

Population dynamics of giant barrel sponges on Florida coral reefs



Steven E. McMurray, Christopher M. Finelli, Joseph R. Pawlik *

Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, NC 28403, USA

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ABSTRACT

The structure of coral reef benthic communities has changed significantly in recent decades and will likely continue to change with the increasing frequency and scale of disturbances. Reef-building corals and macroalgae have been regularly included in assessments of coral reef communities, however very little is known about the long-term dynamics of sponge populations. The giant barrel sponge *Xestospongia muta* is a dominant component of Caribbean coral reef communities, and it was previously reported that populations significantly increased in the Florida Keys over 2000–2006. Using surveys of sponges from the same permanent plots on reefs off Key Largo, Florida, USA, this study extended the investigation of the population dynamics of *X. muta* for 2000–2012 at three depths (15, 20, 30 m). Over 12 years, the density of *X. muta* significantly increased by a mean of 122% (range = 53–336%) on Conch Reef and by a mean of 44% on Pickles Reef. Both the cover and volume of *X. muta* concomitantly increased at all sites and increases in both metrics were greater over 2006–2012 relative to 2000–2006 due to decreased mortality of the largest sponges in the population over time. Population growth accelerated at all sites on Conch Reef due to a significant increase in recruitment and sponge survival, and was greater at deeper relative to shallow depths; on Pickles Reef, recruitment decreased, but survival increased and population growth remained constant over time. Despite mortality due to putative pathogenesis, and in contrast to the persistent decline of reef-building corals, these results suggest that conditions on Florida coral reefs have been increasingly favorable for the growth of barrel sponge populations. Given the long lifespan of *X. muta*, it remains to be seen whether these results represent a persistent change with broad geographic relevance, or stochastic variation in local demographics.

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1. Introduction

The structure of coral reef benthic communities has significantly changed over recent decades because of a number of natural and anthropogenic stressors (Bellwood et al., 2004; Hughes et al., 2003). Among the most pervasive of these changes has been a significant decline in the cover of scleractinian corals, the foundation species of coral reefs (Bruno and Selig, 2007; De'ath et al., 2012; Gardner et al., 2003; Schutte et al., 2010). The long-term depletion of coral populations has been due to both colony mortality and recruitment failure, and these demographic processes have continued to impede coral recovery (Edmunds and Elahi, 2007; Hughes and Tanner, 2000; Williams and Miller, 2011). Given the persistent decline in coral reef resilience and forecasts of chronic disturbance due to climate change and ocean acidification, the community composition of future reefs is likely to be much different than current baselines (Hoegh-Guldberg and Bruno, 2010; Hoegh-Guldberg et al., 2007; Hughes et al., 2003).

Space is a limiting resource for coral reef benthic communities (Connell, 1978) and the decline of cover by scleractinian corals has been associated with compensatory increases in the abundance of

other taxa over varying temporal scales (Dudgeon et al., 2010). On some reefs, the benthos has become dominated by macroalgae (Bruno et al., 2009; McManus and Polsenberg, 2004); on others, species of sponges, soft corals, corallimorpharians, and other taxa that grow fast and have high reproductive output have become dominant (Norström et al., 2009). Aside from these examples of rapid phase shifts in the dominant populations of coral reef communities, however, very little is known about the long-term dynamics of slower-growing non-scleractinian benthic reef fauna (but see Brown and Edmunds, 2013; Colvard and Edmunds, 2011; Ruzicka et al., 2013; Villamizar et al., 2013).

Sponges are important components of Caribbean coral reef benthic communities that perform a variety of functional roles (Bell, 2008; Diaz and Rützler, 2001). Sponges contribute to reef substrate erosion (Rützler, 1975) and accretion (Wulff, 1984), contribute to reef biodiversity through the provision of habitat (Henkel and Pawlik, 2005), and are dominant competitors within the benthic community (Loh et al., 2015). Sponges also mediate the cycling of carbon and nutrients on coral reefs (de Goeij et al., 2013; Southwell et al., 2008; Zhang et al., 2015) via their capacity as efficient suspension feeders (McMurray et al., 2014; Reiswig, 1974) and because they host diverse assemblages of symbiotic microbes (Webster and Taylor, 2011). Despite their ecological importance, however, sponges have been typically excluded from coral reef monitoring

* Corresponding author.

E-mail address: pawlikj@uncw.edu (J.R. Pawlik).

efforts (Bell, 2008). In part, this may be because sponges are generally less abundant than other benthic taxa on the basis of percentage cover, the metric typically used in assessments of coral reef community structure (e.g. Loh and Pawlik, 2014); however, if benthic communities are considered in three dimensions, sponges dominate Caribbean coral reefs on the basis of biomass (Loh and Pawlik, 2014; Southwell et al., 2008; Villamizar et al., 2013; Zea, 1993a). Given the functional roles that sponges perform and the increasing frequency and scale of disturbances to coral reefs, there is a need to better understand the demographics of sponges on Caribbean coral reefs as they have been transformed.

The giant barrel sponge *Xestospongia muta* is a particularly dominant member of sponge communities on Caribbean coral reefs. *X. muta* is a large and long-lived species (McClain et al., 2015; McMurray et al., 2008), populations comprise up to 65% of total sponge community biomass (Southwell et al., 2008), and *X. muta* is the second most abundant sponge on Caribbean coral reefs on the basis of percentage cover (Loh and Pawlik, 2014). Due to its large biomass, *X. muta* is an important component of habitat heterogeneity (Büttner, 1996). Moreover, populations process large volumes of seawater (McMurray et al., 2014) and play important roles in the flux of carbon and nutrients on coral reefs (Southwell et al., 2008).

