

REPORT

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Scale-dependent spatial variability of coral assemblages along the Florida Reef Tract

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Abstract Coral reef communities of the western Atlantic have changed over the past two to three decades, but the magnitude and causes of this change remain controversial. Part of the problem is that small-scale patterns observed on individual reefs have been erroneously extrapolated to landscape and geographic scales. Understanding how reef coral assemblages vary through space is an essential prerequisite to devising sampling strategies to track the dynamics of coral reefs through time. In this paper we quantify variation in the cover of hard corals in spur-and-groove habitats (13–19 m depth) at spatial scales spanning five orders of magnitude along the Florida Reef Tract. A video-graphic sampling program was conducted to estimate variances in coral cover at the following hierarchical levels and corresponding spatial scales: (1) among transects within sites (0.01- to 0.1-km scale), (2) among sites within reefs (0.5- to 2-km scale), (3) among reefs within sectors of the reef tract (10- to 20-km scale), and (4) among sectors of the reef tract (50- to 100-km scale). Coral cover displayed low variability among transects within sites and among sites within reefs. This means that transects from a site adequately represented the variability of the spur-and-groove habitat of the reef as a whole. Variability among reefs within sectors was highly significant, compared with marginally significant variability among sectors. Estimates from an individual reef, therefore, did not adequately characterize nearby reefs, nor did those estimates sufficiently represent variability at the scale of the sector.

The structure and composition of coral reef communities is probably determined by the interaction of multiple forcing functions operating on a variety of scales. Hierarchical analyses of coral assemblages from other geographic locations have detected high variability at scales different from those in the present study. A multiscale analysis should, therefore, precede any management decisions regarding large reef systems such as the Florida Reef Tract.

Key words Scale · Coral reefs · Landscape ecology · Florida Keys · Caribbean · Hierarchical analysis.

Introduction

Ecologists have become increasingly aware that scales of measurement must be adjusted to suit the nature of the system to be studied and the hypotheses to be tested (Stommel 1963; Dayton and Tegner 1984; Menge and Olson 1990). Most ecosystems display variability that differs depending on the spatial and temporal scales of observation (O'Neill et al. 1986; Weins 1989; Underwood 1997). This scale dependence is often due to the interaction of processes possessing distinct rates and scales of effect (Allen and Hoekstra 1992). Considerations of scale are germane to the dynamics of coral reef communities, in which processes operate over spatial scales from the submicroscopic to the global, and temporal scales from the instantaneous to the millennial (Hubbard 1988; Jackson 1991; Hatcher 1997).

Measuring the variability of coral assemblages across multiple scales can elucidate the range of scales at which different patterns occur (Reichelt and Bradbury 1984; Hatcher et al. 1987; Ogden et al. 1994). Surveying over a range of scales may also help uncover links between seemingly unrelated processes operating at different hierarchical levels of organization (Menge

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and Olson 1990; Allen and Hoekstra 1992; Levin 1992; Wu and Loucks 1995). Moreover, multiscale sampling may reveal domains, or ranges of scale, in which the characteristics of a reef system are scale-independent (Weins 1989; Aronson 1994; Aronson and Plotnick 1998). If the scales of interest fall within such a scale-independent domain, then research programs can be optimized to reduce the effort required to sample reefs effectively (Underwood 1997).

Coral reefs of Florida and the Caribbean have changed over the past two to three decades, but the magnitudes, scales, and causes of this change remain controversial (Ginsburg 1994; Hughes 1994; Aronson and Precht in press). In general, the cover of living hard corals has declined and algal cover has increased. Some researchers have suggested that factors operating at small spatio-temporal scales (meters to kilometers and days to years), such as point-source nutrient loading and ship groundings, could be primarily responsible for the decline of coral populations along the Florida Reef Tract (Dustan and Halas 1987; Lapointe and Clark 1992; Ginsburg and Shinn 1994; Lapointe 1997). Others assert that meso- to large-scale processes (tens to thousands of kilometers and decades to millennia), such as larval transport, fishing pressure, disease outbreaks, and climate change, are equally or more important (Lessios 1988; Smith and Buddemeier 1992; Szmant and Forrester 1996; Roberts 1997). An essential prerequisite to formulating and testing hypotheses about temporal dynamics is understanding how reef coral assemblages vary over multiple spatial scales at one time (Schneider 1994). Despite their importance to nearshore food webs, few multiscale analyses have been attempted for corals on reefs (Done 1982; Edmunds and Bruno 1996; Hughes et al. 1999), although studies of this sort are common for coral reef fish (Sale 1980; Victor 1986; Doherty and Fowler 1994).

Until recently, information regarding the condition of Florida's reefs was derived primarily from small-scale surveys (e.g. Dustan and Halas 1987; Porter and Meier 1992; Lapointe 1997). Surveys that encompass the entire reef tract are needed to determine whether the patterns observed and the processes inferred from those small-scale studies can be extrapolated to larger scales (Ogden et al. 1994). Furthermore, the surveying techniques used must have sufficient statistical power to test the hypotheses, an issue that has been largely ignored in the contentious debates about the state of the Florida Reef Tract.

In this paper we test the hypothesis that the cover of hard corals (*Scleractinia* plus *Milleporina*) along the Florida Reef Tract exhibits variability that changes with the spatial scale of observation. We surveyed spur and groove habitats at 13–19 m depth on 16 reefs in 1995 using a hierarchical sampling design. Our results highlight the value of multiscale assessment in making effective management decisions.

Methods

Scales of analysis

The variation in live, hard-coral cover was measured on four hierarchically-nested spatial scales, spanning five orders of magnitude, over the Florida Reef Tract (Figs. 1 and 2). These scales corresponded to four geographic levels of organization (see Allen and Hoekstra (1992) on the distinction between scales and hierarchical levels).

Transects within sites: 0.01- to 0.1-km scale Small-scale ecological variation was measured among transects placed on distinct spurs in the spur-and-groove habitat.

