruitment limitation, whole and partial mortality, being incorporated sequentially into the model. Our optimal model explains the lack of response in *C. tenuis* populations in Glover's Atoll with an accuracy of 98%. We found that space releasing after coral mortality has the potential to promote sponge outbreaks, but outbreaks may be curtailed by competition with macroalgae, which occupy 36% of the substrate. The competitive superiority of macroalgae is not only provided by the completive strength to overgrow the sponge but also the potential to rapidly pre-empt the available space. This asymmetrical interaction, characterized by disparities in size, competitive strength and space colonizing rate of competitors, strongly regulate excavating sponges. In summary, these results show that while reductions in coral cover may temporarily favour the rapid colonization by sponges, the competitive superiority of macroalgae may steal the opportunity from the opportunists.

Keywords: Asymmetrical competition, Porifera, population regulation, macroalgae, coral reefs.

Introduction

Populations are regulated when they persist in time exhibiting bounded fluctuations in abundance as a result of potentially stabilizing mechanisms and/or interactions with a stochastic environment (Murdoch 1994, Sæther 1997, Hixon et al. 2002). In addition to being of theoretical interest, regulating mechanisms are essential for management and conservation, elucidating how human interventions might drive changes in the population structure and growth (Caswell and Cohen 1991). Among marine ecosystems, coral reefs are presently one of the most intensively perturbed, yet a full understanding of the resulting system trajectories is lacking (Halpern et al. 2007). Temporal patterns of reef benthic communities typically show that disturbance drives coral cover down while macroalgal cover increases to the point where reinforcing feedbacks favour their dominance over corals (Mumby 2009). However, the inherent complexity of coral reefs makes it difficult to accurately predict the trajectories the system can take, and the response of many common reef dwelling taxa, such as sponges, remains understudied despite their potential role in determining ecosystem trajectories (Norström et al. 2009, González-Rivero et al. 2011).

Ecological disturbance has the potential to alter species composition as consequence of trade-offs between competitive abilities and resistance to disturbance among species (Petraitis et al. 1989, Dial and Roughgarden 1998, Suding and Goldberg 2001). In space-limited systems, such as those of the marine benthos on hard bottom (Hughes and Jackson 1985, Roughgarden et al. 1985, Muko et al. 2001) disturbance can favour rapid colonization by “fugitive” species (sensu Hutchinson 1951), either through release from competition (Horn and MacArthur 1972, Menge 1976) or by altering the competitive hierarchy among species (Suding and Goldberg 2001, Lenssen et al. 2004). Perhaps, one of the most iconic case studies in benthic systems to represent this idea is that of the sea palm, Postelsia palmaeformis, whose abundance is favoured when disturbance (wave exposure) remove patches of mussels that would interfere with the sea palm opportunity to establish (Paine 1988). Fugitive species in general have the potential to colonize vacated space better than others due to their fast growth rate and/or high recruitment rates, which favour them with a strong resilience to disturbance (Armstrong 1976). These life history characteristics common to fugitive species are found in boring sponges on coral reefs (Rützler 2002, Schönberg et al. 2008, González-Rivero et al. "in review"). However, the manner in which such attributes of excavating sponges interact as the ecosystem degrades is as yet unknown.

Studies of interspecific competition vastly show the importance on this structuring process across different ecosystems, where marine ecosystems are not the exception (Connell 1983, Schoener 1983). Most of the competitive interactions in marine benthos are driven by space availability at a local scale. Traditionally, competition is seen into two separate classes depending one the competitor's attributes: exploitative, by depriving users from the same resource; and by interference, the interaction results in negative effects on one or more competitor (reviewed by Connell 1983). However, evidence show that such competitive attributes can combine in a competitor, creating therefore a disparity in the competitive abilities on interacting individuals (Lawton and Hassell 1981, Connell 1983). Such asymmetrical competition is commonly observed in nature due to disparities in size, growth rate, and the competitive strength *per se* (Schoener 1983, Resetarits 1997, Martinkova and Honek 2011). Though no doubt the importance of competition in coral reefs benthos, uncertainly rise when trying to predict the role of complex competitive networks in perturbed ecosystems. In particular, considering multispecies asymmetrical interactions, as well as the dynamical nature of such interactions and hierarchies (Connell 1983).

Case studies have shown an positive trend in the abundance of bioeroding sponges, possibly as a result of decreases in coral cover, nutrient enrichment, or other stressors (Rützler 2002, Ward-Paige et al. 2005, Carballo 2006, Chiappone et al. 2007, Carballo et al. 2008, Schönberg and Ortiz 2008). The response of excavating sponges appears to be spatially variable and only, few studies have demonstrated increases in the sponge abundance at broad spatial and temporal scales (Ward-Paige et al. 2005, Chiappone et al. 2007, Schönberg and Ortiz 2008), and what control these populations yet remains to be elucidated. Interactions at the community level may make it difficult to understand species-specific responses to habitat degradation. Complex responses to disturbance have previously been explored in terrestrial ecology, where the outbreak potential of disturbance-resistant species is dampened by the competitive strength of other players (McEvoy et al. 1993, Lenssen et al. 2004). In coral reef systems, such complexities are found where interspecific density dependent interactions may influence the outcome of disturbance (Tanner et al. 2009). Given the rapid colonization potential of macroalgae following perturbation (Mumby et al. 2005, Nugues and Bak 2008) and their overgrowing capacity on boring sponges (López-Victoria et al. 2006, Chaves-Fonnegra and Zea 2011, González-Rivero et al. 2012), we hypothesize that macroalgal competition can inhibit potential outbreaks of sponge populations.

While we have focused on competition, other processes such as mortality (Hughes and Connell 1987, Hixon et al. 2002), recruitment limitation (Roughgarden et al. 1985, Hughes 1990) and partial tissue mortality (Bak and Meesters 1998), are common drivers of the structure of populations in marine organisms with indeterminate growth. Here, we explore the importance of these processes in driving the population dynamics of *Cliona tenuis*, a common bioeroding sponge in Caribbean reefs. Using an ecosystem modelling approach, which considers the interactions among common reef taxa, we simulated the population dynamics of *C. tenuis* and quantified the relative importance of each proposed regulating mechanisms in explaining independent field observations from Glover's Atoll, Belize. Based on this approach, here we provide a mechanistic understanding of the processes likely driving the structure of *C. tenuis* populations in the Caribbean.

Methods

Study species

Bioeroding or excavating species often dominate the sponge community of shallow reefs, and most are represented by members of the genus *Aka* and the family Clionaidae (MacGeachy 1977). Individuals of the Clionaide family are the primary excavating sponges, accounting for as much as 95% of reef framework erosion (Scoffin et al. 1980, Peyrot-Clausade et al. 1999).

Among Caribbean clionaids, *Cliona tenuis* is a common brown excavating sponge, and has recently been described within the *Cliona viridis* complex, whose species are symbiotically associated with zooxanthellae (Rützler 2002, Schönberg 2002, Zea and Weil 2003). Clionaids are fast-growing species whose capacity to out-compete corals may be due to their ability to undermine polyps (López-Victoria et al. 2006, Chaves-Fonnegra and Zea 2007). While *C. tenuis* is the fastest growing among Caribbean brown clionaids, competition can reduce its lateral expansion rate in a species-specific fashion, and algal species such as *Lobophora variegate* often overgrow the sponge (López-Victoria et al. 2006, González-Rivero et al. 2012). Life history observations suggest that *C. tenuis* tends to trade-off somatic growth against reproduction, resulting in a seasonal alternation of these processes during the year (González-Rivero et al. "in review"). At Glover's Atoll, our study area, high recruitment rates occur throughout the year, resulting in a total of 2.5 recruits$\cdot m^{-2}\cdot yr^{-1}$ (González-Rivero et al. "in review"). Reproduction occurs once a year and the clionaidae larvae show weak swimming abilities, tending rather to crawl over the substrate, which supports the close stock-recruitment relationship observed in temperate systems (Mariani et al. 2005, Mariani et al. 2006). The depth of tissue penetration into the substrate for species of the *C. viridis* complex is limited to two centimetres, possibly due to light limitation in the autotrophic symbionts (Bergman 1983, Acker and Risk 1985). Therefore, for modelling proposes, we considered *C. tenuis* individuals as bi-dimensional structures of constant thickness, whose growth is defined by their lateral expansion. Although clionaid habitats are typically exposed to fish, predation does not compromise the somatic growth of adult sponges, but incidental predation might play a role controlling the number of juveniles in the population (González-Rivero et al. 2012). These group of clionaid species have a high tolerance towards typical disturbances on coral reefs such as thermal-induced bleaching (Vicente 1990, Schönberg and Loh 2005), sedimentation (Carballo 2006), and hurricanes (López-Victoria and Zea 2004).