Populations of *X. muta* have been monitored in permanent plots on the Florida Keys reef tract for over 18 years, and the demographic trends observed over 2000–2006 were reported previously (McMurray et al., 2010). Among the findings of this work was a 46% increase in the mean density of *X. muta*, but no significant increases in population volume or percent cover due to mortality of the largest individuals as the result of a pathogenic-like condition (Coward et al., 2006). Further, projections of population models indicated that the density of *X. muta* would continue to increase. Given the important functional roles of *X. muta*, changes in the demographics of this species may have important implications for the structure and function of Caribbean coral reefs. Here, an extension and additional analyses of the demographics of *X. muta* in the Florida Keys over 2000–2012 is provided, and recent population trends are compared with those previously reported and projected (McMurray et al., 2010).

2. Material and methods

2.1. Study sites and sponge monitoring

Populations of *X. muta* were monitored over 2000–2012 on Conch Reef (24°56'59" N; 80°27'13"W) and Pickles Reef (24°59'16" N; 80°24'39"W), Key Largo, Florida in 12 permanent 16 m diameter circular plots. On Conch Reef, three plots each at 15, 20, and 30 m depths (CR15, CR20, and CR30, respectively) were established, and on Pickles Reef three plots were established at 15 m depth (PR15). Within each plot, each sponge was mapped and given a unique tag attached to a masonry nail driven into the substratum next to the base of the sponge. Beginning in the spring of 2000, sponges were monitored up to twice yearly; however, due to inclement weather and logistical constraints, not all plots were surveyed during each year. During each survey, the fate of all sponges was assessed and new recruits were identified and tagged. Additionally, each sponge was photographed from above with a slate, held parallel to the plane of the top of the osculum and displaying the unique tag number of each sponge and a 16 cm scale, and sponge size estimates were subsequently obtained using image analysis software (McMurray et al., 2008).

2.2. Population size structure, volume, and percent cover

To compare recent demographic patterns of *X. muta* with those reported previously (McMurray et al., 2010), this study was divided into two equal 6-year time periods: May 2000–May 2006 and May 2006–May 2012. The population structure of *X. muta* was evaluated by

assigning sponges to one of six stages (base, and size classes I–V; McMurray et al., 2010) at the beginning and end of each time interval (i.e. May 2000, May 2006, and May 2012). Bases were defined as sponges with remnant-like morphologies with more than two oscules (see McMurray et al., 2010, Appendix B). The base stage often results from partial mortality and remnants have been observed to grow and fuse over time to eventually restore a cylindrical-like morphology. All other sponges with typical cylindrical morphologies were assigned to size classes based on sponge volume: 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 $\leq 17,383.97 \text{ cm}^3$), and size class V ($> 17,383.97 \text{ cm}^3$). UTHSCA Image Tool image analysis software was used to obtain two measurements of osculum diameter of each sponge from digital images, with the first diameter chosen as the longest possible diameter and the second perpendicular to the first. The volume of each sponge (V_{sponge}) was then estimated from mean osculum diameter using the equation: $V_{\text{sponge}} = 28.514 \times \text{Osculum Diameter}^{2.1}$ ($p < 0.001$, $R^2 = 0.90$; McMurray et al., 2010). Because the volume of sponges in the base stage could not be accurately computed, they were omitted from analysis and total population volume estimates are therefore conservative values.

To determine percentage cover of *X. muta* at the beginning and end of each time interval, the base diameter of each sponge was estimated from osculum diameter measurements using the equation: $\text{Base Diameter} = 4.834 \times \text{Osculum Diameter}^{0.624}$ ($p < 0.001$, $R^2 = 0.84$; McMurray et al., 2010). The area of substratum covered by each sponge was then 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.

2.3. Data analysis

Sponge density, percentage cover and volume were compared among years (2000, 2006, 2012) and between sites (CR15, CR20, CR30, PR15) with 2-way repeated measures ANOVAs with site as the between-subjects factor and time as the within-subject factor. The change in density between each interval (2000–2006 and 2006–2012), a measure of the population growth rate, and recruitment were similarly compared between time intervals and between sites with 2-way repeated measures ANOVAs. Significant site or time effects were followed with Tukey post hoc tests, and significant interactions were evaluated by tests of simple main effects for all repeated-measures ANOVAs. Assumptions of normality and homogeneity of variances were checked with box and residual plots and data were transformed as needed. The assumption of sphericity was tested with Mauchly's test; if violated, the degrees of freedom were corrected using Greenhouse–Geisser estimates of sphericity (Quinn and Keough, 2002).

Log-linear models were used to test for temporal and spatial differences in the number of individuals in each stage (Quinn and Keough, 2002). 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.

