AGRRA

Figure 1. Map of western Atlantic showing AGRRA regional division boundaries and site locations for surveys reported on in this volume.

SYNTHESIS OF CORAL REEF HEALTH INDICATORS FOR THE WESTERN ATLANTIC: RESULTS OF THE AGRRA PROGRAM (1997-2000)

BY

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(On behalf of the AGRRA contributors to this volume)

ABSTRACT

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) sampling strategy is designed to collect both descriptive and quantitative information for a large number of reef vitality indicators over large spatial scales. AGRRA assessments conducted between 1998 and 2000 across a spectrum of western Atlantic reefs with different histories of disturbance, environmental conditions, and fishing pressure were examined to reveal means and variances for 15 indicators. Twenty surveys were compiled into a database containing a total of 302 benthic sites (249 deep, 53 shallow), 2,337 benthic transects, 14,000 quadrats, 22,553 stony corals. Seventeen surveys contained comparable fish data for a total of 247 fish sites (206 deep, 41 shallow), 2,488 fish transects, and 71,102 fishes. Shallow ($\leq$ 5 m) reefs were dominated by *A. palmata*, a good proportion of which was standing dead, while deep (>5m) reefs were nearly always dominated by the *Montastraea annularis* species complex. Fish communities were dominated by acanthurids and scarids with seranids making up less than 1% of the fish seen on shallow reefs and 4% on deep reefs.

AGRRA benthic and fish indicators on deep reefs showed the highest variation at the smallest spatial scale (~<0.1 km), with recent mortality and macroalgal canopy height displaying the largest area and subregional scale (~1-100 km) variation. A mean live coral cover of 26% for the 20 survey areas was determined for the deep sites. Significant bleaching and disease-induced mortality of stony corals associated with the 1998 (El Niño-Southern Oscillation) ENSO event were most apparent in the western Caribbean and Bahamas subregions and the *Montastraea annularis* complex was the most heavily impacted.

The overall low number of sightings for larger-bodied groupers and snappers (~< 1/100 m^2) as a whole suggest that the entire region is overfished for many of these more heavily targeted species. More remote reefs showed as much evidence of reef degradation as reefs more proximal to human coastal development. Characterizing present-day reef condition across the region is a complex problem since there are likely multiple sources of stress operating over several spatial and temporal scales. Not withstanding the many

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limitations of this analysis, the value of making multiple observations across multiple spatial scales that can approximate the "normal" state for the region today is still very high.

INTRODUCTION

Coral reefs in the western Atlantic have undergone massive changes over the past several decades from coral-dominated to algal-dominated states. Widespread impacts such as the 1983 die-off of *Diadema antillarum* and severe overfishing have disrupted herbivory processes. Coral diseases, like the white-band disease epizootic (Green and Bruckner, 2000) and bleaching (Wilkinson, 2000) have decimated previously healthy coral populations. Our understanding of these and other decadal-scale changes comes largely from a limited number of descriptive studies where long-term monitoring has been conducted. Some of the most frequently cited examples are those from Jamaica (Hughes, 1994), Florida Keys (Dustan and Halas, 1987; Porter and Meir, 1992), Curaçao (Bak and Nieuwland, 1995); and Belize (Aronson and Precht, 1997). With the exception of the Caribbean Coastal Marine Productivity (CARICOMP) program (Kjerfve et al., 1998) and the fish surveys of the Reef Environmental and Education Foundation (REEF) (www.reef.org), few studies in the western Atlantic (Caribbean, Gulf of Mexico, Florida, Bahamas, and Brazil) have examined the condition of coral reefs over large spatial scales (100s-1000s km). Moreover, most studies have focused on localized impacts and used diverse sampling methods making statistical comparisons on larger spatial scales impossible. Establishing regional patterns of reef condition is essential for characterizing the extent and severity of decline and developing hypotheses about the causes of decline (Ginsburg and Glynn, 1994).

