

REPRODUCTIVE DEMOGRAPHY OF THE SCLERACTINIAN CORAL *Siderastrea radians*
IN THE ST. MARTINS KEYS, FLORIDA: SPATIAL PATTERNS IN ABUNDANCE, SIZE,
AND REPRODUCTIVE CHARACTERISTICS

By

KATHERINE ELIZABETH LAZAR

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Abstract of Thesis Presented to the Graduate School
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By

Katherine Elizabeth Lazar

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The reproductive demography of corals is reported to play a significant role in their population dynamics by influencing reproductive success. The objectives of this study were to quantify spatial variation in: (1) density, (2) aggregation, (3) size distribution, (4) sexuality, (5) puberty size, and (6) sex ratio in a population of *Siderastrea radians* in the St. Martins Keys, Florida (SMK). Initially, corals were counted and measured at each of 81 sites arrayed in a 16-km² grid during 2006 and 2007. Results indicated that corals were distributed in patches (mean Morisita's Index = 3.74; range = 0.00–10.00), with densities ranging from 0.0 to 86.0 colonies m⁻² (mean = 7.0 colonies m⁻²) in both years. The size-frequency distributions were positively skewed like many other scleractinian populations, with the majority of colonies falling within the smallest size classes. To quantify the relationships among density, aggregation, and sex ratio, corals were collected from 10 sites with different combinations of density and aggregation in July–August 2007. Histological data suggested a gonochoric population; however, planulae were not observed in histological sections. Therefore, a brooding reproductive mode in the SMK populations could not be confirmed. Colonies reached puberty at approximately 32 mm maximum diameter and formed aggregations with sex ratios of

approximately 1:1 at scales of tens and hundreds of meters. In contrast, a puberty size of 20 mm and a female-biased sex ratio have been reported for Caribbean populations. Statistically significant linear regressions showed that numbers of solitary polyps (i.e., recruits) increased with increasing numbers of conspecifics, colonies above puberty size (putative adults), and colonies below puberty size. The relationship with adults was weakest, which indicated that 1) planulae may settle and/or survive better near conspecifics and 2) planulae are likely to disperse at least tens of meters from their parental colonies. Overall, these results pointed to geographic differences in reproductive characteristics across the range of *S. radians*.

CHAPTER 1 GENERAL INTRODUCTION

Contemporary research on scleractinian corals is dominated by efforts to elucidate the causes and consequences of a worldwide decline in coral cover (Bellwood et al. 2004). Accordingly, it is imperative for scientists and managers to understand how corals and coral reefs respond to environmental and physical disturbance. A demographic approach is well-suited to address this issue (Bak & Meesters 1999, Meesters et al. 2001, Edmunds 2005). Demographic research on populations of corals centers on determining numbers, sizes and/or ages, and distributions of recruits and adults of both sexes, and ultimately, it includes spatiotemporal changes in response to changes in key demographic rates (i.e., birth, death, immigration, and emigration). An understanding of the status and changes in the demography of a population has insight into the reproductive ecology of a species as part of its foundation. Reproductive demography, defined here as the spatial analysis of reproductive ecology, contributes to an understanding of interactions between reproductive ecology and population-level processes that result in a population structure at any given point in time. The reproductive strategy employed by a species, including sexuality and reproductive mode that come to be reflected in sex ratios and distributions of sexes, interacts with pre-settlement and post-settlement processes that affect reproductive output, growth, survival, and subsequent reproduction to ultimately result in an observed population structure. For example, the spatial distribution of sexes in a population directly affects fertilization success leading to an indirect effect on recruitment rates. Accordingly, research on responses to disturbance by corals and coral reefs is incomplete without data on both population structure and the reproductive characteristics of the species of interest.

The species of interest in this study is *Siderastrea radians*, commonly known as the lesser starlet coral. This purported brooder (Szmant 1986, Soong 1991) is common throughout the tropical Atlantic, and it is found in highly dynamic environments tolerated by few other scleractinian corals (Lewis 1989, Lirman et al. 2002, Lirman et al. 2003, Moses et al. 2003). For example, in a decade-long study in St. John, U.S. Virgin Islands, small, morphologically simple species such as *S. radians* became relatively more abundant in areas exposed to higher temperatures in contrast to larger, more complex reef-building species such as *Porites astreoides* and *P. furcata* (Edmunds 2004). These observed changes in coral community structure appeared to be linked to higher mean seawater temperature and fewer cold days, and they resulted from enhanced recruitment of *S. radians* and depressed growth rates of *Porites*, *Agaricia*, and *Favia* (Edmunds 2004). Furthermore, anecdotal evidence suggests that, among scleractinian species in the Florida Keys, *S. radians* is usually one of the last to bleach (M. Johnson, The Nature Conservancy, pers. comm.). In general, *Siderastrea radians* and other smaller, morphologically simple species may outcompete or simply survive better than larger, more structurally complex corals such as *P. astreoides* and *P. furcata* (Edmunds 2004). The relative success of *S. radians* may be due to its B5a clade of symbiotic zooxanthellae (LaJeunesse 2002), which is known to tolerate temperatures up to 36°C (Warner et al. 1996). Zooxanthellae in *Symbiodinium* clade B are typically found in shallow-water corals and in portions of large colonies that receive high irradiance (Rowan & Knowlton 1995). Reproductive mode and a spherical morphology also promote the survival of *S. radians*. Lewis (1989) showed that in tide pools and on reef flats where wave action was strong, the survival of *S. radians* increased with colony size and was positively correlated with development of a spherical shape. Because sexual reproduction is its primary mode (Duerden 1904, Vermeij 2005), *S. radians* also may adapt more easily during

periods of environmental fluctuation (Lasker & Coffroth 1999). Many scleractinian species reproduce primarily asexually, i.e., they depend on processes such as budding, fragmentation, and fission for colony growth and propagation (Hughes et al. 1992). Asexual reproduction may be advantageous in physically stable environments, but the absence of genetic variability leaves a large proportion of a genetically uniform population vulnerable to physical and/or biological stress (Richmond 1997, Lasker & Coffroth 1999). Further, fragments and other asexually produced tissues have limited dispersal capabilities, in contrast to most gametes and/or larvae (Richmond 1997). Enhanced genotypic diversity associated with sexual reproduction may decrease a species' susceptibility to extinction, augmenting persistence of a species following environmental disturbance or climate change (Richmond 1997).

Although the SMK population of *Siderastrea radians* does not build reefs, it offers a tractable opportunity to gain insights into interactions between reproductive and demographic characteristics. There is little scientific literature specific to *S. radians* (but see Duerden 1904, Szmant 1986, Soong 1991, Vermeij 2005), and none on this particular population. Therefore, a study of its reproductive demography both adds to the body of knowledge about this species and allows comparisons across geographically disjunct populations.

In the face of global climate change and increasing anthropogenic impacts on marine ecosystems, knowledge of the structure and function of coral communities is imperative if we are to assess impacts and attempt restoration. In the following chapters, intended to stand alone, I detail a multifaceted study of the coral *Siderastrea radians* in the St. Martins Keys, characterize patterns in abundance and aggregation, and combine these data with information on sexuality, puberty size, and sex ratio derived from histology. Information on abundance, distribution, and reproductive characteristics is integral to a more complete understanding of the population

dynamics of coral species. Many corals exhibit variation in these characteristics across their geographic range; accordingly, it is important to understand how coral populations are structured in a variety of locations to determine how they will respond to stressors and other perturbations in different environments. Data that combines both demographic and reproductive information is therefore necessary and relevant to the management and conservation of coral resources.

CHAPTER 2 SPATIAL PATTERNS IN ABUNDANCE AND SIZE OF *Siderastrea radians*

Introduction

Demographic studies are essential to further our understanding of how marine populations are structured by density-independent and density-dependent processes operating before and after larval settlement. This portion of my study focuses on spatial patterns in key demographic parameters, i.e., abundance and size, for the scleractinian coral *Siderastrea radians*. This demographic baseline expands our understanding because: (1) there is no published information on this species in the St. Martins Keys (SMK) and limited information from other locations (Szmant 1986, Soong 1991, Lirman et al. 2003, Moses et al. 2003, Vermeij 2005); (2) *S. radians* essentially exists in a monospecific aggregation in the SMK, which is similar only to pavements of an unusual morphotype found in the Cape Verde Islands (Moses et al. 2003) and unlike populations in the Caribbean (Szmant 1986, Soong 1991); and (3) *S. radians* achieves densities in the SMK that far exceed those recorded in the Caribbean (e.g., Szmant 1986, Soong 1991, this study).

Measures of the abundance and spatial distribution of individuals, especially juveniles, can provide valuable insights into life history strategies (Bak & Engel 1979). However, to be able to quantify these parameters, one must first decide on the unit(s) to be studied. Contemporary research on the evolutionary ecology of corals has generated debate about what comprises an individual and a population.

The term ‘individual’ is applied at three levels in coral biology. First, the polyp constitutes a morphological individual, complete with its own mouth, gastric cavity, and gonads. Second, the colony represents a physiological individual, in that each colony functions as a separate biological unit. Lastly, all polyps and/or colonies that arise from the same zygote form a genetic

individual, or genet. The genet may consist of polyps produced by asexual budding and separate colonies created by fragmentation. Regardless of whether a genet is scattered in space or functionally united to form a colony, it possesses a single genotype that is subject to natural selection. In species where asexual reproduction predominates and recruitment is highly localized, populations may consist of few genets. This fact must be recognized when studying the life histories and population dynamics of clonal organisms. However, the ‘individual’ of choice ultimately depends on the question(s) being asked. Whereas studies of population genetics in corals typically concentrate on the genet, most ecological studies focus on the colony as the individual unit. Studies like this one that explore demographic parameters and reproductive characteristics at a population level use colonies almost exclusively.

What, then, constitutes a population? Hughes et al. (1992) define a population as an ‘interbreeding unit, the spatial extent and size of which is unknown for any coral.’ Studies on population genetics typically focus on the effective population size, N_e , which is an idealized measure of the number of genetically distinct individuals contributing genes to future generations and the evenness of those contributions. In corals, this measure is bound to be dissimilar and, in fact, typically much smaller than the standard measure of population size, N , which is obtained by counting colonies. Notwithstanding the importance of population genetics to the life history and reproductive strategies of a species, it is beyond the scope of this project. Additionally, *Siderastrea radians* reproduces primarily via sexual reproduction (Duerden 1904, Vermeij 2005), and as this process occurs at the colony level, it provides further justification for focusing on the population as comprised of individual colonies.

Although *Siderastrea radians* can be locally abundant, the processes that determine its distribution and abundance are not well known. Because adult colonies are sessile, spatial

patterns initially are determined by the settlement of planulae and subsequent mortality of attached corals. Historically, the prevailing view was that larvae of marine organisms are subjected to stochastic processes that influence recruitment to adult populations (Caley et al. 1996). In the Caribbean, rates of recruitment for small brooding corals, such as *Porites astreoides* and *Agaricia agaricites*, have been found to be highly spatially and temporally variable, which suggests that stochastic, density-independent processes play an important role in population dynamics (Miller et al. 2000). However, variability in recruitment also may be explained by density-dependent processes; for example, the soft coral *Efflatounaria* sp. experiences increased asexual recruitment rates at low densities (Karlson et al. 1996). Contemporary studies focus on how density-dependent and density-independent processes operating before and after settlement combine to structure marine populations. For example, Vermeij (2005) concluded that *S. radians* recruitment, i.e., the point at which newly settled polyps become visible after settlement (Keough & Downes 1982), was limited by habitat availability and structured by adult abundance in the Florida Keys. In addition, shifts in the size structure of a coral population may result from environmental stress acting on recruitment and juvenile survival to create size-specific mortality (see Fig. 6 in Bak & Meesters 1999). Further, changes in density of *Siderastrea* spp. in St. John, U.S. Virgin Islands, appeared to arise from decreased competition for space or other resources stemming from a decrease in the abundance of *Porites*, *Favia*, and *Agaricia* (Edmunds 2004).

Understanding the mechanisms driving patterns in the abundance and size of coral colonies is critical to developing effective management strategies for their long-term conservation. Such information, for example, will help predict success in new or altered landscapes. This portion of my research focused on the population structure of *Siderastrea radians* in the St. Martins Keys,

specifically spatial patterns in abundance and colony size. This survey will yield insights into processes that structure the population and serve as a baseline for future studies.

Materials and Methods

Study Site

The St. Martins Keys (SMK) are located along the north-central Gulf coast of Florida (28°45.5'N, 82°37.1'W), and they are contained within the St. Martins Marsh Aquatic Preserve (SMMAP) and the Chassahowitzka National Wildlife Refuge. The study area (Fig. 2-1) comprised a dense *Thalassia testudinum* (turtle grass) meadow that bordered an extensive salt-marsh complex. The coral assemblage at SMK is comprised of a nearly monospecific assemblage of *Siderastrea radians*, with a few colonies of *S. siderea*.

The study area is subject to marked variations in temperature and salinity. Water temperatures at four fixed stations within and near the SMK ranged from 9.6 to 33.3°C, with a mean of 23.1°C, and salinity at these stations ranged from 12.0 to 36.4 ppt, with a mean of 25.06 ppt (Table 2-1, Fig. 2-2, Jacoby et al. 2008). Variation in salinity is driven primarily by tides that exhibit a semidiurnal range of approximately 1 m (Glancy et al. 2003) and discharge from nearby coastal rivers.

Relatively shallow and clear water allows light to penetrate near the bottom (mean depth = 0.88 m, mean light extinction coefficient = 1.05, mean Secchi depth = 0.87 m, Table 2-1). These conditions are favorable for and should promote the growth of corals.

Population Survey

The abundances and sizes of *Siderastrea radians* in the SMK were quantified at 81 sites arrayed in a 16-km² grid. Sites were identified by laying out parallel gridlines separated by 500 m on a nautical chart. Intersecting coordinates were identified in degrees, minutes, and seconds, and the coordinates were imported into ArcMAP (ArcINFO 9.2, Fig. 2-1).

Between March and July 2006 and again in April and May 2007, the predetermined sites were located with a handheld global positioning system (GPS 12 XL, Garmin). At each site, a 25-m transect was laid out by swimming a predetermined, random number of kicks from the boat to a starting point and then extending a surveyor's tape 25 m along a predetermined, random compass bearing. If the initial starting point and bearing put the transect on land, then a new pair were chosen from the predetermined list. Ten quadrats (0.5 m x 0.5 m) were placed at random points along each transect that were chosen from a predetermined list. In each quadrat, the percent cover of seagrass, drift algae, and attached macroalgae was recorded before drift algae were removed. All coral colonies were subsequently counted and classified as comprising single or multiple polyps, and the presence of bleaching, encrustation by algae and/or sponges, and the sediment was recorded. The maximum basal diameter of each colony was measured to the nearest 0.1 mm. In 2006, heights also were recorded to the nearest 0.1 mm for colonies at 4 sites.

Statistical Analyses

The validity of using maximum diameter as the sole measure of colony size was investigated by linear regression. Coral heights were regressed against maximum diameters, with the line forced through the origin.

The mean sizes of coral colonies in the two years of sampling were compared with a *t*-test. Before the analysis, data were tested for normality with a Ryan-Joiner test and homoscedasticity with Cochran's test. Data were transformed if necessary.

Differences in counts of colonies were analyzed via a two-way analysis of variance (ANOVA) with Year and Site as fixed factors. Before ANOVA, data were tested for normality with a Ryan-Joiner test and homoscedasticity with Cochran's test. Data were transformed if necessary.

The influence of habitat was investigated by relating counts of coral colonies to percent cover of seagrass, drift algae and macroalgae. Pearson product moment correlations were calculated for counts vs. each type of plant or algal coverage.

The spatial distribution of colonies within sites in the SMK sampling grid was investigated using Morisita's Index of Dispersion (I_δ), which was calculated as

$$I_\delta = \frac{q \sum n_i(n_i - 1)}{N(N - 1)} \quad (2-1)$$

where q is the number of quadrats within a single transect, n_i is the number of colonies in the i^{th} quadrat, and N is the total number of colonies in all quadrats along a transect. If colonies are randomly distributed, the expectation is that $I_\delta = 1$; if colonies are uniformly distributed, $I_\delta < 1$; and if colonies are patchily distributed, $I_\delta > 1$. This index is not affected by differences in density, but the maximum possible value is determined by sampling effort. For example, if the number of quadrats sampled at a site is equal to 10, then the maximum value for I_δ will be 10.

Mean Morisita's Indices in the two years of sampling were compared with a t -test. This analysis was conducted using data from sites where coral was found in both years. Before the analysis, data were tested for normality with a Ryan-Joiner test and homoscedasticity with Cochran's test. Data were transformed if necessary.

Results

Colony Size

A linear regression of colony height versus maximum diameter indicated that diameters could be used to predict heights ($r^2 = 0.90$, $p < 0.001$, $n = 646$, Fig. 2-3). Coral colonies tended to be slightly higher than expected for hemispheres of a given maximum diameter. Diameters were used in all analyses of size.

