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Population dynamics of **Montastraea** *spp.*
in the Florida Keys' Fully Protected Zones: modeling future trends

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Abstract

In this study we evaluated patterns of changes in populations of the key reef-building coral species, *Montastraea "annularis"* specis complex and *Montastraea cavernosa* at four sites in the Florida Keys. Recruitment, mortality, growth and shrinkage rates of coral colonies located in permanent quadats at two depths at each site were used to formulate population models based on transition probability matrices. The models for both taxa indicate that low recruitment rates, and high mortality and shrinkage rates resulted in predicted population declines, dropping below 50% of the initial population size in the next 7-10 years. In addition, we assessed the population structure of these two species at our sites in 1998 and 2003 by extracting size frequency distributions of colony sizes from random video transect records. We could not detect any changes in the distributions from 1998 to 2003. Two of our sites were within Fully Protected Zones (Western Sambo Ecological Reserve and Eastern Sambo Research Only Area) and we could not detect differences between these sites and the two adjacent unprotected areas at Middle Sambo and Pelican Shoal. Lack of normality in the data sets limited our analyses and future efforts, using more transects per site, may help to resolve patterns of change and differences between protected and unprotected sites.

A. Introduction

Recent reports have highlighted concerns about the continued decline of coral populations in the Florida Keys and best practices for management in this era (Jameson et al. 2002; Andrews et al. 2005). Extensive monitoring programs have shown localized loss of coral diversity as well as coral coverage along the length of the Keys since 1996 (Wheaton et al. 2001; Beaver et al. 2004). Earlier reef monitoring programs from the 1970's and 1980's documented the loss of *Acropora cervicornis* and *Acropora palmata*, ostensibly to disease (Dustan 1985; Dustan and Halas 1987; Jaap et al. 1988; Miller et al. 2002), but through this period the important reef-building coral *Montastraea "annularis"* (*sensu lato*: referring to the three sibling species of the complex in aggregate, Weil and Knowlton 1994) had maintained or increased its coverage at some locations (Jaap et al. 1988). A recent data set on *M. "annularis"* shows a slight decline from 1996 to 2001 (Wheaton et al. 2001) on a Keys-wide basis, although the drop from 1998 to 1999 followed the passages of Hurricanes Georges and Mitch in 1998. As compelling as these results appear, it is important to understand that these patterns are not uniform across sampling sites or through time, with some sites losing coral and others gaining on a multi-year temporal scale. Also, Miller et al. (2001) reported many healthy coral-dominated reefs along the Florida reef tract in 2001. This spatio-temporal patterning has been documented in other reef systems as well (Edmunds and Bruno 1996).

It is difficult to determine whether there has been a decline in coverage of a key coral species like *M. "annularis"* from the 1970's to the present because of a lack of continuity in monitoring at specific sites, and because of different methods and levels of replication used at different times. For example, Dustan and Halas (1987) noted an overall decline in coverage from 17.9% in 1975 to 10.1 % in 1982 on the Carysfort inner fore-reef terrace. In surveys at the same location in 1992 and 1993, Aronson et al.(1994 and unpublished data) determined coverage to be 13.3% and 14.9% respectively. It is unequivocal that coverage on the four permanent transects surveyed by Dustan and Halas declined, but we cannot know if the coverage estimates and trend over time are truly representative because of the small sample size in this earlier study. The larger sets of 10 randomized video transects taken in 1992 and 1993 have higher statistical power with which to assess trends over time. Murdoch and Aronson (1999) employed this survey method on spur-and-groove reefs at 13-15 m depth on a Keys-wide scale and showed clearly that *Montastraea* spp. were the predominant corals in 1995 and the importance of the scale of sampling necessary to evaluate patterns of coverage within this zone.

The FKMS established a network of protected zones, ecological reserves and Sanctuary Protected Areas along the Florida Reef Tract in 1997. These areas are collectively referred to as Fully Protected Zones or FPZs. Our research teams began a project in 1998 to evaluate the relationships between coral reef community structure (cover and species composition) and population ecological processes (coral recruitment and juvenile coral colony mortality) with respect to no-take management (Aronson et al. 2001; Smith et al. 2005). The project was funded by NOAA's Coastal Ocean Program through 2005. The design used the techniques of video monitoring and permanent photo-quadrats to support a hypothesis-driven research program. The sites included four no-take marine reserves, fully protected from extractive uses, and four adjacent reference sites

where extractive uses are permitted. Our results to date indicate no consistent evidence of increase or decrease in coral coverage or recruitment at the no-take sites compared to the reference areas (Aronson et al. 2001; Smith et al. 2005), in contrast to results of the WQPP EPA project, which has described declines in coral cover at protected and unprotected sites over the same period (Wheaton et al. 2001; Beaver et al. 2005).
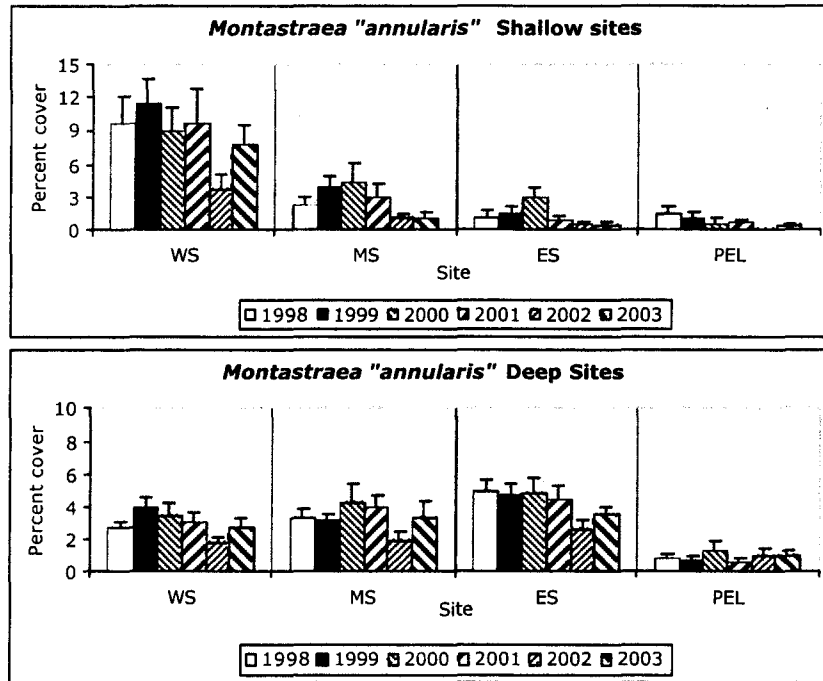

Figure 1. Mean percent coverage ($\pm$ SE) by *Montastraea "annularis"* at protected sites (WS = Western Sambo, ES= Eastern Sambo) and reference areas (MS= Middle Sambo, PEL = Pelican Shoal). The time series runs from 1998 to 2003. Shallow: 7-9m; Deep: 14-18m.