AGRRA was conceived to provide a "snapshot" characterization of a number of structurally or functionally important benthic and fish indicators on western Atlantic coral reefs. When applied synoptically to the entire region, results can be used to develop a biotic index of relative health or condition. The concept of evaluating "ecosystem health" is a rapidly emerging science for which a number of different definitions and approaches have been suggested (e.g., Costanza, 1992; Rapport et al., 1998, 1999). Because health involves the response of structural and functional components of the ecosystem, most approaches have used more than a single indicator. Some of these include naturalness, normality, productivity, organization (species diversity and complexity of interactions), and resilience (Coates et al., 2002). Normality in itself has been shown to be particularly useful since it provides guidelines for the range of system states. The AGRRA approach relies on normality as its principal measure of condition and these norms are meant to represent a baseline for the region. The methodology and indices, which were developed with the advice of specialists and based on current scientific understanding of coral reef dynamics as well as standard monitoring methodologies, are summarized below.

Coral Condition

The condition of the principal scleractinian and hydrozoan corals that contribute most to the construction and maintenance of the three-dimensional framework is critical for determining the long-term integrity of the reef ecosystems (Dustan and Halas, 1987; Done, 1997). Species composition, colony size, mortality, recruitment, disease, bleaching, predation, coral cover, etc., are examined over large spatial scales in the AGRRA assessment. Estimates of colony size provide information on rugosity, architectural complexity, and an approximation of colony age (Hughes and Jackson, 1980, 1985). Visual estimates of the partial mortality of colonies (hereafter partial mortality) are used to distinguish between the amount of moribund tissue considered recently dead (about 1 year) and long dead (more than 1 year). The amount of "recent mortality" indicates current impacts while "old mortality" is primarily an integration of mortality over longer time scales. The AGRRA data, within certain limits, can be used to calculate size frequency distributions (Bak and Meesters, 1998) as well as identify mortality patterns related to size and/or species identity. Given current knowledge it is hypothesized that large percentages of recent partial mortality are a signal of decline yet some level of old mortality is expected, at least in the larger corals (Hughes and Connell, 1999). By examining coral condition indices on many types of reefs throughout the region, patterns should emerge to establish and help formulate hypotheses on causes.

Algae

There has been a noticeable change on many reefs around the wider Caribbean from coral-dominated communities to those dominated by macroalgae (e.g., Done, 1992; Hughes, 1994; Hallock et al., 1993; Dustan and Halas, 1987; Lewis, 1986; Steneck and Detheir, 1994; McClanahan and Muthiga, 1998). The causes for these shifts have been attributed, in part, to a loss of key herbivorous fishes and sea urchins, particularly *Diadema antillarum*. *Diadema* affects coral reef structure and composition, including algal composition and abundance, by competition with other grazers, particularly certain fishes, and by erosion of coral skeletons (e.g., Steneck and Dethier, 1994; Roberts, 1995; McClanahan and Muthiga, 1998). The dramatic decline of *Diadema* that occurred after its 1983 die-off (Lessios et al., 1984) led to the dominance of many reefs in Jamaica by fleshy and calcareous macro algae, increased coral mortality and decrease in coral recruitment (Hughes, 1994). Recent reports have suggested the abundance of *Diadema* has been increasing in localized areas but little regional information is available on its recovery and subsequent influence on the condition of reefs (but see Edmunds and Carpenter, 2001).

The objective of assessing algae is to quantify the relative abundance of several key functional groups (crustose corallines, macroalgae and, initially, turf algae), and to relate these abundances with herbivorous fish biomass and coral condition. Given that reefs in decline often have high fleshy (noncalcified) macroalgal biomass, sometimes accompanied by a high biomass of *Halimeda*, it is expected that reefs with a low macroalgal:crustose coralline ratio, or a low macroalgal index (= macroalgal abundance x

macroalgal height) are more biologically intact than those with a high ratio (after Steneck and Dethier, 1994).

