Ecology, 91(2), 2010, pp. 560–570

Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys

Steven E. McMurray, Timothy P. Henkel, and Joseph R. Pawlik[1]

Department of Biology and Marine Biology, Center for Marine Science, University of North Carolina, Wilmington, North Carolina 28409 USA

Abstract. The structure of Caribbean coral reef communities has been altered by numerous anthropogenic and natural stressors. Demographic studies of key functional groups have furthered efforts to describe and understand these changes. Little is known, however, about the demographics of sponges on coral reefs, despite their abundance and the important functions they perform (e.g., increased habitat complexity, water filtration). We have monitored permanent plots on reefs off Key Largo, Florida, USA, to study the demography of a particularly important species, the giant barrel sponge, *Xestospongia muta*. From 2000 to 2006, population densities of *X. muta* significantly increased at sites on Conch Reef by a mean of 46% (range = 16–108%) and on Pickles Reef by a mean of 33%. In 2006, densities of *X. muta* on Conch Reef ranged from 0.134 to 0.277 sponges/m^2, and mean sponge volume was 1488 cm^3/m^2, with the largest size class of sponges constituting 75% of the total volume. Increased population density resulted from a significant increase in the number of sponges in the smallest size class. Recruit survival did not significantly change through time; however, a significant interaction between season and year on recruitment suggests that large recruitment pulses are driving population increases. Mean yearly recruitment rates ranged from 0.011 to 0.025 recruits·m^{-2}·yr^{-1}, with pulses as high as 0.036 recruits/m^2.

To explore the demographic processes behind the population increase and determine future population growth of *X. muta* under present reef conditions, a stage-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; however population growth may be negatively affected by continued mortality of the largest individuals from a recently described pathogenic syndrome.

Key words: demography; Florida Keys, USA; giant barrel sponge; invertebrate; matrix model; population dynamics; Porifera; Xestospongia muta.

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 anthropogenic influences of climate change, overfishing, eutrophication, and diseases (Halpern et al. 2008). The result has been significant changes in coral reef community structure and dynamics, particularly in the Caribbean (Gardner et al. 2003, Norström et al. 2009). Since the 1970s, populations of the historically dominant Caribbean framework-building coral, *Acropora* spp., have declined to threatened status (Precht et al. 2004, Federal Register 2006); in the 1980s, there was mass mortality of the herbivorous sea urchin *Diadema antillarum* (Lessios et al. 1984); and over the past several decades, populations of fish and other large consumers have been substantially reduced (Roberts 1995, Jackson et al. 2001). A better understanding of community dynamics on coral reefs has come from studies of groups that perform critical functional roles (e.g., reef-building corals, herbivorous fish; Bellwood et al. 2004). In this regard, studies of coral reef sponges have been notably lacking, especially considering their abundance and diversity on Caribbean coral reefs (Targett and Schmahl 1984, Suchanek et al. 1985).

Sponges filter large amounts of water, providing an important link in benthic–pelagic coupling (Southwell et al. 2008). Sponges also serve as habitat for numerous reef organisms (Henkel and Pawlik 2005), they are dominant competitors within the benthic community (Suchanek et al. 1985), and they harbor diverse assemblages of bacteria that can take part in nitrification and carbon fixation (Southwell et al. 2008). Surveys have provided distribution and abundance information for sponges on coral reefs (e.g., Targett and Schmahl 1984, Wilkinson 1987), but studies describing their population

---

Manuscript received 6 November 2008; revised 28 April 2009; accepted 30 April 2009. Corresponding Editor: R. B. Aronson.

[1] Corresponding author. E-mail: pawlikj@uncw.edu

dynamics have been limited (e.g., Reiswig 1973, Cropper et al. 2001). In particular, demographic studies that evaluate both the structure and dynamics of coral reef sponge populations have been lacking. Similar studies have provided insight into the underlying dynamics of changing coral populations (e.g., Hughes 1984, Hughes and Tanner 2000, Edmunds and Elahi 2007).

We have monitored the demographics of the giant barrel sponge *Xestospongia muta* since 1997 at sites off Key Largo, Florida, USA, 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 (Buettner 1996). Individual sponges can reach >1 m in height and diameter and live for hundreds to thousands of years (McMurray et al. 2008). Populations of this species occupy >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).

