The influence of habitat selection and density on the population dynamics of stony coral species of the Bahamian Archipelago

Kathleen L. SEMON*, Kathleen SULLIVAN SEALEY, and Vanessa L. NERO

Department of Biology, University of Miami, Coral Gables, FL, 33124 USA
*Corresponding author: K. Semon
Phone: 1-305-284-3013, Fax: 1-305-284-3039, e-mail: ksemon@bio.miami.edu

Abstract Although stony corals are most frequently studied on high-relief reef structures, many coral species occur in a wide variety of nearshore tropical habitats, including mangrove creeks, seagrass beds and rocky platforms. This study estimated overall population size, potential reproductive output, and population structure for several species across sandy-bottom, hard-bottom, and patch reef habitats. The density of coral colonies, area of available habitat, and size distribution of resident *Siderastrea radians, Favia fragum,* and *Diploria clivosa* colonies were recorded for several island bank systems across habitat types in the central Bahamas. Nearshore patch reefs generally exhibited larger population sizes and higher density of colonies, and contained more larger or older colonies. Nearshore hardbar communities had smaller population sizes and a lower density of colonies, and supported more small colonies, which may either be recruits or asexual clones. High numbers of larger colony sizes observed in dense patch reefs indicate a high sexual reproductive potential. A greater proportion of smaller individuals distributed widely across space in hardbar habitats indicate low sexual reproductive potential, and either high recruitment or high cloning rates.

Keywords Scleractinia, population dynamics, size-frequency distribution, patch reef, nearshore hardbar, Bahamas

Introduction

Coral distribution and abundance patterns have been shown to closely reflect environmental history at multiple spatial scales, and it is widely accepted that corals are not distributed randomly throughout habitats (Pandolfi et al. 1999). In some habitats, corals accrete and form reefs, but corals are not confined to reefal habitats. The key to coral persistence may lie in their ability to utilize a wide array of habitat types, and shape populations to ensure success through adaptive life history strategies.

Populations are generally defined by reproductive output and recruitment, growth, and mortality rates. The demographics of organisms that "build their own habitats," such as corals, are subject to a combination of biological and environmental parameters. Growth and survival are influenced by environmental factors such as temperature, salinity, turbidity, and storm events. Some aspects of population parameters should be density-dependent (either on coral conspecifics or other species). Growth may be limited in crowded species, while reproduction may be limited in low-density habitats with long distances (100's of meters vs. meters) between coral colonies. Recruitment is limited by space and substrate.

Population dynamics of *Siderastrea radians* (Pallas 1766) and *Favia fragum* (Esper 1795) were compared between hard bottom ("locally referred to as "hard bar" in The Bahamas) and patch reef habitats. In addition to the habitat comparisons, this project contrasted populations from similar habitats adjacent to developed and undeveloped coastlines. Both corals are weedy species; these corals are described as short-lived (years instead of decades), generally small, and brood their larvae (Szmant-Froelich et al. 1985, Szmant 1986, Vaughn 1915, Loya 1976, Jones 1977). These species are less likely to be impacted by chronic land-based sources of pollutants. Due to their general small size, these corals are more likely to be impacted by acute events such as sedimentation or burial. Population dynamics for the broadcast spawning coral *Diploria clivosa* (Ellis and Solander 1786) were contrasted to the *S. radians* and *F. fragum* dynamics. *D. clivosa* is described as being longer-lived, reaches a larger colony size, and, based on disease patterns, is more likely impacted by chronic pollutants and pathogens (Soong 1991, Williams and Bunkley-Williams 1990) .

Abiotic and biotic variables of habitats allow for a particular density of colonies. Differing distributions and spacing of colonies will require differing life history strategies in order for a population to persist. We hypothesize that there should be observable patterns or trends between a species' occurrence in a particular habitat and its life history strategy. We predicted that species with similar life history strategies would occur in similar habitats. This study focused on near shore seagrass, patch reef, and windward hardbar environments in the central Bahamas.

Materials and Methods

The Bahamian Archipelago covers 6 degrees of latitude, and represents the largest shallow water bank system in the insular Caribbean. Large tracts of water are divided into bank systems based on placement of islands, which consist of larger landmasses or smaller discontinuous cays. “Marginal” habitats such as sand, seagrass, and hard bar dominate the shallow water bank systems, while true, accreting reefs cover a relatively small area. Hard bottom and seagrass habitats are critical fisheries habitats, and support large populations of corals that occur at low colony densities. See Sullivan Sealey et al. (2002) for further habitat descriptions.