Our results show patterns of stability for populations of several coral species (e.g. *M. "annularis"*; Fig. 1) when assessed in terms of coverage. Some taxa have shown consistent recruitment and survival of juvenile corals (poritids, agariciids, *Siderastrea* spp.), but other species have shown remarkable recruitment failure in the Keys, particularly massive reef-building corals such as *M. "annularis"*. Only eighteen new recruits of *M. "annularis"* have been observed in 384 permanent quadrats (a total area of 237 m^2) from 1998 to 2003. The challenge is to understand these patterns in a meaningful way that helps predict future population trajectories. We believe that tracking trends in coverage over time is a useful monitoring approach but the trends have to be explored further with assessments of population structure and population modeling, based on recruitment and survival of individual corals over appropriate temporal and spatial scales. In our proposal we outlined how products of this project (recruitment data, time series of photographic records of individual colonies) were available to develop population models of two key reef-building corals (*M. "annularis"* and *M. cavernosa*) at four sites in the Lower Keys using data from 1998 to 2003.

Population models based on demographic trends are powerful tools that have been applied successfully to reef corals (Babcock 1991; Lasker 1991; Hughes 1996; Fong and Glynn 1998; Hughes and Tanner 2000). Hughes and Tanner (2000) have clearly shown the precarious status of some coral populations in Jamaica, where recruitment rates are low to nonexistent and rates of asexual growth are no longer sufficient to sustain the populations. As adult colony mortality rates reduce population size, the trend is towards localized extinction due to recruitment failure. Historically, massive reef-building corals (such as *Montastraea* spp.) fit a *K*-selected life history, in which adult longevity offset low recruitment rates to provide population stability. However, under the current environmental regime in the Keys (reduced water quality, bleaching stress and increasing disease incidence; Santavy et al. 2005), Florida's adult corals may be losing the battle for long-term survival. Population models, based on transition matrix methods, use empirically-derived recruitment, survival and growth rates to simulate future population trends (Hughes and Tanner 2000).

A key point of concern about the long-term survival of *Montastraea* spp. colonies is an appreciation of the relationship between coral size and fecundity (Szmant 1991). Partial mortality reduces coral size and may shift a colony from high to low fecundity or even sexual immaturity. Hughes et al. (2000) demonstrated how important fecundity is to local recruitment. However, coral coverage and fecundity are not necessarily correlated. That is, a local population dominated by many smaller colonies with high coverage will have much lower fecundity rates and produce fewer propagules compared to a population dominated by fewer but much larger and more fecund colonies, with lower coverage. If Florida's corals are declining in coverage, via partial mortality in response to agents such as diseases or bleaching, then a concomitant reduction in fecundity will ensue and recruitment rates will also be reduced. The rare largest colonies have a strongly disproportionate effect on the gene pool of any new recruits, because of their high fecundity (Hughes et al. 1992). Thus it is important, over time, to see many coral colonies within a population continuing to grow to large size classes, with increased fecundity that adds to the genetic diversity of new recruits.

Another recent approach to assess the status of coral populations has been to examine population size structure (Bak and Meesters 1998; Meesters et al. 2001; Webster and Smith 2002). The size-frequency distribution curve for a species can indicate the relative proportion of small and large colonies in a particular area and can be interpreted as an index of successful recruitment and survival of juvenile corals and well as the survival of older adult colonies (Meesters et al. 2001; Webster and Smith 2002). The frequency distribution curves and shape parameters (skewness and kurtosis) are used to compare statistically between sites or between species. Changes in the structure of the curves over time can also be evaluated statistically to assess temporal changes and estimate population trajectories. In our proposal we sought to determine if our video transect records could be used to derive population structure data for *M. "annularis"* and *M. cavernosa* and whether trends over time could be detected from 1998 to 2003. We also sought to evaluate the changes in the broader spatial scale patterns of distribution of *Montastraea* spp. at our study sites as a context for the patterns of change observed in the permanent quadrats.

B. Methods

The study sites were located in the Lower Keys and included two Fully Protected Zones (Western Sambo Ecological Reserve, Eastern Sambo Research Only Area) and two unprotected reefs (Middle Sambo and Pelican Shoal) chosen as reference sites with which to evaluate potential benefits of the FPZs in our COP project. At each site there were 32 quadrats at each of two depths, 7-9m and 15-18m. Each quadrat was 95 x 65cm.

Coral population dynamics: recruitment, growth and survival

We analyzed changes in two-dimensional areas of images of *Montastraea* colonies (>5 cm diameter) in the permanent quadrats from 1998 to 2003. Each image was processed in Adobe Photoshop to enhance the clarity and contrast of the colony margins. Each colony image was measured three times using a digital planimetry program (Carnoy 2.0), reducing measurement error to about 1%. The colonies were measured in 1998, 1999, 2000, 2001, 2002 and 2003. If a colony was not observed in one year (either not visible or due to a missing photograph) but appeared the following year it was assigned the size it had in the year prior to the missing year. The analyses generated annual size-specific rates of mortality, shrinkage and growth for *Montastraea "annularis"* and *M. cavernosa*. The *"annularis"* colonies were all *M. favelota* and *M. franksi*, as well as could be determined from the photographs, but uncertainty in identification of the small colonies required that all the colonies be pooled as *"annularis"*.

Recruitment rates and juvenile colony (=5cm diameter) growth and mortality rates were derived from the COP project analyses of changes in the permanent quadrats and were included in the models. Recruitment rates were determined from the annual visual censuses of the 128 permanent quadrats at the 4 sites representing an area of approximately 80 m². The average diameters of the juvenile colonies in the quadrats were measured directly in the field using calipers (±1mm). The rates of recruitment, and colony growth, shrinkage, stasis or mortality over the five yearly intervals were used to develop transition matrices and population models following the methods of Hughes and Tanner (2000). The models were run using MatLab software.

We marked 7 or 8 larger colonies (20 cm to 2-4 m diameter) of each *Montastraea* species at each depth at each site. These supplemental colonies were located in the area of the permanent photo-quadrats. The colonies were videotaped with a scale bar adjacent to each colony. An image of each colony was extracted from the video records and the two-dimensional surface area determined by planimetry as described above.

Coral population size structure

We constructed size-frequency distributions of colonies of *M. "annularis"* and *M. cavernosa* from the video transect data series using data from 1998 and 2003. Ten haphazardly located 25 m x 0.4 m transects were recorded at both the shallow and deep sites. Transects were laid along the axes of relict spurs. Digitized video frames containing the *Montastraea* colonies were extracted from the video records and each target coral's 2-dimensional area determined by planimetry using Carnoy 2.0 as described above. Sufficient ambiguity in trying to identify the smaller colonies (as either *favelota*, *franksii* or *annularis*) required that we pooled all colonies as *"annularis"*.