The Florida Keys reef tract was designated as a National Marine Sanctuary in 1990. As in the broader Caribbean, reefs in the Florida Keys have experienced dramatic reductions in coral cover since the 1980s (Gardner et al. 2003). More recently, mean coral cover has continued to decrease (from ~12% in 1996 to 6% in 2006); the cover of macroalgae and octocorals has fluctuated (mean cover in 2006 was ~10% and 12%, respectively), while sponge cover has remained at ~2% along the Florida Keys reef tract since 1996 (Callahan et al. 2007). The purpose of this study was to investigate the temporal and spatial demographic patterns of *X. muta* populations off Key Largo, Florida. Despite the reported stability of sponge cover along the Keys reef tract, our findings demonstrate that populations of *X. muta* on Pickles and Conch Reefs are remarkably dynamic.

METHODS

Study sites and monitoring

Populations of *X. muta* were studied at permanent 16 m diameter circular plots 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, as part of a long-term monitoring program begun in 1997. On Conch Reef, the *Aquarius* habitat was used as a diving platform to establish three plots at 15, 20, and 30 m depth (CR15, CR20, and CR30, respectively), and at Pickles Reef, three plots were established at 15 m depth (PR15). Within each plot, 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, monitoring was conducted twice per year at all plots. 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 with a digital camera from above and in profile. 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, with the slate displaying the unique tag number of each sponge and a 16-cm scale marker. The analyses presented herein are for data from 2000 to 2006, corresponding to the period for which digital images were available.

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 (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. Transition probabilities and stage-specific mortality rates were calculated from sponge fates over each interval. 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. Transition probabilities for each time interval were calculated from a data set of pooled transitions over the three depths on Conch Reef. Similarly, site summary matrices, $\mathbf{A}^{(\mathrm{CR15})}$, $\mathbf{A}^{(\mathrm{CR20})}$, $\mathbf{A}^{(\mathrm{CR30})}$, and $\mathbf{A}^{(\mathrm{PR15})}$ were constructed to investigate spatial patterns by pooling transitions over the two time intervals for each site. The population parameters λ and ρ and elasticities were calculated for each matrix using PopTools 2.7.5 (Hood 2006). The dominant eigenvalue, λ, describes the population growth rate and the damping ratio ($\lambda_1/|\lambda_2|$), ρ, 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 2009), we 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, λ describes the rate of decline of a population over time and is less than 1 (Hughes 1984).

Sponges were assigned to one of six categories based on sponge volume or stage: base, 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). Size classes were chosen to encompass the range of sponge sizes found in the population while minimizing sample and distribution errors (Caswell 2001). 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 (Appendix A). The equation used to calculate sponge (sp) volume from osculum diameter was determined to be: $V_{\mathrm{sp}} = 28.514 \times$ osculum diameter$^{2.1}$ ($P < 0.001$, $R^2 = 0.901$). 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: base diameter $= 4.834 \times$ osculum diameter$^{0.624}$ ($P < 0.001$, $R^2 = 0.835$; Appendix A).

The typical morphology of *X. muta* is cylindrical; however the base stage results from partial mortality and usually consists of a thin ring of multi-oscule remnants having a variable morphology (Appendix B). 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 five 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 λ across temporal and spatial scales (Appendix C). 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 $\mathbf{A}^{(\mathrm{CR}15)}$, $\mathbf{A}^{(\mathrm{CR}20)}$, $\mathbf{A}^{(\mathrm{CR}30)}$, and $\mathbf{A}^{(\mathrm{PR}15)}$ were similarly completed to examine population-level differences between sites (Appendix D). 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 three-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, we examined the role of observed recruitment on population growth by adding a recruitment vector, **r**, to the population vector at each projection interval (Hughes 1984). 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 **r**. The final two projections examined the demographic role of mortality and the potential of recruitment to regulate population size. To examine the demographic role of mortality, we projected differing matrices, $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$, with the same recruitment vector, $\mathbf{r}^{(00-03)}$. To examine the potential of recruitment to regulate population size, the same matrix, $\mathbf{A}^{(00-03)}$, was projected under the differing recruitment regimes, $\mathbf{r}^{(00-03)}$ and $\mathbf{r}^{(03-06)}$ (Hughes 1990).

Data analysis

Sponge density from 2000 to 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 were used; site was the between-subjects factor and year was the within-subjects factor. Post hoc multiple comparisons were conducted with a Bonferroni procedure. The assumption of sphericity was tested with Mauchly's test for all repeated-measures ANOVAs. If violated, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

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.