Fishes

Reef fish, as predators or grazers, play important roles in the community dynamics of coral reefs through their interactions with corals, algae and other herbivores (Roberts, 1995). Fish communities respond to disturbance in various ways depending on the type and degree of perturbation. Various combinations of commercial, subsistence and recreational fishing, particularly of herbivores, constitute some of the most widespread and greatest anthropogenic impacts on coral reefs (Roberts, 1995). In particular, the loss of certain indicator species and guilds causes both direct and indirect shifts in fish community structure as well as in other components of reef ecosystems (Munro and Williams, 1985; McClanahan and Muthiga, 1988; Hughes, 1993, 1994). Disruption in the balance of reef fish assemblages can result in decreased coral cover and increased algal abundance (Roberts, 1995, 1997; McClanahan et al., 1996). Yet only a few studies have examined the response of fish communities to degradation or changes in habitat structure and composition (Jones and Syms, 1998). Whereas visual fish censuses have been conducted throughout the Caribbean and Gulf of Mexico, relatively few are comparable interregionally because of the various methodologies used (Sale, 1998).

The AGRRA approach includes two distinct assessment methods that provide complementary"snapshots" of fishes at a given site although they do not fully account for the daily, tidal, and seasonal changes known to occur in reef habitats (Ault and Johnson, 1998; Bellwood, 1988; Willis, 2001). While subtle differences among fish assemblages can be difficult to detect with this level of sampling, robust patterns across large number of assessments can be revealed. It is expected that areas near human populations will have lower abundance of fishes, particularly commercially significant species.

In this paper I have synthesized the AGRRA data on coral reef condition collected between 1998 and 2000 by a network of scientists from 20 distinct locations in the western Atlantic extending over 1,000 km (Table 1). The areas presented in this synthesis include a wide spectrum of situations with respect to history of disturbance, environmental conditions, and fishing pressure from humans. The principal goals of this synthesis are to examine over various spatial scales (0.1-100 km):

1) variability of coral condition (mortality, recruitment, disease, damage),
2) the relative abundances of major algal functional groups and factors contributing to any differences in macroalgal index,
3) patterns of spatial variability of the abundance and size of targeted fish species or key guilds such as herbivores to evaluate the degree of overfishing, and
4) the integration of indices into a biotic "reef health index" that can be used in an exploratory way to examine patterns and form hypotheses for future experimental testing.

This synthesis is unique in providing the first regional perspective on coral reef condition in the western Atlantic that is based on multiple indicators and in its

examination of spatial variation and trends of reef condition on multiple spatial scales. The results summarized here originate entirely from the data generously contributed by the authors of this volume to the AGRRA database and may differ slightly from that reported in their papers because of differences in the way the data have been analyzed. The reader is referred to individual papers in this volume for more specific information about each of the assessment areas.

METHODS

Sampling Design

A map of the western Atlantic showing AGRRA regional division boundaries and geographic location (indicated by identification number) for the 20 assessments reported on in this volume is shown in Figure 1. All data submitted by individual AGRRA teams in the form of preformated spreadsheets were checked for errors and standardized to uniform species codes. The timing of the assessments spans a three-year period, many of which (~12) were conducted during the wet-season months (June-August) in much of the wider Caribbean. To synthesize results from the many assessments, an Access database was developed that allows users to manage large quantities of data, make statistical comparisons across various spatial scales, and provide this information to other AGRRA scientists, resource managers and interested researchers. A version of the database (Version 1.1) covering the period from 1997-2000 is currently available and newer versions will be released in the future. Fish data collected using the Roving Diver Technique are not discussed here as they are not part of the AGRRA database but instead are housed in the REEF database (www.reef.org).