Coral populations in different habitats were compared from North Andros Island, New Providence, Exuma Cays Land and Sea Park, and Great Guana Cay, Abaco. Habitats (ecotypes) were classified according to NOAA standards in terms of geomorphology and life form coverage (Allee et al. 2000). Survey methods previously used in the region (see Sluka et al. 1996, Chiappone and Sullivan 1994) were used to note total number of colonies, total number of species, and colony area. Survey areas for hard bar and patch reefs were 20 m^2, while areas surveyed in the low-density seagrass habitats were 2500m^2 in 50 m by 50 m quadrats. Density across habitats was defined as the number of colonies per hectare of habitat type. Colony area was determined by measuring the widest diameter and the diameter perpendicular to it, and size was used as a proxy for age.

Colony size measurements were made to the nearest millimeter using calipers. Size data was transformed to log (x+1) and size frequency distributions were created in SYSTAT 10.2 (see Bak and Meesters 1998).

Survey areas were also scored for degree of development impact using methods described in Sullivan Sealey et al. 2004 and Sullivan Sealey 2004. Areas were ranked based on: i) physical restructuring of the shoreline, ii) destructive land use, iii) native vegetation loss and replacement by invasive exotics, and iv) degree of coastal development. Islands had varying degrees of coastal development impacts; New Providence Island was the most developed island in the archipelago with 70% of the population of The Bahamas and the capital city of Nassau (about 225,000 people from the 2000 census, one of the most densely populated islands in the tropical Atlantic with over 2800 people per square mile). Surveys in the Exuma Cays Land and Sea Park included assessments of patch reefs off islands with low development (less than 2 people per square mile). The coastal development impact assessment was not a function of human population size, but an assessment of the four ranking criteria presented earlier.

Results

Coral colony average density (number of colonies/hectare), diversity, and dominance for each habitat type are summarized in Table 1. Average density was highest in patch reefs, and decreased dramatically through hardbar, sparse seagrass, and patchy/dense seagrass. The highest species diversity also occurred in patch reefs. The most abundant species across all habitats were *S. radians, F. fragum,* and *Porites astreoides* (Lamarck 1816).

Table 1 Coral Diversity, Density, and Dominance across near shore habitats in The Bahamas (New Providence, Andros, Great Exuma, Abaco)

	Patch Reefs	Nearshore Hardbar	Sand - sparse seagrass	Sand - patchy/ dense seagrass
Area surveyed	240 m^2	260 m^2	240 m^2	140 m^2
Mean Number of Colonies	456	54	18.4	10.5
Standard Deviation	166.34	71.23	14.05	0.71
Number of Sites Surveyed	11	13	12	3
Density of Colonies (#/ha)	1.9X10^4	2.08X10^3	7.67X10^2	11.56
Total Number of Coral Species	30	18	7	3
Dominant Species by colony number	*S. radians* *F. fragum* *Porites astreoides*	*S. radians* *F. fragum* *Porites astreoides*	*S. radians* *F. fragum* *Porites astreoides*	*S. radians* *F. fragum* *Porites astreoides*
Dominant species by area covered	*D. clivosa* *Montastrea annularis* *Porites porites*	*D. clivosa* *Montastrea annularis* *Porites porites*	*S. radians* *Manicina areolata* *Porites porites*	*S. radians* *Porites astreoides* *Porites porites*

Size-frequency distributions were created for *S. radians* and *F. fragum* observed in different habitat types (Fig. 1-2). A difference in density was evident between areas of high and low coastal development, yet size-frequency distribution curves appear similar in both undeveloped and developed habitat types. Large individuals were present in all distributions, but relatively little difference exists between their representation in developed and undeveloped habitats. Overall, more small colonies were observed in hardbar environments. More large colonies existed in patch reefs than hardbar, but corals in patch reefs tended to exist largely in the middle size classes (3-7 cm²). *F. fragum* and *S. radians* patch reef populations tended to follow a bell shaped curve, while hardbar *F. fragum* and *S. radians* populations tended to be skewed towards smaller individuals. The largest *F. fragum* colonies tended to occur in undeveloped hardbar habitats. The most common colony sizes occurring in both habitat types and degree of alteration tended to be of middle size ranges.