Sites within reefs: 0.5- to 2-km scale Ecological variation within the spur-and-groove zones of reefs was examined by comparing the differences among sites within three of the 16 study reefs. The dimensions of these sites were ~ 100 m along the depth contours of the reef by 25 m along the spurs perpendicular to those depth contours, between the 13 and 19 m depth contours. A site represented the area of a reef that could be effectively sampled in an 8-h period by a team of divers with other tasks to accomplish. Sites were separated by distances of 0.5–2 km. Sites within reefs could, hypothetically, experience different small-scale hydrographic and biological conditions influencing coral cover.

Reefs within sectors: 10- to 20-km scale Landscape-scale differences among the spur-and-groove habitats of different reefs were also compared. Reefs were defined as the spur-and-groove zones of discrete areas of hard substratum at least 2 km long, isolated from neighboring areas by stretches of soft substratum. Reefs were generally 10–15 km apart. Coral composition was expected to vary from reef to reef due to historical differences in disturbance regimes, fishing pressure, and localized recruitment events (Hughes 1989; Russ 1991; Smith 1992), as well as for hydrographic and physiographic reasons (Shinn et al. 1989; Lidz and Shinn 1991; Lidz et al. 1997).

Sectors within the reef tract: 50- to 100-km scale At the largest spatial scale, we compared differences among sectors of the Florida Reef Tract. Each sector was a continuous swath of the reef tract ~ 50 km long. Sectors were defined according to two geographic classification schemes, described below in study areas. These sectors possess distinct hydrographic and geological characteristics that could cause geographic differences in the composition of coral assemblages (Shinn et al. 1989; Klein and Orlando 1994; Lee et al. 1994).

Study areas

Videographic data sets were collected during the three research cruises of the Keyside Coral Reef expedition in August–October, 1995. The purpose of the Expedition was to provide a synoptic survey of the biota of the Florida Keys National Marine Sanctuary (FKNMS) for future comparison. Twenty reefs from Biscayne Bay to the Dry Tortugas were selected for sampling and assigned letter designations. They were chosen haphazardly based on (1) evidence of a deep-water spur-and-groove zone in aerial photographs, when available, and (2) visual assessment of the occurrence of hard substratum in the 13–19 m depth range. Most of the reefs were characterized by areas of emergent reef that were landward of the depth range sampled. Since mooring buoys in the FKNMS are generally located near the emergent portions of reefs, we conducted our surveys lateral to and seaward of these emergent portions to avoid areas subject to the heaviest human use.

Of the 20 reefs sampled, 16 (Fig. 1) were characterized by a deep-water spur-and-groove habitat at 13–19 m depth. Their geomorphology represents relict spur-and-groove development, with reef accretion apparently inhibited at present in that depth range (Shinn

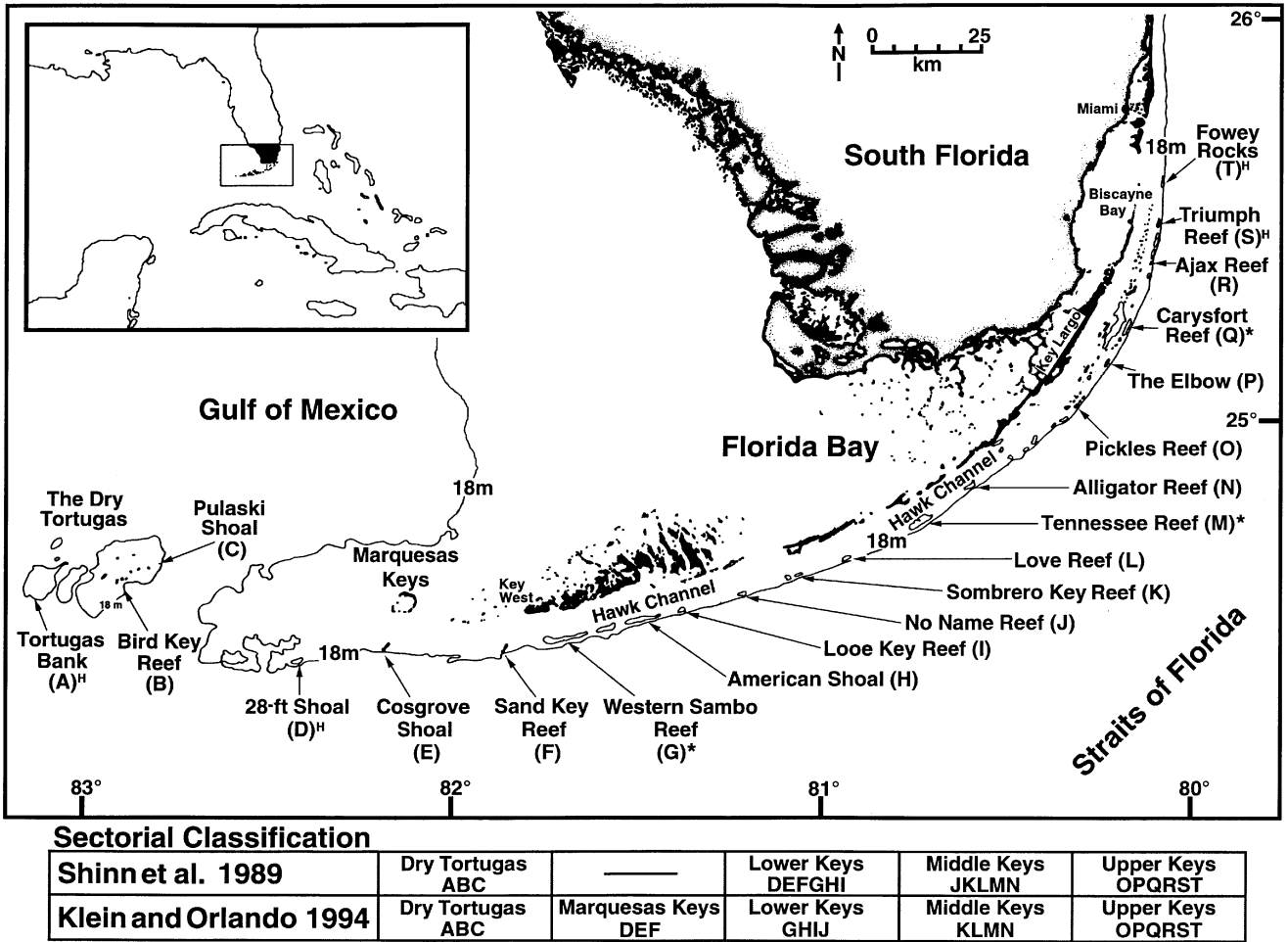


Fig. 1 Map of the Florida Reef Tract showing the reefs studied. Three sites were surveyed on each of three intensively sampled reefs (*): Western Sambo Reef (G), Tennessee Reef (M), and Carysfort Reef (Q). Four reefs (H) were hardgrounds at 13–19 m depth and were not considered in the analysis: Tortugas Bank (A), 28-ft Shoal (D), Triumph Reef (S), and Fowey Rocks (T). Modified from Shinn et al. (1989). Also included are the sectorial classification schemes used in the analysis

et al. 1989). The remaining four study areas were limestone pavements. These hardgrounds were excluded from the present analysis to control for habitat type in testing our hypothesis of scale-dependent variation.