A synopsis of the AGRRA methodology is provided in Appendix One (this volume). The majority of the AGRRA teams used Version 2 of the protocol. Conceptually, the AGRRA sampling design is based on principles of stratified two-stage sampling (Cochrane, 1977). A hierarchical multiscale sampling approach and associated spatial scales are shown in Figure 2. The sampling domain, defined as the western Atlantic *region*, is subdivided spatially into *subregions, areas, reefs,* and *sites*. Eight subregions are recognized in the western Atlantic: Gulf of Mexico, Bahamas, western Caribbean, central Caribbean, eastern Caribbean, southern Caribbean, Brazil, and Florida. AGRRA data have been collected from each of these subregions except Florida, for which an assessment is scheduled in summer 2003.

Further stratification of reef types can be accomplished using a combination of depth, cross-shelf position, and geomorphology to delineate areas of similarity over any specified geographic area. One aim of AGRRA sampling is to select a series of "typical" sites that are representative of the geographic area. For the purpose of this synthesis, however, *sites* were only distinguished based on the mean benthic transect depth into "shallow" ($\leq$5 m, mostly reef crests and patch reefs) and "deep" (> 5m, mostly fore-reef slopes) categories.

The appropriate sampling effort needed to characterize sites, areas, and sub-regions can vary from location to location depending on the spatial variation of coral,
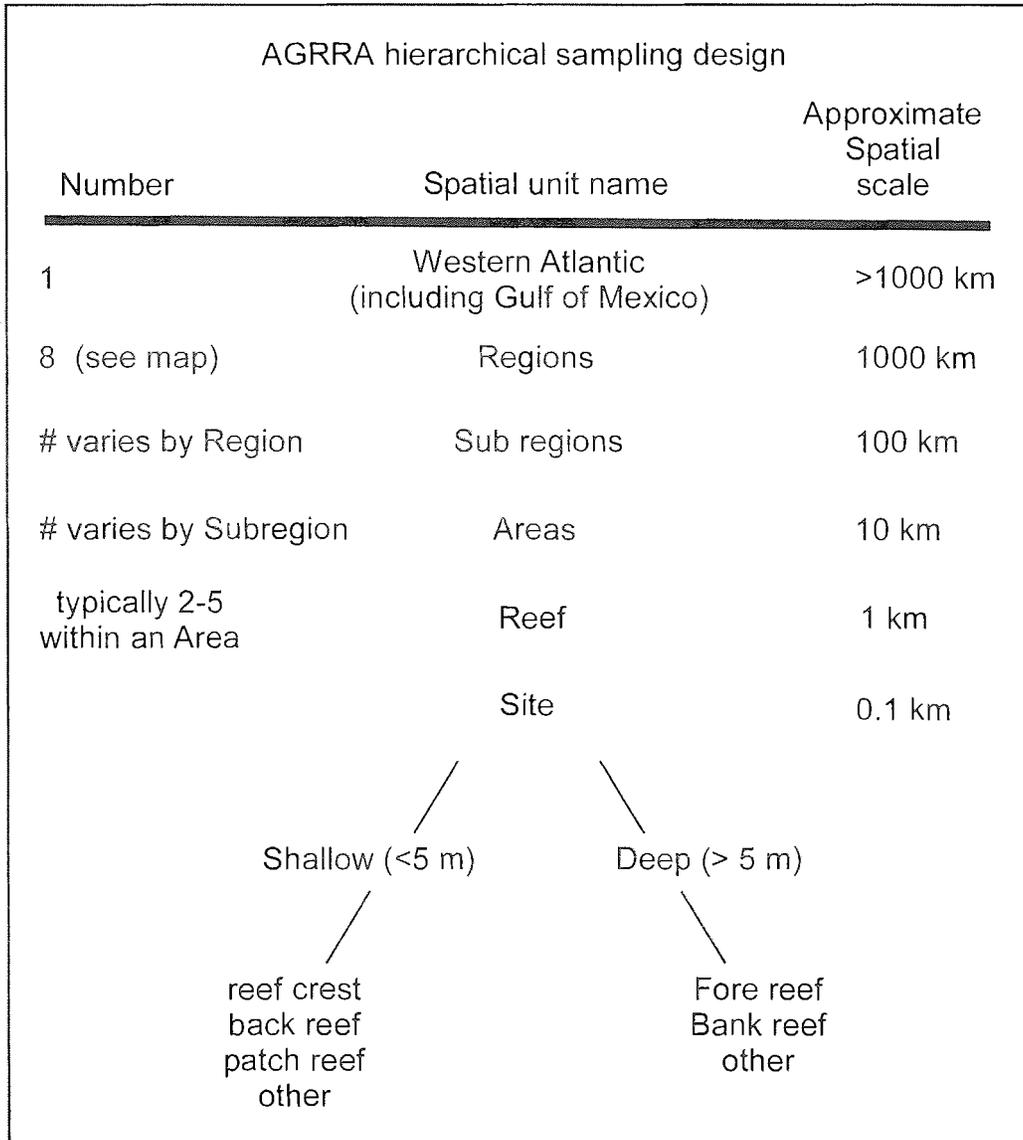
Figure 2. Hierarchical sampling scheme and associated spatial scales for AGRRA surveys. Sites are also classified hierarchically based on depth, geomorphology, relief, and additional modifiers. For the purpose of this synthesis, sites are only distinguished based on depth into shallow (≤5 m) and deep (>5 m).