Size-frequency distributions from the two years of sampling were skewed to the right as is typical of scleractinian coral species (Bak & Meesters 1998). Over 50% of the colonies had diameters less than 25 mm in both 2006 and 2007, which meant that over half of all colonies fell in the first 20% of the overall size range (Fig. 2-4). Maximum diameters were not normally distributed or homoscedastic; therefore, the data were square root transformed. However, transformed data remained non-normal and heteroscedastic. Given the number of replicates, a *t*-test for data with unequal variances was deemed sufficiently robust to these violations of assumptions. The *t*-test indicated that the mean sizes of coral colonies measured as maximum diameters were significantly smaller in 2006 than 2007 ($t = -4.38$, $df = 2811$, $p < 0.0001$). However, the mean maximum diameters differed by less than 3 mm (mean maximum diameter \pm standard error for 2006 = 24.54 ± 0.47 and for 2007 = 27.02 ± 0.52), which did not suggest a biologically significant change in the population from one year to the next.

Colony Abundance

Coral colonies were found in 32 and 24 of the 81 sites in 2006 and 2007, respectively. Transformed data [$\log_{10}(\text{count} + 1)$] remained non-normal, but were homoscedastic. Conservative interpretation of the two-way ANOVA indicated that coral abundances varied among combinations of years and sites (Table 2-2). Although mean counts did vary between years, sites that had corals in 2006 also tended to have corals in 2007 (Fig. 2-5). Across both years, densities of *Siderastrea radians* ranged from 0.0 to 86.0 colonies m^{-2} . In both years, densities appeared to be concentrated on the western side of the islands, with the highest densities occurring in the southwest region of the sampling grid (Figs. 2-6 to 2-8). The mean density calculated from combined data was 7.03 colonies m^{-2} , which extrapolated to 112.48×10^6 colonies across the 16- km^2 grid.

Coral counts were significantly correlated with all three types of plant and algal coverage. Counts were negatively correlated with the percent cover of seagrass ($r = -0.38$, $p < 0.001$) and positively correlated with percent cover of drift algae ($r = 0.30$, $p < 0.001$) and macroalgae ($r = 0.14$, $p < 0.001$).

Siderastrea radians colonies typically were healthy (Table 2-3). The incidence of bleaching in *S. radians* colonies was 3.29% in 2006 and 1.71% in 2007. Encrustation by algae or sponges occurred in 4.41% and 9.94% of colonies in 2006 and 2007, respectively. Sediment was found on 2.24% and 2.10% of colonies sampled in 2006 and 2007, respectively.

Patterns in Aggregation

Siderastrea radians in the SMK were aggregated in both years. Values of I_{δ} ranged from 0.00 to 10.00, with less than 5% of the values being less than 1.09.

\log_{10} -transformed I_{δ} -values from the fifteen sites where coral was found in both years were normal and homoscedastic. A t -test indicated that mean I_{δ} -values did not vary between years ($t = 0.68$, $df = 28$, $p = 0.50$). The back-transformed mean for 2006 was 3.61 with lower and upper 95% confidence limits of 2.79 and 4.55, and the back-transformed mean for 2007 was 2.81 with lower and upper 95% confidence limits of 1.94 and 3.85.

Discussion

Results indicated that diameters of *Siderastrea radians* colonies were good predictors of their heights, although colonies were not perfectly hemispherical. Therefore, maximum diameter alone should serve as a useful proxy for age. In fact, colony size frequently is used as a proxy for age in demographic studies of corals (Lewis 1989) because it is related to settlement, growth, reproduction, and mortality, which are important processes that structure populations (Hughes 1984). The relationship between size and age does not hold true in many scleractinian corals because of partial colony mortality, fusion, and fission. However, *S. radians* appears less

susceptible to these factors, which have been recorded in only 2–3% of small colonies in the Caribbean (Lewis 1989). Indeed, evidence of partial colony mortality due to bleaching, encrustation, and/or the presence of sediment was low in the SMK, reaching levels of 9.9% and 13.7% for colonies of all sizes in 2006 and 2007, respectively.

Size-frequency distributions can provide key information on the processes structuring a population. In most coral populations, the majority of colonies fall within the smallest size classes (Bak & Meesters 1999). Results from surveys of *Siderastrea radians* in this study conformed to this trend, with the majority of colonies being less than 25 mm in diameter or in the lower 20% of the size range in both years. In fact, the mean diameter of coral colonies in the two years differed by less than 3 mm. The large proportion of colonies within the smallest size classes in both years indicates that there is recent recruitment, and based on the size-frequency distributions, the larger size classes appear to be stable. However, the difference in mean maximum diameter between years is primarily a result of lower numbers in the smallest 3 size classes (0–15 mm max diameter). This shift could be indicative of a difference in the strength or timing of recruitment in 2007 or a difference in mortality of the smallest size classes. Further monitoring of settlement, recruitment, and subsequent survival of *S. radians* in the SMK may help determine the relative importance of pre-settlement and post-settlement processes resulting in the observed size-frequency distribution.

Additionally, population models of corals suggest that increases in the frequency and/or intensity of disturbance tends to skew size-frequency distributions toward the right (Done 1987), and such an effect could have been operating in the SMK. For example, *S. radians* at this location were subject to over 20°C changes in temperature and over 20 ppt changes in salinity. These ranges exceed typical conditions for more tropical populations of *S. radians* (e.g., Cubit et

al. 1989). Overall, *S. radians* has been reported to be highly tolerant of stresses, including shading and sedimentation (Lewis 1989), and this characteristic was confirmed by the low incidence of bleaching and other indicators of poor health among corals counted during the surveys. However, threshold levels of environmental stress have yet to be determined for the SMK population of *S. radians*.

Siderastrea radians was aggregated at most sites in both years. Values of I_{δ} were consistently higher than 1.00, with values reaching the maximum possible value of 10.00 for some sites. Thus, corals were patchy at the scale of tens of meters (area sampled at each site = 25 m²). In addition, densities of *S. radians* varied across the 81 sites in the sampling grid, which provided evidence of patchiness at the scale of hundreds of meters. The significant variation in counts among combinations of Sites and Years was no unexpected, given the sampling design applied to a sessile, marine organism exhibiting an aggregated distribution at the scale of tens of meters. Regardless, results of the two surveys indicated that corals tended to occur at the same sites in both years.

Patchiness can arise from several processes and their interactions. It may reflect variation in exogenous factors such as habitat suitability and/or availability, or endogenous factors such as larval dispersal, or selective settlement and/or survival of larvae. The significant negative correlation between seagrass coverage and coral abundance suggested that not all substrates in the sampling grid were suitable for settlement and/or survival of *Siderastrea radians*. Qualitative observations indicated that locations with dense seagrass typically had deeper and softer substrates than those with sparse or no seagrass. *Siderastrea radians* also exhibited a weak, but statistically significant, positive correlation with macroalgal coverage. This relationship probably arose because both organisms attach to a hard substrate or survived better if they were attached

to one. Corals typically settle on hard substrate (Harrison & Wallace 1990), be it limestone bedrock or another coral (pers. obs.). In contrast, the positive correlation between coral abundance and percent cover of drift algae probably reflected the tendency of drift algae to become trapped on coral colonies rather than a relationship centered on suitable habitat. The relatively low correlation coefficients indicated that factors other than substrate were influencing the distribution of coral colonies. Further research on substrate characteristics (e.g., depth and composition) coupled with data on *S. radians* abundance could yield an improved understanding of how substrate affects the distribution of coral colonies. Additionally, more information is needed on the dispersal of *S. radians* in the SMK to determine the relative importance of endogenous vs. exogenous factors in determining the observed aggregation patterns (see van Teeffelen & Ovaskainen 2007).

The presence of conspecifics may interact with substrate composition to affect settlement and mortality of the early life stages of *Siderastrea radians* in the SMK, as Vermeij (2005) has found for *S. radians* populations in the Florida Keys. Planulae may use the presence of conspecifics as a cue for settlement, resulting in aggregations of corals. Optimal distance for fertilization success also may play a role in creating aggregated distributions. In fact, spatial aggregation and a female-biased sex ratio are expected in populations of brooding corals, including *S. radians* populations in the Caribbean (Shinkarenko 1981, Szmant 1986, Soong 1991, Ben-Yosef & Benayahu 1999). Females clustered around one or several males are thought to garner increased reproductive success. Analyses of patterns in recruits, adults, and males and females will shed light on the processes that yield aggregated distributions of colonies within the SMK (Chapter 3).

Conclusions

In summary, the observed distributions of size and density of *Siderastrea radians* colonies within and among sites in the SMK indicate that there is recent recruitment to the population. Large numbers of small colonies and stable numbers of larger colonies indicate that the population is stable, if not growing. Aggregation values coupled with a significant negative correlation between *S. radians* abundance and seagrass coverage highlight the patchy distribution of this population, which may be indicative of substrate suitability and/or availability. The addition of data on the reproductive characteristics of this species in the SMK will further augment our understanding of its population dynamics.

Table 2-1. Environmental conditions at four sampling stations near the Homosassa River and the St. Martins Keys. Values based on data collected monthly from November 1996 through December 2007 (Jacoby et al. 2008). SE = standard error.

| Parameter | | Homosassa Station | | | |
|---|---------|-------------------|-------|-------|-------|
| | | 1 | 2 | 3 | 6 |
| Depth (m) | Mean | 0.79 | 0.53 | 0.82 | 1.37 |
| | SE | 0.03 | 0.02 | 0.04 | 0.02 |
| | Minimum | 0.2 | 0.1 | 0.2 | 0.8 |
| | Maximum | 1.8 | 1.5 | 2.6 | 2.2 |
| Temperature (°C) | Mean | 22.90 | 23.30 | 23.30 | 22.70 |
| | SE | 0.50 | 0.50 | 0.50 | 0.50 |
| | Minimum | 10.0 | 10.4 | 10.0 | 9.6 |
| | Maximum | 32.4 | 33.3 | 33.1 | 32.3 |
| Salinity (ppt) | Mean | 24.67 | 26.89 | 22.49 | 26.19 |
| | SE | 0.38 | 3.35 | 0.37 | 0.38 |
| | Minimum | 12.0 | 14.8 | 13.0 | 15.9 |
| | Maximum | 33.5 | 35.4 | 33.2 | 36.4 |
| Light Extinction Coefficient (k_d ; m^{-1}) (based on readings at depths ≥ 0.5 m) | Mean | 0.98 | 1.03 | 1.17 | 1.04 |
| | SE | 0.06 | 0.08 | 0.06 | 0.04 |
| | Minimum | 0.2 | 0.4 | 0.3 | 0.2 |
| | Maximum | 2.4 | 2.9 | 2.2 | 2.4 |
| Secchi Depth (m) (based on replacing readings of Bottom with depths) | Mean | 0.79 | 0.53 | 0.80 | 1.37 |
| | SE | 0.03 | 0.02 | 0.03 | 0.02 |
| | Minimum | 0.2 | 0.1 | 0.2 | 0.7 |
| | Maximum | 1.8 | 1.5 | 2.3 | 2.2 |

Table 2-2. Results of two-way ANOVA using $\log_{10}(\text{coral counts} + 1)$.

| Factor | df | SS | MS | F | p |
|-------------|-----|--------|-------|-------|-------|
| Year | 1 | 0.248 | 0.248 | 2.10 | 0.148 |
| Site | 41 | 72.590 | 1.771 | 14.99 | 0.000 |
| Year x Site | 41 | 30.670 | 0.748 | 6.33 | 0.000 |
| Error | 754 | 89.053 | 0.118 | | |

Table 2-3. Evidence of partial colony mortality due to bleaching, encrustation by algae and/or sponge, and presence of sediment for *Siderastrea radians* colonies in the St. Martins Keys.

| Year | Number of colonies | Partial colony mortality (no. colonies) | | | Total % mortality |
|------|--------------------|---|--------------|---------------|-------------------|
| | | Bleaching | Encrustation | Sedimentation | |
| 2006 | 1609 | 53 | 71 | 36 | 9.9% |
| 2007 | 1288 | 22 | 128 | 27 | 13.7% |

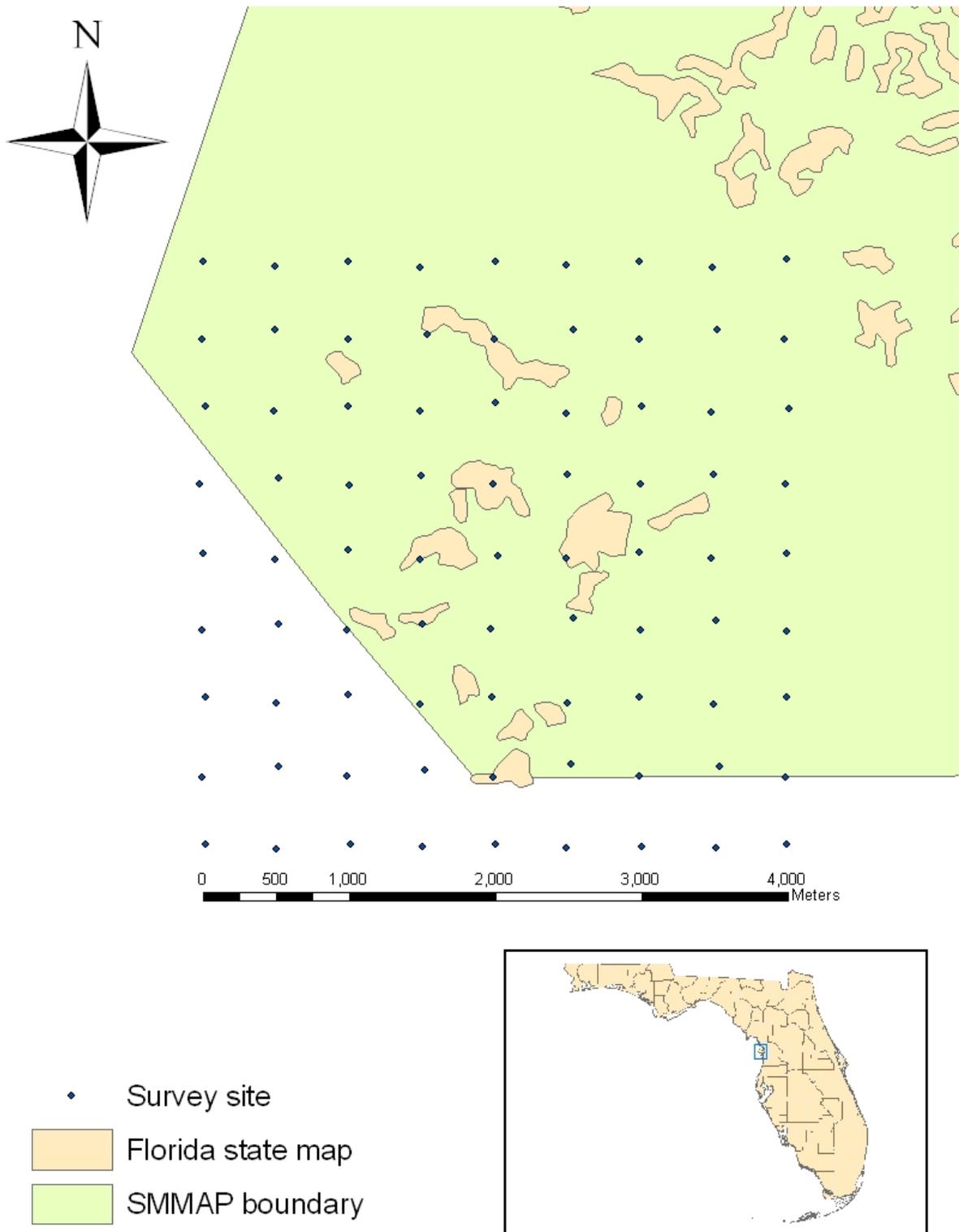


Figure 2-1. St. Martins Keys, Florida, showing study sites for the 2006 and 2007 surveys. The distance between any two neighboring sites is 500 m. SMMAP = St. Martins Marsh Aquatic Preserve.