Study area

Data to parameterize and validate the model used in the present study was collected in Glover’s Reef Atoll, Belize, which is located approximately 50 km off the Central American mainland and 15 km east of the Mesoamerican Barrier Reef. Surveys were conducted within the boundary of the Glover’s Atoll Marine Reserve, on shallow (8-10m) *Montastraea* dominated fore reefs, at three sites, two exposed to wave energy E1 and E2 and one protected W1 (Fig V-20). In recent decades, coral reefs at Glover’s Atoll have been impacted by a number of hurricanes and bleaching events (Mumby 1999, Mumby et al. 2005). As a consequence, structural changes have been observed along time in both lagoonal patch and fore-reefs (McClanahan and Muthiga 1998, Mumby et al. 2005, McClanahan and Karnauskas 2011).

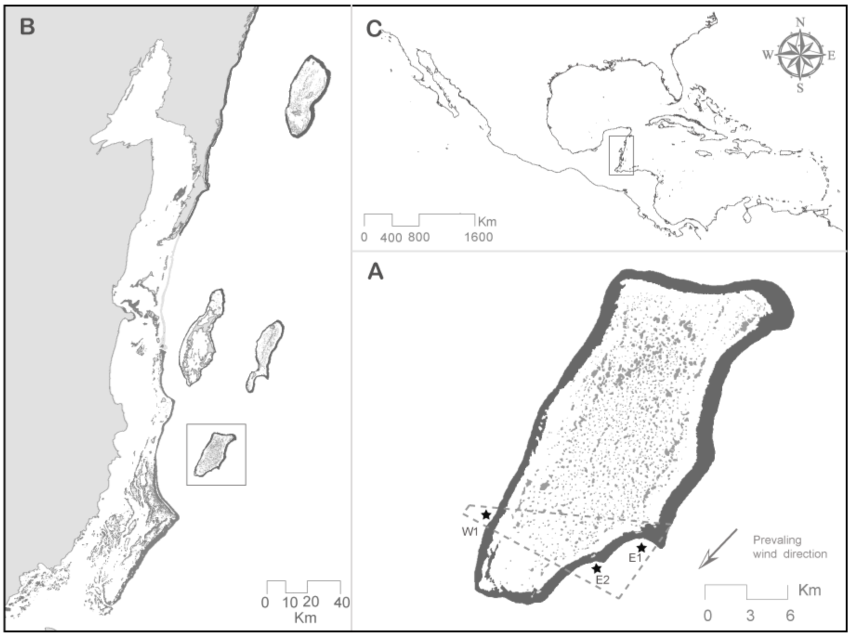

Figure V-20 Location of study sites at Glover’s Atoll (A) in the Mesoamerican Barrier Reef, Belize (B), and the relative location of the atoll in the wider Caribbean region (C). Dashed line show the approximate boundaries of the Glover’s Atoll Marine Reserve. Vital rates of the *Cliona tenuis* populations were obtained from site E1, while sites E1, E2 and W1 were monitored over time and used for testing the model simulations. Map Source data: global coastline by the Global Self-consistent, Hierarchical, High-resolution Shoreline database (GSHHS) and Mesoamerican coastline and reef locations by the Millennium Coral Reef Mapping project (MCRM).

Population modelling of *Cliona tenuis* in an ecosystem context

Scope: The simulation model employed in the present study was originally designed to represent mid-depth (5-15m) fore-reefs in the Caribbean, which typically have the highest biomass and diversity of reef organisms (Mumby 2006, Mumby et al. 2006c). The parameterization was based on reefs with little or no mangrove connectivity and little sediment deposition. During this research, the model was modified to include bioeroding sponges and simulate the dynamics of their population. The model was parameterized using vital rates and population structure data gathered from Glover's Atoll in 2009 at site E1 (Table V-4). Model outputs were compared to a separate data set from three sites in the same area (Fig V-20), and the relative role of the processes driving the population structure was explored using a perturbation analysis approach (inclusion/exclusion) where the simulated size structure is compared against field observations. Below, we (1) give an overview of the simulation model; (2) explain the putative drivers of the structure of the population of *C. tenuis* included during the simulations; and (3) explain the procedures followed to test the performance of the model and compare the relative role of the putative drivers of *C. tenuis* population dynamics.

Overview of the model: Using an individual-based spatial simulation approach, we modelled the dynamics of the main benthic components of a tropical coral reef (massive growth forms of corals, algal turf, dominant species of macroalgae and bioeroding sponges), including their recruitment, growth, mortality and competitive rates in a spatially explicit framework. The model is structured in a square lattice of 400 cells each of which represents 0.25m^2 of reef and can be occupied by a combination of living and dead substrata. Individual cells in the model comprise multiple coral colonies, algal patches and sponges, so the interactions occur at individual scales as they do *in situ.* Grazing affects all algal classes and grazed patches become algal turf. Corals and sponges are subject to size-dependent fecundity and mortality. Acute disturbance occurs from hurricanes, and bleaching disturbance is considered in the background whole-colony mortality of corals. The initial conditions at the start of each simulation are given by the size structure of corals and sponges in 1998. Each model simulation was run for 22 time steps (11 years), and 50 simulations were carried out to determine the average population attributes. Full details of the parameters of the model are given in Appendix A, and a more detailed description of the performance of the model and its validation can be found in Mumby (2006b, 2006c), Mumby et al. (2007) and Edwards et al. (2011). New extensions to the model, to include the dynamics of *C. tenuis* populations, are described below.

Table V-4 Full detail of the parameterization of the demographic rates of *Cliona tenuis*

Parameter	Details
Growth	Sponge growth (*G*) is subject of the amount and intensity of competition (Eq. 5). Sponge size is quantified as the cross-sectional, basal area of a hemispherical individual (cm^2). The final area after each time step is calculating by the linear extension (le) of the sponge in from each competitor (i : cropped algae, *Dictyota*, *Lobophora* or coral) assuming a circular grow form, and weighted by the proportion of tissue in contact with each competitor (*p*), whereby: $G = \sum \frac{\pi(r+le_i)^2}{p_i}$ (Eq. 5) Where *r* is the radius of the sponge and p is calculated as the average local cover of the competitor (in the von Neumann 5-cell neighbourhood). The linear extension rates (le) for each competitor were: Cropped algae: 0.35·cm·6mo^{-1}; (see section below) *Dictyota*: 0.14 cm·mo^{-1} (González-Rivero et al. 2012) *Lobophora*: -0.56 cm·6mo^{-1} (González-Rivero et al. 2012) Coral: 1.02 cm·6mo^{-1} (González-Rivero et al. 2012)
Recruitment	Sponge recruit on cropped algae at a rate of 0.315 ind per 0.25 m^2 of cropped algae per time interval(~2.5 ind/m2.y, González-Rivero et al. "in review"). Recruit size is 1 cm^2.
Fecundity	Fecundity is assumed to be a linear function of size, as bigger sponges will contain a proportionally higher number of reproductive propagules, and assuming that the number of propagules per unit area of tissue remains independent of size. Therefore, sponge reproduction is a function of the existing population structure in the previous time steep. Refer to stock-recruitment in section bellow for more details.
Whole-individual mortality of juvenile and adult sponges	Probability of mortality follows an exponential decay function of size which parameters are estimated combining the mortality registered in small individuals and an optimization algorithm to fit the model to the size structure of the population at Glover's Atoll in 2009. Please refer to section bellow for more details.

Modelling hypothesized drivers of the population structure

We hypothesize that four mechanisms could drive the population structure of *Cliona tenuis:* macroalgal competition, stock-recruitment dynamics, mortality, and/or partial tissue mortality, as discussed in turn below.

Competition: The growth rate of *Cliona* spp. is strongly dependent on the intensity of competition, given by the identity of the competitor and the proportion of tissue in direct contact (Cebrian and Uriz 2006, López-Victoria et al. 2006, Chaves-Fonnegra and Zea 2011). Pairwise competition coefficients, such as the rate of advance or retreat during confrontation, were obtained from a previous field study at Glover's atoll (E1 in Figure V-1) during 2009 (González-Rivero et al. 2012), and the results are summarized in Table V-4.

