

7-2008

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Rutten, Leanne M.; Chiappone, Mark; Swanson, Dione W.; and Miller, Steven, "Stony Coral Species Diversity and Cover in the Florida Keys Using Design-Based Sampling" (2008). *Marine & Environmental Sciences Faculty Proceedings, Presentations, Speeches, Lectures*. 487.

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Stony coral species diversity and cover in the Florida Keys using design-based sampling

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Abstract. Large-scale sampling of stony coral species richness, species distribution, and cover was undertaken at 423 Florida Keys sites between Miami and SW of Key West during 2005 and 2007. A two-stage, stratified random sampling design employed belt transects to enumerate numbers of species and point-intercept surveys to quantify cover. The sampling design incorporated ten reef and hard-bottom habitats from < 1 m to 27 m depth, as well as oceanographic regions and areas inside and outside of protected management zones. These data provide insights into the spatial extent and factors influencing stony coral biodiversity. For stony corals, a pool of ~50 taxa encompassing the Orders Milleporina and Scleractinia, including species and morphotypes, was recorded. Significant differences were found in species richness and cover among cross-shelf habitats, with great values on inner shelf margin patch reefs, followed by deeper fore-reef slope habitats that extended to the 27 m depth limit sampled. In contrast, the shallow fore-reef, especially in areas historically dominated by the branching coral *Acropora palmata*, yielded relatively low numbers of species and cover that are presently dominated by smaller, brooding corals such as *Porites astreoides* and *Favia fragum*.

Key words: Benthic, cover, coral, habitat, species richness, stratified sampling.

Introduction

Coral reefs are in a state of decline worldwide from multiple stressors, including physical impacts, water quality changes, overfishing, disease outbreaks, and climate change (Pandolfi et al. 2003; Bellwood et al. 2004). Coral reefs in a degraded state are often characterized by one or more symptoms, including low abundances of top-level predators, herbivores, and reef-building corals with higher abundances of ahermatypic organisms such as seaweeds (Gardner et al. 2003). Like many coral reef ecosystems, the Florida Keys have experienced symptoms of "degradation" in recent decades, including declines in urchins and corals, particular *Acropora*, that have also occurred in the wider Caribbean (Dustan and Halas 1987; Chiappone et al. 2002). There are also a considerable array of natural phenomena affecting Florida Keys reefs such as atmospheric cold fronts, continental influence (Florida Bay-Atlantic Ocean exchange), and destructive tropical storms. This multitude of stressors makes it challenging to discern the degree to which human activities have comprised ecological integrity relative to natural variability (Sommerfield et al. 2008).

Part of the uncertainty in understanding the factors driving decreases in populations of the coral reef ecosystem stems from the quality of the data used to document spatial patterns and temporal changes. Many historical studies lacked the statistical rigor

necessary to adequately evaluate changes at the population-scale; in other words, the ecosystem area inhabited by a closed, interbreeding unit (Gardner et al. 2003). Generally, sampling has been at habitat-scales, that is, limited to a few reef sites within particular habitat types in restricted portions of the spatial domain (Dustan and Halas 1987; Porter and Meier 1992; Chiappone and Sullivan 1997). Frequently, selection of sampling sites within a given habitat did not follow standard randomization protocols, and consequently, the derived abundance metrics may not have been representative of the sampled habitats (Murdoch and Aronson 1999).

For the Florida Keys, we contend that the documented temporal changes and current views of spatial distribution and abundance patterns of coral reef benthos, particularly stony corals, are partly biased by the selection of particular reef habitats in particular locations that may not be representative of the larger ecosystem. For example, there is no doubt that areas historically dominated by *Acropora* corals, particularly the shallow (< 6 m) and deeper (8-15 m) fore-reef, have changed substantially, largely due to Caribbean-wide disease events (Dustan and Halas 1987; Chiappone and Sullivan 1997) and bleaching (Sommerfield et al. 2008). However, debate has ensued for at least 25 years on the causes of coral reef decline (Porter and Meier 1992; Sommerfield et al. 2008), thus making it tenuous for resource managers to determine

which courses of action to take to minimize localized threats in lieu of larger-scale factors such as climate change (Murdoch and Aronson 1999). In this short communication, we report on a large-scale sampling effort that encompassed hundreds of sites across the south Florida shelf to determine patterns of stony coral richness, species distribution, and cover. The 2005 and 2007 surveys were a continuation of previous efforts dating back to 1999 to quantify the abundance and condition of coral reef benthos throughout the FKNMS and built upon pre-existing data from hundreds of sites to guide the sampling design (Miller et al. 2002). Our purpose here is to illustrate the significant spatial variation in stony coral richness and cover, which has implications for reporting “average” reef status and underscores the significant inter-reef variability in this system (Murdoch and Aronson 1999; Somerfield et al. 2008).