Statistical analyses followed the procedures outlined in Meesters et al. (2001) using NCSS software. The data were log-transformed and tested for normality with the Shapiro-Wilk W test. Changes in the size-frequency distributions for both M. "annularis" and M. cavernosa at each site from 1998 to 2003 were assessed using two sample Kolmogorov-Smirnov tests. Changes in the size-frequency distribution curve parameters (skewness and kurtosis) were compared for each species at each site between 1998 and 2003. The M. "annularis" colonies were divided into 9 size classes (< 50 cm^2, 51-100 cm^2, 101-200 cm^2, 201-400 cm^2, 401-600 cm^2, 601- 800 cm^2, 801 -1000 cm^2, 1001-2000 cm^2 and >2000 cm^2). The M. cavernosa colonies were divided into 8 size classes (< 50 cm^2, 51-100 cm^2, 101-200 cm^2, 201-400 cm^2, 401-600 cm^2, 601-800 cm^2, 801-1000 cm^2, 1001-2000 cm^2). The similarity of the size class distributions for each species at each site between 1998 and 2003 was compared by Spearman rank correlations.

Results
Coral population model for M. "annularis".

The patterns of survival, and growth or shrinkage of colonies of M. "annularis" in the permanent quadrats were assessed at the deep sites from 1998 to 2003. Many of these colonies were obvious fragments of adjacent larger colonies but their fates were treated individually. The initial population of colonies greater than 5 cm^2 in 1998 was 85, of which only 52 survived over the five years. The initial population of colonies less than 5 cm^2 was 16, which turned over frequently and was reduced to 7 in 2003. The number of colonies available for measurement varied each year depending on several factors: fusion or fission of colonies during the year, visibility in the photographs or lack of photographs, especially in 2001 when no photographs were taken at Middle Sambo. During this period the annual recruitment rates were 2, 4, 4, 2, and 6 per year in 1998-1999, 1999-2000, 2000-2001, 2001-2002 and 2002-2003 respectively.

The individual colonies present and measureable each year were placed in the following six size categories: < 5 cm^2, 5.1- 10 cm^2, 10.1 – 50 cm^2, 51 – 100 cm^2, 101 – 200 cm^2 and > 200 cm^2. The largest observed colonies in the quadrats were about 460 cm^2. The fate of each colony was assessed from year to year in terms of remaining in the same size class (within a 1% measurement error), growth out of a size class, shrinkage to a smaller size class, or complete mortality. For each size-class the pooled changes for all colonies occurring in that size class across the five annual assessment periods (1998-1999, 1999-2000, 2000-2001, 2001-2002, 2002-2003) were used to determine the probability of remaining in the specific size class (stasis), probability of growth to a higher size-class, probability of shrinkage to a lower size class and the probability of mortality, q_x. These probabilities represent an average value for each category of change over a five year period. The probability matrix is presented in Table 1.

The probabilities of stasis, growth, shrinkage and mortality for each of the six size classes were used to formulate a transition matrix with which to simulate progressive changes over time in the populations of colonies in each size class on an annual basis. A simple model was iterated for 15 years using the same probability transition matrix in each year. The model output for each year was the calculated number of colonies in each

size class and these data used as the starting population for the next model iteration. The only variable in each model year was the recruitment rate, randomly selected from one of the five possible rates (2, 4, 4, 2, or 6 new colonies/year) observed over the 5-year study. The new colonies were added to the smallest size class at the beginning of a model year.

Table 1. Transition matrix for *M. "annularis"* colonies at the four deep sites. Probabilities are averaged values over a five year period from 1998 to 2003 in six colony size classes (in cm^2). The initial *n* values are the number of colonies observed in that class over the five years (1998 to 2003).

Classes	=5	5.1 to 10	10.1 to 50	50.1 to 100	101 to 200	>200
=5	0.389	0.087				
5.1 to 10	0.14	0.565	0.131			
10.1 to 50		0.188	0.676	0.195		
50.1 to 100			0.089	0.646	0.258	
101 to 200				0.097	0.661	0.123
>200					0.081	0.837
Mortality, q_x	0.474	0.159	0.103	0.061	0	0.041
Initial *n*	57	69	145	82	62	49

The main-diagonal values represent stasis, or the probability of remaining in the same class. The bottom number in each column represents the probability of growth up to the next highest size class and the upper numbers are the probabilities of shrinking down to the next lowest size class. The relatively high probability of mortality [(1- (stasis - growth - shrinkage)] in each size class, combined with low probability of growth into higher size classes and a very low recruitment rate, resulted in declines in all size classes over the 15-year model run (Figure 2). The population shrank to less than 50% of the initial size by Year 10.
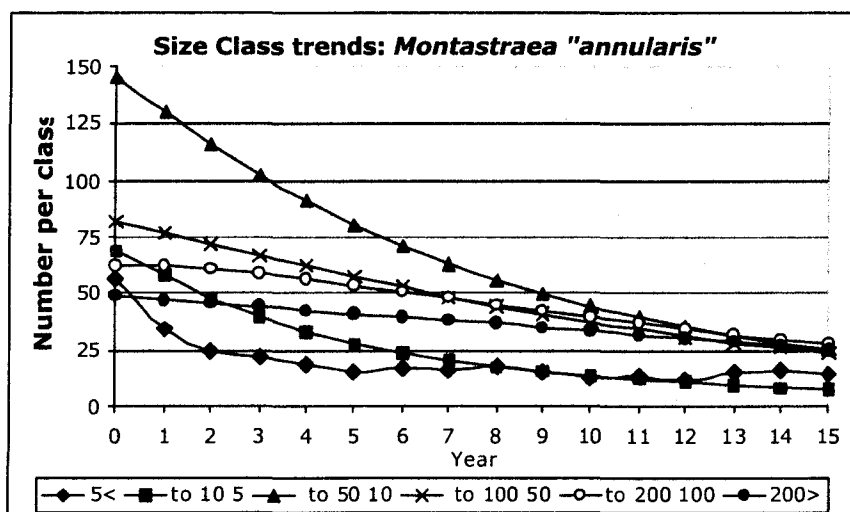

Figure 2. Model simulation of changes in number of *M. "annularis"* colonies in six colony size classes (in cm^2) over a 15 year run. Recruitment rates were varied each year.

Coral population model for M. cavernosa

The patterns of survival, growth or shrinkage of colonies of *M. cavernosa* in the permanent quadrats were assessed at the deep sites from 1998 to 2003. Nearly all the colonies remained whole through the study period with very little fission or fusion The initial population of colonies greater than 5 cm^2 in 1998 was 36 colonies, of which 18 survived over the five years. The initial number of colonies less than 5 cm^2 was 90, which turned over frequently and was reduced to 85 in 2003. The number of colonies available for measurement varied each year depending on visibility in the photographs or lack of photographs, especially in 2001 when no photographs were taken at Middle Sambo.

The individual colonies present and measureable each year were placed in the following six size categories: < 5 cm^2, 5.1- 10 cm^2, 10.1 – 50 cm^2, 51 – 100 cm^2, and >100 cm^2. The largest observed colonies in the quadrats were about 400 cm^2. The fate of each colony was assessed from year to year in terms of remaining the same (within a 1% difference between years), growth out of a size class, shrinkage into a smaller size class or mortality. For each specific size-class the pooled changes for all colonies occurring in that size class across the five annual assessment periods (1998-1999, 1999-2000, 2000-2001, 2001-2002, and 2002-2003) were used to determine the probability of remaining in the specific size class, probability of growth to a higher size-class, probability of shrinkage into a lower size class and the probability of mortality, q_x. These probabilities represent an average value for each category of change over a 5-year period. The probability transition matrix is presented in Table 2.