During that research, we observed that the linear extension of *C. tenuis* in competition with cropped algae, or turf, significantly varied as a function of the developing state of this algal *community*, indicating that the competitive strength of turf increase as it get denser and taller (González-Rivero et al. 2012). Here we estimate growth of the sponge in confrontation with the average cropped algae state at Glover's Atoll (including tall and short turf algae). From tagged sponges in 2009 at E1 (see González-Rivero et al. 2012 for details), we selected those individuals which withstood over 90% of their perimeter in competition with turf algae (95.6 ± 0.2 %; mean ± $CI_{0.95}$, n = 27). Assuming a radial expansion of *C. tenuis*, average linear extension was estimated by calculating the difference between the radius of the sponge (Δr) at two time steps (0 and 286 days during year 2009) from each individual (Equation 1).

$$\Delta r = 1.35 \cdot \frac{A_f^{1/2} - A_i^{1/2}}{\pi^{1/2}} \qquad \text{Eq 1}$$

Where *A* is the size of the individual at 0 (*Ai*) and 286 days (*Af*), estimated from video footage using the software VidAna (v 1.2.1; Hedley 2006). Linear extension (Δr) is linearly extrapolated to a year, using the constant coefficient of 1.35. The average growth of the sponge in confrontation with major benthic components is presented in the Table V-4.

Stock-recruitment dynamics: Given the poor swimming capabilities of clionaid larvae their abundance is strongly spatially correlated to the abundance of adults (Mariani et al. 2005, Mariani et al. 2006). Therefore, the modelled populations are assumed to be sustained by stock-recruitment dynamics determined by the number of individuals and the fecundity associated with each. Fecundity is a function of colony size (Ramirez Llodra 2002), and although the exact nature of the fecundity-size relationship has not yet been determined in clionaids, here we assume a simple linear increase in fecundity with tissue area. The reproductive index is the proportion of propagules per unit of tissue, and assuming that this index remains constant with size, the number of propagules and larvae produced will proportionately increase with the individual size of the sponge.

Whole-individual mortality: Newly settled individuals are prone to high mortality rates caused by extrinsic physical or biological selective pressures, and as individuals increase in size they become less vulnerable, eventually reaching a size at which they escape from these sources of mortality (Gosselin and Qian 1997). Thus, whole-individual mortality rates tend to decrease as benthic invertebrates grow (Jackson et al. 1985, Hughes and Connell 1987, Babcock 1991). Here we modelled mortality as a negative power function of size (Peterson and Wroblewski 1984).

$$M = 0.16 \cdot size^{-1.42} \qquad \text{Eq 1}$$

where the parameters were estimated by the non-linear least square regression fitting, and *size* is the initial area of the sponge, described below. Equation 1 was used to calculate the mortality rate per year. We then divided this value by two to obtain the rate per time step in the model (6 months).

253 sponges were randomly tagged in January 2009 at E1 (Fig V-20), and followed during 286 days (see González-Rivero et al. 2012, González-Rivero et al. "in review" for details). The number of dead individuals was recorded at the end of this period, and the initial size of each individual was estimated from high definition footage videos, using the software VidAna (Hedley 2006). The probability of mortality as a function of size was then calculated by subdividing the dataset into 5 cm^2 size classes. The no-linear regression was fitted using R and the ‘nls’ package.

Partial tissue mortality: The age and size structure of sessile organisms are largely decoupled, and this especially true in marine ecosystems (Hughes 1984, Hughes and Connell 1987, Bak and Meesters 1998). Individuals of a given age can vary considerably in size by sustaining large partial tissue mortality or shrinkage (Hughes and Connell 1987, Bak and Meesters 1998). Here we modelled the partial tissue mortality of sponges by using the probability of shrinking per individual at each time step and, the probable extent of tissue mortality as a proportion of size.

Shrinking of the tagged sponges was commonly observed in the field. Although partial mortality is generally overlooked in demographic studies of benthic organisms, this attribute could be important for the dynamics of these populations. To calculate the per capita probability of occurrence and intensity of partial mortality we followed sponges that were not subjected to macroalgae or coral competition throughout the year in 2009. These sponges had 95.6 ± 0.2 % (mean ± CI0.95, n = 27) of the perimeter in contact with turf, therefore minimizing any possible confounding effect of competition in the estimates of partial mortality. The probability of partial mortality was then calculated as a proportion of shrinking sponges against those that did not change in size.

Testing the model performance

The population structure of *Cliona tenuis* and the abundance of other benthic components, such as macroalgae and corals, were evaluated over eleven years at Glover's Atoll (between 1998 and 2009). Data were gathered using videos of 1-m2 quadrats, although 10 m^2 belt transects were surveyed in 1998, at two sites on the windward side of the atoll (E1 and E2 in Fig V-20), and one site on the leeward side of the atoll (W1 in Fig V-20). Footage was analysed using the software *VidAna* to calculate the size (area) and number of individuals within each quadrat (Hedley 2006). The population attributes of *C. tenuis*, such as frequency size distribution, kurtosis, skewness, geometric mean size, percentage cover and population size were evaluated at four time periods: 1998, 2003, 2007 and 2009. Size of individuals was dived into six evenly distributed classes, containing individuals within 200 cm2. Additionally, two size classes were incorporated to accommodate newly recruited individuals (<10 cm2) and juveniles (>10 and <100 cm2), summing to a total of eight size classes. Changes in population size structure attributes were compared among periods and sizes using Kruskal-Wallis Analysis of Variance (K-W). Size-frequency distribution at each period was compared against a lognormal distribution using Kolmogorov-Smirnov (K-S) normality test on log-transformed data. Sample size and sampled area are shown in Table V-5.

The accuracy of the model to simulate the dynamics of major benthic groups, including sponges, was evaluated against field observations (1998-2009), independent from the dataset used to parameterize the model. To how well the model captured *in situ* population dynamics, we compared the size-frequency classes produced by the simulation against the size-frequency classes observed in the field. As a metric of goodness fit, we used a standardized distance (δ)

whereby the absolute difference between each simulated (*S*) and observed (*O*) frequency class (*i*) is expressed as a proportion of that observed frequency class, and these differences are summed for the eight size classes (Equation 2).

$$\delta = \sum_{i=1}^{8} \frac{|S_i - O_i|}{O_i} \qquad \text{(Eq 2)}$$

Understanding the role of regulating mechanisms

Here we propose that interspecific competition with macroalgae (C), whole-individual mortality (M), stock-recruitment dynamics of a closed population (SR) and partial tissue mortality (PM) can each contribute to regulating *Cliona tenuis* populations. To explore their relative importance in explaining the population structure of *C. tenuis* observed *in situ* in 2009, we compared the results of the simulations to the field data when each proposed mechanism was incorporated to the model. A null model, including only background sponge growth rates (1.65 $\text{cm}\cdot\text{yr}^{-1}$; linear extension over short turf), a constant recruitment rate (2.5 $\text{ind}\cdot\text{yr}^{-1}$) and negligible effects of competition or mortality, was used as a baseline (i.e. null hypothesis). This approach reassembles a hypothesis testing design, whereby a ‘null model’ is used to simulate the scenario where none of the proposed mechanisms is incorporated (see Gotelli and Graves 1996). We used an orthogonal design that considers each mechanism independently as well as their interactions. We calculated the accuracy of fit of each simulation (θ_i) as a metric to quantify the relative importance of each mechanism and their interactions (Equation 3). Accuracy of fit (θ) it is calculated as a proportion, using the standardized distance produced by each scenario (δ_i) against the metric obtained from the null model scenario (δ_0), such that:

$$\theta_i = 100 \cdot \left(1 - \frac{\delta_i}{\delta_0}\right) \qquad \text{(Eq 3)}$$

Results

The populations of *Cliona tenuis* at Glover's Atoll have maintained their size structure and density over time (Fig V-21, Table V-5) despite two coral bleaching events and three hurricane impacts. In eight out of ten cases, the size structure followed a lognormal distribution (Table V-5), being strongly skewed to the right (3.9 ± 1.7; mean ± $CI_{0.95}$ for all sites and years: Table V-5). Size distributions were typically leptokurtic, described by a low variation around the mean and a high "peakedness" (Kurtosis, 27.1 ± 17.9: Table V-5). On average, 95 ± 3 % of the populations were represented by individuals smaller than 100 cm^2, and with a geometric mean of 13.8 ± 4.7 cm^2.

When parameterized for a typical Caribbean coral reef and initialized with the observed attributes of the reef in 1998, the model successfully simulated the dynamics of the dominant benthic taxa (corals, algae and sponges) at Glover's Atoll over an eleven-year period (Fig V-22). Despite a decrease in coral cover (Fig V-22A) and a small increase in macroalgae cover (Fig V-22B), the abundance of *Cliona tenuis* did not vary either in cover (Fig V-22C) or density (Fig V-22D) over time. The model successfully captured this trend, simulating a size-frequency distribution that is within the 95% confidence intervals of the observed populations at Glover's Atoll (Fig V-22).