Mortality was assessed separately for the standing population (i.e. those sponges present at the beginning of each time interval) and recruits. Temporal and spatial differences in the mortality of the standing population were tested with log-linear models. Analyses were based on a four-way contingency table with the response variable fate, F , (mortality or survival). 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 . Four-way tables were then decomposed into three-way contingency tables for each state. Log-linear models were similarly used to test for temporal and spatial

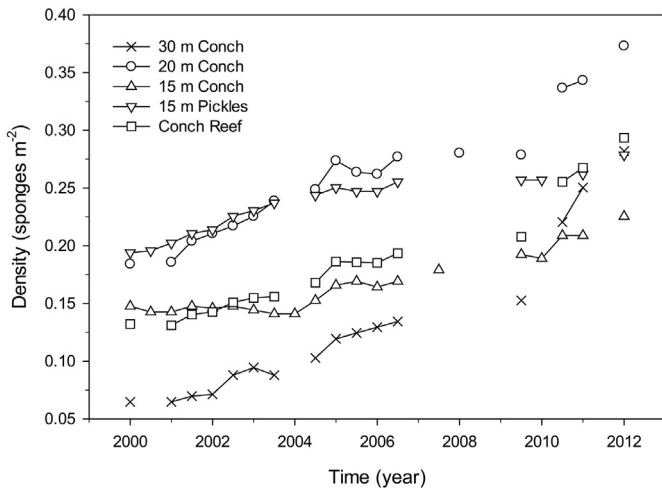


Fig. 1. Mean density of *Xestospongia muta* at 30, 20, and 15 m depth sites on Conch Reef and at 15 m depth on Pickles Reef, Key Largo, Florida, from May 2000 to May 2012. Also plotted is the mean density over all sites on Conch Reef.

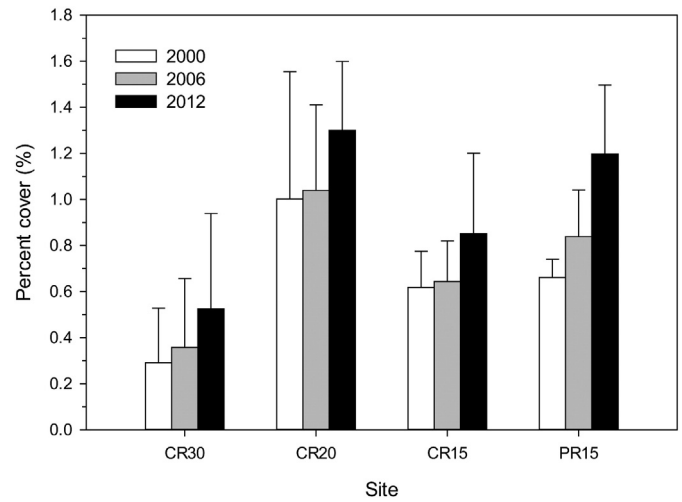


Fig. 2. Mean (\pm SD) percentage substratum covered by *Xestospongia muta* at 30, 20, and 15 m depth sites on Conch Reef (CR) and 15 m depth on Pickles Reef (PR) in 2000, 2006, and 2012.

differences in recruit mortality; analyses were based on a three-way contingency table with the null hypothesis TL, F . Statistical analyses were conducted with SPSS (version 19 for Windows; IBM) statistical software.

3. Results

The mean density of *X. muta* significantly varied over time ($F_{1,06,8,48} = 71.28, p < 0.001$) and between sites ($F_{3,8} = 4.12, p = 0.048$). Additionally, differences in sponge densities between sites significantly varied through time (site x time interaction: $F_{3,18,8,48} = 4.98, p = 0.027$, Fig. 1, Table 1). Comparisons of simple main effects revealed that the density at all sites significantly increased over time (CR15: $F_{1,06,8,48} = 5.82, p = 0.039$; CR20: $F_{1,06,8,48} = 31.15, p < 0.001$; CR30: $F_{1,06,8,48} = 42.94, p < 0.001$; PR15: $F_{1,06,8,48} = 6.30, p = 0.034$). Densities significantly varied between sites in 2000 ($F_{3,8} = 9.34, p = 0.005$) and in 2006 ($F_{3,8} = 5.79, p = 0.021$), but not in 2012 ($F_{3,8} = 2.43, p = 0.140$) and these results were largely driven by a large increase in sponge density at CR30 relative to other sites (Fig. 1). In 2000, sponges were least abundant at CR30; however, by 2012, sponge density at CR30 exceeded that at CR15 and was similar to that for PR15. From 2000–2012, mean sponge density increased by 0.08, 0.22, 0.19, and 0.09 sponges m^{-2} at CR15, CR20, CR30, and PR15 sites, respectively (Table 1).

The rate of population increase significantly varied over time ($F_{1,8} = 48.52, p < 0.001$), between sites ($F_{3,8} = 4.53, p = 0.039$), and between sites over time (site x time interaction: $F_{3,8} = 18.93, p = 0.001$). Simple main effects indicated that the rate of population increase was similar between sites over 2000–2006 ($F_{3,8} = 2.02, p = 0.190$), but significantly varied between sites over 2006–2012 ($F_{3,8} = 10.58, p = 0.004$). Pairwise comparisons revealed that, for 2006–2012, population growth

was significantly greater at CR30 compared to CR15 ($p = 0.004$) and PR15 ($p = 0.001$) and that population growth at CR20 was significantly greater than that at PR15 ($p = 0.009$); all other comparisons between sites were not significant. Additionally, the rate of population increase accelerated over 2006–2012 relative to 2000–2006 for all sites on Conch Reef (CR15: $F_{1,8} = 18.69, p = 0.003$; CR20: $F_{1,8} = 10.26, p = 0.013$; CR30: $F_{1,8} = 72.03, p < 0.001$), but remained the same over time at Pickles Reef ($F_{1,8} = 4.33, p = 0.071$, Fig. 1).