The probabilities of stasis, growth, shrinkage and mortality for each of the five size classes were used to formulate a transition matrix with which to simulate progressive changes over time in the populations of colonies in each size class on an annual basis. A simple model was iterated for 15 years using the same probability transition matrix in each year. The model output for each year was the calculated number of colonies in each size class and the outputs used as the starting population for the next model iteration. In each model year the recruitment rate was randomly selected from one of the five possible rates (53, 23, 25, 42, and 27 new colonies/year in 1998-1999, 1999-2000, 2000-2001, 2001-2002, and 2002-2003 respectively) observed over the 5-year study and these new colonies were added to the smallest size class at the beginning of a model year. Similarly, the probability of mortality for the =5 cm^2 colonies was randomly selected from the five annual rates determined from the visual census data from 1998 to 2003 (0.24, 0.15, 0.41, 0.38, and 0.12 in 1998-1999, 1999-2000, 2000-2001, 2001-2002, and 2002-2003 respectively).

The diagonal values of the transition matrix again represent stasis, or the probability of remaining in the same class. The bottom number in each column represents the probability of growth up to the next highest size class and the upper numbers are the probabilities of shrinking down to the next lowest size class. The relatively high probability of mortality in each size class, combined with low probability of growth into higher size classes, resulted in declines in all size classes over the 15 year model run (Figure 3). The population shrank to less than 50% of the initial size by Year 7.

Table 2. Transition matrix for *M. cavernosa* colonies at the four deep sites. Probabilities are averaged values over a five year period from 1998 to 2003 in five colony size classes (in cm^2). The initial *n* values are the total number of colonies observed in that class over the five years (1998 to 2003)

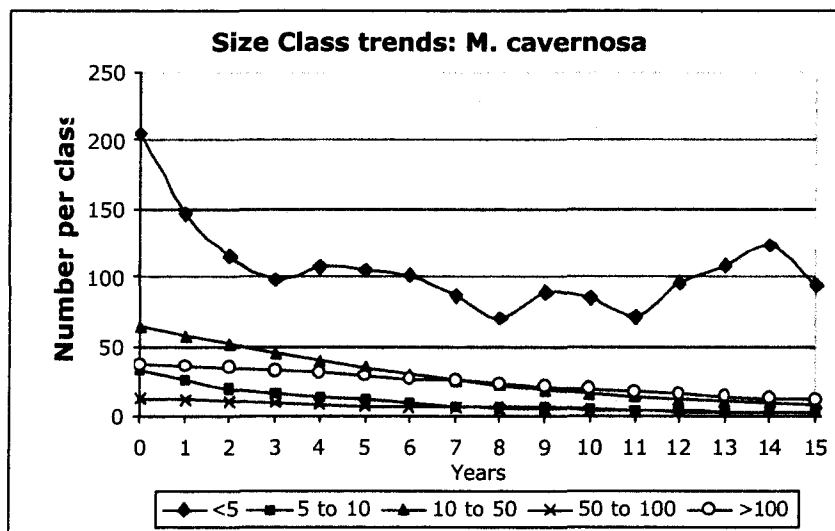| Classes	_5	5.1 to 10	10.1 to 50	50.1 to 100	>100
_5	0.714	0.03			
5.1 to 10	0.026	0.65	0.109		
10.1 to 50		0.1	0.781	0.462	
50.1 to 100			0.016	0.308	0.135
>100				0.077	0.838
Mortality, q_x	0.12 - 0.41	0.25	0.094	0.154	0.027
Initial *n*	205	32	64	13	37

Figure 3. Model simulation of changes in number of *M. cavernosa* colonies in five size classes over a 15 year run. The recruitment and the mortality rates for the $=5cm^2$ class were randomly selected for each year of the model run and this accounts for the fluctuations in the smallest size class.

The relatively high rate of mortality in each size class, combined with a low probability of growth into higher size classes and an insufficient recruitment rate resulted in steady declines in all size classes (except the < 5 cm^2) over the 15-year model run (Figure 3). The recruitment rate of *M. cavernosa* was usually an order of magnitude greater than that of *M. annularis*. The range in recruitment rates (23- 53 colonies per year) and variable mortality rates for the smallest size class does stabilize the population around one third of its initial size after Year 7, masking the continued losses of the largest colonies. There was a very high rate of shrinkage (46%) for the 50.1 to 100 size class, which limited the growth of the population. In contrast, the *M. "annularis"* population declined monotonically because of the narrow range of recruitment per year (2-6 colonies per year) and no variation in the mortality rate for the smallest classes due to the small number of colonies observed in the quadrats from 1998 to 2003 (Figure 4).
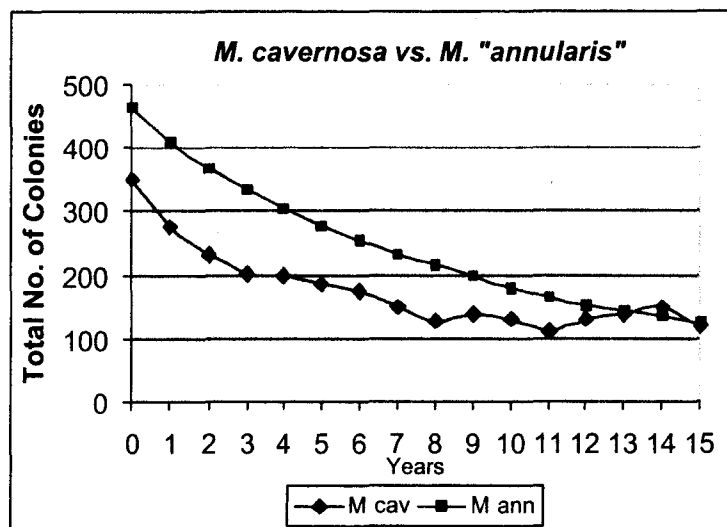
Figure 4. Comparison of the total population trajectories of *M. cavernosa* and *M. "annularis"* over a 15 year model run. Totals are the sum of all size classes shown in Figures 2 and 3.

Frequency distribution of M. *"annularis" colonies observed in the video transects*

The size-class distributions of *M. "annularis"* at each of the four sites are shown in Figure 5 and the frequency distributions are presented after log transformation in Figure 6. The distribution curve parameters for the log-transformed data are shown in Table 3. The log-transformed colony frequency distributions approximated bell-shaped normal distribution curves. However, the populations at Western Sambo in 1998 and 2003 and at Pelican Shoal in 1998 were significantly different than normal after transformation (Table 3). At all four sites no significant differences were detected between the 1998 and 2003 frequency distributions (two sample Kolmogorov-Smirnov tests) and no significant differences were detected between the log-transformed size-class distributions (Table 4).