Fore-reef slopes in Florida generally do not descend monotonically with depth. In many places ridges rise to within 10 m of the surface (Lidz et al. 1991, 1997). Sampling was done on the seaward-most spur-and-groove habitat, in order to ensure that each reef was sampled in its area of maximum wave exposure.

Three reefs from three different sectors of the reef tract were arbitrarily chosen for analysis of within-reef variation. Western Sambo Reef (reef G), in the Lower Keys, was characterized by moderate coral cover; Tennessee Reef (reef M), in the Middle Keys, had high coral cover; and Carysfort Reef (reef Q), in the Upper Keys, had low coral cover (Fig. 1). Three sites were sampled on each of these reefs. Sites were separated by 0.5–2 km, as discussed above.

Among-reef and among-sector variability was assessed by sampling two to five reefs within each sector of the Florida Reef Tract. We performed the sectorial analysis using two classification schemes (Fig. 1). The Florida Reef Tract traditionally has been partitioned into sectors based on geographic criteria (Ginsburg and Shinn 1964; Shinn et al. 1989). According to this scheme, the sectors are the Upper Keys, Middle Keys, Lower Keys, and Dry Tortugas. More

recently, Klein and Orlando (1994) developed a hierarchical framework based on large-scale, quantifiable, physical and hydrographic features. In this scheme, the sectors are the Upper Keys, Middle Keys, Lower Keys, Marquesas Keys, and Dry Tortugas.

Known physical and hydrographic differences led to some a priori predictions of among-sector differences in coral assemblages. The Dry Tortugas sector, for example, is isolated from the terrestrial and anthropogenic influences that pervade the rest of the Florida Reef Tract (Klein and Orlando 1994; Lee et al. 1994; 1995). As a result, we expected higher coral cover in the Dry Tortugas than in the other sectors. In contrast, reefs of the Middle Keys sector are exposed to water from Florida Bay, which reaches them through numerous passes between islands (Marszalek et al. 1977). Florida Bay water is in many respects inimical to coral growth (Ginsburg and Shinn 1964, 1994), and we therefore expected lower coral cover in the Middle Keys than elsewhere.

Data collection and analysis

Transects were videotaped and the data analyzed following procedures described in Aronson et al. (1994) and Aronson and Swanson

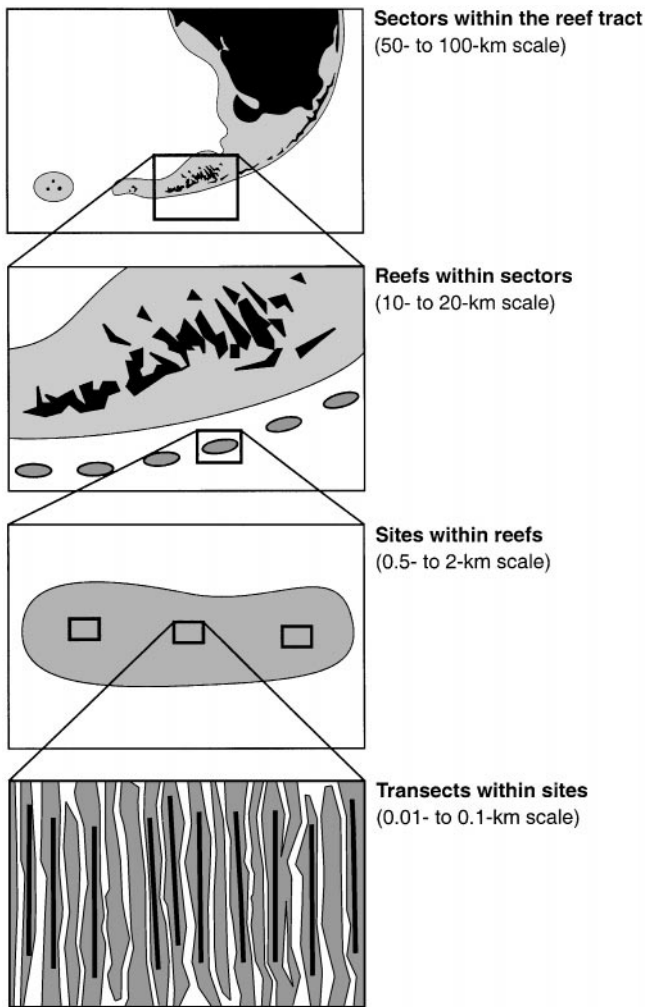


Fig. 2 Hierarchical levels and spatial scales of analysis

(1997). Divers stretched a 25-m long waterproof surveyor's tape down the middle of each of ten haphazardly selected spurs within the site to be sampled. Transects were generally 3–10 m apart. Care was taken to avoid laying the transect lines over sand or off the ends of spurs. Once each transect line was in place another diver slowly swam its length, videotaping a 0.4 m wide \times 25 m long swath of the reef.

The transects were videotaped in plan view and at a constant height from the substratum using a high resolution (Hi-8) video camera. The camera was enclosed in a underwater housing and equipped with a wide-angle lens and two 50-W waterproof lights. A stainless steel rod projected forward from the camera housing. The rod was used as a guide so that the diver could maintain a set distance of 40 cm between the camera lens and the reef surface. A 15-cm gray plastic bar was mounted on the end of the rod. The plastic bar provided scale in the videotaped images. The camera was held perpendicular to the reef surface, with the scale bar maintained at a distance of less than 2 cm from the substratum.