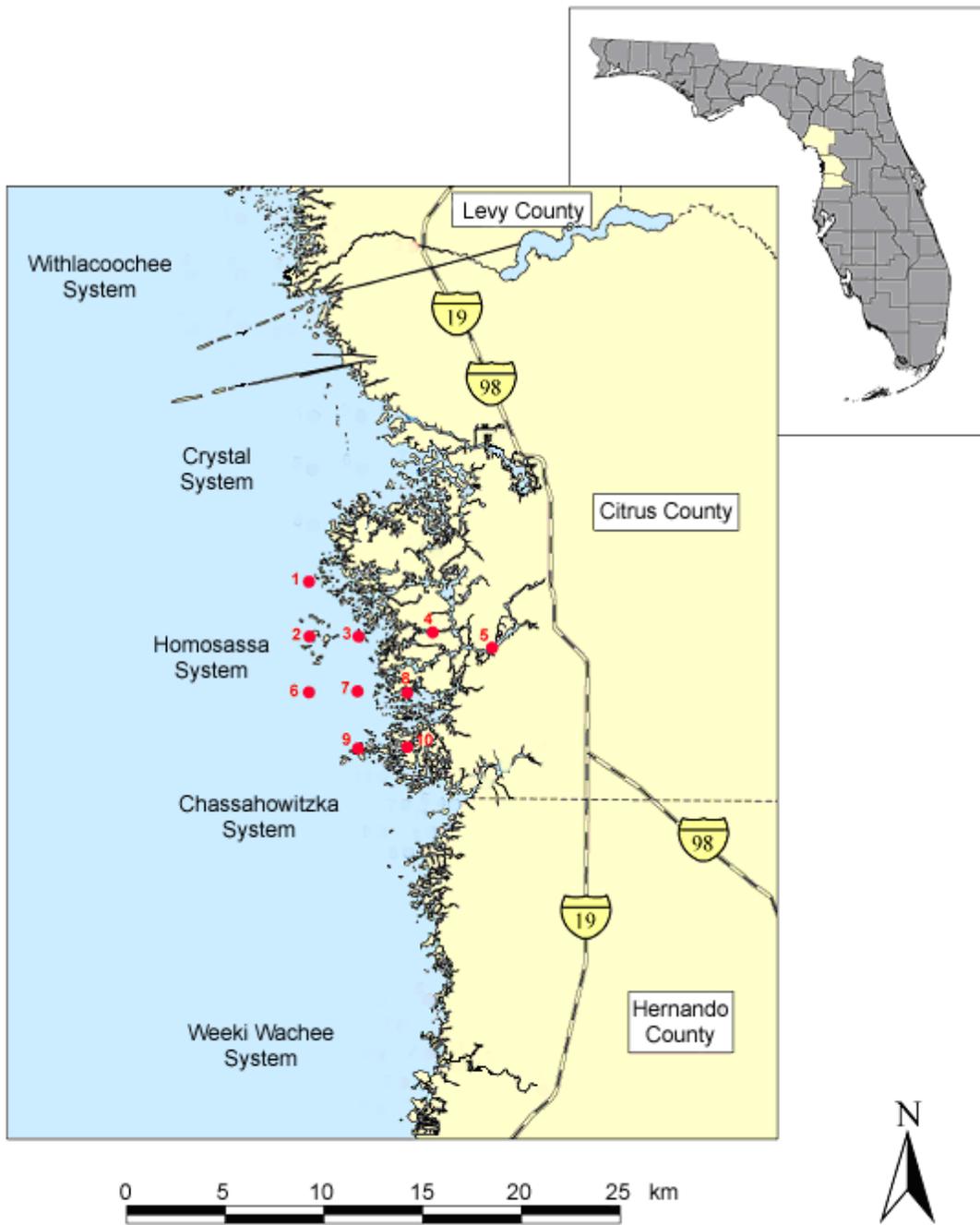


Figure 2-2. Sampling stations for environmental data (modified from Jacoby et al. 2008).

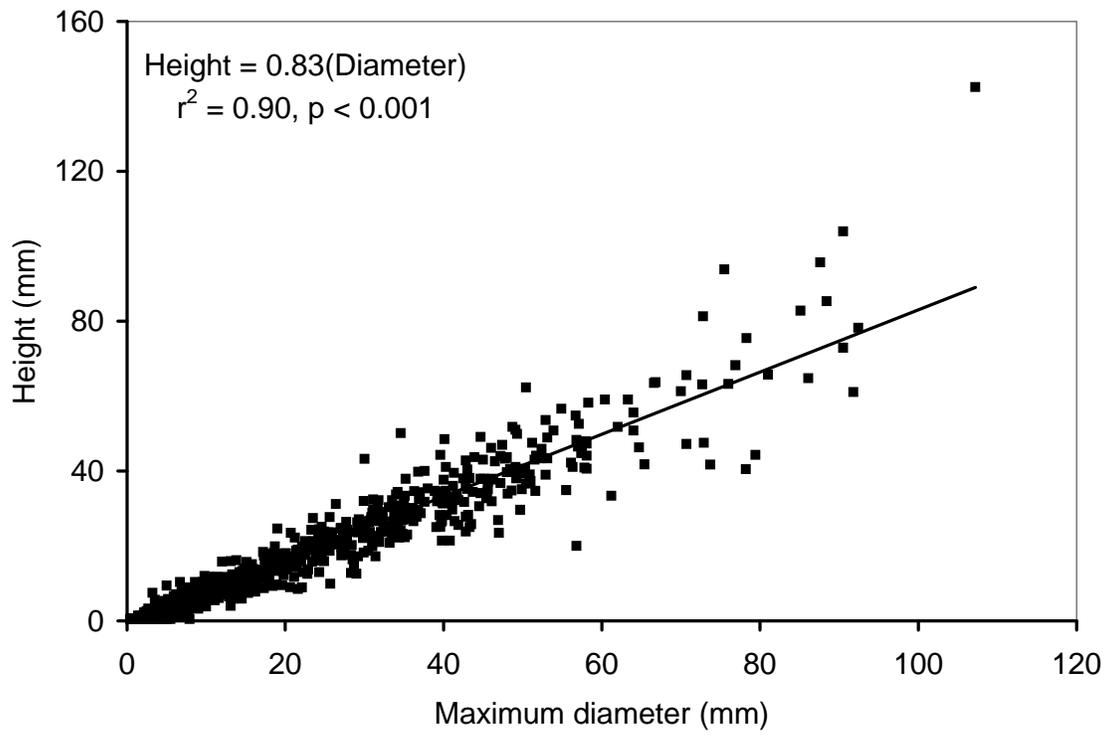


Figure 2-3. Linear regression of *Siderastrea radians* colony heights vs. maximum diameters.

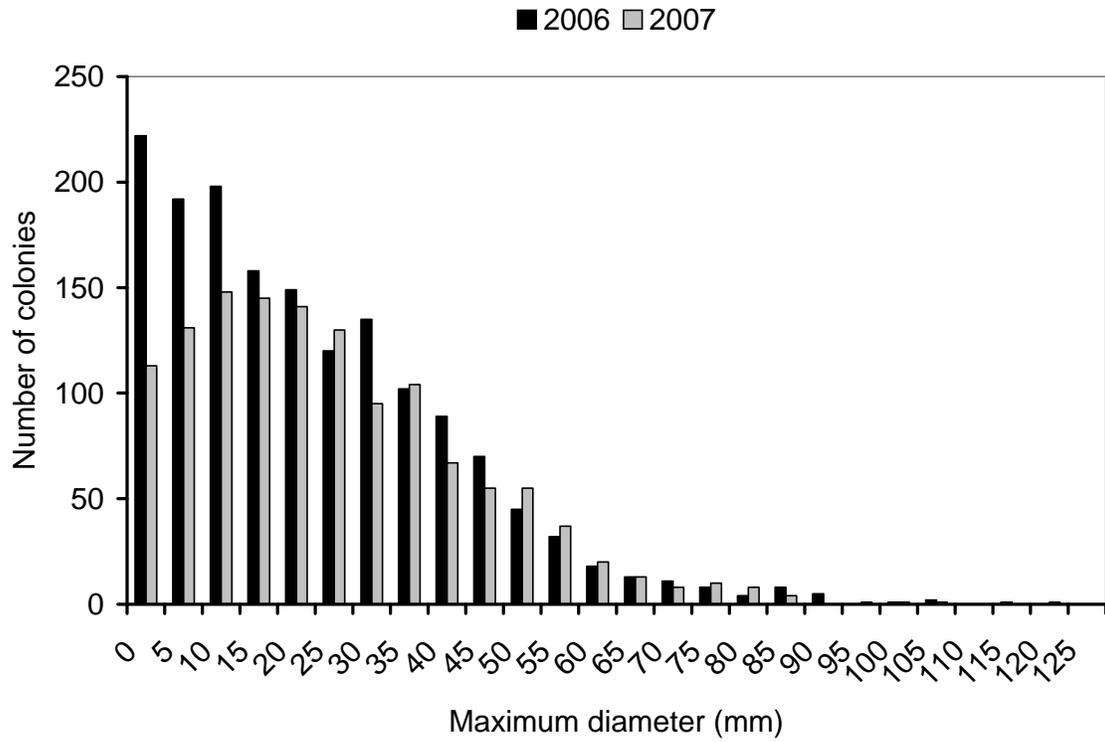


Figure 2-4. Size-frequency distributions of *Siderastrea radians* colonies in 2006 and 2007.

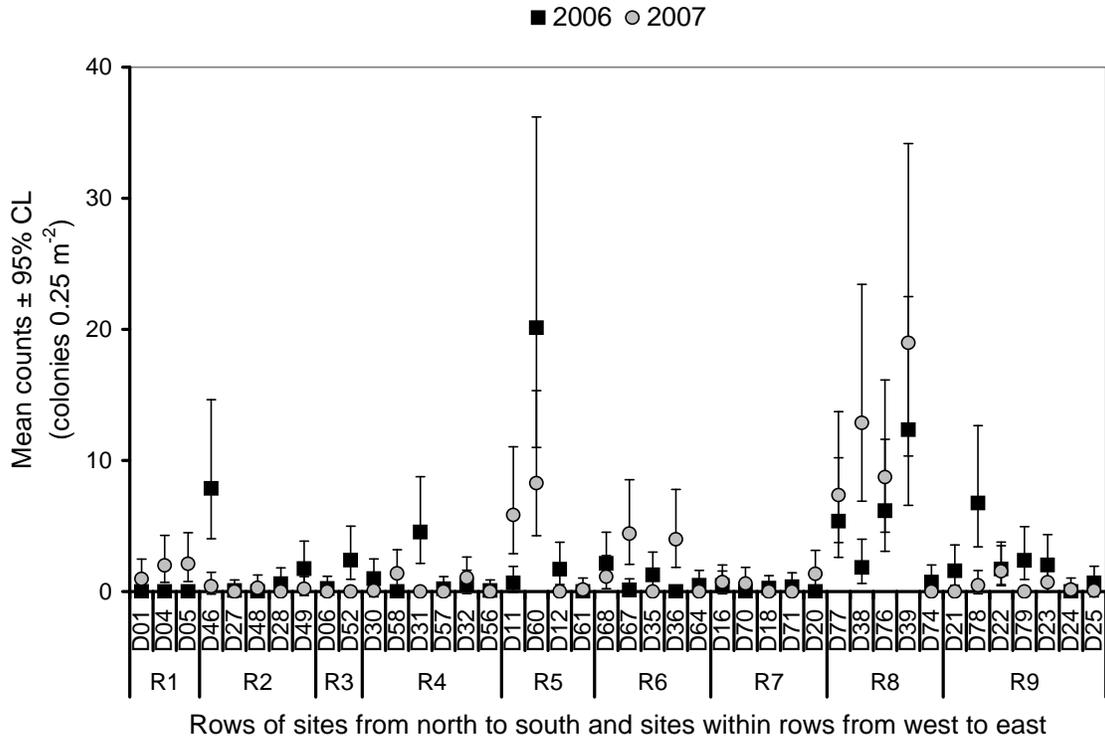


Figure 2-5. Back-transformed mean counts of *Siderastrea radians* colonies ± 95% confidence limits (CL).

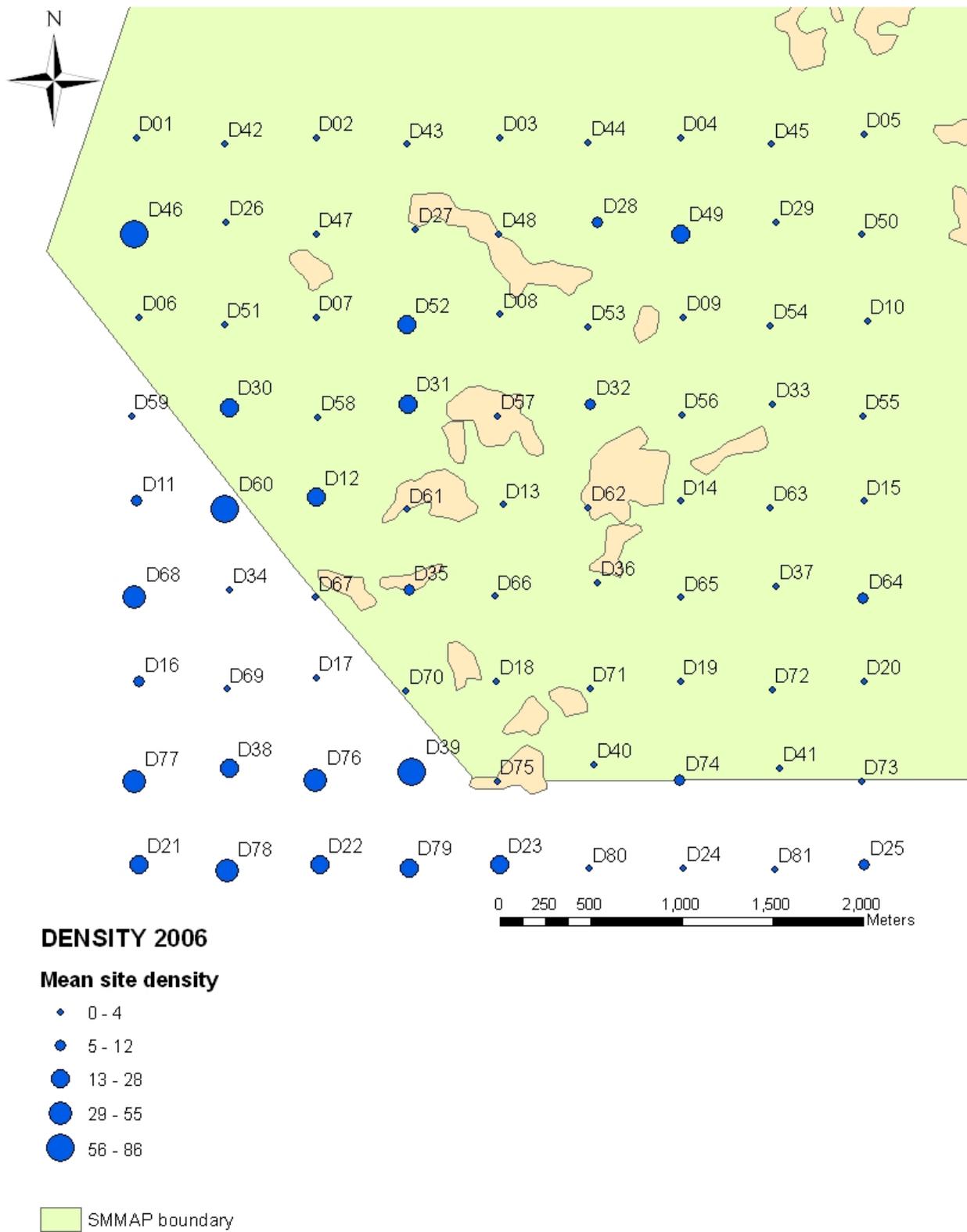


Figure 2-6. Mean densities of *Siderastrea radians* (colonies m^{-2}) in 2006. SMMAP = St. Martins Marsh Aquatic Preserve.

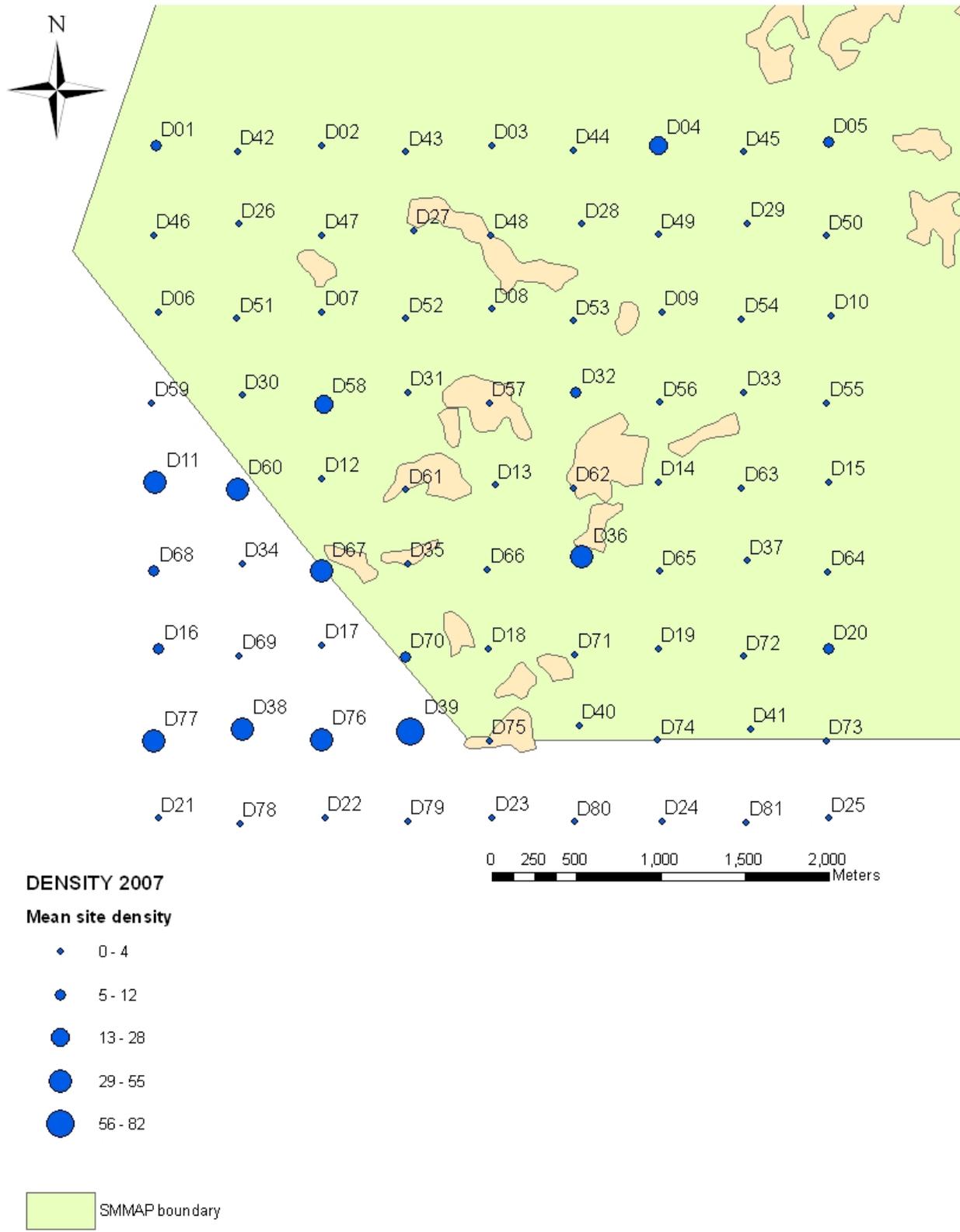


Figure 2-7. Mean densities of *Siderastrea radians* (colonies m^{-2}) in 2007. SMMAP = St. Martins Marsh Aquatic Preserve.

