

DEMOGRAPHY OF THE GIANT BARREL SPONGE *XESTOSPONGIA MUTA*  
IN THE FLORIDA KEYS

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## ABSTRACT

Coral reefs are in decline worldwide, prompting research toward a better understanding of the demographics of dominant organisms that comprise reef communities. Sponges are an especially abundant and diverse group on Caribbean coral reefs that perform key community functions, however little is known about sponge demography. The giant barrel sponge *Xestospongia muta* a particularly important species; populations constitute a significant amount of overall reef biomass, are an important component of habitat heterogeneity, and filter large amounts of seawater. Since 1997, the Pawlik laboratory has monitored permanent transects on reefs off Key Largo, Florida, to study the demography of *X. muta*. This long-term dataset was used, along with experimental approaches, to address topics on the demography, growth, bleaching, and conservation of *X. muta*.

In the first chapter, I examined the population dynamics and structure of *X. muta* on reefs off the Florida Keys. Population densities of *X. muta* were found to significantly increase over 6 years at sites on Conch and Pickles Reefs. To explore the demographic processes behind the population increase and determine future population growth under present reef conditions, a size-based matrix modeling approach was used. Variable recruitment pulses and mortality events were hypothesized to be large determinants of the demographic patterns observed for *X. muta*. Elasticity and life table response analysis revealed that survival of individuals in the largest size class has the greatest effect on population growth. Projections indicate that populations of *X. muta* will continue to increase under present conditions, and therefore maintain the alternate reef community. While populations of *X. muta* remain resilient to current coral reef degradation, population growth may be negatively affected by continued mortality of the largest individuals from a recently described pathogenic syndrome.

*Xestospongia muta* has been called the ‘redwood of the reef’ because of its large size (often >1 m height and diameter) and presumed long life. In chapter two, I examined the growth and age of *X. muta*. Measurements of sponges were taken in the field and from digital images to examine morphological scaling and growth dynamics. Five models were fit to volume estimates to determine which best described growth. Growth was variable, and specific growth rates decreased with increasing sponge size. Negative growth rates occurred over short temporal scales and growth varied seasonally, significantly faster during the summer. No differences in specific growth rate were found between transects at 3 different depths (15, 20, 30 m) or at 2 different reef sites. Spongocoel volume was positively allometric with increasing sponge size and scaling between the vertical and horizontal dimensions of the sponge indicated that morphology changes from a frustum of a cone to cylindrical as volume increases. Growth of *X. muta* was best described by the general von Bertalanffy and Tanaka growth curves. The largest sponge within transects was estimated to be 127 years old. Although age extrapolations for very large sponges are subject to more error, the largest sponges on Caribbean reefs may be in excess of 2300 years, placing *X. muta* among the longest-lived animals on earth.

*Xestospongia muta* has commonly been reported as an affected species during coral reef bleaching events. While water temperature is regarded as the primary causative agent of coral bleaching, the cause and impact of sponge bleaching was unknown. In the third chapter, I examined the relationship between anomalous water temperatures and bleaching of *X. muta*. Bleaching and temperature data was collected over the period 2000 to 2005 at three depths on Conch Reef, Florida. Bleaching increased significantly with depth and was significantly greater in the fall compared to the spring. The percentage of days in which there was a positive or negative 0.5°C anomaly within two weeks prior to bleaching surveys was found to best explain

the relationship between temperature and bleaching. Bleaching significantly increased with positive 0.5°C anomalies at 30 m in the spring and fall, and with negative 0.5°C anomalies in the spring, but there were not similar effects at the other two depths. Unlike bleaching in corals, bleaching of *X. muta* appears to be a response by cyanobacteria symbionts that have little effect on their host sponge.

When damaged or dislodged, large sponges usually die because they are unable to reattach to the reef substratum. Because suitable methods for reattaching dislodged sponges are lacking, they are typically excluded from coral reef restoration efforts. In the final chapter, I present a novel technique for the reattachment of large sponges that was tested using *X. muta*. Transplants of *X. muta* were conducted at 15 and 30 m depth off Key Largo, Florida. Despite the active hurricane season of 2005, 90% of deep and 35% of shallow transplants survived, with nearly 80% reattaching to the substratum and growing after 2.3 – 3 years. This technique may be generally adapted for securing large sponges in coral reef restoration efforts.

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## DEDICATION

Dedicated to Pop – feed and speed.

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CHAPTER 1. DEMOGRAPHICS OF INCREASING POPULATIONS OF THE GIANT  
BARREL SPONGE *XESTOSPONGIA MUTA* IN THE FLORIDA KEYS

ABSTRACT

Caribbean coral reefs have been altered by a number of anthropogenic and natural stressors, resulting in a state dominated by sponges, gorgonians and macroalgae. While sponges are a diverse and abundant component of Caribbean coral reefs, little is known about their demography. Permanent transects on reefs off Key Largo, Florida, have been monitored since 1997 to study the demography of a particularly important species, the giant barrel sponge *Xestospongia muta*. Population densities of *X. muta* significantly increased over 6 years at sites on Conch Reef by a mean of 46% (range:16 - 108%) and by a mean of 33% on Pickles Reef. In 2006, densities of *X. muta* on Conch Reef ranged from 0.134 to 0.277 sponges/m<sup>2</sup>, and mean sponge biomass was 1488 cm<sup>3</sup>/m<sup>2</sup>, with the largest size class of sponges constituting 75% of the total biomass. Increased sponge density resulted from a significant increase in individuals of the smallest size class. Recruitment and recruit survival did not significantly change through time; however a significant interaction between season and year on recruitment suggests large recruitment pulses are driving population increases. Mean yearly recruitment rates ranged from 0.011 to 0.025 recruits/m<sup>2</sup> year<sup>-1</sup>, with pulses as high as 0.036 recruits/m<sup>2</sup>. To explore the demographic processes behind the population increase and determine future population growth under present reef conditions, a size-based matrix modeling approach was used. Variable recruitment pulses and mortality events were hypothesized to be large determinants of the demographic patterns observed for *X. muta*. Elasticity and life table response analysis revealed that survival of individuals in the largest size class has the greatest effect on population growth.

Projections indicate that populations of *X. muta* will continue to increase under present conditions, and therefore maintain the alternate reef community. While populations of *X. muta* remain resilient to current coral reef degradation, population growth may be negatively affected by continued mortality of the largest individuals from a recently described pathogenic syndrome.

## INTRODUCTION

Coral reefs are dynamic ecosystems, with high biodiversity maintained by periodic natural disturbances (Connell 1978). In recent decades, however, the disturbance regime has been altered by humans, resulting in declines of coral reefs worldwide, and particularly in the Caribbean (Gardner et al. 2003; Wilkinson 2004). Numerous factors have been linked to coral reef degradation, including climate change, overfishing, eutrophication, and diseases (Halpern et al. 2008). Coral reef degradation has been marked by significant changes in coral reef community structure. For example, beginning in the 1970s, populations of the historically dominant framework-building coral species in the Caribbean, *Acropora* spp., have been reduced to endangered status (Aronson and Precht 2001; Precht et al. 2004); in the 1980s the Caribbean experienced a mass-mortality of the herbivorous sea urchin *Diadema antillarum* (Lessios et al. 1984); outbreaks of the coral-eating crown-of-thorns seastar have occurred in the Indo-Pacific (Moran 1988); and populations of fish and other large consumers have declined on reefs worldwide (Roberts 1995; Jackson et al. 2001).

It is now apparent that coral reef communities may persist in alternate states (Knowlton 1992, 2004). Most notably, macroalgae are now a prominent component of benthic communities once dominated by reef-building corals on many reefs (eg. Hughes 1994; Gardner et al. 2003). It is therefore not surprising that the interactions of reef-building corals and macroalgae have been

forefront in research to advance our understanding of community dynamics on coral reefs (Done 1992; McManus and Polsenberg 2004). However, a better understanding of shifting community structure may be obtained by considering other dominant groups on coral reefs that perform critical functional roles (Bellwood et al. 2004).

Sponges are an especially abundant and diverse group on Caribbean coral reefs (Targett and Schmahl 1984; Suchanek et al. 1985) that perform key functions in coral reef communities (Diaz and Rützler 2001; Bell 2008). Sponges filter large amounts of water, and are a predominant link in benthic-pelagic coupling on reefs (Reiswig 1971; Pile et al. 1997); they serve as habitat to numerous reef organisms (Duffy 1992, Henkel and Pawlik 2005); they are dominant competitors within the benthic community (Suchanek et al. 1985; Aerts 1998; Engel and Pawlik 2005); and they harbor diverse assemblages of bacteria that can take part in nitrification and carbon fixation (Rützler 1985; Diaz and Ward 1997; Southwell et al. 2008).

Surveys have provided distribution and abundance information for sponges on coral reefs (eg. Targett and Schmahl 1984; Schmahl 1985; Wilkinson 1987), but studies describing the population dynamics of coral reef sponges are limited (Reiswig 1973; Wulff 1991; Cropper et al. 1999; Cropper and DiResta 1999). In light of continued shifts in the composition of benthic communities on coral reefs, demographic approaches that evaluate both the structure and dynamics of coral reef sponge populations are needed. Similar studies have provided insight into the underlying dynamics of changing coral populations (Hughes 1984; Hughes and Tanner 2000; Edmunds and Elahi 2007).

The demographics of the giant barrel sponge *Xestospongia muta* have been monitored since 1997 at sites off Key Largo, Florida to study this important coral reef species.

*Xestospongia muta* is a conspicuous and abundant component of reef communities at depths

greater than 10 m throughout the Caribbean (Humann 1992, Buettner 1996). Individual sponges can reach > 1 m in height and diameter and live to be hundreds to thousands of years old (McMurray et al. 2008). Populations of this species occupy greater than 9% of the available reef substrate on some Caribbean reefs (Zea 1993), where the biomass of this species, and its seawater-filtering capacity, exceeds that of any other benthic invertebrate (Southwell et al. 2008; Weisz et al. 2008).

The Florida Keys reef tract was designated as a National Marine Sanctuary in 1990. As for the Caribbean in general, reefs in the Florida Keys have experienced dramatic reductions in coral cover and increases in macroalgal cover since the 1980s (Dustan and Halas 1987; Porter and Meier 1992; Gardner et al. 2003; Callahan et al. 2007; Somerfield et al. 2008). Data from a long-term monitoring study of the Florida Keys reef tract suggest that reefs have undergone a phase shift from coral to macroalgal and sponge dominated communities (Maliao et al. 2008), but no previous studies have described the demographics of coral reef sponges off the Florida Keys.

The purpose of this study was to describe the temporal and spatial demographic patterns of *X. muta* populations off Key Largo, Florida. First, I described spatial and temporal patterns of population structure in terms of density, size frequency, biomass, and percent cover. Second, I examined the processes of mortality, growth and recruitment to explain demographic patterns. Finally, I used matrix modeling to further investigate population dynamics. Because *X. muta* exhibits plastic growth and the ability to suffer partial mortality (Schmahl 1999; McMurray et al. 2008), demographic patterns are best described by size rather than age (Hughes 1984). I therefore developed stage-based matrix models that included processes of partial mortality and shrinkage, in addition to standard parameters of growth and survival. By excluding recruitment,

an open system was modeled to examine temporal and spatial patterns in the depletion of the standing population. Elasticity analyses were used to identify the relative importance of different transitions in population growth rates. Life table response analyses were used to identify the contribution of each transition to the observed temporal and spatial differences in population growth rates. Finally, matrix projections were used to further examine temporal and spatial demographic patterns by considering recruitment.

## METHODS

### *Study sites and monitoring*

Populations of *Xestospongia muta* were studied at permanent 16 m-diameter circular transects on Conch Reef [24°56.996 N; 80°27.223 W] and Pickles Reef [24°59.272 N; 80°24.660 W], Key Largo, Florida, as part of a long-term monitoring program begun in 1997 (Appendix A). On Conch Reef, the *Aquarius* habitat was used as a diving platform to establish 3 transects at 15, 20, and 30 m depth (CR15, CR20 and CR30, respectively), and at Pickles Reef, 3 transects were established at 15 m depth (PR15). Within each transect, each sponge was mapped and given a unique stainless steel tag attached with a plastic cable-tie to a masonry nail driven into the limestone substratum next to the base of the sponge. Starting in the spring of 2000, twice-yearly monitoring was conducted at all transects. Due to inclement weather, surveys were not conducted in the fall of 2000 and the spring of 2004. During each survey, new recruits were identified and tagged and the fate of each sponge was assessed. Additionally, each sponge was photographed from above and in profile with a digital camera. A slate was photographed in each digital image, held parallel to the central axis of each sponge in side images and parallel to the

plane of the top of the osculum in top images, displaying the unique tag number of each sponge and a 16 cm scale marker.

### *Demographic modeling*

Stage-classified matrix models in the form  $\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$  were used to examine the population dynamics of *X. muta*, where  $\mathbf{A}$  is a population projection matrix that gives the transitions of individuals between stages through the processes of growth, shrinkage, or partial mortality, and the vector  $\mathbf{n}(t)$  describes the number of individuals in each stage at time  $t$  (Lefkovich 1965, Caswell 2001). To investigate spatial and temporal demographic patterns, the study was divided into two equal time periods and matrices were constructed for each location (CR15, CR20, CR30, PR15) for the periods 2000-2003 and 2003-2006. A full factorial analysis was not completed due to the limited number of transitions at low density sites. Therefore, to investigate temporal changes in the overall dynamics of the Conch Reef population over each time interval, summary matrices,  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , were constructed by pooling transitions over the three depths on Conch Reef. Similarly, site summary matrices,  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$ , were constructed to investigate spatial patterns by pooling transitions over the two time intervals for each site. Transition probabilities and stage-specific mortality rates were calculated from sponge fates over each interval. The population parameters  $\lambda$  and  $\rho$ , and elasticities were calculated for each matrix using PopTools 2.7.5. The dominant eigenvalue,  $\lambda$ , describes the population growth rate and the damping ratio ( $\lambda_1 / |\lambda_2|$ ),  $\rho$ , describes the rate of convergence to the stable stage distribution. Elasticity is the proportional effect of perturbations of transition probabilities on population growth rate (Caswell 2001). Because *X. muta* has larvae that disperse in the plankton (López-Legentil and Pawlik 2008), I modeled an open system

by omitting fecundities from the projection matrix. In addition, unlike some sponge species, *X. muta* has not been observed to reproduce asexually. Excluding reproduction from the matrix,  $\lambda$  describes the rate of decline of a population over time and is less than 1 (Hughes 1984, Hughes and Tanner 2000, Edmunds and Elahi 2007).

Size was used as a state variable because the indeterminate growth and partial mortality of *X. muta* may decouple age from size (McMurray et al. 2008). Sponge volume was estimated from osculum diameter measurements at the start and end of each three-year interval. Two measurements of osculum diameter, with the first diameter chosen as the longest possible diameter and the second perpendicular to the first, were taken from top images of sponges with UTHSCA Image Tool software. If a sponge was not photographed during a census, osculum diameter measurements were taken from pictures from adjacent field seasons and its osculum diameter was estimated by interpolation.

The volume of *X. muta* was found to be reliably predicted from the osculum diameter of the sponge. To determine this relationship, measurements of height, base diameter, and osculum diameter were taken on 104 sponges spanning a broad range of sizes present in the population. Volume was calculated using the equation for the geometric model of a frustum of a cone, which applies to the three most common morphologies of *X. muta*: cylinder, frustum of a cone, and inverse frustum of a cone. Sponge volume was then corrected for spongocoel volume by subtracting the volume of the central cavity of the sponge (McMurray et al. 2008). Because a predictive relationship was sought, ordinary least squares regression was performed on  $\log_e$ -transformed volume and osculum diameter data (Sokal and Rohlf 1995, Warton et al. 2006). Bias in the scaling coefficient estimate resulting from the conversion from log to arithmetic units was corrected with a logarithmic correction factor (Sprugel 1983). The equation used to calculate

sponge volume from osculum diameter was determined to be:

$$V_{\text{sponge}} = 28.514 * \text{OsculumDiameter}^{2.1} (P < 0.001, R^2 = 0.901).$$

Sponges were assigned to one of six categories based on sponge volume or stage: Base, size class I ( $\leq 143.13 \text{ cm}^3$ ), size class II ( $> 143.13 \text{ cm}^3$  but  $\leq 1077.13 \text{ cm}^3$ ), size class III ( $> 1077.13 \text{ cm}^3$  but  $\leq 5666.32 \text{ cm}^3$ ), size class IV ( $> 5666.32 \text{ cm}^3$  but  $\leq 17383.97 \text{ cm}^3$ ), and size class V ( $> 17383.97 \text{ cm}^3$ ). Size classes were chosen to encompass the range of sponge sizes found in the population while minimizing sample and distribution errors (Caswell 2001).

The typical morphology of *X. muta* is cylindrical; however the Base stage results from partial mortality and usually consists of a ring of multi-oscule remnants with a low growth form and highly variable morphology (Fig. 1). The volume of this stage is hard to quantify, yet it is an important part of the life history of *X. muta*. Remnants are observed to grow and fuse, with a reduction of oscules, and may eventually restore a cylindrical-like morphology. Therefore, any sponge with a remnant-like morphology was classified as a Base. Sponges in any size class have the potential of contributing to this stage after partial mortality. Likewise, a Base may contribute to any one of the 5 size classes depending on the size of the resulting sponge after remnant fusion.

Life table response analyses were conducted to determine the contribution each vital rate had to differences in  $\lambda$  across temporal and spatial scales. In contrast to elasticity, which measures the potential effect of a change in a given transition on  $\lambda$ , a life table response analysis can be used to decompose the population effect of a treatment (i.e. time) into the effect on the underlying transitions (Caswell 1996, 2001). In the first analysis, changes in  $\lambda$  from the 2000-2003 to the 2003-2006 Conch Reef summary matrices were examined. From the mean matrix of  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , a matrix of sensitivities was calculated. Then, with  $\mathbf{A}^{(00-03)}$  used as a

reference matrix, a matrix of contributions was calculated by multiplying each element of the matrix of sensitivities by the respective element of  $\mathbf{A}^{(03-06)} - \mathbf{A}^{(00-03)}$  (Caswell 1996). In the second analysis, differences in  $\lambda$  between sites were examined. Analyses were completed as described above, with the exception that a mean matrix of the transition matrices from all sites was constructed and used as a reference matrix in which comparisons with each site was made (Caswell 2001).

To examine the population-level effect of conditions experienced by the Conch Reef population over the 2000-2003 and 2003-2006 time intervals, projections of  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$  were conducted (Caswell 2001). Projections of  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$  were similarly completed to examine population-level differences between sites. Population vectors in 2000, describing the initial population structure of Conch Reef or at each site, were used to multiply matrices for each projection. Using a 3 year projection interval, each matrix was projected over 51 years. Four projections were completed for  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ . For the first projection, recruitment was assumed to be zero so that the depletion of the population could be examined. Next, I examined the role of observed recruitment on population growth by adding a recruitment vector,  $\mathbf{r}$ , to the population vector at each projection interval (Hughes 1984, 1990). For each time interval, 2000-2003 and 2003-2006, the number of sponges that recruited to the population and survived to the end of the interval served as  $\mathbf{r}$ . Results of the life table response analysis indicated that there was a population-level effect of increased mortality of size-class V over 2003-2006. To examine the demographic role of mortality, I projected differing matrices,  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , with the same  $\mathbf{r}$ . Finally, to examine the potential of recruitment to regulate population size, the same matrix,  $\mathbf{A}^{(00-03)}$ , was projected under the differing recruitment regimes observed over 2000-2003 and 2003-2006, respectively (Hughes 1990). For each site summary

matrices,  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$ , two projections were completed. For the first projection, depletion of the population was examined by assuming zero recruitment. For the second projection, a recruitment vector,  $\mathbf{r}$ , was added to the population vector at each projection interval. The mean number of sponges that recruited to each site over 2000-2003 and 2003-2006 and survived to the end of each interval was used as  $\mathbf{r}$  for projections.

### *Data analysis*

Sponge density from 2000-2006 was compared among years and between sites with repeated measures ANOVA. Because density was not expected to significantly vary between consecutive twice-yearly censuses, density data from the spring of each year was used. The assumption of sphericity was tested with Mauchly's Test for all rm ANOVAs. If violated, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. Multiple comparisons were conducted using Bonferroni-adjusted multiple comparison tests.

Log-linear models were used to test for temporal and spatial differences in the number of individuals in each stage (Sokal and Rohlf 1995). Analyses were based on a three-way contingency table with the response variable state, S, (six stages), and explanatory variables time, T, (three years), and location, L, (four sites). The null hypothesis, the model TL, S, describes state as independent of time and location. Both marginal and conditional analyses were used in hierarchical model comparisons.

To determine percent cover of *X. muta* at the study sites, the base diameter of each sponge at each interval was estimated from osculum diameter measurements using the equation:  $BaseDiameter = 4.834 * OsculumDiameter^{0.624}$  ( $P < 0.001$ ,  $R^2 = 0.835$ ). This relationship was determined by the method described for the osculum diameter and volume relationship. The area

of substrate covered by each sponge was estimated by solving for the area of a circle. For sponges in the Base stage, surface area was traced from top images using UTHSCA Image Tool. Percent cover data was arcsine-transformed to meet assumptions of ANOVA and repeated measures ANOVA was used to test for differences in sponge cover between sites and among time intervals (2000, 2003, 2006). The volumes of sponges in each size class were summed and repeated measures ANOVA was similarly used to test for spatial and temporal changes in sponge biomass. Because the volumes of sponges in the Base stage could not accurately be computed they were omitted from analyses. Examination of the resulting temporal and spatial patterns of biomass and the number of sponges in the Base stage revealed that the exclusion of the Base stage had no effect on the outcome.

Sponge mortality from 2001-2006 was compared between sites, years, and seasons, using the Scheirer-Ray-Hare extension of the Kruskal Wallis test (Sokal and Rohlf 1995). The same test was used to compare recruitment between sites, years and seasons. Incomplete data from 2004 was omitted from analyses. Post hoc multiple comparisons were completed with the simultaneous test procedure (STP) (Sokal and Rohlf 1995). The survivorship of annual cohorts of recruits from 2001-2006 was compared with the logrank test (Pyke and Thompson 1986, Hutchings et al. 1991).

Log-linear analyses were used to test the independence of sponge fate from historical effects (Horvitz and Schemske 1995). I examined whether fate of a sponge in 2006,  $F_t$ , was independent of its state in 2000,  $S_{t-2}$ , given its state in 2003,  $S_{t-1}$ , by comparing the null model  $S_{t-2} S_{t-1} F_t$ , with a model that included the  $S_{t-2} F_t$  interaction. This analysis was performed for the Conch Reef population and each site individually and only included sponges with known states at every census.

The effects of time and location on sponge transitions were examined with log-linear analyses. Analyses were based on a four-way contingency table with the response variable fate, F, (6 stages + mortality). The null hypothesis STL, FS was used to examine the independence of sponge fate, conditional upon initial state, S, from the factors time, T, and location, L (Caswell 2001). Four-way tables were then decomposed into three-way contingency tables for each state. Log-linear models were similarly used to examine the effects of time and location on sponge fate for each state (Horvitz and Schemske 1995).

Randomization tests were used to determine if population growth rate and the damping ratio were affected by time or location (Manly 1997, Caswell 2001).  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$  were compared to examine temporal differences and  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$  were compared to examine location differences. The records of state and fate of individuals were randomly permuted among the treatments being compared, keeping sample sizes fixed. For each permutation, population matrices were constructed and  $\lambda$  and  $\rho$  were calculated. For temporal comparisons of population growth rate, a two-tailed test of the null hypothesis  $\lambda^{00-03} = \lambda^{03-06}$  was conducted with the statistic  $\theta = \left| \lambda^{00-03} - \lambda^{03-06} \right|$  from a set of 10,000 permutations (Brault and Caswell 1993, Caswell 2001). Similar tests were conducted with  $\rho$  between time intervals and both population parameters between sites.

Bootstrap calculations were used to generate 95% confidence intervals for the population parameters  $\lambda$  and  $\rho$  and stage-specific mortality rates. Individuals and their records were resampled with replacement until a fixed sample size was drawn. For each of 10,000 resampled datasets, population matrices were constructed and  $\lambda$ ,  $\rho$ , and stage-specific mortality rates were calculated. Confidence intervals were taken as the 0.025 and 0.975 percentiles of the distribution of each parameter. The percentile intervals were corrected for median bias of the bootstrap

estimates (Efron and Tibshirani 1993, Caswell 2001). Bootstrap calculations and randomization tests were conducted using Resampling Stats software (vers. 3.2 for Excel, Resampling Stats, Arlington, Virginia, USA). All other analyses were conducted with SPSS (vers. 14.0.0 for Windows, SPSS, Inc., Chicago Illinois, USA).

## RESULTS

The number of sponges at all study sites significantly increased through time ( $F = 30.448$ ,  $df = 1.441$ ,  $P < 0.001$ ) (Fig. 2). Over six years, mean sponge density increased 16, 49, 108, and 33 % at the Conch Reef 15, 20, and 30 m sites and the Pickles Reef 15 m site, respectively. Considering all depths on Conch Reef collectively, mean sponge density increased 46%. Sponge density also significantly differed between sites ( $F = 9.544$ ,  $df = 3$ ,  $P = 0.005$ ) (Fig. 2). Post hoc tests revealed that both the Conch Reef 20 m (CR20) and Pickles Reef 15 m (PR15) sites had significantly greater sponge densities compared to the Conch Reef 30 m (CR30) site. The mean ( $\pm$  SD) densities of sponges at CR15, CR20, CR30 and PR15 in spring 2000 were  $0.148 \pm 0.022$ ,  $0.186 \pm 0.047$ ,  $0.065 \pm 0.038$ , and  $0.191 \pm 0.021$  sponges/m<sup>2</sup>, respectively, compared to fall 2006 densities of  $0.171 \pm 0.045$ ,  $0.277 \pm 0.035$ ,  $0.134 \pm 0.074$ , and  $0.254 \pm 0.017$  sponges/m<sup>2</sup>.

As the density of sponges increased, the size-frequency distributions significantly changed (Table 1). The Conch Reef population and all sites individually became increasingly dominated by smaller sponges (Fig. 3, Appendix B). For Conch Reef, the number of individuals in each stage, with the exception of size class III and the Base stage, increased through time; however size class I experienced the largest increase in sponges (Appendix C). The number of sponges in size class I on Conch Reef increased by 30 sponges (130%) from 2000 to 2003 and 47

sponges (89%) from 2003 to 2006. In general, size classes I and II observed greater increases than size classes IV and V for Conch Reef and all sites (Appendix C). Size-frequency distributions also significantly differed between sites (Table 1). The number and proportion of sponges in the Base stage was greatest at the 15 m site on Conch Reef and decreased with increasing depth. The size frequency distributions of sponges at both CR20 and CR30 were negatively skewed in 2000 to 2003 but the sponges in size class I outnumbered sponges in size class V from 2003 to 2006. The size frequency distribution of sponges at PR15 was largely positively skewed from 2003 to 2006 compared to 2000-2003 (Appendix B).

The percent cover of sponges increased throughout the study at all sites, however this change was not significant ( $F = 2.390$ ,  $df = 1.271$ ,  $P = 0.150$ ) (Appendix D). Additionally, percent cover did not differ between sites ( $F = 3.684$ ,  $df = 3$ ,  $P = 0.062$ ). Spatial patterns of sponge cover paralleled patterns of sponge density, with cover greatest at CR20 and PR15 and lowest at CR30 (Appendix D). The mean ( $\pm$  SD) sponge cover at CR15, CR20, CR30 and PR15 for spring 2006 were  $0.64 \pm 0.18$ ,  $1.04 \pm 0.37$ ,  $0.36 \pm 0.30$ , and  $0.84 \pm 0.20$  % respectively. The area covered by each stage on Conch Reef increased with the exception of the Base stage and size class III.

The mean biomass of sponges at the study sites did not change through time ( $F = 2.699$ ,  $df = 2$ ,  $P = 0.098$ ). Though not significant, biomass increased over the 2000 – 2003 interval and decreased over the 2003 – 2006 interval for all sites on Conch Reef. At PR15, biomass continually increased over the study period. The mean ( $\pm$  SD) biomass on Conch Reef for all sites in 2000, 2003, and 2006 was  $1420 \pm 1242$ ,  $1529 \pm 1241$ , and  $1488 \pm 1175$   $\text{cm}^3/\text{m}^2$  respectively. Individuals of the largest size class contributed most to the total biomass at each site. For all sites at Conch Reef, the total biomass of size class V exceeded that of size classes I-

IV combined (Appendix E). In 2000 size class V comprised 77% of the total biomass of *X. muta* on Conch Reef and 75% in 2006. There was no significant difference in sponge biomass between sites ( $F = 2.357$ ,  $df = 3$ ,  $P = 0.148$ ). Spatial patterns of biomass were similar to patterns of density and percent cover. The mean ( $\pm$  SD) biomass of sponges at CR15, CR20, CR30 and PR15 for spring 2000 were  $1266.42 \pm 402.05$ ,  $2418.76 \pm 1750.92$ ,  $575.97 \pm 584.87$ , and  $1304.59 \pm 344.25$   $\text{cm}^3/\text{m}^2$ , respectively, compared to fall 2006 biomass of  $1305.90 \pm 326.43$ ,  $2577.01 \pm 1440.66$ ,  $581.74 \pm 530.20$ , and  $1737.11 \pm 674.01$   $\text{cm}^3/\text{m}^2$ .

The total number of recruits over each time interval increased over 2003 to 2006 for all sites on Conch Reef. A total of 191 recruits were recorded from the fall of 2000 to the fall of 2006 on Conch Reef; of these 70 recruited from the fall of 2000 to the spring of 2003 while 100 recruited from the fall of 2003 to the spring of 2006 and 21 recruited in the fall of 2006. At Pickles Reef, 70 total recruits were observed from the fall of 2000 to the fall of 2006, with 34 and 30 recruiting in the first and second time intervals, respectively. Recruitment was significantly different between sites ( $H = 14.556$ ,  $df = 3$ ,  $P = 0.002$ ) (Fig. 4). STP post hoc tests revealed that CR15 experienced significantly less recruitment compared to CR20. The mean ( $\pm$  SD) yearly recruitment of sponges at CR15, CR20, CR30 and PR15 was  $0.011 \pm 0.010$ ,  $0.025 \pm 0.010$ ,  $0.017 \pm 0.016$ , and  $0.018 \pm 0.008$  recruits/ $\text{m}^2$  year<sup>-1</sup>, respectively. Recruitment was generally greater over the summer compared to the winter, but was temporally variable, with very low or no recruitment for some sites over a given season and occasional large recruitment pulses (significant year\*season interaction,  $H = 22.021$ ,  $df = 4$ ,  $P = 0.0002$ ) (Fig. 4). The largest pulse ( $0.028 \pm 0.006$  recruits/ $\text{m}^2$ ) occurred over the winter of 2004 at CR20.

Survival was found to be similar for annual cohorts of recruits at all sites on Conch Reef ( $LR = 4.07$ ,  $df = 4$ ,  $P = 0.42$ ) (Fig. 5). Additionally, there was no significant difference in recruit

survival when analyzed for each site independently. Survival was similar between sites, with 16.7, 17.6, 18, and 21.4 % mortality observed for all new sponges throughout the study for CR15, CR20, CR30 and PR15, respectively. Recruits had the greatest chance of mortality in their first year and survival increased over time. Age-specific mortality rates for 1, 2, 3, 4, and 5 year old recruits on Conch Reef were 10, 5.9, 6.2, 4.8, and 0 % respectively. For all sites at Conch Reef, 90% of the sponges that recruited from 2000 to 2003 survived to 2003 while 95% of the recruits from 2003 to 2006 survived to 2006. In addition, the number of sponges that recruited and survived to the end of each three year interval increased for all sites except for PR15 (Appendix D). At Pickles Reef, 31 sponges recruited from 2000 to 2003 and survived to 2003 while 28 sponges recruited from 2003 to 2006 and survived to 2006. For all sites at Conch Reef there was a > 50 % increase in the number of sponges that recruited and survived over the two intervals: 63 new recruits survived to 2003 while 95 new recruits survived to 2006.

Mortality did not differ between years ( $H = 5.332$ ,  $df = 4$ ,  $P = 0.255$ ), seasons ( $H = 0.300$ ,  $df = 1$ ,  $P = 0.5839$ ), or sites ( $H = 3.042$ ,  $df = 3$ ,  $P = 0.385$ ) (Fig. 6). Mortality was generally low and variable, ranging from a mean of  $0.004 \pm 0.004$  to  $0.01 \pm 0.009$  sponges/m<sup>2</sup> year<sup>-1</sup> on Conch Reef. A relatively large mortality event occurred over the summer of 2005 when a mean 0.02 sponges/m<sup>2</sup> died at CR20 due to a pathogenic-like condition (Cowart et al. 2006). The mean ( $\pm$  SD) yearly mortality rates at CR15, CR20, CR30 and PR15 were  $0.007 \pm 0.005$ ,  $0.01 \pm 0.008$ ,  $0.005 \pm 0.004$ , and  $0.001 \pm 0.008$  sponges/m<sup>2</sup> year<sup>-1</sup>, respectively.

### *Transition matrices*

Over each time interval, stasis, growth, shrinkage, mortality, and partial mortality into the Base stage were observed (Table 2; Appendix E). Not all transitions were observed at each site

for a given time interval (Appendix F). For the lowest density site, CR30, there were initially no sponges present in size class I, and no mortality was observed for the two largest size classes. To allow for analytical comparisons between sites, transitions over each time interval were pooled to parameterize site summary matrices (Table 3).