Material and Methods

The Florida Keys are an archipelago of limestone islands stretching more than 360 km from near Miami to the Dry Tortugas, representing the only region of extensive reef development in the continental U.S. The islands are part of the south Florida shelf, a submerged Pleistocene platform 6-35 km wide and generally < 12 m deep (Lidz et al. 2003). The primary influences reef distribution and development are paleotopography and fluctuating sea level (Shinn et al. 1989; Lidz et al. 2003). Bedrock throughout the area is Pleistocene limestone, either exposed on the seafloor or lying underneath Holocene reefs and sands (Shinn et al. 1989). From inshore to offshore of the Pleistocene islands, a nearshore rock ledge extends ~2.5 km seaward and consists of hard-bottom, seagrass, and some inshore patch reefs (FDEP 1998). Further seaward is Hawk Channel, a broad trough-like depression dominated by non-coralline, non-oolitic grainstone, but also harboring several thousand patch reefs whose distribution is affected by the number and width of tidal passes (Marszalek et al. 1977). Bands of rock ridges exist further offshore along the outer shelf and on the upper slope from 30-40 m depth before tapering off into the Florida Straits. The semi-continuous reef tract is emergent in places, where Holocene reefs sit atop a Pleistocene coral ridge (~86-78 ka), forming a shelf-margin ledge (Lidz et al. 2003). Coral reef distribution reflects exchange processes between Florida Bay and the Atlantic Ocean (Marszalek et al. 1977; Shinn et al. 1989), which, is related to the size and orientation of the Pleistocene islands, the locations of major tidal passes, and the proximity of the Florida Current to the platform margin (Smith 1994).

At each site, four random sampling points per targeted site were generated in a GIS and located in

the field using a differential GPS. Four 15-m transects were deployed per site. For stony coral species richness, an area 0.5-m out from each transect side was searched for the presence of any species present. Along the same transects, coral cover was estimated using the point-intercept method, in which the bottom type every 15 cm along the transect was recorded for a total of 400 points per site.

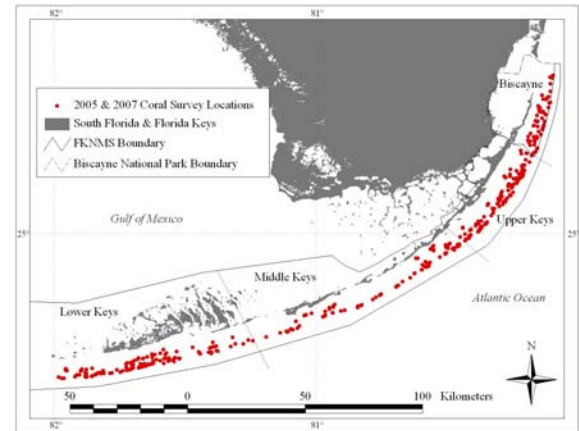


Figure 1: Survey locations sampled for stony coral species richness and cover during 2005 and 2007 in the Florida Keys National Marine Sanctuary and Biscayne National Park.

Table 1: Sampling effort for stony corals in the Florida Keys during 2005 and 2007. Available sites reflect the number of 200 m x 200 m cells with particular habitat based upon FDEP (1998) data

Habitat	Sites (% effort)	Sample area (m ²)	Sites available
Mid-channel patch reef (MPR)	87 (20.6)	5,220	3,532
Offshore patch reef (OPR)	69 (16.3)	4,140	1,243
Inner line spur and groove (IRT)	13 (3.1)	780	87
Shallow hard-bottom (LHBS)	39 (9.2)	2,340	972
High-relief spur and groove (HSG)	70 (16.6)	4,200	238
Patchy hard-bottom (PHBD)	32 (7.6)	1,920	1,247
Deeper hard-bottom (LHBD)	40 (9.5)	2,400	2,395
Low-relief spur and groove (LSG)	47 (11.1)	2,820	1,763
Fore reef 15-20 m (FRS20)	17 (4.0)	1,020	880
Fore reef 22-22 m (FRS27)	9 (2.1)	540	671
Sampling Design Total	423 (100)	25,380	13,028

Statistical estimation procedures for population abundance metrics (proportional transect frequency, cover) for a two-stage stratified random sampling design were adapted from Cochran (1977). Site species richness, species frequency of occurrence, and total coral cover were calculated for each site, and then pooled for sampling strata, consisting of

combinations of habitat, regional location, and management zone factors. Data reported herein emphasize habitat-related patterns. Statistical comparisons among habitats for mean site species richness, species frequency of occurrence, and cover were accomplished by computing confidence intervals (CI) based on the equation: $CI = \text{mean} \pm t_{\alpha, df} \cdot \text{standard error}$. Standard errors were estimated by the two-stage, stratified random sampling design (Cochran 1977) and confidence intervals were adjusted for multiple comparisons using the Bonferroni procedure. The experiment-wise error rate was held at $\alpha = 0.05$ and the comparison-wise error rate was adjusted based on the number of multiple comparisons as follows: comparison-wise error rate = α/c , where $c = k(k-1)/2$ and $k = \text{number of categories}$ (e.g. habitat classes).