As the density of *X. muta* increased, the percentage cover also significantly increased over time ($F_{1,16,9,25} = 17.57, p = 0.002$, Fig. 2). Post hoc tests revealed that percentage cover did not vary between 2000 and 2006 ($p = 0.468$), but was significantly greater in 2012 ($p < 0.001$). Percentage cover was similar between sites ($F_{3,8} = 3.35, p = 0.076$) and did not vary between sites through time ($F_{3,47,9,25} = 0.56, p = 0.676$, Fig. 2). The mean (\pm SD) percentage cover of *X. muta* in 2012 was $0.85 \pm 0.35, 1.30 \pm 0.30, 0.52 \pm 0.42$, and $1.20 \pm 0.30\%$ at CR15, CR20, CR30, and PR15, representing increases of 38, 30, 80, and 81%, respectively, over the 12 year period. For all sites on Conch Reef collectively, sponge cover increased by 40% over the study to a mean of $0.89 \pm 0.46\%$ in 2012; 79% of sponge cover in 2012 was attributed to sponges initially present in 2000 that survived and grew, while the input and growth of new recruits since 2000 represented 74% of the increase in sponge cover for 2000–2012.

Similar to findings for percentage cover, the mean volume of sponges at the study sites significantly increased over time ($F_{1,21,9,68} = 18.65, p = 0.001$, Fig. 3). Sponge volume was similar between 2000 and 2006 ($p = 0.384$) and was significantly greater in 2012 ($p = 0.002$). Volume was similar between sites ($F_{3,8} = 3.08, p = 0.091$) and did not vary between sites through time ($F_{3,63,9,68} = 1.99, p = 0.178$, Fig. 3). Between 2000 and 2012, mean sponge volume at CR15, CR20, CR30, and PR15 increased by 40, 38, 43, and 111%,

Table 1
Densities of *Xestospongia muta* over time at sites on Conch and Pickles Reefs.

Site	Mean (\pm SD) density m^{-2}			Percent change (%)		
	2000	2006	2012	2000–2006	2006–2012	2000–2012
Conch	0.13 (0.06)	0.19 (0.07)	0.29 (0.09)	40	59	122
CR30	0.06 (0.04)	0.13 (0.28)	0.28 (0.11)	100	118	336
CR20	0.18 (0.04)	0.26 (0.02)	0.37 (0.01)	42	42	103
CR15	0.15 (0.02)	0.16 (0.05)	0.23 (0.07)	11	37	53
PR15	0.19 (0.02)	0.25 (0.02)	0.28 (0.01)	27	13	44

The first row represents all depths on Conch Reef combined.

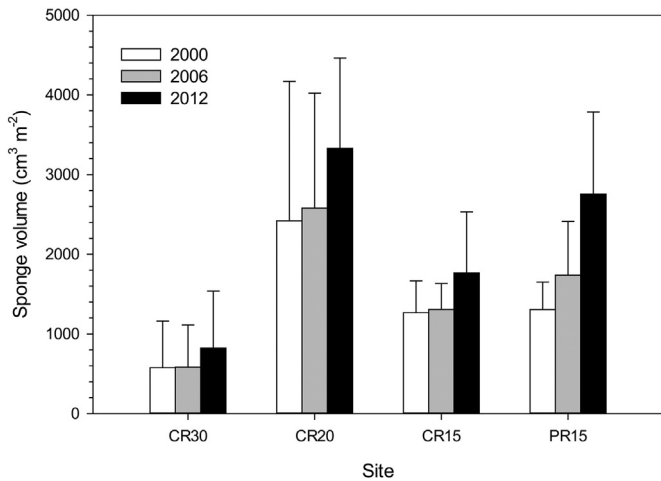


Fig. 3. Mean (\pm SD) volume of *Xestospongia muta* at 30, 20, and 15 m depth sites on Conch Reef (CR) and 15 m depth on Pickles Reef (PR) in 2000, 2006, and 2012.

respectively; for all sites on Conch Reef, volume increased by 39%. The largest individuals consistently contributed most to the mean sponge volume on Conch Reef (\approx 18 and 76% for size classes IV and V, respectively), while size class I contributed < 1%.

The population structure of *X. muta* significantly varied over time ($G^2 = 81.24$, $df = 10$, $p < 0.001$), between sites ($G^2 = 53.52$, $df = 15$, $p < 0.001$), and between sites over time ($G^2 = 60.49$, $df = 30$, $p < 0.001$, Fig. 4). This was largely the result of large increases in the number of smaller sponges and differences in the abundance of size class I individuals between sites and over time. For 2000–2012, the mean abundance of individuals in size class I increased 275, 655, and 48% at CR15, CR20, and PR15, respectively. At CR30, there were initially zero individuals in size class I, however the density of this size class had increased by a mean (\pm SD) of 0.13 ± 0.04 sponges m^{-2} by 2012.

Considering all sites on Conch Reef collectively, the density of individuals in the Base, I, II, III, IV, and V stages changed by -33 , 800 , 200 , 18 , 43 , and 31% , respectively, for 2000–2012 (Fig. 5).