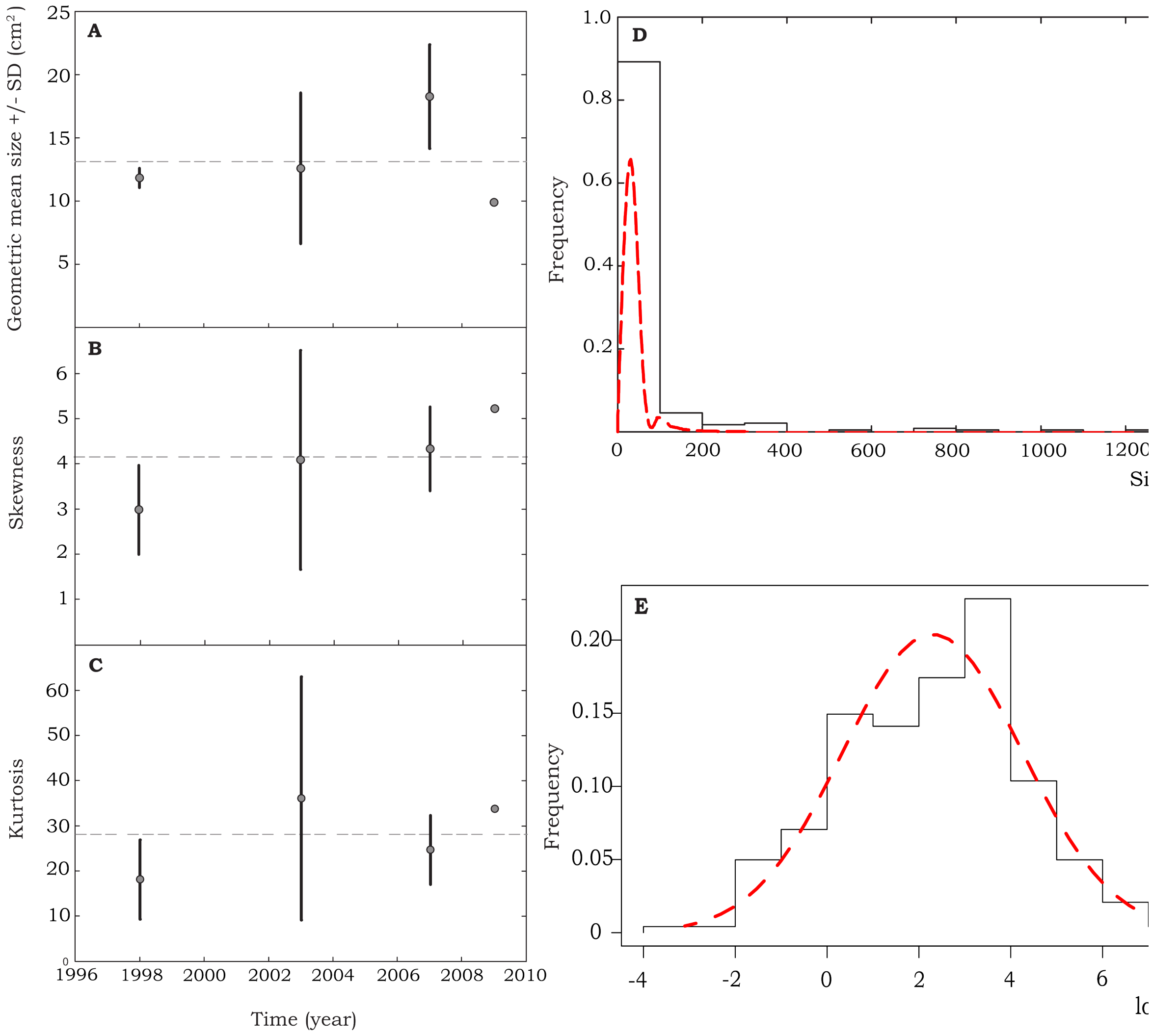

Figure V-21 Demographic attributes of *Cliona tenuis* populations between 1998 and 2009. The dotted line in panned A to C show the global averages among sites and years, dots represent averages among sites, and vertical bars denote the 95% confidence intervals. A) Geometric mean size of individuals. B) Skewness. C) Kurtosis. In panels D and E, the bars indicate the observed size frequency distribution and the red dashed lines show the fitted log-normal size frequency distribution given the mean and standard deviation. D) Size-frequency distribution of *C. tenuis* in 2009. E) The same distribution when size is log-transformed.

Table V-5 Demographic attributes of *Cliona tenuis* at Glover's Atoll from 1998 to 2009, showing the skewness, kurtosis, geometric mean size, K-S normality test of the log transform sample (W Kolmogorov- Smirnov statistic, p: significance level), and the sampling effort (sampled area, number sampling units and of sampled individuals) for specific sponge populations at each site and time. Populations were sampled in time and space using 1-m^2 quadrats, which two exceptions highlighted in the table with the asterisks.

Year	**Site**	**Skewness**	**Kurtosis**	**Geometric mean Size (cm^2)**	**Log-Normality test**		**Sampling effort**		
					W	p	Area (m^2)	Sampling units	Ind.
1998	E1	5.14	38.81	12.65	0.984	0.279	30	6*	100
	E2	0.96	2.64	9.97	0.960	0.694	5	1*	15
	W1	2.86	12.96	12.85	0.988	0.684	15	3*	79
2003	E1	1.12	3.22	27.06	0.958	0.087	13	13	47
	E2	1.15	2.93	7.12	0.888	0.092	18	18	13
	W1	10.01	102.13	3.57	0.953	**0.001**	19	19	106
2007	E1	5.69	34.20	14.82	0.968	0.341	23	23	38
	E2	5.24	33.95	28.18	0.959	**0.043**	40	40	60
	W1	2.08	5.93	11.78	0.934	0.095	30	30	26
2009	E1	5.22	33.78	9.89	0.993	0.291	100/10 **	10	241

* Belt transects (0.5 x 10 m)

** Belt transects (1 x 10 m) for sponge and quadrats (1m2) for other benthic taxa

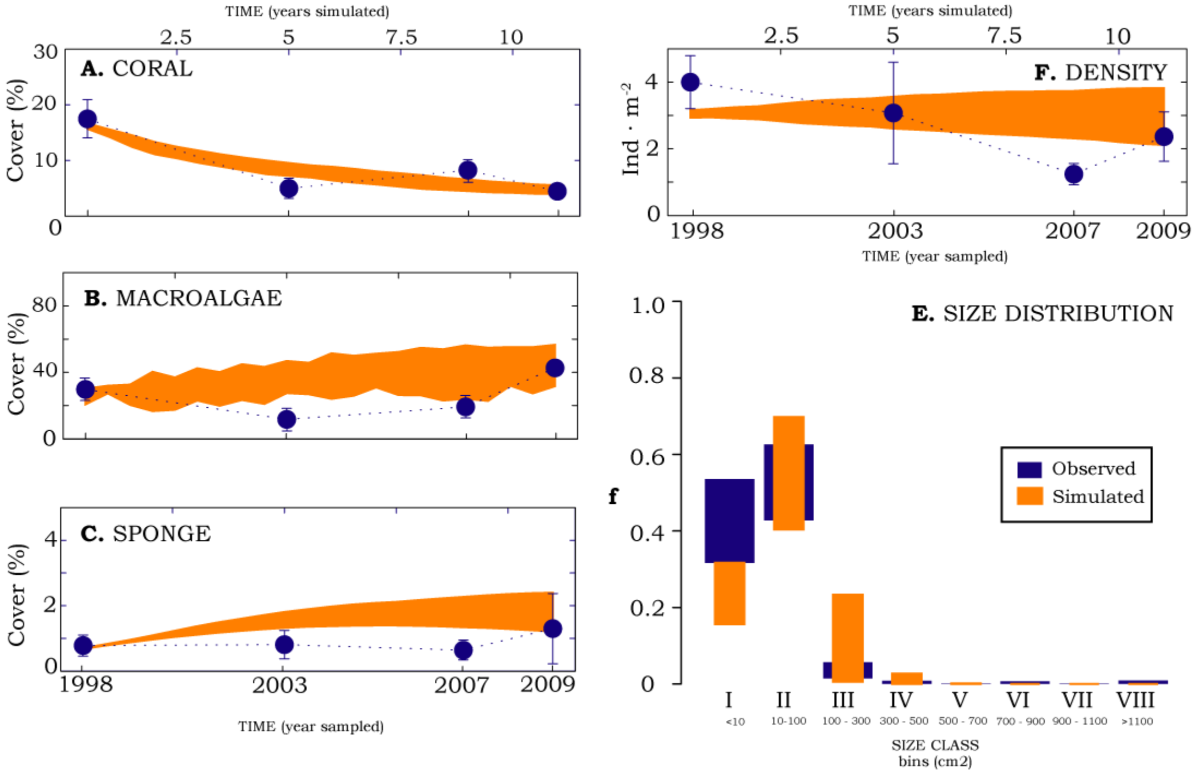

Figure V-22 Validation of the model performance when contrasted against the observed trend of the coral reefs at Glover's atoll over the past 11 years. Left panels show temporal changes in cover of Corals (A), Macroalgae (B) and Sponges (C; *Cliona tenuis*). The density of sponge individuals is depicted in panel F, as well as the size-frequency distribution of the population in E. 95%-confidence intervals, among sites and years, is showed in dark blue, while the modelled attributes over this period are shown ins light grey.