The size-class distribution patterns at Western Sambo, Eastern Sambo and Middle Sambo (Figs 5 and 6) show robust population distributions with relatively high proportions of small colonies (representing both juveniles and many fragments of larger colonies) and relatively few larger and older colonies. The number of small colonies at these sites appeared to increase from 1998 to 2003, although the overall distributions did not change from 1998 to 2003 (Table 4). Pelican Shoal had low proportions of small colonies that dropped slightly from 1998 to 2003.

The distributions of *M. "annularis"* colonies at Western Sambo were skewed with positive values (right skewed) in both 1998 and 2003. Middle Sambo, Eastern Sambo and Pelican Shoal distributions became more negative from 1998 to 2003, increasingly left skewed due to reductions in the number of smaller colonies. The patterns of kurtosis at Western Sambo shifted from being leptokurtic (positive value, flatter than a normal distribution) to slightly platykurtic (negative value, more peaked than normal) from 1998 to 2003 while the opposite pattern was detected at Middle Sambo. The distributions at Eastern Sambo and Pelican Shoal became less leptokurtic from 1998 to 2003.
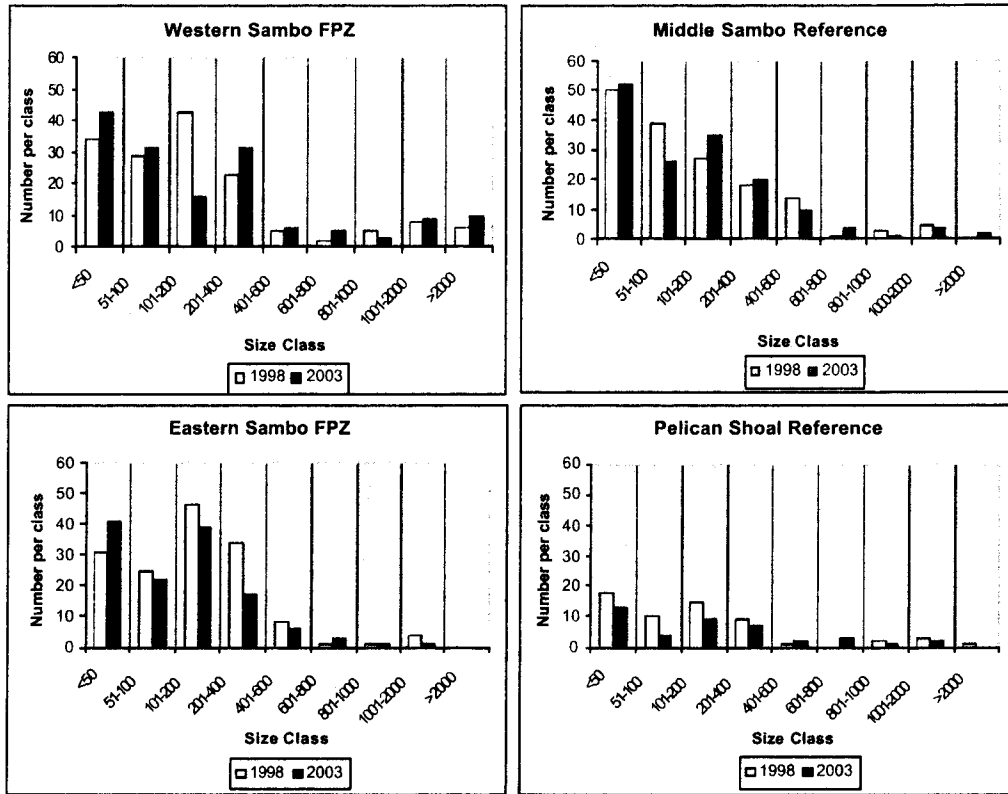
Figure 5. Size-class distributions of *M. "annularis"* colonies extracted from the video transect records at the four study sites from 1998 and 2003. Size classes are in cm^2.

Table 3. Curve parameters for log-transformed colony sizes of *M. "annularis"* and *M. cavernosa* extracted from the video transect records in 1998 and 2003. Negative skewness values indicate populations with the distributions to the right, positive skewness values have the distributions to the left. Negative kurtosis values indicate a platykurtic distribution; positive values indicate a leptokurtic distribution. P*norm* values below 0.05 indicate significant departure from a normal distribution.

Montastraea "annularis"

Parameter	Western 1998	Western 2003	Middle 1998	Middle 2003	Eastern 1998	Eastern 2003	Pelican 1998	Pelican 2003
Mean, μ	2.11	2.11	1.95	1.95	2.08	1.93	1.94	2.01
Skewness, $g1$	1.0119	1.8842	0.6773	-0.516	-1.205	-1.6026	-0.5655	-1.9035
Kurtosis, $g2$	1.745	-0.3776	-0.9376	0.8539	1.1083	0.0247	0.8877	0.5601
Probability, P*norm*	0.02	0.04	0.61	0.77	0.22	0.13	0.32	0.11
Sample size, n	155	160	157	154	150	130	59	41