Recruitment significantly varied over time ($F_{1,8} = 78.43$, $p < 0.001$), between sites ($F_{3,8} = 4.83$, $p = 0.033$), and between sites over time (site \times time interaction: $F_{3,8} = 54.32$, $p < 0.001$; Table 2). Simple main effects indicated that recruitment was similar between sites for 2000–2006 ($F_{3,8} = 2.93$, $p = 0.099$) but significantly varied between sites for 2006–2012 ($F_{3,8} = 10.32$, $p = 0.004$). Over the second time interval, recruitment was significantly greater at CR20 and CR30 compared to CR15 and PR15 ($p < 0.05$ for all comparisons); all other comparisons between sites were not significant. Over time, recruitment significantly increased at all sites on Conch Reef (CR15: $F_{1,8} = 14.30$, $p = 0.005$; CR20: $F_{1,8} = 43.13$, $p < 0.001$; CR30: $F_{1,8} = 157.19$, $p < 0.001$), but decreased at Pickles Reef ($F_{1,8} = 26.77$, $p = 0.001$, Table 2).

Mortality of recruits significantly decreased over time ($G^2 = 7.27$, $df = 1$, $p = 0.007$) and did not differ between sites ($G^2 = 6.87$, $df = 3$, $p = 0.076$) or between sites over time ($G^2 = 3.94$, $df = 3$, $p = 0.269$). The number of sponges that recruited over a 6-year time interval and survived to the end of that interval changed by 50, 19, 136, and -28% for 2006–2012 compared to 2000–2006 at CR15, CR20, CR30, and PR15, respectively. For all sites on Conch reef, the number of sponges that recruited and survived increased by 76% (Table 2).

Mortality of the standing population was generally greatest for size class I and the base stage and generally decreased with sponge size (Fig. 6). Of the 239 sponges initially tagged in 2000, 78% survived to 2006 and 66% survived to 2012. Log-linear analysis indicated that mortality varied over time ($G^2 = 13.23$, $df = 6$, $p = 0.039$) and between sites ($G^2 = 30.82$, $df = 18$, $p = 0.030$), but the site \times time interaction was not significant ($G^2 = 20.85$, $df = 18$, $p = 0.287$, Table 3). When four-way tables were decomposed into three-way contingency tables for each state, mortality was found to decrease for the base stage ($G^2 = 4.11$, $df = 1$, $p = 0.043$) and size class V over time ($G^2 = 7.10$, $df = 1$, $p = 0.008$); for all other stages, mortality did not significantly vary over the two time intervals (Fig. 6). Between-site comparisons

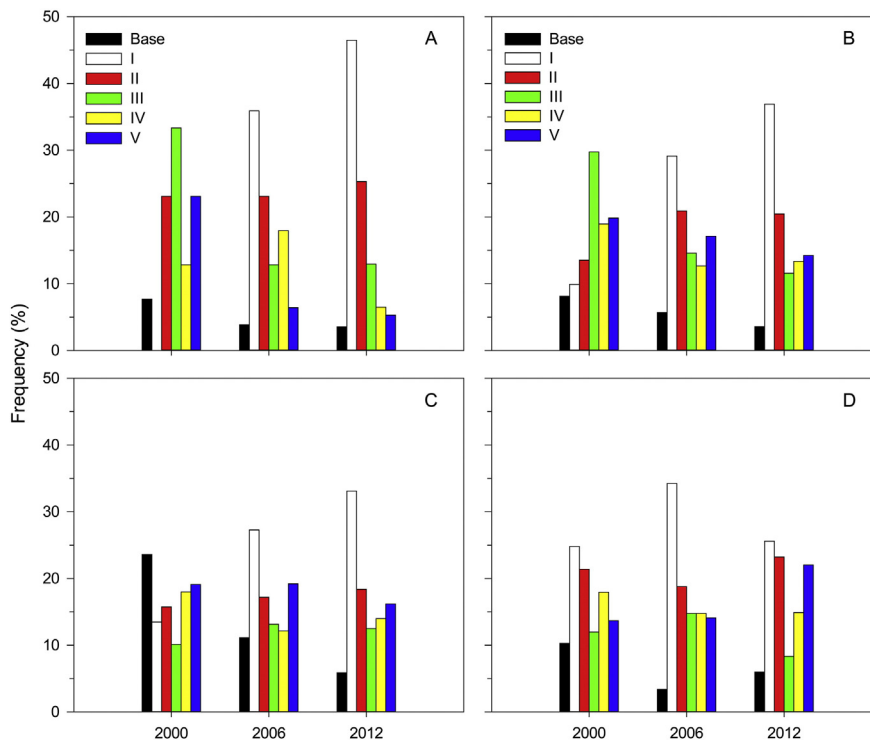


Fig. 4. Population structure of *Xestospongia muta* in 2000, 2006, and 2012 at (A) CR30, (B) CR20, (C) CR15, and (D) PR15 sites.