Sponge mortality from 2001 to 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 were 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 to 2006 was compared with the log rank (LR) test (Pyke and Thompson 1986).

The effects of time and location on sponge transitions were examined with log-linear models. Analyses were based on a four-way contingency table with the response variable fate, F, (six 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.

Randomization tests were used to determine whether population growth rate and the damping ratio differed between time intervals or locations (Appendix E). Bootstrap calculations were used to generate 95% confidence intervals for the population parameters (Appendix E). Analyses were conducted with SPSS (version 14.0.0 for Windows; SPSS, Chicago Illinois, USA).

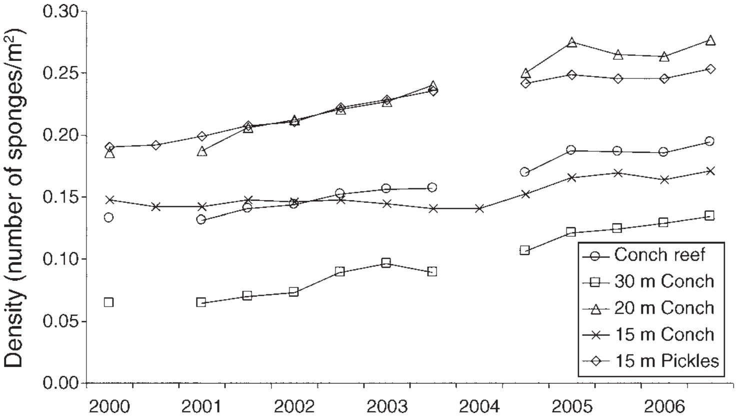

FIG. 1. Mean density of the giant barrel sponge, *Xestospongia muta*, at different depths at sites on Conch and Pickles Reefs, Key Largo, Florida, USA, from May 2000 to November 2006. Also plotted is the mean density over all sites on Conch Reef.

RESULTS

The number of sponges at all study sites significantly increased through time ($F = 30.448$, df $= 1.441, 11.529$, $P < 0.001$; Fig. 1). 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 $= 3, 8$, $P = 0.005$; Fig. 1). Post hoc tests revealed that both the CR20 and PR15 sites had significantly greater sponge densities compared to the CR30 site. The densities of sponges at CR15, CR20, CR30, and PR15 in spring 2000 were 0.148 ± 0.022, 0.186 ± 0.047, 0.065 ± 0.038, and 0.191 ± 0.021 sponges/m^2 (mean ± SD), respectively, compared to fall 2006 densities of 0.171 ± 0.045, 0.277 ± 0.035, 0.134 ± 0.074, and 0.254 ± 0.017 sponges/m^2.

As the density of sponges increased, the size–frequency distributions significantly changed (Fig. 2; Appendix F). The Conch Reef population and all sites individually became increasingly dominated by smaller sponges. 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 (Table 1). 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 (Table 1). Size–frequency distributions also significantly differed between sites (Appendix F).

The total number of recruits over each time interval increased over 2003–2006 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

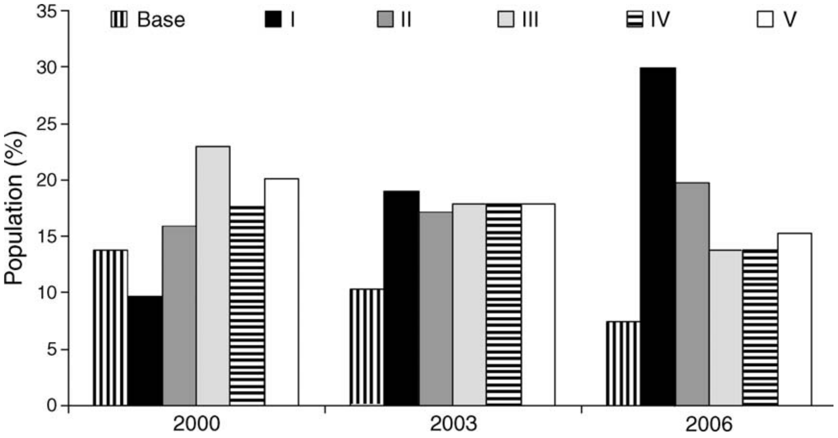

FIG. 2. Size–frequency distributions of *Xestospongia muta* over all sites on Conch Reef in 2000, 2003, and 2006. Sponges were assigned to one of six stages based on volume or stage: base (see Appendix B), size class I ($\leq$143.13 cm^3), size class II ($>$143.13 cm^3 but $\leq$1077.13 cm^3), size class III ($>$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).