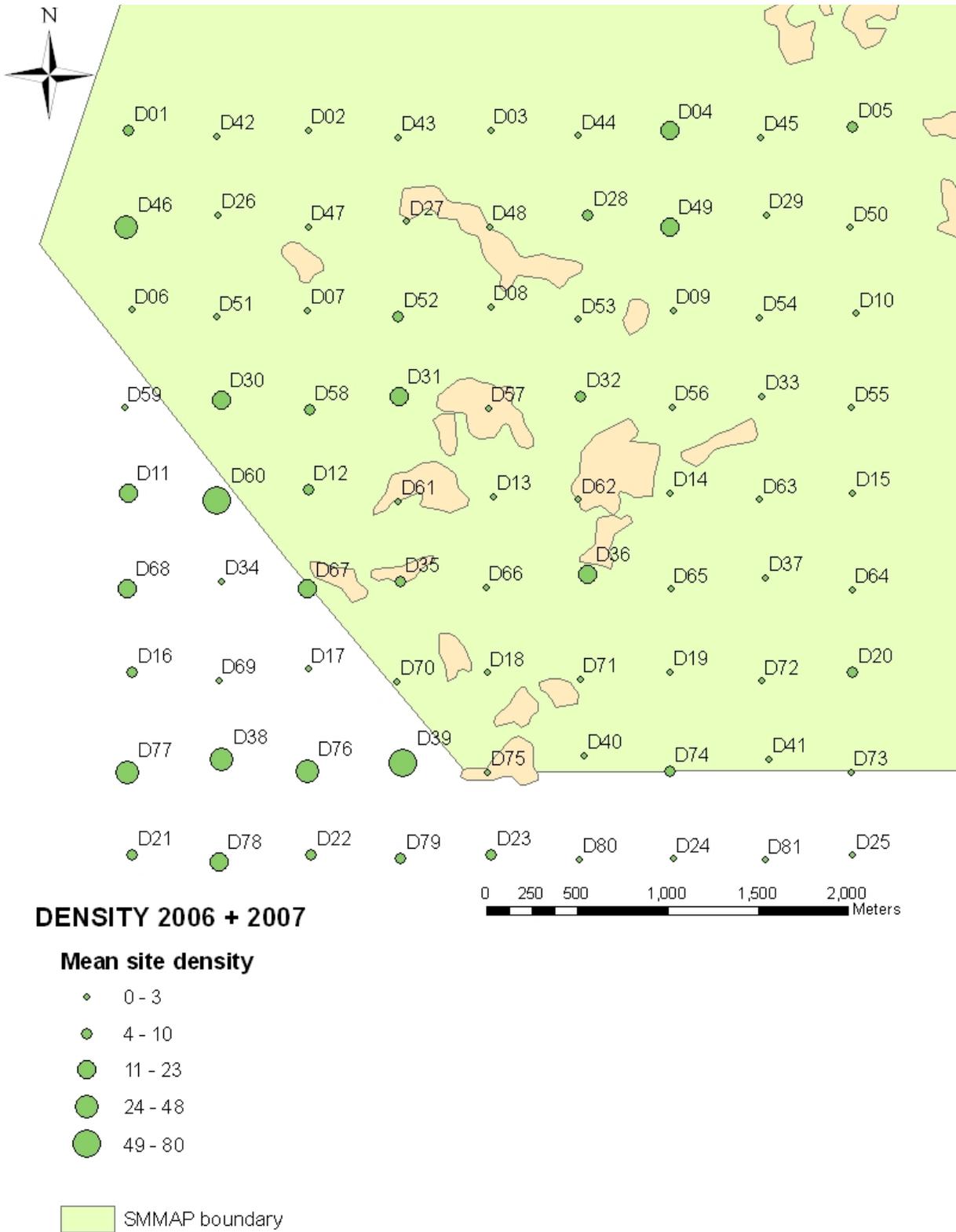


Figure 2-8. Mean densities of *Siderastrea radians* (colonies m⁻²) for 2006 and 2007. SMMAP = St. Martin's Marsh Aquatic Preserve.

CHAPTER 3
REPRODUCTIVE CHARACTERISTICS OF *Siderastrea radians*

Introduction

Most marine invertebrates exhibit complex life cycles that include a planktonic larval phase. The genetic structure and survival of populations, along with the species composition of assemblages are dependent on the outcome of processes affecting this phase and the subsequent addition of new recruits to populations (Vermeij 2005). The settlement and subsequent recruitment of larvae are therefore crucial life history characteristics, and many studies of marine benthic invertebrates have, consequently, focused on the survival and dispersal of larvae. Notwithstanding the importance of larval dynamics, research within the past thirty years has begun to focus on the reproductive ecology of benthic invertebrates as a potential factor controlling population dynamics and an important component in the evolution of life histories (see Pennington 1985). The results of such investigations should be particularly important for protection and restoration of corals, which are under stress worldwide, because reproductive ecology should play a role in determining the functional roles, interchangeability, and contributions to resilience for different species of corals (Bellwood et al. 2004). Beyond larval dispersal, key aspects of reproductive ecology include sexuality, reproductive mode, seasonality and timing of reproduction, fecundity, sex ratio, and variations in these characteristics with variations in abundance and level of aggregation.

In corals, there are typically four patterns of sexual reproduction, consisting of gonochoric or hermaphroditic species with broadcast spawning or brooding modes of development. The sexuality of a coral refers to whether the species is gonochoric or hermaphroditic. A gonochoric species is represented by two distinct sexes, whereas a hermaphroditic species may contain both sexes either at the same time (simultaneous) or at different stages in the life history (sequential).

Sexuality is typically conserved within a species throughout its range (Harrison & Wallace 1990). In contrast to sexuality, reproductive mode may vary between geographically separated populations of a given species and within local populations (Harrison & Wallace 1990). For example, populations of the reef coral *Goniastrea aspera* in Palau were found to brood and release planulae (Abe 1937, Motoda 1939), but Babcock (1984) suggested that they were hermaphroditic, broadcast spawners on the Great Barrier Reef. Populations of this same coral in Okinawa have been reported to be both hermaphroditic, broadcast spawners and to brood planulae (Heyward et al. 1987, Hayashibara et al. 1993). Therefore, one should not assume that reproductive mode would remain consistent across the entire range of a species.

Sex ratios in species with separate sexes tend to approximate 1:1 (Fisher 1930, Hamilton 1967). Even hermaphroditic species should allocate approximately equal resources to male and female gametes (Maynard Smith 1971). Darwin (1871) and Fisher (1930) recognized that sex ratios evolve through frequency-dependent selection on the relative reproductive success of male and female offspring. In other words, imbalances in sex ratios are self-correcting because offspring of the minority sex will generally experience greater than average reproductive success, which, in turn, can lead to an increase in production of the minority sex if this trait is heritable; a balancing of the sex ratio leads to a stable evolutionary equilibrium.

Nevertheless, species do exhibit biased sex ratios. A bias toward males, for example, has been reported for the brittle star *Ophiactis savignyi* (McGovern 2002) and Richardson's ground squirrels *Spermophilus richardsonii* (Schmutz et al. 1979). Female-biased sex ratios occur in a wide range of coral taxa, including gorgonians (*Acabaria biserialis*, Ben-Yosef & Benayahu 1999), red corals (*Corallium rubrum*, Santangelo et al. 2003), and stony corals, such as *Siderastrea stellata* (De Barros et al. 2003).

Biased sex ratios have been attributed to various causes, such as asexual propagation (Sammarco 1982), inbreeding or parthenogenesis (Hamilton 1967), sex changes in adult colonies (Rinkevich & Loya 1987), developmental activation of ova by sperm of other species (Stenseth & Kirkendall 1985), and environmental determination of sex (Charnov & Bull 1977).

Furthermore, if male reproductive output is capable of greatly exceeding that of females, a female-biased sex ratio may be evolutionarily advantageous. For this reason, the presence of a skewed sex ratio in gonochoric, brooding corals is not unexpected (Harrison & Wallace 1990).

The reproductive success of a gonochoric, brooding coral is related to an interaction between the spatial distribution of colonies and the sex ratio in the population (Ben-Yosef & Benayahu 1999). In populations where only the females brood, the number of female colonies is likely to become the factor that limits reproductive success because sperm from a single male colony can fertilize multiple eggs, which become the planulae brooded by multiple female colonies. In this scenario, a female-biased sex ratio should evolve because colonies that produce a higher proportion of females transmit their genes more successfully and garner increased fitness (Maynard Smith 1978, Charnov 1982). In contrast to brooders, broadcast spawners, such as *Siderastrea siderea*, typically exhibit a 1:1 sex ratio (Soong 1991).

In addition to sex ratio, the presence of a uniform, random, or aggregated distribution of males and females is also a critical influence on reproductive success. In plants, a random distribution over relatively large spatial scales is considered optimal for pollen distribution and seed dispersal (Bawa & Opler 1977). This situation may differ for sessile invertebrates if the threshold distance for successful fertilization becomes a limiting factor. The likelihood of successful fertilization may decrease significantly if males and females are separated by a few

meters, as shown in *Plexaura cuna*, a broadcast spawning octocoral (Coma & Lasker 1997), and other marine invertebrates (Pennington 1985, Levitan 1991, Brazeau & Lasker 1992).

However, aggregated distributions also may be the result of other influences. For example, corals depend on various environmental or chemical cues when timing settlement and/or larval metamorphosis. The presence of crustose coralline algae has been shown to induce larval settlement and metamorphosis in both soft (Slattery et al. 1999) and hard corals (Heyward & Negri 1999). Furthermore, habitat characteristics, such as water depth (Edmunds et al. 2004), sediment depth, or substrate composition (Vermeij 2005), also influence settlement and subsequent recruitment.

The processes that yield a particular spatial distribution of males and females may be influenced by density. Density in plants and insects has been shown to affect secondary sexual characteristics (Lovett Doust et al. 1987) and sex ratios (Myers et al. 1998), respectively. The difference between the sex ratios of a Costa Brava population of the red coral *Corallium rubrum* and a population in Italy (Santangelo et al. 2003) has been hypothesized to be due to differences in density and larval recruitment between the two sites (Tsounis et al. 2006). Optimal fertilization rates and, consequently, sex ratios in gorgonians are affected by population density (Brazeau & Lasker 1990). In addition, the presence and/or density of adult conspecifics may influence larval settlement in many marine invertebrates. For example, adult density was shown to positively influence recruit abundance in *Siderastrea radians* populations in the Florida Keys (Vermeij 2005).

In summary, several key questions that bear on reproductive success and, ultimately, population structure, relate to the reproductive characteristics of corals. Do colonies exhibit gonochorism or hermaphroditism across the species' geographic range? Are sex ratios balanced

or biased between and within populations? Does density or level of aggregation affect sex ratios? In addition, variation in reproductive characteristics has broad implications for how a species will respond to environmental stressors and natural and anthropogenic disturbances. Therefore, basic information on reproductive characteristics for a species with a cosmopolitan distribution, like *Siderastrea radians*, represents a significant contribution to the field of coral ecology.

Typically, small massive corals like *Siderastrea radians* exhibit life history characteristics that differ from large massive species. Massive corals with surface areas under 100 cm² generally brood larvae, reproduce often and throughout the year, reach puberty at a small size, and exhibit high recruitment rates (see Soong 1993). In fact, some of these reproductive characteristics have been identified for specific populations of *S. radians* (Duerden 1904, Szmant 1986, Soong 1991, Soong & Lang 1992).

Sexuality and reproductive mode appear to be known for *Siderastrea radians*. Although an initial report detailing *S. radians* postlarval development suggests that the species may be hermaphroditic (Duerden 1904), subsequent studies indicate that it is more likely to be gonochoric (Szmant 1986, Soong & Lang 1992). In addition, populations of *S. radians* in Panama have been shown to exhibit brooding as a reproductive mode (Soong 1991), which may increase reproductive success (Szmant 1986). Planulae of brooding species often settle within hours of release and near their point of release (Duerden 1904, Lewis 1974, Vermeij 2005), thereby escaping the relatively high rate of mortality associated with planktonic development (Szmant 1986). In addition, brooding generally is coupled with multiple reproductive cycles per year, resulting in more opportunities for recruitment than a single spawning cycle. Although many scleractinian coral species (especially broadcast spawners) reproduce on a lunar or seasonal basis, *S. radians* in Panama exhibits protracted reproduction and broods year-round

(Soong 1991). Furthermore, there was no evidence of lunar synchrony in larval development or release. However, latitudinal variation in the timing of gametogenesis has been linked to differences in water temperature due to upwelling for species such as *Siderastrea stellata* (De Barros et al. 2003). If geographically distinct populations of *S. radians* experience differences in sea surface temperatures, spawning and gametogenesis may differ from what has been observed in the Caribbean.

The sex ratio of *Siderastrea radians* populations in both Puerto Rico and Panama was found to be skewed towards females (1:20, Szmant 1986; 24:526, Soong 1991), and populations in Bermuda also exhibit a highly female-biased sex ratio (S. de Putron, University of Swansea in Wales, pers. comm.). It is unlikely that the proliferation of females in *S. radians* populations can be explained by asexual reproduction based on the morphology and habitat of this species (Harriott 1983). Selective mortality of male planulae and/or colonies also is unlikely to produce a skewed sex ratio given the stochastic nature of mortality and the early age at which most mortality occurs (Hughes 1983). This study focused on the sex ratio of the reproductively active component of the population, i.e., the operational sex ratio, which represents the outcome of all processes operating earlier in the life history.

To tease out interactions among reproductive characteristics, abundance or density, and aggregation, I employed a sampling regime designed to quantify these parameters for *Siderastrea radians* in the St. Martins Keys, Florida (SMK). This portion of my research focused on two main goals: (1) to elucidate the key reproductive characteristics of sexuality, reproductive mode, sex ratio, and puberty size for the SMK population; and (2) to quantify the relationship between recruit and conspecific abundance.

Materials and Methods

Corals cannot be sexed in the field unless planula and/or sperm release is observed; therefore, the reproductive characteristics of *Siderastrea radians* in the SMK were determined by histological examination of tissue samples from colonies collected at study sites selected to reflect variation in density and aggregation as measured by Morisita's Index (I_{δ} ; Eq. 2-1).

The histological results were combined with counts of colonies and measures of maximum diameters to elucidate key aspects of the reproductive demography, or variation in reproductive ecology, of *Siderastrea radians*. The presence of ova, sperm, and/or planulae indicated maturity and sexuality. Size-frequency distributions of mature and non-reproductive colonies provided estimates of size at puberty. Comparisons of sex ratios among sites yielded insights into potential interactions with density and aggregation, as did evaluation of the relationship between recruits and conspecifics.

Coral Surveys

Based on the results of surveys in 2006 and 2007, 17 sites were selected to: (1) represent different combinations of density and aggregation (Table 3-1), and (2) encompass the north, west, and southwest regions of the sampling grid (Fig. 3-1). Between 26 and 28 June 2007, eight 50-m transects were deployed at each site from the coordinate identifying the site. Bearings started at 0° (N), were incremented by 45°, and ended at 315° (NW). Along each transect, three 0.25-m² quadrats were placed at distances chosen with the aid of random numbers. In each of the resulting 24 quadrats, corals were counted and assigned to one of four size categories based on maximum diameters: (1) 0.0–4.9 mm, (2) 5.0–19.9 mm, (3) 20.0–49.9 mm, and (4) >50.0 mm. These size categories captured variation seen in size-frequency distributions generated from surveys in 2006 and 2007, as well as size categories deemed important in the reproductive biology of *Siderastrea radians* in the Caribbean (Soong & Lang 1992). For example, the first

size category (0.0–4.9 mm) was designed to encompass immature corals, and the third category (20.0–49.9 mm) began at the puberty size of *S. radians* in Panama (Soong & Lang 1992). Coral counts were used to confirm variation in density and aggregation. These results were used to identify 10 sampling sites for coral collection.

Coral Collection

Siderastrea radians colonies were relatively small, with most being less than 100 mm in diameter; therefore, whole colonies were collected. Attempts to extract cores from large colonies using either a pneumatic drill or an arch punch failed to yield suitable samples or destroyed the colony. During collection, the basal attachment of the colonies was severed with a hammer and masonry chisel.