To compare the relative roles of the four candidate mechanisms in controlling the observed population structure of *Cliona tenuis*, we iteratively included each mechanism in the model and compared the results against those of a null model (Fig V-23 and Fig V-24). Algal competition is the most important driver of population size structure of *C. tenuis* at Glover's atoll, explaining a great deal of the simulations fit (92%) and constraining the abundance of individuals to the smallest size classes (Fig V-24E). When competition is negligible (null hypothesis model), the population size structure rapidly shifts to a left-skewed distribution, where large individuals represent the bulk of the population and pre-empt the space (Fig V-24A). Although partial mortality (Fig V-24C) and stock-recruitment dynamics of a fully-closed population (Fig V-24B) did not make large individual contributions to the goodness of fit, their interaction with competition explains much of the observed leptokurtic and strongly right-skewed population size structure (Fig V-24E). When interacting in the model, competition and partial mortality constrain the majority of the population to the small size classes (Fig V-24F). Lastly, the size-frequency distribution is best modelled when also including stock-recruitment dynamics, coupling the rate of new recruits to the abundance of adults in the local population (improving the goodness of fit to 98.7%: Fig V-24G). Overall, when affected by competition and partial mortality, the somatic growth of the sponge is the most sensitive vital rate determining changes in the size and structure of populations of *C. tenuis*.

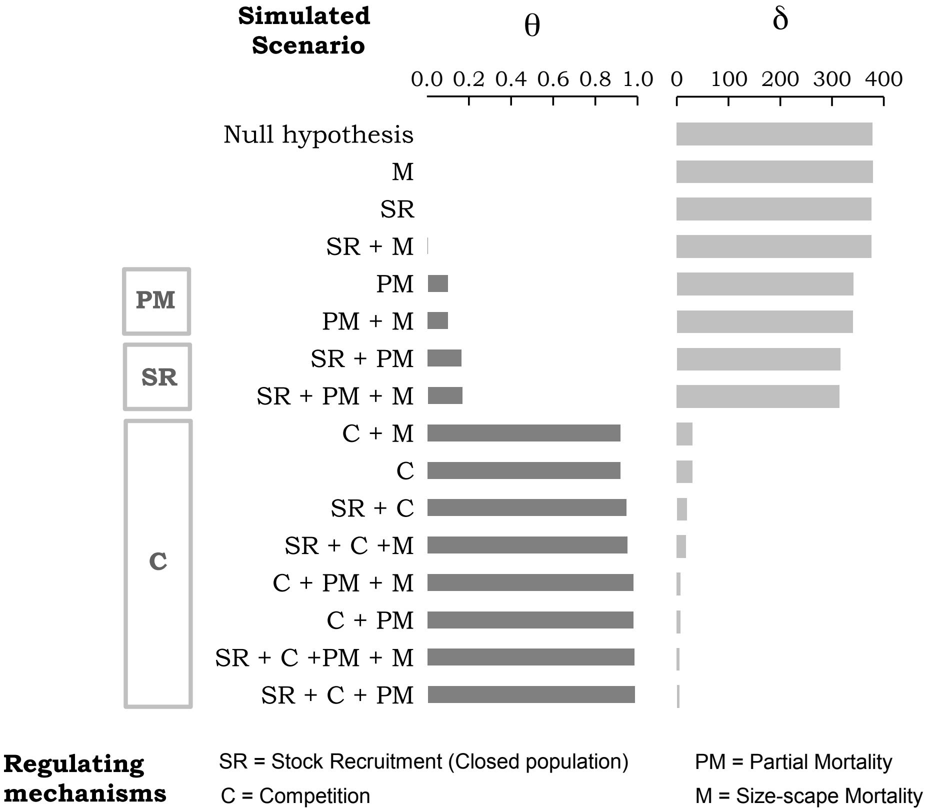

Figure V-23 Quantitative metrics of the fit of the simulated size structure of *Cliona tenuis* when hypothesized regulating mechanisms are modelled for 11 years. Light grey bars represent the simulated scenarios incorporating each regulating mechanism and their interactions. Dark grey bars show the accuracy of fit (θ) of the simulation to the data, when compared to the null hypothesis, where none of the drivers are modelled. The standardized distance (δ) between the observed and simulated size structure is depicted by light grey bars. The boxes on the left of the plot highlight the main mechanisms driving the increase in θ and respective decrease in δ.