The videotaped transects were analyzed in the laboratory with a Hi-8 video cassette recorder (VCR) wired to a high-resolution color monitor. Each video transect was sampled at 50 regularly spaced, non-overlapping frames, displayed by pausing the VCR. For each frame, one of ten clear plastic sheets marked with ten random points was laid over the monitor screen, and the sessile organisms or

substrate types present under the points were identified and recorded. The videotape was then advanced to the next frame and a new sheet of dots haphazardly selected. Percent covers of coral species were calculated for each transect from the resulting set of 500 point counts. A sample size of ten transects, analyzed in this manner, allows statistically powerful, univariate and multivariate comparisons of coral cover among sites (Aronson et al. 1994; Aronson and Swanson 1997).

Point counts are biased against the inclusion of rare species, particularly when cover is low (Aronson et al. 1994; Hayek and Buzas 1997). To examine patterns of species presence and absence, we recorded all coral species appearing in each video transect. Rarefaction analysis in an earlier study showed that a sample of ten transects is inadequate to estimate coral species richness on western Atlantic reefs; therefore, ten additional transects of the same dimensions were surveyed visually in the field and the coral species recorded, providing a sufficient sample size of $N = 20$ (Aronson et al. 1994). Presence-absence data were only compared at the 10- to 20-km (reefs within sectors) and the 50- to 100-km (among-sector) scales. Time constraints did not permit us to sample ten visual transects at each of the three sites on Western Sambo, Tennessee, and Carysfort Reefs.

Statistical analysis

Univariate coral cover data from the transects were analyzed using a two-level nested analysis of variance (ANOVA) design. One ANOVA compared the variance among sites to the variance among reefs, with sites nested within reefs. Two additional ANOVAs compared the variance among reefs to the variance among sectors, with reefs nested within sectors; a separate ANOVA was calculated for each sectorial classification scheme. For the three intensively sampled reefs (i.e. Western Sambo, Tennessee, and Carysfort) the site that was chronologically the first sampled was used to represent that reef in the latter two ANOVAs. The error terms in the three ANOVAs represented estimates of the variance among transects.

Prior to ANOVA, the point count data were expressed as proportions. The data were then tested for conformity to the parametric assumptions of normality and homogeneity of variances, using the Lilliefors and F_{max} tests, respectively. Arcsine transformation was necessary to make the data satisfy the assumptions of ANOVA.

Cluster analysis was used to determine if sites within the three intensively sampled reefs were more similar to each other in the composition of their coral assemblages than they were to sites from other reefs. The point count data were pooled by coral species across transects within sites. Dissimilarity matrices were calculated for the nine sites (three on each reef), and the sites were clustered by the average linkage method. Two dissimilarity measures were used in separate cluster analyses: Euclidean distance and Bray-Curtis dissimilarity. Both are weighted toward the most abundant species, but the Bray-Curtis measure is a more robust, reliable measure (Faith et al. 1987).

The same approach was used to determine if spur-and-groove habitats on reefs within sectors were more similar to each other than to spur-and-groove habitats on reefs from other sectors. In this case the Euclidean distance and Bray-Curtis dissimilarity matrices were calculated from the vectors representing species-specific point count values on the 16 reefs, and the reefs were again clustered by the average linkage method. Since the Euclidean and Bray-Curtis measures are weighted toward the dominants, we performed a third cluster analysis of reefs, in which all species were weighted equally. The 16 reefs were analyzed based on the species presence-absence data, using a matrix of Jaccard dissimilarities and clustering by the average linkage method. All univariate and multivariate statistical calculations were performed using the SYSTAT 8.0 statistical package.

A power analysis was performed for each nested ANOVA. The power of the performed test was calculated to determine the probability of detecting among-reef differences in the first comparison

(sites nested within reefs) and among-sector differences in the second (reefs within sectors). In addition, we calculated the minimum detectable difference, δ , in arcsine-transformed proportional coral cover among reefs and, separately, among sectors. The minimum detectable difference is an estimate of the difference in coral cover that one can reasonably expect to detect in future studies using the same design. Calculations were performed according to Zar (1984) and Cohen (1988).

Following convention, the power was set at $(1 - \beta) = 0.80$ and the significance level was set at $\alpha = 0.05$ to calculate minimum detectable differences. The calculated values of δ in the two analyses were converted to untransformed coral cover for ease of interpretation. First, δ was added to the (transformed) lowest group mean in the analysis, that value was back-transformed to actual percent cover, and the difference was calculated between the back-transformed value and the observed (untransformed) lowest group mean. Second, δ was subtracted from the (transformed) highest group mean, that value was back-transformed, and the difference was taken between the observed (untransformed) highest mean and the back-transformed value. These calculations were used to estimate the range of the minimum detectable difference in actual percent cover, corresponding to the range of group means in each of the ANOVAs (Aronson et al. 1994).

Results

Reefs, sites, and transects

To compare the variability among reefs to the variability among sites within reefs and among transects within sites, 90 video transects from nine sites on three reefs were analyzed. Thirty-five species of hard corals were recorded from the nine sites. The cover of hard corals, estimated from a data set of 45 000 point counts, varied considerably among the three reefs (Fig. 3). The five most abundant species, in descending order of overall cover, were *Montastraea franksi*, *Siderastrea siderea*, *M. faveolata*, *M. cavernosa*, and *Colpophyllia natans*. These species accounted for 68.4% of the total cover. All other species were rare: no other species accounted for more than 5.3% of the total cover.

There was little variation in mean coral cover among sites in the spur-and-groove habitat within the three intensively sampled reefs. Furthermore, coral cover was relatively homogeneous among transects within sites, judging from the small errors. A two-level nested ANOVA, with sites nested within reefs, revealed no significant among-site effects, but there was a highly significant among-reef effect (Table 1). Among-transect variation accounted for 13.7% of the total variance (calculated from the mean square estimates; see for example Underwood 1997), among-site variation accounted for $\sim 0\%$ of the total variance, and among-reef variation accounted for 86.3% of the total. Tukey HSD a posteriori pairwise comparisons showed that coral cover on each of the three reefs was significantly different from coral cover on both other reefs ($P < 0.002$ in all cases).