For the Conch Reef summary matrices,  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , a total of 239 sponges were tracked from 2000 to 2003 and 280 sponges were tracked from 2003 to 2006. The number of sponges that survived and remained in a particular size class (stasis) was generally greater for larger size classes compared to smaller size classes (Table 2). For example, there was only 39 % stasis for size class I between 2000 and 2003 compared to 88% for size class V. Stasis for the Base stage was comparable to stasis for size class IV. Sponge mortality was generally greatest for size class I and the Base stage (Appendix G). For the 2003 to 2006 matrix, mortality of the largest size classes was also relatively high, with 14 and 18 % mortality for size classes IV and V, respectively. Mortality for size classes II and III ranged from approximately 4 to 8 % over the two time intervals (Table 2; Appendix G). Sponge growth followed an inverse relationship with sponge size and was generally lower for larger size classes. Between 2000 and 2003 on Conch Reef, 35 and 34 % of sponges in size classes I and II transitioned into the next size class, compared to 29 and 19 % of sponges in size classes III and IV that transitioned into the next size class (Table 2). Sponges in the Base stage grew and contributed to all size classes, but not all transitions were observed in a given three year interval. The recovery and growth of sponges in the Base stage to a typical morphological form was less than the growth of all other size classes. Sponge shrinkage was variable and sponges from size classes II through V were observed to shrink to the next smallest size class. Partial mortality into the Base stage occurred for size

classes II through V. Partial mortality occurred at low levels and ranged from 0 to 5 % for these size classes over a given three year interval (Table 2).

For the site summary matrices,  $\mathbf{A}^{(\text{CR15})}$ ,  $\mathbf{A}^{(\text{CR20})}$ ,  $\mathbf{A}^{(\text{CR30})}$ , and  $\mathbf{A}^{(\text{PR15})}$ , sponge stasis was again generally found to increase with increasing size (Table 3). One exception to this trend was  $\mathbf{A}^{(\text{CR30})}$ , where 12 and 6 % of size class V sponges were found to shrink to the next smallest size class or transition to the Base stage, respectively. Sponge mortality was greatest for size class I for all matrices and greatest mortality of size class V occurred for  $\mathbf{A}^{(\text{CR15})}$  (Table 3). Growth was more variable between sites compared to  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$  and an inverse relationship between growth and size did not hold for all site summary matrices. In particular, growth of size class I for  $\mathbf{A}^{(\text{CR20})}$  and  $\mathbf{A}^{(\text{CR30})}$  was low compared to growth of size classes II and III for these matrices. Sponge shrinkage and partial mortality was variable among and between sites with transitions to the next smallest size class or the Base stage observed for size classes II through V. Interestingly, no sponges were observed to transition to the Base stage at Pickles Reef (Table 3).

Given the size-frequency distributions among sites and years, transition probabilities were not significantly different between sites or time intervals (Appendix H). When each stage was tested separately, the independence of sponge fate from time and location remained for each stage with the exception of size class II, whose fate significantly varied between sites in both marginal and conditional tests (Appendix H). No mortality of size class II sponges was found at the 20 m Conch Reef site. The fates of sponges at all sites and on Conch Reef were independent of historical effects ( $\chi^2 = 27.27$ ,  $df = 30$ ,  $P = 0.609$ ).

The rate of population depletion,  $\lambda$ , for the Conch Reef summary matrices was determined to be 0.923 for  $\mathbf{A}^{(00-03)}$  and 0.836 for  $\mathbf{A}^{(03-06)}$  (Table 2). Comparison of these rates indicates that population decline accelerated over the second time interval by 9.4%.

Randomization tests revealed that this difference was not significant ( $P = 0.069$ ). Spatially, there was a direct relationship between population decline and depth on Conch Reef, with the deepest site having the slowest rate of depletion (Table 3). Randomization tests indicated that population depletion was significantly faster at CR15 compared to CR30 ( $P = 0.044$ ). Comparisons between all other sites were nonsignificant. The damping ratio for  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$  did not significantly change over time ( $P = 0.841$ ; Table 2). The damping ratio increased with increasing depth on Conch Reef (Table 3).  $\mathbf{A}^{(CR30)}$  had a significantly greater  $\rho$  compared to  $\mathbf{A}^{(CR15)}$  ( $P = 0.007$ ) and  $\mathbf{A}^{(CR20)}$  ( $P = 0.016$ ).  $\mathbf{A}^{(PR15)}$  also had a significantly greater  $\rho$  compared to  $\mathbf{A}^{(CR15)}$  ( $P = 0.041$ ) and  $\mathbf{A}^{(CR20)}$  ( $P = 0.05$ ).

Elasticities were calculated to determine the proportional effect of changes in vital rates on the population growth rate (Caswell 2001). Large elasticities indicate transitions that have proportionately large effects on  $\lambda$  when perturbed. Elasticities of the Conch Reef summary matrices indicated that the stasis of the largest size class (V) has the greatest proportional influence on  $\lambda$ . The elasticity of size class V sponges decreased over the second time interval, but the elasticities of this transition remained the largest compared to all other stages over both intervals (Appendix I). The stasis of size class IV individuals had the second-greatest contribution to  $\lambda$  over the first interval and remained high over the second interval. For sponges in the Base stage, stasis had a larger influence on  $\lambda$  over the second time interval and remained the largest contribution for this stage. In general, for a given stage, transitions into smaller stages (shrinkage) had smaller elasticities, compared to transitions of growth, and stasis. Stasis generally had the greatest potential to affect  $\lambda$  for a given size class (Appendix I). To compare the proportional contribution of each stage to  $\lambda$ , total elasticity was calculated by summing the elasticities for each stage (Fig. 7). Total elasticities indicate that the largest size class has the

greatest influence on  $\lambda$ . Total elasticities decreased with decreasing sponge size for both time intervals. Over the second interval, total elasticity of stages IV and V decreased and the total elasticity of all other stages increased.

A life table response analysis was performed to identify the transitions that had the greatest influence on the decrease of  $\lambda$  over time for  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ . The same analysis was performed to identify the transitions responsible for differences in  $\lambda$  between  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$ . Tables 4 and 5 present the contributions of each transition to differences in  $\lambda$  between matrices. Positive values indicate a particular transition contributed to positive population growth and negative values indicate transitions that contributed to negative population growth. The summation of all contributions approximates the observed difference in population growth rate over the matrices compared (i.e.  $\lambda^{(00-03)} - \lambda^{(03-06)}$ , Table 4). For comparison of  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , sponges in the largest size classes that, instead of dying, suffered partial mortality and transitioned to the Base stage contributed positively to population growth. However, the largest contributions were due to the mortality of sponges in the largest two size classes, which largely contributed to the accelerated population decline over the two time intervals. Site summary matrices were compared to a matrix that was the mean of all transition frequencies at the four sites. Again, transitions of size classes IV and V contributed the most to observed differences in  $\lambda$  between sites. Significantly greater  $\lambda$  for  $\mathbf{A}^{(CR30)}$  compared to  $\mathbf{A}^{(CR15)}$  was largely due to a large positive contribution from stasis of size class IV individuals at the 30 m Conch Reef site (Table 5). This is in agreement with the high elasticity value for this transition (Appendix I) and the higher frequency of this transition for  $\mathbf{A}^{(CR30)}$  compared to  $\mathbf{A}^{(CR15)}$ .

Projections indicated that the Conch Reef population behaved differently over the two time intervals. As expected from the dominant eigenvalues,  $\lambda$ , of  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , the rate of population depletion accelerated over 2003-2006 compared to 2000-2003 (Fig. 8A). Without recruitment, the population would be effectively depleted in 195 years under 2000-2003 conditions and 90 years under the conditions experienced over 2003-2006.

Projections were next completed to examine the role of recruitment in the population dynamics of *X. muta* over the two time intervals. Of the 63 surviving recruits over the 2000-2003 interval, 43 were in size class I, 15 were in size class II, 3 were in size class III, and 2 were in the Base stage when measured in 2003. Of the 95 surviving recruits over the 2003-2006 interval, 72 and 23 were in size classes I and II, respectively in 2006. These figures served as  $\mathbf{r}^{(00-03)}$  and  $\mathbf{r}^{(03-06)}$  for subsequent projections of  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ , respectively. The population increased with the addition of recruitment under the conditions of both intervals (Fig. 8B). In addition, the larger input of recruits over 2003-2006 offset the accelerated rate of population depletion for this interval and the population was found to increase faster compared to projection of  $\mathbf{A}^{(00-03)}$  with added recruitment. Figure 9 shows the projected population structure under the conditions of  $\mathbf{A}^{(03-06)}$ . In this projection, size class V composes 20.1% of the initial population while 9.6% of the population is in size class I. Through time, the population becomes increasingly positively skewed, with 13.6 and 23.8% of the population composed of individuals in size classes V and I, respectively.

Projections of both matrices with the same recruitment vector,  $\mathbf{r}^{(00-03)}$ , allowed for comparison of population growth under different mortality regimes. Specifically, the primary difference between the two matrices was increased mortality of size-class V individuals over 2003-2006. Initial population growth rate and asymptotic population size was found to be

greater under conditions of  $\mathbf{A}^{(00-03)}$  (Fig. 10). In addition, the size-frequency distributions differed after 51 years;  $\mathbf{A}^{(00-03)}$  conditions resulted in a negatively skewed distribution, while conditions under  $\mathbf{A}^{(03-06)}$  resulted in higher abundances of smaller size classes (Fig. 10). Projections of the same matrix,  $\mathbf{A}^{(00-03)}$ , with different recruitment vectors,  $\mathbf{r}^{(00-03)}$  and  $\mathbf{r}^{(03-06)}$ , allowed for comparison of population growth under different recruitment regimes. The initial population growth rate and asymptotic population size was found to be greater under conditions of  $\mathbf{r}^{(03-06)}$  (Fig. 11).

Projections of the site summary matrices indicate that populations behaved differently over spatial scales. Population depletion slowed with increasing depth on Conch Reef (Fig. 12A). The rate of population depletion at PR15 was more similar to CR20 and CR30 than CR15. Projections indicate that, without recruitment, populations at CR15, CR20, CR30 and PR15 would be depleted in 87, 123, 207, and 195 years, respectively, under 2000-2006 conditions.

Populations increased under the conditions experienced at all sites (Fig. 12B). Recruitment vectors added to the population at each iteration were 14 size class I and 3 size class II for  $\mathbf{A}^{(CR15)}$ , 27 size class I, 8.5 size class II, 1 size class III, and 0.5 Base stage for  $\mathbf{A}^{(CR20)}$ , 16.5 size class I, 7.5 size class II, 1 size class III, and, 0.5 Base stage for  $\mathbf{A}^{(CR30)}$ , and 26 size class I, 3.5 size class II and 0.5 Base stage for  $\mathbf{A}^{(PR15)}$ . The fastest rates of population growth were exhibited at CR20 and PR15. In addition, higher recruitment at CR20 offset the faster population depletion at this site compared to PR15 and the population was found to increase at a faster rate (Fig. 12B). Of all sites, CR15 had both the fastest population depletion and lowest recruitment, and projections indicate that population increases were slowest at this site (Fig. 12B).

## DISCUSSION

### *Population dynamics and structure*

Similar to Caribbean-wide patterns, significant reductions in coral cover and increases in the cover by macroalgae have occurred on reefs along the Florida Keys over recent decades (Dustan and Halas 1987; Porter and Meier 1992; Gardner et al. 2003; Callahan et al. 2007; Somerfield et al. 2008; Maliao et al. 2008). At the start of the present study, macroalgae dominated by the genus *Dictyota*, covered a large portion of the available substrate on Conch Reef (Beach et al. 2003) and cover of stony corals was low (Chiappone and Sullivan 1997). Coral cover in the Upper Keys has remained relatively unchanged since a significant decline observed from 1996 to 1999 while cover by macroalgae has remained high (Callahan et al. 2007; Maliao et al. 2008). In addition, since 1996 sponge cover has remained at about 2% throughout the Florida Keys (Callahan et al. 2007). Despite the apparent stability of sponges along the Keys reef tract, my findings show that populations of *X. muta* on Pickles and Conch Reefs are remarkably dynamic.

At both reef sites and at the three depths studied, populations of *Xestospongia muta* significantly increased over a six year period. In addition, projections indicate that the Conch Reef population is increasing at a faster rate (Fig. 8B). No statistically significant increase in recruitment rate or recruit survival through time was found, however both metrics trended upward throughout the study. Thus, the faster rate of population increase over 2003-2006 is likely the result of a combined effect of moderate increases in both recruitment and recruit survival. These findings are opposite those from work on reef-building corals that have documented population declines resulting from recruitment failure (Hughes and Tanner 2000). Additionally, a significant season\*year effect on sponge recruitment rate suggests that variability

over short temporal scales and recruitment pulses are important. Because adult sponge survival is relatively high, the effects of such recruitment pulses are “stored” in the population and limit declines during low recruitment years (Warner and Chesson 1985).

Mortality and size transitions of *X. muta* did not change through time, however even a small, statistically insignificant increase in mortality of the largest individuals was found to have a dramatic population-level effect. Accelerated decline of the standing Conch Reef population over 2003-2006 compared to 2000-2003 is attributed to increased mortality of sponges in the largest size classes (Table 4). In 2005, mortality of many of the largest sponges at CR20 was observed to result from a pathogenic condition termed sponge orange band (SOB) (Cowart et al. 2006). After symptoms of SOB appear, most sponges died and were reduced to a white mass of spicules within 6 weeks. Because of the rapid pace of the syndrome, it is likely that the high mortality of large sponges observed at other sites over 2003-2006 was attributable to SOB. Interestingly, in his sponge population study on Jamaican reefs, Reiswig (1973) described a similar disease that predominantly affected large individuals of the massive sponge *Mycale* sp.. Because water filtration increases with sponge size (Reiswig 1971), large sponges may have a greater chance of contacting potential pathogens in the water column compared to small sponges. Alternatively, the rapid mortality of affected sponges may bias observations in favor of larger sponges.

Stochastic variations in both mortality and recruitment appear to be important determinants of population dynamics. While population increases were observed over both study intervals, analyses of the summary matrices for Conch Reef indicate that the underlying demographics of these increases have changed. The standing population declined at a faster rate over 2003-2006 compared to 2000-2003, but the number of sponges that recruited and survived

was greater over this period, resulting in greater increases than those observed over 2000-2003. Therefore, increases over 2000-2003 resulted from relatively low mortality and recruitment, while there was greater turnover in the population over 2003-2006 due to both higher mortality and recruitment.

The temporal dynamics of the *X. muta* on Conch Reef indicate that the population is limited by recruitment, as is true for other benthic invertebrate species (Caley et al. 1996). Specifically, mortality was found to be independent of population density and changes in population density were correlated with recruitment. Additionally, it was found that variations in mortality obscure the relationship between recruitment and population density. Projections of the two Conch Reef summary matrices with the addition of the same recruitment vector yielded different results (Fig. 10). Population size was found to be larger under 2000-2003 conditions when both matrices were projected with the same recruitment vector. The population level difference in the two matrices resulted from increased mortality of large individuals over 2003-2006.

While sponge density increased throughout this study, both percent cover and biomass of *X. muta* did not significantly change. This is due to the proportionally high contribution of the largest sponges to these metrics. Increases of percent cover and biomass through the processes of growth and recruitment were largely negated by mortality of size class IV and V individuals over the 2003-2006 interval. These findings further illustrate the limitation of such metrics to describe the underlying dynamics of populations (Hughes 1996; Hughes and Tanner 2000) and should be considered in future monitoring efforts of coral reef sponges.

Density, cover, and biomass of *X. muta* were found to be greatest at 20 m depth and lowest at 30 m depth on Conch Reef. This is in agreement with Schmahl (1985), who found *X.*

*muta* abundance increased with depth to 20 m, the maximum depth surveyed, on reefs in the upper Florida Keys. My density and biomass estimates of 0.17 sponges/m<sup>2</sup> and 1.3 L/m<sup>2</sup>, respectively at 15 m depth on Conch Reef are in close agreement with findings by Southwell et al. (2008) who reported density and biomass estimates of *X. muta* to be 0.20 sponges/m<sup>2</sup> and 2.33 L/m<sup>2</sup> at approximately the same depth on Conch Reef. Percentage cover of *X. muta* in this study was lower than that on reefs off St. Croix (0.47% cover at 20-24 m depth; Targett and Schmahl 1984) and Colombia (0.82 % on 12-20 m deep reef terrace and 9.82% cover on 30-36 m deep reef base; Zea 1993).

Sponge abundance and distribution may be affected by a number of factors, including competition (Aerts 1998; Engel and Pawlik 2005), predation (Pawlik 1997, 1998), sedimentation (Reiswig 1971), ultraviolet light (Jokiel 1980), wave-surge and hurricanes (Reiswig 1973; Wulff 1995), disease (Webster 2007), and nutrition (Wilkinson and Cheshire 1990; Lesser 2006). Abiotic factors are likely to define the upper limit of *X. muta* on Conch Reef ( $\approx$  10 m) (Lopez-Legentil et al. 2008). Post-settlement processes are likely to influence population structure, but fail to explain the bathymetric patterns observed on Conch Reef. Within its range, *X. muta* is commonly found in spatially competitive interactions with neighboring biota, however bathymetric patterns of competitive interactions are unknown (Engel and Pawlik 2005). *Xestospongia muta* has variable chemical and physical defenses against predation (Chanas and Pawlik 1997; Jones et al. 2005). Although bite marks from fish and turtles are commonly observed on some individuals (Pawlik unpublished data), predation is not likely a significant source of mortality as *X. muta* can regenerate and heal tissue loss rapidly (Schmahl 1999; Walters and Pawlik 2005; McMurray et al. 2008). Greater picoplankton abundance at 30 m depth compared to 15 m was found to correlate with increased rates of growth and biomass of

the common tube sponge *Callyspongia vaginalis* on Conch Reef (Lesser 2006; Trussell et al. 2006), however decreased growth (Appendix F; McMurray et al. 2008) and biomass of *X. muta* are observed at 30 m compared to other depths. Because mortality does not significantly differ between sites, recruitment processes may best explain patterns of distribution of *X. muta* on Conch Reef.

Recruit and adult survival was similar among both temporal and spatial scales and independent of sponge density. These findings suggest that larval supply and settlement may be an important determinant of population structure. Mariani et al. (2000) found that abundance of the sponge *Cliona viridis* in the Mediterranean was positively correlated with larval abundance. Additionally, projections of the same matrix under different recruitment regimes demonstrated the potential of recruitment to regulate population size (Fig. 11). This occurs because the per capita recruitment rate decreases with increasing population density, becoming effectively density dependent (Hughes 1990; Caley et al. 1996). Survival of immediate post-settlement stages may also be important, as the time from settlement to observable size is unknown (Keough and Downes 1982). Pre-settlement processes have been shown to significantly influence recruitment for mass-spawning coral species (Hughes et al. 2000).

Little is known about the reproductive biology and larval ecology of *X. muta* and sponges in general (Maldonado 2006). Unlike some rope sponges that predominantly reproduce asexually (Wulff 1991), reproduction of *X. muta* is entirely sexual. Individuals are gonochoric and oviparous, with reproduction occurring at least twice a year during synchronous broadcast spawning events (Ritson-Williams et al. 2005; McMurray pers obs). Fecundity is expected to be high; Fromont and Bergquist (1994) estimated that a female of the closely related Indo-Pacific barrel sponge, *Xestospongia bergquistia*, spawned 1.4 million eggs with 71.4% fertilization.

Eggs occur in gelatinous masses and are negatively buoyant (Lindquist and Hay 1996; Ritson-Williams et al. 2005). This may aid in the local retention of recruits (Fromont and Bergquist 1994), however gametes are frequently observed to be swept into the water column during spawning events of *X. muta* (McMurray pers. obs.). Larvae are likely lecithotrophic (Maldonado 2004) and are chemically defended against significant fish predation (Lindquist and Hay 1996). The duration of the dispersal phase is unknown, however population genetics of *X. muta* throughout the Caribbean indicate that dispersal distances can be substantial (López-Legentil and Pawlik 2008). The fecundity of source populations, as well as biotic and abiotic processes acting on the larval stage, likely influence local recruitment (Hughes et al. 2000).

If pre-settlement processes have a predominant effect on population structure, recruitment patterns should correlate with adult populations. Recruitment at CR20 and PR15 support this pattern: both sites supported the highest population densities and highest recruitment rates. However, recruitment rates failed to fully explain population densities at CR15 and CR30. It is unclear why there was an inverse relationship between recruitment and density for CR15 and CR30. Because of the long lifespan of *X. muta*, stochastic variation in mortality may mask patterns of recruitment at these sites and the low density at 30 m may be an artifact of a historical mortality event (Caley et al. 1996). This hypothesis is supported by changes that were found to occur temporally when recruitment is fixed and mortality is variable. Alternatively, recruitment patterns may vary temporally among the spatial scales examined by this study (Caley et al. 1996). For example, the size-frequency distribution of the population in 2000 is deficient in size class I sponges compared to 2006 (Fig. 3, Appendices B and C). This suggests that recruitment rates prior to this study may have differed with the rates currently observed. Because of the long lifespan of *X. muta*, populations are the product of many past recruitment events (the storage

effect, Warner and Chesson 1985). Therefore, ultimate elucidation of the relationship between recruitment and population size will require monitoring over larger temporal scales.

A number of mechanisms acting on presettlement processes may be hypothesized to explain spatial and temporally variable patterns of recruitment. Larval behavior and numerous physical factors affect sponge settlement (Fell 1974; Maldonado and Young 1996; Uriz et al. 1998; Maldonado 2006; Mariani et al. 2006; Whalan et al. 2008). Higher than normal water temperatures induced stress and the production of heat shock proteins by *X. muta* (López-Legentil et al. 2008), and increased water temperatures may affect the larval ecology of the sponge *Rhopaloeides odorabile* (Whalan et al. 2008). Thus, increased water temperatures may favor recruitment to deeper portions of the reef. The distributions of recruits for many benthic invertebrates are influenced by selective settlement of larvae to specific substrata (Pawlik 1992; Baird et al. 2003). Sponge larvae exhibit both selective (Hartman 1958; Woollacott and Hadfield 1996; Jackson et al. 2002; Whalan et al. 2008) and non-selective (Warburton 1966) settlement. Nonetheless, temporal and spatial changes in the benthic community may influence the availability of suitable substratum for settlement and resulting recruitment patterns. Meroz and Ilan (1995) found the distribution of the opportunistic sponge *Mycale fistulifera* reflected the availability of suitable substrata for settlement. Settlement and post-settlement survival of corals and octocorals are influenced by the presence of crustose coralline algae (Morse et al. 1988; Lasker and Kim 1996; Harrington et al. 2004); and several species of macroalgae and cyanobacteria affect coral recruitment (Kuffner and Paul 2004; Kuffner et al. 2006). In a study by Kuffner et al. (2006), macroalgae and cyanobacteria were found to inhibit both coral larvae settlement and immediate post-settlement stage recruit survival. This study further found recruitment inhibition by *Dictyota* spp., the dominant macroalgae on Conch Reef (Beach et al.

2003, 2006). The percent cover of *Dictyota* on Conch Reef was found to be significantly greater at 7 and 21 m depths compared to 32 m (Beach et al. 2006). This may explain higher recruitment rates of *X. muta* at 30 m compared to 15 m, but high recruitment at 20 m undercuts this explanation. The temporal cover of *Dictyota* and other algae on the Florida reef tract is dynamic (Lirman and Biber 2000; Beach et al. 2006), but studies of sponge recruitment and algal dynamics conducted on similar temporal scales are needed to determine if a relationship exists.

Ultimately, population dynamics and structure are likely governed by temporal variation in the frequency and intensity of biotic and physical disturbances that act on both the pre- and post-settlement phases of the life history of *X. muta*. Variation in the scales and types of disturbances of reef communities has similarly been found to largely explain population dynamics of reef-building corals (Connell et al. 1997). In addition to the analysis in the present study, data from the longest running transects (two transects established in 1997 and spring of 1998, respectively) at the 15 m site provide important historical insights. Specifically, a large mortality event (loss of  $0.032 \pm 0.011$  sponges/m<sup>2</sup>) was observed to coincide with Hurricane Georges in the fall of 1998, and in the subsequent year, a large pulse of recruitment was observed (increase of  $0.036 \pm 0.014$  sponges/m<sup>2</sup>).

#### *Cause of increasing populations*

Population increases were associated with a shift in size-frequency distributions. High recruitment into size class I and relatively constant growth and mortality of other size classes resulted in a positively skewed size-frequency distribution in 2006 compared to 2000. The relative lack of size class I individuals in 2000 compared to 2006 suggests that recruitment rates observed over the present study may be higher than those in recent history prior to 2000. In

addition, over the study interval, the number of sponges that recruited and survived was observed to increase. The literature on sponge ecology offers a number of hypotheses that may explain the population increases of *X. muta*.

In a conceptual model of the influence of nutrition on community structure developed by Birkeland (1988), sponges and other heterotrophic suspension feeders are hypothesized to be favored by increased levels of nutrient input and associated elevated levels of water column productivity. The density and biomass of benthic suspension feeders may parallel gradients of nutrients at a number of temporal and spatial scales (Highsmith 1980; Pastorok and Bilyard 1985; Birkeland 1987, 1988). Moreover, there is a large literature on correlative distribution patterns of sponges and organic content of the water column. Wilkinson (1987) and Wilkinson and Cheshire (1990) found larger mean sponge size and five times greater sponge biomass on Caribbean reefs compared to the Great Barrier Reef and attributed this difference to higher productivity in the former. In both locations, sponge biomass was also correlated with gradients of land-derived productivity, with greater biomass on nearshore reefs compared to oceanic reefs (Wilkinson 1987; Wilkinson and Cheshire 1989, 1990). In the Florida Keys, sponge biomass increases with depth (Schmahl 1985; Lesser 2006), correlating with gradients of water column productivity (Lesser 2006). Abundance and population increases of boring sponges are positively correlated with elevated nutrients (Rose and Risk 1985; Zea 1994; Holmes 1997, 2000; Holmes et al. 2000; Ward-Paige et al. 2005), and sponge populations have been found to increase in areas influenced by sewage outfalls (Smith et al. 1981; Rose and Risk 1985; but see López-Victoria and Zea 2005).

Coral reef sponges may meet energy requirements from photosymbionts or by filtering particles from the water column (Wilkinson 1983; Erwin and Thacker 2008). *Xestospongia muta*

has a thin peripheral layer of cyanobacteria; however available evidence indicates that these commensals provide no benefit to the sponge (Thacker 2005; López-Legentil et al. 2008). While land-based eutrophication of nearshore waters in the Florida Keys has been documented (Lapointe and Clark 1992; Lapointe and Matzie 1996; Szmant and Forrester 1996), its impact on the reef tract is thought to be minimal (Szmant and Forrester 1996). Internal tidal bores are responsible for a significant pulsed delivery of nutrients and plankton to Conch Reef; with the duration and magnitude of delivery events increasing with depth (Leichter et al. 1998, 2003). The abundance of picoplankton also increases with depth on Conch Reef, irrespective of the occurrence of internal tidal bores; and there is a positive correlation reported between picoplankton abundance and the biomass of a common tube sponge, *Callyspongia vaginalis*, on Conch Reef (Lesser 2006; Trussell et al. 2006). While *X. muta* appears reliant on heterotrophy to meet energy requirements, spatial patterns of density and biomass on Conch Reef do not correlate with food availability. Food availability may favor increased fecundity of source populations of *X. muta*; however water quality data do not indicate increased phytoplankton availability in offshore waters of the Florida Keys (Boyer and Briceño 2006). Eutrophication and water-column productivity are therefore unlikely to explain the observed population increases of *X. muta*.

Increases in *X. muta* may be related to the availability of suitable substrata for recruitment. Space is limiting on coral reefs and space once occupied by reef-building corals may provide opportunity for sponge population increases. Data from a long-term monitoring program in the Florida Keys has shown that sites in the Upper Keys experienced both the greatest increases in clionid sponges, which bore into reef limestone, and the greatest decreases in relative coral cover, compared to the Lower Keys (Porter et al. 2002; Ward-Paige et al. 2005).

Ward-Paige et al. (2005) attributed both patterns to land-based sources of eutrophication; however, regardless of the cause of the coral decline, the observed increase of sponges may be an artifact of the ability of those sponges to exploit increases in available substratum. López-Victoria and Zea (2005) found that distribution patterns of three clionid sponges on Colombian reefs did not correlate with patterns of eutrophication. Rather, the authors concluded that, because of selective occupation of coral skeletons, recruitment was enhanced on recently dead coral compared to heavily fouled coral surfaces (López-Victoria and Zea 2005). The availability of substratum for recruitment is recognized as a predominant influence on the abundance and distribution of boring sponges (Kiene and Hutchings 1994; Schönberg 2001; Schönberg and Wilkinson 2001; Carballo et al. 2008). Macroalgae now dominate much of the benthic community on Conch Reef (Beach et al. 2003, 2006), but recruitment of *X. muta* does not appear to be affected by algal cover (see discussion above).

#### *Implications of increasing populations and changing population structure*

Despite degradation of coral reefs throughout the Caribbean (Gardner et al. 2003; Wilkinson 2004), populations of *X. muta* off the Florida Keys were found to be remarkably resilient. Populations of *X. muta* recovered from disturbance events (hurricanes, disease) because of high recruitment rates. Under current conditions, projections indicate populations will continue to increase, and *X. muta* may become an even more dominant component of Florida coral reef communities.

Population increases of *X. muta* may have both positive and negative implications for the coral reef community. Sponges serve as habitat to numerous fish and benthic invertebrates (Diaz and Rützler 2001). In addition, the large size of *X. muta* offers an important source of reef

habitat complexity (Buettner 1996). Sponges can filter large volumes of water and thus influence the coupling of water-column and benthic processes on coral reefs (Reiswig 1971; Diaz and Ward 1997; Southwell et al. 2008). This filtration ability can influence water clarity (Peterson et al. 2006) and may indirectly effect coral and algal populations that are dependent on light availability. Because of its high abundance and large biomass in some communities, *X. muta* may play a particularly important role in the remineralization of organic matter and nitrification (Southwell et al. 2008). As discussed by Southwell et al. (2008), the release of high concentrations of dissolved inorganic nitrogen from sponges may alter community structure. Sponges are dominant competitors for space on coral reefs (Suchanek et al. 1985; Aerts 1998; Engel and Pawlik 2005), and I have frequently observed and photographed *X. muta* outcompeting juvenile corals, gorgonians, and other sponges while monitoring our transects. Increased monopolization of space by sponges may limit coral recruitment, contributing to the maintenance of an alternate community on Florida reefs dominated by sponges, algae, and gorgonians.

While populations of *X. muta* remain resilient to current coral reef degradation, population growth may ultimately be negatively affected by continued mortality of the largest individuals. Elasticity analyses showed that changes in the mortality rates of the largest individuals have the greatest potential to negatively affect population growth. This potential was further confirmed by life table response analyses, as a small increase in the mortality of the largest individuals contributed greatly to the accelerated decline of the standing population over 2000-2003 to 2003-2006. The largest sponges account for significant portions of overall population biomass and substratum occupation. In addition, because of their slow growth, it may take over 100 years for a recruit to reach the size of the largest sponges measured in this study

(McMurray et al. 2008). Large sponges also constitute the largest proportion of reproductive potential. As fecundity is expected to exponentially increase with increasing sponge size, the largest sponges along the Florida Reef tract are potentially the greatest source of new recruits to upstream populations. Because of their abundance and importance, there is a need for increased conservation of large *X. muta* for effective management of this species (McMurray and Pawlik in press).

Similar to findings for reef-building corals (Gardner et al. 2003; Wilkinson 2004), evidence suggests that anthropogenic and natural disturbances of coral reef sponges are increasing. Large disturbances of sponge populations can have long-term ecosystem-level effects (Butler et al. 1995; Wulff 2006). There has been an increase in the number of reports of sponge disease affecting coral reef sponges over the last decade (Webster 2007). Moreover, mortality of many large *X. muta* on Conch Reef recently resulted from a pathogenic condition (Coward et al. 2006). In addition, *X. muta* is particularly vulnerable to damage and mortality from vessel groundings and marine debris, particularly as fishing lines and ropes are dragged along the bottom during storm events (Schmahl 1999; Chiappone et al. 2002; 2005). Finally, on a larger scale, populations of *X. muta* may be negatively affected by increasing seawater temperatures (López-Legentil et al. 2008) and increases in the frequency and intensity of hurricanes predicted by global climate change (Gardner et al. 2005). The demographic data on *X. muta* provided by this study may be used to detect future anthropogenic influences on coral reefs.

## LITERATURE CITED

- Aerts, L. A. M. 1998. Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. *Marine Ecology Progress Series* 175:241–249.
- Aronson, R. B., I. G. Macintyre, C. M. Wapnick, and M. W. O’Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* 85:1876–1891.
- Aronson, R. B. and W. F. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38.
- Aronson, R. B., W. F. Precht, M. A. Toscano, and K. H. Koltjes. 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology* 141:435–447.
- Baird, A. H., R. C. Babcock, and C. P. Mundy. 2003. Habitat selection by larvae influences the depth distribution of six common coral species. *Marine Ecology Progress Series* 252:289–293.
- Beach, K., L. Walters, and H. Borgeas. 2006. Irradiance and nutrient limitation of *Dicytota* spp. populations on Conch Reef, Florida Keys, USA. *Journal of Experimental Marine Biology and Ecology* 329:101–112.
- Beach, K., L. Walters, H. Borgeas, C. Smith, J. Coyer, and P. Vroom. 2003. The impact of *Dicytota* spp. on *Halimeda* populations of Conch Reef, Florida Keys. *Journal of Experimental Marine Biology and Ecology* 297:141–159.
- Bell, J. J. 2008. The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* 79:341–353.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Birkeland, C. 1987. Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological processes, and productivity. Pages 45–97 in C. Birkeland, editor. *Unesco Reports in Marine Science*. UNESCO, Norwich, UK.
- Birkeland, C. 1988. Geographic comparisons of coral reef community processes. Pages 211–220 in J. H. Choat, M.A. Borowitzka, J. C. Coll, P. J. Davies, P. Flood, B. G. Hatcher, D. Hopley, P. A. Hutchings, D. Kinsey, G. R. Orme, M. Pichon, P. F. Sale, P.W. Sammarco, C. C. Wallace, C. R. Wilkinson, E. Wolanski, and O. Bellwood, editors. *Proceedings of the sixth international coral reef symposium*. Executive Committee, Townsville, Australia.