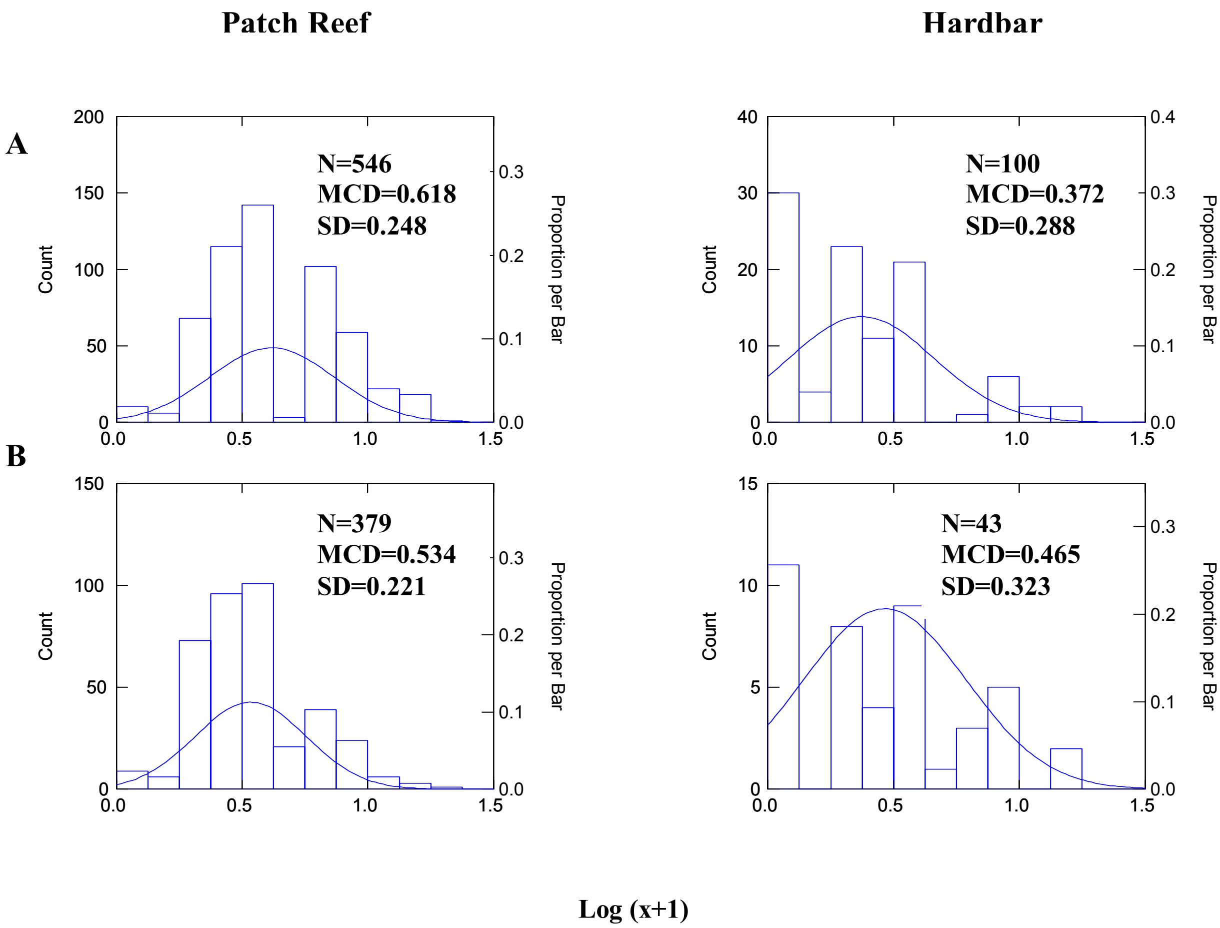

Fig. 1 *F. fragum* size-frequency distributions. **A** (top) graphs represent reefs adjacent to low coastal development impact sites; **B** (bottom) graphs represent sites with high coastal development impacts. Y-axis "Count" represents the number of coral colonies occurring within a size class, represented by one bar. Z-axis "Proportion per Bar" represents overall proportion of colonies included in each size class bar. Colony areas (cm²) were transformed to log (x+1). Mean colony diameter (MCD) for colonies located near low coastal development impacts was 0.618, equivalent to log (3.896 cm² +1) for patch reef species, and 0.534 or log (2.922 cm² +1) for hardbar species. Mean colony diameter (MCD) for colonies located near high coastal development impacts was 0.372, equivalent to log (2.031 cm² +1) for patch reef species, and 0.465 or log (2.748 cm² +1) for hardbar species.