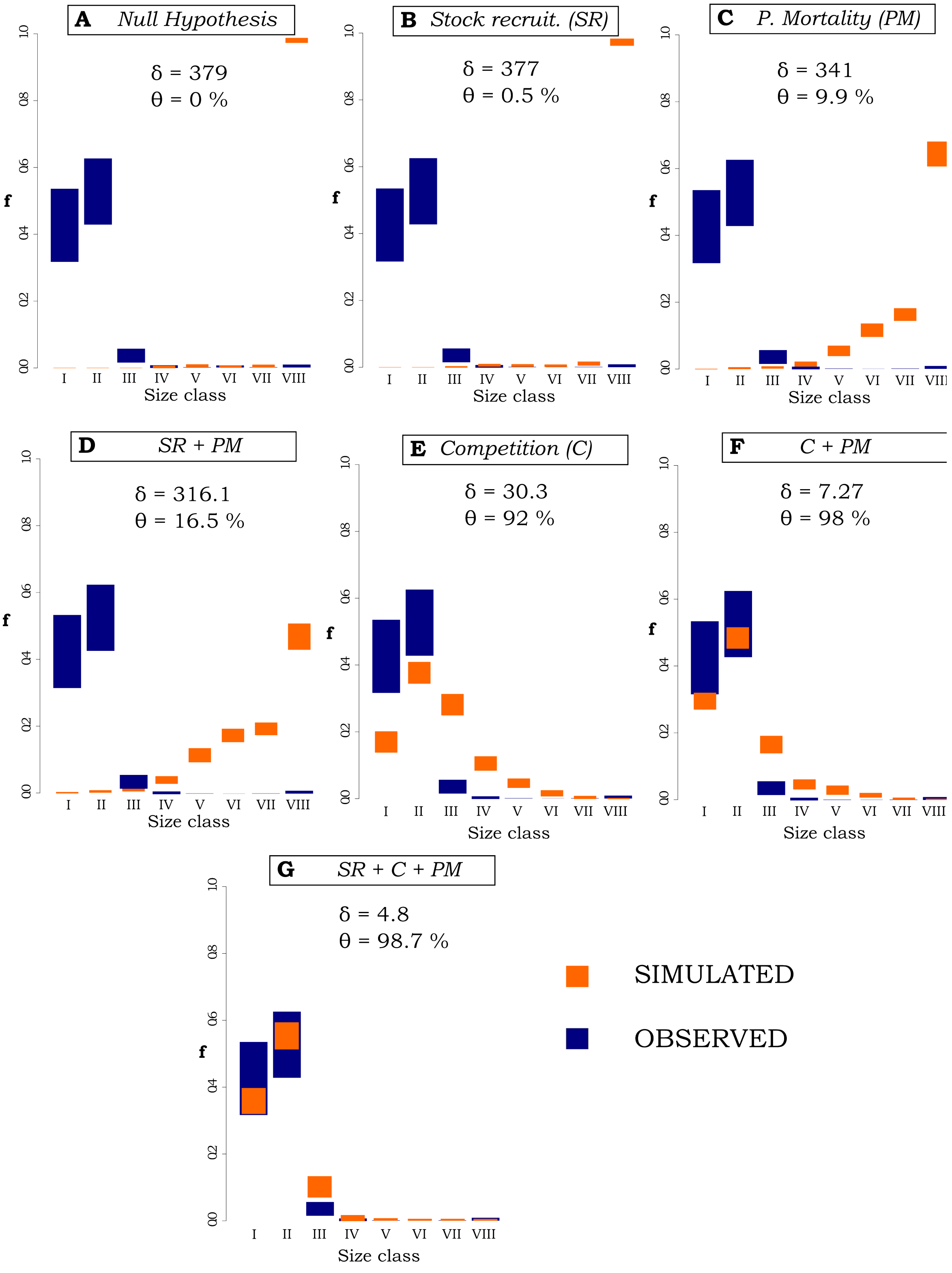

Figure V-24 The relative role of each candidate-regulating driver of the size structure of *Cliona tenuis*, showing simulated (grey) and observed results (blue). Blue bars represent the observed frequency of individuals, representing the variability within 95% confidence of intervals among the study sites and years at Glover's atoll. The simulated frequency of individuals per size class is depicted by grey bars, which represent the upper and lower boundary of the frequency with the standard deviation of the mean. The figure also include the standardized distance (δ) and the percentage of fit explained (θ) when the followed scenarios are modelled: **A**. Null hypothesis, when none of the hypothesised drivers are modelled; **B**. Stock-recruitment dynamics of a closed population; **C**. Partial mortality; **D**. Stock-recruitment and partial mortality; **E**. Competition; **F**. Stock-recruitment and Competition; and **G**. Stock-recruitment, competition and partial mortality.

Discussions

Overall, the population structure of *C. tenuis* at Glover's atoll remained constant in time even in spite of an important reduction in coral cover. Small-size individuals, describing a right-skewed size-frequency distribution, characterized the population structure of sponges. Competition is the most important driver of the dynamics resulting on this population size-structure. In general, the model here presented captures well *in situ* observations of the population dynamics of *C. tenuis*, tested against field observations during eleven years at Glover's Atoll.

The role of disturbance in structuring highly competitive systems has been supported by studies in many systems, including forests (Wright 2002), grasslands (Olff and Ritchie 1998), intertidal rocky shores (Dayton 1971, Paine 1988), coral reefs (Connell 1978, Porter et al. 1982) and deep sea bottom communities (Dayton and Hessler 1972). Here we demonstrate how multispecies interactions following disturbance can be used to predict the response of individual populations, even in complex systems. We show that a fugitive species, a species adapted to colonize newly disturbed habitats, such as *Cliona tenuis* has the potential to respond rapidly to the opportunity provided by disturbance, and how such potential is dampened by macroalgal competition exerting a stabilizing effect on the sponge population.

Over the 11 years covered by our data set, coral cover decreased by 74% on average, probably attributable to hurricane and bleaching events (see Mumby 1999, Mumby et al. 2005). Following such perturbation, a release from space limitation may promote the rapid colonization by *Cliona tenuis* given its resistance to disturbance and fast growth rate (Vicente 1990, Schönberg and Wilkinson 2001, Wulff 2006). However, populations of *C. tenuis,* at Glover's Atoll have remained largely unchanged over the past decade, at low in cover and density, and maintaining a strongly right-skewed size-frequency distribution. This lognormal size pattern is common in many taxa, resulting from the evolution of life history strategies and is modulated by the biotic and abiotic environment (Hutchinson and MacArthur 1959, Kirchner et al. 1980). Many coral species exhibit lognormal size-frequency distributions, whose attributes vary among species and disturbance regimes (Meesters et al. 2001). For these clonal organisms, the size-frequency distribution has been explained by extrinsic processes such as competition for space constraining the transition of juvenile corals to lager classes (Muko et al. 2001), or attributed to partial mortality of the tissue in clonal individuals, which increases with size and restricts the abundance of large sizes (Hughes and Jackson 1985, Babcock 1991, Bak and Meesters 1998). In the case of *C. tenuis*, we show that modelling both processes can explain the stable skewed size-frequency distribution over time, although largely more explained by competition. However, while these conclusions can be extrapolated to most Caribbean coral reefs, the importance of these processes may change and thus the structuring forces that regulate the sponge populations.

As highlighted in the literature, rapid growth and high recruitment can combine to support a positive numerical response of *Cliona* spp populations as much as pre-empting available space (Rützler 2002, Ward-Paige et al. 2005, Schönberg and Ortiz 2008). Nonetheless, interspecific competition strongly inhibits *C. tenuis* outbreaks and explains a large proportion of the unaltered behaviour of their populations over time at Glover's atoll (92% of the fit). Additionally, the stabilizing effect of macroalgal competition acts in a density-dependent manner to regulate the sponge populations, where a decrease in macroalgae cover can induce a rapid positive response from the sponge (data not shown). This is supported by the observed shift in dominance of a encrusting and competitive sponge, *Chondrilla nucula*, after bleaching-induced coral mortality under high levels of herbivory (Aronson et al. 2002). Density-dependent demography has been widely investigated in plants, and most studies consider only the density only of the studied species. However, density-dependent regulation of sessile organisms, both in terrestrial and marine ecosystems, may frequently occur at community level, rather than only within particular species (Goldberg et al. 2001, Tanner et al. 2009). Our results add to the growing knowledge of community-level density-dependant interactions as an important driver of community assemblages (Lenssen et al. 2004, Feagin et al. 2005, Tanner et al. 2009).

Other examples, particularly from terrestrial systems, support our findings. In meadows, weed outbreaks can be promoted by seed storage and localize soil disturbances, but the overall trend of the populations is strongly regulated by plant competition and insect herbivory (McEvoy et al. 1993). In flood plains, although some plants tolerate floods better than others, the disturbance does not favour weak competitors. Therefore, high tolerance to disturbance in combination with traits enhancing competitive ability after flooding can ensure persistence in disturbed sites (Lenssen et al. 2004). In coral communities, hurricanes can release the competition pressure for space by diminishing the cover of highly competitive species such as macroalgae, and temporarily favouring fugitive species, that are tolerant to the disturbance and rapidly colonize the substrate as a result of their higher recruitment rates (Connell et al. 2004). Nevertheless, when cover is increasing, branching corals of *Acropora* genus grow quickly, overgrowing the fugitive species and thus reducing their populations (Connell et al. 2004), by asymmetrical competitive abilities.

In combination with interspecific competition, although to a lesser extent, intrinsic aspects of *Cliona tenuis* populations, such as partial tissue mortality and the strong stock-recruitment dynamics typical of closed populations may also modulate their population size structure. Partial mortality in modular organisms, such as corals, has been attributed to age-related failure of the individual to repair physical damage, therefore exhibiting an asymptotic increase in mortality with size (Meesters et al. 1994, Bak and Meesters 1998), as observed after the optimization exercise. Competition and partial mortality may act as growth constraints, limiting the transition of small individuals to larger size classes. On the other hand, based on the assumption of a closed population in clionaids (Mariani et al. 2000, Mariani et al. 2001, Mariani et al. 2005), the sparse abundance of large individuals help to refine the fitting of the simulations by incorporating recruitment limitation. However, at this stage, our data only partly highlight our limited understanding of partial mortality and stock-recruitment dynamics. We highlight the need for further research to understand how environmental conditions can moderate the role of these two processes in sponge population dynamics. It would be particularly crucial to understand which factors can alter the competitive ability and, thus, the ‘invasibility’ of the sponge into perturbed systems, *sensu* the hypothesis of competitive change (Suding and Goldberg 2001). It predicts that certain species can increase in competitive ability relative to other species followed perturbations (Wedin and Tilman 1993, Suding and Goldberg 2001, Lenssen et al. 2004).

Disturbance may be expected to favour weaker competitors by releasing them from competition when the abundance of stronger competitors diminishes followed disturbance (Horn and MacArthur 1972, Goldberg et al. 2001). Alternatively, the competitive attributes of a particular species may change as disturbance occurs, shifting the competitive hierarchy in the system, competitive change hypothesis (Suding and Goldberg 2001, Lenssen et al. 2004). Disturbance may thus change the size structure and relative abundance of a particular species by favouring its competitive abilities relative to other species in the community, as observed in changes in nutrient content in soil altering the competitive hierarchy of plants (Wedin and Tilman 1993, Suding and Goldberg 2001). Our study highlights the importance of asymmetrical competition, represented by disparities in size, competitive strength and colonization rate, as a structuring driver in populations of excavating sponges, when disturbance affects the abundance of competitors. Nonetheless, sources of disturbance, such a nutrient enrichment in coastal waters, are likely to affect the competitive abilities of sponges (Rose and Risk 1985, Ward-Paige et al. 2005) and theses aspects in context of population dynamics still remain understudied.