Cluster analysis of the multivariate point count data, using Euclidean distances and Bray-Curtis dissimilar-

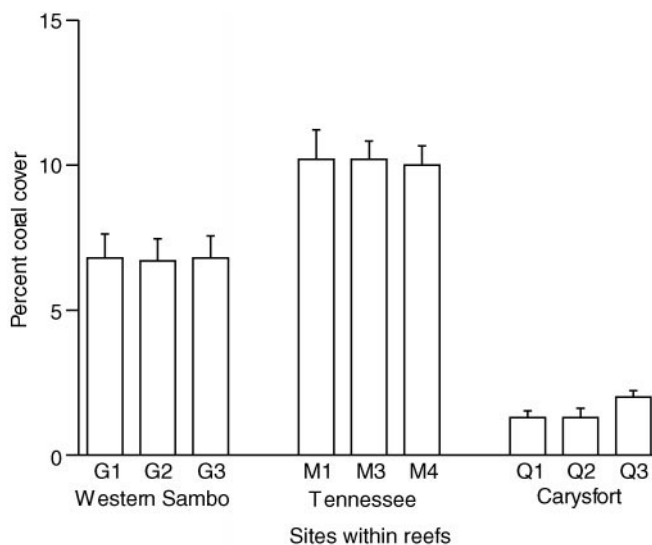


Fig. 3 Mean percent coral cover for nine sites within three intensive-sampled reefs on the Florida Reef Tract (three sites at each reef; ten video transects at each site). Error bars represent one standard error of the sample mean

Table 1 Results of two-level nested ANOVA on arcsine-transformed proportional coral cover along the Florida Reef Tract, comparing the variation among reefs with the variation among sites within reefs and among transects within sites (error term). The Site{Reef} and Error variances were not pooled to calculate the denominator mean square for testing the effect of Reef, following Zar (1984) but contrary to Sokal and Rohlf (1981). The F -test for Reef is highly significant despite being more conservative than if the variances had been pooled

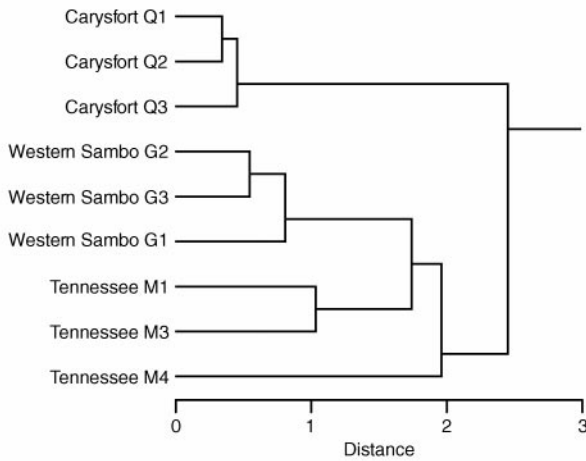
Source	Sum of Squares	df	Mean Square	F	P
Reef	0.6451	2	0.3225	329.81	7.32×10^{-7}
Site{Reef}	0.0059	6	0.0010	0.5607	0.760
Error	0.1413	81	0.0017		

ities, showed similar patterns of scale dependence (Fig. 4). Sites were more similar to other sites on the same reef than they were to sites on either of the other reefs, with the exception of Tennessee Reef site M4 in the Euclidean analysis. Tennessee Reef and Western Sambo Reef clustered together, and they were distinct from Carysfort Reef. In the Bray-Curtis analysis, sites within Carysfort Reef were more different from each other than Western Sambo and Tennessee Reefs were from each other.

Sectors, reefs, and transects

The low variance among sites within reefs provided the rationale for collapsing the reef and site levels and using 10 transects from a single site to represent the spur-and-groove habitat of an entire reef. Comparison of the variation among sectors to the variation among reefs within sectors involved the analysis of 160 video

A Euclidean Distance



B Bray-Curtis Dissimilarity

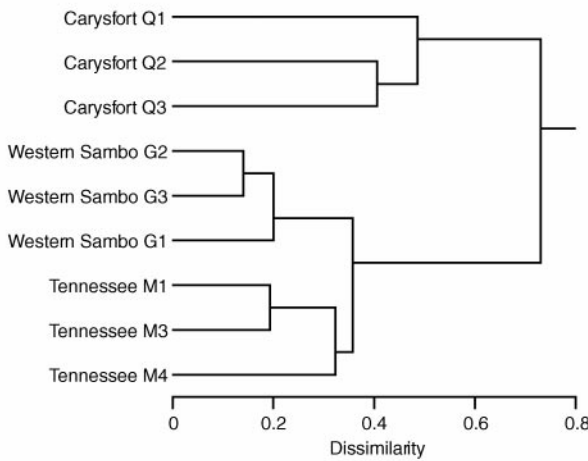


Fig. 4 A,B Cluster diagrams showing the relationships of species-specific coral cover among nine sites on three intensively sampled reefs within the Florida Reef Tract. Sites were clustered by the average linkage method based on: **A** Euclidean distance and **B** Bray-Curtis dissimilarity

transects from 16 reefs. Thirty-eight species of hard corals were recorded from the 16 reefs. Total coral cover, estimated from a data set of 80,000 point counts, showed substantial among-reef variation (Fig. 5). The five dominant species were, in descending order, *Montastraea franksi*, *M. faveolata*, *M. cavernosa*, *Siderastrea siderea*, and *Millepora alcicornis*. Together they accounted for 69.4% of the total coral cover. All other species were rare: no other species accounted for more than 4.8% of the total cover.