Table 2: Physical characteristics of stony coral survey sites in the Florida Keys. Values are the ranges in transect depth (m), maximum vertical relief (cm), and site distance from shore (km). See Table 1 for habitat abbreviations

Habitat	Depth (m)	Max. vertical relief (cm)	Shore distance (km)
MPR	0.9-9.9	29-211	1.6-7.5
OPR	2.1-14.6	33-165	4.1-9.9
IRT	1.5-6.1	55-168	5.3-7.2
LHBS	2.7-7.0	20-92	5.5-9.6
HSG	0.6-9.4	32-253	5.9-10.2
PHBD	4.6-11.3	21-68	5.6-9.5
LHBD	5.7-13.7	10-80	4.6-10.6
LSG	7.6-16.2	14-98	5.5-10.7
FRS20	15-19.2	53-129	7.1-10.6
FRS27	21.6-27	84-144	6.4-10.3

Results

Surveys of the 423 Florida Keys sites yielded 49 stony coral taxa. Independent of region and management zone, mean (± 1 SE) stony coral site species richness (no. species/60 m²) ranged from 12.1 \pm 0.8 to 19.7 \pm 0.4 among the 10 habitats (Table 3). Precision estimates (coefficient of variation) among habitats ranged from 2% to 7%. Stony coral species richness was positively correlated with mean percent coral cover (Pearson correlation coefficient $r = 0.630$), indicating that sites with greater numbers of coral species tended to yielded higher coral abundance. Among the 10 habitats sampled, maximum transect depth ($r = 0.264$) and distance from shore ($r = 0.469$) were only weakly correlated with site species richness, while maximum vertical relief was more highly correlated ($r = 0.852$). Species richness on mid-channel and offshore patch reefs was significantly greater ($P < 0.002$, Bonferroni-adjusted α) than on shallow (< 6 m), low-relief and high-relief fore-reef habitats. Particularly noteworthy was the low species richness of shallow fore-reef areas historically dominated by *Acropora palmata*. Although patch reefs yielded the highest mean site species richness,

there was substantial variability from reef to reef, with species richness among mid-channel and offshore patch reefs ranging from 9-28 and 9-29 species per site, respectively. Deeper (6-15 m and 15-20 m) low-relief spur and groove habitat also yielded significantly greater numbers of species than shallow fore-reef habitats.

Mean stony coral cover ranged from 0.5% to 43.3% among the 423 sites surveyed (Table 3). There was substantial variability both among sites within habitats and among habitats. Mean coral cover was greatest on mid-channel (16.2%) and offshore patch reefs (8.5%), but was less than 8% for all other habitats. Relatively high coral cover on patch reefs was represented by massive framework species such as *Colpophyllia natans*, *Montastraea* spp., *Siderastrea siderea*, and *Stephanocoenia michelini*. Total coral cover was significantly greater on patch reefs ($P < 0.002$, Bonferroni-adjusted α) compared to low-relief low-relief and high-relief habitats on the shallow platform margin, and then increased again on the deeper fore-reef slope, especially below 15-m.

Table 3: Habitat summary of stony coral species richness (no. species per 60 m²) and cover at 423 Florida Keys sites