TABLE 1. Summary matrices $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ for 2000–2003 and 2003–2006, respectively, for the giant barrel sponge, *Xestospongia muta* on Conch Reef, Key Largo, Florida, USA.

Stage/size class or statistic	Stage or size class (2000–2003)						Stage or size class (2003–2006)					
	Base	I	II	III	IV	V	Base	I	II	III	IV	V
Base	0.697	0	0.053	0.018	0.024	0	0.655	0	0.021	0.04	0.04	0.02
I	0.03	0.391	0	0	0	0	0.069	0.472	0.021	0	0	0
II	0.03	0.348	0.526	0.073	0	0	0.034	0.283	0.521	0.04	0	0
III	0.03	0	0.342	0.582	0.024	0	0	0	0.354	0.52	0.04	0
IV	0.061	0	0	0.291	0.714	0.042	0.034	0	0	0.32	0.56	0.02
V	0	0	0	0	0.19	0.875	0.034	0	0	0	0.22	0.78
q_x	0.152	0.261	0.079	0.036	0.048	0.083	0.172	0.245	0.083	0.08	0.14	0.18
n	33	23	38	55	42	48	29	53	48	50	50	50

Notes: Values are transition probabilities calculated by pooling transitions over all sites on Conch Reef. Zeroes indicate that there is a zero probability for a given stage to transition to the stage in question. The damping ratio, ρ, for the 2000–2003 Conch Reef is 1.155 (CI = 1.060, 1.317) and for 2003–2006 Conch Reef is 1.175 (CI = 1.027, 1.351). The dominant eigenvalue describing the rate of population depletion, λ, for the 2000–2003 Conch Reef is 0.923 (CI = 0.852, 0.974) and for 2003–2006 Conch Reef is 0.836 (CI = 0.756, 0.894). Other statistical abbreviations are: q_x, stage-specific mortality rate; n, sample size.

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, $P = 0.002$; Appendix G). The STP post hoc tests revealed that CR15 experienced significantly less recruitment compared to CR20. The yearly recruitment of sponges at CR15, CR20, CR30, and PR15 was 0.011 ± 0.010, 0.025 ± 0.010, 0.017 ± 0.016, and 0.018 ± 0.008 recruits·m^{-2}·yr^{-1}, 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, $P = 0.0002$; Appendix G). The largest pulse (0.028 ± 0.006 recruits/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, $P = 0.42$; Appendix G). Additionally, 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 on 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. 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, $P = 0.385$; Appendix H). Mortality was generally low and variable, ranging from 0.004 ± 0.004 to 0.01 ± 0.009 sponges·m^{-2}·yr^{-1} on Conch Reef. A relatively large mortality event occurred over the summer of 2005 when a mean of 0.02 sponges/m^2 died at CR20 due to a pathogenic condition (Cowart et al. 2006). The yearly mortality rates at CR15, CR20, CR30, and PR15 were 0.007 ± 0.005, 0.01 ± 0.008, 0.005 ± 0.004, and 0.001 ± 0.008 sponges·m^{-2}·yr^{-1}, respectively.

Transition matrices

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 1). Sponge mortality was generally greatest for size class I and the base stage (Table 1). For the 2003–2006 matrix, mortality of the largest size classes was also relatively high, with 14% and 18% mortality for size classes IV and V, respectively. Sponge growth generally followed an inverse relationship with sponge size (Table 1). Sponges in the base stage grew and contributed to all size classes, but not all transitions were observed in a given three-year interval. 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 at levels ranging from 0% to 5% over a given three-year interval (Table 1). Transitions for the site summary matrices followed similar

TABLE 2. Contributions of transitions to the accelerated population decline of the giant barrel sponge, *Xestospongia muta*, from 2000–2003 to 2003–2006 on Conch Reef.

Stage or size class	Stage or size class					
	Base	I	II	III	IV	V
Base	−0.0029	0.0000	−0.0006	0.0009	0.0025	**0.0138**
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	**−0.0273**	**−0.0171**
V	0.0023	0.0000	0.0000	0.0000	0.0043	**−0.0623**

Notes: Negative values indicate transitions that contributed to accelerated population decline and positive values indicate transitions that slowed population decline. The summation of all contributions approximates the observed difference in population growth rate, $\lambda^{(00-03)} - \lambda^{(03-06)}$, over the matrices compared ($\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$). Boldface values indicate contributions greater than ±0.01.

patterns to those described for $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$, but were more variable (Appendix I).