- Boyer, J. N., and H. O. Briceño. 2006 annual report of the Water Quality Monitoring Project for the water quality protection program of the Florida Keys National Marine Sanctuary. Southeast Environmental Research Center, Miami.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454.
- Buettner, H. 1996. Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch, 1787) and associated fishes in Colombia. *Bulletin of Marine Science* 58:248–260.
- Butler, M. J., J. H. Hunt, W. F. Herrnkind, M. J. Childress, R. Bertelsen, W. Sharp, T. Matthews, J. M. Field, and H. G. Marshall. 1995. Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series* 129:119–125.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Reviews of Ecology and Systematics* 27:477–500.
- Callahan, M., J. Wheaton, C. Beaver, S. Brooke, D. Johnson, J. Kidney, S. Kupfner, J. W. Porter, M. Meyers, S. Wade, M. Colella, and M. Bertin. 2007. Coral Reef Evaluation and Monitoring Project, 2006 Executive Summary. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, Florida.
- Carballo, J. L., E. Bautista-Guerrero, and G. E. Leyte-Morales. 2008. Boring sponges and the modeling of coral reefs in the east Pacific Ocean. *Marine Ecology Progress Series* 356:113–122.
- Caswell, H. 1996. Analysis of life table response experiments. II. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling* 88:73–82.
- Caswell, H. 2001. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.
- Chanas, B., and J. R. Pawlik. 1997. Variability in the chemical defense of the Caribbean reef sponge *Xestospongia muta*. Pages 1363–1368 in H. Lessios and I. G. Macintyre, editors. *Proceedings of the Eighth International Coral Reef Symposium*. Volume 2. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
- Chiappone, M., H. Dienes, D. W. Swanson, S. L. Miller. 2005. Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. *Biological Conservation* 121:221–230.
- Chiappone, M., and K. M. Sullivan. 1997. Rapid assessment of reefs in the Florida Keys: results from a synoptic survey. Pages 1509–1514 in H. Lessios and I. G. Macintyre, editors. *Proceedings of the Eighth International Coral Reef Symposium*. Volume 2. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.

- Chiappone, M., A. White, D. W. Swanson, and S. L. Miller. 2002. Occurrence and biological impacts of fishing gear and other marine debris in the Florida Keys. *Marine Pollution Bulletin* 44:597–604.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67:461–488.
- Cowart, J. D., T. P. Henkel, S. E. McMurray, and J. R. Pawlik. 2006. Sponge orange band (SOB): a pathogenic-like condition of the giant barrel sponge *Xestospongia muta*. *Coral Reefs* 25:513.
- Cropper Jr., W. P., and D. DiResta. 1999. Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. *Ecological Modeling* 118:1–15.
- Cropper Jr., W. P., D. Lirman, S. C. Tosini, D. DiResta, J. Luo, and J. Wang. 2001. Population dynamics of a commercial sponge in Biscayne Bay, Florida. *Estuarine, Coastal and Shelf Science* 53:13–23.
- Diaz, M. C., and K. Rützler. 2001. Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science* 69:535–546.
- Diaz, M. C., and B. B. Ward. 1997. Sponge-mediated nitrification in tropical benthic communities. *Marine Ecology Progress Series* 156:97–107.
- Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132.
- Duffy, J. E. 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Marine Ecology Progress Series* 90:127–138.
- Dustan, P., and J. C. Halas. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* 6:91–106.
- Edmunds, P. J., and R. Elahi. 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* 77:3–18.
- Efron, B. and R. J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman and Hall, New York, New York, USA.
- Engel, S., and J. R. Pawlik. 2005. Interactions among Florida sponges: I. Reef habitats. *Marine Ecology Progress Series* 303:133–144.

- Erwin, P. M., and R. W. Thacker. 2008. Phototrophic nutrition and symbiont diversity of two Caribbean sponge-cyanobacteria symbiosis. *Marine Ecology Progress Series* 362:139–147.
- Fell, P. E. 1974. Porifera. Pages 51-132 in A. C. Giese, and J. S. Pearse editors. *Acoelomate and pseudocoelomate metazoans*. Academic Press, New York and London.
- Fromont, J. and P. R. Bergquist. 1994. Reproductive biology of three sponge species of the genus *Xestospongia* (Porifera: Demospongiae: Petrosida) from the Great Barrier Reef. *Coral Reefs* 13:119–126.
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–960.
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology* 86:174–184.
- Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A global map of human impact on marine ecosystems. *Science* 319:948–952.
- Harrington, L., K. Fabricius, G. De'ath, A. Negri. 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428–3437.
- Hartman, W. D. 1958. Natural history of the marine sponges of southern New England. *Bulletin of the Peabody Museum of Natural History* 12:1–155.
- Henkel, T. P., and J. R. Pawlik. 2005. Habitat use by sponge-dwelling brittlestars. *Marine Biology* 146:301–313.
- Highsmith, R. C. 1980. Geographic patterns of coral bioerosion: a productivity hypothesis. *Journal of Experimental Marine Biology and Ecology* 46:177–196.
- Holmes, K. E. 1997. Eutrophication and its effect on bioeroding sponge communities. Pages 1411–1416 in H. A. Lessios and I. G. Macintyre editors. *Proceedings of the Eight International Coral Reef Symposium*. Vol 2. Smithsonian Tropical Research Institute, Panama.
- Holmes, K. E. 2000. Effects of eutrophication on bioeroding sponge communities with the description of new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae). *Invertebrate Biology* 119:125–138.

- Holmes, K. E., E. N. Edinger, Hariyadi, G. V. Limmon, and M. J. Risk. 2000. Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. *Marine Pollution Bulletin* 40:606–617.
- Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* 65:155–192.
- Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *The American Naturalist* 123:778–795.
- Hughes, T. P. 1990. Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71:12–20.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes, T. P. 1996. Demographic approaches to community dynamics: a coral reef example. *Ecology* 77:2256–2260.
- Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81:2241–2249.
- Hughes, T. P., and J. E. Tanner. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2263.
- Humann, P. 1992. Reef creature identification. New World Pub., Jacksonville, Florida.
- Hutchings, M. J., K. D. Booth, and S. Waite. 1991. Comparison of survivorship by the logrank test: criticisms and alternatives. *Ecology* 72:2290–2293.
- Jackson, D., S. P. Leys, V. F. Hinman, R. Woods, M. F. Lavin, and B. M. Degnan. 2002. Ecological regulation of development: induction of marine invertebrate metamorphosis. *International Journal of Developmental Biology* 46:679–686.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Jokiel, P. L. 1980. Solar ultraviolet radiation and coral reef epifauna. *Science* 207:1069–1071.

- Jones, A. C., J. E. Blum, and J. R. Pawlik. 2005. Testing for defensive synergy in Caribbean sponges: bad taste or glass spicules. *Journal of Experimental Marine Biology and Ecology* 322:67–81.
- Keough, M. J., and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54:348–352.
- Kiene, W. E., and P. A. Hutchings. 1994. Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs* 13:91–98.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32:674–682.
- Knowlton, N. 2004. Multiple “stable” states and the conservation of marine ecosystems. *Progress in Oceanography* 60:387–396.
- Kuffner, I. B., and V. J. Paul. 2004. Effects of the benthic cyanobacterium *Lyngbya majuscula* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs* 23:455–458.
- Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series* 323:107–117.
- Lapointe, B. E., and M. W. Clark. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries* 15:465–476.
- Lapointe, B. E., and W. R. Matzie. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. *Estuaries* 19:422–435.
- Lasker, H. R., and K. Kim. 1996. Larval development and settlement behavior of the gorgonian coral *Plexaura kuna* (Lasker, Kim and Coffroth). *Journal of Experimental Marine Biology and Ecology* 207:161–175.
- Lefkovich, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21:1–18.
- Leichter, J. J., G. Shellenbarger, S. J. Genovese, and S. R. Wing. 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? *Marine Ecology Progress Series* 166:83–97.
- Leichter, J. J., H. L. Stewart, and S. J. Miller. 2003. Episodic nutrient transport to Florida coral reefs. *Limnology and Oceanography* 48:1394–1407.
- Lesser, M. P. 2006. Benthic-pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. *Journal of Experimental Marine Biology and Ecology* 328:277–288.

- Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335–337.
- Lindquist, N., and M. E. Hay. 1996. Palatability and chemical defense of marine invertebrate larvae. *Ecological Monographs* 66: 431–450.
- Lirman, D., and P. Biber. 2000. Seasonal dynamics of macroalgal communities of the northern Florida reef tract. *Botanica Marina* 43:305–314.
- López-Legentil S., B. Song, S. E. McMurray, and J. R. Pawlik. 2008. Bleaching and stress in coral reef ecosystems: *hsp70* expression by the giant barrel sponge *Xestospongia muta*. *Molecular Ecology* 17:1840–1849.
- López-Legentil S., and J. R. Pawlik. 2008. Genetic structure of the Caribbean giant barrel sponge *Xestospongia muta* using the I3-M11 partition of COI. *Coral Reefs in press*.
- López-Victoria, and S. Zea. 2005. Current trends of space occupation by encrusting excavating sponges on Colombian coral reefs. *Marine Ecology* 26:33–41.
- Maldonado, M. 2004. Choanoflagellates, choanocytes, and animal multicellularity. *Invertebrate Biology* 123:1–22.
- Maldonado, M. 2006. The ecology of the sponge larva. *Canadian Journal of Zoology* 84:175–194.
- Maldonado, M., and C. M. Young. 1996. Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Marine Ecology Progress Series* 138:169–180.
- Maliao, R. J., R. G. Turingan, and J. Lin. 2008. Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. *Marine Biology* 154:841–853.
- Manly, B. F. J. 1997. *Randomization and Monte Carlo methods in biology*. Second edition. Chapman and Hall, New York, New York, USA.
- Mariani, S., M.-J. Uriz, and X. Turon. 2000. Larval bloom of the oviparous sponge *Cliona viridis*: coupling of larval abundance and adult distribution. *Marine Biology* 137:783–790.
- Mariani, S., M.-J. Uriz, X. Turon, and T. Alcoverro. 2006. Dispersal strategies in sponge larvae: integrating the life history of larvae and the hydrologic component. *Oecologia* 149:174–184.
- McManus, J. W., and J. F. Polsenberg. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60:263–279.

- McMurray, S. E., J. E. Blum, and J. R. Pawlik. 2008. Redwood of the reef: growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Marine Biology* 155:159–171.
- McMurray, S. E., and J. R. Pawlik. A novel technique for the reattachment of large coral reef sponges. *Restoration Ecology in press*.
- Meroz, E., and M. Ilan. 1995. Life history characteristics of a coral reef sponge. *Marine Biology* 124:443–451.
- Moran, P. J. 1988. The *Acanthaster* phenomenon. The Australian Institute of Marine Science Monograph Series 7:1–177.
- Morse, D. E., N. Hooker, A. N. C. Morse, and R. A. Jensen. 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. *Journal of Experimental Marine Biology and Ecology* 116:193–217.
- Pastorok, R. A., and G. R. Bilyard. 1985. Effects of sewage pollution on coral-reef communities. *Marine Ecology Progress Series* 21:175–189.
- Pawlik, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology: An Annual Review* 30:273–335.
- Pawlik, J. R. 1997. Fish predation on Caribbean reef sponges: an emerging perspective of chemical defenses. Pages 1255–1258 in H. Lessios and I. G. Macintyre, editors. *Proceedings of the Eighth International Coral Reef Symposium. Volume 2*. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
- Pawlik, J. R. 1998. Coral reef sponges: do predatory fish affect their distribution? *Limnology and Oceanography* 43:1396–1399.
- Peterson, B. J., C. M. Chester, F. J. Jochem, and J. W. Fourqurean. 2006. Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Marine Ecology Progress Series* 328:93–103.
- Pile, A. J., M. R. Patterson, M. Savarese, V. I. Chernykh, and V. A. Fialkov. 1997. Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux. *Limnology and Oceanography* 42:178–184.
- Porter, J. W., and O. W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. *American Zoologist* 32:625–640.
- Porter, J. W., V. Kosmynin, K. L. Patterson, K. G. Porter, W. C. Jaap, J. L. Wheaton, K. Hackett, M. Lybolt, C. P. Tsokos, G. Yanev, D. M. Marcinek, J. Dotten, D. Eaken, M. Patterson, O. W. Meier, M. Brill, and P. Dustan. 2002. Detection of coral reef change by the Florida

- Keys coral reef monitoring project. Pages 749–769 in J. W. Porter and K. G. Porter, editors. The Everglades, Florida Bay, and coral reefs of the Florida Keys: an ecosystem sourcebook. CRC, Boca Raton.
- Precht, W. F., M. L. Robbart, and R. B. Aronson. 2004. The potential listing of *Acropora* species under the US Endangered Species Act. *Marine Pollution Bulletin* 49:534–536.
- Pyke, D. A., and J. N. Thompson. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67:240–245.
- Reiswig, H. M. 1971. In situ pumping activities of tropical Demospongiae. *Marine Biology* 9:38–50.
- Reiswig, H. M. 1973. Population dynamics of three Jamaican Demospongiae. *Bulletin of Marine Science* 23:191–226.
- Ritson-Williams, R., M. A. Becerro, and V. J. Paul. 2005. Spawning of the giant barrel sponge *Xestospongia muta* in Belize. *Coral Reefs* 24:160.
- Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* 9:988–995.
- Rose, C. S. and M. J. Risk. 1985. Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of Grand Cayman fringing reef. *P. S. Z. N. I. Marine Ecology* 6:345–363.
- Rützler, K. 1985. Associations between Caribbean sponges and photosynthetic organisms. Pages 455–466 in K. Rützler editor. *New perspectives in sponge biology*. Smithsonian Institution Press, Washington D. C.
- Schmahl, G. P. 1985. Community structure and ecology of sponges associated with four southern Florida coral reefs. Pages 376–383 in K. Rützler editor. *New Perspectives in Sponge Biology*. Smithsonian Institution Press, Washington, D.C.
- Schmahl, G. P. 1999. Recovery and growth of the giant barrel sponge (*Xestospongia muta*) following physical injury from a vessel grounding in the Florida Keys. *Memoirs of the Queensland Museum* 44:532.
- Schönberg, C. H. L. 2001. Small-scale distribution of Great Barrier Reef bioeroding sponges in shallow water. *Ophelia* 55:39–54.
- Schönberg, C. H. L., and C. R. Wilkinson. 2001. Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69–76.

- Smith, S. V., W. J. Kimmerer, E. A. Laws, R. E. Brock, and T. W. Walsh. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35:279–395.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64:209–210.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. W. H. Freeman and Co. New York.
- Somerfield, P. J., W. C. Jaap, K. R. Clarke, M. Callahan, K. Hackett, J. Porter, M. Lybolt, C. Tsokos, and G. Yanev. 2008. Changes in coral reef communities among the Florida Keys 1996–2003. *Coral Reefs* DOI 10.1007/s00338-008-0390-7
- Southwell, M. W., J. B. Weisz, C. S. Martens, and N. Lindquist. 2008. In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnology and Oceanography* 53:986–996.
- Suchanek, T. H., R. C. Carpenter, J. D. Witman, and C. D. Harvell. 1985. Sponges as important space competitors in deep Caribbean coral reef communities. Pages 55–59 in M. L. Reaka editor. *The Ecology of Deep and Shallow Coral Reefs*, Symposia Series for Undersea Research 3(1), NOAA/NURP: Rockville, Maryland.
- Szmant, A. M., and A. Forrester. 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs* 15:21–41.
- Targett, N. M., and G. P. Schmahl. 1984. Chemical ecology and distribution of sponges in the Salt River Canyon, St. Croix, U.S.V.I. NOAA Technical Memorandum OAR NURP-1, Rockville, Maryland.
- Thacker, R. 2005. Impacts of shading on sponge-cyanobacteria symbioses: a comparison between host-specific and generalist associations. *Integrative and Comparative Biology* 45:369–376.
- Trussell, G. C., M. P. Lesser, M. R. Patterson, and S. J. Genovese. 2006. Depth-specific differences in growth of the reef sponge *Callyspongia vaginalis*: role of bottom-up effects. *Marine Ecology Progress Series* 323:149–158.
- Uriz, M.-J., M. Maldonado, X. Turon, and R. Martí. 1998. How do reproductive output, larval behaviour, and recruitment contribute to adult spatial patterns in Mediterranean encrusting sponges? *Marine Ecology Progress Series* 167:137–148.
- Walters, K. D., and J. R. Pawlik. 2005. Is there a trade off between wound-healing and chemical defenses among Caribbean reef sponges? *Integrative and Comparative Biology* 45:352–358.
- Warburton, F. E. 1966. The behavior of sponge larvae. *Ecology* 47:672–674.

- Ward-Paige, C. A., M. J. Risk, O. A. Sherwood, and W. C. Jaap. 2005. Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570–579.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist* 125:769–787.
- Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81:259–291.
- Webster, N. S. 2007. Sponge disease: a global threat? *Environmental Microbiology* 9:1363–1375.
- Weisz, J. B., N. Lindquist, and C. S. Martens. 2008. Do associated microbial abundances impact marine demosponge pumping rates and tissue densities? *Oecologia* 155:367–376.
- Whalan, S., P. Ettinger-Epstein, C. Battershill, and R. de Nys. 2008. Larval vertical migration and hierarchical selectivity of settlement in a brooding marine sponge. *Marine Ecology Progress Series* 368:145–154.
- Whalan, S., P. Ettinger-Epstein, and R. de Nys. 2008. The effect of temperature on larval pre-settlement duration and metamorphosis for the sponge, *Rhopaloeides odorabile*. *Coral Reefs* DOI 10.1007/s00338-008-0400-9.
- Wilkinson, C. R. 1983. Net primary productivity in coral reef sponges. *Science* 219:410–412.
- Wilkinson, C. R. 1987. Interocean differences in size and nutrition of coral reef sponge populations. *Science* 236:1654–1657.
- Wilkinson, C. ed. 2004. Status of coral reefs of the world. 2004. (vols 1 and 2). Australian Institute of Marine Science, Cape Ferguson and Dampier.
- Wilkinson, C. R. and A. C. Cheshire. 1989. Patterns in the distribution of sponge populations across the central Great Barrier Reef. *Coral Reefs* 8:127–134.
- Wilkinson, C. R. and A. C. Cheshire. 1990. Comparisons of sponge populations across the barrier reefs of Australia and Belize: evidence for higher productivity in the Caribbean. *Marine Ecology Progress Series* 67:285–294.
- Woollacott, R. M., and M. G. Hadfield. 1996. Induction of metamorphosis in larvae of a sponge. *Invertebrate Biology* 115:257–262.
- Wulff, J. L. 1991. Asexual fragmentation, genotype success, and population dynamics of erect branching sponges. *Journal of Experimental Marine Biology and Ecology* 149:227–247.

- Wulff, J. L. 1995. Effects of a hurricane on survival and orientation of large erect coral reef sponges. *Coral Reefs* 14:55–61.
- Wulff, J. L. 2006. Rapid diversity and abundance decline in a Caribbean coral reef sponge community. *Biological Conservation* 127:167–176.
- Zea, S. 1993. Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. *Caribbean Journal of Science* 29:75–88
- Zea, S. 1994. Patterns of coral and sponge abundance in stressed coral reefs at Santa Marta, Colombian Caribbean. Pages 257–264 *in* R. W. M. van Soest, T. M. G. van Kempen, and J. C. Braekman editors. *Sponges in Time and Space*. Balkema, Rotterdam.

Table 1. Log-linear analysis of size-frequency data. Analyses were based on a three-way contingency table with the response variable state, S, (six stages), and explanatory variables time, T, (three years), and location, L, (four sites).

Model	$G^2$	$df$	$P$	Contrast	Effect	$\Delta G^2$	$\Delta df$	$P$
$M_1 = TL, S$	134.895	55	<0.001	$M_2$ vs. $M_1$	T	42.065	10	<0.001
$M_2 = TL, TS$	92.830	45	<0.001	$M_4$ vs. $M_3$	T	42.252	10	<0.001
$M_3 = TL, LS$	79.193	40	<0.001	$M_3$ vs. $M_1$	L	55.702	15	<0.001
$M_4 = TL, TS, LS$	36.941	30	0.179	$M_4$ vs. $M_2$	L	55.889	15	<0.001
$M_5 = STL$	0	0	1.000	$M_5$ vs. $M_4$	$T \times L$	36.941	30	0.222

Table 2. Conch Reef summary matrices  $A^{(00-03)}$  and  $A^{(03-06)}$  for 2000–2003 and 2003–2006, respectively. Transition probabilities were calculated by pooling transitions over all sites on Conch Reef.  $q_x$  = stage-specific mortality rate,  $n$  = sample size,  $\lambda$  = dominant eigenvalue describing rate of population depletion,  $\rho$  = damping ratio and CI = 95% confidence intervals.

2000–2003 Conch Reef						
Size class	Size class					
	Base	I	II	III	IV	V
Base	0.697	0	0.053	0.018	0.024	0
I	0.03	0.391	0	0	0	0
II	0.03	0.348	0.526	0.073	0	0
III	0.03	0	0.342	0.582	0.024	0
IV	0.061	0	0	0.291	0.714	0.042
V	0	0	0	0	0.19	0.875
$q_x$	0.152	0.261	0.079	0.036	0.048	0.083
$n$	33	23	38	55	42	48
$\rho$ (CI)	1.155	(1.060, 1.317)				
$\lambda$ (CI)	0.923	(0.852, 0.974)				

2003–2006 Conch Reef						
Size class	Size class					
	Base	I	II	III	IV	V
Base	0.655	0	0.021	0.04	0.04	0.02
I	0.069	0.472	0.021	0	0	0
II	0.034	0.283	0.521	0.04	0	0
III	0	0	0.354	0.52	0.04	0
IV	0.034	0	0	0.32	0.56	0.02
V	0.034	0	0	0	0.22	0.78
$q_x$	0.172	0.245	0.083	0.08	0.14	0.18
$n$	29	53	48	50	50	50
$\rho$ (CI)	1.175	(1.027, 1.351)				
$\lambda$ (CI)	0.836	(0.756, 0.894)				

Table 3. Site summary matrices  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$  for 15, 20, and 30 m Conch Reef and 15 m Pickles Reef sites, respectively. Transition probabilities for each site were calculated by pooling transitions over 2000–2003 and 2003–2006.  $q_x$  = stage-specific mortality rate,  $n$  = sample size,  $\lambda$  = dominant eigenvalue describing rate of population depletion,  $\rho$  = damping ratio and CI = 95% confidence intervals.

Location	Size class	Size class					
		Base	I	II	III	IV	V
15 m Conch	Base	0.667	0	0	0.053	0.067	0
	I	0.056	0.36	0.032	0	0	0
	II	0.028	0.4	0.516	0	0	0
	III	0	0	0.323	0.684	0	0
	IV	0.056	0	0	0.263	0.633	0
	V	0.028	0	0	0	0.233	0.829
	$q_x$	0.167	0.24	0.129	0	0.067	0.171
	$n$	36	25	31	19	30	35
	$\lambda$ (CI)	0.829 (0.704, 0.892)		$\rho$ (CI) 1.027 (1.0, 1.092)			
20 m Conch	Base	0.737	0	0.057	0.033	0.021	0
	I	0.053	0.487	0	0	0	0
	II	0	0.282	0.543	0.083	0	0
	III	0.053	0	0.4	0.517	0.042	0
	IV	0.053	0	0	0.3	0.563	0.022
	V	0	0	0	0	0.229	0.870
	$q_x$	0.105	0.231	0	0.067	0.146	0.109
	$n$	19	39	35	60	48	46
	$\lambda$ (CI)	0.890 (0.809, 0.955)		$\rho$ (CI) 1.093 (1.011, 1.247)			
30 m Conch	Base	0.571	0	0.05	0	0	0.059
	I	0	0.5	0	0	0	0
	II	0.143	0.167	0.5	0.038	0	0
	III	0	0	0.3	0.538	0.071	0
	IV	0	0	0	0.346	0.857	0.118
	V	0	0	0	0	0.071	0.706
	$q_x$	0.286	0.333	0.15	0.077	0	0.118
	$n$	7	12	20	26	14	17
	$\lambda$ (CI)	0.957 (0.837, 1.0)		$\rho$ (CI) 1.415 (1.248, 1.884)			
15 m Pickles	Base	0.652	0	0	0	0	0
	I	0.043	0.5	0.115	0	0	0
	II	0.043	0.278	0.538	0	0	0
	III	0.087	0.014	0.308	0.581	0.023	0.029
	IV	0	0	0	0.355	0.75	0.029
	V	0	0	0	0.032	0.205	0.857
	$q_x$	0.174	0.208	0.038	0.032	0.023	0.086
	$n$	23	72	52	31	44	35
	$\lambda$ (CI)	0.933 (0.844, 0.991)		$\rho$ (CI) 1.335 (1.235, 1.635)			

Table 4. Contributions of transitions to the accelerated population decline from 2000–2003 to 2003–2006 on Conch Reef. Negative values indicate transitions that contributed to accelerated population decline and positive values indicate transitions that slowed population decline. Contributions  $> \pm 0.01$  are in bold.

Size class	Size class					
	Base	I	II	III	IV	V
Base	-0.0029	0.0000	-0.0006	0.0009	0.0025	<b>0.0138</b>
I	0.0030	0.0007	0.0005	0.0000	0.0000	0.0000
II	0.0005	-0.0008	-0.0002	-0.0020	0.0000	0.0000
III	-0.0030	0.0000	0.0003	-0.0036	0.0036	0.0000
IV	-0.0021	0.0000	0.0000	0.0013	<b>-0.0273</b>	<b>-0.0171</b>
V	0.0023	0.0000	0.0000	0.0000	0.0043	<b>-0.0623</b>

Table 5. Contributions of transitions to differences in  $\lambda$  between sites. Contributions were calculated by comparing each site summary matrix to a reference matrix, which is a mean of all site summary matrices. Negative values indicate transitions that contributed to accelerated population decline and positive values indicate transitions that contributed to slowed population decline compared to the reference matrix. Contributions  $> \pm 0.01$  are in bold.

Location and size class		Size class					
	Base	I	II	III	IV	V	
<b>15 m Conch</b>							
Base	0.0008	0	-0.0006	0.0018	0.0082	<b>-0.0118</b>	
I	0.0017	-0.0012	-0.0001	0	0	0	
II	-0.0033	0.0019	-0.0003	-0.0030	0	0	
III	-0.0044	0.0001	-0.0003	0.0098	-0.0099	-0.0091	
IV	0.0024	0	0	-0.0034	<b>-0.0134</b>	<b>-0.0368</b>	
V	0.0012	0	0	-0.0004	0.0064	0.0077	
<b>20 m Conch</b>							
Base	0.0043	0	0.0005	0.0006	-0.0002	<b>-0.0101</b>	
I	0.0008	0.0002	-0.0007	0	0	0	
II	-0.0044	0	0.0005	0.0040	0	0	
III	0.0013	0	0.0015	-0.0042	0.0016	-0.0065	
IV	0.0015	0	0	-0.0009	<b>-0.0227</b>	<b>-0.0150</b>	
V	-0.0004	0	0	-0.0004	0.0068	<b>0.0370</b>	
<b>30 m Conch</b>							
Base	-0.0029	0	0.0003	-0.0010	-0.0049	0.0081	
I	-0.0014	0.0001	-0.0005	0	0	0	
II	0.0062	-0.0005	-0.0007	0.0008	0	0	
III	-0.0029	0	-0.0012	-0.0049	<b>0.0207</b>	-0.0033	
IV	-0.0022	0	0	0.0035	<b>0.0843</b>	<b>0.0336</b>	
V	-0.0004	0	0	-0.0006	<b>-0.0383</b>	<b>-0.0305</b>	
<b>15 m Pickles</b>							
Base	-0.0001	0	-0.0002	-0.0012	-0.0041	-0.0071	
I	0.0002	0.0002	0.0007	0	0	0	
II	-0.0004	0	0.0002	-0.0028	0	0	
III	0.0022	0.0001	-0.0003	0.0001	-0.0037	<b>0.0180</b>	
IV	-0.0010	0	0	0.0032	<b>0.0143</b>	<b>-0.0100</b>	
V	-0.0002	0	0	0.0016	0.0045	<b>0.0241</b>	
<b>Reference matrix</b>							
Base	0.6568	0	0.0268	0.0215	0.0219	0.0147	
I	0.0379	0.4618	0.0369	0	0	0	
II	0.0535	0.2816	0.5244	0.0304	0	0	
III	0.0349	0.0035	0.3326	0.5800	0.0340	0.0071	
IV	0.0270	0	0	0.3160	0.7007	0.0420	
V	0.0069	0	0	0.0081	0.1846	0.8153	

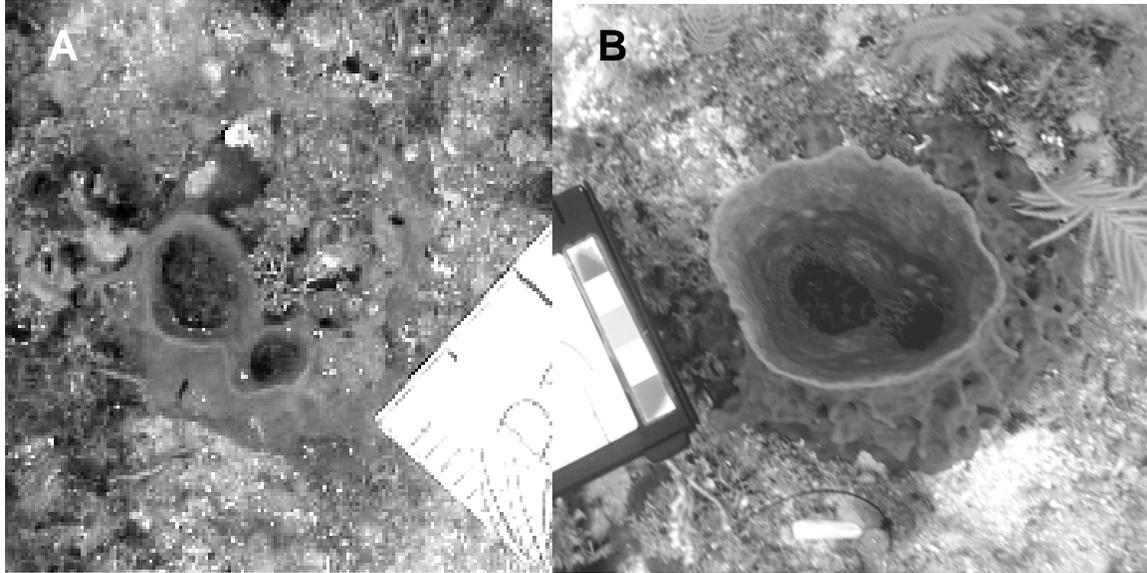


Figure 1. Specimen of *Xestospongia muta* on Conch Reef, top view (A) after suffering partial mortality and transitioning to the Base stage, and (B) 5 years later after growth and transition to size class II.

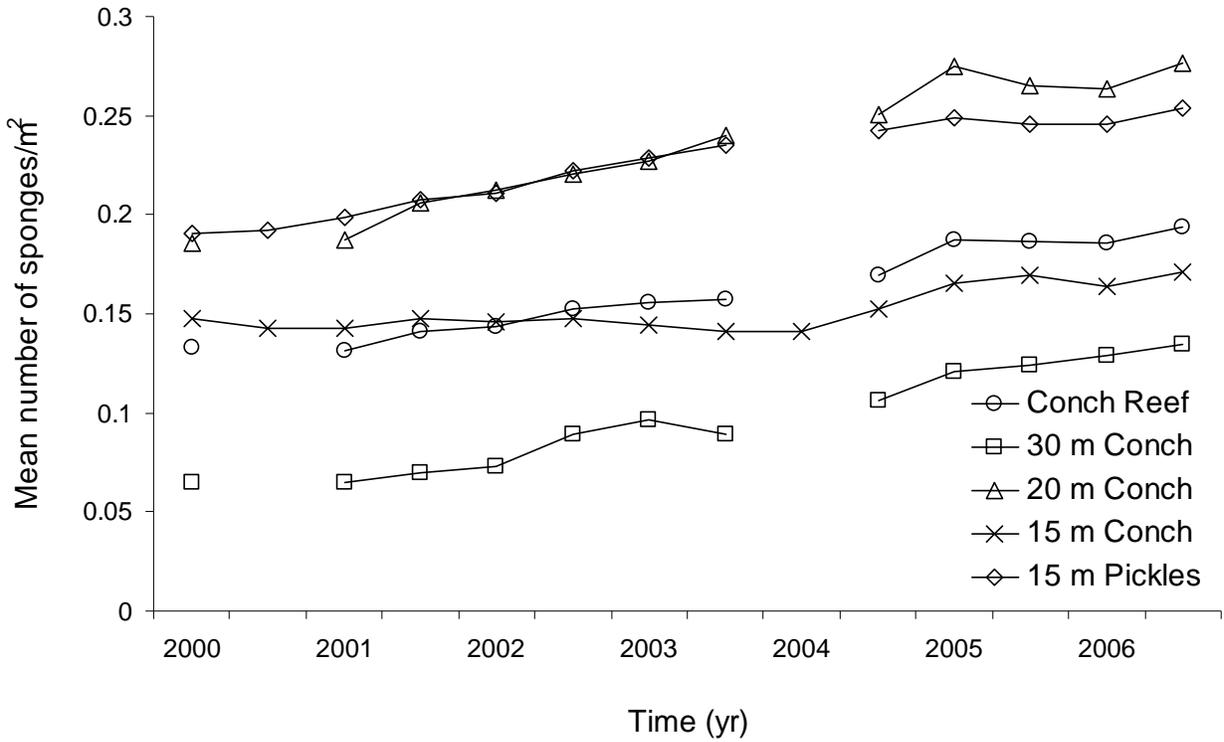


Figure 2. Mean density of *Xestospongia muta* at sites on Conch and Pickles Reefs from May 2000 to November 2006. Also plotted is the mean density over all sites on Conch Reef.