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Appendix

Appendix A. Estimation vital rates of *Cliona tenuis* and general model parameterization

Table A-1. Full detail of the model parameterization.

Parameter	Details
Coral recruitment	Corals recruit to cropped algae, because algal turfs are not heavily sediment-laden. Recruit at size 1 cm2. Recruitment rate of brooders and spawners (respectively): 2 and 0.2 per 0.25 m2 of cropped algae per time interval. Recruitment rate was adjusted for rugosity (~2) and the cover of cropped algae at Glovers Reef (Mumby 1999).
Coral growth	Coral size is quantified as the cross-sectional, basal area of a hemispherical colony (cm2). BC have a lateral extension rate of 0.8 cm · yr^{-1} and SC grow slightly faster at 0.9 cm · yr-1 (based on median rates for *Porites astreoide*s, *P. porites*, *Siderastrea siderea, Montastraea annularis, Colpophyllia natans* and *Agaricia agaricite*s) (Maguire and Porter 1977, Highsmith et al. 1983, Huston 1985, Chornesky and Peters 1987, Van Moorsel 1988)).
Coral reproduction	Excluded, assume constant rate of coral recruitment from outside reef (i.e. no stock-recruitment dynamics).
Colonisation of cropped algae	Cropped algae arise (i) when macroalgae is grazed and (ii) after all coral mortality events (Jompa and McCook 2002a) except those due to macroalgal overgrowth (see coral-algal competition below).
Colonisation of macroalgae	Macroalgae have a 70% chance of becoming established if cropped algae are not grazed for 6 months (mostly *Dictyota*) and this increases to 100% probability after 12 mo of no grazing (mostly *Lobophora*). Rates acquired from detailed centimeter-resolution observations of algal dynamics with and without grazing, (Box and Mumby unpub. data, Mumby et al. 2005).
Macroalgal growth over dead coral (cropped algae)	In addition to arising from cropped algae that are not grazed (above), established macroalgae also spread vegetatively over cropped algae (mostly *Lobophora* as *Dictyota* spread shows little pattern with grazing (Mumby et al. 2005). The probability that macroalgae will encroach onto the algal turf within a cell, PA→M, is given by (1) where M4cells is the percent cover of macroalgae within the von Neumann (4-cell) neighbourhood (de Ruyter van Steveninck and Breeman 1987). This is a key method of algal expansion and represents the opportunistic overgrowth of coral that was extirpated by disturbance. PA→M = M4cells (1)
Competition between corals	If corals fill the cell (2500 cm2), the larger coral overtops smaller corals (chosen at random if more than one smaller coral share the cell). If corals have equal size, the winner is chosen at random (Lang and Chornesky 1990).
Competition between corals and cropped algae	Corals always overgrow cropped algae (Jompa and McCook 2002a).
Competition between corals and macroalgae 1: effect of macroalgae on corals	a) Growth rate of juvenile corals (area <60 cm^2) set to zero if M4cells ≥ 80%, and reduced by 70% if 60% ≤ M4cells < 80%. Parameters based on both *Dictyota* and *Lobophora* (Box and Mumby 2007). b) Growth rate of juvenile and adult corals (area ≥ 60cm2) reduced by 50% if M4cells ≥ 60% (Tanner 1995, Jompa and McCook 2002a, b).

	c) Limited direct overgrowth of coral by macroalgae can occur (Lirman 2001, Nugues and Bak 2006, Hughes et al. 2007) found that the upper 95% CL of the mean area of overgrowth ranged from 0-18 cm^2 pa across a ~7cm length of coral edge, with an overall mean of 8 cm^2 pa. This translates to 4 cm^2 in each 6-mo time step of the model. Overgrowth (cm^2), OC→M, was scaled to entire colonies using (2) where M4cells is the proportion of macroalgae in the von Neumann 4-cell neighbourhood and Pi is the perimeter of the coral. $OC \rightarrow M = M4cells \times Pi/7 \times 4$ (2) Note that Nugues and Bak (2006)) did not find significant effects of Lobophora on all coral species studied. Whilst this was the correct interpretation of their data, the published results strongly suggest that an effect does exist and that a larger sample size may well have resulted in significant differences. Other studies have found negative effects of macroalgae on both massive (Lirman 2001) and branching corals (Jompa and McCook 2002a).
Competition between corals and macroalgae 2: effect of corals on macroalgae	The probability with which macroalgae spread vegetatively over cropped algae, PA→M (1) is reduced by 25% when at least 50% of the local neighbourhood includes coral (de Ruyter van Steveninck et al. 1988, Jompa & McCook 2002a) ()proportion of coral, 2500BCSCC+= (3a) $PA \rightarrow M = 0.75 \times M4cells$ if $C5cells \geq 0.5$ (3b) $PA \rightarrow M = M4cells$ if $C5cells < 0.5$, (3c) where C5cells is the proportion of corals in the 5 cell neighbourhood comprising the focal cell and the 4-cell von Neumann neighbourhood.
Grazing by fishes & impact of fishing	Grazing is spatially-constrained (Williams et al. 2001, Mumby 2006, Mumby et al. 2006a). The dynamic basis of this grazing threshold is poorly understood seeing as most measures of grazing take place at scales of seconds and most studies of algal dynamics take place on monthly scales (hence the use of a 6 month time step). Nonetheless empirical studies (Mumby 2006b), and experimental results scaled to the complex forereef (Williams et al. 2001), have identified a grazing limit of 30%-40% of the reef during 6 months. This value allows for a numeric positive response by parrotfish after severe coral mortality events during which colonisation space for algae increases dramatically. For example, an increase in parrotfish biomass over 5 years maintained the cover of cropped algae at Glovers Reef at 35% after Hurricane Mitch caused extensive coral mortality and liberated new settlement space for macroalgae (Mumby et al. 2005) (i.e. grazing impact remained at around 30% 6 mo.-1 even though coral cover dropped from around 60% to 20%, suggesting that the approach is robust during phase changes). The reasons for this are not fully understood. All parrotfish species graze algal turfs and in doing so constrain the colonisation and vegetative growth of macroalgae. Direct removal of macroalgae occurs through the grazing of larger sparisomid species (up to 50% of bites in S. viride, Mumby unpub. data) and natural fluctuations in algal dynamics including annual spawning events during which their cover is decimated (Hoyt 1907). Of course, macroalgae increase once the availability of settlement space exceeds the grazing threshold (e.g. as coral cover declines from disturbance). During a given time interval, cells are visited in a random order and all algae consumed until the total grazing impact is reached. This approach implies spatially-intensive grazing which appears to be more biologically-accurate than a spatially-extensive approach because parrotfish feed repeatedly at particular sites on time scales of days to weeks (Mumby unpublished data). All turf and macroalgae are consumed (and converted to A6) until the constraint is reached.

Partial-colony mortality of corals	Size-dependent, following empirical observations from Curaçao before major bleaching or hurricane disturbances (Meesters et al. 1997). State variables reported in literature converted to dynamic variables using least squares optimization until equilibrial state in model matched observed data. Implementation uses equations (4a) and (4b) where Ppm is the probability of a partial mortality event, Apm is the area of tissue lost in a single event, and χ is the size of the coral in cm^2: $Ppm = 1-[60+(-12 \ln(\chi))]$ (4a) $\mathrm{Ln}[(Apm \times 100)+1] = -0.5 + (1.1 \ln(\chi))$ (4b)
Whole-colony mortality of juvenile and adult corals	Incidence of mortality in juvenile corals (60-250 cm^2), 2% per time interval (~4% per annum). Halved to 1% (2% pa) for mature colonies (>250 cm^2) (Bythell et al. 1993). These levels of mortality occur in addition to macroalgal overgrowth. Algal overgrowth and predation affects juvenile corals (see above and below).
Predation on coral recruits	Instantaneous whole-colony mortality occurs from parrotfish predation at a rate of 15% each 6 month iteration of the model (Box & Mumby 2007) Predation is confined to small corals of area $\leq 5cm^2$, based on Meesters et al (1997) where between 60% and 95% of bite-type lesions were of this size.
Environmental disturbance	Hurricane incidence was measured using the Atlantic Hurricane dataset (1851-2008), which tracks the location and intensity of the eye of tropical cyclones every six hours (Jarvinen et al. 1984). We confined the analyses to storms that reached hurricane intensity (wind speeds higher than 166 km h-1). Hurricane-force winds may extend several kilometers from the hurricane track. We calculated the frequency of hurricanes in any given location using the approach described by Edwards et al. (2010). Essentially, the area of influence of each hurricane is captured in buffers (up to 160 km wide) that take into account the intensity of the storm, its asymmetry (because of the Coriolis force) and the reduction in wind speed with distance from the hurricane track (Keim and Muller 2007). Using this approach, we mapped the total frequency of hurricanes for each Saffir-Simpson intensity class for the entire record at 1 km2 spatial resolution. Hurricanes can affect corals and macroalgae, but we assumed no effects on the sponge, giving its encrusting growth from, sheltered from the breakage effects of water movement during hurricanes (Wulff 2006).