Montastraea cavernosa

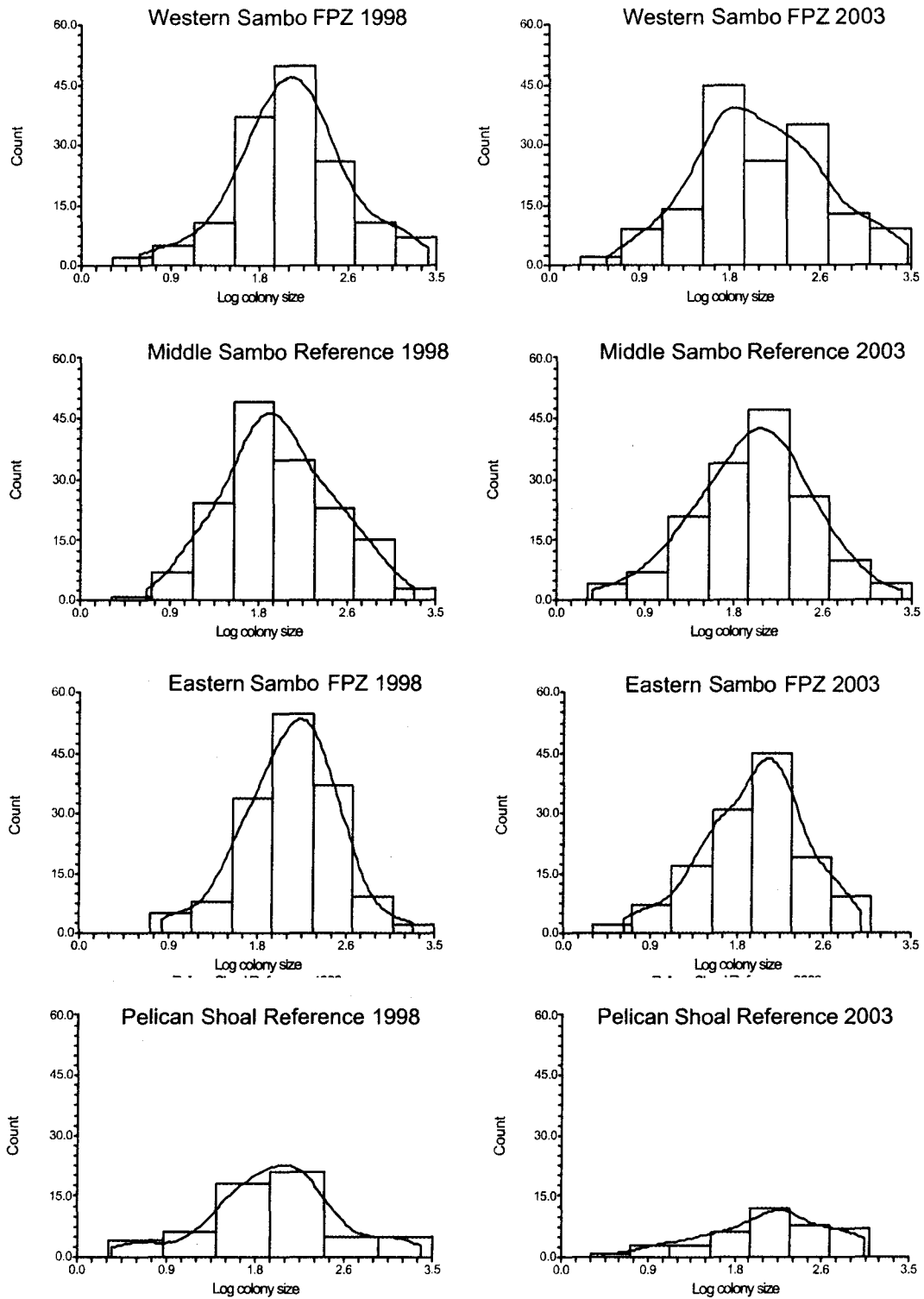| Parameter	Western 1998	Western 2003	Middle 1998	Middle 2003	Eastern 1998	Eastern 2003	Pelican 1998	Pelican 2003
Mean, μ	1.72	2.05	1.857	1.857	1.8	2.15	2.27	2.23
Skewness, $g1$	0.6382	-0.648	-0.8437	0.2155	-1.5908	-0.1173	-2.684	-1.861
Kurtosis, $g2$	-0.9153	-1.5	-0.9262	-2.7456	-0.3402	-3.3941	1.643	0.4701
Probability, P*norm*	0.69	0.11	0.44	0.12	0.06	0.02	0.004	0.036
Sample size, n	27	33	31	52	36	20	21	23

Figure 6. Frequency distributions of *M. "annularis"* colonies extracted from the video transect records at the four study sites from 1998 and 2003. Colony sizes were log transformed.

Table 4. Tests of significance in the log-transformed colony frequency distributions for *M. "annularis"* and *M. cavernosa* between 1998 and 2003 (Kolomgorov-Smirnov tests, p < 0.05 are significantly different) and tests of significance between untransformed size class distributions of colonies in 1998 and 2003 for *M. "annularis"* and *M. cavernosa* (Spearman Rank correlations).

| | *Montastraea "annularis"* | |
Site	Kolmogrov-Smirnov 1998 vs 2003	Spearman Rank 1998 vs 2003
Western Sambo	0.374	0.848
Middle Sambo	0.373	0.921
Eastern Sambo	0.071	0.878
Pelican Shoal	0.413	0.768

| | *Montastraea cavernosa* | |
Site	Kolmogrov-Smirnov 1998 vs 2003	Spearman Rank 1998 vs 2003
Western Sambo	0.085	0.783
Middle Sambo	0.855	0.879
Eastern Sambo	0.008	0.233
Pelican Shoal	0.264	0.392

Frequency distribution of M. cavernosa *colonies observed in the video transects*

The size-class distributions of *M. cavernosa* at each of the four sites are shown in Figure 7 and then presented after log transformation in Figure 8. The distribution curve parameters for the log-transformed data are shown in Table 3. The colony frequency distributions generally did not approximate bell-shaped normal distribution curves except for Western Sambo 1998 and Middle Sambo in 1998 and 2003. The departures from normality are probably due in part to the relatively small number of colonies observed at all four sites. No significant differences were detected between the 1998 and 2003 frequency distributions (two sample Kolmogorov-Smirnov tests) and no significant differences were detected between the log transformed size class distributions (Table 4).

The distributions of *M. cavernosa* colonies at Western Sambo were skewed with positive values (right-skewed) in 1998 but shifted to a negative value (left-skewed) in 2003 due to an increase in the number of larger colonies and a reduction in the number of smaller colonies. Middle Sambo distributions changed from negative to positive from 1998 to 2003, due to strong increases in the number of smaller colonies. Eastern Sambo and Pelican Shoal distributions became less negative from 1998 to 2003, increasingly left skewed due to reductions in the number of smaller colonies at Eastern Sambo and increase in the number of larger colonies at both sites. The patterns of kurtosis at Western Sambo, Middle Sambo and Eastern Sambo remained strongly platykutic from 1998 to 2003. Pelican Shoal became less leptokurtic from 1998 to 2003 as more larger colonies were observed in 2003. It is important to note that relatively smaller numbers of colonies were observed at all sites in both year (<50) compared to the numbers observed for *M. "annularis"*. (>150, except at Pelican Shoal with <60 colonies).
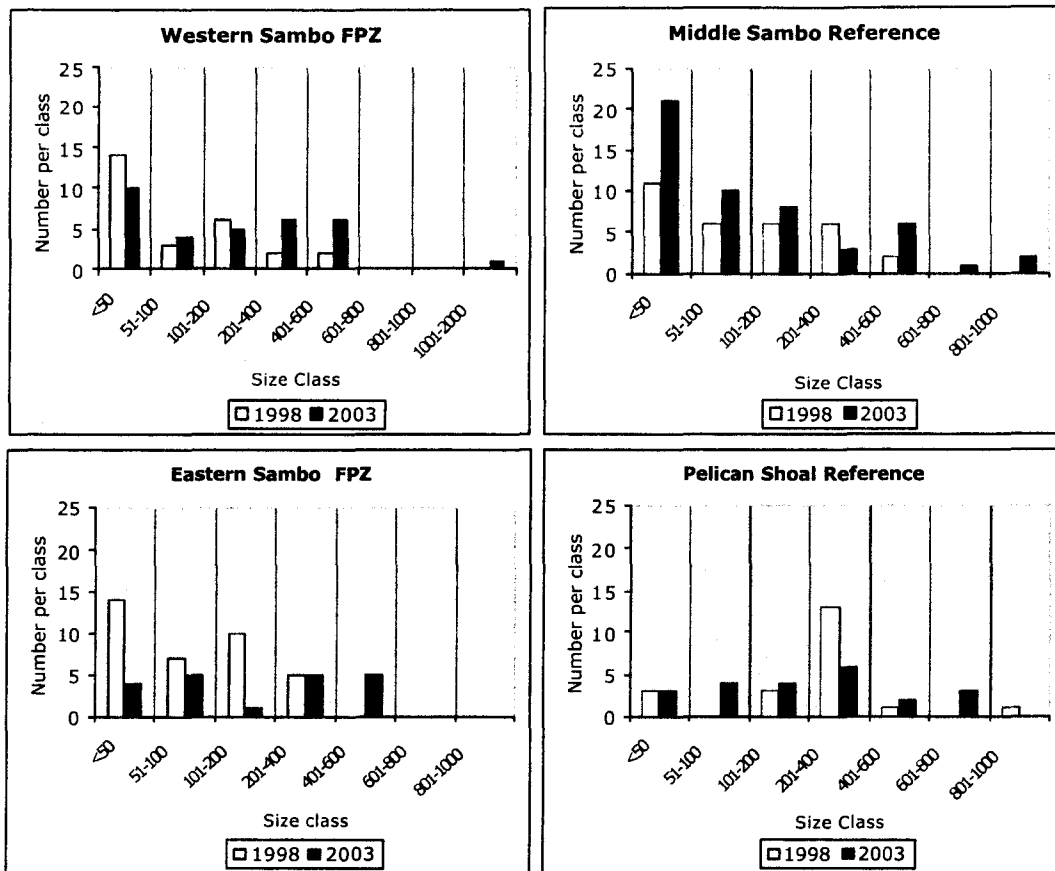
Figure 7. Size class distributions of *M. cavernosa* colonies extracted from the video transect records at the four study sites from 1998 and 2003. Size classes are in cm^2.