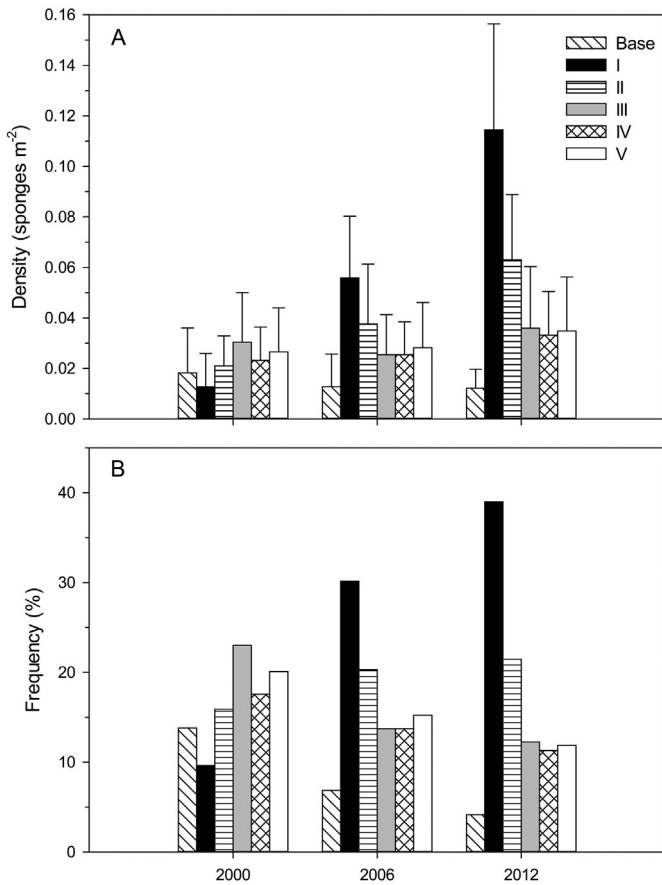


Fig. 5. Population structure of *Xestospongia muta* over all sites on Conch Reef in 2000, 2006, and 2012. (A) mean (\pm SD) density and (B) frequency of individuals in each of six stages. Sponges were assigned to stages based on volume or stage: bases are multi-oscule remnant-like individuals; stages I–V represent sponge size classes.

revealed significant differences in the mortality of size classes III ($G^2 = 12.42$, $df = 3$, $p = 0.006$) and IV ($G^2 = 10.9$, $df = 3$, $p = 0.012$); for all other stages, mortality did not significantly vary between sites. Mortality of size class III was greatest at CR30 (30%) and lowest at CR15 (0%), while mortality of size class IV was greatest at CR20 (17%) and lowest at PR15 (0%).

4. Discussion

For 2000–2012, populations of hard corals on reefs in the Florida Keys (Ruzicka et al., 2013; Toth et al., 2014) and elsewhere in the Caribbean (e.g. Edmunds, 2013) have continued to decrease in abundance due to a variety of stressors. In contrast, over the same time period, the density of *X. muta* has increased by 44% on Pickles Reef and has more than doubled (122% increase) on Conch Reef. Further, population growth was found to have accelerated for 2006–2012 compared to 2000–2006 at 3 of the 4 sites surveyed. These results are largely

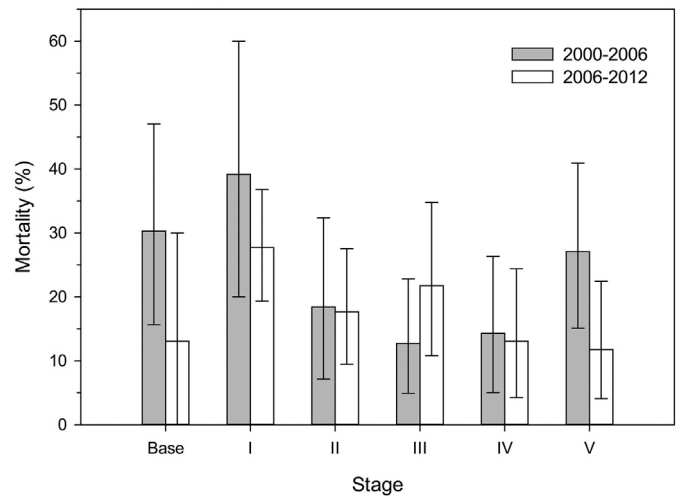


Fig. 6. Percentage mortality for each stage of *Xestospongia muta* over all sites on Conch Reef between 2000–2006 and 2006–2012. Error bars are 95% bootstrap confidence intervals.

consistent with those from the Florida Keys Coral Reef Evaluation and Monitoring Project (CREMP), which has documented significant increases of *X. muta* throughout the Florida Keys reef tract since CREMP monitoring of this species began in 2007 (Bertin and Callahan, 2008; R. Ruzicka pers. comm.). Given current rates of population growth, it is predicted that populations of *X. muta* will continue to increase under present conditions.

Although few studies have quantified the long-term dynamics of sponge populations on coral reefs over recent decades, these results support growing evidence that sponges are increasing on Caribbean coral reefs (Bell et al., 2013). In some cases, sponge populations have increased rapidly to dominate the benthic community (Aronson et al., 2002; Norström et al., 2009); however, more typically, population growth has been less pronounced, protracted, and has not led to defined shifts in benthic community structure (Colvard and Edmunds, 2011; Ruzicka et al., 2013; Villamizar et al., 2013; Ward-Paige et al., 2005). Further, on the basis of percentage cover, the metric typically used to monitor coral reef benthic community structure, significant changes in sponge abundance can be difficult to detect for slower-growing massive species (McMurray et al., 2010). In the Florida Keys, there have been two recent reports on the long-term changes in the cover of sponges. Toth et al. (2014) found that sponge cover increased from 1998 to 2011 at six sites at 15–18 m depths, but that this change was not significant; while a broader survey of 32 sites along the Florida Keys reef tract at 10–20 m depths found a significant increase in sponge cover over from 1999 to 2009 (Ruzicka et al., 2013). The disparity of these findings may reflect the inclusion of deeper sites surveyed by Ruzicka et al. (2013), as coral reef sponge abundance in shallow waters is generally low and limited by physical disturbance due to turbulence from storm events (Pawlik et al., 2015); not surprisingly, sponge cover remained unchanged at sites spanning 2–9 m depths (Ruzicka et al., 2013; Toth et al., 2014). Regardless, both studies suggest that increases in

Table 2
Recruitment of *Xestospongia muta* and recruit mortality over 6-year intervals at sites on Conch and Pickles Reefs.