Two-level nested ANOVAs, using both sectorial classification schemes, detected highly significant differences among reefs and marginally significant differences among sectors (Table 2). Using the Klein and Orlando (1994) sectorial classification scheme, among-transect variation accounted for 17.6% of the total

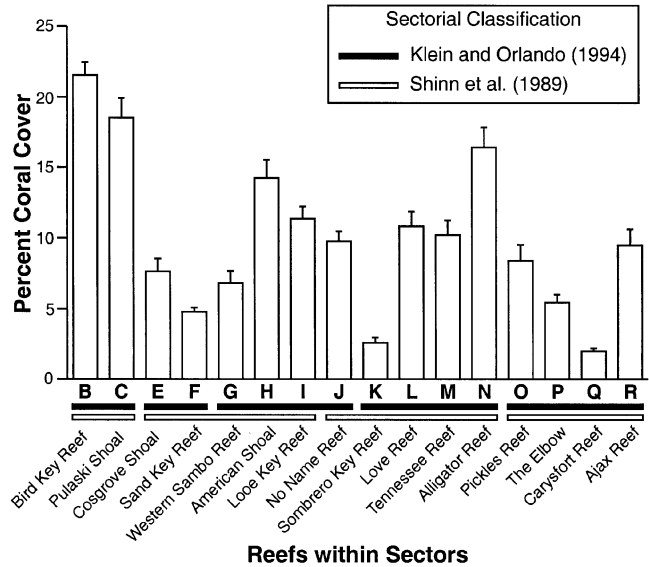


Fig. 5 Mean percent coral cover for 16 reefs on the Florida Reef Tract (one site comprising ten transects at each reef). The two sectorial classification schemes are denoted by filled and open horizontal bars. Error bars represent one standard error of the mean

variance, among-reef variation accounted for 34.8% of the total, and among-sector variation accounted for 47.6% of the total. Using the Shinn et al. (1989) classification, among-transect variation accounted for 16.6% of the total variance, among-reef variation accounted for 36.6% of the total, and among-sector variation accounted for 46.9% of the total.

These ANOVAs comparing among-sector to among-reef variation were unbalanced. Although the sample size (number of transects) was the same for each reef, the number of reefs sampled was not the same within each sector. Thus, the *F*-tests for the among-reef effect are exact, but the tests for among-sector effects are only approximate. Although SYSTAT corrects for unbalanced designs, the significant among-sector effects should be interpreted cautiously, especially since the *P*-values were marginal in both cases.

Because we had a priori expectations about how the Dry Tortugas would compare with the rest of the reef tract, coral cover in the Dry Tortugas was compared with cover in all the other sectors by the method of orthogonal contrasts. As predicted, the Dry Tortugas had significantly higher coral cover ($P < 0.01$, using either sectorial classification), although it should be borne in mind that only two reefs were sampled in that sector. When the Middle Keys were compared with all other sectors by the same method, there was no significant difference, contrary to our expectation that coral cover would be lower in the Middle Keys ($P \geq 0.35$, using either classification). For both classifications, Tukey HSD a posteriori pairwise comparison of sectors revealed that the Dry Tortugas had significantly

Table 2 Results of two-level nested ANOVAs on arcsine-transformed proportional coral cover, comparing the variation among sectors to the variation among reefs within sectors and among transects within reefs (error term), for two different sectorial classification schemes of the Florida Reef Tract

A. Sectorial classification of Klein and Orlando (1994)					
Source	Sum of Squares	df	Mean Square	<i>F</i>	<i>P</i>
Sector	0.7990	4	0.1997	4.0051	0.030
Reef{Sector}	0.5486	11	0.0498	20.589	$< 5.00 \times 10^{-10}$
Error	0.3464	143	0.0024		
B. Sectorial classification of Shinn et al. (1989)					
Source	Sum of Squares	df	Mean Square	<i>F</i>	<i>P</i>
Sector	0.6521	3	0.2174	3.7723	0.041
Reef{Sector}	0.6915	12	0.0576	23.439	$< 5.00 \times 10^{-10}$
Error	0.3516	143	0.0025		

higher coral cover than the Upper Keys ($P < 0.03$ in both cases), but that no difference in cover between any other pair of sectors was significant.

Cluster analysis of the point counts using Euclidean distances and Bray-Curtis dissimilarities confirmed that variability was high among reefs within sectors (Fig. 6). Reefs did not cluster into either sectorial classification scheme. The two reefs sampled in the Dry Tortugas formed a distinct cluster in each analysis, but they were very different from each other in the Euclidean analysis. This Tortugas cluster separated from all other reefs in the Euclidean analysis (Fig. 6A) but not in the Bray-Curtis analysis (Fig. 6B). Cluster analysis of the species presence-absence data using Jaccard dissimilarities, which weighted all species equally, showed no geographic pattern of reef clustering (Fig 6C).

Power and sample size

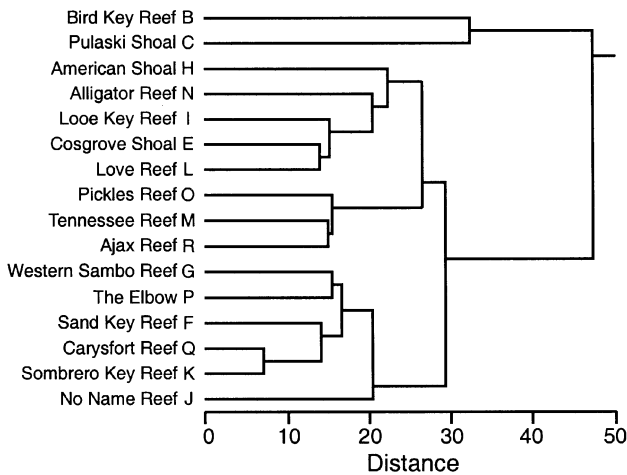
The nested ANOVA comparing among-reef with among-site variation (Table 1) detected a significant among-reef difference as low as 3.38% cover, between Western Sambo and Tennessee Reefs. The power of the test of among-reef differences was $(1 - \beta) > 0.99$. This high power reflects both the low among-site variance and the differences in coral cover among the reefs sampled. Since these reefs encompassed a reasonably large range of coral covers, the low *P*-value and high power are not surprising. In fact, even smaller among-reef differences can be detected with this design: the calculated range of the minimum detectable difference was $0.71 \leq \delta \leq 1.53\%$ cover at $\alpha = 0.05$ and $(1 - \beta) = 0.80$. These calculations used the among-site variance as the error term, so the range of the minimum detectable difference is for the nested design reported in Table 1. When the among-site and the among-transect variances were combined into a maximum error term, the calculated range increased to $0.95 \leq \delta \leq 1.97\%$ cover. This range is the minimum detectable difference that can be expected in a one-way (unnested) ANOVA comparing three reefs. Note that these calculations are

based on the observed variability among sites within reefs: they are not driven by the mean coral covers of the particular reefs examined.