~ VI ~

GENERAL DISCUSSION

Sponges contribute critically to coral reef ecosystem dynamics. This has been established by studies that demonstrate their role in ecosystem processes or attributes, such as competition (Aerts 1998, Wulff 2006, Chadwick and Morrow 2011), nutrient cycling (Scheffers et al. 2004, de Goeij et al. 2008, Hoffmann et al. 2009), bioerosion/construction of the physical framework (Scoffin et al. 1980, Wulff 1984, Acker and Risk 1985, Hutchings 1986), and ultimately biodiversity (Díaz and Rützler 2001, Ribeiro et al. 2003, van Soest 2007). However, this intriguing group of organisms often challenge further developments in their ecology as a consequence of their taxonomical complexity, remarkable plasticity in function and form to the environment, and the difficulty maintaining them in experimental conditions for long periods of time (Bergquist 1978, Rützler 2004, Wulff 2006); thus resulting in a noticeable paucity of sponge ecological knowledge (Becerro 2008). Consequently, important knowledge gaps still require investigation, which constitute urgently needed information when predicting the ecosystem role of sponges as coastal environments experience greater levels of disturbance. As pointed out in the literature, bioerosion is one the sponge-driven processes proposed to increase followed disturbances, as excavating sponges are proposed to readily benefit from coral mortality, while resisting to major disturbance regimes (Rützler 2002, Schönberg and Ortiz 2008). In particular, it is proposed that sponge bioerosion can be facilitated as reefs rapidly degrade under the effects of nutrient enrichment, hurricanes, sea temperature rise and sedimentation (Rützler 2002, López-Victoria and Zea 2004, Ward-Paige et al. 2005, Carballo et al. 2008). Nonetheless, much of our current understanding relay on individual-based studies on bioeroding sponges, where integrative approaches considering their interaction with other reef taxa (i.e., community and ecosystem) remain poorly studied (see Becerro 2008).

This thesis investigates the sponge biology and ecology and contributes to a more holistic understanding of the ecology of bioeroding sponges and their putative response in the face of disturbance; thus, adding to the general knowledge of the reef trajectories in the face of perturbations. I have shown that excavating sponges potentially benefit from disturbances of coral reef ecosystems and have the capacity to alter ecological dynamics of these systems. Additionally, the thesis also emphasizes the overriding importance of multispecies interactions to predict the response of sponge populations in complex systems accurately. Ultimately, this contribution generates, investigates, and provides hypotheses for further studies, which are outlined in further detail bellow.

Biological attributes of clionaids have been widely studied to understand the mechanisms of bioerosion and competition, with particular focus on interactions with corals (Rützler 1974, Rützler 1975, Schönberg and Wilkinson 2001, Rützler 2002, Schönberg 2006, Chaves-Fonnegra and Zea 2007, Chaves-Fonnegra et al. 2008, Chaves-Fonnegra and Zea 2011). My results contribute to the growing understanding of interspecific interactions of sponges with other taxa, such as competition with macroalgae, and predation by parrotfish (Cebrian and Uriz 2006, López-Victoria et al. 2006, Cebrian 2010). In addition, this work describes for the first time clionaid life history traits, such as sexual reproduction and growth, highlighting a seasonal trade-off in these traits. Trade-offs in biological functions are the consequence of evolutionary pressures favouring the fitness of species in a particular environment (Tuomi et al. 1983, Roff 1984, Reich et al. 2003). Therefore, trade-offs are perhaps one of the most obvious, and still largely understudied, aspects of sponge ecology to explore in response to disturbances. Phenology, the study of annually recurring life cycle events such as reproduction, migration and growth, can provide useful insights into the response of populations to a perturbed environment. Mostly represented in terrestrial ecology, studies on the effects of disturbances on the phenology of species have found a remarkable impact on the overall response of the population (Nylehn and Totland 1999, Cotton 2003), and more recently at the ecosystem level (Crawley 2004, Edwards and Richardson 2004).

In the context of a globally changing climate, studies of terrestrial systems using long-term data sets, have observed phenological trends that likely reflect responses to climate change (see Walther et al. 2002). Increasing evidence of changes in the timing of spring activities include earlier breeding or first singing of birds, earlier arrival of migrants (Cotton 2003), appearance of butterflies, choruses and spawning in amphibians and shooting/flowering of plants, has been associated to global warming (Walther et al. 2002, Parmesan and Yohe 2003). More recently applied to marine pelagic environments, studies show that large-scale phenological shifts in traits can importantly alter the ecosystem dynamics (Edwards and Richardson 2004, Pörtner and Farrell 2008). In coral reefs, these aspects remain understudied, despite our rapidly increasing body of knowledge in the context of a changing climate (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010).

With global concerns of increased reef erosion and decreased accretion under climate change (Hoegh-Guldberg 2011), there is an urgent need to understand the magnitude of the effects on significant bioeroders, such as sponges. Environmental drivers, such as temperature, are documented in the literature and supported by our results to be important phenological triggers of traits such as growth and reproduction (Rützler 2002, Ettinger-Epstein et al. 2007, Schönberg et al. 2008). However, the extent and direction at which the projected temperature increase (sensu IPCC 2007) can affect clionaid populations remain largely understudied (but see Márquez et al. 2006, Schönberg et al. 2008). Furthermore, as disturbances are not acting independently, other sources of anthropogenic activities may interact as climate changes, which combined effects on marine sponges remain unknown (Nyström et al. 2000, Hoegh-Guldberg and Bruno 2010). Such interactions, for example among nutrient enrichment, hurricanes, ocean acidification and overfishing may alter the competitive hierarchy of the benthic community of coral reefs, and our limited knowledge on the combined effects on bioeroding sponges, given the complexity of species interactions in coral reefs, combined with the complexity of coral reefs, severely constrain our understanding of the system trajectories.

From the holistic view of an ecosystem, emergent properties arise when scaling-up observations from individuals and populations. These include a special case in which heightened competitive ability of macroalgae versus coral in the face of sponge competition may counter-intuitively prove to be advantageous to the persistence of corals, suggesting intransitive interactions. Analytical and simulation models provide different angles to understand complex dynamics, since they are different, but complementary, approaches. On one hand, analytical models represent a simplistic view of the system where we focused on the importance of competition among three major taxa on the reef. This simplistic approach allowed us to explore the sensitivity of the model to multiple competitive parameters affecting the dynamics of the taxa and to project the state of the system until reaching multiple equilibria states. On the other hand, simulation models allowed an expansion of the complexity of the system by incorporating multiple species and processes in a spatially explicit context. By being more realistic, this approach is computationally more challenging and only allowed us to explore the role of particular processes at a shorter and high-resolution time scale. Using both approaches we showed that incorporating sponges into ecological models of reef could alter current predictions of reef trajectories because of the intrinsic attributes of their populations. However the simulation approach also demonstrates an asymmetrical competition between macroalgae and sponges, which dampens the potential of clionaid outbreaks when space is released by coral mortality

Further work is needed on a number of sponge dynamics. For example, our work demonstrates that macroalgal competition can reduce the rapid expansion of clionaids, but other studies suggest that this interaction may be more complex. Recent studies on Caribbean reefs have shown that algae and other benthic taxa can be important sources of nutrition for sponges, by leaking dissolved organic matter (van Duyl et al. 2011). These findings support the nature of intransitive interactions in benthic ecosystems, by suggesting a non-linear and rather interconnected network of interactions among benthic taxa (sensu Buss 1980, Laird and Schamp 2006, Edwards and Schreiber 2011). Therefore, provided that these complex intransitive networks can facilitate the coexistence of highly competitive species (Edwards and Schreiber 2011), the study of unexplored interactions on highly competitive species such as sponges and macroalgae can provide great insights to understand the trajectory of perturbed system.

Moreover, understanding these complex intransitivity networks under interacting disturbances, such as nutrient enrichment, sedimentation and thermal stress, will contribute to an accurate prediction of the fate of these ecosystems.

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