Based on the results of counts, corals were collected from 10 sites chosen to differ in density of colonies and degree of aggregation between 30 July and 10 August 2007. Starting at the central coordinate, each site was divided into 8 quadrants of 45°. The area was further divided into 16 subquadrants, with 8 subquadrants running 0–50 m from the central coordinate and the remaining 8 subquadrants running 50–100 m from the central point. Using a randomized list of the first 8 subquadrants, one subquadrant was selected, the area was scanned for coral, and a 0.25-m² quadrat was haphazardly placed in a location that contained coral colonies. Coordinates of all quadrats were recorded with a handheld global positioning system (GPS 12 XL, Garmin) contained in a dry bag. All corals within the quadrat were collected and placed into a Ziploc bag containing ambient seawater. This process was repeated until a minimum of three quadrats with coral were identified and at least 50 corals were collected. The more distant set of subquadrants was used only if these conditions were not satisfied by sampling in the 0–50 m subquadrants. Corals were transported to the boat and transferred from bags to jars

filled with a 1:4 solution of Z-Fix (buffered zinc formalin, Anatech Ltd. USA) and ambient seawater, respectively. Each jar contained one coral colony, with a label comprising a unique identification number, the site number, and the quadrat number. Corals were transported to the laboratory for histology.

Histological Analysis

Containers with corals were agitated every 2 h for the first 8 h to ensure penetration of the fixative into the tissue. Samples were left in the fixative solution for at least 48 h. Used fixative was disposed according to protocols approved by University of Florida Environmental Health and Safety Division.

The calcium carbonate skeleton of the colonies needed to be removed to facilitate sectioning and allow for examination of tissues. In an effort to promote efficient and effective decalcification, a 30 mm x 40 mm portion of colonies larger than 50 mm in diameter was removed using a wet tile saw. Central polyps were chosen based on reports that infertile polyps generally were associated with margins of colonies (Chornesky & Peters 1987). Remnants of large colonies were disposed according to University of Florida Environmental Health and Safety protocols.

All specimens were decalcified using a solution consisting of 2.5% hydrochloric acid and a chelating agent, ethylenediaminetetraacetic acid (EDTA), according to standard procedures (E. Peters unpubl. data). Decalcification times varied according to the size of the specimens.

Following decalcification, one or two tissue samples (~7.5 mm x 15.0 mm) were cut from each specimen and placed in tissue cassettes under running tap water for 24 h. After rinsing, cassettes were stored in 75% ethanol until they were processed.

Tissue samples were dehydrated and embedded in paraffin (Paraplast) in preparation for sectioning with a microtome. Samples were serially sectioned at a thickness of 6 μm , which

yielded approximately 60 sections per specimen. Sections were floated onto five to ten precleaned slides that were rubbed with L-Lysine (Fisher Scientific) prior to section placement. Slides were dried overnight on a slide warmer or in an oven. Three to five slides per specimen were stained using hematoxylin and eosin-Y (Hematoxylin 7211, Eosin-Y 7111, Richard-Allan Scientific), which is an approach commonly used to distinguish various cell and tissue components. A coverslip was added to each slide using Permount (Fisher Scientific). Each stained slide was examined under light microscopy for gonadal material, which was used to identify the sex of individual polyps.

Sex Ratio

Sex ratios were calculated from the results of histological examination of corals. Chi-square tests were used to compare sex ratios (calculated as males:females) calculated across all sites to sex ratios reported for *Siderastrea radians* in Puerto Rico and Panama (Szmant 1986, Soong 1991).

A two-way analysis of variance (ANOVA) was used to test for significant variation in sex ratios among sites with differing densities and degrees of aggregation. Sex ratio was operationally defined as the number of mature males divided by the number of mature females. Sites were classified according to the densities and Morisita's Indices calculated from counts in the 24 quadrats comprising the June 2007 coral surveys. The resulting classes were treated as levels of fixed factors. Before the analysis, data were tested for normality with a Ryan-Joiner test and homoscedasticity with Cochran's test. Data were transformed if necessary.

Puberty Size

Cumulative size-frequency distributions were prepared for non-reproductive coral colonies, females, and males using the results of histological examinations. These distributions were used to define puberty size, or the average size at first reproduction. Differences in mean

maximum diameters among males, females, and non-reproductive colonies were investigated with a one-way ANOVA. Before the analysis, data were tested for normality with a Ryan-Joiner test and homoscedasticity with Cochran's test. Data were transformed if necessary.

Puberty size was calculated using several methods. In one calculation, colonies were ranked according to increasing size, and puberty size represented the maximum diameter of the smallest colony in the first group of 20 colonies that contained 90% or more fertile colonies (i.e., 18 or more fertile colonies; Soong & Lang 1992). In contrast, puberty size also was calculated as (1) the colony size below which there was no evidence of mature gonads (Hall & Hughes 1996), and (2) the colony size at which 50% of colonies exhibited mature gonads.

Distribution of Recruits Relative to Conspecifics

Relationships between recruits, which were operationally defined to be solitary polyps, and conspecifics were investigated using linear regression. Numbers of recruits and conspecifics were drawn from the pooled data collected during the 2006 and 2007 surveys, with counts being sums across ten, 0.25-m² quadrats along each transect.

Three relationships were examined. Numbers of recruits were regressed against (1) numbers of all conspecifics, (2) numbers of mature conspecifics, which were operationally defined as colonies equal to or larger than puberty size, and (3) numbers of immature conspecifics, operationally defined as colonies smaller than puberty size. Before the analyses, data were tested for normality with a Ryan-Joiner test and homoscedasticity with Cochran's test. Data were transformed if necessary.

Results

Coral Surveys

The majority of corals surveyed fell into the 20.0–49.9 mm and 5.0–19.9 mm size classes (Fig. 3-2). In addition, 41% of corals were in the two smallest size classes, 0.0–4.9 mm

and 5.0–19.9 mm. Thus, the size frequency distribution was similar to earlier surveys (see Fig. 2-4). Densities at the 17 selected sites ranged from 0.0 to 36.5 colonies m^{-2} (Fig. 3-3). The overall mean density for all sites was 9.78 colonies m^{-2} . Morisita's Indices (I_{δ}) ranged from 0.00 to 24.00 across the 17 sites (Fig. 3-3). As expected for an index designed not to correlate with density, I_{δ} -values at densities less than 5.0 colonies m^{-2} varied from 2.3 to 24.0 (Fig. 3-3). Ten of the 17 sites were selected for coral collection (Fig. 3-3). These sites covered nearly the full range of densities and levels of aggregation.

Reproductive Strategy

The 598 colonies collected from the 10 sites had maximum diameters ranging from 0.2 mm to 170.7 mm, with a mean \pm standard error of 26.6 ± 0.85 mm. The size-frequency distribution (Fig. 3-4) was similar to that found in the 2006 and 2007 surveys (see Fig. 2-6), with 54% of corals being smaller than 25 mm in maximum diameter.

Of the 581 colonies examined, 357 contained no identifiable sperm, eggs or planulae. All polyps examined in every mature colony were of the same sex, which provided no evidence of hermaphroditism and reasonable evidence that *Siderastrea radians* in the SMK are gonochoric. Planulae were not observed, so there was no evidence that the corals are brooders.

Sex Ratio

The colonies containing evidence of gonads comprised 108 males and 116 females. This sex ratio, calculated here as males:females, 0.93:1.00, does not differ significantly from 1:1 ($\chi^2 = 0.286$, $p = 0.593$), but it is significantly different from the female-biased sex ratios of 1:20 and 1:22 reported from Puerto Rico and Panama (Szmant 1986, $\chi^2 = 933.011$, $p < 0.0001$; Soong 1991, $\chi^2 = 1022.278$, $p < 0.0001$). Sex ratios, expressed as males:females, calculated

for individual sites ranged from 0.28:1.00 to 1.33:1.00, with a mean \pm standard error of 0.89:1.00 \pm 0.10 (Table 3-2).

Across all sites, 38% of colonies exhibited reproductive activity, and values for individual sites ranged from 18% to 64% (Table 3-2). Inactive colonies, or those above the puberty size as defined by Soong & Lang (1992), comprised 45 of the 581 collected colonies (Table 3-2). The frequency of fertile colonies increased in larger size classes, but the frequencies were always lower than those reported by (Soong & Lang 1992) for Panamanian *Siderastrea radians* (Table 3-3).

Based on data from 24 quadrats sampled in each site, the 10 sites were classified into high and low categories for both density of *Siderastrea radians* colonies and level of aggregation as measured by Morisita's Indices (Table 3-4, Fig. 3-5). The ratios of males to females were normal and homoscedastic. The ratio of males to females did not vary significantly among classes of density, classes of aggregation, or a combination of the two (Table 3-5, Figs. 3-6 & 3-7).

Puberty Size

Estimated puberty size varied according to the methods applied. Applying the methods of Soong & Lang (1992) yielded a puberty size of 39.8 mm, compared with a puberty size of 20.0 mm reported for *Siderastrea radians* in Panama. The smallest colony with mature gonads was 3.8 mm in diameter (method of Hall & Hughes 1996). Alternatively, 50% of colonies exhibited gonadal material at 32.8 mm maximum diameter, and this estimate of puberty size was used in further analyses (Fig. 3-8).

Square-root transformed maximum diameters were homoscedastic, but non-normal. A conservative interpretation of the results of ANOVA indicated that the mean maximum diameters of males were larger than those of females, which were larger than those of non-reproductive colonies ($F = 115.9$, $df = 2, 578$, $p < 0.001$, Fig. 3-8). The back-transformed mean

maximum diameter for non-reproductive colonies was 15.6 mm with lower and upper 95% confidence limits of 13.4 and 17.8 mm. The back-transformed mean maximum diameter for female colonies was 32.6 mm with lower and upper 95% confidence limits of 29.5 and 39.8 mm. The back-transformed mean maximum diameter for male colonies was 42.2 mm with lower and upper 95% confidence limits of 38.7 and 45.9 mm.

Distribution of Recruits Relative to Conspecifics

Counts of solitary polyps and larger colonies summed over the 10 quadrats sampled in each of 81 sites during the 2006 and 2007 surveys were normal and homoscedastic following the appropriate log-transformation. A regression based on counts from quadrats with solitary polyps showed a significant positive relationship between numbers of solitary polyps and numbers of all other conspecifics ($r^2 = 0.27$, $p < 0.001$, Fig. 3-9). Mature conspecifics could be identified by applying the puberty size derived from the maximum diameter at which 50% of colonies displayed gonads, i.e., colonies equal to or larger than 32.8 mm in maximum diameter. A regression showed a positive, but weaker, relationship between numbers of solitary polyps and mature conspecifics ($r^2 = 0.15$, $p = 0.0008$, Fig. 3-10). Further, a regression between solitary polyps and conspecifics smaller than the puberty size showed the strongest positive relationship ($r^2 = 0.32$, $p < 0.001$, Fig. 3-11).

Discussion

Variation in reproductive characteristics has been described for several anthozoans (Rinkevich & Loya 1979, Benayahu & Loya 1983, Kojis 1986, Soong 1991, Fan & Dai 1995, Sakai 1997, Kramarsky-Winter & Loya 1998, Santangelo et al. 2003, Tsounis et al. 2006, Gori et al. 2007). For example, studies have shown intraspecific variation in reproductive mode, sex ratio (Benayahu & Loya 1983, Tsounis et al. 2006, Gori et al. 2007), and interspersions of males and females (Kramarsky-Winter & Loya 1998) across various spatial scales in a wide variety of

species, including sea anemones (Rossi 1975), gorgonians (Gori et al. 2007) and scleractinian corals (Rinkevich & Loya 1979). Harrison & Wallace (1990) suggested that although some facets of reproductive strategy (e.g., sexuality) may be genetically determined and consistent across a species' geographic range, other aspects (e.g., reproductive mode, size at maturity, and reproductive season) may be influenced by local environmental variables. In fact, even 'genetically determined' sexuality may exhibit variation (see Tomascik & Sander 1987).

Sexuality

Sexuality is generally evaluated through histological analysis of tissue samples when organisms lack other sexually dimorphic characteristics. In the present study, all specimens with gonadal material were sexually dichotomous, i.e., only eggs or sperm were found in any individual colony. This evidence of gonochorism is consistent with studies of Caribbean populations of *Siderastrea radians* (Szmant 1986, Soong 1991), and, in combination, these findings corroborate the concept that sexuality generally remains consistent within each scleractinian family throughout its geographic range (Harrison & Wallace 1990).

Although Caribbean and SMK populations of *Siderastrea radians* are purported to be gonochoric, available results do not exclude the possibility of sequential hermaphroditism because the sexuality of individual colonies has not been traced through time. Thus, the possibility that *S. radians* is a sequential hermaphrodite remains to be explored. However, sequential hermaphroditism in sessile organisms is not common, with few corals exhibiting this reproductive strategy (Marshall & Stephenson 1933, Glynn et al. 2000, Neves & Pires 2002). In addition, skewed sex ratios characterize populations of these species (Szmant 1986, Soong 1991). The sex ratio of the SMK population of *S. radians* was not skewed and males and females were abundant across all size ranges; therefore, sequential hermaphroditism in this population is unlikely.

Sex Ratio

Geographic variation in the reproductive strategy of *Siderastrea radians* was exemplified by differences in sex ratios between populations in the SMK and the Caribbean. The sex ratio in the SMK differed significantly from ratios reported for Panamanian (24:526, Soong 1991) and Puerto Rican populations (1:20, Szmant 1986). The observed sex ratio in the SMK population was approximately 1:1 and the sample size was large ($n = 581$), so it is unlikely that the estimate was inaccurate. However, samples were only collected during a two-week period from 30 July to 10 August 2007, unlike the year-long sampling regimes utilized by Soong (1991) and Szmant (1986). This snapshot of the operational sex ratio of *S. radians* at the SMK may be affected by seasonal or cyclic maturation of gonads. However, inaccurate sex ratios typically present as highly skewed or comprising only one sex (e.g., Duerden 1904). This is not to say that a highly skewed sex ratio is inherently inaccurate.

In fact, female-biased sex ratios are common in brooding species. Szmant (1986) suggested that sexual reproduction via brooding solely in females of gonochoric species should naturally result in a female-biased sex ratio, as seen in *Siderastrea radians* in Puerto Rico and Panama. Only the females brood in most coral species adopting this reproductive strategy, and the limited space available for brooding within each polyp may exert a selective pressure for an increase in the proportion of female colonies (Szmant 1986). However, there are reported cases of gonochoric, brooding corals with a 1:1 sex ratio, including *Balanophyllia elegans* (Fadlallah & Pearse 1982), *Porites porites* (Tomascik & Sander 1987), and *Leptopsammia pruvoti* (Goffredo et al. 2006). The population of *S. radians* in the SMK may belong in this group as evidenced by the absence of significant variation in sex ratios across two spatial scales, i.e., within and among sites.

Sex ratios also may be affected by spatial distributions of conspecifics. Regardless of whether sex determination occurs pre-settlement (e.g., facultative sex determination determined by temperature) or post-settlement (e.g., environmental sex determination due to social interactions), one would expect a sex ratio of approximately 1:1 at low densities, because it facilitates interactions between the sexes. At higher densities, a single male may successfully fertilize many females, which could result in a female-biased sex ratio. Although there was no significant variation in sex ratio across sites that differed in density and degree of aggregation, the spatial distribution of colonies may indirectly affect the observed sex ratio of *Siderastrea radians*. Thus, future research could determine if the presence and/or sex of conspecifics act as cues for settlement of *S. radians* larvae and, if so, how these cues interact with density, aggregation, and distance between conspecifics (see Vermeij 2005) to affect sex ratios.

An increase in asexual reproduction at low densities also may result in skewed sex ratios, as has been reported for female-dominated populations of *Siderastrea radians*, *Porites lutea*, and *P. lobata* (Kojis & Quinn 1981, Tomascik & Sander 1987), or even the absence of one sex, as reported by Duerden (1904) who observed only female colonies of *S. radians*. In fact, Ayre & Miller (2006) argue that the optimal life-history strategy for brooding corals involves some level of inbreeding or selfing (i.e., asexual reproduction). Although sexual reproduction may be the predominant strategy, asexual reproduction can serve to augment recruitment, particularly when a population has suffered environmental stress or disturbance (Highsmith et al. 1980). A flexible strategy may favor sexual reproduction when both sexes are in close proximity and asexual reproduction or increased inbreeding when adult densities are low (Ayre & Miller 2006). Although beyond the scope of this study, fecundity has been suggested for use as a biological

indicator of environmental stress (Kojis & Quinn 1984), and future studies of *S. radians* in the SMK could combine data on fecundity and sex ratios to detect evidence of stress.

Puberty Size

Colonies without gonadal material were present across a broad size range. Although populations of *Siderastrea radians* are thought to reproduce year-round (Duerden 1904) and eggs, sperm, and planulae were observed in histological sections of *S. radians* in Puerto Rico almost year-round (Szmant 1986), seasonal reproductive cycles may become more pronounced with increasing latitude (Harrison & Wallace 1990). In addition, reproductive cycles could be staggered among colonies. In fact, this population of *S. radians* is, to my knowledge, near the northernmost limit of the species' range in the Gulf of Mexico, and, although highly stress tolerant, it may respond to fluctuations in temperature and salinity. Effects of environmental stress and/or disturbance (e.g., collection) also may manifest through premature abortion of gametes or planulae (Fadlallah 1983, Brown & Howard 1985). Future research should entail sequential sampling of individual colonies across the breeding season to determine if there is seasonal variability in the production of gametes.