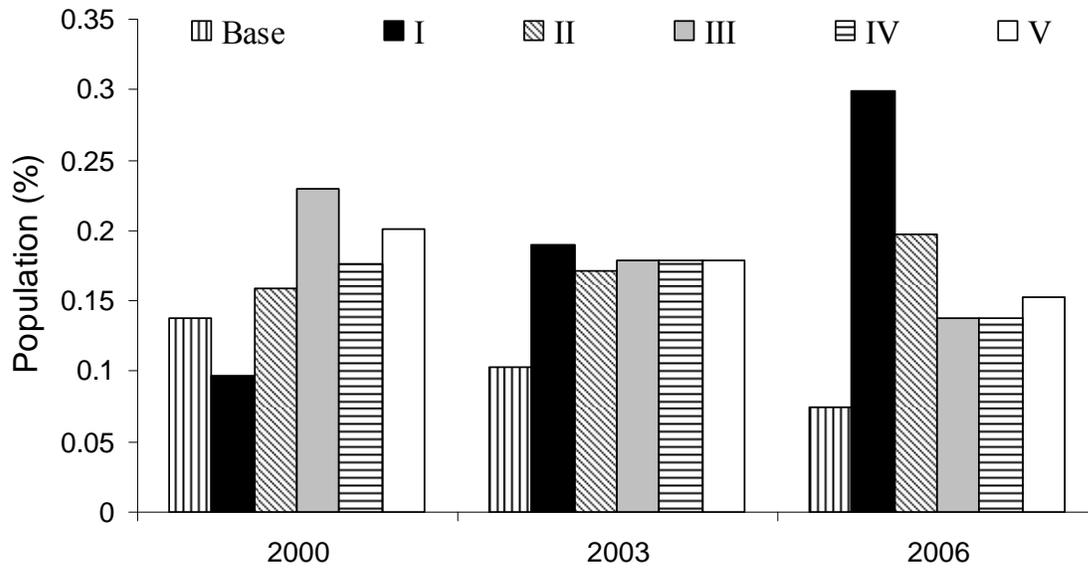


Figure 3. Size-frequency distributions of *Xestospongia muta* over all sites on Conch Reef in 2000, 2003, and 2006.

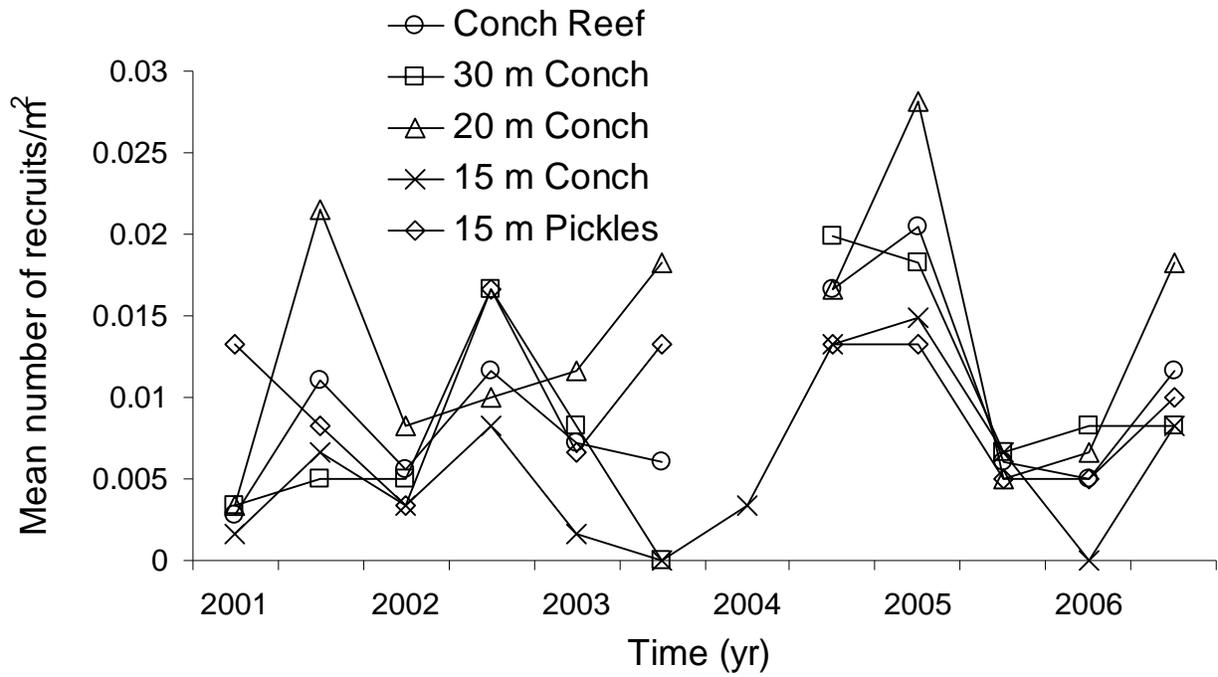


Figure 4. Mean number of recruits of *Xestospongia muta* at sites on Conch and Pickles Reefs from May 2000 to November 2006. Also plotted is the mean recruitment over all sites on Conch Reef.

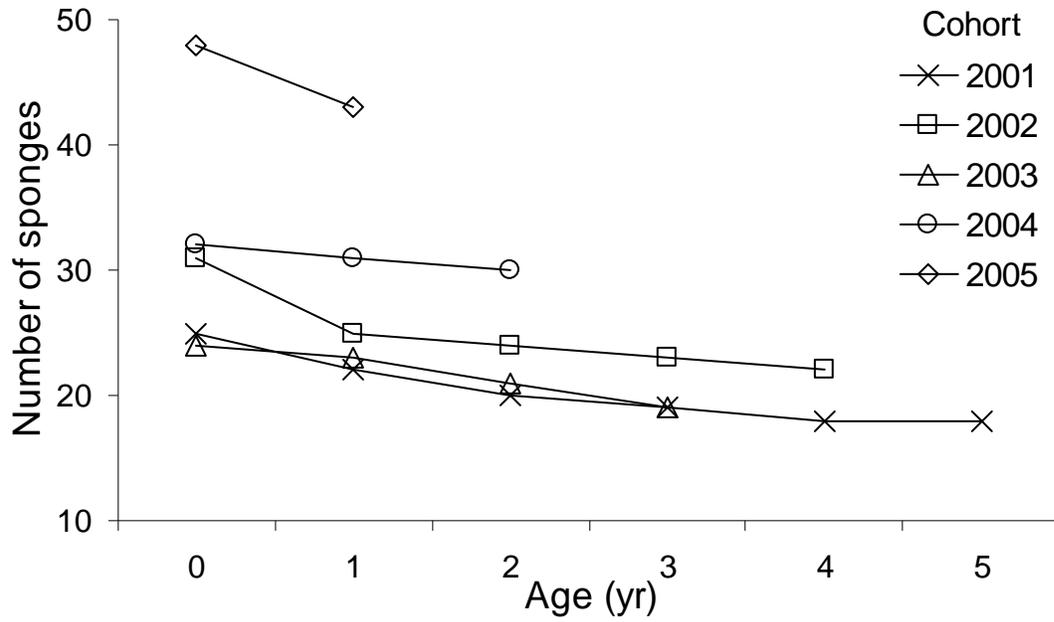


Figure 5. Survival of yearly cohorts of *Xestospongia muta* after recruiting into the population over 15, 20, and 30 m Conch Reef sites combined.

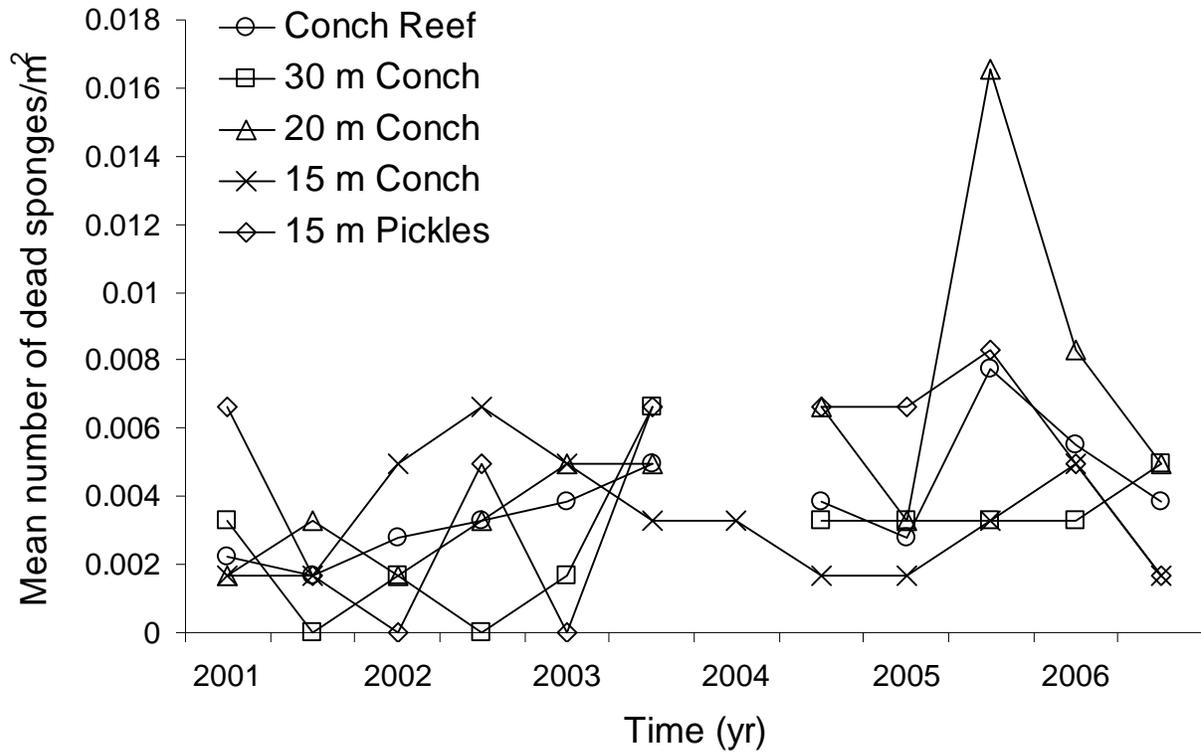


Figure 6. Mean number of dead *Xestospongia muta* at sites on Conch and Pickles Reefs from May 2000 to November 2006. Also plotted is the mean mortality over all sites on Conch Reef.

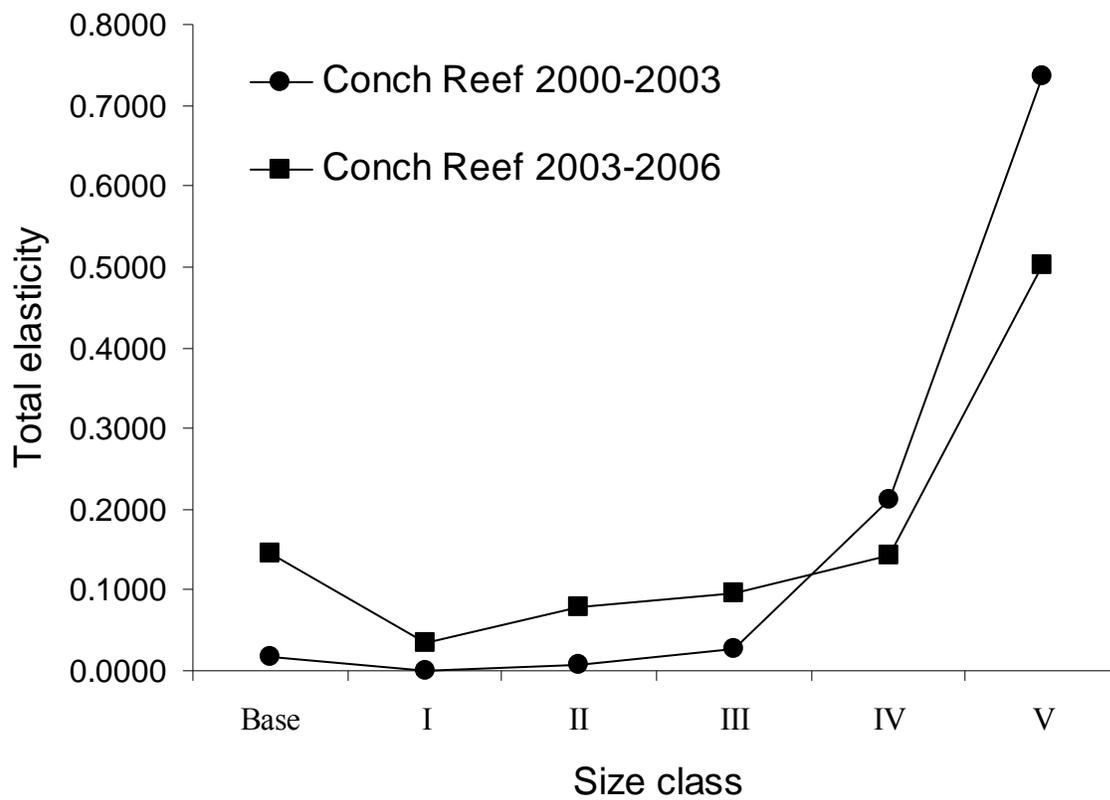


Figure 7. Total elasticities for each stage of *Xestospongia muta* over 2000–2003 and 2003–2006 for the Conch Reef summary matrices  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$ . Total elasticities were calculated as the sum of all elasticities for each stage from elasticity matrices (Appendix H).

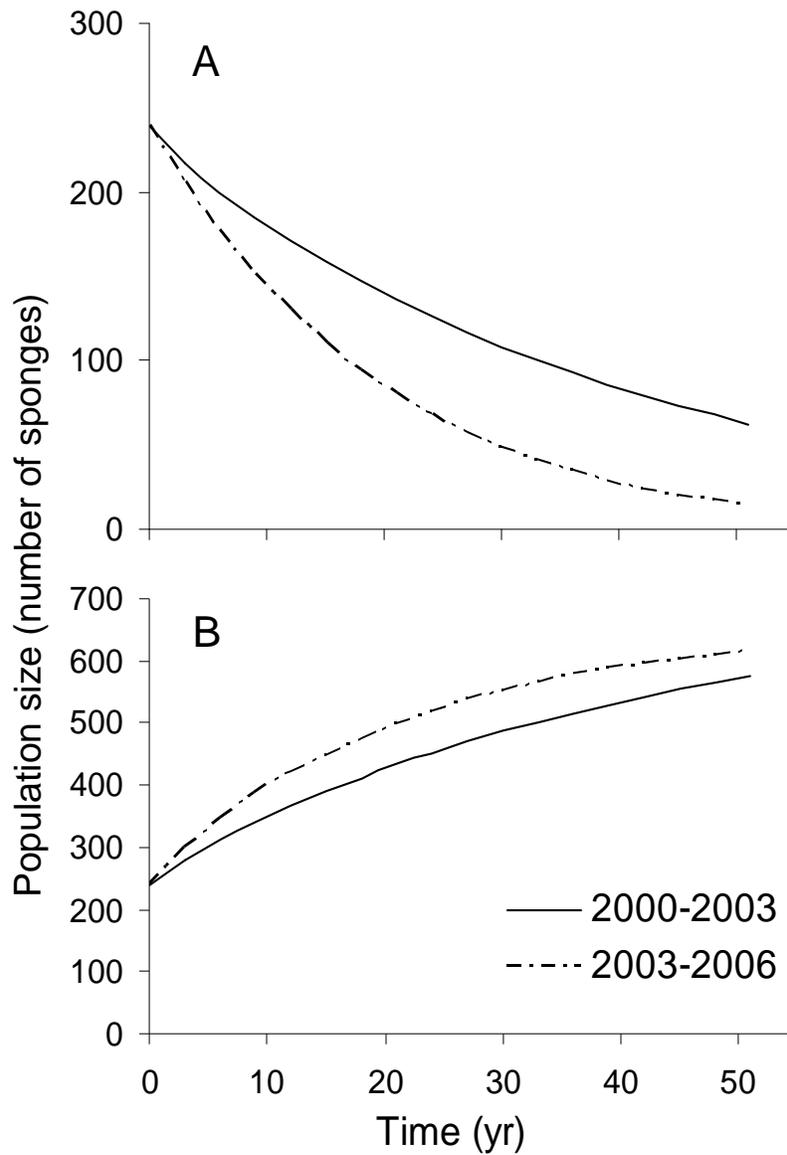


Figure 8. Projections of the Conch Reef summary matrices  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$  over 51 years (A) without recruitment of *Xestospongia muta* to observe the rate of population decline, and (B) with the addition of a recruitment vector,  $\mathbf{r}$ , at each iteration to observe the importance of recruitment on population growth.  $\mathbf{r}^{(00-03)} = 43$  size class I, 15 size class II, 3 size class III, and 2 Base stage;  $\mathbf{r}^{(03-06)} = 72$  size class I and 23 size class II.

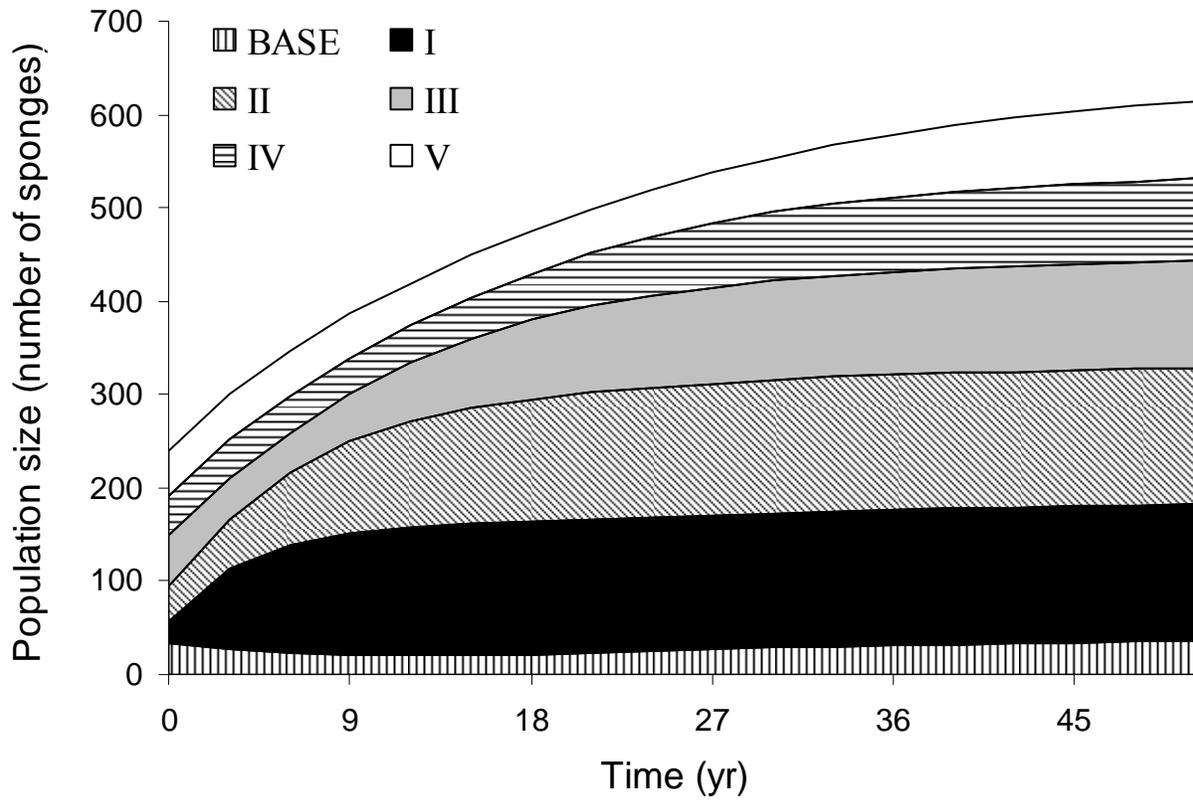


Figure 9. Projection as in Figure 8B for  $A^{(03-06)}$  illustrating changes in the population structure of *Xestospongia muta* through time.

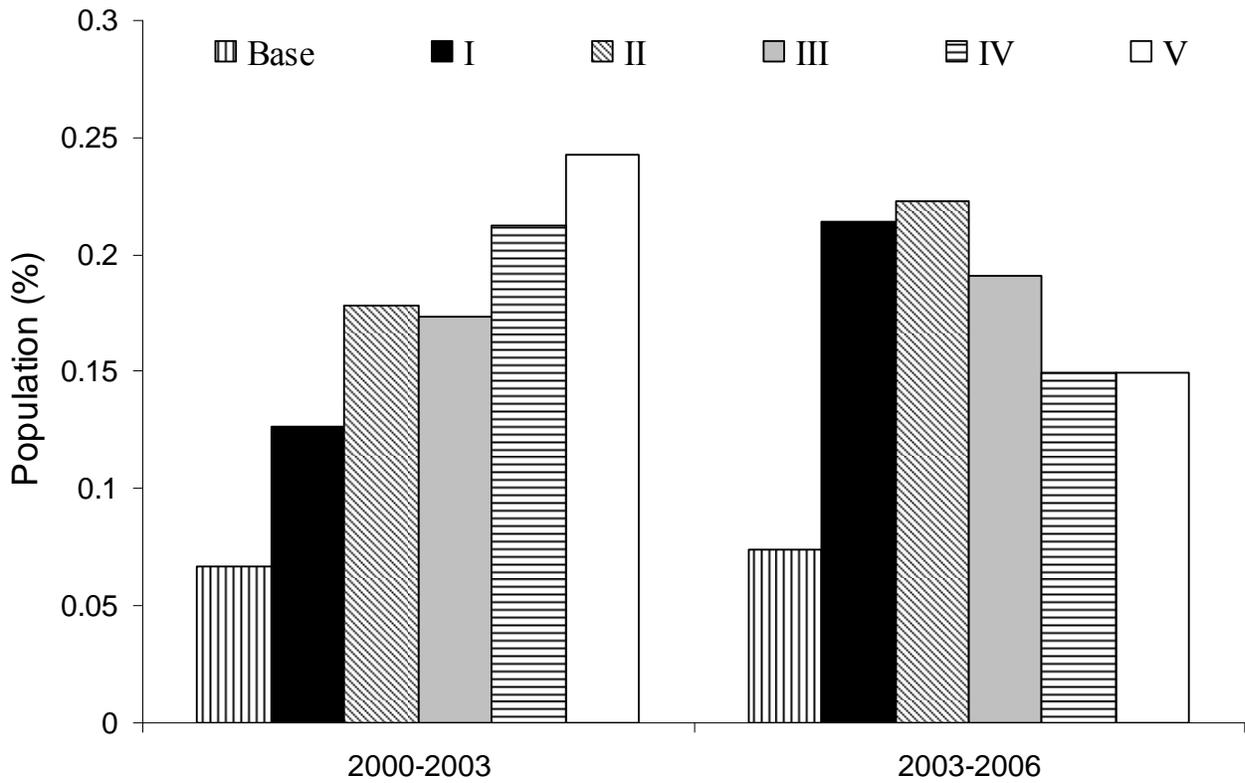


Figure 10. Resulting population structure of *Xestospongia muta* after 51 year projections of  $\mathbf{A}^{(00-03)}$  and  $\mathbf{A}^{(03-06)}$  with addition of the same recruitment vector,  $\mathbf{r}^{(00-03)}$ . Projections demonstrate the effect of contrasting mortality regimes (2000–2003 compared to 2003–2006) on population structure.

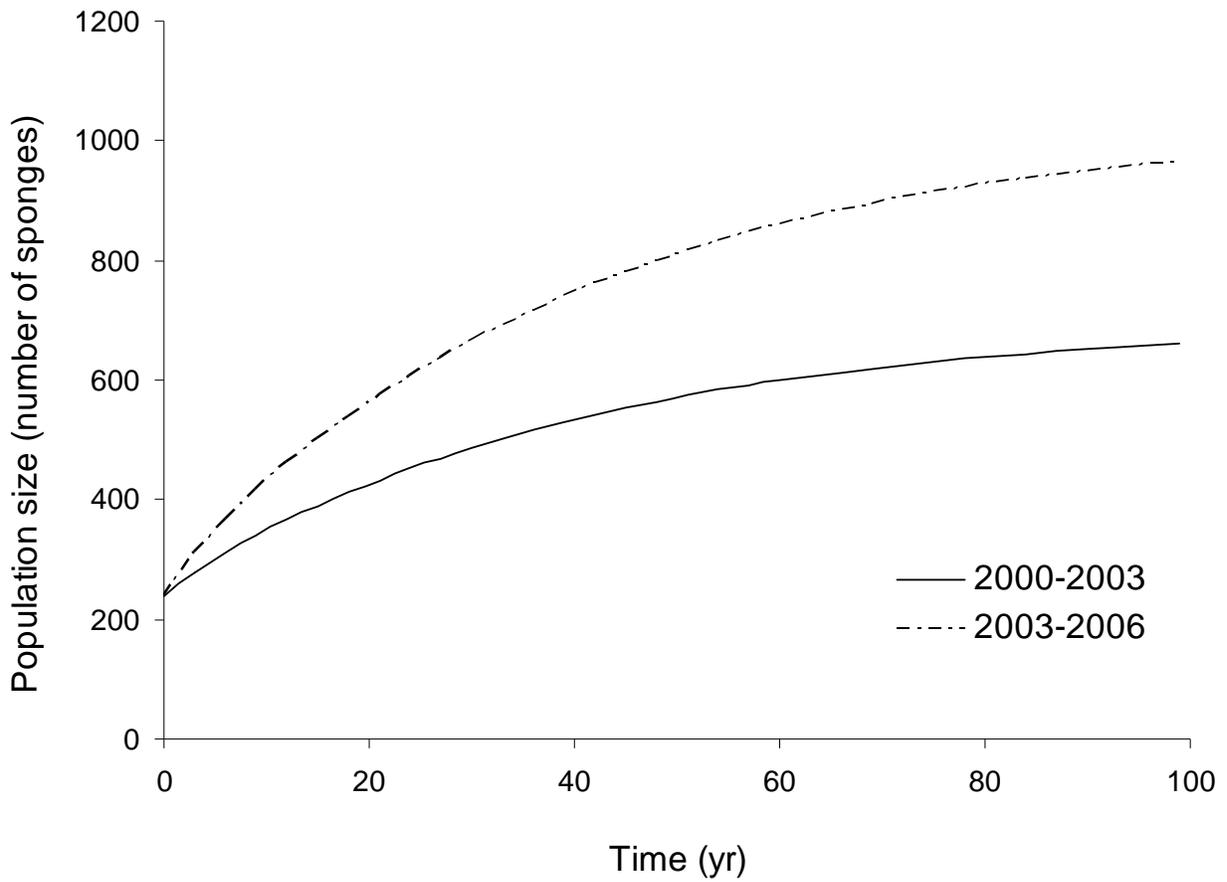


Figure 11. Projections of  $\mathbf{A}^{(00-03)}$  over 99 years with addition of  $\mathbf{r}^{(00-03)}$  and  $\mathbf{r}^{(03-06)}$ . Projections illustrate regulation of the population size of *Xestospongia muta* by recruitment.

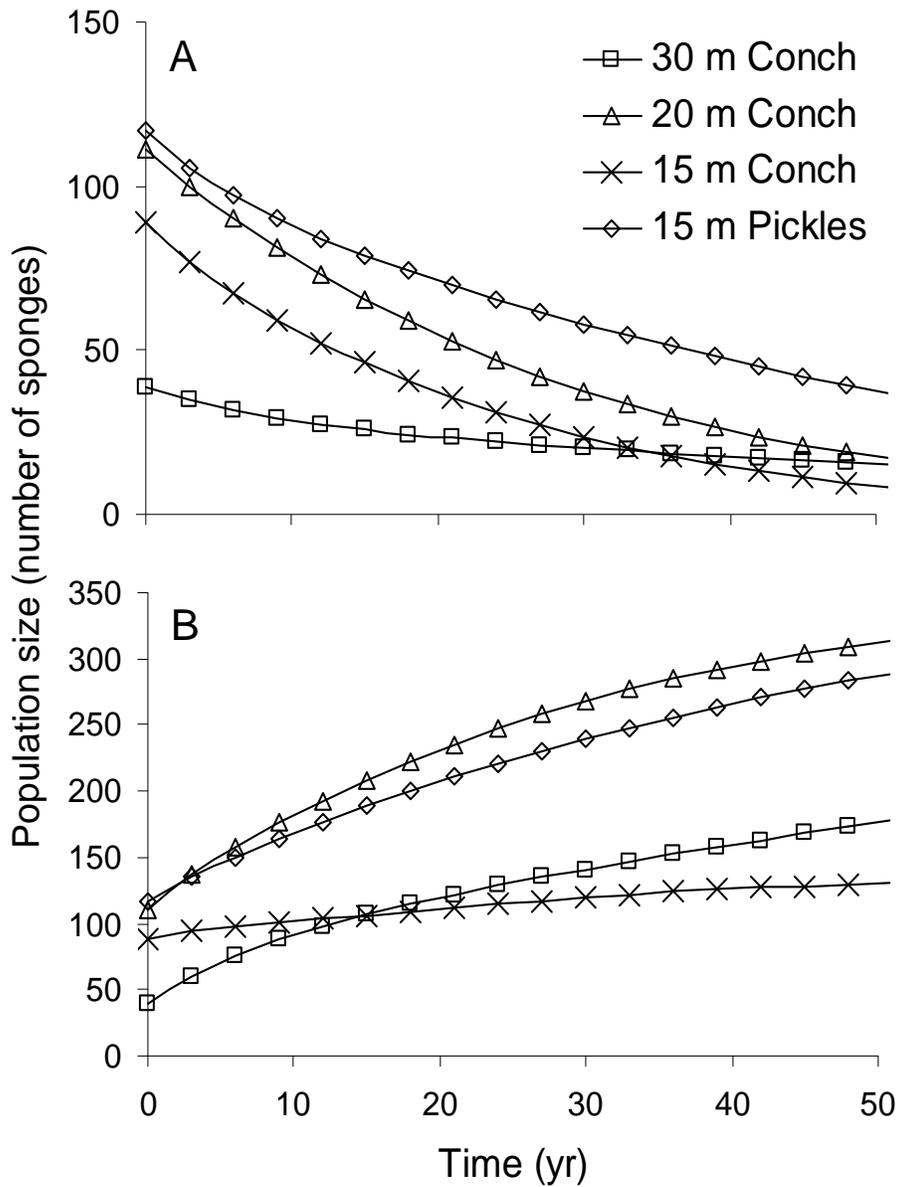


Figure 12. Projections of the site summary matrices  $\mathbf{A}^{(CR15)}$ ,  $\mathbf{A}^{(CR20)}$ ,  $\mathbf{A}^{(CR30)}$ , and  $\mathbf{A}^{(PR15)}$  over 51 years (A) without recruitment of *Xestospongia muta* to observe the rate of population decline, and (B) with the addition of a recruitment vector,  $\mathbf{r}$ , at each iteration to observe the importance of recruitment on population growth.  $\mathbf{r}^{(CR15)}$  = 14 size class I and 3 size class II,  $\mathbf{r}^{(CR20)}$  = 27 size class I, 8.5 size class II, 1 size class III, and 0.5 Base,  $\mathbf{r}^{(CR30)}$  = 16.5 size class I, 7.5 size class II, 1 size class III, and, 0.5 Base, and  $\mathbf{r}^{(PR15)}$  = 26 size class I, 3.5 size class II and 0.5 Base.

CHAPTER 2. REDWOOD OF THE REEF: GROWTH AND AGE OF THE GIANT BARREL  
SPONGE *XESTOSPONGIA MUTA* IN THE FLORIDA KEYS

Abstract

The growth of animals in most taxa has long been well described, but the phylum Porifera has remained a notable exception. The giant barrel sponge *Xestospongia muta* dominates Caribbean coral reef communities, where it is an important spatial competitor, increases habitat complexity, and filters seawater. It has been called the ‘redwood of the reef’ because of its size (often >1 m height and diameter) and presumed long life, but very little is known about its demography. Since 1997, 12 permanent 16 m diameter circular transects on the reef slope off Key Largo, Florida, have been established and monitored to study this important species. Over a 4.5-year interval, I measured the volume of 104 tagged sponges using digital images to determine growth rates of *X. muta*. Five models were fit to the cubed root of initial and final volume estimates to determine which best described growth. Additional measurements of 33 sponges were taken over 6-month intervals to examine the relationship between the spongocoel, or inner-osculum space, and sponge size, and to examine short-term growth dynamics. Sponge volumes ranged from 24.05 to 80,281.67 cm<sup>3</sup>. Growth was variable, and specific growth rates decreased with increasing sponge size. The mean specific growth rate was  $0.52 \pm 0.65 \text{ year}^{-1}$ , but sponges grew as fast or slow as 404 or 2% year<sup>-1</sup>. Negative growth rates occurred over short temporal scales and growth varied seasonally, significantly faster during the summer. No differences in specific growth rate were found between transects at three different depths (15, 20, 30 m) or at two different reef sites. Spongocoel volume was positively allometric with increasing sponge size and scaling between the vertical and horizontal dimensions of the

sponge indicated that morphology changes from a frustum of a cone to cylindrical as volume increases. Growth of *X. muta* was best described by the general von Bertalanffy and Tanaka growth curves. The largest sponge within the transects (1.23 × 0.98 m height × diameter) was estimated to be 127 years old. Although age extrapolations for very large sponges are subject to more error, the largest sponges on Caribbean reefs may be in excess of 2,300 years, placing *X. muta* among the longest-lived animals on earth.

## Introduction

Sponges are important components of coral reef ecosystems (Diaz and Rützler 2001). In the Caribbean, sponges rival reef-building corals in diversity and abundance (Targett and Schmahl 1984; Suchanek et al. 1985). They filter large amounts of water (Reiswig 1971; Pile et al. 1997) and compete for space in the benthic community (Suchanek et al. 1985; Engel and Pawlik 2005). Additionally, coral reef sponges serve as habitat for a large number of other invertebrate taxa (e.g., Duffy 1992; Henkel and Pawlik 2005) and host a diverse array of microbes that may take part in primary production or nitrification (Rützler 1985; Diaz and Ward 1997).

Growth, form, and size influence the ecology and functional significance of an organism in its community (Peters 1983; Werner and Gilliam 1984). In addition, the size of an organism may explain patterns in life histories (Blueweiss et al. 1978). Despite the importance of understanding growth, size, and other demographic data, limited information exists for sponges. Some studies have been conducted on species that are encrusting (Elvin 1976; Ayling 1983; Turon et al. 1998; Garrabou and Zabala 2001; Tanaka 2002), rope-form (Wulff 1985) and tubular (Lesser 2006; Trussell et al. 2006), but less is known about massive species (Reiswig

1973; Hoppe 1988). Studies of sponge growth rates have been hindered by many difficulties: most species grow slowly (Reiswig 1973) requiring long-term monitoring, they have high inter- and intra-specific variation in morphology, and they exhibit indeterminate growth (Sebens 1987). In addition, growth rates of sponges may be highly variable (e.g., Duckworth and Battershill 2001; Garrabou and Zabala 2001), many species do not tolerate or are too large for manipulation, and there are no morphological or internal structures that accrete regularly so as to indicate age.