Given the size–frequency distributions among sites and years, transition probabilities were not significantly different between sites or time intervals. 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 ($\chi^2 = 24.04$, df = 12, $P = 0.02$). No mortality of size class II sponges was found at the 20-m Conch Reef site.

The rate of population depletion, λ, 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 1). Comparison of these rates indicated that population decline accelerated over the second time interval by 9.4%. Randomization tests revealed that this difference was not significant ($P = 0.069$). The damping ratio for $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ did not significantly change over time ($P = 0.841$; Table 1). Spatially, there was a direct relationship between λ and ρ and depth on Conch Reef, with the deepest site having the slowest rate of depletion and fastest rate of convergence to the stable stage distribution (Appendix I).

Elasticities of the Conch Reef summary matrices indicated that the stasis of the largest size class (V) has the greatest proportional influence on λ (Appendix J). In general, for a given stage, transitions into smaller stages (shrinkage) had smaller elasticities compared to transitions of growth and stasis. To compare the proportional contribution of each stage to λ, total elasticity was calculated by summing the elasticities for each stage (Appendix J). Total elasticities indicate that the largest size class has the greatest influence on λ. Total elasticities decreased with decreasing sponge size for both time intervals (Appendix J).

A life table response analysis was performed to identify the transitions that had the greatest influence on the decrease of λ over time for $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ and to identify the transitions responsible for differences in λ between $\mathbf{A}^{(CR15)}$, $\mathbf{A}^{(CR20)}$, $\mathbf{A}^{(CR30)}$, and $\mathbf{A}^{(PR15)}$ (Appendix C). 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 (Table 2). 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 (Table 2). Similarly, transitions of the largest size classes contributed the most to observed differences in λ between sites (Appendix C).

Projections indicated that the Conch Reef population behaved differently over the two time intervals. As

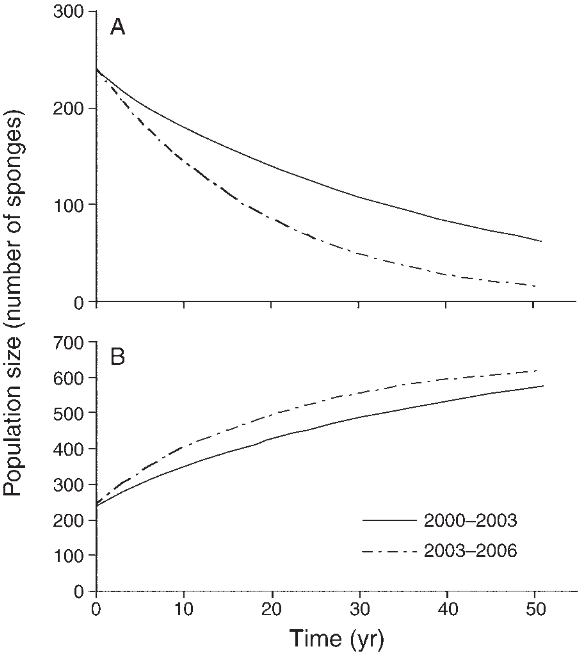

FIG. 3. Projections of the Conch Reef summary matrices $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ over 51 years (A) without recruitment of *Xestospongia muta* to observe the rate of population decline and (B) with the addition of a recruitment vector, **r**, at each iteration to observe the importance 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.