Site	2000–2006			2006–2012			2000–06 vs 2006–12 Percent change in recruitment (%)
	Mean (\pm SD) recruits m^{-2}	Percent recruitment (%)	Percent recruit mortality (%)	Mean (\pm SD) recruits m^{-2}	Percent recruitment (%)	Percent recruit mortality (%)	
Conch	0.09 (0.04)	71.1	12.9	0.16 (0.06)	85.1	8.4	67.6
CR30	0.09 (0.05)	135.9	11.3	0.19 (0.05)	148.7	4.3	118.9
CR20	0.13 (0.02)	72.1	13.8	0.19 (0.02)	71.5	9.7	41.3
CR15	0.06 (0.04)	41.6	13.5	0.09 (0.04)	56.6	14.3	51.4
PR15	0.11 (0.01)	54.7	21.9	0.06 (0.02)	25.5	5.3	–40.6

The first row represents all depths on Conch Reef combined. Percent recruitment is equivalent to per capita recruitment over each time interval.

Table 3
Mortality of the standing population of *Xestospongia muta* over 6-year intervals at sites on Conch and Pickles Reefs.

Site	2000–2006		2006–2012	
	Mean (\pm SD) mortality m^{-2}	Percent mortality (%)	Mean (\pm SD) mortality m^{-2}	Percent mortality (%)
Conch	0.028 (0.014)	21.8	0.036 (0.021)	19.4
CR30	0.013 (0.008)	20.5	0.032 (0.006)	24.4
CR20	0.037 (0.013)	19.8	0.058 (0.016)	22.2
CR15	0.037 (0.003)	24.7	0.018 (0.014)	11.1
PR15	0.030 (0.005)	15.4	0.028 (0.003)	11.4

The first row represents all depths on Conch Reef combined.

sponge populations have been relatively gradual compared to well-documented shifts in the abundance of other benthic taxa (e.g. soft corals, corallimorpharians, macroalgae) that have occurred on some Caribbean coral reefs (Bruno et al., 2009; McManus and Polsenberg, 2004; Norström et al., 2009).

Both low mortality and high recruitment contributed to the population growth of *X. muta* for 2000–2012 and these findings are in direct contrast with those for reef-building corals, for which both recruitment failure and colony mortality have contributed to population declines (Edmunds and Elahi, 2007; Hughes and Tanner, 2000; Williams and Miller, 2011). Consistent with previous findings, both temporal and spatial patterns of mortality and recruitment were independent of sponge density (McMurray et al., 2010). There are few relevant comparative data for Caribbean sponge fauna, however sexual recruitment of *X. muta* is much lower than rates reported for fast-growing species (e.g. *Amphimedon compressa*, *Mycalaxia laxissima*), but generally greater than other relatively long-lived species (e.g. *Tectitethya crypta*, *Verongula reiswigi*). Also, mortality rates of *X. muta* are generally lower than rates for fast-growing species and approximate those for slower-growing species (Mercado-Molina et al., 2011; Reiswig, 1973).

Relative abundance aside, particularly striking is that population growth of *X. muta* has accelerated on Conch Reef. In fact, previous projections from population models, parameterized using data observed over 2003 to 2006, underestimate 2012 sponge densities by 27% (McMurray et al., 2010). A comparison of the demographics observed for 2000–2006 versus 2006–2012 indicates that the accelerated population growth observed on Conch Reef was driven by a combination of increased recruitment and decreased mortality. On Pickles Reef, population growth was relatively constant over time because, although sponge mortality decreased for 2006–2012 compared to 2000–2006, this site experienced decreased recruitment for 2006–2012.

Interestingly, while mortality of the standing population largely did not differ between sites, the increased recruitment and consequent accelerated population growth at Conch Reef sites were especially pronounced at deeper depths. Population growth and recruitment were similar between sites for 2000–2006, but were significantly greater at deeper sites (CR30, CR20) relative to shallow sites (CR15, PR15) for 2006–2012. When monitoring began in 2000, the density of sponges was lowest at CR30 and there were no individuals in size class I, suggesting historically low recruitment to this site. Since then, however, sponge density at CR30 has increased the most of any site (336%) due to high recruitment. While a historical mortality event may partially explain the initial low density at CR30, there is clear evidence that recruitment has increased for 2000–2012, suggesting that current rates of recruitment exceed historical baselines.

It is unclear why recruitment has increased on Conch Reef and why recruitment has become greater at deep relative to shallow sites. *X. muta* is oviparous and broadcasts eggs during mass spawning events, with reproduction occurring at least twice a year (McMurray et al., 2008; Ritson-Williams et al., 2004). Fecundity is likely very high (Fromont and Bergquist, 1994), eggs are negatively buoyant (Ritson-Williams et al., 2004) and unpalatable to fish predators (Lindquist and Hay, 1996), and larval dispersal is influenced by ocean currents

(López-Legentil and Pawlik, 2008). Sponge recruitment is dependent on larval production (Abdul Wahab et al., 2014a; Mariani et al., 2000); therefore, increases in recruitment may reflect an increase in the survivorship of the largest *X. muta*, which constitute the largest proportion of reproductive potential and may be enhancing the supply of viable larvae to the reef. Larval behavior and numerous physical factors affect sponge settlement (Abdul Wahab et al., 2014b; Maldonado, 2006; Mariani et al., 2006) and it may be that changes in coral reef benthic community structure have increased the availability of suitable substrate (Whalan and Webster, 2014; Whalan et al., 2012). Additionally, increased water temperatures may favor recruitment to deeper portions of the reef (Whalan et al., 2008). The time from settlement to observable size is unknown, however an increase in the survivorship of recruits at all sites suggests that early post-settlement survivorship may have increased as well (Keough and Downes, 1982). In some cases, sponge recruitment and recruit survival may be higher around adult sponges (Zea, 1993b), however the distribution of recruits relative to adult *X. muta* has been found to be random (Deignan and Pawlik, 2014). Given the long lifespan of *X. muta*, monitoring over longer temporal scales and at more reef locations will be necessary to ultimately determine whether these results represent a persistent change with broad geographic relevance, or stochastic variation in local recruitment (Caley et al., 1996).