The size-frequency distribution generated by coral collection was similar to those generated by surveys in 2006 and 2007; therefore, estimates of puberty size should be unbiased. Both sampling efforts recorded large numbers of small colonies, which is typical for scleractinian coral species (Bak & Meesters 1999). Based on Soong & Lang's (1992) criteria for puberty, colonies in the SMK mature, on average, at twice the size of colonies in Panama. In addition, there is also a significant difference in reproductive activity between Panamanian and SMK populations. In Panama, 96% to 100% of large colonies were fertile, whereas only 56% to 63% of large colonies were fertile in the SMK. Given the lower proportion of fertile colonies in the SMK, the 90% level of reproductive activity that Soong & Lang (1992) used to determine

puberty size was replaced with the size at which 50% of the population was observed to be reproductive. The resulting estimate of 32.8 mm still indicated an average onset of maturity at a larger size than in Panama.

In general, brooding species tend to become reproductive at smaller sizes than broadcast spawners (Harrison & Wallace 1990); however, the minimum size at which reproduction occurs is not the same as puberty size, which is an estimate of the average size at first reproduction for a population. Kojis & Quinn (1985) suggested that colony size determines whether a coral is reproductive, whereas polyp age influences size at first reproduction and fecundity. Harvell & Grosberg (1988) suggested that the presence of a threshold size above which reproduction occurs indicates that either extrinsic factors (e.g., food availability, temperature and lunar cycle) or intrinsic factors (e.g., size) interact with spatial distribution to initiate sexual maturity. Beyond the threshold, a combination of age and extrinsic factors may modify actual size at first reproduction. Ultimately, the optimal size for first reproduction likely results from balancing growth, survival, and reproduction (Stearns 1976). Many long-lived clonal species delay reproduction throughout unfavorable conditions until attaining some minimum size. In addition, it is not uncommon for scleractinian corals to exhibit intraspecific variation in size at sexual maturity. In *Montastrea annularis*, puberty size varies widely within a single population (Szmant-Froelich 1985). Relatively late maturation in the SMK population of *Siderastrea radians* may indicate a different balance among influences. For example, *S. radians* in the SMK could allocate more resources to growth at small sizes. However, mature males and females were found among the smallest colonies; therefore, colony size may not be the only important influence. Future research could examine the onset of reproduction as affected by extrinsic factors, such as density and resource availability.

Reproductive Mode

Reproductive mode refers to how a species breeds, and scleractinian corals utilize two primary modes. Most species spawn gametes that are fertilized externally, and they are classified as broadcast spawners. A smaller proportion of species brood planula larvae internally and subsequently release them, and these species are classified as brooders. Broadcast spawners are thought to disperse larvae across great distances, whereas brooders are considered to be poor dispersers (Harriott 1992). However, larvae of some brooding species may exhibit protracted planktonic existences (Szmant 1986), such as *Pocillopora damicornis* planulae that can remain in the plankton for up to two months (Szmant & Gassman 1991). Consequently, a brooding reproductive strategy does not preclude long-distance dispersal. Therefore, reproductive mode can combine with hydrology and other abiotic factors to have an important effect on gene flow and population structure (Ayre et al. 1997, Ayre & Hughes 2000, Nishikawa & Sakai 2005).

Although reproductive mode is generally conserved within a given species, intraspecific variation does exist (Richmond & Hunter 1990, Ward 1992). Geographic variation in reproductive mode does occur in species with wide latitudinal ranges. For example, *Acropora humilis* broadcast spawns in the Great Barrier Reef and the Red Sea, but it broods planulae at Enewetak in the Marshall Islands (Richmond 1987a, b, Ward 1992). Variation in reproductive mode also has been linked to habitat; with brooders typically occupying shallow water where disturbance is relatively high and broadcast spawners residing in calmer, deeper waters (Stimson 1978, Ward 1992).

The reproductive mode of a species is difficult to determine when the reproductive cycle is not known. In fact, inaccurate conclusions regarding reproductive mode and/or sex ratio can result from small sample sizes or missed reproductive cycles (Harrison & Wallace 1990). Corals do exhibit reproductive cycles, especially at high latitudes where breeding seasons and spawning

periods tend to be shorter than in tropical regions (Harrison & Wallace 1990). In fact, Duerden (1904) observed larval release in *Siderastrea radians* in Kingston Harbor, Jamaica, in late June and during July (n = 5), but *S. radians* was shown to release planulae year-round in Panama (Soong 1991). Additionally, the laboratory spawning period of *S. radians* in Bermuda is seasonal, with planulae release occurring in July, August, and September (S. de Putron, University of Swansea in Wales, pers. comm.).

Collection of large numbers of specimens (n = 623) over a year-long period should have accurately characterized brooding as the reproductive mode of *Siderastrea radians* in Panama (Soong 1991). The present study utilized a large sample size (n = 581); however, samples were collected over a two-week period from 30 July to 10 August 2007. Thus, the lack of planulae could have reflected seasonality in reproductive timing; however, based on laboratory reports of Bermudian *S. radians* releasing planulae in July, August, and September (S. de Putron, University of Swansea in Wales, pers. comm.), one might expect to see planulae in histological sections of *S. radians* collected in July and August at the SMK, a lower latitude population. Absence of planulae also may result from either a response to stressful conditions that caused release or premature abortion of planulae (Fadlallah 1983, Brown & Howard 1985), or geographic variation in reproductive mode. Intraspecific variation in reproductive timing and mode among allopatric populations may be a reflection of either plasticity or local adaptation to environmental conditions and stimuli (Richmond & Hunter 1990). Future research could investigate seasonality in reproduction for *S. radians* in the SMK, and such research could incorporate experimental manipulation of exposure to environmental conditions to distinguish between plasticity and local adaptation.

Distribution of Recruits Relative to Conspecifics

In populations of sessile marine invertebrates, analyses of the spatial distributions of males, females, and recruits across variations in density and aggregation provide insights into reproductive strategies and even sex determination. Spatial distributions yield insights because settlement and recruitment have significant effects on reproductive success in sessile organisms that reproduce sexually.

Settlement refers to the point at which larvae attach themselves to the substrate, and recruitment is the stage at which newly settled polyps become visible (Keough & Downes 1982, Connell 1985). Logistics precluded direct observations of settlement and subsequent recruitment of *Siderastrea radians* in the SMK. However, several lines of evidence suggested that solitary polyps, with maximum diameters of 0.1–5.8 mm, served as a reliable proxy for new recruits. Harrison & Wallace (1990) suggest that recently settled coral polyps are typically smaller than 2 mm in diameter; not much larger than the planulae from which they developed. Duerden (1904) described the pear-shaped planulae of *S. radians* as being 2 mm in length, and Soong (1991) reported a maximum length of 0.8 mm for planulae. In fact, most corals recruit approximately 8 to 10 months after settlement, and individuals rarely reach diameters of 10 mm after one year of growth (Harrison & Wallace 1990).

Populations of many marine organisms have been considered demographically open, i.e., local recruitment is not dependent on local reproduction, with planktonic larvae recruiting from distant sources (Caley et al. 1996). Previous reports suggest that *Siderastrea radians* larvae are brooded internally and then released into the water column (Duerden 1904), but the mere presence of planktonic larvae does not imply an open population, as evidenced by many philopatric coral species. Philopatric larvae, although capable of planktonic dispersal, settle next to or close to parent colonies. Although larvae of *S. radians* are typically not thought to crawl

directly to the substrate and settle (but see Vermeij 2005), the duration of their free-swimming and competency periods have been demonstrated in the laboratory to be on the order of hours to days (Duerden 1904). Therefore, it is likely that larval supply to the SMK population is predominately local. In fact, the majority of recruitment by corals on the Great Barrier Reef has been shown to be local, especially for brooding corals (Ayre & Hughes 2000). Thus, the distribution of recruits within the SMK population can provide insights into local processes.

Results from the present study confirmed that at a scale of tens of meters, recruits of *Siderastrea radians* occur in higher abundances where conspecifics are more abundant. Such a result was not unexpected given the aggregated nature of this population and reports that the species reproduces via brooding (Szmant 1986, Soong 1991). The significant linear regression between recruits and conspecifics was suggestive of localized dispersal, with larvae settling close to their natal colonies. In fact, Goreau et al. (1981) showed that larvae of the brooding coral, *Porites porites*, displayed non-random, aggregated settling behavior in the laboratory, and other studies have provided evidence for a direct relationship between juvenile abundance and adult cover (Bak & Engel 1979, Rylaarsdam 1983). However, at least three hypotheses could explain the spatial distribution of recruits in the SMK population of *S. radians*: (1) larvae are stimulated to attach to or settle near conspecifics; (2) settlement is random, but survival is increased through attachment to or settlement near conspecifics; or (3) larvae settle in response to physical characteristics of the environment, which makes settlement near conspecifics more likely (Connell 1973). These hypotheses are not mutually exclusive; it is likely that a combination of these and other factors, such as larval source and transport, resulted in the distribution of recruits and conspecifics seen in this study.

Although all three relationships between recruits and conspecifics were statistically significant, the relationship between recruits and potential parents, i.e., conspecifics equal to or larger than the estimated 32.8 mm puberty size, was weak. Further, the relationship between recruits and immature colonies was strongest. This finding corroborates the finding that the presence of mature colonies was not a strong indicator of recruit abundance, and it further supports the need to investigate hypotheses related to other influences. Additionally, these relationships indicate that larval input to a site may be unrelated to the reproductive output of the resident adults. In other words, larvae may disperse beyond the site where they were released. There are two seemingly competing views on dispersal and competency periods of brooded larvae. The first postulates that brooded larvae are able to settle more quickly than larvae from broadcast spawners. The second suggests that because of their large energy reserves, including high lipid content (Richmond 1981), brooded larvae may have competency periods that are longer than larvae of broadcast spawners (Richmond 1988). However, the prevailing view seems to be that larvae of brooding corals exhibit relatively short competency periods, with settlement occurring relatively quickly and close to the natal colony. Duerden (1904) reported laboratory competency periods of a few hours to days for *Siderastrea radians*. However, a recent study of *S. radians* in Brazil (Neves et al. 2008) suggested that laboratory experiments underestimate actual competency periods and the effective dispersal distance generated by local oceanographic conditions. Protracted competency periods and increased dispersal may contribute to creating the 1:1 sex ratio observed for *S. radians* in the SMK by making its reproductive strategy more similar to broadcast spawning.

Ultimately, an understanding of potential dispersal distance and the effects of various influences on actual dispersal will be important in assessing the resilience of reef ecosystems or

coral communities subject to disturbances, such as bleaching (Magalon et al. 2005). Therefore, further study of dispersal in conjunction with data on spatial patterns in abundance, aggregation, and reproductive strategies should improve the way corals resources are managed.

Conclusions

In summary, the gonochoric nature of *Siderastrea radians* in the Caribbean is conserved in the SMK population. However, a brooding reproductive mode cannot be confirmed. The lack of planulae in histological sections, coupled with the observed 1:1 sex ratio, is inconsistent with typical reproductive patterns of brooding coral species. However, this could be attributed to the short collection period, and may reflect seasonality in reproductive timing as is exhibited by many coral species at higher latitudes. Nonetheless, the 1:1 sex ratio and larger size at puberty of *S. radians* in the SMK highlight the geographic variation in reproductive characteristics among observed populations.

The observed relationships between recruit and conspecific abundance suggest that although colonies were aggregated, the distribution of recruits was not tightly related to the distribution of reproductively mature colonies. This points to the importance of other factors affecting settlement and establishment of larvae, such as dispersal distance and substrate availability and/or quality. Again, these results call into question the prevalence of a brooding reproductive mode for *Siderastrea radians* in the SMK.

Ultimately, this study demonstrates that *Siderastrea radians* exhibits a wide degree of geographic variation in reproductive characteristics. Such variation may have implications for a population's response to stress, climate change, and other perturbations. This variation is important to factor into management and conservation of coral resources.

Table 3-1. Densities and Morisita's Indices based on pooled data from 2006 and 2007 for sites selected for coral surveys in June 2007.

| Values for 2006 and 2007 combined | | |
|--|--|---|
| Site | Density (colonies m⁻²) | Morisita's Index (I_δ) |
| D24 | 0.6 | 20.00 |
| D18 | 1.0 | 12.00 |
| D48 | 1.2 | 13.33 |
| D71 | 1.6 | 9.29 |
| D74 | 3.6 | 10.59 |
| D28 | 3.8 | 9.71 |
| D16 | 6.4 | 5.08 |
| D52 | 8.4 | 4.53 |
| D32 | 10.4 | 6.38 |
| D31 | 11.6 | 2.66 |
| D23 | 11.8 | 3.20 |
| D49 | 12.6 | 5.46 |
| D68 | 18.0 | 3.66 |
| D67 | 18.0 | 3.88 |
| D11 | 22.8 | 2.29 |
| D60 | 63.0 | 1.32 |
| D39 | 79.6 | 1.48 |

Table 3-2. Reproductive characteristics of *Siderastrea radians* colonies at the 10 coral collection sites. Immature colonies are classified as those less than the puberty size of 39.8 mm maximum diameter (sensu Soong & Lang 1992); inactive colonies are those larger than or equal to puberty size that did not contain gonads in histological sections. Percent reproductive = percentage of all collected colonies at each site that contained gonads in histological sections.

| Site | Number of colonies | | | | | Percent reproductive | Sex ratio M:M |
|-------------|---------------------------|--------------|----------------|---------------------------------------|---------------------------------|-----------------------------|--------------------------|
| | Total | Males | Females | Immature (<39.8 mm) | Inactive (≥ 39.8 mm) | | |
| D11 | 55 | 15 | 13 | 25 | 2 | 51 | 1.15 |
| D18 | 64 | 9 | 11 | 27 | 17 | 31 | 0.82 |
| D23 | 51 | 2 | 7 | 32 | 10 | 18 | 0.28 |
| D24 | 51 | 6 | 8 | 32 | 5 | 27 | 0.75 |
| D39 | 86 | 10 | 14 | 58 | 4 | 28 | 0.71 |
| D48 | 49 | 14 | 12 | 22 | 1 | 53 | 1.17 |
| D49 | 64 | 9 | 12 | 43 | 0 | 32 | 0.75 |
| D52 | 55 | 20 | 15 | 20 | 0 | 64 | 1.33 |
| D67 | 54 | 8 | 12 | 33 | 1 | 37 | 0.67 |
| D68 | 52 | 15 | 12 | 20 | 5 | 52 | 1.25 |
| All sites | 581 | 108 | 116 | 346 | 45 | 38 | 0.93 |

Table 3-3. Frequency of fertile *Siderastrea radians* colonies by size class.

| Source | Maximum diameter (mm) | | | |
|---------------------|-----------------------|------|-------|--------|
| | 0-4 | 4-15 | 15-60 | 60-250 |
| This study | | | | |
| Percent fertile | 3 | 7 | 56 | 63 |
| Number of colonies | 38 | 176 | 321 | 46 |
| Soong & Lang (1992) | | | | |
| Percent fertile | 50 | 86 | 97 | 100 |
| Number of colonies | 64 | 206 | 208 | 23 |

Table 3-4. Densities, Morisita's Indices (I_{δ}), and density and aggregation classes (H: high; L: low) based on surveys of *Siderastrea radians* colonies in 24 quadrats at each of 10 sites.

| Site | Mean | | Class | |
|------|---------|--------------|---------|--------------|
| | Density | I_{δ} | Density | I_{δ} |
| D49 | 64.0 | 10.00 | H | H |
| D67 | 55.0 | 10.00 | H | H |
| D39 | 114.7 | 1.08 | H | L |
| D11 | 55.0 | 4.78 | H | L |
| D24 | 40.8 | 10.00 | L | H |
| D18 | 36.6 | 6.00 | L | H |
| D48 | 28.0 | 6.67 | L | H |
| D68 | 52.0 | 1.99 | L | L |
| D23 | 51.0 | 2.58 | L | L |
| D52 | 44.0 | 2.26 | L | L |

Table 3-5. Results of 2-way ANOVA using ratios of numbers of males to numbers of females.

| Factor | df | SS | MS | F | p |
|----------------------------|----|--------|--------|------|-------|
| Density | 1 | 0.0305 | 0.0305 | 0.21 | 0.664 |
| Morisita's Index | 1 | 0.0439 | 0.0439 | 0.30 | 0.604 |
| Density x Morisita's Index | 1 | 0.0197 | 0.0197 | 0.13 | 0.727 |
| Error | 6 | 0.8781 | 0.1463 | | |