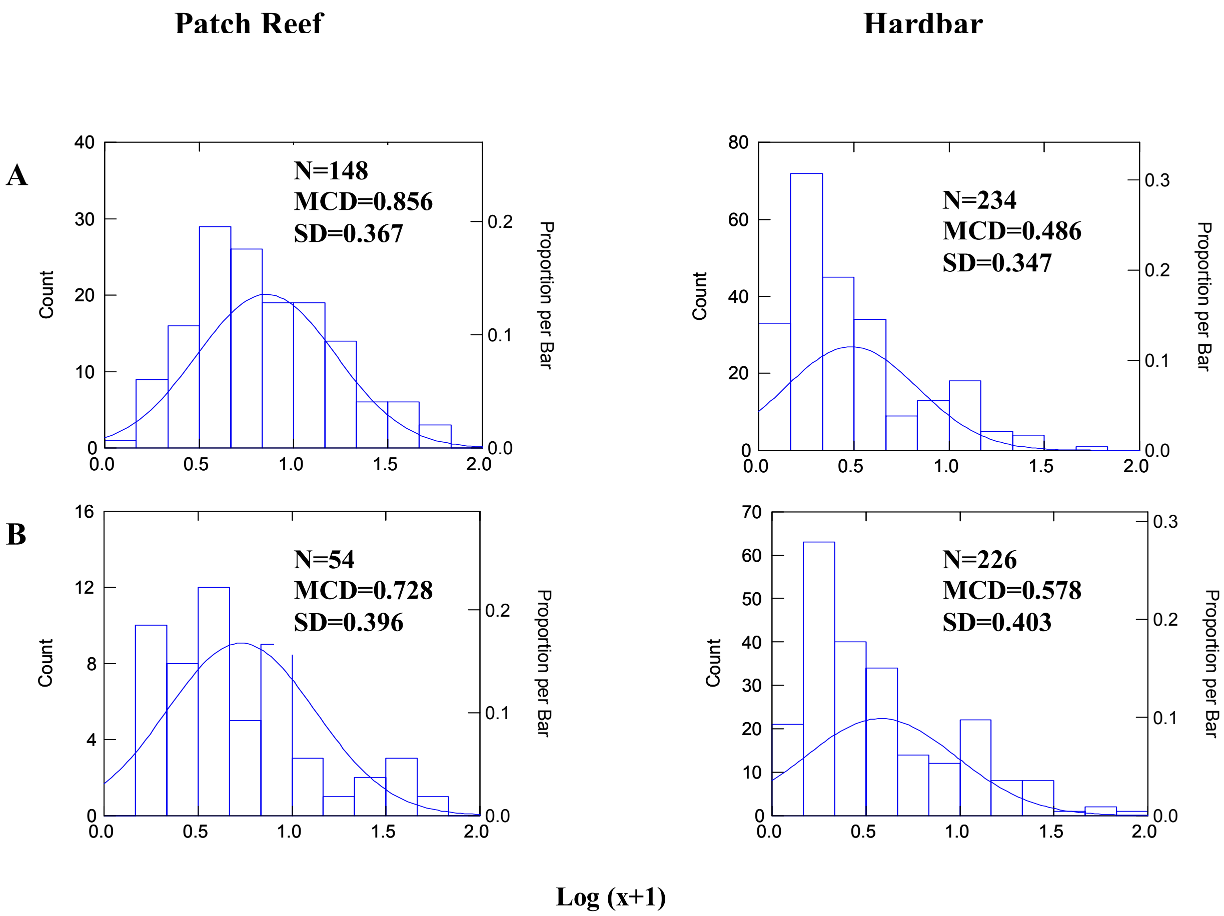

Fig. 2 *S. radians* size-frequency distributions. **A** graphs represent reefs adjacent to low coastal development impact sites. **B** graphs represent sites with high coastal development impacts. Y-axis "Count" represents the number of coral colonies occurring within a size class, represented by one bar. Z-axis "Proportion per Bar" represents overall proportion of colonies included in each size class bar. Colony areas (cm^2) were transformed to log (x+1). Mean colony diameter (MCD) for colonies located near low coastal development impacts was 0.856, equivalent to log (9.562 cm^2 +1) for patch reef species, and 0.486 or log (3.606 cm^2 +1) for hardbar species. Mean colony diameter (MCD) for colonies located near high coastal development impacts was 0.728, equivalent to log (7.746 cm^2 +1) for patch reef species, and 0.578 or log (5.575 cm^2 +1) for hardbar species.