Mortality remained low for all sites and was similar through time for the majority of stages; however, there was a significant decrease in mortality of bases and size class V. The decrease in mortality of the largest individuals likely reflects a decrease in the incidence of disease. In 2005, there was a relatively large mortality event of the largest individuals on Conch Reef due to the pathogenic-like condition sponge orange band (SOB) (Coward et al., 2006; McMurray et al., 2010); however, while observed consistently at other sites on the same reef, the incidence of SOB has remained low since the 2005 event. Another likely contributor to increased survivorship of size class V is the decreased hurricane activity experienced by the Florida Keys for 2006–2012 relative to 2000–2006. The year 2005 had a large number of intense storms, with tropical storm Dennis and hurricanes Wilma, Rita, and Katrina hitting the Florida Keys. Large sponges are particularly susceptible to detachment and subsequent mortality as the result of strong ocean surges and the movement of marine debris during storms (McMurray and Pawlik, 2009; Mercado-Molina and Yoshioka, 2009; Reiswig, 1973). Decreased mortality of bases also likely reflects a decrease in hurricane activity. Specifically, bases, which result from partial mortality, are particularly susceptible to mortality when sponges first transition to this stage and mortality has been observed to decrease over time as regeneration and growth occurs. Lower mortality of bases is hypothesized to reflect a decrease in sponges of other size classes suffering partial mortality and transitioning to this stage during 2006–2012 relative to 2000–2006.

Both the cover and volume of *X. muta* significantly increased at all sites for 2000–2012, and primarily occurred for 2006–2012. In addition to greater recruitment and survivorship for 2006–2012, and the growth of individuals in all size classes, increased cover and volume largely resulted from reduced mortality of the largest size class, which accounted for a significant portion of both population metrics. While the percentage cover of *X. muta* in 2012 was significantly greater than 2000 baselines at all study sites, this increase likely does not represent what would be defined as a phase shift in the benthic community structure of Florida coral reefs (Dudgeon et al., 2010). Nonetheless, this should not diminish the potential ecological significance of the population growth reported here, as volume is a more appropriate metric for assessing the functional roles of massive sponge species such as *X. muta*. Given the large increases in volume observed for 2000–2012, the functional role of *X. muta* on Florida coral reefs has likely become even more substantial.

The demographic changes in populations of *X. muta* for 2000–2012 suggest that conditions on Florida coral reefs were increasingly favorable for population growth. Sponges remained susceptible to many of

the same stressors negatively affecting coral populations, and there had been reports of localized declines of some sponge assemblages (e.g. Butler et al., 1995; Wulff, 2006), but evidence suggests that sponges have been relatively less affected by these stressors (Bell et al., 2014, 2015). On reefs off Brazil, many benthic taxa suffered mass mortalities as a result of thermal stress due to the 1997–1998 El-Niño Southern Oscillation, however sponge assemblages were largely unaffected and subsequently increased in abundance (Kelmo et al., 2013). A number of species have been found to be unaffected by changes in seawater pH and temperature that are predicted to occur by the end of this century (Bell et al., 2013; Duckworth et al., 2012; Simister et al., 2012; Webster et al., 2011), however, others, including *X. muta*, may have lower tolerance to increased seawater temperatures (López-Legentil et al., 2008; Massaro et al., 2012). Interspecific differences in resilience will likely lead to differences in the population trajectories of sponge species, as has been demonstrated for corals and other benthic taxa (Pandolfi et al., 2011). For example, Colvard and Edmunds (2011) found that the mean density of sponges on reefs of St. John, US Virgin Islands increased from 1992 to 2007; however, finer taxonomic analysis revealed that only 3 of the 4 sponge species considered had increased in abundance. It remains to be seen whether the increased cover of sponges along the Florida Reef tract (Ruzicka et al., 2013) is attributable to several species, or perhaps largely driven by increases in the abundance of *X. muta*, which is a dominant member of coral reef sponge communities in the Florida Keys and throughout the Caribbean (Loh and Pawlik, 2014; Southwell et al., 2008).

Large declines of sponge assemblages are known to have long-term effects on marine ecosystem function (Butler et al., 1995; Peterson et al., 2006). The implications of large increases in sponge populations, such as those reported here, are unclear, but may be expected to have similar effects on the function of coral reef ecosystems (Bell et al., 2013; González-Rivero et al., 2011). Growing recognition of the influence of sponges on water-column processes (de Goeij et al., 2013; Maldonado et al., 2012; McMurray et al., 2014; Southwell et al., 2008; Zhang et al., 2015) and the long-term population growth of *X. muta* reported here highlight the need to further consider the ecology of sponges on modern Caribbean coral reefs.

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