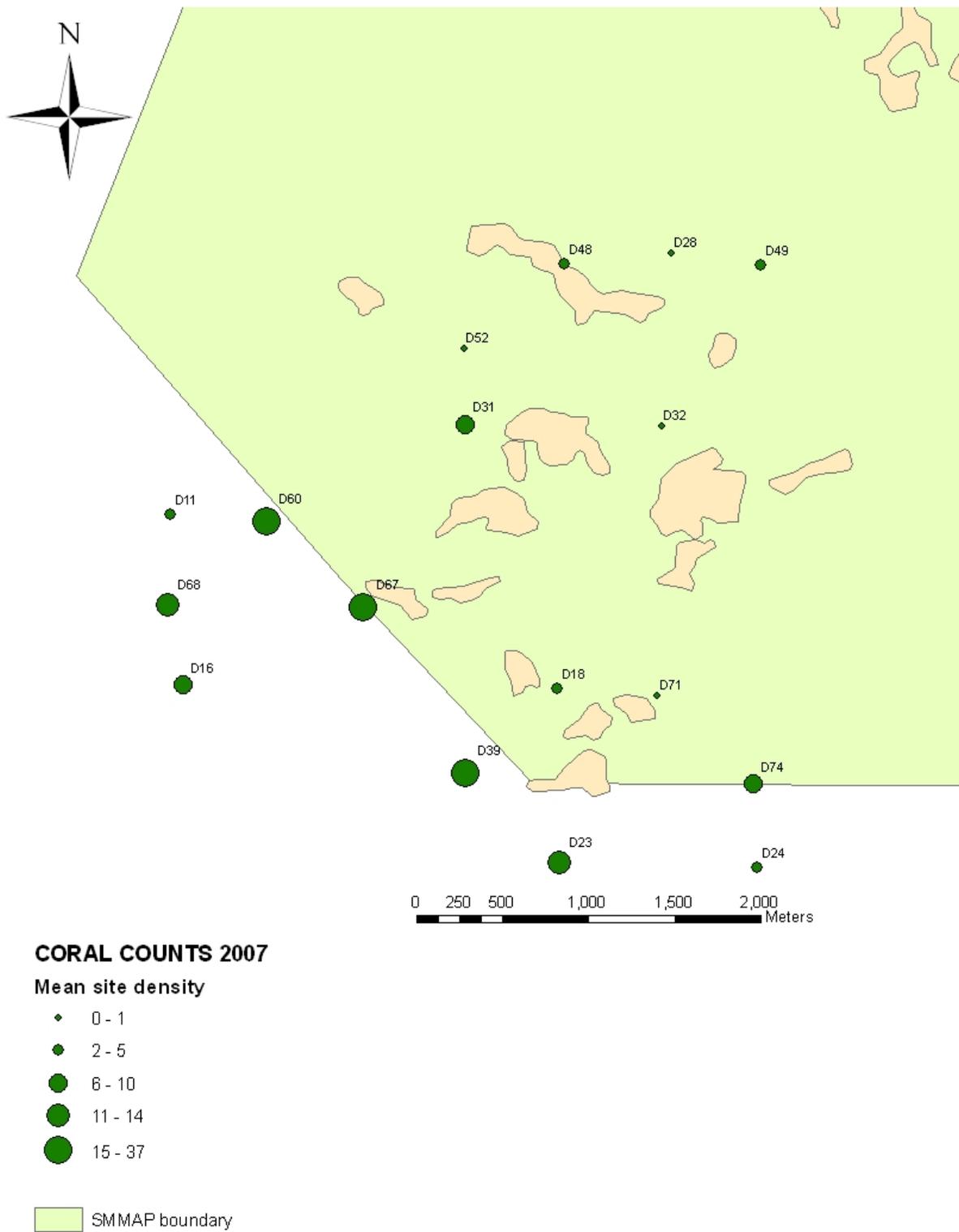


Figure 3-1. Mean densities of *Siderastrea radians* (colonies m^{-2}) from surveys in June 2007. Data were used to determine sites for coral collections. SMMAP = St. Martins Marsh Aquatic Preserve.

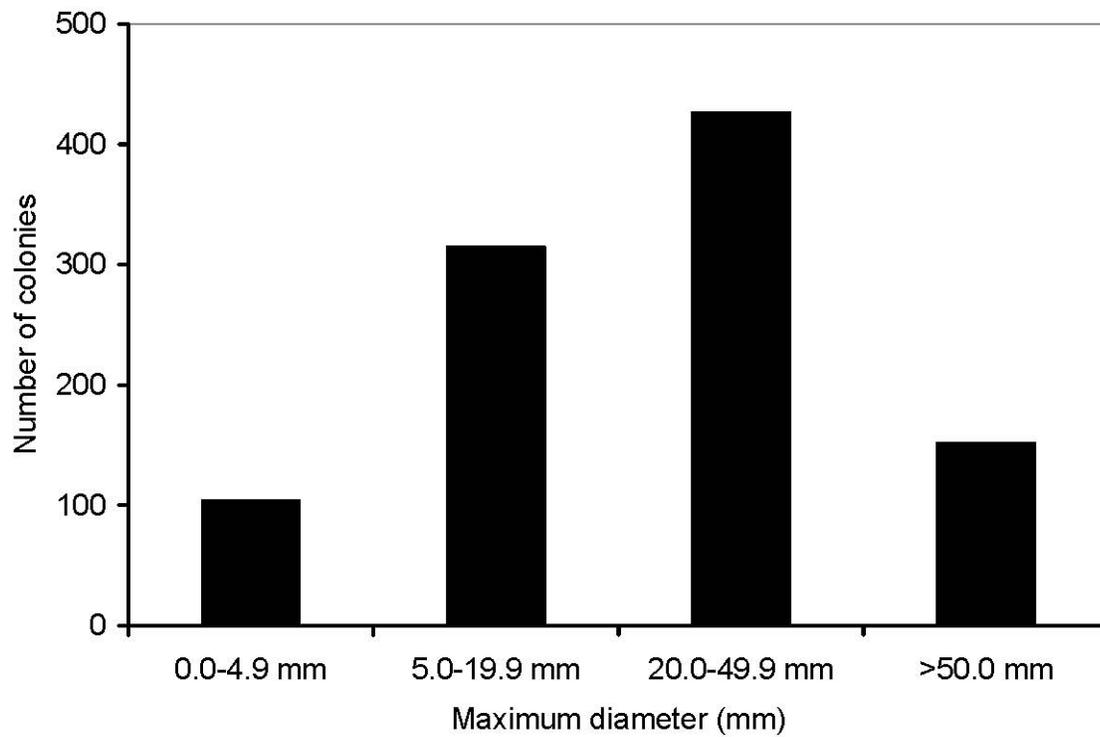


Figure 3-2. Size-frequency distribution for *Siderastrea radians* colonies sampled in June 2007.

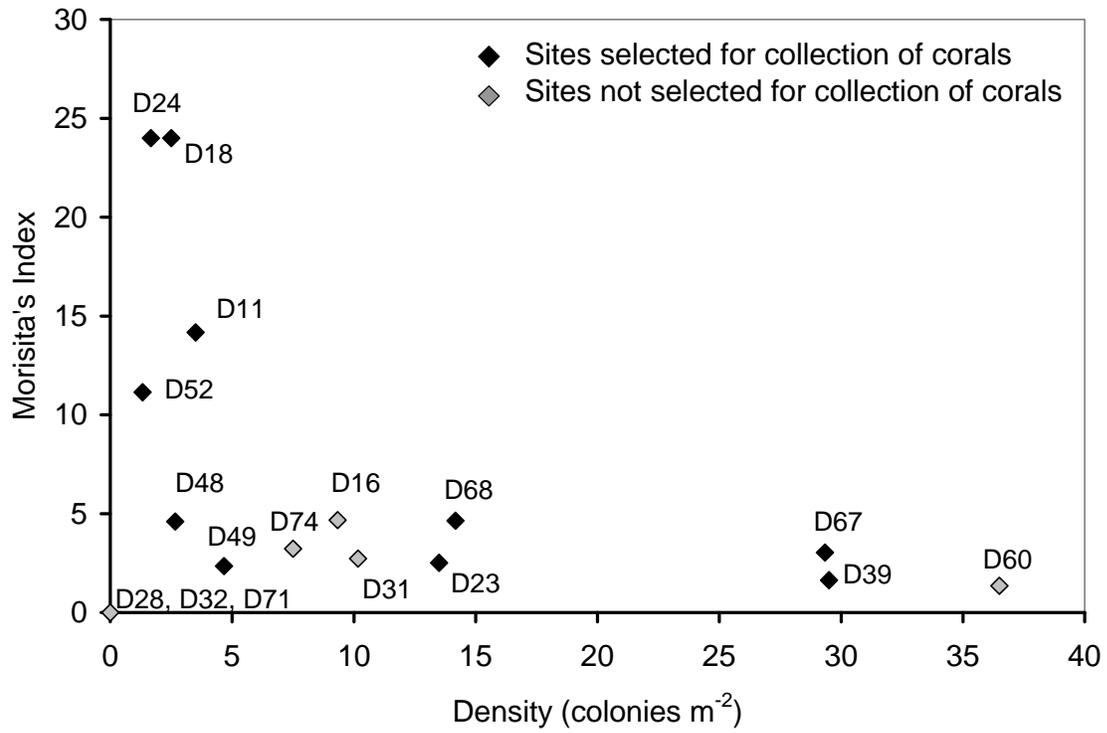


Figure 3-3. Mean densities of *Siderastrea radians* and Morisita's Indices from coral surveys in June 2007.

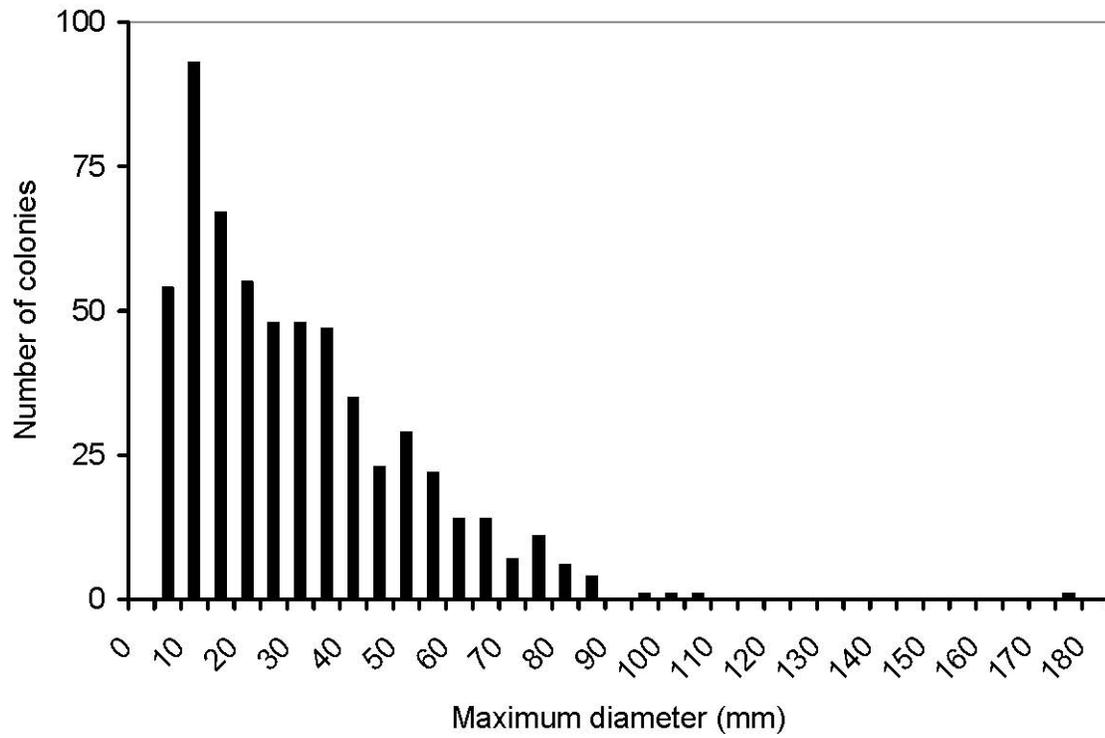


Figure 3-4. Size-frequency distribution of *Siderastrea radians* colonies collected for histology.

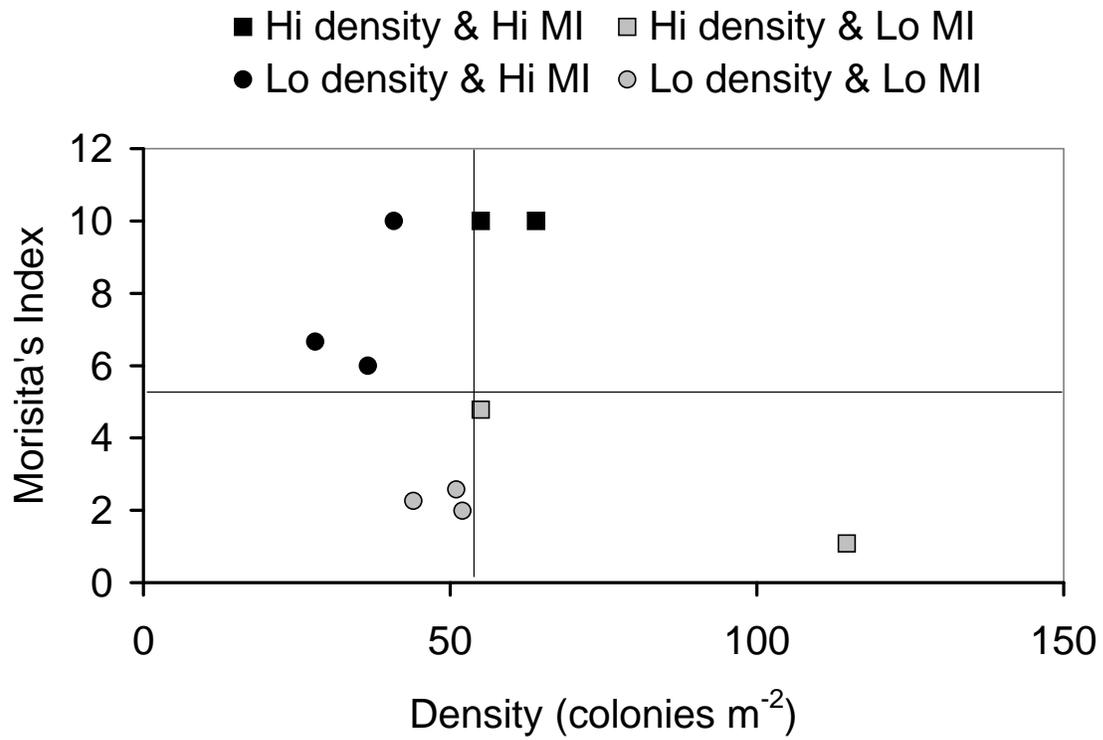


Figure 3-5. Classes of density and aggregation (based on Morisita's Indices) for July–August 2007 coral collection sites. MI = Morisita's Index.

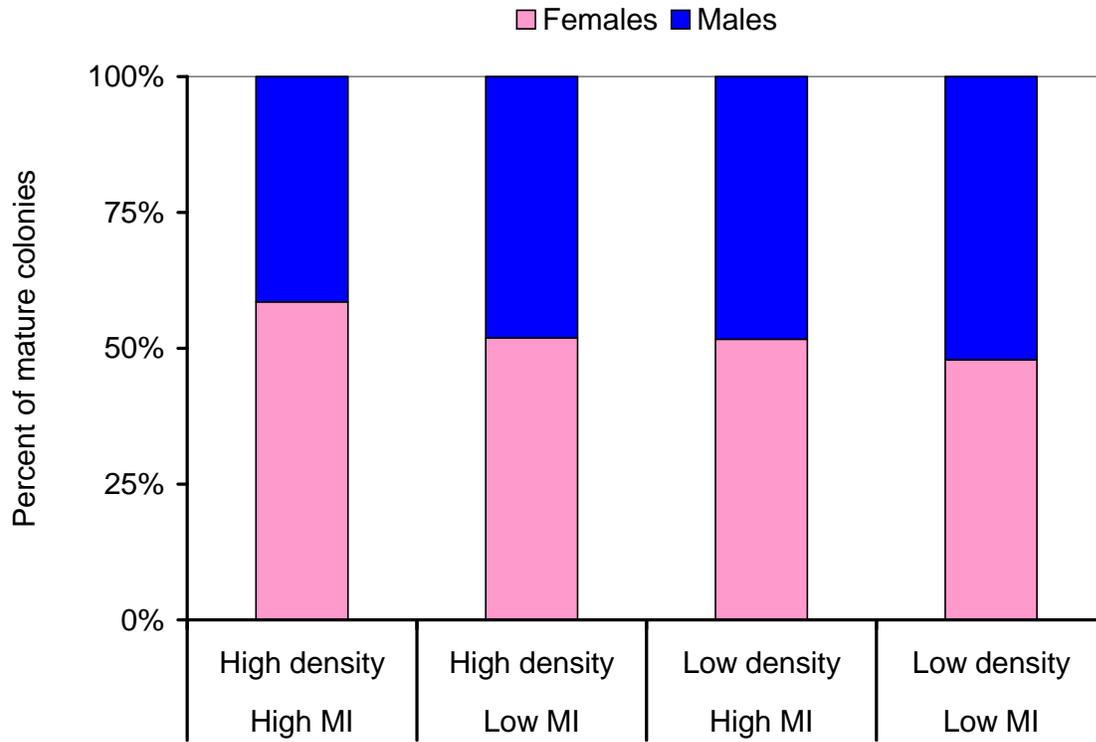


Figure 3-6. Percent of mature male and female *Siderastrea radians* colonies across differing densities and degrees of aggregation. MI = Morisita's Index.