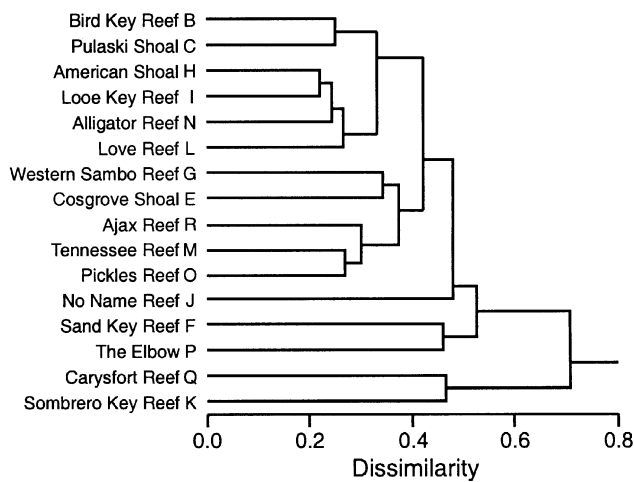
The high sample size, 30 transects per reef, contributed strongly to the sensitivity of the sampling design for detecting differences in coral cover of $< 2\%$ among reefs. Given that sampling is normally constrained to ten video transects per reef or per site (Aronson et al. 1994; Aronson and Swanson 1997), it is important to know the minimum detectable difference that can be expected at this lower sample size. To obtain this estimate, we performed a one-way ANOVA comparing one site from each of the three intensively sampled reefs. We chose the site that was chronologically the first sampled on each reef, since this was the site used in the comparison of sectors and reefs along the Florida Reef Tract. Results of this ANOVA of arcsine-transformed, proportional cover data again indicated a significant among-reef effect (Table 3). The calculated range of the minimal detectable difference was $2.37 \leq \delta \leq 3.79\%$ cover at $\alpha = 0.05$ and $(1 - \beta) = 0.80$ for a comparison of three reefs or sites. Tukey HSD a posteriori comparisons showed that each of the three samples was significantly different from the other two ($P < 0.02$ in all cases), and the minimum difference actually detected was 3.38% cover, between Tennessee and Western Sambo Reefs. This value is close to the minimum between-reef difference of 3.6% cover detected by Aronson et al. (1994), using the same protocol in the same depth range on four western Atlantic reefs. For a comparison of ten reefs, the range of the minimum detectable difference would be $4.99 \leq \delta \leq 6.29\%$ cover. These results agree with estimates of δ presented in Aronson et al. (1994).

The nested ANOVAs comparing among-sector to among-reef variation indicated a marginally significant effect of sector (Table 2). The power of these tests was high, at $(1 - \beta) = 0.80$ using the Klein and Orlando (1994) sectorial classification scheme and $(1 - \beta) = 0.70$ using the Shinn et al. (1989) classification. Because of the high variability among reefs within sectors, the calculated range of the minimum detectable difference

A Euclidean Distance



B Bray-Curtis Dissimilarity



C Jaccard Dissimilarity

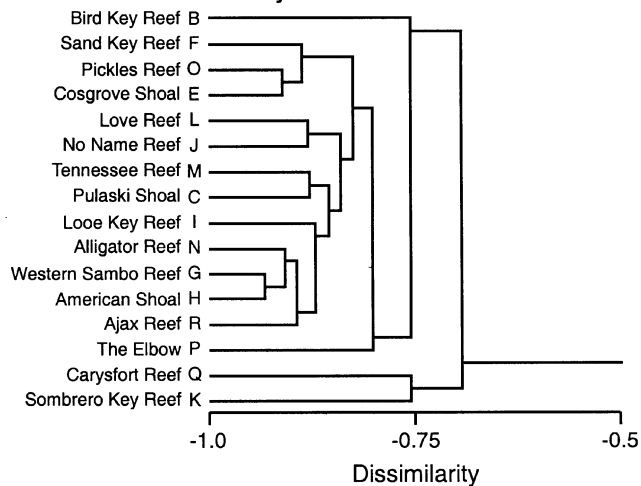


Fig. 6A–C Cluster diagrams showing the relationships among 16 reefs along the Florida Reef Tract. Sites were clustered by the average linkage method based on: **A** Euclidean distance calculated from species-specific coral cover, **B** Bray-Curtis dissimilarity calculated from species-specific coral cover, and **C** Jaccard dissimilarity calculated from species presence-absence data

Table 3 Results of one-way ANOVA on arcsine-transformed proportional coral cover, comparing variation among single sites at Western Sambo, Tennessee, and Carysfort Reefs to variation among transects within sites (error term) along the Florida Reef Tract

Source	Sum of Squares	df	Mean Square	F	P
Sites	0.2378	2	0.1189	53.897	3.74×10^{-10}
Error	0.0596	27	0.0022		

among sectors was $13.70 \leq \delta \leq 13.79\%$ cover, assuming a balanced, nested design and using the Klein and Orlando (1994) classification. In fact, the analysis detected a (possibly) significant difference of 13.94% cover between the Dry Tortugas and the Upper Keys. The minimum significant between-reef difference in coral cover, detected between Sand Key Reef (reef F) and Carysfort Reef (reef Q), was 2.8% (Tukey test, $P < 0.025$), which again agrees with Aronson et al. (1994). Similar results were obtained from calculations using the Shinn et al. (1989) classification.

Discussion

Patterns of variability at different scales

Coral assemblages of the Florida Reef Tract exhibited different degrees of variability in cover depending on the spatial scale surveyed. Coral cover varied little within and among sites on a single reef, yet it varied substantially from reef to reef. Had the Dry Tortugas sector not exhibited high coral cover, landscape-scale (among-reef) variation would have overwhelmed any intersectorial differences.

The higher coral cover observed in the Dry Tortugas could have been a result of their isolation from natural and anthropogenic sources of coral mortality from Florida Bay and the rest of the Florida Reef Tract. The Dry Tortugas are also exposed to gyres that may return locally-generated larvae to the sector, promoting coral recruitment (Lee et al. 1994, 1995). Research into the genetic variability of gorgonians indicates that populations in the Dry Tortugas are distinct from those along the rest of the Florida Reef Tract (D. Brazeau pers. comm.). The same could be true for one or more coral species, especially those with a short larval lifespan (see Carlton and Olson 1993).