The giant barrel sponge *Xestospongia muta* is a conspicuous and abundant member of reef communities throughout the Caribbean, where it is an important component of habitat heterogeneity (Humann 1992; Buettner 1996). Populations of this species occupy greater than 9% of the available reef substrate in some regions (Zea 1993); on the reefs off Key Largo, Florida, mean densities of *X. muta* are  $\sim 0.2$  sponges  $m^{-2}$  (McMurray and Pawlik, unpublished data), and the biomass of this species exceeds that of any other benthic invertebrate. Individuals are often very large, with heights and diameters in excess of 1 m, and *X. muta* is believed to be long lived, with anecdotal estimates ranging from 100 to >1,000 years old (Humann 1992; Gammill 1997), although little is known about the growth of this species.

The purpose of this study was to measure growth rates of *X. muta* by applying image-analysis measurement techniques to repeated digital images of sponges in situ. Measurements were conducted across different temporal and spatial scales to identify patterns of sponge growth. Scaling of sponge dimensions was assessed to examine changes in sponge morphology with increased size. Growth functions were fitted to measurement data to describe sponge growth and obtain age estimates for this species.

## Materials and methods

## Study sites and monitoring

Growth of *X. muta* was studied at permanent 16 m-diameter circular transects on Conch Reef [24°56.996N; 80°27.223W] and Pickles Reef [24°59.272N; 80°24.660W], Key Largo, Florida, as part of a long-term monitoring program begun in 1997. On Conch Reef, 3 transects were established at 15, 20 and 30 m depth, and at Pickles Reef (~ 6 km from Conch Reef), 3 transects were established at 15 m depth. Because of bottom-time limitations of SCUBA-diving at depth, transects at 20 and 30 m at Conch Reef were set-up using NOAA's underwater habitat "Aquarius" as a base of operations. Subsequent twice-yearly monitoring was undertaken by SCUBA diving from surface vessels using compressed air or nitrox. Within each transect, each sponge was mapped and given a unique stainless steel tag attached with a plastic cable-tie to a masonry nail driven into the limestone substratum next to the base of the sponge. Sponges were surveyed and each was photographed from above and in profile with a digital camera in the spring and fall of each year from 2000 to 2007. Due to inclement weather and limitations presented in the field, every sponge was not always photographed during each field season. A slate was photographed in each digital image, held parallel to the central axis of each sponge in side images and parallel to the plane of the top of the osculum in top images, displaying the unique tag number of each sponge and a 16 cm scale marker. For the purposes of this study, the spongocoel is defined as the central cavity of *X. muta*.

## Field measurements

Field measurements were performed on sponges in permanent transects on Conch and Pickles reefs to test the accuracy of the digital image measurement technique (see below), examine the relationship between sponge volume and spongocoel volume, and determine if a

seasonal pattern of growth exists for *X. muta*. Initial measurements of 33 sponges were taken in May 2006 and these sponges were revisited in November 2006 and May 2007. The 6 month interval between May and November 2006 was considered the summer season and the final 6 month interval was considered the winter season. Sponge height, base circumference, and osculum diameter were measured with a flexible plastic measuring tape (to  $\pm 0.5$  cm). Volume was calculated using the equation for the geometric model of a frustum of a cone:

$$V_{sponge} = \frac{1}{12} \pi h (od^2 + (od)(bd) + bd^2) \quad (1)$$

where  $V_{sponge}$  = sponge volume ( $\text{cm}^3$ );  $h$  = height (cm);  $od$  = osculum diameter (cm); and  $bd$  = base diameter (cm) (Fig. 1).

Equation 1 applies to the three most common morphologies of *X. muta*: cylinder, frustum of a cone, and inverse frustum of a cone. Additional measurements of spongocoel depth and inner diameter were performed and spongocoel volume was calculated by applying the equation for the frustum of a cone:

$$V_{spongocoel} = \frac{1}{12} \pi sd (sb^2 + (sb)(od) + od^2) \quad (2)$$

where  $V_{spongocoel}$  = spongocoel volume ( $\text{cm}^3$ );  $sd$  = depth of spongocoel (cm);  $sb$  = spongocoel base diameter (cm); and  $od$  = osculum diameter (cm) (Fig. 1).

The relationship between spongocoel volume and sponge volume was described by the allometric equation:

$$V_{spongocoel} = \alpha V_{sponge}^{\beta} \quad (3)$$

Field data was  $\log_e$ -transformed so that the equation becomes:

$$\log_e V_{spongocoel} = \log_e \alpha + \beta \log_e V_{sponge} \quad (4)$$

Linear regression was performed to determine the scaling coefficient,  $\alpha$ , and the scaling exponent,  $\beta$  of Eq. 4. Because a predictive relationship was sought, ordinary least squares

regression (OLS) was used (Sokal and Rohlf 1995; Warton et al. 2006). A logarithmic correction factor was applied to eliminate bias in the scaling coefficient estimate resulting from the conversion from log to arithmetic units (Baskerville 1971; Sprugel 1983). The actual slope was tested against an isometric slope of  $\beta = 1$  with a  $t$ -test. Analysis of covariance (ANCOVA) was used to test for differences between sampling periods with sponge volume as the covariate and measurement period (May 2006, November 2006, May 2007) as a fixed factor.

Specific growth rates were calculated as:

$$G = \frac{V_2 - V_1}{V_1} * \frac{1}{dt} \quad (5)$$

where  $G$  = specific growth rate ( $\text{year}^{-1}$ );  $V_1$  = initial volume ( $\text{cm}^3$ );  $V_2$  = final volume ( $\text{cm}^3$ ); and  $t$  = time (years). Spearman rank correlation was used to examine the relationship between initial volume and specific growth rate for each season. Differences in specific growth rates between summer and winter seasons were tested with a paired sample  $t$ -test.

#### Digital image measurements

A cross-sectional approach was employed to study growth of *X. muta*. Size-increment data were obtained from digital images taken in May 2001 and December 2005, a period spanning 4.5 years. These timepoints were chosen because they included the largest number of measurable sponges with initial and final photographs compared to other field seasons. A total of 104 sponges, representing a broad range of sizes present in the population, were selected for study. Sponges from both Conch and Pickles reefs and from all three depths at Conch Reef were measured, but only sponges with characteristic “barrel” morphologies that had not experienced any obvious damage or tissue loss were included.

Measurements of sponges from digital images were made with UTHSCA Image Tool software. Measurements of sponge height and base diameter were taken from side images and two perpendicular measurements of osculum diameter were taken from top images (to  $\pm 0.5$  cm). For the two osculum diameter measurements, the first diameter was chosen as the longest possible diameter, with the second perpendicular to the first. Volume was calculated by applying Eq. 1 for a frustum of a cone (Fig. 1).

A paired-sample *t*-test was used to test for differences between volume estimates from digital image measurements and from field measurements, uncorrected for spongocoel volume, for data from November 2006. As digital image estimates assume a solid geometry and do not account for the volume of the spongocoel, Eq. 3 was used to obtain spongocoel volume estimates for sponges measured with digital image analysis. Spongocoel estimates were then subtracted from original sponge volume estimates to correct for spongocoel volume. Specific growth rates were calculated by applying Eq. 5. Spearman rank correlation was used to examine the relationship between initial volume and specific growth rate estimates for digital image data, corrected for spongocoel volume.

A Walford (1946) plot was constructed with  $\log_e$  final volume on the ordinate and  $\log_e$  initial volume on the abscissa. Differences in growth between depths were tested with a one-way ANCOVA with initial volume as the covariate and depth (10, 20 and 30 m) as a fixed factor. Differences in growth between Pickles and Conch reefs at 15 m depth were similarly tested with a one-way ANCOVA. Following Trussell (1997), OLS regressions were used because techniques for model II ANCOVA are unavailable (Sokal and Rohlf 1995).

To examine the relationship between size and morphology, scaling relationships between height, base diameter, and osculum diameter were determined. Relationships between final and

initial sizes of each dimension were similarly determined. The geometric mean of initial and final measurements was used in regressions between differing dimensions. Measurements were  $\log_{10}$ -transformed and reduced-major-axis (RMA) regression was used because of measurement error in the independent variable (Ricker 1973). To test actual slope against an isometric slope of  $\beta = 1$ , the  $T$  statistic and degrees of freedom were calculated with equations from McArdle (1988).

### Growth models

Five commonly used growth functions were fit to size-increment data to determine which model best described growth of *X. muta*: the general von Bertalanffy growth formula (gVBGF), specialized von Bertalanffy growth formula (sVBGF), Gompertz, Richards, and Tanaka growth functions. Growth equations were obtained from Brey (2001) and Tanaka (1982).

For the following equations,  $S_1$  is the initial size (cm) and  $S_2$  is the final size (cm) after time interval  $dt$  (4.5 years);  $S_t$  is a continuous function of  $t$  (years) and  $S_0$  is size at time zero and  $t_0$  is the theoretical age at zero size. For the sVBGF, gVBGF, Gompertz, and Richards functions (Eqs. 6–15) parameters included:  $S_\infty$  = asymptotic size (cm);  $K$  = defines rate of growth ( $\text{yr}^{-1}$ );  $D$  = influences shape of curve.

The specialized von Bertalanffy growth formula (von Bertalanffy 1938):

$$S_2 = S_1 + (S_\infty - S_1)(1 - e^{-K(dt)}) \quad (6)$$

Or

$$S_t = S_\infty(1 - e^{-K(t-t_0)}) \quad (7)$$

is the commonly used form of the von Bertalanffy growth function. It has no inflection point and growth approaches an asymptote. For theory and derivation of this model see Beverton and Holt (1957) and Pauly (1981).

The generalized von Bertalanffy growth formula (Pauly 1981):

$$S_2 = \left( S_\infty^{1/D} (1 - e^{-K(dt)}) + S_1^{1/D} e^{-K(dt)} \right)^D \quad (8)$$

Or

$$S_t = S_\infty \left( 1 - e^{-K(t-t_0)} \right)^D \quad (9)$$

is asymmetrical sigmoid and approaches an asymptote. See Richards (1959) and Pauly (1981) for theory and derivation of this model.

The Gompertz function (Gompertz 1825):

$$\ln S_2 = \ln S_\infty \left( 1 - e^{-K(dt)} \right) + \ln S_1 e^{-K(dt)} \quad (10)$$

Or

$$S_t = S_\infty e^{-e^{-K(t-t_0)}} \quad (11)$$

was initially developed to describe survival and has been successfully used to describe individual growth (Winsor 1932). Like the gVBGF, it is asymmetrical sigmoid and approaches an asymptote.

The Richards function (Richards 1959, Ebert 1980):

$$S_2 = \left( S_\infty^{-1/D} (1 - e^{-K(dt)}) + S_1^{-1/D} e^{-K(dt)} \right)^{-D} \quad (12)$$

Or

$$S_t = S_\infty \left( 1 + (1/D) e^{-K(t-t_0)} \right)^{-D} \quad (13)$$

is asymptotic and has an additional parameter,  $D$ , which makes it a very flexible curve. This model includes several other functions as special cases, including the gVBGF, sVBGF, Gompertz and logistic models.

The Tanaka function (Tanaka 1982):

$$S_2 = (1/f^{0.5}) \ln(2G + 2(G^2 + fa)^{0.5}) + d \quad (14)$$

where:  $G = (E/4) - (fa/E) + f$ ,  $E = e^{(r^{0.5})(s_1-d)}$

Or

$$S_t = (1/f^{0.5}) \ln(2f(T-c) + 2(f^2(T-c)^2 + fa)^{0.5}) + d \quad (15)$$

where:  $T = t/dt$ ,  $c = (a/E) - (E/4f)$ ,  $E = e^{(r^{0.5})(s_0-d)}$

is sigmoid with an initial period of slow growth, and a period of exponential growth followed by growth that slows but never reaches an asymptote. The biological meanings associated with the parameters are:  $a$  = related to maximum growth rate ( $\approx 1/a^{0.5}$ );  $c$  = age at which growth is maximum;  $d$  = shifts size at which growth is maximum;  $f$  = measure of the rate of change of the growth rate (Tanaka 1982, 1988). The influence of each parameter on the shape of the curve is demonstrated in Ebert et al. (1999) and Ebert (1999).

The cube root of volume estimates, corrected for spongocoel volume, was used as an average linear size to model growth of *X. muta*. The difference equations of the models were fitted to final and initial linear sizes on a Walford plot by nonlinear regression (NLIN procedure SAS).

The sum of squared error (SSE), coefficient of determination and Akaike (1973) Information Criterion (AIC) were used to evaluate model fit. The AIC selects the most parsimonious candidate model by evaluating the trade-off between model bias that results from

too few parameters versus variance that results from too many (Burnham and Anderson 2002). Therefore, AIC values can be used to evaluate any differences between the 2- and 3-parameter models that may otherwise be neglected through use of the SSE as the sole fitting criteria. In model selection, the model with the lowest SEE and AIC is sought. Because sample size,  $n$ , was small with respect to the number of model parameters,  $K$ , ( $n/K < 40$ ), the second-order correction,  $AIC_c$  was used (Burnham and Anderson 2002). The model selection criteria AIC differences,  $\Delta_i$ , give a measure of each model relative to the best model; and Akaike weights,  $w_i$ , are normalized relative likelihood values which give the probability that a given model is the best of the candidate models (Burnham and Anderson 2002).

Parameter estimates were used to produce size-at-age curves using the integrated forms of the growth functions. Growth functions were then cubed to obtain volume-at-age plots. In contrast to the four determinate models, Tanaka parameters described growth for 4.5 year intervals because the time interval between initial and final sizes is not included in the difference equation for this model. To determine parameters for yearly growth, nonlinear regression was performed to refit the curve. The parameter  $t_0$  was determined by solving each function at  $t = 0$ . The size of the smallest sponge measured in the dataset was used as size at  $t = 0$  for all curves. Analyses were conducted with SPSS (vers. 14.0.0 for Windows, SPSS, Inc., Chicago, IL, USA) and SAS (vers. 9.1.3 for Windows, SAS Institute Inc., Cary, NC, USA) statistical software.

## Results

### Growth rates

Estimates of volume of individual *X. muta* from field measurements did not significantly differ from estimates using digital images (paired  $t$ -test;  $P = 0.26$ ,  $t_{31} = -1.16$ ). Initial volume

estimates from digital image analysis, corrected for spongocoel volume, ranged from 24.05 to 80,281.67 cm<sup>3</sup>. There was a significant negative correlation between specific growth rate and initial volume ( $r_s = -0.798$ ,  $P \leq 0.01$ ). All sponges had positive growth over the study interval and there was large variation in growth rates. The mean ( $\pm 1$  SD) specific growth rate was  $0.52 \pm 0.65$  year<sup>-1</sup>. Growth rates as fast as 4.04 year<sup>-1</sup> and as slow as 0.02 year<sup>-1</sup> were observed. In terms of volume, sponges gained an average of  $1,955.37 \pm 2,221.09$  cm<sup>3</sup>year<sup>-1</sup>. ANCOVA analysis of log<sub>e</sub>-transformed initial and final volume data indicated that there was no significant effect of depth ( $F_{2,68} = 2.75$ ,  $P = 0.07$ ) or reef location ( $F_{1,60} = 1.55$ ,  $P = 0.22$ ) on growth rate. Although not significant, mean growth was greater for sponges at 20 and 15 m depths compared to sponges at 30 m.

The initial volumes of sponges measured in the field ranged from 26.69 to 150,492.90 cm<sup>3</sup>. Specific growth rate during the summer was negatively correlated with initial volume ( $r_s = -0.69$ ,  $P \leq 0.01$ ), but no significant correlation was found between initial volume and specific growth rate during winter ( $r_s = -0.105$ ,  $P = 0.56$ ). Growth over the entire year was significantly correlated with initial volume, with rates decreasing with increasing volume ( $r_s = -0.67$ ,  $P \leq 0.01$ ). Sponges grew significantly faster in summer compared to winter (paired  $t$ -test;  $P = 0.001$ ,  $t_{32} = 3.65$ ). Mean ( $\pm 1$  SD) specific growth rates during the summer and winter were  $0.94 \pm 1.20$  and  $0.14 \pm 0.42$  year<sup>-1</sup> respectively. The mean specific growth rate over the entire year was  $1.15 \pm 1.42$  year<sup>-1</sup>. In terms of volume, sponges gained an average of  $4,195.53 \pm 4,080.01$  cm<sup>3</sup> during summer compared to  $1,472.40 \pm 6,173.16$  cm<sup>3</sup> during winter. Growth was variable and 3 sponges experienced negative growth in summer while 10 decreased in size over winter. When these sponges were omitted from analyses, positive growth rates remained significantly greater in the summer compared to winter (paired  $t$ -test;  $P = 0.003$ ,  $t_{19} = 3.37$ ).

## Spongocoel volume

Spongocoel volumes measured in the field ranged from 0.61 to 57,543.51 cm<sup>3</sup> for sponges with non-corrected volumes (i.e., uncorrected for spongocoel volume) of 27.31 and 223,529.96 cm<sup>3</sup> respectively. There was no significant effect of measurement period on the relationship between spongocoel volume and non-corrected sponge volume (ANCOVA;  $F_{2,98} = 0.793$ ,  $P = 0.46$ ). Data from all three measurement periods were therefore pooled and used to determine the parameters of the allometric equation (Eq. 3). Spongocoel volume was found to allometrically increase with increasing sponge volume and is reliably predicted from sponge volume ( $t_{97} = 9.73$ ,  $r^2 = 0.97$ ,  $P < 0.001$ ) (Fig. 2). The allometric equation relating spongocoel volume to sponge volume was determined to be:

$$V_{spongocoel} = 0.01946 * V_{sponge}^{1.214} \quad (16)$$

## Scaling

The ranges of heights, base diameters, and osculum diameters of measured sponges were 2.28–65.79, 3.84–51.95, and 0.48–46.05 cm respectively. Mean growth rates ( $\pm 1$  SD) were  $1.85 \pm 1.10$  cm year<sup>-1</sup> in height,  $1.45 \pm 0.88$  cm year<sup>-1</sup> in base diameter, and  $0.98 \pm 0.67$  cm year<sup>-1</sup> in osculum diameter. Scaling equations that describe the relationship between sponge dimensions and change in each dimension are given in Table 1. The slopes of regressions of final versus initial size, in terms of height, base diameter, and osculum diameter, were significantly less than 1, indicating that growth in all dimensions decreases with increasing size. For regressions of base diameter versus sponge height, and osculum diameter versus sponge height, slopes did not significantly differ from those predicted for isometry. In contrast, an allometric relationship was

found between base diameter and osculum diameter, with increases in osculum diameter occurring faster than increases in base diameter.

## Growth models

Because *X. muta* has a variety of morphologies (i.e., low growth form with base diameter greater than height, high growth form with base diameter less than height), no one linear measurement best characterized sponge size. Moreover, the Tanaka growth model failed to converge when modeling volumetric growth. Therefore, the cube root of digital image volume estimates, corrected for spongocoel volume, was used to model growth of *X. muta*. This measurement of size is useful because it inherently accounts for the spongocoel correction and morphology of the sponge.

Parameter estimates for each of the five growth models are presented in Table 2. A number of fitting criteria were used to assess the fit of the models (Table 3). The models, in order of best fit are: gVBGF = Richards > Tanaka > sVBGF > Gompertz (Table 3). The Richards model converged on the gVBGF as one of its special cases. Therefore further mention of the gVBGF will refer to both models.  $AIC_c$  values were in agreement with the SSE and did not indicate substantial differences between the models. Akaike weights revealed that there is a 22 and 21% chance, respectively, of the gVBGF and Tanaka being the best of the candidate models. Low Akaike weights are indicative of the large variation in observed growth and inclusion of poor models (e.g., sVBGF and Gompertz) in the set of candidate models.

The gVBGF and Tanaka models were selected for further analysis, as the best of the candidate models, based on model fit. An evidence ratio, the ratio of Akaike weights, indicates that the gVBGF is only 1.07 times more likely to be the best model, given the set of candidate

models. A Walford plot of final and initial sizes with the fitted models is presented in Fig. 3. Both models describe initial growth that gradually increases to a maximum and slowly attenuates with increasing size. Initial growth is slightly overestimated and the models start to diverge at larger size classes. The primary difference between the two models is the description of growth for the largest size classes. A plot of the two growth curves for both linear size and volume (Fig. 4a, b) shows the same patterns observed in Fig. 3. The gVBGF describes faster growth for larger individuals and approaches an asymptotic size of 6,612.11 cm. The Tanaka curve describes relatively constant growth rates for larger size classes. Extrapolation of the Tanaka curve to 3,000 years shows slowly attenuating growth that never reaches an asymptote (Fig. 4c). The age estimates obtained from the gVBGF and Tanaka curves for the largest sponge measured over the 4.5 year interval are 53 and 55 years, respectively.

## Discussion

### Redwood of the reef?

Although *X. muta* is a dominant member of Caribbean coral reef ecosystems, with average densities of  $\sim 0.2$  individuals  $\text{m}^{-2}$  (McMurray and Pawlik, unpublished data), and covering  $> 9\%$  of available hard substratum on some reefs (Zea 1993), remarkably little is known of its demography. This species has been anecdotally reported to be long-lived (Humann 1992; Gammill 1997), but no measurement data related to age could be found in the scientific literature. Using our data and the Tanaka growth model, I can confirm the extreme longevity of *X. muta*, and can calculate ages of very large specimens based on their dimensions. The largest sponge within our transects (1.23 m high, 0.98 m diameter) is estimated to be 127 years old. In June 2007, I measured two specimens of *X. muta* at 30 m depth off Plana Cay, Bahamas

[22°36.441N, 73°37.555W]: one was 170 cm in height, 305 cm in base circumference, and 81.5 cm average osculum diameter, while the second was 140, 300 and 96.5 cm, respectively (Fig. 5). The volume estimates for these sponges, corrected for spongocoel volume, were 662,147.30 and 632,912.80 cm<sup>3</sup>; and age estimates, obtained from the Tanaka growth model, were 258 and 242 years, respectively. Size estimates of an even larger specimen of *X. muta* from Curaçao (photograph in Nagelkerken et al. 2000) provide an age estimate of ~2,300 years, although age estimates of sponges of this size are rather significant extrapolations and may be subject to more error than for smaller sponges. Nevertheless, this estimate greatly surpasses the age of the oldest reported individual (non-clonal) animal, the Ocean Quahog *Arctica islandica*, at 374 years (Schone et al. 2005), and places it on par with the oldest known redwood tree, *Sequoia sempervirens* (~2,000 years old) in Humboldt Redwoods State Park, California (HRIA 2006). Considering their large size and great age, “redwood of the reef” is an apt designation for *X. muta*.

#### Growth rates

Specific growth rates of *X. muta* were found to decrease with increasing sponge volume. The same trend has been observed for many sponge species (Reiswig 1973; Hoppe 1988; Leys and Lauzon 1998; Garrabou and Zabala 2001). In contrast, Duckworth and Battershill (2001) found no differences in growth rates among the range of size classes studied. Wulff (1985) observed decreased growth rates with increasing size in only one of three rope-form species. It was hypothesized that relatively constant surface area to volume ratios of rope-form species allow for less influence of size on growth rates (Wulff 1985). For *X. muta*, physiological or mechanical limits may constrain growth in larger size classes while there may be a selective

advantage for relatively faster growth of small sponges. The observed variability in growth rates is characteristic of sponges (Reiswig 1973; Dayton et al. 1974; Fell and Lewandrowski 1981; Ayling 1983; Wulff 1985; Hoppe 1988; Leys and Lauzon 1998; Duckworth and Battershill 2001; Garrabou and Zabala 2001) and other indeterminately growing species (Sebens 1987).

Growth rates did not differ for *X. muta* from three depths (15, 20, 30 m) on Conch Reef. In contrast, a common tube sponge, *Callyspongia vaginalis*, was found to grow significantly faster on the deeper slope of Conch Reef (25 m), where picoplankton concentrations were demonstrated to be higher, compared to shallower parts of the reef (14 m; Lesser 2006; Trussell et al. 2006), prompting these authors to conclude that food availability was the cause of the observed bathymetric growth pattern. Our study bracketed the same depth range on the same reef, but no significant effect of depth on growth of *X. muta* was observed, suggesting that differences in picoplankton abundance (Lesser 2006; Trussell et al. 2006) may not be important determinants of growth for all sponge species.

Cross-species comparisons of sponge growth rates are difficult to make, because specific growth rates decrease with increasing sponge size for *X. muta* (this study) and for other species (e.g., Reiswig 1973; Hoppe 1988), and average growth rates are influenced by the range of sizes measured. Comparisons are further complicated by the different methods used to measure growth rates. Nevertheless, Hoppe (1988) found average volume increases of 7.7–19.4% year<sup>-1</sup> for *Neofibularia nolitangere*, *Ircinia strobilina*, and *Agelas clathrodes*, all large sponges on the reefs around Curaçao. Reiswig (1973) found increases ranging from < 5 to 60 % year<sup>-1</sup> for *Mycale* sp., *Verongia gigantea*, and *Tethya crypta* on Jamaican reefs. The average specific growth rate of 52 % year<sup>-1</sup> for *X. muta* reported in this study is comparable to these species, given the wide interspecific variation in reported growth rates.

In a study documenting regeneration of *X. muta*, Schmahl (1999) monitored the recovery of injured sponges following the grounding of a vessel on the Florida reef tract. Sponges were tracked for 13 months and linear growth in height was measured. Growth was variable, and 27% of the sponges did not grow. Sponges that grew increased an average of 1.94 cm in height, and growth rates were greatest during the peak of warm water temperatures. However, regeneration rates are known to differ from normal growth rates (Hoppe 1988) and involve separate processes (Simpson 1984). In another study that examined regeneration, Walters and Pawlik (2005) found *X. muta* capable of healing the area of a wound at a rate of 6.5% day<sup>-1</sup>. In the present study, specimens of *X. muta* were specifically chosen to be free of physical injury so that normal rates of growth could be determined, and the average yearly rate of growth in height, 1.85 cm, suggests that normal growth rates may be less than regeneration rates reported by Schmahl (1999) and Walters and Pawlik (2005). Moreover, I observed substantial damage to other specimens of *X. muta* in our permanent transects caused by the movement of rope debris, and these exhibited very rapid subsequent regeneration; in one case, approximately twice the rate observed by Schmahl (1999).

Sponges grew significantly faster in summer compared to winter. This pattern is consistent with findings for smaller species (Elvin 1976; Fell and Lewandrowski 1981; Barthel 1986; Turon et al. 1998; Duckworth and Battershill 2001; Garrabou and Zabala 2001; Tanaka 2002). Johnson (1979) found the opposite pattern of growth for calcareous sponges, while others have found no seasonal growth (Ayling 1983; Hoppe 1988; Tanaka 2002). Based on historical average water temperatures on Conch Reef (Leichter and Miller 1999), faster growth rates of *X. muta* occurred in the summer months when the metabolic rate would be expected to increase.

Trade-offs of energy allocation to processes of reproduction and chemical defense may also influence temporal changes in growth rate. A trade-off between growth and chemical defense has been found for the sponge *Crambe crambe* in the Mediterranean (Turon et al. 1998), but a relationship between growth and reproduction has yet to be established. The chemical defense of *X. muta* is variable and is not correlated to sponge size (Chanas and Pawlik 1997); however, no study has examined temporal patterns of metabolite production in this species. Likewise, little is known about reproduction of *X. muta*. The age of first reproduction is unknown and little information exists on the timing of reproduction. Spawning has been observed in both spring and late summer (May 2004: Ritson-Williams et al. 2005; May 2005: McMurray, personal observation; and September 2007, O. Rutten, personal communication). Recruitment has also been observed in the spring and fall (Pawlik, unpublished data), suggesting that *X. muta* reproduces at least twice yearly. Growth rates are expected to decrease with increased reproduction if a trade-off in energy allocation between these two processes exists. Energy diverted from growth to gamete production may occur over several months, which could explain lower growth rates in the winter, prior to spawning in May. However, not all sponges in the population spawn during any one season (Pawlik, unpublished data), and some spawn in the fall, so there is not a clear trade-off between reproduction and growth.

Coral reef sponges may obtain food as picoplankton from the water column (Lesser 2006), or derive it from symbiotic algae (Frost and Williamson 1980; Hill 1996). Picoplankton availability as a function of depth may influence spatial differences in growth rates of some tube sponges (Lesser 2006; Trussell et al. 2006) but a similar relationship was not observed for *X. muta*, and seasonal picoplankton abundance on Conch Reef would not be expected to vary sufficiently to explain seasonal differences in sponge growth. In a study of the growth of the

sponge *Halichondria panacea*, Barthel (1986) found that temporal patterns were explained by water temperature and not correlated with food. Seasonal variation in light levels would be important if photoautotrophic cyanobacterial symbionts provided nutrition to *X. muta*, as has been demonstrated for other coral reef sponges (Wilkinson and Cheshire 1988). While *X. muta* does harbor cyanobacteria, available evidence suggests that they are commensals that do not benefit the host sponge (Thacker 2005; López-Legentil et al. 2008).

Field measurements revealed variable growth of *X. muta*, with shrinkage occurring for some sponges. It has been well documented that sponge growth is highly plastic (Reiswig 1973; Barthel 1986; Turon et al. 1998; Garrabou and Zabala 2001), and shrinkage rates are also known to be lower than rates of growth (Garrabou and Zabala 2001). Plasticity is a common characteristic of indeterminate growth (Sebens 1987). The patterns of seasonal growth and short-term shrinkage events highlight the influence that the temporal scale of measurements has on observed growth rates. Field measurements over half-year intervals revealed dynamic growth processes, while the image-analysis technique, used over a much longer time interval, integrated short-term processes and provided smoothed growth rates.

### Spongocoel volume

The spongocoel has been excluded in geometric volume approximations of sponge size in previous studies of large reef species (e.g., Reiswig 1973), and the present study is the first to address scaling of the spongocoel with sponge size. Spongocoel volume was positively allometric with increasing sponge size, necessitating the correction of geometric approximations for spongocoel volume across a broad range of sponge size-classes. In the present study, sponge volumes and growth rates would be overestimated without correcting for this relationship. It is

unclear why larger sponges have a proportionally larger spongocoel, but two important functions are likely responsible: water pumping (Reiswig 1971) and reproduction (Ritson-Williams et al. 2005). The spongocoel functions as the excurrent site for water pumped through the sponge. The relationship between pumping rates and spongocoel volume is unknown; however pumping rates are known to increase proportionally with tissue volume (Reiswig 1975). Increased spongocoel volume may aid pumping rates as sponges grow larger, thus potentially reducing physiological problems associated with large size (Schmidt-Nielson 1974). The positive allometry between spongocoel volume and sponge volume also increases the ratio of surface area to sponge volume. The outer surface of a sponge is covered with ostia for water intake, and subsequently, food capture, waste removal, and gas exchange (Reiswig 1971). During reproduction, the spongocoel is the excurrent site for gametes during spawning events (Ritson-Williams et al. 2005). Reproductive output is expected to increase with sponge size and this may require an increasingly larger spongocoel, with a proportionally greater surface area, as sponges grow larger.

## Scaling

Scaling relationships between sponge dimensions characterize the form of sponge growth (Schmidt-Nielson 1974). The way in which an organism grows has many ecological implications (Werner and Gilliam 1984). For example, Hoppe (1988) found significantly faster vertical rates of growth compared to horizontal for the sponge *Ircinia strobilina* and attributed this difference as a strategy to avoid competition. In the present study, growth in height, base diameter, and osculum diameter were compared. Both horizontal measures of base and osculum diameter increased at the same rate as vertical growth (height). While a significant allometric relationship

was not found between these dimensions, examination of the slopes of the regressions reveals a tendency for base diameter to increase slower than height and for osculum diameter to increase faster than height (Table 1). Osculum diameter was found to widen significantly faster than base diameter. As *X. muta* grows, its morphology changes from a frustum of a cone to a cylinder, or barrel-shape, with osculum diameter equal or larger than base diameter. There are, of course, exceptions to this generality and growth form may be influenced by an array of physical (e.g., water flow) and biological factors (e.g., damage by fish or turtle grazing).

#### gVBGF and Tanaka growth models

Among all the growth models considered, the gVBGF and Tanaka growth models were found to provide the best fit to the data. The Walford plot of size-increment data (Fig. 3) shows that, indicative of indeterminate growth, all sponges were actively growing. Both curves fit the wide range of size classes measured for the current study. The primary difference in the fit of the two curves lies within the large size-classes: the gVBGF extrapolates growth beyond the largest measured sponge to approach an asymptote, while the Tanaka describes slowly attenuating growth. Much larger individuals of *X. muta* exist on Conch Reef, and throughout the Caribbean, than those included in this study (e.g., Nagelkerken et al. 2000). In fact, estimated volumes for the largest individuals exceed the asymptote of all asymptotic growth curves studied. The Tanaka curve does not have an asymptote and is therefore the most relevant model to describe growth of *X. muta*. The Tanaka function has previously been used to describe growth of other marine invertebrates, including sea urchins (Ebert et al. 1999; Rogers-Bennett et al. 2003) and molluscs (Tanaka 1988).

The growth curve determined for *X. muta* is conservative in several aspects. First, the volume used at time zero, 24.05 cm<sup>3</sup>, is an overestimation of true volume at settlement. Measuring growth of recruits is imposed by the limits of detection in the field. Recruits that are approximately 5 cm<sup>3</sup> were frequently observed and larvae of *X. muta* have been reported to be 0.1–0.2 mm in length (Lindquist and Hay 1996). The growth of these earliest stages is presently unknown and may occur over a significant length of time. Because of their plastic nature, a decoupling of sponge size and age may exist in some cases. Sponges have the ability to lose large amounts of volume and regenerate (Henry and Hart 2005). When *X. muta* suffers partial mortality, a ring of multi-oscule remnants may regenerate at the base of the sponge. Through time, remnants have been observed to grow and fuse with reduction in the number of osculae as the sponge grows, although the resulting form is not typical. Should a regenerated sponge grow sufficiently to restore single-osculum morphology, the application of the Tanaka growth curve to establish its age would result in an underestimation.

