Population dynamics of giant barrel sponges on Florida coral reefs

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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

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 (Cowart 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 cm^3), size class II (>143.13 cm^3 but $\leq$1077.13 cm^3), size class III (>1077.13 cm^3 but $\leq$5666.32 cm^3), size class IV (>5666.32 cm^3 but $\leq$17,383.97 cm^3), and size class V (>17,393.97 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: $V_{sponge} = 28.514 \times$ 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: Base Diameter = $4.834 \times$ 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