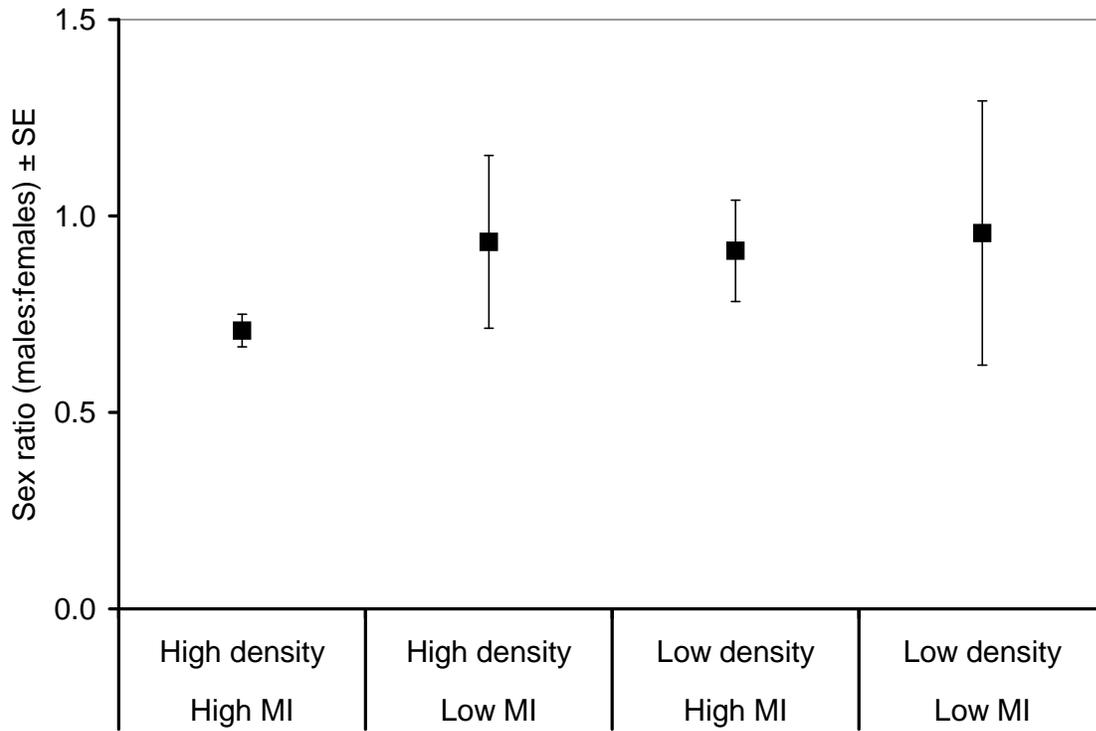


Figure 3-7. Mean ratios of male to female *Siderastrea radians* ± standard errors (SE) as measured across differing densities and degrees of aggregation. MI = Morisita's Index.

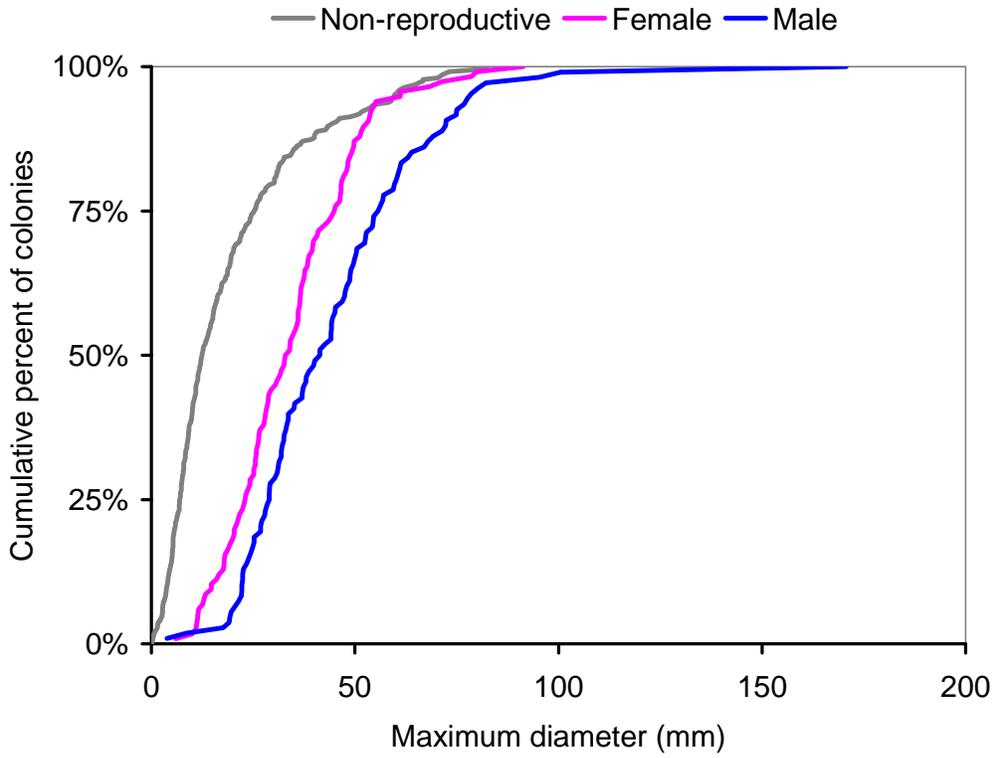


Figure 3-8. Cumulative frequency distributions for non-reproductive, female, and male *Siderastrea radians* colonies vs. maximum diameters.

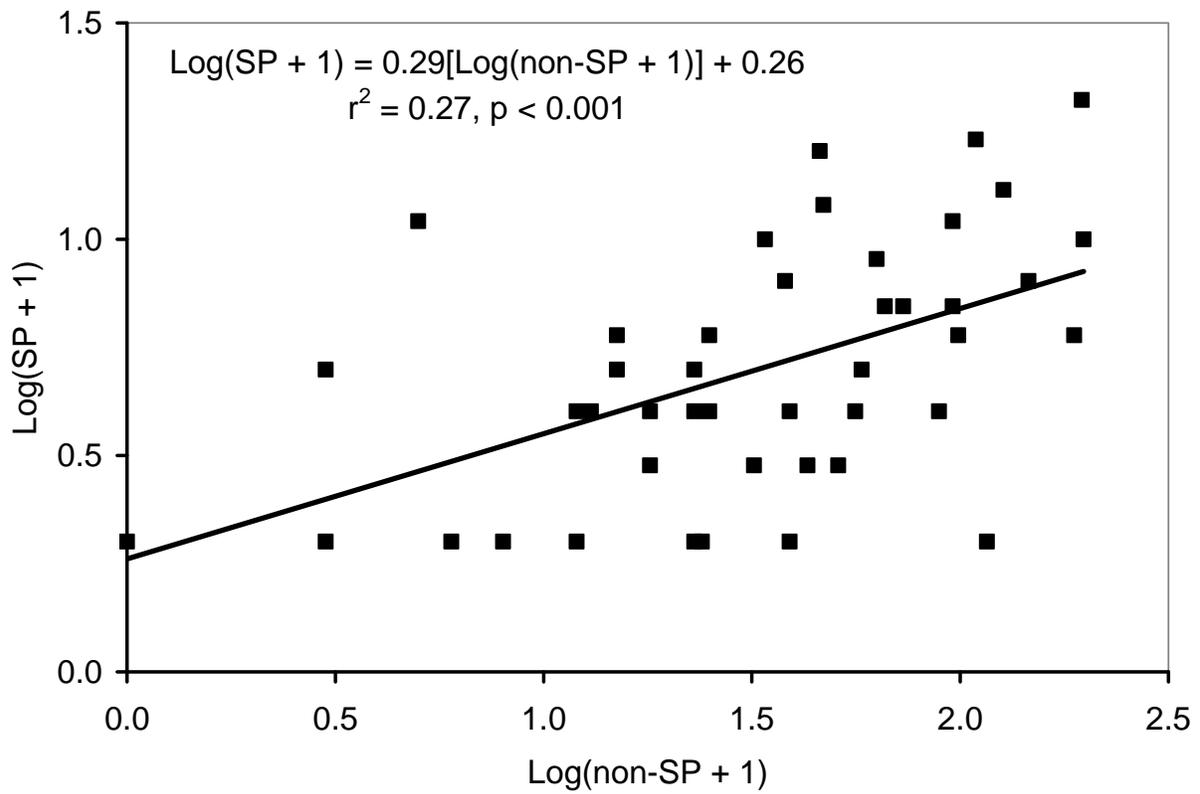


Figure 3-9. Linear regression of numbers of *Siderastrea radians* recruits (solitary polyps) vs. total numbers of all other conspecifics. Data were log(sum + 1) transformed. SP = solitary polyps, non-SP = colonies with more than one polyp.

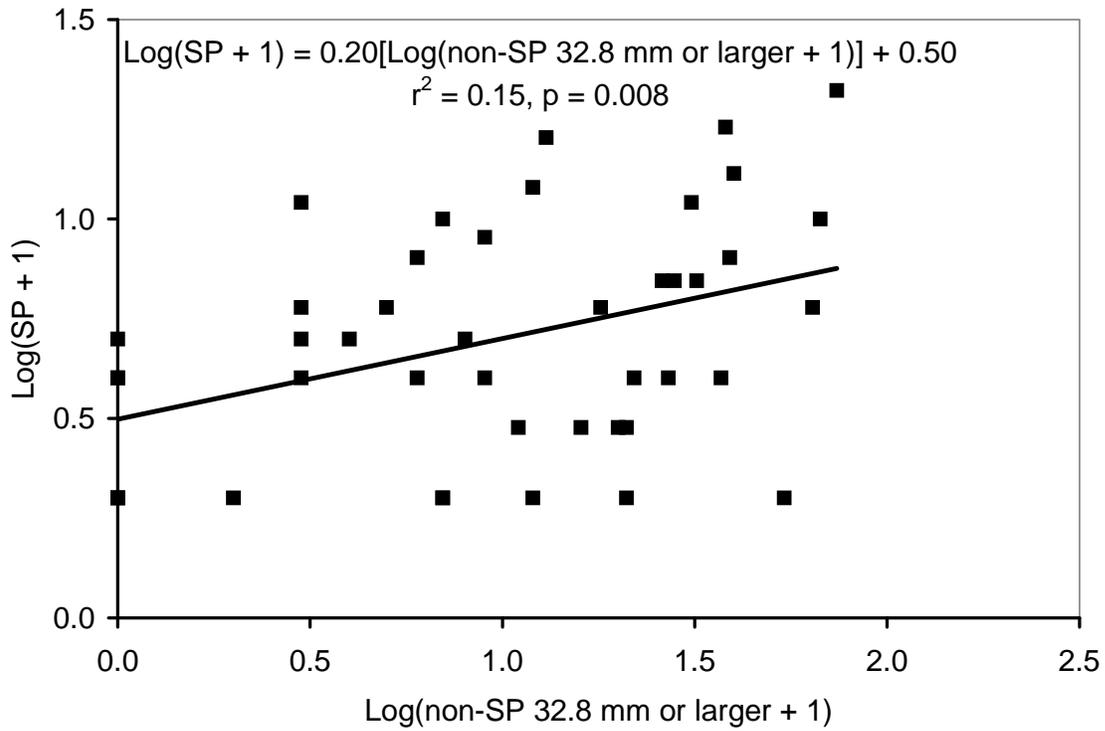


Figure 3-10. Linear regression of numbers of *Siderastrea radians* recruits (solitary polyps) vs. numbers of conspecifics ≥ 32.8 mm in maximum diameter (mature colonies). Data were $\log(\text{sum} + 1)$ transformed. SP = solitary polyps, non-SP = colonies with more than one polyp.

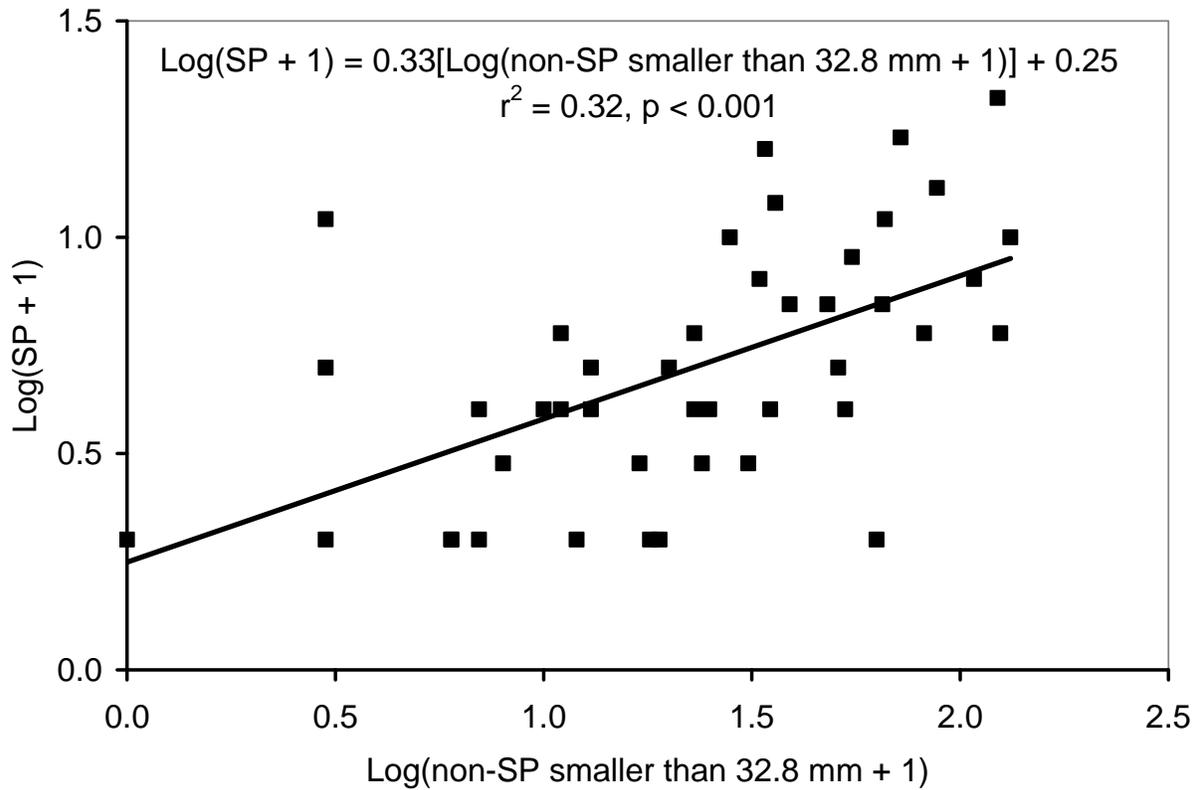


Figure 3-11. Linear regression of numbers of *Siderastrea radians* recruits (solitary polyps) vs. numbers of conspecifics < 32.8 mm in maximum diameter (immature colonies). Data were log(sum + 1) transformed. SP = solitary polyps, non-SP = colonies with more than one polyp.

CHAPTER 4 GENERAL CONCLUSIONS

Given the relative stability in mean density and level of aggregation documented by all sampling in this study, results detailing reproductive characteristics in sites can be scaled to the 16-km² grid and probably to the St. Martins Keys and nearby regions. However, care should be taken when applying information across populations, because intraspecific variation may exist. For example, *Siderastrea radians* populations are gonochoric in Panama and the St. Martins Keys, but there is significant variation in sex ratio between these two locations. In fact, variation in reproductive characteristics is found across a wide range of coral species, and it is exemplified by geographic and environmental variation in sex ratio, spawning cycles, and even reproductive mode. Such intraspecific variation in reproductive characteristics may reflect plasticity or local adaptations to environmental conditions, or they may be attributed to taxonomic problems or errors in interpreting data (Harrison & Wallace 1990). Overall, we must take care when extrapolating the results of any study.

Improved understanding of reproductive strategies and population dynamics of *Siderastrea radians* and other coral species has obvious implications for coral reef restoration and rehabilitation, especially when environmental disturbances and perturbations continue to degrade coral communities worldwide. Environmental stress may affect a species' reproductive strategy as manifest by intraspecific variation in sexuality and sex ratio across a species' range. In addition, reproductive strategies are intimately tied to larval dispersal and recruitment dynamics, and thus, source vs. sink dynamics, which affect recovery rates after disturbances. Thus, future research on *S. radians* in the St. Martins Keys should include long-term monitoring of recruitment, growth, and mortality coupled with collection of data on sediment characteristics,

dissolved oxygen concentrations, salinities, temperatures, nutrient concentrations and other potential stressors.

Lastly, this research is the first quantitative study of *Siderastrea radians* in the St. Martins Keys, and it is one of the few studies that focuses on this species of coral (but see Duerden 1904, Soong & Lang 1992, Vermeij 2005). The study provides information on the reproductive characteristics of a globally abundant species from an unstudied area, thus it enables broader comparisons. Despite these insights, further investigations into factors affecting geographic variation in reproductive characteristics are needed and warranted.

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BIOGRAPHICAL SKETCH

A native Californian, Kate Lazar grew up in the San Francisco Bay Area before heading south to the University of California, San Diego (UCSD), where she received her Bachelor of Science degree in ecology, behavior, and evolution. While attending UCSD, she traveled to Monteverde, Costa Rica, for an education abroad program, where she was introduced to tropical ecology. After graduating, Kate volunteered in Panama for a sea turtle research program, and then worked for the California Department of Fish and Game on their Pacific herring and California market squid research programs. In preparation for life on a graduate student salary, Kate also worked at REI, where they give great employee discounts on tents and sleeping bags. While researching squid fecundity, Kate was accepted into graduate school at the Department of Fisheries and Aquatic Sciences at the University of Florida (UF). She received her Master of Science in summer 2008. She is currently living in England and working as a freelance copy editor for several scientific journals.