D. clivosa, a large broadcasting species, was also commonly observed in hardbar areas (Fig. 3). Larger colonies occurred more frequently in populations located near undeveloped coastlines, and large individuals were noticeably absent off developed shores.

Discussion

Colony density is important, but habitat area may be critical. Reefs boast a high density of coral heads but are relatively limited in the area they cover; habitats such as hard bar may be more important to coral population persistence as this habitat is much more common and covers a wider area than reefs. Area of reefs in The Bahamas is estimated at less than 1 percent of total bank area, but there are huge coral populations supported on hard bar and seagrass habitats.

Both *S. radians* and *F. fragum* size-frequency distributions from patch reefs were skewed towards middle to larger colonies sizes, indicating a smaller proportion of these populations as occupied by recruits or juveniles. These populations are most likely recruitment-limited, due to the high density of colonies present and inherently little available space on which recruits might settle. Most patch reef colonies exist in middle size class ranges, and few reach a large size. Hardbar habitats tended to be dominated by many small individuals, and few large colonies. These lower-density habitats are not limited in available space, and may therefore be more attractive to recruits. *F. fragum* and *S. radians* hardbar populations did not appear to be greatly impacted by development, as size-frequency distributions were similar in both undeveloped and developed habitats. These species are likely not sensitive to chronic pollutants, and share characteristics typical of "weedy" species: *F. fragum and S. radians* are generally small colonies, have high growth rates, and most likely reproduce frequently by asexual fission,

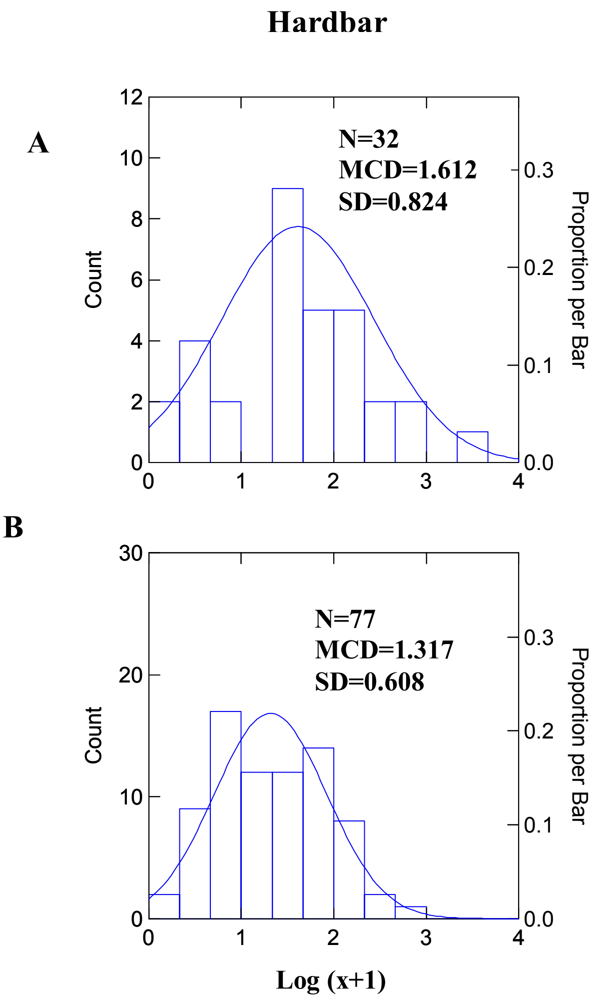

Fig. 3 *D. clivosa* size-frequency distributions for hard bar habitat. **A** graph represents hard bar adjacent to low coastal development impacts; **B** graph represents hard bar adjacent to high coastal development impacts. Y-axis "Count" represents the number of coral colonies occurring within a size class, represented by one bar. Z-axis "Proportion per Bar" represents overall proportion of colonies included in each size class bar. Colony areas (cm^2) were transformed to log (x+1). Mean colony diameter (MCD) for colonies located near low coastal development impacts was 1.612, equivalent to log (193.896 cm^2 +1), and mean colony diameter (MCD) for colonies located near high coastal development impacts was 1.317, equivalent to log (338.668 cm^2 +1).

in addition to their ability to release of sexually-produced larvae year-round (Soong 1991 and Szmant-Froelich et. al 1985).

D. clivosa is a broadcasting coral, longer lived (decades) and does accrete and form patch reefs. An absence of larger colonies off developed shorelines may be due to higher sensitivity to chronic coastally-originated stressors, resulting in large colony mortality or an inability to reach a large colony size.