Can the growth model derived herein be used to estimate the age of specimens of *X. muta* at other locations in the tropical and subtropical Western Atlantic? A definitive answer awaits additional research, but our data indicate little reason to believe otherwise. Physical and biological parameters are remarkably similar on coral reefs throughout the greater Caribbean (e.g., Goreau et al. 1993), which may partially explain the consistency of the flora and fauna over such a large biogeographic region. I detected no differences in growth of *X. muta* as a function of depth, despite differences in temperature and picoplankton availability along this cline (Lesser 2006; Trussell et al. 2006). Seasonal cycles of temperature are common to Caribbean reefs at all latitudes, with an offset of temperature between northern and southern reefs of only a few degrees (Goreau et al. 1993). Further, there is no reason to believe that growth rates of *X. muta*

have changed over decadal to millennial scales; our recent transect data show population increases in *X. muta* over the past decade (McMurray and Pawlik, unpublished data), suggesting that sponges are generally healthy. Interestingly, it remains to be seen whether growth and age may reliably be predicted from our data for the closely related Indo-Pacific giant barrel sponge, *Xestospongia testudinaria*, which occur at similar sizes and densities on Australia's Great Barrier Reef (Fromont and Bergquist 1994).

#### Implications for conservation and management

The worldwide decline of coral reef ecosystems has prompted many local restoration efforts (Jaap 2000; Precht 2006). Funding devoted to restoration can be substantial; for example, one 1994 ship grounding on a coral reef resulted in a \$3.9 million remediation settlement (NOAA 1997). Efforts typically focus on reattachment of reef-building corals (e.g., Hudson et al. 2007), but based on our data, greater emphasis should be placed on large coral reef sponges. Future remediation settlements should take into consideration the importance of barrel sponges to habitat complexity, as well as their great age. In addition to damage from vessel groundings, *X. muta* may be affected by the cutting movements of chain, rope, or monofilament fishing line, particularly as these items are dragged during storm events (Schmahl 1999; Chiappone et al. 2002, 2005). After these events, detached large sponges are commonly found, still alive and intact, between reef spurs on sand or rubble where they slowly erode under the action of oscillating currents. I have recently developed new techniques for the reattachment of dislodged *X. muta* to the reef substratum (McMurray and Pawlik 2008).

Perhaps greater than the threat of physical damage affecting *X. muta* populations is the increasing evidence of disease affecting large coral reef sponges (Webster 2007). A recently

described syndrome “sponge orange band” (SOB), usually results in the death of *X. muta* on which it is observed (Cowart et al. 2006). In fact, the largest and oldest sponge (~ 130 years) in our permanent transects succumbed to this syndrome within 6 weeks in July 2005 (Cowart et al. 2006). The same syndrome was likely responsible for the death of the very large sponge described from Curaçao by Nagelkerken et al. (2000), estimated at ~ 2,300 years old. I have observed that the number of sponges affected by this syndrome is highly patchy within sponge populations, and its intensity changes greatly from year to year. It is not clear if this syndrome is a new phenomenon, but if sponges in the population have an equal probability of contracting it in any given year, the likelihood that any individual sponge will survive to a great age would diminish. If diseases of sponges similar to SOB are becoming more prevalent (Webster 2007), I would predict profound changes in the age structure of long-lived coral reef sponges such as *X. muta*.

## References

- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Proceedings of the 2nd international symposium on information theory. Akademiai Kiado, Budapest, pp. 267–281
- Ayling AL (1983) Growth and regeneration rates in thinly encrusting Demospongiae from temperate waters. Biol Bull 165:343–352
- Barthel D (1986) On the ecophysiology of the sponge *Halichondria panacea* in Kiel Bight. I. Substrate specificity, growth and reproduction. Mar Ecol Prog Ser 32:291–298
- Baskerville GL (1971) Use of logarithmic regression in the estimation of plant biomass. Can J For Res 2:49–5
- Bertalanffy L von (1938) A quantitative theory of organic growth (inquires on growth laws II). Human Biol 10:181–213
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Fisheries Investigations of the Ministry of Agriculture and Fisheries, Food in Great Britain (2. Sea Fish), 19. Fascimile reprint 1993, Fish and Fisheries Series, Number 11, Chapman and Hall, London
- Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37:257–272
- Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. Alfred Wegener Institute for Polar and Marine Research, Germany. <http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Hand-book/main.html>. Accessed 26 March 2007
- Buettner H (1996) Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch, 1787) and associated fishes in Colombia. Bull Mar Sci 58:248–260
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretical approach. Springer, New York
- Chanas B, Pawlik JR (1997) Variability in the chemical defense of the Caribbean reef sponge *Xestospongia muta*. In: Lessios HA, Macintyre IG (eds) Proceedings of the 8th international coral reef symposium, vol 2. Smithsonian Tropical Research Institute, Balboa, pp 1363–1368
- Chiappone M, Dienes H, Swanson DW, Miller SL (2005) Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. Biol Conserv 121:221–230

- Chiappone M, White A, Swanson DW, Miller SL (2002) Occurrence and biological impacts of fishing gear and other marine debris in the Florida Keys. *Mar Pollut Bull* 44:597–604
- Cowart JD, Henkel TP, McMurray SE, Pawlik JR (2006) Sponge orange band (SOB): a pathogenic-like condition of the giant barrel sponge *Xestospongia muta*. *Coral Reefs* 25:513
- Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol Monogr* 44:105–128
- Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. *Bull Mar Sci* 69:535–546
- Diaz MC, Ward BB (1997) Sponge-mediated nitrification in tropical benthic communities. *Mar Ecol Prog Ser* 156:97–107
- Duckworth AR, Battershill CN (2001) Population dynamics and chemical ecology of New Zealand Demospongiae *Latrunculia* sp. nov. and *Polymastia croceus* (Poecilosclerida: Latrunculiidae: Polymastiidae). *N Z J Mar Freshw Res* 35:935–949
- Duffy JE (1992) Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Mar Ecol Prog Ser* 90:127–138
- Ebert TA (1980) Estimating parameters in a flexible growth equation, the Richards function. *Can J Fish Aquatic Sci* 37:687–692
- Ebert TA (1999) Plant and animal populations: methods in demography. Academic Press, San Diego
- Ebert TA, Dixon JD, Schroeter SC, Kalvass PE, Richmond NT, Bradbury WA, Woodby DA (1999) Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. *Mar Ecol Prog Ser* 190:189–209
- Elvin DW (1976) Seasonal growth and reproduction of an intertidal sponge *Haliclona permollis* (Bowerbank). *Biol Bull* 151:108–125
- Engel S, Pawlik JR (2005) Interactions among Florida sponges: I. Reef habitats. *Mar Ecol Prog Ser* 303:133–144
- Fell PE, Lewandrowski KB (1981) Population dynamics of the estuarine sponge, *Halichondria* sp., within a New England eelgrass community. *J Exp Mar Biol Ecol* 55:49–63
- Fromont J, Bergquist PR (1994) Reproductive biology of three sponge species of the genus *Xestospongia* (Porifera: Demospongiae: Petrosida) from the Great Barrier Reef. *Coral reefs* 13:119–126

- Frost TM, Williamson CE (1980) *In situ* determination of the effect of symbiotic algae on the growth of the fresh water sponge *Spongilla lacustris*. Ecology 61:1361–1370
- Gammill ER (1997) Identification of coral reef sponges. Providence Marine Publishing, Inc, Tampa
- Garrabou J, Zabala M (2001) Growth dynamics in four Mediterranean demosponges. Estuar Coastal Shelf Sci 52:293–303
- Gompertz B (1825) On the nature of the function expressive of human mortality, and on a new mode of determining the value of life contingencies. Philos Trans R Soc Lond, Series B 115:513–585
- Goreau T J, Hayes RL, Clark JW, Basla DJ, Robertson CN (1993) Elevated sea surface temperatures correlate with Caribbean coral reef bleaching. In: Geyer RA (ed) A global warming forum: scientific, economic and legal overview. CRC Press, Boca Raton, pp 225–255
- Henkel TP, Pawlik JR (2005) Habitat use by sponge-dwelling brittlestars. Mar Biol 146:301–313
- Henry L-A, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals—a review. Int Rev Hydrobiol 90:125–158
- Hill MS (1996) Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge *Anthosigmella varians* forma *variens*. Mar Biol 125:649–654
- Hoppe WF (1988) Growth, regeneration and predation in three species of large coral reef sponges. Mar Ecol Prog Ser 50:117–125
- HRIA (2006) Coast Redwood. Humboldt Redwoods Interpretive Association. <http://www.humboldtredwoods.org/>. Accessed 20 December 2007
- Hudson JH, Anderson J, Franklin EC, Schittone J, Stratton A (2007) M/V Wellwood coral reef restoration monitoring report, monitoring events 2004–2006. Florida Keys National Marine Sanctuary Monroe County, Florida. Marine Sanctuaries Conservation Series NMSP-07-02. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, 50 pp
- Humann P (1992) Reef creature identification. New World Pub., Jacksonville
- Jaap WC (2000) Coral reef restoration. Ecol Eng 15:345–364
- Johnson MF (1979) Recruitment, growth, mortality and seasonal variations in the calcareous sponge *Clathrina coriacea* (Montagu) and *C. blanca* (Miklucho-Maclay) from Santa Catalina Island, California. In: Lévi C, Boury-Esnault N (eds) Biologie des Spongiaires. Colloques Internationaux du CNRS 291, Paris, pp. 325–334

- Leichter JJ, Miller SL (1999) Predicting high frequency upwelling: spatial and temporal patterns of temperature anomalies on a Florida coral reef. *Cont Shelf Res* 19:911–928
- Lesser MP (2006) Benthic-pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. *J Exp Mar Biol Ecol* 328:277–288
- Leys SP, Lauzon NRJ. (1998) Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. *J Exp Mar Biol Ecol* 230:111–129
- Lindquist N, Hay ME (1996) Palatability and chemical defense of marine invertebrate larvae. *Ecol Monogr* 66:431–450
- López-Legentil S, Song B, McMurray SE, Pawlik JR (2008) Bleaching and stress in coral reef ecosystems: *hsp70* expression by the giant barrel sponge *Xestospongia muta*. *Mol Ecol* 17:1840–1849
- McArdle BH (1988) The structural relationship: regression in biology. *Can J Zool* 66:2329–2339
- McMurray SE, Pawlik JR (2008) A novel technique for the reattachment of large coral reef sponges. *Restoration Ecol* (in press)
- Nagelkerken I, Aerts L, Pors L (2000) Barrel sponge bows out. *Reef Encounter* 28:14–15
- NOAA (1997) NOAA gears up for reef restoration at Looe Key: university agrees to \$3.9 million settlement for damage in Florida Keys Sanctuary. Press Release. <http://www.publicaffairs.noaa.gov/pr97/nov97/noaa97-r423.html>
- Pauly D (1981) The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforsch* 28:251–282
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Pile AJ, Patterson MR, Savarese M, Chernykh VI, Fialkov VA (1997) Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux. *Limnol Oceanogr* 42:178–184
- Precht WF (2006) *Coral reef restoration handbook*. CRC Press, Boca Raton
- Reiswig HM (1971) *In situ* pumping activities of tropical Demospongiae. *Mar Biol* 9:38–50
- Reiswig HM (1973) Population dynamics of three Jamaican Demospongiae. *Bull Mar Sci* 23:191–226

- Reiswig HM (1975) The aquiferous systems of three marine Demospongiae. *J Morphol* 145:493–502
- Richards FJ (1959) A flexible growth function for empirical use. *J Exp Bot* 10:290–300
- Ricker WE (1973) Linear regressions in fishery research. *J Fish Res Board Canada* 30:409–434
- Ritson-Williams R, Becerro MA, Paul VJ (2005) Spawning of the giant barrel sponge *Xestospongia muta* in Belize. *Coral Reefs* 24:160
- Rogers-Bennett L, Rogers DW, Bennett WA, Ebert TA (2003) Modeling red sea urchin (*Strongylocentrotus franciscanus*) growth using six growth functions. *Fish Bull* (Wash DC) 101:614–626
- Rützler K (1985) Associations between Caribbean sponges and photosynthetic organisms. In: Rützler K (ed) *New perspectives in sponge biology*. Smithsonian Institution Press, Washington DC, pp 455–466
- Schmahl GP (1999) Recovery and growth of the giant barrel sponge (*Xestospongia muta*) following physical injury from a vessel grounding in the Florida Keys. *Mem Queensl Mus* 44:532
- Schmidt-Nielson K (1974) Scaling in biology: the consequences of size. *J Exp Zool* 194:287–307
- Schone BR, Fiebig J, Pfeiffer M, Gleb R, Hickson J, Johnson A, Dreyer W, Oschmann W (2005) Climate records from a bivalved Methuselah (*Arctica islandica*, Mollusca; Iceland). *Palaeogeogr Palaeoclimatol Palaeoecol* 228:130–14
- Sebens KP (1987) The ecology of indeterminate growth in animals. *Ann Rev Ecol Syst* 18:371–407
- Simpson TL (1984) *The cell biology of sponges*. Springer, New York
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*. 3rd edn. W. H. Freeman and Co, New York
- Sprugel D (1983) Correcting for bias in log-transformed allometric equations. *Ecology* 64:209–210
- Suchanek TH, Carpenter RC, Witman JD, Harvell CD (1985) Sponges as important space competitors in deep Caribbean coral reef communities. In: Reaka ML (ed) *The ecology of deep and shallow coral reefs, symposia series for undersea research* 3(1), NOAA/NURP: Rockville, pp 55–59

- Tanaka K (2002) Growth dynamics and mortality of the intertidal encrusting sponge *Halichondria okadai* (Demospongiae, Halichondrida). *Mar Biol* 140: 383–389
- Tanaka, M (1982) A new growth curve which expresses infinitive increase. *Pub Amakusa Mar Biol Lab, Kyushu Univ* 6:167–177
- Tanaka M. (1988) Eco-physiological meaning of parameters of ALOG growth curve. *Pub Amakusa Mar Biol Lab, Kyushu Univ* 9:103–106
- Targett NM, Schmahl GP (1984) Chemical ecology and distribution of sponges in the Salt River Canyon, St. Croix, U.S.V.I. NOAA Tech Mem OAR NURP-1
- Thacker R (2005) Impacts of shading on sponge-cyanobacteria symbioses: a comparison between host-specific and generalist associations. *Integ Comp Biol* 45:369–376
- Trussell GC (1997) Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* 8:1033–1048
- Trussell GC, Lesser MP, Patterson MR, Genovese SJ (2006) Depth-specific differences in growth of the reef sponge *Callyspongia vaginalis*: role of bottom-up effects. *Mar Ecol Prog Ser* 323:149–158
- Turon X, Tarjuelo I, Uriz MJ (1998) Growth dynamics and mortality of the encrusting sponge *Crambe crambe* (Poecilosclerida) in contrasting habitats: correlation with population structure and investment in defence. *Funct Ecol* 12:631–639
- Walford LA (1946) A new graphic method of describing the growth of animals. *Biol Bull* 90:141–147
- Walters KD, Pawlik JR (2005) Is there a trade off between wound-healing and chemical defenses among Caribbean reef sponges? *Integ Comp Biol* 45:352–358
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Webster NS (2007) Sponge disease: a global threat? *Environ Microbiol* 9:1363–1375
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Ann Rev Ecol Syst* 15:393–425
- Wilkinson CR, Cheshire AC (1988) Growth rate of Jamaican coral reef sponges after Hurricane Allen. *Biol Bull* 175:175–179
- Winsor CP (1932) The Gompertz curve as a new growth curve. *Proc Nat Acad Sci USA* 18:1–8

Wulff JL (1985) Patterns and processes of size change in Caribbean Demosponges of branching morphology. In: Rützler K (ed) *New perspectives in sponge biology*. Smithsonian Institution Press, Washington, DC, pp 425–435

Zea S (1993) Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. *Carib J Sci* 29:75–8

Table 1. Reduced-major axis regression equations for scaling analysis of linear measurements of *Xestospongia muta*

Regression	$r^2$	$df$	$T$
log base diameter ( $Y$ ) vs. log height ( $X$ ) log $Y = 0.82 \log X + 0.27$	0.79 <sup>***</sup>	75	1.95 <sup>NS</sup>
log osculum diameter ( $Y$ ) vs. log height ( $X$ ) log $Y = 1.21 \log X - 0.52$	0.74 <sup>***</sup>	76	1.62 <sup>NS</sup>
log base diameter ( $Y$ ) vs. log osculum diameter ( $X$ ) log $Y = 0.68 \log X + 0.61$	0.85 <sup>***</sup>	73	4.40 <sup>***</sup>
log height <sub><math>t+D_t</math></sub> ( $Y$ ) vs. log height <sub><math>t</math></sub> ( $X$ ) log $Y = 0.80 \log X + 0.42$	0.88 <sup>***</sup>	72	2.94 <sup>**</sup>
log base diameter <sub><math>t+D_t</math></sub> ( $Y$ ) vs. log base diameter <sub><math>t</math></sub> ( $X$ ) log $Y = 0.74 \log X + 0.47$	0.88 <sup>***</sup>	72	3.73 <sup>***</sup>
log osculum diameter <sub><math>t+D_t</math></sub> ( $Y$ ) vs. log osculum diameter <sub><math>t</math></sub> ( $X$ ) log $Y = 0.72 \log X + 0.47$	0.89 <sup>***</sup>	72	4.35 <sup>***</sup>

The  $T$  statistic was used to test actual slope against an isomeric slope of  $\beta = 1$  for each regression  
<sup>\*\*\*</sup>  $P < 0.001$ , <sup>\*\*</sup>  $P < 0.01$ , NS = not significant

Table 2. Parameter estimates for growth functions fitted to cubed root of final and initial volumes;  $n = 104$

gVBGF	Richards	Tanaka	sVBGF	Gompertz
$S_{\infty} = 66.1211$	$S_{\infty} = 66.1213$	$a = 0.5548$	$S_{\infty} = 138.3$	$S_{\infty} = 52.4541$
$k = 0.0388$	$k = 0.0388$	$f = 0.00254$	$k = 0.0102$	$k = 0.0711$
$d = 1.8972$	$d = -1.8972$	$d = 68.9563$		

Function parameters were estimated by nonlinear regression (NLIN procedure SAS)

Table 3. Growth function fitting criteria

Model	$K$	$r^2$	SSE	$AIC_c$	$\Delta_i$	$w_i$
gVBGF	3	0.935	689.3	202.7	0	0.2213
Richards	3	0.935	689.3	202.7	0	0.2213
Tanaka	3	0.935	690.2	202.8	0.1357	0.2068
sVBGF	2	0.933	705.2	203.1	0.2505	0.1952
Gompertz	2	0.933	708.3	203.5	0.7067	0.1554

$K$  number of parameters,  $r^2$  coefficient of determination,  $SSE$  sum of squared error,  $AIC_c$  second order correction for the Akaike Information Criterion,  $\Delta_i$  Akaike differences,  $w_i$  Akaike weights

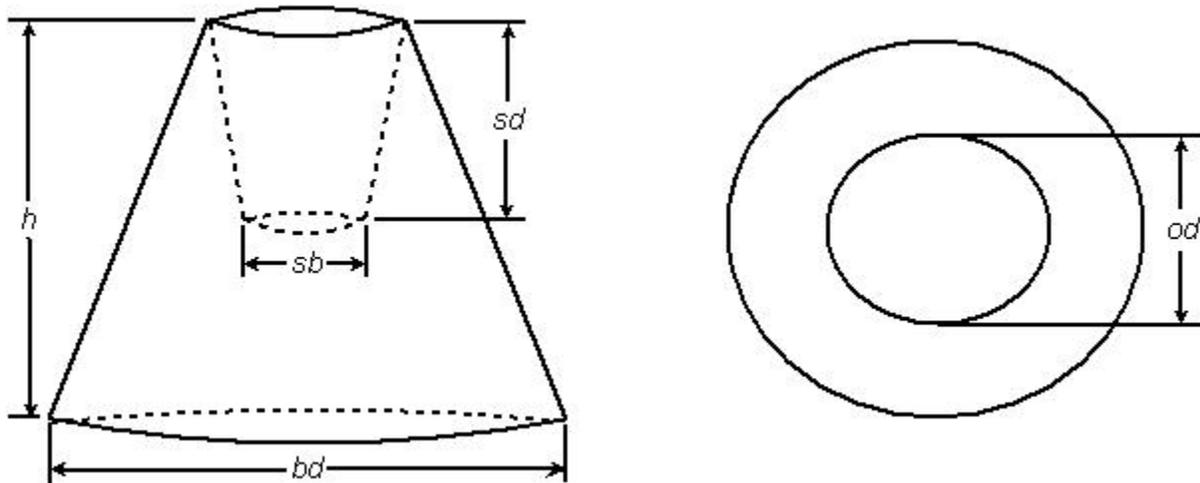


Fig. 1. Frustum of a cone geometric approximation of *X. muta*, side and top view. Measurements used for digital image analysis were:  $h$  sponge height;  $bd$  base diameter,  $od$  osculum diameter. Additional measurements taken in the field were:  $sd$  spongocoel depth;  $sb$  spongocoel base diameter.

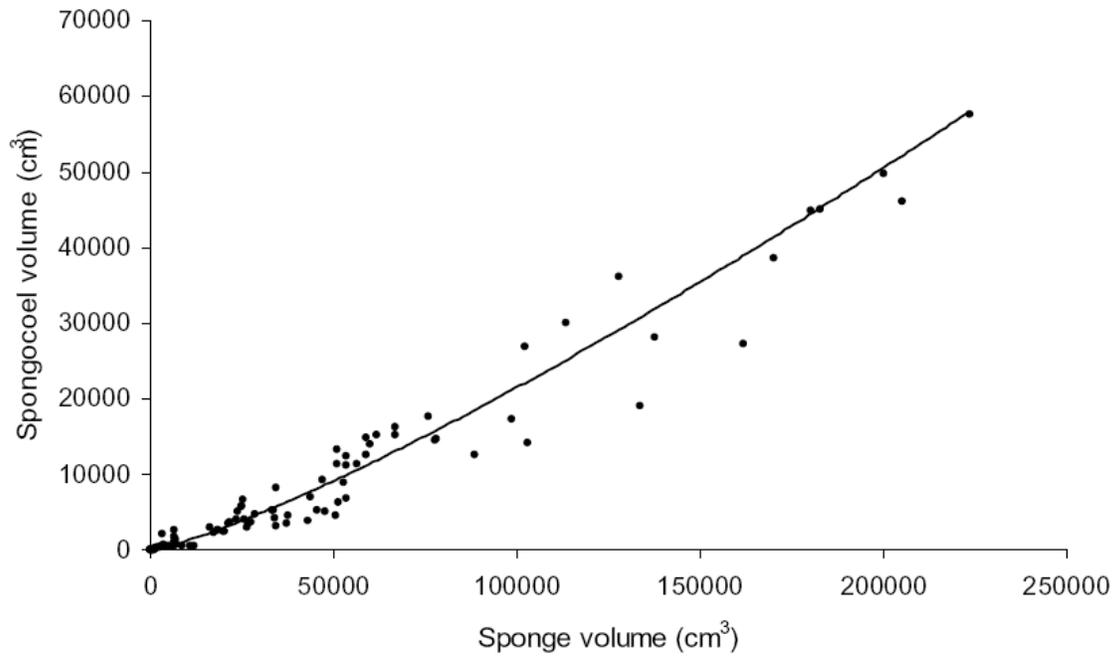


Fig. 2. Relationship between spongocoel volume and sponge volume for sponges measured in the field. Fitted line is the allometric equation (Eq. 16).

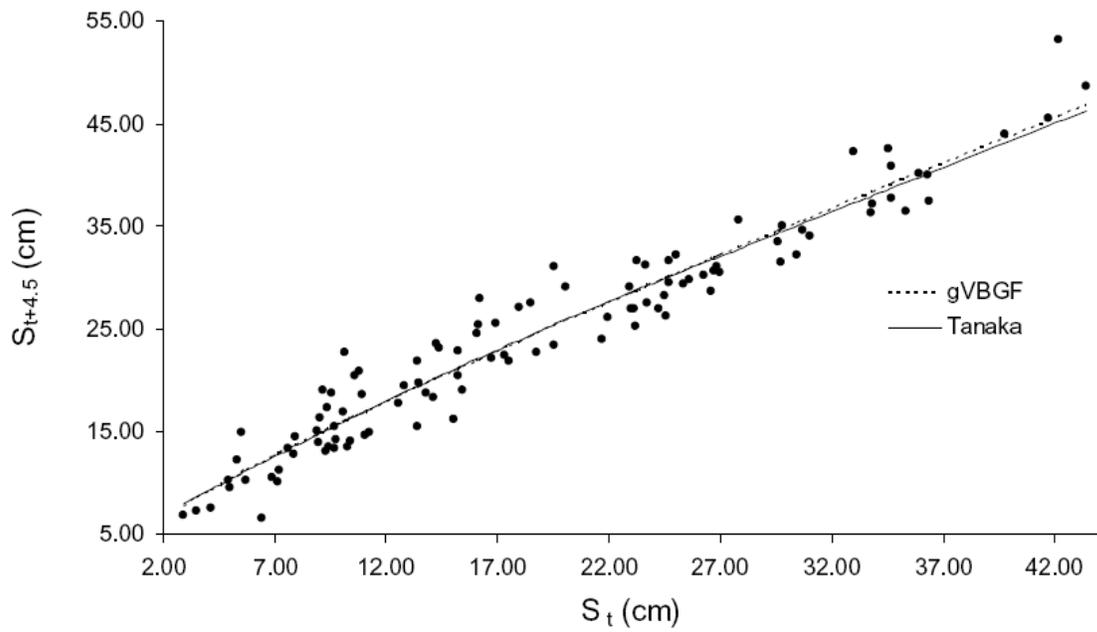


Fig. 3. Walford plot of initial size ( $S_t$ ) and size 4.5 years later ( $S_{t+4.5}$ ). Plotted sizes are the cube root of volume estimates. Fitted lines are the gVBGF and Tanaka function with parameters from Table 2.

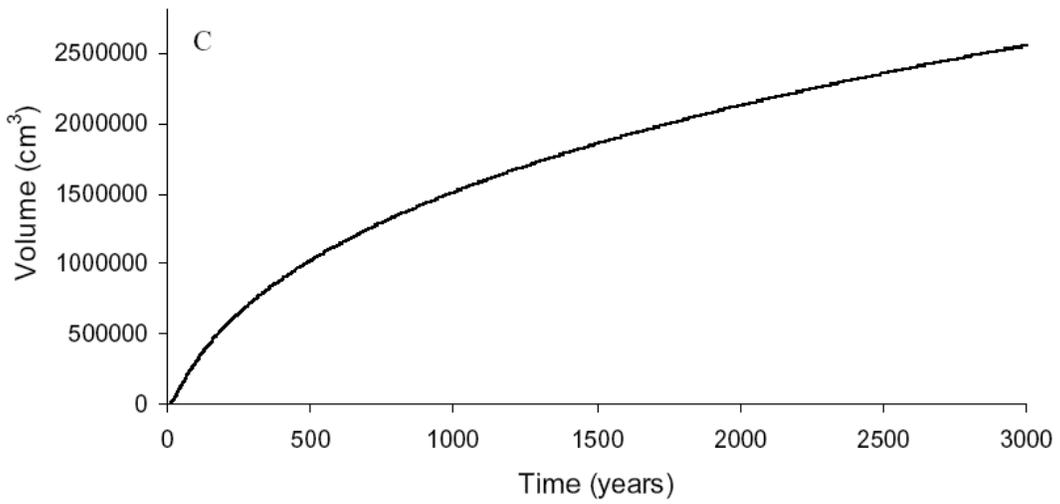
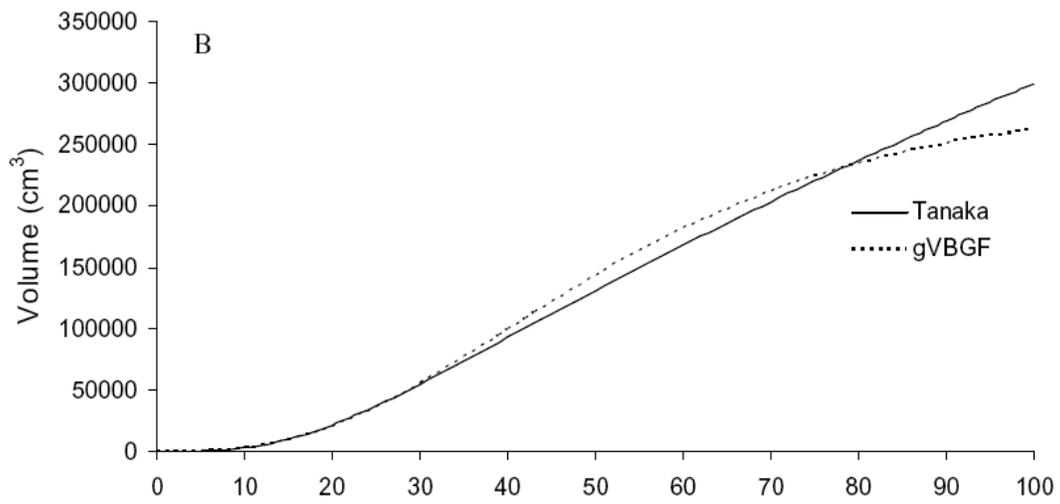
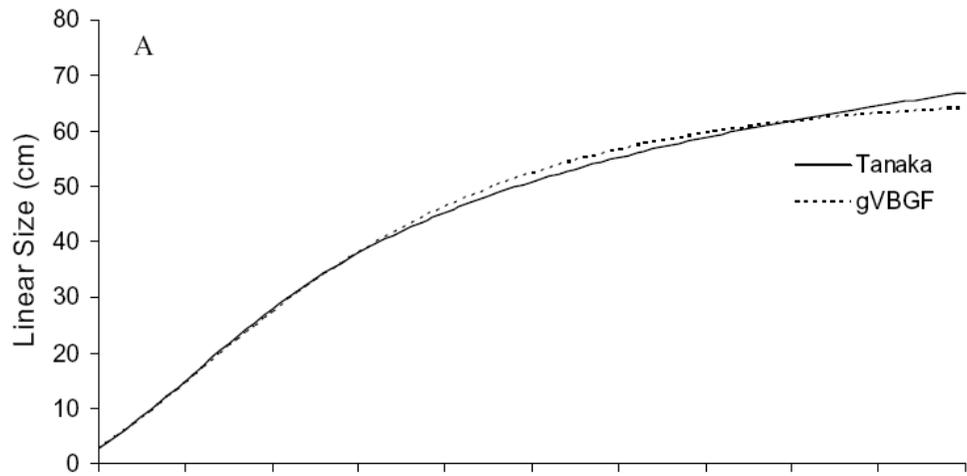


Fig. 4. gVBGF and Tanaka growth curves from parameter estimates in Table 2. **a** linear size as a function of time; **b** linear sizes from **(a)** cubed for volume as a function of time; **c** same curve as **(b)** with time expanded out to 3,000 years.

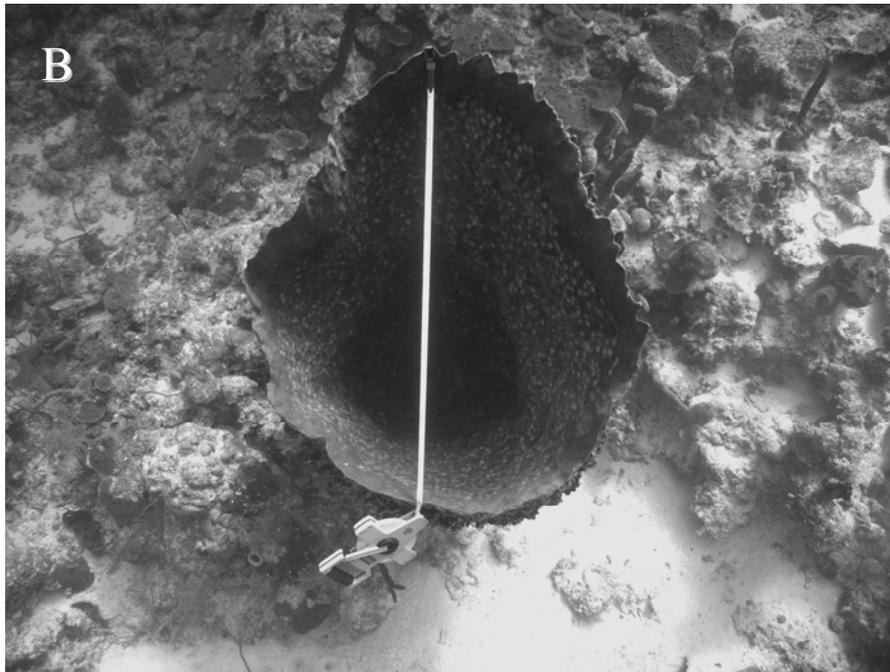


Fig. 5. Specimen of *Xestospongia muta* measured at 30 m depth off Plana Cay, Bahamas **a** side view **b** top view. Distance under tape is 1 m.

## CHAPTER 3. BLEACHING OF THE GIANT BARREL SPONGE *XESTOSPONGIA MUTA* IN THE FLORIDA KEYS

### Abstract

Coral bleaching has been the subject of considerable research for more than 2 decades. More recently, sponge bleaching has been documented during coral bleaching events. The Caribbean giant barrel sponge *Xestospongia muta* is particularly affected, but the cause and impact of sponge bleaching was unknown. This study investigated the relationship between temperature and bleaching of *X. muta* on Conch Reef, Florida. Bleaching and temperature data were collected from 2000 to 2005 at three depths (15, 20, 30 m). Bleaching increased significantly with depth and was greater in fall compared to spring. Bleaching significantly increased with positive 0.5°C anomalies at 30 m in the spring and fall, and with negative 0.5°C anomalies in the spring, but there were not similar effects at the other two depths. Unlike bleaching in corals, bleaching of *X. muta* appears to be a response by cyanobacteria symbionts that have little effect on their host sponge.