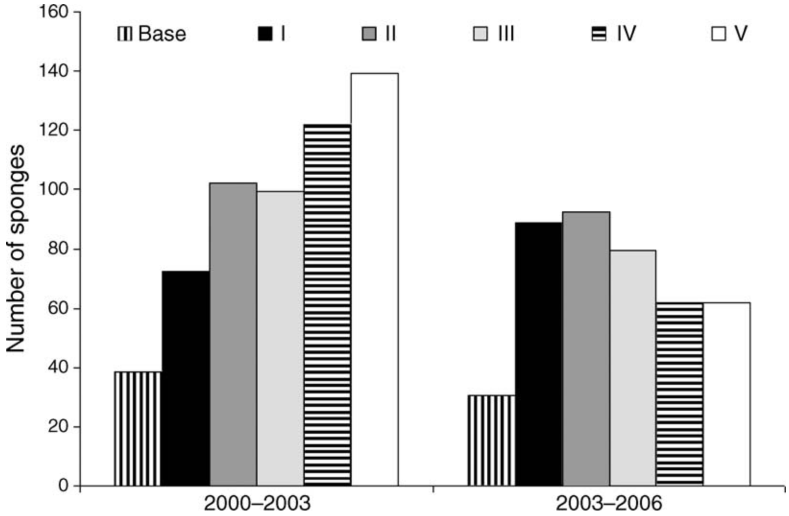

FIG. 4. Resulting population structure of *Xestospongia muta* after 51-year projections of $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ with addition of the same recruitment vector, $\mathbf{r}^{(00-03)}$. Projections demonstrate the effect of contrasting mortality regimes (2000–2003 compared to 2003–2006) on population size and the distribution of sponges in each size class.

expected from the dominant eigenvalues, λ, of $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$, the rate of population depletion accelerated over 2003–2006 compared to 2000–2003 (Fig. 3A). 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. 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. 3B). 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. The projected population structure of $\mathbf{A}^{(03-06)}$ was found to become increasingly positively skewed through time (Appendix D). Projections of the site summary matrices indicate that populations behaved differently over spatial scales (Appendix D).

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. Projections of $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ with the same recruitment vector, $\mathbf{r}^{(03-06)}$, allowed for comparison of population growth under different mortality regimes. Initial population growth rate and asymptotic population size was found to be greater under conditions of $\mathbf{A}^{(00-03)}$ (Fig. 4). In addition, the distributions of sponges in each size class 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. 4). 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. 5).

DISCUSSION

Populations of *X. muta* on Pickles and Conch Reefs are remarkably dynamic. At both reef sites and at the three depths studied, populations of *X. muta* significantly increased over a six-year period. In addition, projections indicate that the Conch Reef population is increasing at a faster rate (Fig. 3B). The faster rate of population increase over 2003–2006 compared to 2000–2003 is the result of a combined effect of increases in both recruitment and recruit survival. These findings

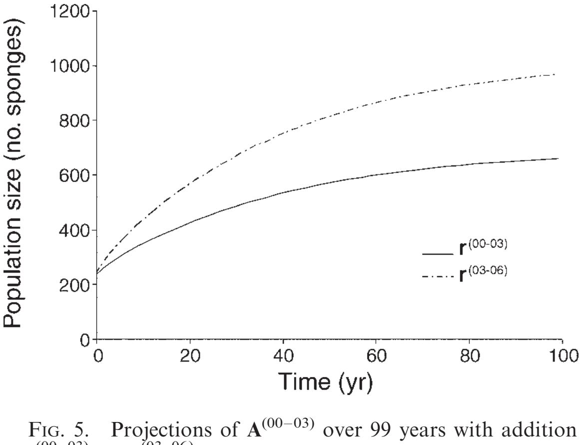

FIG. 5. Projections of $\mathbf{A}^{(00-03)}$ over 99 years with addition of $\mathbf{r}^{(00-03)}$ and $\mathbf{r}^{(03-06)}$. Projections demonstrate regulation of the population size of *Xestospongia muta* by recruitment.

contrast those for reef-building corals, for which recruitment failure has played a large role in population declines (Hughes and Tanner 2000). Additionally, a significant season × year effect on sponge recruitment rate suggests that variability over short temporal scales is important. Because adult sponge survival is relatively high, the effects of 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 population at Conch Reef over 2003–2006 compared to 2000–2003 is attributed to increased mortality of sponges in the largest size classes (Table 2). In 2005, mortality of many of the largest sponges at CR20 resulted from a pathogenic condition termed sponge orange band (SOB; Cowart et al. 2006). After symptoms of SOB appeared, most sponges died within six 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, 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 for *X. muta*. 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. Compared to 2000–2003, the standing population declined at a faster rate over 2003–2006, but the number of sponges that recruited and survived was greater over the latter period, resulting in greater increases than those observed over 2000–2003 (Fig. 3A, B). 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.

While sponge density increased throughout this study, both percentage cover and volume of *X. muta* did not significantly change (Appendix A). This is due to the proportionally high contribution of the largest sponges to these metrics. Increases of percent cover and volume 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 limitations of metrics that ignore size structure in describing the underlying dynamics of populations (Hughes and Tanner 2000).