Coral population structure also reflects disturbance history, as *S. radians* and *F. fragum* populations tend to be recruitment-limited on patch reefs, and experienced periodic mortalities in nearshore hardbar habitats after hurricane events. Hardbar environments tend to be most impacted by the acute scouring activity of hurricane events, and the skewed curves toward small colony sizes may be a result of recovery from hurricanes that impacted the Bahamas in 1999 and 2001. Patch reefs tend to dissipate wave energy, and may be more affected by chronic disturbances.

Patch reef populations are dense collections of colonies representing mostly middle to large size classes, and thus have high sexual reproductive potentials. Colonies tend to be of reproductive sizes, and are located in close proximity to each other, facilitating gamete exchange. Larvae produced on patch reefs may be settling elsewhere in lower-density habitats, like hardbar areas. Hardbar populations are dominated by small colonies, but survival of small colonies tends to be low, as evidenced by fewer colonies representing middle to large size classes. These habitats may be highly desirable to recruits, or larger colonies may be contributing to lower size classes through asexual fission.

A large proportion of the total population *can* survive and persist in non-reef habitats. Characterization of populations by habitat is essential in determining developmental effects. Coral species can persist in different habitats by exhibiting some form of plasticity in life history strategies, distributing energy throughout growth and reproduction, depending on habitat characteristics. Future studies will involve monitoring permanent plots to further characterize population structure for a particular habitat, using species presence, counts, and diameters of colonies as a proxy for habitat health rather than coral percent cover. Additionally, future research will focus on the source of this habitat occupation plasticity by exploring both coral and symbiont population genetics.

Acknowledgements

This work was supported by the Earthwatch Institute Coastal Ecology of The Bahamas project, the University of Miami, the Environmental Defense Academic Mini-grant fund, and the College of The Bahamas. Data collection would not have been possible without the help of over 100 Earthwatch volunteers who participated in the Coastal Ecology of the Bahamas expeditions from 2002 to date.

References

Allee RJ, Dethier M, Brown D, Deegan L, Ford RG, Hourigan TF, Maragos J, Schoch C, Sealey K, Twilley R, Weinstein MP and Yoklavich M (2000) Marine and estuarine ecosystem and habitat classification. NOAA Technical Memorandum NMFS-F/SPO-43

Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. Marine Ecology Progress Series 162:301-306

Chiappone M, Sullivan KM (1994) Ecological structure and dynamics of nearshore hard-bottom communities of the Florida Keys. Bulletin of Marine Science 54:747-456

Jones JA (1977) Morphology and development of southeastern Florida patch reefs. Proc 3rd Int Coral Reef Symp 2:231-235

Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rico corals. Bulletin of Marine Science 26:450-466

Pandolfi JM, Llewellyn G, Jackson JBC (1999) Pleistocene reef environments, constituent grains, and coral community structure: Curacao, Netherlands Antilles. Coral Reefs 18:107-122

Sullivan Sealey KM (2004) Large-scale ecological impacts of development on tropical island systems: comparisons of developed and undeveloped islands in the central Bahamas. Bulletin of Marine Science 75:295-320

Sullivan Sealey KM, Brunnick S, Luton C, Nero V, Flowers L (2002) An ecoregional plan for the Bahamian Archipelago. Taras Oceanographic Foundation, Jupiter Florida

Sullivan Sealey KM, Flowers AL, Nero VL, Semon KL, Wilson J (2004) Characterization and ranking of coastal environments of the Bahamian Archipelago: a database for protection and policy. Bahamas Journal of Science 10:12-25

Sluka RM, Chiappone M, Sullivan KM, Wright R (1996) Habitat and life in the Exuma Cays, The Bahamas: The status of groupers and coral reefs in the northern cays. Media Publishing Ltd, Nassau Bahamas

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43-53

Szmant-Froelich AM, Reutter M, Riggs L (1985) Sexual reproduction of *Favia fragum* (Esper): lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. Bulletin of Marine Science 37:880–892

Soong K (1991) Sexual reproductive patterns of shallow-water reef corals in Panama. Bulletin of Marine Science 49:832-846

Vaughn TW (1915) The geological significance of the growth-rate of the Floridian and Bahamian shoal-water corals. Journal of the Washington Academy of Sciences 5:591-600

Williams EH Jr, Bunkley-Williams L (1990) The world-wide coral reef bleaching cycle and related sources of coral mortality. Atoll Research Bulletin 335:1-71