### Introduction

Associations between benthic invertebrates and photosynthetic symbionts are a common feature of coral reef communities. The coral-zooxanthellae symbiosis has attracted significant attention since reports of large-scale coral bleaching events first appeared in the 1980's (Glynn 1991). Bleaching is a process in which the host loses coloration because of symbiont loss or photobleaching of algal pigments (Glynn and D'Croz 1990). Bleaching is not limited to reef-building corals, however, and can potentially affect all photosymbiotic reef species (Glynn 1996). In addition to corals, commonly affected hosts include hydrozoans, sea anemones, zoanthids, and sponges. Because of its widespread occurrence across several taxa of reef

organisms, it has been suggested that the phenomenon be termed ‘coral reef bleaching’ (Williams and Bunkley-Williams 1990). While it has been intensively studied for reef-building corals, bleaching is poorly understood for other ecologically important reef species.

Sponges are important constituents of coral reefs (Diaz and Rützler 2001), where their abundance and diversity in these communities often rivals that of dominant reef-building corals (Suchanek et al. 1985). Similar to reef building corals, many sponges form complex associations with photoautotrophic endosymbionts, including zooxanthellae (Sarà and Liaci 1964) and cyanobacteria (Erwin and Thacker 2007; 2008). While the majority of sponges harboring photosymbionts appear to be unaffected during coral reef bleaching events, the sponge *Xestospongia muta* has commonly been reported to bleach (Williams and Bunkley-Williams 1988; Vincente 1990; Dennis and Wicklund 1993).

In the Caribbean, the giant barrel sponge *Xestospongia muta* is a common member of the benthic community at depths greater than 10 m. Individuals can reach > 1 m in height and diameter and live to hundreds or thousands of years old (McMurray et al. 2008). Populations constitute a significant amount of overall reef biomass (McMurray et al. unpublished data), are an important component of habitat heterogeneity (Buettner 1996), and filter large amounts of seawater (Southwell et al. 2008). Peripheral tissues harbor cyanobacteria of the genus *Synechococcus* that are responsible for the reddish-brown coloration of unbleached individuals (Gomez et al. 2002; Erwin and Thacker 2007). During bleaching, sponges undergo a lightening of this characteristic coloration (Vincente 1990) to the point that they may appear creamy-white. *Xestospongia muta* has been observed to undergo cycles of bleaching and recovery of pigmentation (Coward et al. 2006). Bleaching can be moderate, affecting only localized areas of the sponge, or it can be severe.

Several stressors can cause reef-building corals to bleach, however anomalously high water temperatures are the primary causative agent of widespread bleaching events (Jokiel and Coles 1990; Glynn 1996; Hoegh-Guldberg 1999). The occurrence of bleaching of *X. muta* during large coral bleaching events (Williams and Bunkley-Williams 1988; Vincente 1990; Dennis and Wicklund 1993) suggests that the causes of bleaching in both cases may be similar. The purpose of this study was to determine whether a correlation exists between water temperature and bleaching of *X. muta*.

## Materials and methods

Surveys of bleaching of *Xestospongia muta* were conducted from May 2000 to December 2005 on Conch Reef (24°56.9''N, 80°27.2''W), Florida. Three permanent 16 m-diameter circular transects were established at 15, 20 and 30 m depths. Within each transect, each sponge was mapped and given a unique tag on a masonry nail driven next to the base of the sponge. Surveys were conducted in the spring and fall of every year, but because of inclement weather, surveys were not conducted in the fall of 2000 and the spring of 2004 at the 20 and 30 m sites. Sponge pigmentation was scored as either normal, exhibiting spotted bleaching, lightly bleached, or severely bleached. For purposes of analysis, sponge pigmentation was categorized as bleached (spotted, lightly, or severely bleached) and not bleached (normal pigmentation).

Temperature data on Conch Reef were collected at 10, 20, and 30 m depths from January 1997 to December 2005 (Leichter et al. 2003). Ryan Tempmentors and Onset Computers Stowaway loggers were fixed 1 m above the substratum and recorded at 20 min intervals. Additional Onset Computers HOBO Water Temp Pro loggers were deployed at 10, 15, 20, and 30 m depths from March to December 2005. For each day from 1997 to 2005, the mean at each

depth was calculated. Using data collected during 2005, a ridge estimator was used to interpolate the temperature series at 15 m. The equation used to interpolate 15 m daily mean temperatures was:  $T_{15m} = -0.074897 + 0.597144T_{10m} + 0.401723T_{20m}$ , where  $T_{15m}$ ,  $T_{20m}$ , and  $T_{30m}$  are the mean daily temperatures at 15, 20, and 30 m depths, respectively. For each site, a daily temperature climatology was produced from measurements for each day over 1997 to 2005. Daily positive and negative temperature anomalies were calculated as the difference between the daily mean temperature and the daily climatology.

Several temperature metrics, analogous to those used in studies of coral bleaching (e.g. Podestá and Glynn 2001), were developed that considered acute thermal stress, cumulative thermal stress, and thermal shock. Binomial regression was used to model the relationship between temperature and sponge bleaching. Generalized estimating equations were used to estimate parameters of each model (Hardin and Hilbe 2003). The deviance statistic was used to assess model fit. Analyses were conducted with SAS (vers. 9.1.3 for Windows, SAS Institute Inc., Cary, NC, USA) statistical software.

## Results and discussion

Coral bleaching typically occurs during the summer or fall when temperatures are the highest or near the end of a prolonged warming period (Williams and Bunkley-Williams 1990; Glynn 1991). In contrast, bleaching of *X. muta* was observed in both the spring and fall of every year surveyed (Figure 1). Bleaching was, however, significantly greater in the fall compared to the spring for all depths (15 m:  $\chi^2 = 18.32$ ,  $df = 1$ ,  $P < 0.0001$ ; 20 m:  $\chi^2 = 10.76$ ,  $df = 1$ ,  $P = 0.001$ ; 30 m:  $\chi^2 = 72.05$ ,  $df = 1$ ,  $P < 0.0001$ ). These findings are similar to those of Fitt et al. (2000), who found that corals from all depths experienced seasonal cycles of bleaching, although

not always visually obvious, with lowest algal densities experienced in the late summer or fall and highest densities during the coldest part of the year.

Bleaching significantly increased with depth on Conch Reef, but this relationship varied with season (Figure 1). In the fall, significantly less bleaching occurred at 15 m compared to 20 m ( $\chi^2 = 5.44$ ,  $df = 1$ ,  $P = 0.0197$ ) and 30 m ( $\chi^2 = 40.61$ ,  $df = 1$ ,  $P < 0.0001$ ), and less at 20 m compared to 30 m ( $\chi^2 = 24.77$ ,  $df = 1$ ,  $P < 0.0001$ ). In the spring, bleaching remained significantly less at 15 m compared to 20 m ( $\chi^2 = 16.5$ ,  $df = 1$ ,  $P < 0.0001$ ) and 30 m ( $\chi^2 = 10.23$ ,  $df = 1$ ,  $P = 0.0014$ ), but bleaching did not differ between 20 and 30 m depths. Incidence of bleaching is usually greatest for reef-building corals at shallow depths, but bleaching also affects deep-water corals (Glynn 1996). In some areas, deep-water corals were affected before and to a greater extent than shallow water species (Warner et al. 1999). Fitt et al. (2000) have suggested that deep-water corals appear lighter in color before shallower corals because they normally harbor fewer zooxanthellae. Decreased light intensity has been shown to reduce cyanobacterial abundance in *X. muta* and may explain why bleaching is greater at depth (see below; Gómez et al. 2002; López-Legentil et al. 2008).

The percentage of days in which there was a 0.5°C anomaly within two weeks prior to bleaching surveys was found to best explain the relationship between temperature and bleaching. The ratio of deviance to degrees of freedom was 1.2571, indicating a good fit of the model. The incidence of bleaching was found to significantly increase with the number of days in which there was a positive 0.5°C anomaly in both the spring ( $P < 0.0001$ ) and fall ( $P = 0.024$ ) at 30 m ( $P < 0.0001$ ), but not at 15 or 20 m (Figure 2). The incidence of bleaching was found to significantly increase with the number of days in which there was a negative 0.5°C anomaly in the spring ( $P < 0.0001$ ) at 30 m ( $P < 0.0001$ ), but not in the fall or at 15 and 20 m (Figure 3).

In a study by López-Legentil et al. (2008), bleaching of *X. muta* did not coincide with an increase in the expression of the heat-shock protein *hsp70*, which is an indication of tissue stress. This corroborates findings for a congeneric species of sponge that contains *Synechococcus* symbionts (Thacker 2005), and for which it was concluded that the commensal blue-green bacteria provided no clear benefits to the host sponge. Bleaching is therefore likely to be a response by the cyanobacteria rather than by the host sponge.

Corals host a diverse group of dinoflagellates belonging to the genus *Symbiodinium* (Rowan and Powers 1991) which vary in their response to bleaching (Rowan et al. 1997). Similarly, *Synechococcus* harbored by sponges have been found to be a diverse group with a range of host specificities (Erwin and Thacker 2008). Both a generalist and a host-specific clade of *Synechococcus* have been found in *X. muta* (Erwin and Thacker 2008). It remains to be seen if, as for *Symbiodinium*, these groups of cyanobacteria differ physiologically or can acclimatize to environmental stress (Rowan et al. 1997; Brown et al. 2002); however these hypotheses may explain the seasonal and bathymetric patterns of bleaching observed for *X. muta* on Conch Reef. In addition, differences in susceptibilities to bleaching among *Synechococcus* clades may partially explain different bleaching responses between adjacent sponges and sponges that undergo spotted bleaching.

Laboratory investigations have confirmed that temperature changes are the causative agent of bleaching for reef-building corals (e.g. Glynn and D’Croze 1990). While the findings of the present study support a correlation between anomalous water temperature and bleaching of *X. muta* at one depth, further experimental work is needed to determine if this correlation reflects a casual relationship. In laboratory experiments, fifteen hour exposure of *X. muta* to water temperatures ranging from 10–40°C did not cause bleaching (López-Legentil et al. 2008), but

longer exposures may be required to elicit a response. Available evidence indicates that cyanobacterial abundance in the tissues of *X. muta* is dependent on light intensity. Both shading experiments and transplantation of *X. muta* to deeper depths resulted in decreases in cyanobacterial abundance (Gómez et al. 2002; López-Legentil et al. 2008). Moreover, completely white, aposymbiotic *X. muta* have been observed under overhangs and in caves (Steindler et al. 2005). Decreased light availability could explain the greater incidence of bleaching with depth, but fails to fully explain why adjacent individuals can be affected dissimilarly, and this may be explained by cladal differences.

In conclusion, bleaching of *X. muta* was found to correlate with positive temperature anomalies in the spring and fall and negative temperature anomalies in the spring at 30 m, but not at 15 or 20 m depths. Bleaching also appears to be a cyclic response by the cyanobacteria symbionts of *X. muta* that has no negative effect on the host sponge (Gómez et al. 2002; López-Legentil et al. 2008). In contrast to *X. muta*, some sponge species appear to gain benefits from cyanobacteria symbionts (Thacker 2005) and bleaching may be predicted to have deleterious effects on these host sponges (e.g. Fromont and Garson 1999).

## References

- Brown BE, Dunne RP, Goodson MS, Douglas AE (2002) Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs* 21:119–126
- Buettner H (1996) Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch, 1787) and associated fishes in Colombia. *Bull Mar Sci* 58:248–260
- Cowart JD, Henkel TP, McMurray SE, Pawlik JR (2006) Sponge orange band (SOB): a pathogenic-like condition of the giant barrel sponge *Xestospongia muta*. *Coral Reefs* 25:513
- Dennis GD, Wicklund RI (1993) The relationship between environmental factors and coral bleaching at Lee Stocking Island, Bahamas in 1990. In: case histories for the colloquium and forum on global aspects of coral reefs: health, hazards and history, pp F15–F21
- Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. *Bull Mar Sci* 69:535–546
- Erwin PM, Thacker RW (2007) Incidence and identity of photosynthetic symbionts in Caribbean coral reef sponge assemblages. *J Mar Biol Assoc UK* 87:1683–1692
- Erwin PM, Thacker RW (2008) Cryptic diversity of the symbiotic cyanobacterium *Synechococcus spongiarum* among sponge hosts. *Mol Ecol* 17:2937–2947
- Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol Oceanogr* 45:677–685
- Fromont J, Garson M (1999) Sponge bleaching on the West and East coasts of Australia. *Coral Reefs* 18:340
- Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol Evol* 6:175–179
- Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. *Glob Change Biol* 2:495–509
- Glynn PW, D'Croz L (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8:181–191
- Gomez R, Erpenbeck D, Van Dijk T, Richelle-Maurer E, Devijver C, Braekman JC, Woldringh C, Van Soest RWM (2002) Identity of cyanobacterial symbiont of *Xestospongia muta*. *Boll Mus Ist Biol Univ Genova* 66-67:82–83

- Hardin, JW, Hilbe JM (2003) Generalized estimating equations. Chapman & Hall/CRC, Boca Raton.
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshwater Res* 50:839–866
- Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–162
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48:1394–1407
- López-Legentil S, Song B, McMurray SE, Pawlik JR (2008) Bleaching and stress in coral reef ecosystems: hsp70 expression by the giant barrel sponge *Xestospongia muta*. *Mol Ecol* 17:1840–1849
- McMurray SE, Blum JE, Pawlik JR (2008) Redwood of the reef: growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Mar Biol* 155:159–171
- Podestá GP, Glynn PW (2001) The 1997-98 El Niño event in Panama and Galápagos: an update of thermal stress indices relative to coral bleaching. *Bull Mar Sci* 69:43–59
- Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388:265–269
- Rowan R, Powers DA (1991) A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbioses. *Science* 251:1348–1351
- Sarà M, Liaci L (1964) Symbiotic association between zooxanthellae and two marine sponges of the genus *Cliona*. *Nature* 203:321–322
- Southwell MW, Weisz JB, Martens CS, Lindquist N (2008) In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnol Oceanogr* 53:986–996
- Steindler L, Huchon D, Avni A, Ilan M (2005) 16S rRNA phylogeny of sponge-associated cyanobacteria. *Appl Environ Microb* 71:4127–4131
- Suchanek TH, Carpenter RC, Witman JD, Harvell CD (1985) Sponges as important space competitors in deep Caribbean coral reef communities. In: Reaka ML (ed) *The Ecology of Deep and Shallow Coral Reefs*, Symposia Series for Undersea Research 3(1), NOAA/NURP: Rockville, Maryland, p 55–59
- Thacker RW (2005) Impacts of shading on sponge-cyanobacteria symbiosis: a comparison between host-specific and generalist associations. *Integr Comp Biol* 45:369–376

- Vincente VP (1990) Response of sponges with autotrophic endosymbionts during the coral-bleaching episode in Puerto Rico. *Coral Reefs* 8:199–202
- Warner ME, Fitt WK, Schmidt GW (1999) Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. *Proc Natl Acad Sci USA* 96:8007–8012
- Williams EH, Bunkley-Williams L (1990) The world-wide coral bleaching cycle and related sources of coral mortality. *Atoll Res Bull* 335:1–71
- Williams Jr EH, Bunkley-Williams L (1988) Bleaching of coral reef animals in 1987-1988: an updated summary. In: Ogden J, Wicklund R (eds) *Mass bleaching of coral reefs in the Caribbean: a research strategy*. National Undersea Research Program, Research Report 88-2, 51pp

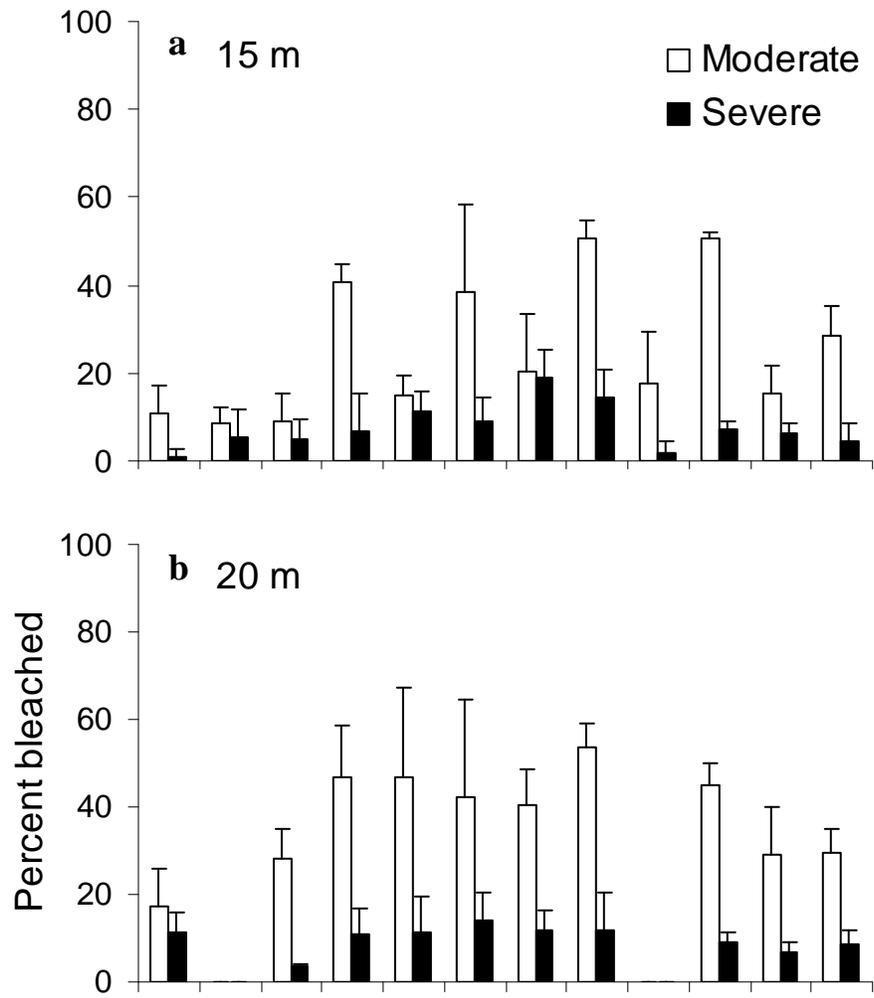


Figure 1 continued

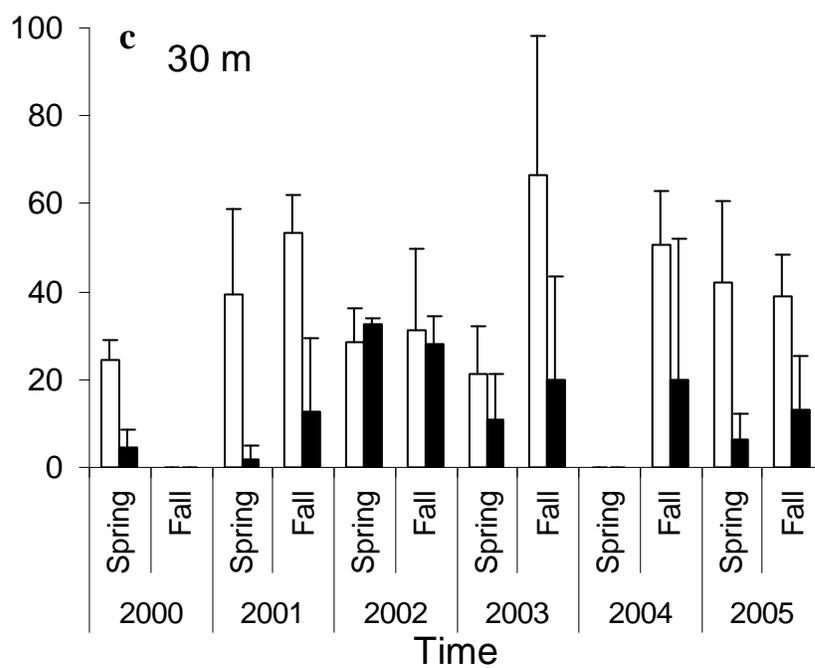


Figure 1. Mean ( $\pm$  SD) percent of *Xestospongia muta* exhibiting moderate (light and spotted) and severe bleaching from 2000 to 2005 at (a) 15, (b) 20, and (c) 30 m depths on Conch Reef

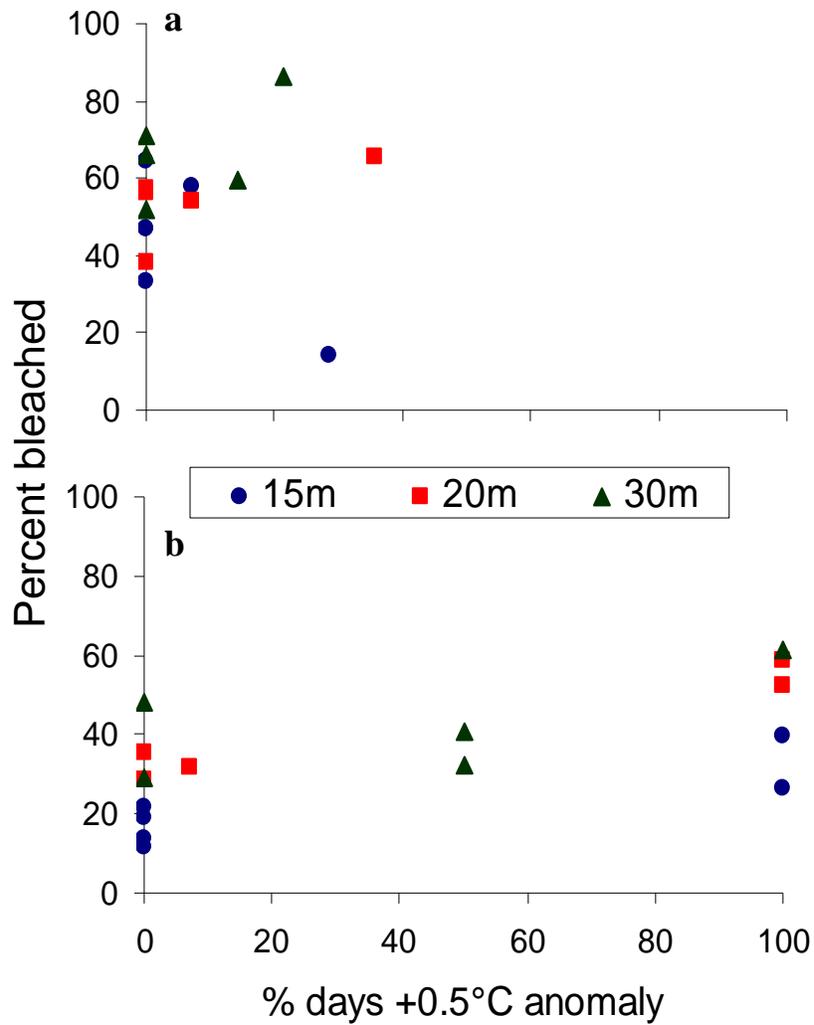


Figure 2. Scatterplots of the percent of bleached sponges versus the percentage of days in which there was a +0.5°C temperature anomaly within two weeks prior to bleaching surveys for 15, 20, and 30 m depths (a) in the fall (b) in the spring

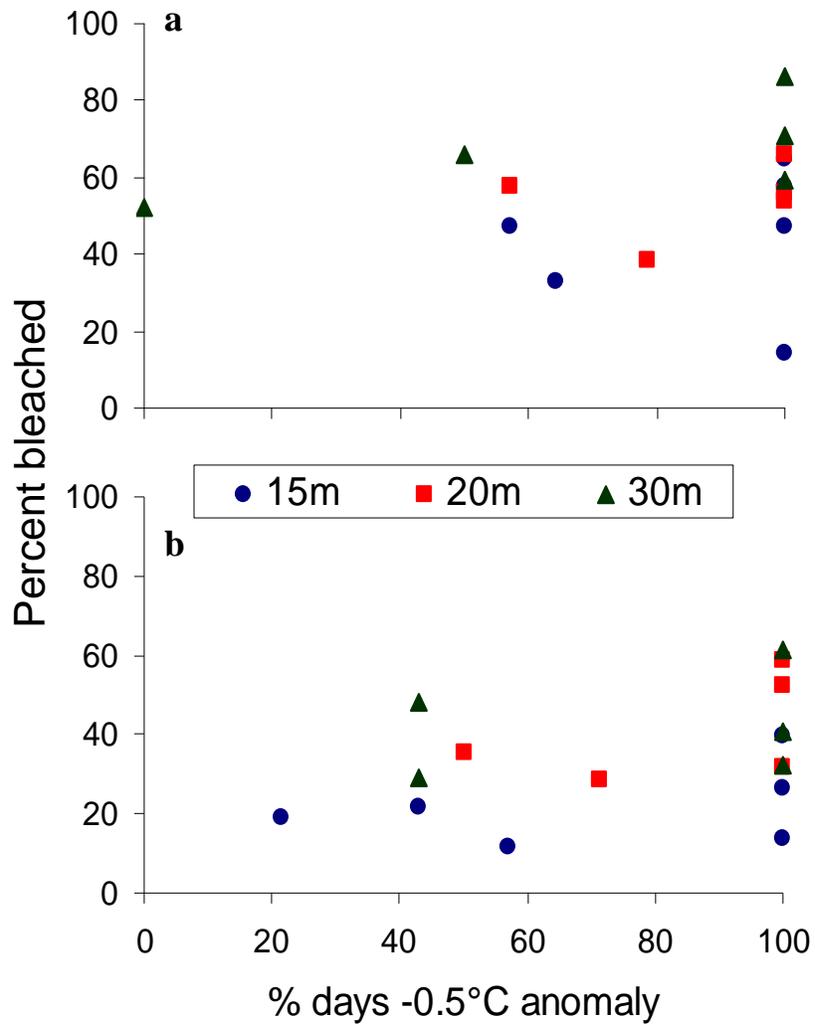


Figure 3. Scatterplots of the percent of bleached sponges versus the percentage of days in which there was a  $-0.5^{\circ}\text{C}$  temperature anomaly within two weeks prior to bleaching surveys for 15, 20, and 30 m depths (a) in the fall (b) in the spring

## CHAPTER 4. A NOVEL TECHNIQUE FOR THE REATTACHMENT OF LARGE CORAL REEF SPONGES

### Abstract

Sponges are dominant components of coral reef ecosystems, often exceeding reef-building corals in abundance. Large sponges, often more than 1 m in diameter, may be hundreds to thousands of years old. When damaged or dislodged, large sponges usually die because they are unable to reattach to the reef substratum. Because suitable methods for reattaching dislodged sponges are lacking, they are typically excluded from coral reef restoration efforts. Here I present a novel technique for the reattachment of large sponges that was tested using the Caribbean giant barrel sponge, *Xestospongia muta*. Transplants of *X. muta* were conducted at 15- and 30-m depth off Key Largo, Florida. Despite the active hurricane season of 2005, 90% of deep and 35% of shallow transplants survived, with nearly 80% reattaching to the substratum and growing after 2.3–3 years. This technique may be generally adapted for securing large sponges in coral reef restoration efforts.

### Introduction

The worldwide decline of coral reef ecosystems has prompted many local restoration efforts (Jaap 2000, Precht 2006). Funding devoted to restoration can be substantial; for example, one 1994 ship grounding on a coral reef resulted in a \$3.9 million remediation settlement (NOAA 1997). Efforts typically focus on reattachment of reef-building corals (e.g., Hudson et al. 2007). Despite their dominance on coral reefs (Diaz & Rutzler 2001), large sponges are

generally excluded from restoration efforts because of a lack of suitable methods for sponge reattachment.

Small, fast-growing reef sponges often employ fragmentation as a form of asexual reproduction, and quickly recover after disturbance events. In contrast, large sponges do not reattach to the substratum when dislodged. In particular, the giant barrel sponges *Xestospongia muta* in the Caribbean and *X. testudinaria* in the Indo-Pacific are species having large individuals that may exceed 100 years of age, and sometimes more than 1,000 years old (McMurray et al. 2008).

Large sponges may be damaged by a variety of natural events and human activities including severe storms, vessel groundings, and the cutting movements of chain, rope, or monofilament line moved along with debris by strong currents (Schmahl 1999; Chiappone et al. 2002, 2005). After these events, detached large sponges are commonly found, still alive and intact, between reef spurs on sand or rubble where they slowly erode under the action of oscillating currents. The success of past attempts at reattaching sponges using cement or epoxy has been limited (Jaap 2000; Collier et al. 2007) because adhesives do not bind to sponge tissue. Herein I describe a novel technique for reattaching *X. muta* that could be generally applied to the restoration of other large sponge species dislodged by human activities or storm events.

## Methods

This sponge reattachment technique was developed as part of two experiments conducted on Conch Reef, Florida (lat 24.95°N, long 80.45°W) that required detached sponges to be held in place for subsequent monitoring; full details of the experimental design will be presented elsewhere (McMurray, unpublished. data). For both experiments, 10 *Xestospongia muta*, about

20 to 30 cm in height and base diameter, were transplanted from the adjacent reef Conch Wall (about 80-m distance), to both a shallow (15 m) and deep (30 m) site on Conch Reef. The first experiment was conducted on 6–8 November 2004, and the second, 25–26 July 2005. For both experiments, sponge reattachment was examined and a qualitative assessment of sponge condition was conducted monthly for 6–7 mo, and then 1 year and 2.3–3 years following transplantation.

Sponges were detached at the level of the substratum using long knives and transported underwater to their reattachment sites. For each sponge, an area of about 1 m<sup>2</sup> bare flat limestone substratum was cleaned of loose debris and algae with a wire brush prior to sponge reattachment. Two pairs of sponge holders (Fig. 1) were positioned perpendicularly with 10- to 20-cm distance between each holder and the sponge surface (Fig. 2). Each holder consisted of a slotted piece of polyvinyl chloride pipe anchored in a concrete block that was set on a plastic (vexar) mesh base (Fig. 1). The plastic mesh base of each holder was secured by driving three to four washer nails through the mesh and into the substratum. Each sponge was skewered horizontally through the slots in two opposing holders with each of two 60-cm stainless steel threaded rods, perpendicular to each other, at a height of about 15 cm from the substratum (Fig. 2). Once the cut surface of the sponge was seated tightly against the substratum, the sponge was secured to the holders by tightening down stainless steel washers and zinc-plated nuts along the ends of the threaded rods (Fig. 2).

Temporal and spatial differences in survival and reattachment were tested using log-linear models (Sokal and Rohlf 1995). Analyses were conducted for each of the two transplants separately due to differences in survey dates between the two experiments. For each experiment, analyses were based on separate three-way contingency tables with the explanatory

variables time,  $T$ , and depth,  $D$  for both tables and the response variables survival,  $S$ , and attachment,  $A$ , for the two tables, respectively. The null hypotheses, the models  $TD$ ,  $S$ , and  $TD$ ,  $A$ , were compared with marginal models containing the  $TS$ ,  $DS$ ,  $TA$ , and  $DA$  interactions.

## Results

The sponge reattachment technique was originally designed solely to keep sponges stationary for 2 manipulative experiments (McMurray, unpublished data); however, it was discovered that some sponges were reattaching to the substratum after only 6 months. For the first experiment, all but one sponge was healthy after 6 months, and six had reattached to the substratum at the deep site. Sponges transplanted to the deep site had significantly greater survival compared to sponges at the shallow site ( $\chi^2 = 30.432$ ,  $df = 1$ ,  $p < 0.001$ ) and survival did not significantly change through time. All sponges survived tropical storm Arlene, which passed Key Largo about 7 months after transplantation, but seven sponges from the shallow site that had yet to reattach disappeared as a result of hurricane Dennis, about 8 months after transplantation (sponge holders remained intact) (Table 1). The 13 surviving sponges were alive and healthy after 1 year, and 6 had reattached to the substratum. After 3 years, two sponges that were reattached became dislodged, but an additional five sponges had reattached. No difference in sponge reattachment was found between sites or through time. A total of 12 sponges survived and 9 had reattached to the substratum (Table 1).

Again for the second experiment, survival of sponges was significantly greater at the deep compared to the shallow site ( $\chi^2 = 4.054$ ,  $df = 1$ ,  $p = 0.044$ ), but it did not significantly change through time. All sponges were healthy until exposed to storm events. Hurricanes Katrina, Rita, and Wilma passed about 2, 3, and 4 months after transplantation, respectively,

removing five sponges from the shallow site (again, sponge holders remained intact). Two sponges at the deep site subsequently died from a disease-like condition, “sponge orange band,” which also killed *X. muta* on adjacent reefs at the same time (Coward et al. 2005). Sponge reattachment was found to significantly increase over time ( $\chi^2 = 4.434$ ,  $df = 1$ ,  $p = 0.035$ ) and did not differ between sites. All 13 surviving transplants were alive and healthy after 1 year and 6 had reattached to the substratum (Table 1). After 2.3 years, all 13 surviving sponges were still alive, all 6 that had reattached after one year remained attached, and an additional 5 had reattached to the substratum, for an 85% reattachment rate (Table 1). After the final survey for both transplants, the apparatus was successfully removed from all sponges that had reattached.

## Discussion

Twenty specimens of the Caribbean giant barrel sponge were reattached at Conch Reef using the technique described herein, despite an unusually rigorous testing regime that included four hurricanes. Despite these storm events, 62.5% of sponges in both experiments survived at least 2.3–3 years, and 90% of the sponges at the deep site survived.

Sponges reattached to the substratum after being held stationary by sponge holders for as little as 6 months. About 20% of the surviving sponges did not reattach because unevenness in the substratum prevented complete contact between the sponge base and the substratum; in other cases currents induced by storm events “rocked” the sponges in their holders to prevent attachment. Attachment success was clearly greater when the base of the sponge was in firm contact with the substratum, and when sponges were reattached at greater depths where storm events had less effect. Removal of the rods after reattachment left small wounds, which healed rapidly (Walters & Pawlik 2005). It is advisable to remove the apparatus as soon as

reattachment is complete, because it may become entangled in debris during storm events, promoting dislodgement.

Although *Xestospongia muta* is the dominant large sponge on Caribbean coral reefs, the technique described herein may also be useful for attaching less common large species, particularly *Geodia neptuni*, *Agelas conifera* and *Verongula gigantea*. Of these species, the first has a stony tissue consistency similar to that of *X. muta*, while the second and third have progressively more elastic tissue that may be difficult to fix in place, and additional modification of the attachment method may be required.

#### Implications for Practice

- Dislodged specimens of the Caribbean giant barrel sponge, *Xestospongia muta*, can be reattached to the reef substratum in as little as 6 months using the apparatus described herein.
- Sponges have greater potential for survival if reattached on deep-water reefs where damage from storms during reattachment is less likely.
- The apparatus should be removed as soon as reattachment is complete.
- This technique may be used to reattach other species of large sponges that become dislodged.