The pattern of high reef-to-reef variability within sectors was presumably the result of environmental gradients acting at spatial scales equal to or larger than individual reefs but smaller than sectors. Such environmental gradients could be caused by water crossing the Florida Platform from the Atlantic Ocean and from Hawk Channel (Pitts 1994), or by water from Florida Bay reaching the reefs via passes between the Keys (Smith 1994). Water from Hawk Channel and Florida

Table 4 Variability of coral cover at different hierarchical levels in this and other studies

Study	Locality	Variability at level of			
		Transect	Site	Reef	Sector
This study	Florida Reef Tract	Low	Low	High	High
Edmunds and Bruno (1996)	Jamaica	Low	—	High	—
Hughes et al. (1999)	Great Barrier Reef	High	High	Low	Low

Bay possesses several characteristics that probably inhibit coral growth and survival, including extreme variability in temperature and salinity as well as high nutrient and sediment loads (Ginsburg and Shinn 1964, 1994; Roberts et al. 1983, 1992; Burns 1985; Shinn et al. 1989; Chiappone and Sullivan 1994; Szmant and Forrester 1996). Sombrero Key Reef (reef K), which is near a large pass to Florida Bay, exhibited particularly low coral cover, whereas American Shoal and Alligator Reef (reefs H and N), which are opposite islands and therefore blocked from exposure to Florida Bay water, had high coral cover (Figs. 1, 5). Thus, water from Florida Bay apparently did not depress coral cover uniformly throughout the Middle Keys. The Middle Keys, therefore, cannot be treated as a unit for the purpose of management.

Our results differed somewhat from those of Edmunds and Bruno (1996), who surveyed reefs in Jamaica. Although they also observed high among-reef variability in coral cover (Table 4), their reefs were separated by one to several kilometers, a spatial scale on which we found low variability. Patterns of variation were also different on the Great Barrier Reef, where Hughes et al. (1999) studied coral colony abundance at a variety of scales. Again, the spatial scales were different from ours: sectors covered 250–500 km in Hughes et al. (1999), as opposed to 50–100 km in the present study, and their reefs were separated by hundreds of meters to tens of kilometers. The low among-reef variability observed by Hughes et al. (1999) could have been due to the clumped distribution of reefs sampled within sectors. The physical and biological factors that underlie variability in reef coral assemblages may act at different scales and hierarchical levels in different geographic locations. Thus, although all three studies detected high variability at some scale, none could have predicted the scales of maximum and minimum variability at other locales.

This study examined spatial variability among coral assemblages, but the species within those assemblages are themselves biologically variable. Corals exhibit interspecific differences in morphology, endosymbiosis, fragmentation rate, dispersal pattern, reproductive mode, recruitment rate, and survivorship relative to gradients of stress and disturbance (Jackson 1979; Highsmith 1982; Hughes and Jackson 1985; Tomascik and Sander 1987; Smith 1992, 1997; Soong 1993; Edinger and Risk 1995; Chiappone and Sullivan 1996;

Rowan 1998). These differences determine which species will dominate under benign conditions and which will do better in the face of chronic stress or disturbance (Aronson and Precht in press). Patterns of spatial variability may be distinct at different taxonomic levels or for different functional groups (Bradbury and Loya 1978; Sullivan and Chiappone 1993; Edinger and Risk 1995; Hughes et al. 1999), possibilities we are currently exploring for the corals of the Florida Reef Tract.

Sampling strategies for science and management

Based on our results, surveys taken at different sites within the spur-and-groove habitat on a reef along the Florida Reef Tract should yield similar estimates of coral cover. In other words, the three reefs we sampled intensively appeared to exist within a domain of scales over which coral cover and species composition were relatively homogeneous (i.e. scale-independent). The common practice of sampling over a minimal area can be justified within the scale-independent domain of each reef (Wiens 1989, Underwood 1997). Since reefs differed from their neighbors, however, researchers and environmental managers in Florida should survey numerous reefs to determine the state of the coral assemblages at the 10- to 20-km scale and at larger scales. The direction and rate of change of the coral assemblage of each reef may be different from that of its neighbors (cf. Kay 1991; Edmunds and Bruno 1996).

Coral reef surveys are almost always limited by time and money, necessitating short, “snapshot” visits to individual reefs. Power analysis showed that an investigator can reasonably expect to detect differences on the order of 3–7% coral cover when comparing spur-and-groove habitats on up to ten reefs in the 13–19 m depth range along the Florida Reef Tract, using a sample size of ten transects per reef. If the study requires detection of smaller differences or involves more than ten reefs, then more transects may be necessary.

Complex patterns of change through time cannot be assessed by short-term, synoptic surveys such as the one described in this paper. Long-term, hypothesis-driven sampling is needed to detect relative changes in assemblage composition over different temporal scales in such systems. Until such time-series data are collected for the majority of the reefs along the Florida Reef Tract, it will not be possible to ascertain which

reefs are undergoing the most dramatic changes in assemblage structure (Rogers 1988; Ray and Grassle 1991; Ogden et al. 1994). In Florida and the Caribbean, an independent sampling approach, with ten transects haphazardly positioned in the spur-and-groove habitat of the study reef at each sampling time, provides a simple, inexpensive, statistically powerful alternative to the traditional repeated measures design, in which permanent transects or quadrats are resampled each time (see also Aronson et al. 1994). It may also be desirable to collect long-term data on changes in the condition or health of coral colonies, as well as on processes such as recruitment, mortality, and herbivory, but such decisions must depend on the hypotheses guiding the study.

Single factors rarely provide sufficient explanations in ecology. The goal of ecological analysis should be to understand the relative contributions of multiple processes to observed patterns (Quinn and Dunham 1983). Thus, for example, although water from Florida Bay may affect reef development in the Middle and Lower Keys, it is by no means the only influence (e.g. Leichter et al. 1996, 1998). Multiple factors combine to determine patterns of community composition along the Florida Reef Tract. Multiscale analyses of complex reef systems like the Florida Reef Tract are expensive and time-consuming, but they are crucial to realistic science and effective management.

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