Density, cover, and volume 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. Our density and volume estimates of 0.17 sponges/m^2 and 1.3 L/m^2, respectively, at 15-m depth on Conch Reef are in close agreement with findings by Southwell et al. (2008), who reported density and volume estimates of *X. muta* to be 0.20 sponges/m^2 and 2.33 L/m^2 at approximately the same depth on Conch Reef. Percent 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, predation, sedimentation, ultraviolet light, wave surge and hurricanes, disease, and nutrition. Post-settlement processes are likely to influence population structure, but fail to explain the temporal and bathymetric patterns observed on Conch Reef. Recruit and adult survival was similar among both temporal and spatial scales and independent of sponge density, suggesting that larval supply and settlement may be important determinants of population structure (Mariani et al. 2000).

The temporal increases of *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). In addition, projections of the same matrix under different recruitment regimes demonstrated the potential of recruitment to regulate population size (Fig. 5). 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). The fecundity of source populations as well as biotic and abiotic processes acting on larval stages significantly influence recruitment for broadcast-spawning coral species (Hughes et al. 2000).

If pre-settlement processes have a predominant effect on population structure, recruitment patterns should also correlate with adult populations over spatial scales. 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 obscure the relationship between recruitment and population size and the low density at CR30 may be an artifact of an historical mortality event (Caley et al. 1996). This hypothesis is supported by changes that were found to occur when recruitment is fixed and mortality is variable; population size was found to be larger under 2000–2003 conditions when both Conch Reef summary matrices were projected with the same recruitment vector (Fig. 4). The population level difference in the two matrices resulted from increased mortality of large individuals over 2003–2006. Alternatively, recruitment patterns may vary temporally among the spatial scales examined by this study (Caley et al. 1996). For example, the size–frequency distribution at CR30 in 2000 is deficient in size class I sponges compared to 2006 (Appendix F). This suggests that recruitment rates prior to this study may have differed with the rates currently observed. Populations of long-lived species such as *X. muta* are the product of many past recruitment events (Warner and Chesson 1985). Therefore, ultimate elucidation of the relationship between recruitment and population size will require monitoring over longer temporal scales or finer-scale population genetic techniques.

Ultimately, population dynamics and structure are likely governed by 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 our longest running plots (two plots established in 1997 and spring of 1998, respectively) at our 15-m site provide important historical insights. Specifically, a large mortality event (loss of 0.032 ± 0.011 sponges/m^2) 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 ± 0.014 sponges/m^2).

Under current conditions, projections indicate populations of *X. muta* will continue to increase, which may have both positive and negative implications for the Florida coral reef community. Populations may provide increased habitat for 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 (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 reminiralization 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. Finally, it has been shown that a population increase of one species, coincident with a decrease in the abundance of a dominant species, can result in a shift in community structure to a new state over relatively short temporal scales. On coral reefs, these "phase shifts" generally result from a decrease in the abundance of reef-building corals and an increase in the abundance of fast-growing opportunistic species (e.g., macroalgae, encrusting sponges; Norström et al. 2009). Decreases in the abundance of reef-building corals have occurred throughout the Florida Keys reef tract, but it remains to be seen whether a phase shift may occur as the result of population increases of slower-growing, longer-lived species such as *X. muta*.

While populations of *X. muta* are increasing, 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 the source of new recruits to downstream populations along the Florida Reef tract. 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 2009).

Evidence suggests that anthropogenic and natural disturbances of sponge populations are increasing and that these disturbances can have long-term ecosystem-level effects (Butler et al. 1995). Diseases affecting coral reef sponges have been observed more frequently over the last decade (Webster 2007), including one targeting *X. muta* (Cowart et al. 2006). In addition, *X. muta* is particularly vulnerable to damage and mortality from vessel groundings and marine debris (Schmahl 1999, Chiappone et al. 2005). Finally, on a broader 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. The demographic data on *X. muta* provided by this study may be helpful in detecting anthropogenic influences on coral reefs in future comparative analyses.

ACKNOWLEDGMENTS

This study was funded by grants to J. R. Pawlik from the National Undersea Research Program at UNCW (NOAA NA96RU-0260) and from the National Science Foundation, Biological Oceanography Program (OCE-0095724, 0550468).