Growth and survival of supplemental large colonies of M. cavernosa *and* M. "annularis" *from 2003 and 2005*

The large colonies of the two target species showed consistent patterns of growth or shrinkage according to site (Figure 9). Both species had consistent positive growth at Western Sambo Deep site, where five of the seven large M. *"annularis"* colonies showed growth and six of the seven *M. cavernosa* colonies showed positive growth. In contrast, four of the six M. *"annularis"* colonies at Middle Sambo Deep site shrank in size as did five of the seven *M. cavernosa* colonies. More colonies of both species were marked at the shallow depth of Western Sambo and Middle Sambo and at the Eastern Sambo and Pelican Shoal sites but the analyses have not been completed to date.
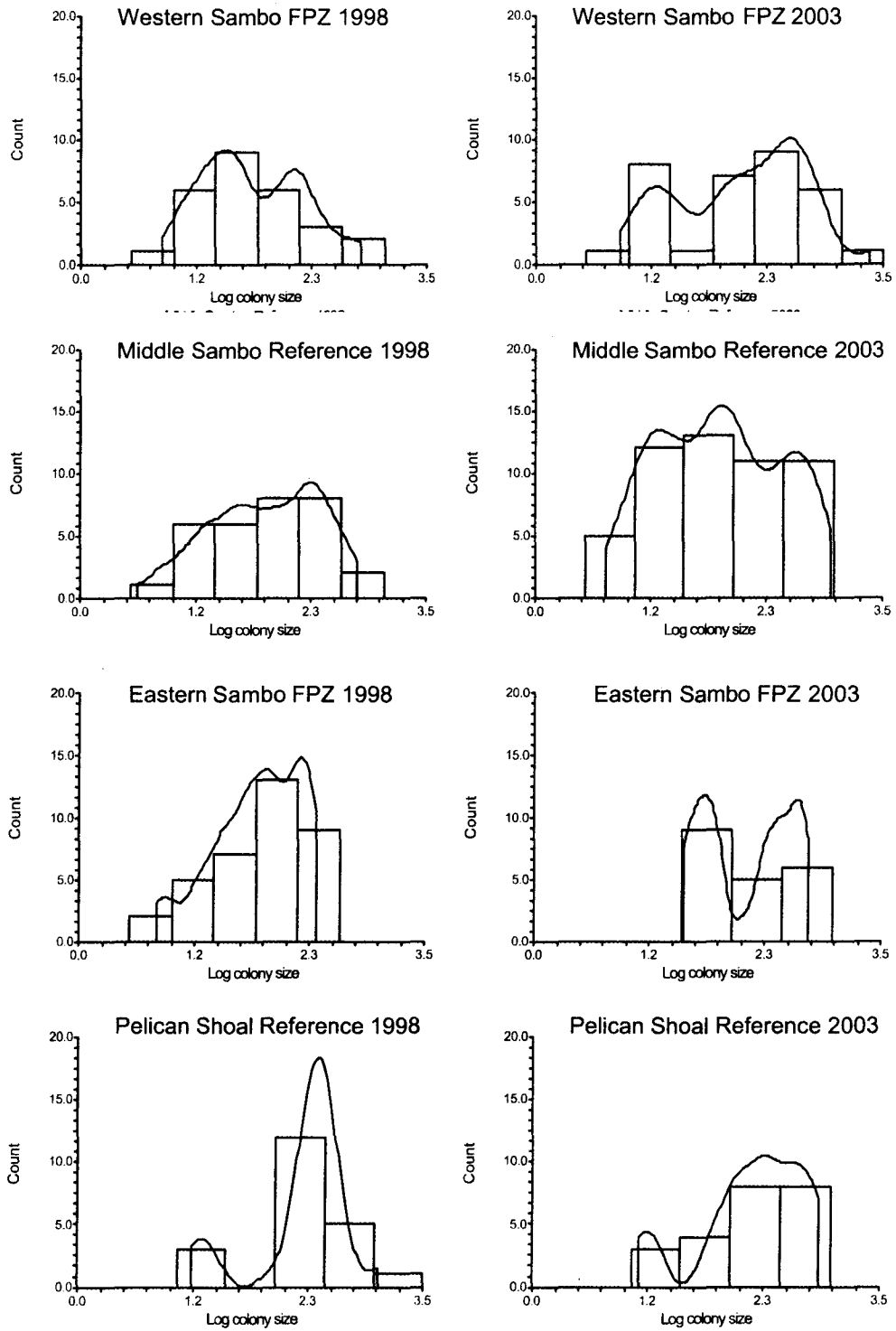
Figure 8. Frequency distributions of *M. cavernosa* colonies extracted from the video transect records at the four study sites from 1998 and 2003. Colony sizes were log transformed.
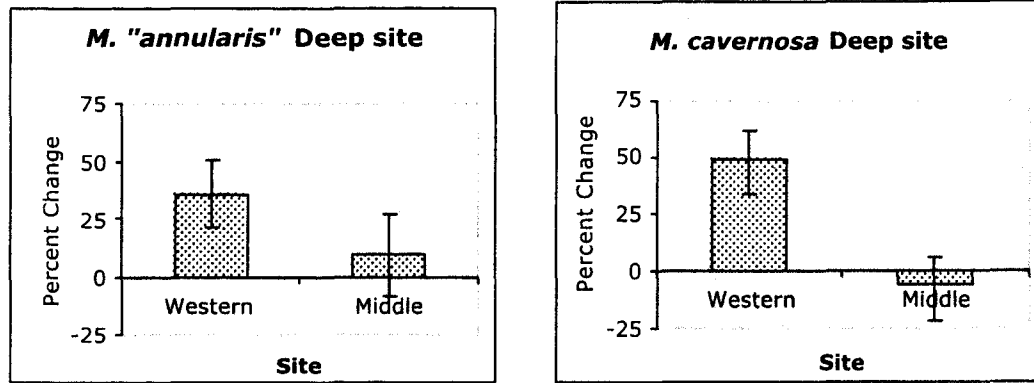
Figure 9. Change in mean size (± SE) of *M. "annularis"* and *M. cavernosa* colonies from 2003 to 2005. These were supplemental colonies of much larger size than the colonies observed in the permanent quadrats. Initial sizes for both species ranged from 400 to 4000 cm^2.