## Literature cited

- Chiappone, M., H. Dienes, D. W. Swanson, S. L. Miller. 2005. Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. *Biological Conservation* **121**:221–230.
- Chiappone, M., A. White, D. W. Swanson, and S. L. Miller. 2002. Occurrence and biological impacts of fishing gear and other marine debris in the Florida Keys. *Marine Pollution Bulletin* **44**:597–604.
- Collier, C., R. Dodge, D. Gilliam, K. Gracie, L. Gregg, W. Jaap, M. Mastry, and N. Poulos. 2007. Rapid response and restoration for coral reef injuries in southeast Florida. ([http://www.dep.state.fl.us/coastal/programs/coral/reports/MICCI/MICCI\\_Project2\\_Guidelines.pdf](http://www.dep.state.fl.us/coastal/programs/coral/reports/MICCI/MICCI_Project2_Guidelines.pdf)). Accessed 08 November 2007.
- Cowart, J. D., T. P. Henkel, S. E. McMurray, and J. R. Pawlik. 2006. Sponge orange band (SOB): a pathogenic-like condition of the giant barrel sponge *Xestospongia muta*. *Coral Reefs* **25**:513.
- Diaz, M. C., and K. Rutzler. 2001. Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science* **69**:535–546.
- Hudson, J. H., J. Anderson, E. C. Franklin, J. Schittone, and A. Stratton. 2007. M/V Wellwood coral reef restoration monitoring report, monitoring events 2004–2006. Florida Keys National Marine Sanctuary Monroe County, Florida. Marine Sanctuaries Conservation Series NMSP-07-02. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, Maryland.
- Jaap, W. C. 2000. Coral reef restoration. *Ecological Engineering* **15**:345–364.
- McMurray, S.E., J.E. Blum, and J.R. Pawlik. 2008. Redwood of the reef: Growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Marine Biology* **155**:159–171.
- NOAA. 1997. NOAA gears up for reef restoration at Looe Key: university agrees to \$3.9 million settlement for damage in Florida Keys Sanctuary. Press Release. (<http://www.publicaffairs.noaa.gov/pr97/nov97/noaa97-r423.html>). Accessed 08 November 2007.
- Precht, W. F., editor. 2006. Coral reef restoration handbook. CRC Press, Boca Raton, Florida.
- Schmahl, G. P. 1999. Recovery and growth of the giant barrel sponge (*Xestospongia muta*) following physical injury from a vessel grounding in the Florida Keys. *Memoirs of the Queensland Museum* **44**:532.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. W. H. Freeman and Co. New York.

Walters, K. D., and J. R. Pawlik. 2005. Is there a trade off between wound-healing and chemical defenses among Caribbean reef sponges? *Integrative and Comparative Biology* **45**:352–358.

Table 1. Total number of 10 *Xestospongia muta* attached to the substratum, unattached, and dead after 1 and 2.3 – 3 years at shallow and deep sites for both transplants.

<i>Transplant</i>	<i>Time After Transplant (Years)</i>	<i>Depth</i>	<i>No. Attached</i>	<i>No. Unattached</i>	<i>No. Dead</i>
1	1	Shallow	0	3	7
1	3	Shallow	2	0	8
1	1	Deep	6	4	0
1	3	Deep	7	3	0
2	1	Shallow	3	2	5
2	2.3	Shallow	4	1	5
2	1	Deep	3	5	2
2	2.3	Deep	7	1	2

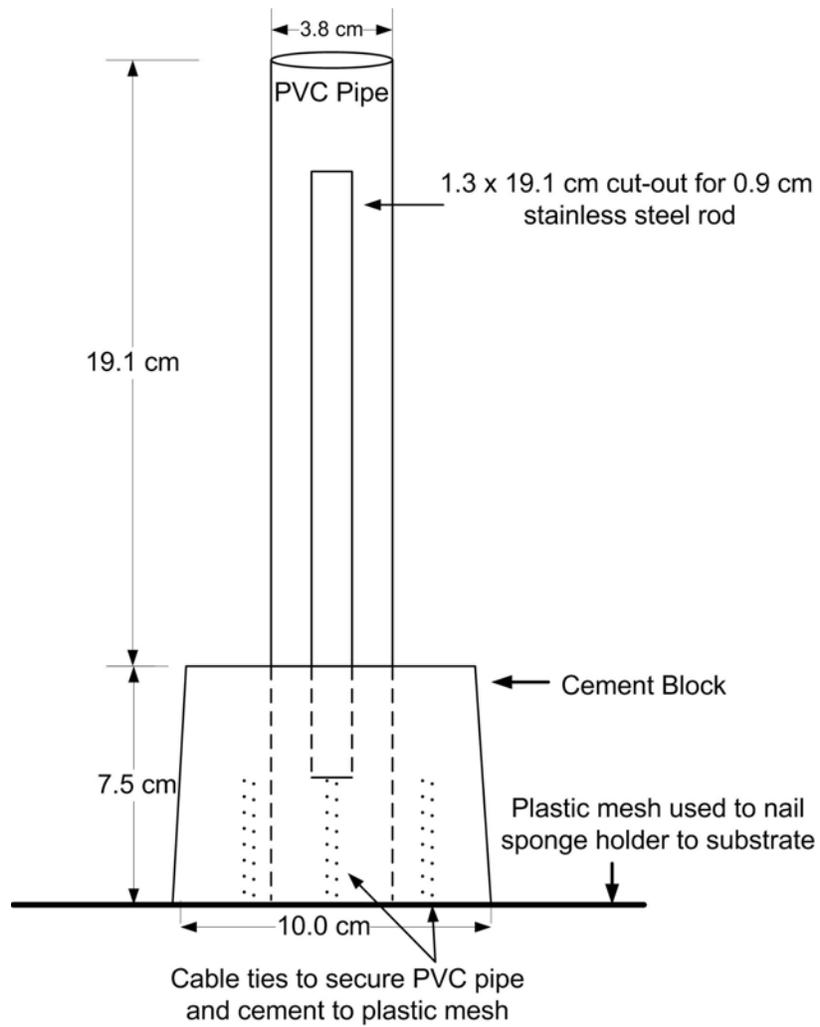


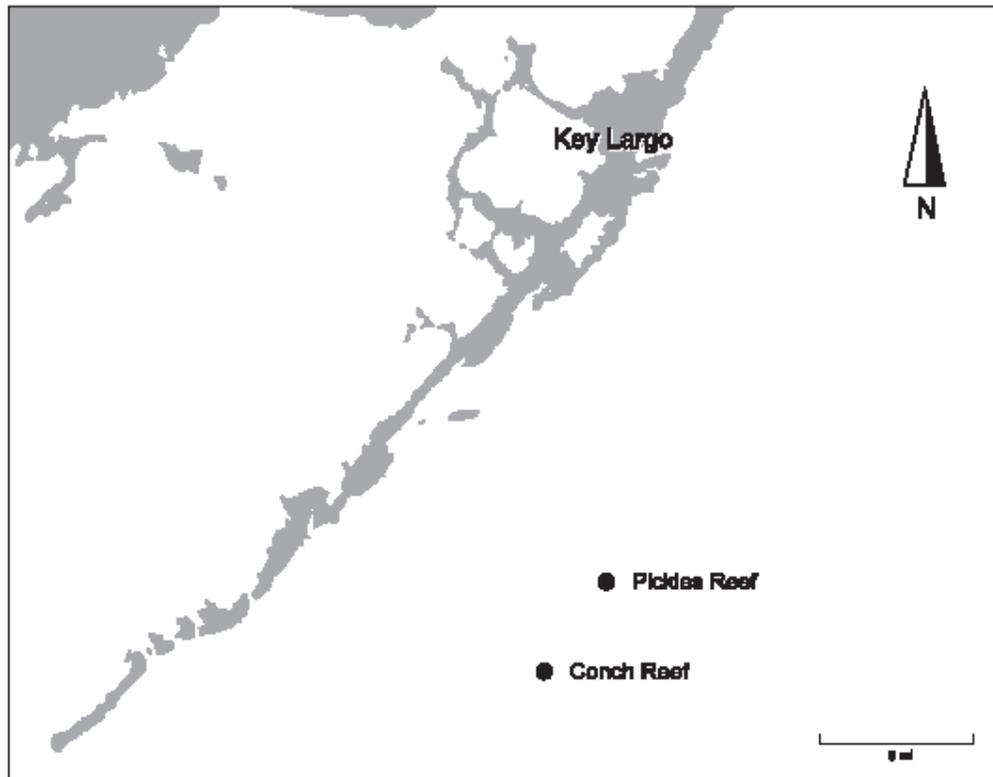
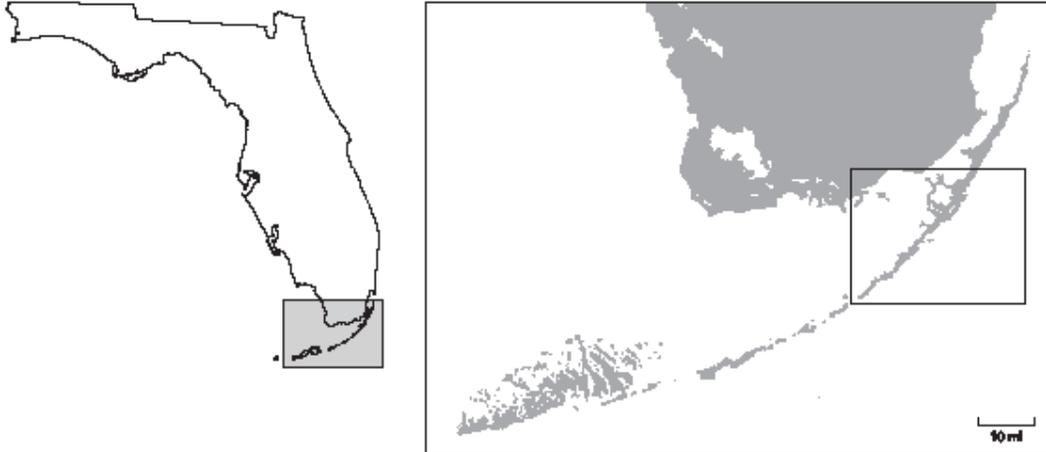
Fig. 1. Schematic of sponge holder. Two pairs of holders were used to secure each sponge.



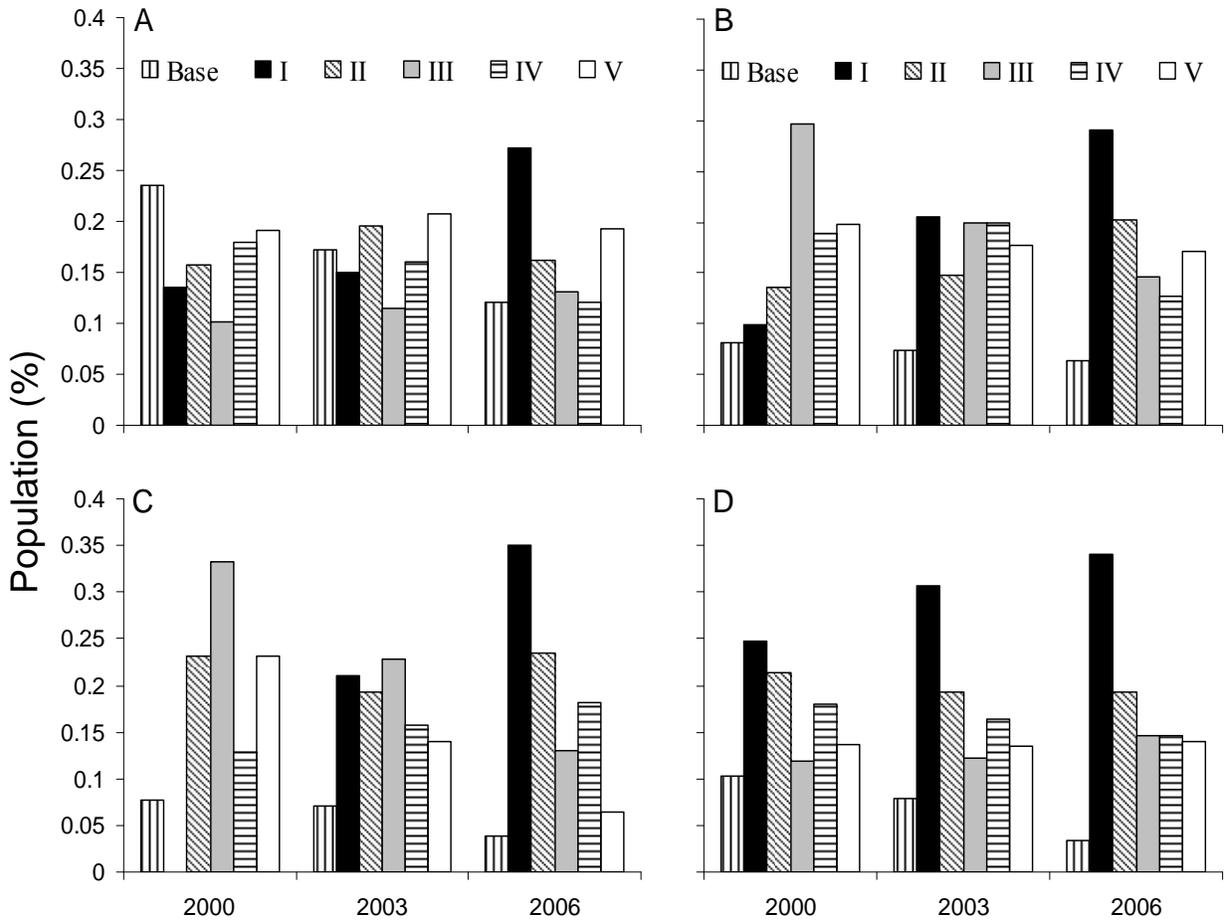
Fig. 2. Specimen of *Xestospongia muta* secured to the substratum at 15-m depth, Conch Reef, Florida. (A) Side view. Long edge of slate is 16 cm. (B) Same sponge, top view.

## APPENDIX

Appendix A. Map of Key Largo, Florida depicting the location of Conch Reef and Pickles Reef study sites.



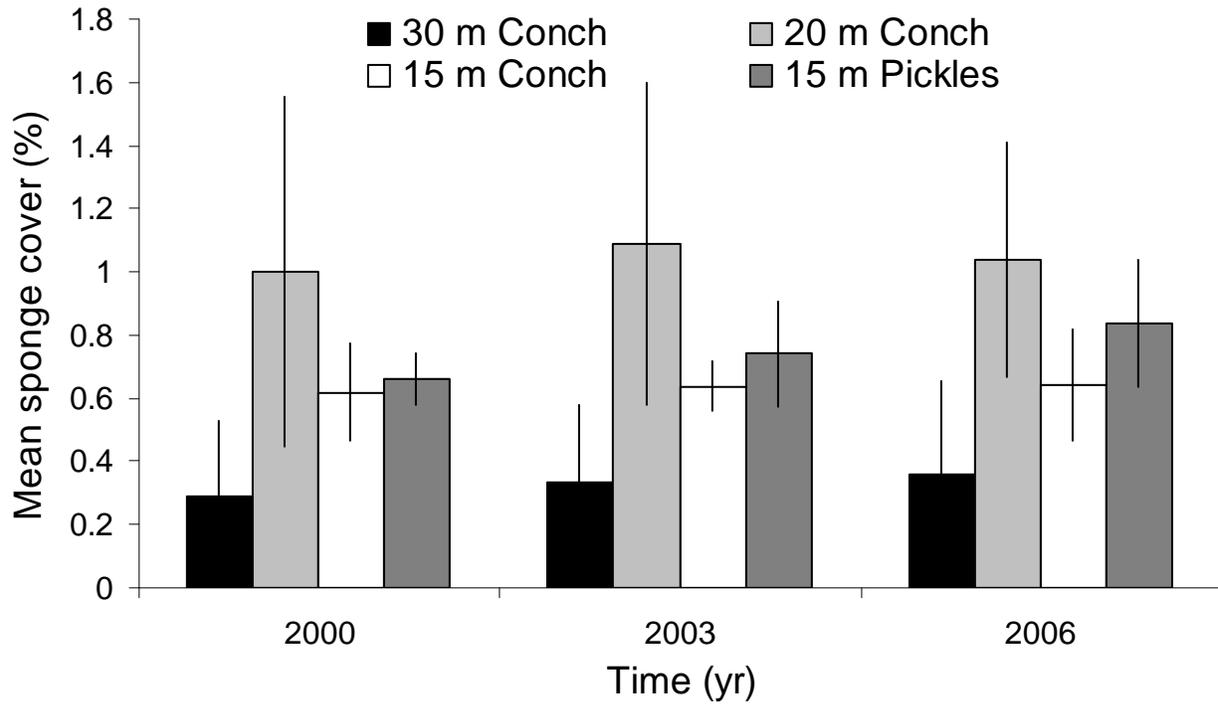
Appendix B. Size-frequency distributions of *Xestospongia muta* at (A) 15 m Conch Reef, (B) 20 m Conch Reef, (C) 30 m Conch Reef, and (D) 15 m Pickles Reef in 2000, 2003, and 2006.



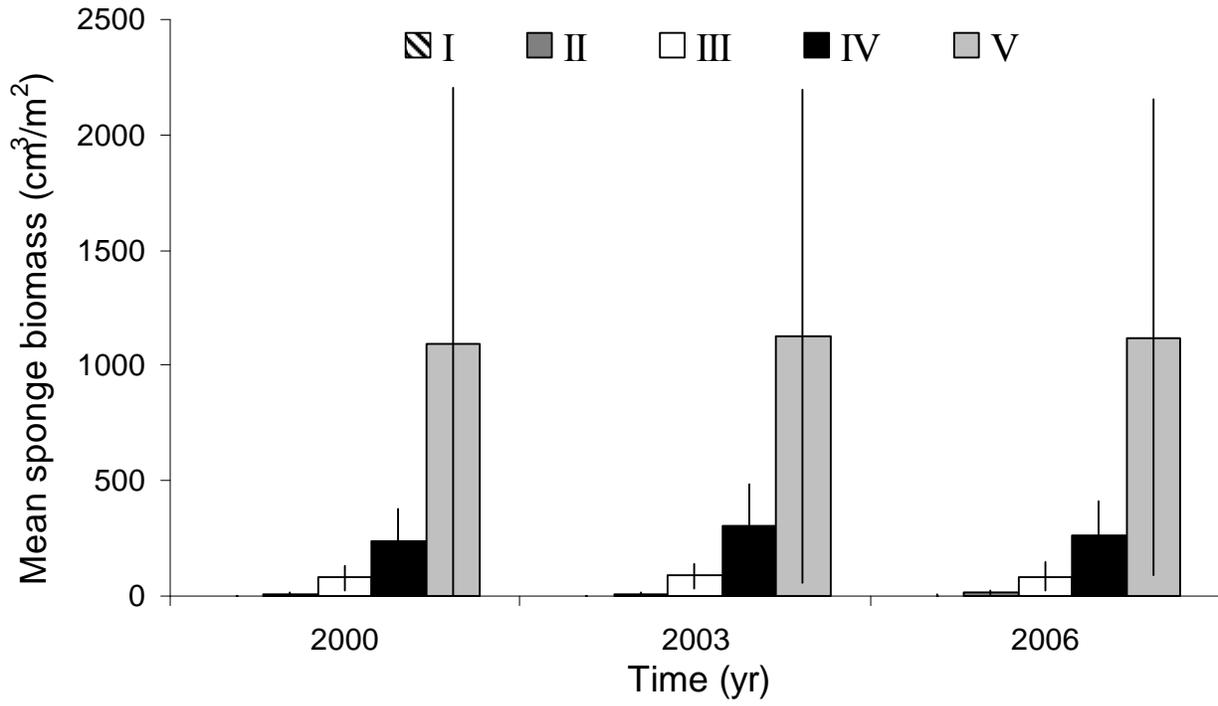
Appendix C. Population vectors describing the population structure at each site in 2000, 2003, and 2006.

Location	Size class	Year		
		2000	2003	2006
15 m Conch	Base	21	15	12
	I	12	13	27
	II	14	17	16
	III	9	10	13
	IV	16	14	12
	V	17	18	19
20 m Conch	Base	9	10	10
	I	11	28	46
	II	15	20	32
	III	33	27	23
	IV	21	27	20
	V	22	24	27
30 m Conch	Base	3	4	3
	I	0	12	27
	II	9	11	18
	III	13	13	10
	IV	5	9	14
	V	9	8	5
15 m Pickles	Base	12	11	5
	I	29	43	51
	II	25	27	29
	III	14	17	22
	IV	21	23	22
	V	16	19	21
Conch Reef (total)	Base	33	29	25
	I	23	53	100
	II	38	48	66
	III	55	50	46
	IV	42	50	46
	V	48	50	51

Appendix D. Mean ( $\pm$ SD) percent substratum covered by *Xestospongia muta* at each site in 2000, 2003, and 2006.



Appendix E. Mean ( $\pm$ SD) biomass of *Xestospongia muta* in each size-class at all sites on Conch Reef. Biomass of size classes I and II are  $< 100 \text{ cm}^3/\text{m}^2$ .



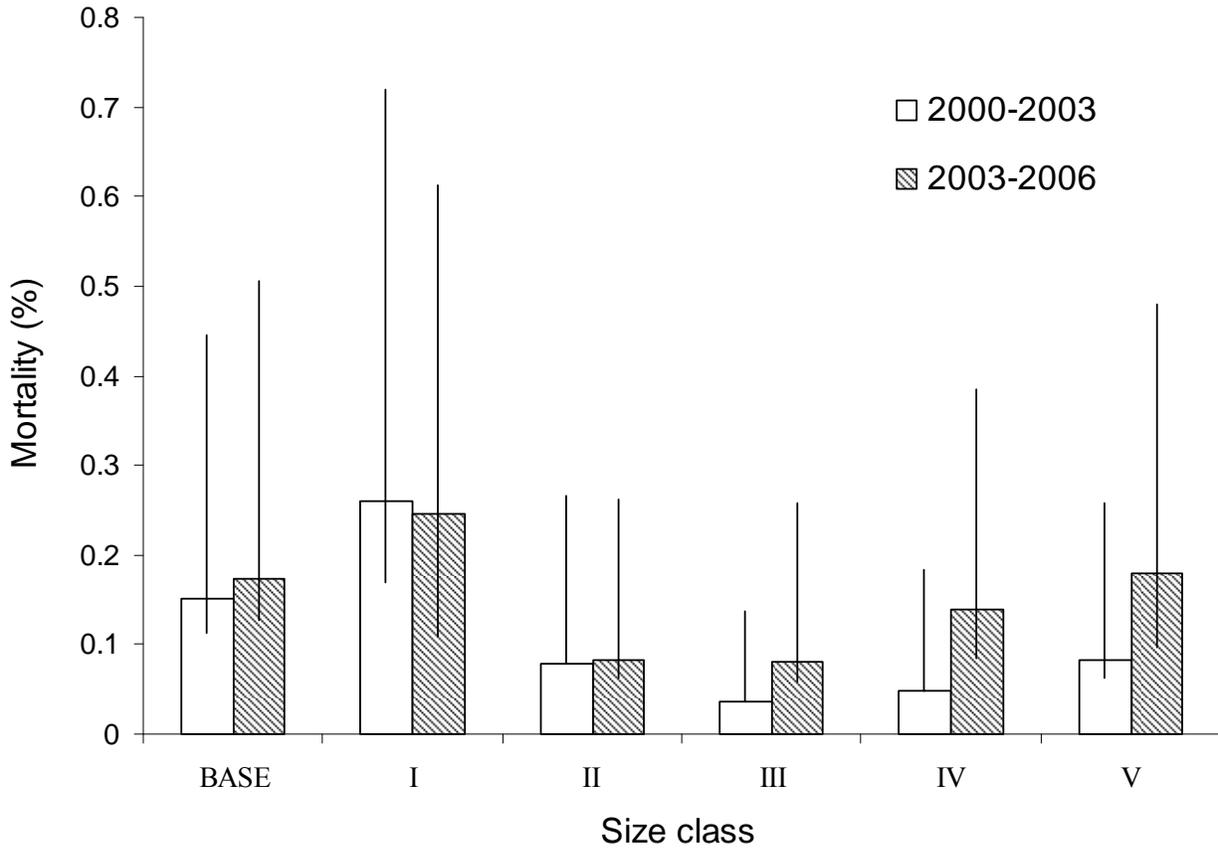
Appendix F. Transition matrices for 15, 20, and 30 m Conch Reef and 15 m Pickles Reef sites, respectively over 2000-2003 and 2003-2006. Because relatively few transitions were observed for some matrices, site summary matrices and Conch Reef summary matrices were used in spatial and temporal analyses (Tables 2 and 3).  $q_x$  = stage-specific mortality rate,  $n$  = sample size.

Location	Size class	2000-2003					
		Base	I	II	III	IV	V
15 m Conch	Base	0.667	0	0	0	0.063	0
	I	0.048	0.333	0	0	0	0
	II	0	0.333	0.643	0	0	0
	III	0	0	0.214	0.778	0	0
	IV	0.048	0	0	0.222	0.688	0
	V	0	0	0	0	0.25	0.824
	$q_x$	0.238	0.333	0.143	0	0	0.176
	$n$	21	12	14	9	16	17
20 m Conch	Base	0.778	0	0.067	0.03	0	0
	I	0	0.455	0	0	0	0
	II	0	0.364	0.4	0.121	0	0
	III	0.111	0	0.533	0.485	0.048	0
	IV	0.111	0	0	0.333	0.714	0
	V	0	0	0	0	0.143	0.955
	$q_x$	0	0.182	0	0.03	0.095	0.045
	$n$	9	11	15	33	21	22
30 m Conch	Base	0.667	0	0.111	0	0	0
	I	0	0	0	0	0	0
	II	0.333	0	0.556	0	0	0
	III	0	0	0.222	0.692	0	0
	IV	0	0	0	0.231	0.8	0.222
	V	0	0	0	0	0.2	0.778
	$q_x$	0	0	0.111	0.077	0	0
	$n$	3	0	9	13	5	9
15 m Pickles	Base	0.833	0	0	0	0	0
	I	0.083	0.448	0.08	0	0	0
	II	0	0.345	0.56	0	0	0
	III	0.083	0.034	0.36	0.429	0	0
	IV	0	0	0	0.429	0.81	0
	V	0	0	0	0.071	0.19	0.875
	$q_x$	0	0.172	0	0.071	0	0.125
	$n$	12	29	25	14	21	16

Appendix F continued.

Location	Size class	2003-2006					
		Base	I	II	III	IV	V
15 m Conch	Base	0.667	0	0	0.1	0.071	0
	I	0.067	0.385	0.059	0	0	0
	II	0.067	0.462	0.412	0	0	0
	III	0	0	0.412	0.6	0	0
	IV	0.067	0	0	0.3	0.571	0
	V	0.067	0	0	0	0.214	0.833
	$q_x$	0.067	0.154	0.118	0	0.143	0.167
	$n$	15	13	17	10	14	18
20 m Conch	Base	0.7	0	0.05	0.037	0.037	0
	I	0.1	0.5	0	0	0	0
	II	0	0.25	0.65	0.037	0	0
	III	0	0	0.3	0.556	0.037	0
	IV	0	0	0	0.259	0.444	0.042
	V	0	0	0	0	0.296	0.792
	$q_x$	0.2	0.25	0	0.111	0.185	0.167
	$n$	10	28	20	27	27	24
30 m Conch	Base	0.5	0	0	0	0	0.125
	I	0	0.5	0	0	0	0
	II	0	0.167	0.455	0.077	0	0
	III	0	0	0.364	0.385	0.111	0
	IV	0	0	0	0.462	0.889	0
	V	0	0	0	0	0	0.625
	$q_x$	0.5	0.333	0.182	0.077	0	0.25
	$n$	4	12	11	13	9	8
15 m Pickles	Base	0.455	0	0	0	0	0
	I	0	0.535	0.148	0	0	0
	II	0.091	0.233	0.519	0	0	0
	III	0.091	0	0.259	0.706	0.043	0.053
	IV	0	0	0	0.294	0.696	0.053
	V	0	0	0	0	0.217	0.842
	$q_x$	0.364	0.233	0.074	0	0.043	0.053
	$n$	11	43	27	17	23	19

Appendix G. Stage-specific mortality rates for *Xestospongia muta* for all sites on Conch Reef over the sampling intervals 2000-2003 and 2003-2006. Error bars are 95% confidence intervals.



Appendix H. Log-linear analysis of transition matrices (Appendix 8) used to test the effects of time and location on sponge transitions. Analyses were based on a four-way contingency table with the response variable fate, F, (6 stages + mortality) and explanatory variables time, T, (three years), and location, L, (four sites).

$G^2$							Sum (df)
3-way models (df)	Base	I	II	III	IV	V	4-way model
Analysis 1: marginal test of the effect of year on fate							
TL, F	39.65 (42)	9.55 (21)	34.55 (28)	29.45 (35)	31.41 (28)	26.58 (28)	171.18 (252)
TL, TF	34.95 (36)	6.08 (18)	32.48 (24)	26.91 (30)	26.23 (24)	22.97 (24)	149.62 (216)
TF	4.70 (6)	3.47 (3)	2.07 (4)	2.54 (5)	5.18 (4)	3.61 (4)	21.56 (36)
Analysis 2: marginal test of the effect of location on fate							
TL, F	39.65 (42)	9.55 (21)	34.55 (28)	29.45 (35)	31.41 (28)	26.58 (28)	171.18 (252)
TL, LF	26.22 (24)	4.86 (12)	11.03 (16)	13.09 (20)	13.71 (16)	13.53 (16)	82.44 (144)
LF	13.43 (8)	4.69 (9)	23.52* (12)	16.36 (15)	17.70 (12)	13.05 (12)	88.74 (108)
Analysis 3: conditional test of the effect of year on fate							
TL, LF	26.22 (24)	4.86 (12)	11.03 (16)	13.09 (20)	13.71 (16)	13.53 (16)	82.44 (144)
TL, TF, LF	21.12 (18)	2.25 (9)	8.44 (12)	10.37 (15)	8.18 (12)	9.70 (12)	60.05 (108)
TF (given L)	5.10 (6)	2.61 (3)	2.59 (4)	2.72 (5)	5.53 (4)	3.83 (4)	22.39 (36)
Analysis 4: conditional test of the effect of location on fate							
TL, TF	34.95 (36)	6.08 (18)	32.48 (24)	26.91 (30)	26.23 (24)	22.97 (24)	149.62 (216)
TL, LF, TF	21.12 (18)	2.25 (9)	8.44 (12)	10.37 (10)	8.18 (12)	9.70 (12)	60.05 (108)
LF (given T)	13.83 (18)	3.83 (9)	24.04* (12)	16.54 (10)	18.05 (12)	13.27 (12)	89.57 (108)
Analysis 5: test of the three-way interaction term LTF							
TL, LF, TF	21.12 (18)	2.25 (9)	8.44 (12)	10.37 (10)	8.18 (12)	9.70 (12)	60.05 (108)
LTF	0	0	0	0	0	0	
PYF (given all two-ways)	21.12 (18)	2.25 (9)	8.44 (12)	10.37 (10)	8.18 (12)	9.70 (12)	

\*  $P < 0.05$

Appendix I. Elasticity matrices of the Conch Reef summary matrices  $A^{(00-03)}$  and  $A^{(03-06)}$  (Table 2). Elasticities greater than 0.01 are shown in bold. Elasticities for each column were summed to calculate total elasticity of each size class (Figure 7).

<u>Conch Reef 2000-2003</u>						
	<u>Size class</u>					
<u>Size class</u>	<u>Base</u>	<u>I</u>	<u>II</u>	<u>III</u>	<u>IV</u>	<u>V</u>
Base	<b>0.0128</b>	0	0.0003	0.0003	0.0035	0
I	0.0006	0.0004	0	0	0	0
II	0.0009	0.0006	0.0047	0.0021	0	0
III	0.0010	0	0.0032	<b>0.0175</b>	0.0060	0
IV	0.0017	0	0	0.0079	<b>0.1631</b>	<b>0.0380</b>
V	0	0	0	0	<b>0.0380</b>	<b>0.6975</b>

<u>Conch Reef 2003-2006</u>						
	<u>Size class</u>					
<u>Size class</u>	<u>Base</u>	<u>I</u>	<u>II</u>	<u>III</u>	<u>IV</u>	<u>V</u>
Base	<b>0.1142</b>	0	0.0013	0.0039	0.0081	<b>0.0181</b>
I	<b>0.0136</b>	<b>0.0196</b>	0.0015	0	0	0
II	0.0088	<b>0.0151</b>	<b>0.0490</b>	0.0057	0	0
III	0	0	<b>0.0267</b>	<b>0.0596</b>	0.0094	0
IV	0.0051	0	0	<b>0.0265</b>	<b>0.0953</b>	<b>0.0153</b>
V	0.0040	0	0	0	<b>0.0294</b>	<b>0.4695</b>

## BIOGRAPHICAL SKETCH

Steven Edward McMurray was born August 14<sup>th</sup>, 1982, in Ashtabula, Ohio and grew up in North Kingsville, Ohio. In 2004, he graduated *magna cum laude* from Hiram College Ohio with a Bachelor of Arts degree in biology and minor in chemistry. At Hiram College, he was mentored by his academic advisor Dr. Dennis Taylor, who instilled in him a passion for biology and interest in ecology. During his undergraduate career, Steve participated in an internship at the Darling Marine Center, University of Maine, and a NSF Research Experiences for Undergraduates program at the University of Alaska. Steve was inducted into the national honor society, Phi Beta Kappa, upon graduating from Hiram College. After graduating, Steve joined the research laboratory of Dr. Joseph Pawlik at the University of North Carolina Wilmington. During his graduate career, Steve participated in three research cruises in the Bahamas aboard the *R/V Seward Johnson* and ten research missions at the National Underwater Research Center in Key Largo, Florida, including two missions that included the use of technical and mixed-gas decompression SCUBA diving techniques. Working under Dr. Pawlik, Steve completed a thesis on the growth, demographics, bleaching, and conservation of the Caribbean giant barrel sponge, *Xestospongia muta*, using a long-term monitoring data set established by Pawlik's group and field-based approaches. In 2008, Steve was awarded the Knauss Fellowship from NOAA and will serve in the executive branch of the U.S. government upon graduating from UNCW.