Particular thanks to the staff of NOAA/NURC in Key Largo, Florida, for logistical support. Assistance in the field was provided by Alan Bright, Jonathan Cowart, Sebastian Engel, Nick Foster, James Gavin, Adam Jones, Sarah Kelly, Wai Leong, Susanna López-Legentil, Tse-Lynn Loh, Greg McFall, Shobu Odate, Will O'Neal, Sven Rhode, David Swearingen, Kyle Walters, and Kristen Whalan.

LITERATURE CITED

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. Nature 429:827–833.

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, USA.

Caswell, H. 2001. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.

Chiappone, M., H. Dienes, D. W. Swanson, and 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.

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 condition of the giant barrel sponge *Xestospongia muta*. Coral Reefs 25: 513.

Cropper, W. P., Jr., 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.

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.

Federal Register. 2006. Endangered and threatened species: Final listing determinations for Elkhorn and Staghorn Corals. Federal Register Notice 71(89):26852–26872.

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.

Halpern, B. S. et al. 2008. A global map of human impact on marine ecosystems. Science 319:948–952.

Henkel, T. P., and J. R. Pawlik. 2005. Habitat use by sponge-dwelling brittlestars. Marine Biology 146:301–313.

Hood, G. M. 2006. PopTools. Version 2.7.5. ⟨http://www.cse.csiro.au/poptools⟩

Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. 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., 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.

Jackson, J. B. C. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

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.

Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science 226:335–337.

López-Legentil, S., and J. R. Pawlik. 2009. Genetic structure of the Caribbean giant barrel sponge *Xestospongia muta* using the I3-M11 partition of COI. Coral Reefs 28:157–165.

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.

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.

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. 2009. A novel technique for the reattachment of large coral reef sponges. Restoration Ecology 17:192–195.

Norström, A. V., M. Nyström, J. Lokrantz, and C. Folke. 2009. Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Marine Ecology Progress Series 376:295–306.

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.

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. 1973. Population dynamics of three Jamaican Demospongiae. Bulletin of Marine Science 23:191–226.

Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. Conservation Biology 9:988–995.

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., USA.

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. Third edition. W. H. Freeman, New York, New York, USA.

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). National Oceanic and Atmospheric Administration, National Undersea Research Program, Rockville, Maryland, USA.

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. Technical Memorandum OAR NURP-1. National Oceanic and Atmospheric Administration, Rockville, Maryland, USA.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 125:769–787.

Webster, N. S. 2007. Sponge disease: A global threat? Environmental Microbiology 9:1363–1375.

Wilkinson, C. R. 1987. Interocean differences in size and nutrition of coral reef sponge populations. Science 236:1654–1657.

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.

APPENDIX A

Additional methods and results of percent cover and volume determinations (*Ecological Archives* E091-040-A1).

APPENDIX B

Digital images depicting the transition of the base stage (*Ecological Archives* E091-040-A2).

APPENDIX C

Additional methods of life table response analysis and results for site summary matrices (*Ecological Archives* E091-040-A3).

APPENDIX D

A figure depicting the projected population structure under the conditions of $\mathbf{A}^{(03-06)}$; and projections of the site summary matrices $\mathbf{A}^{(\mathrm{CR15})}$, $\mathbf{A}^{(\mathrm{CR20})}$, $\mathbf{A}^{(\mathrm{CR30})}$, and $\mathbf{A}^{(\mathrm{PR15})}$ (*Ecological Archives* E091-040-A4).

APPENDIX E

Additional methods of randomization tests and bootstrap calculations (*Ecological Archives* E091-040-A5).

APPENDIX F

Size–frequency distributions at each site in 2000, 2003, and 2006; and results of log-linear analysis of Conch Reef size–frequency data (*Ecological Archives* E091-040-A6).

APPENDIX G

A figure depicting recruitment over time at study sites and a figure depicting the survival of yearly cohorts (*Ecological Archives* E091-040-A7).

APPENDIX H

A figure depicting mean mortality over time at the study sites (*Ecological Archives* E091-040-A8).

APPENDIX I

Site summary matrices $\mathbf{A}^{(\mathrm{CR15})}$, $\mathbf{A}^{(\mathrm{CR20})}$, $\mathbf{A}^{(\mathrm{CR30})}$, and $\mathbf{A}^{(\mathrm{PR15})}$ and additional results (*Ecological Archives* E091-040-A9).

APPENDIX J

Elasticity matrices of the Conch Reef summary matrices $\mathbf{A}^{(00-03)}$ and $\mathbf{A}^{(03-06)}$ and a figure depicting total elasticity for each size class (*Ecological Archives* E091-040-A10).