Habitat (no. sites)	Richness	Cover
Mid-channel patch reef (87)		
Range	9-28	1.8-43.3
Mean \pm 1 SE	19.7 \pm 0.4	16.2 \pm 1.3
Offshore patch reef (69)		
Range	9-29	0.5-22.5
Mean \pm 1 SE	18.8 \pm 0.6	8.5 \pm 1.2
Inner line reef tract (13)		
Range	7-18	6.0-9.3
Mean \pm 1 SE	12.1 \pm 0.8	7.0 \pm 0.6
Shallow hard-bottom (39)		
Range	8-18	0.8-3.0
Mean \pm 1 SE	12.4 \pm 0.4	1.6 \pm 0.2
High-relief spur and groove (70)		
Range	7-21	0.5-13.8
Mean \pm 1 SE	12.4 \pm 0.4	5.1 \pm 0.7
Patchy hard-bottom (32)		
Range	7-22	0.3-4.5
Mean \pm 1 SE	15.2 \pm 0.7	1.5 \pm 0.3
Deeper hard-bottom (38)		
Range	7-25	0.5-13.0
Mean \pm 1 SE	14.8 \pm 0.6	2.8 \pm 0.6
Low-relief spur and groove (49)		
Range	5-26	0.5-21.0
Mean \pm 1 SE	16.1 \pm 0.6	3.3 \pm 1.2
Fore reef (15-20 m) (17)		
Range	14-24	0.5-21.0
Mean \pm 1 SE	18.9 \pm 0.7	7.0 \pm 4.9
Fore reef (22-27 m) (9)		
Range	13-20	3.0-13.0
Mean \pm 1 SE	16.3 \pm 0.9	7.2 \pm 1.1

Mean proportional transect frequency, or the percentage of transects where species were encountered, allowed for the partitioning of species into rare, common, and very common based upon habitat distribution and frequency of occurrence (Fig. 3). Relatively rare species (e.g. *Acropora palmata*,

Mycetophyllia aliciae, *Mussa angulosa*) were observed in few habitats, and when they did occur, were usually absent on 70+% of transects. Common species, which include many of the framework corals such as *Colpophyllia natans* and *Montastraea faveolata*, were present in most or all habitat types, but exhibited patterns in frequency of occurrence that were strongly habitat dependent (e.g. *C. natans* and *Solenastrea bournoni*). Very common species such as *Porites astreoides* and *Siderastrea siderea* were not only found in all habitat types, but frequency of occurrence values were also very high (> 75%).

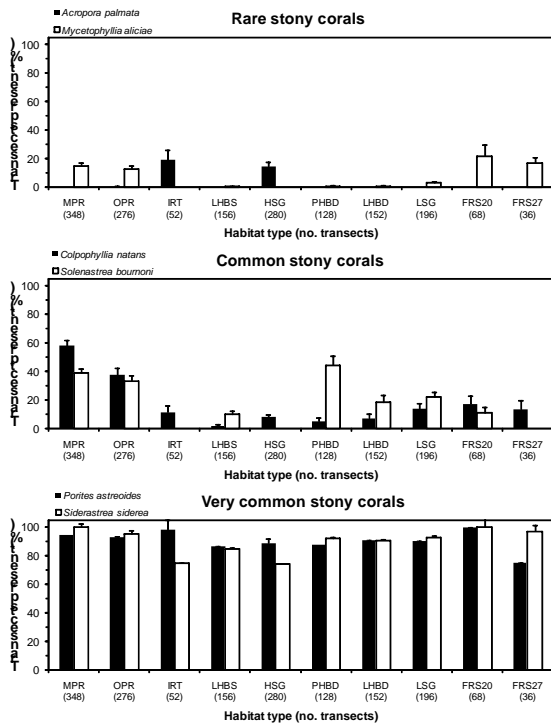


Figure 3: Mean proportional frequency (% of transects recorded) for selected coral species in the Florida Keys, ranging from very common to rare by habitat type. Error bars are +1 SE and numbers in parentheses on the x-axis are the number of 15-m x 4-m transects sampled in each habitat. See Table 1 for habitat abbreviations.

Mid-channel patch reefs were noted for their relatively high coral species richness and cover (Table 3). Figure 4 shows inter-reef variability in these two metrics for 51 mid-channel patch reef sites along ~200 km of the Florida Reef Tract, illustrating reef-to-reef variability, as well as regional variations. For both metrics, coral species richness and cover tended to be greater in the middle and lower Florida Keys, particularly in areas outside of FKNMS no-take zones, relative to the upper Keys and Biscayne National Park.

Discussion

Many biological phenomena are scale dependent, conclusions can be affected by the scale of observation, and caution needs to be exercised in

scaling up results from small-scale studies to spatial and temporal patterns that were not sampled (Edmunds and Bruno 1996). Sampling at multiple spatial scales is usually necessary to determine whether patterns at one spatial scale are indicative of regional patterns (Murdoch and Aronson 1999). The interpretation of spatiotemporal changes in community structure is also made complex by biases introduced by site selection. For example, reefs with high coral cover, selected at the start of a monitoring program, can only remain unchanged or deteriorate once monitoring is initiated (Miller et al. 2002).