Discussion
Coral population models

The model results for *M. "annularis"* and *M. cavernosa* showed similar trends over time even though they have dissimilar underlying parameters for recruitment, growth and mortality. Both populations declined steadily over time due to insufficient recruitment to offset mortality rates and low growth rates of the smaller colonies. The distinctions between these two species were an order of magnitude higher recruitment rate for *M. cavernosa* compared to *M. "annularis"*. *M. cavernosa* also had a much higher survival rate (0.714) for the smallest size class compared to *M. "annularis"* (0.389) but a much lower probability of growth out of this class (0.026 vs. 0.14). Another distinction was a high shrinkage rate for *M. cavernosa* in the 50.1 to 100 cm^2 size class. The changes measured in this size class may not be robust as only 13 colonies were observed and the loss or shrinkage of just one colony had a strong impact on the rates of change of corals in this size class.

The model results point to an inability of both species to recruit sufficient numbers of new colonies with adequate survival rates of small colonies to maintain the populations on these reefs. The pattern of downward decline in *Montastraea "annularis"* populations was reported by Hughes and Tanner (2000) for Jamaican reefs because of the same underlying mechanisms. They reported an extremely low larval recruitment rate of one (1) new colony in 12 quadrats (each 1 m^2) over 16 years for *M. "annularis"*, compared to the 2-6 colonies observed per year in the 128 quadrats (about 80 m^2) in our surveys. The mortality rates for the Jamaican corals were similar to the rates observed in our study, about 40% for the smallest size class, declining to<5% for the largest class. Our shrinkage rates (8-10%for the smallest classes) were lower than those reported in the Jamaican study (22-58%). Hughes and Tanner (2000) pointed to the effects of Hurricanes Allan and Gilbert as well as competitive overgrowth by reef algae as responsible agents of mortality and shrinkage, but our sites also suffered from the impact of Hurricanes Mitch and George in the very first year of the study in 1998.

Our models do not encompass the full spectrum of colony sizes on the study reefs, as indicated in the distributions observed in the video transects, and therefore we cannot conclude that the populations are at risk for extinction at these sites. The model results show the populations diminishing to low numbers of the largest colonies which, by virtue of their large size, could take a very long time to expire at the current rates of shrinkage. We have attempted to supplement the changes that were observed in the permanent quadrats by marking larger colonies of both species at the sites in 2003. Preliminary results from the two sites analyzed to date (Middle Sambo and Western Sambo) showed that survival rates were 100% and that growth by *M. "annularis"* was more positive than that for *M. cavernosa*. This is not surprising given that these are K-selected species, but it is still encouraging in that the colonies had not shrunk very much and appeared to be disease-free. Nevertheless, a two year interval is a very short period of evaluation. A prolonged study of the colonies in the quadrats and the larger colonies marked in 2003 will hopefully provide a more complete picture of patterns of growth and survival, leading to better transition matrix models over a wider ranges of colony sizes.

Size-class distributions of M. "annularis" *and* M cavernosa *colonies*

The patterns observed for *M. "annularis"* at our sites indicated relatively little change in the colony distributions from 1998 to 2003. The number of smaller colonies (<400 cm^2) at Western and Middle Sambo remained that same or increased from 1998 to 2003. Eastern Sambo and Pelican Shoal experienced reductions in the numbers of small colonies observed in 2003. Meesters et al. (2001) interpreted the right-skewed distributions as indicating relatively strong patterns of recruitment. However, we know from the permanent quadrat study that recruitment was not very substantial for *M. "annularis"* from 1998 to 2003. Most likely the slight changes in the distributions are the result of random sampling error, given that there was little change in coverage by this species from 1998 to 2003 (Figure 1). Some of the increases in the number of smaller colonies observed in 2003 could be due to colony fission which was observed in the colonies in the permanent quadrats. Fluctuations in the numbers of large colonies observed can only be accounted for in terms of sampling error as the colonies are incapable of sufficient growth to achieve the largest sizes over that short a time period. A consistent reduction in the number of observed large colonies occurs over time would indicate the loss of a critical proportion of the population but that did not appear to occur from 1998 to 2003 at our four sites.

The patterns observed for *M. cavernosa* were more difficult to assess because the colony densities were much lower than those observed for *M. "annularis"*. Only Middle Sambo showed an increase in the number of small colonies from 1998 to 2003, which might be feasible given the relatively high recruitment rates observed from 1998 to 2003 There was a consistent difference in the number of larger colonies, with more observed at all sites in 2003. This is an encouraging result that runs counter to the predicted declines of the model, but the model included much smaller colonies that the ones observed in the video transects. It is more likely that the differences between 1998 and 2003 are the result of random sampling error. It is difficult to determine if a true change occurred or not because we only have two time points. An analysis of the distribution patterns in the intervening years (1999- 2002) might reveal a trend.

An important dimension of the video-based data sets is that they are pooled from the shallow and deep sites in order to boost the sample sizes, especially for *M. cavernosa*. Further evaluation of trends in the distributions should probably be done by separating the distribution data into their respective depth categories. In order to do this, but not suffer a reduction in sample sizes, we added another two video transects at each depth at each site in 2003 (and again in 2004 and 2005). The data from the extra transects were not included in these analyses since we only had ten transects from 1998 for comparison, but it will enhance the data set for future analyses. An increase in sample sizes might allow for normality in the distributions after transformation and permit us to apply parametric statistical analyses for more robust evaluations of trends over time.

There does not appears to be any consistent differences in the changes in the distributions observed with respect to the protective status of the reefs for either species observed from 1998 to 2003. This may be due to a lack of change in response to the management of human activity on the Fully Protected reefs (Western Sambo and Eastern Sambo) or the limitations of the video transect technique to assess the changes due to random sampling and relatively low population sizes. Meesters et al. (2001) encountered similar densities of colonies as in our studies and were able to discriminate patterns on different reefs with respect to water quality effects. But it was unclear if their sampling regime was comparable to ours as they did not specify the number of transects they surveyed. Hopefully, by increasing our sampling effort to 12 transects per depth per site we will achieve a better discrimination of changes over time and whether distinctions do exist between the protected and reference sites.

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