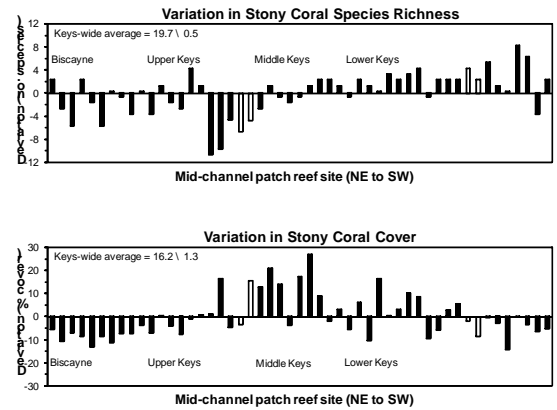


Figure 4: Deviations in stony coral species richness (no. species/60 m²) (top) and percent coral cover (bottom) from domain-wide averages for Florida Keys mid-channel patch reefs. Open bars are sites within Sanctuary no-take zones.

The patterns and processes governing species richness and community structure are complex and scale-dependent (Murdoch and Aronson 1999). Species richness inventories can emphasize biodiversity hotspots, cold-spots, or the full gradient of species richness values. In addition, there have been attempts to identify indicator species whose occurrence patterns are correlated with the species richness of a larger group of organisms. For our Florida Keys study, taxon richness was measured in terms of the number of stony coral species identified in standardized search areas along belt transects sampled at each site. One of the most significant factors related to species distribution in the Florida Keys is habitat type, which reflects a combination of distance from shore, depth, and geomorphology (i.e. Pleistocene topography) (Shinn et al. 1989; Lidz et al. 2003). Greater numbers of coral species were recorded from inner shelf-margin patch reefs, followed by deeper fore-reef slope habitats that extended to the 27 m depth limit of this study. In other words, the greatest species richness of corals was recorded on either side of the main reef tract, including inner shelf margin patch reefs and offshore

of the main reef tract on the deeper fore-reef slope. In contrast, the shallow fore-reef, especially in areas historically dominated by the branching coral *Acropora palmata*, yielded relatively low numbers of species that are either widely distributed and frequently encountered (*Porites astreoides*) or species that are relatively rare in other habitats.

Relative to species richness, coral cover on Florida Keys reefs was more variable among sites within particular habitats, as well as among habitat types, but exhibited similar cross-shelf patterns to species richness. Coral cover was greater on patch reefs closer to shore and was significantly lower on the shallow platform margin, even on highly structured reefs where live *Acropora* cover was historically more abundant. Massive, mounding coral species dominated coverage inshore and some of these same species are prevalent on the deeper fore-reef, but not on the shallower platform margin. Previous large-scale surveys encompassing a large spatial area (Murdoch and Aronson 1999; Chiappone and Sullivan 1997; Miller et al. 2002) or timeframe (Somerfield et al. 2008) confirm the substantial inter-reef variability in the Florida Keys. Overlain on the geologic history of particular sites (Shinn et al. 1989; Lidz et al. 2003) and along-shelf position (Marszalek et al. 1977) are the responses of individual reefs to disease and bleaching episodes (Somerfield et al. 2008).

Cover and species richness are most frequently used with a focus on corals, because after all, corals are often the dominant organism or they are of high interest to managers. However, when coral cover is regionally low for most habitats as it currently is in the Florida Keys, a broader suite of metrics may be needed to evaluate ecosystem health and condition (Miller et al. 2002). In addition, there are so many potential indirect effects that might result from various management measures (e.g. no-take zones), in addition to larger-scale system variability, none of which can be predicted with any degree of certainty. Many previous and ongoing studies of coral reef community structure in the Florida Keys and elsewhere have focused on benthic cover as the abundance metric of choice for stony corals (e.g. Dustan and Halas 1987; Porter and Meier 1992; Somerfield et al. 2008). Benthic cover represents the net outcome of population dynamic rate processes such as colony recruitment, growth, and survivorship, whereas density and size structure, the two basic components of cover, provide information on the rate processes themselves, as well as on the net outcome. For example, a particular area with high densities of mostly small colonies versus another area with low densities of mostly large colonies may produce similar estimates of stony coral cover, but the two areas reflect very different demographic histories.

Spatially explicit estimates of coral population density and size structure not only allow for tracking changes in abundance metrics over time, but can also serve as baseline data for subsequent studies of population and community dynamics (Smith et al. in press).

Acknowledgement

Financial and logistical support was provided by the Florida Keys National Marine Sanctuary, NOAA's Coral Reef Conservation Program, Emerson Associates International, and NURC/UNCW. The authors thank O. Rutten, B. Keller, R. Curry, B. Altmeier, S.G. Smith, and J.S. Ault. Research was conducted under National Marine Sanctuary Permit FKNMS-074-98 and National Park Service Permit BISC-2005-SCI-0039.

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