algal and fish indicators. Often AGRRA surveys are the first to be conducted in an area and/or little or no suitable baseline data exist to determine the appropriate level of sampling that would be needed to characterize the area fully. Furthermore, each indicator will have a separate distribution and desired degree of precision. A power analysis was conducted for several of the AGRRA indicators to examine the tradeoff between sampling effort and precision at both the site and subregional spatial scales. To assess how many transects were needed to adequately estimate *site* means for each indicator, within-site variance as a function of sampling effort was examined at one site in each of four areas.

Data Analysis

The database used for this synthesis contained a total of 302 benthic sites (249 deep, 53 shallow), 2,337 benthic transects, 14,000 quadrats, 22,553 corals, 247 (206 deep, 41 shallow) fish sites, 2,488 fish transects, and 71,102 fishes. For this initial analysis, I divided the sites into either shallow ($\leq$5 m) or deep ($>$5 m) depth categories based on the mean depth of the benthic transects, whereas sites were categorized by depth ranges or by mean depth of the habitat in some of the individual assessments in this volume. In several cases (e.g., Curaçao and the Virgin Islands) the same geographic site was assessed at different times. I treated these sites as independent samples whereas in the individual assessment papers they are grouped together as a single site. Not all results described in the individual assessments were included in the synthesis either due to inconsistencies in the way the methodology was implemented or because of missing data for individual transects or entire sites. The cylindrical (volumetric) fish counts used in Belize and San Salvador, Bahamas (see both papers by Peckol et al., this volume) could not be directly compared to the belt transect data. The 1997 Andros, Bahamas survey followed an early version of the protocol and differed enough from later versions that only data collected during 1998 were used.

To equalize sampling effort, results in the synthesis have only incorporated a maximum of the first 10 transects/site in calculated averages for either fish or benthic parameters, despite larger sample numbers for some sites. Statistical analysis was performed using STATISTICA software, Version 6.0 (StatSoft, Inc., 2002). The percent live coral cover, percent partial-colony mortality (recent, old, total), standing dead (i.e., completely dead and still in original growth position, and calculated as a percentage of the total), mean colony size, prevalence of disease and bleaching, and relative algal abundance were calculated and summarized. Only data from corals that were $\geq$25cm in maximum diameter was included. I chose to remove standing dead colonies from old partial mortality averages; thus, averages in the synthesis should be lower than those in the individual papers for sites with significant amounts of standing dead coral. The macroalgal index, a proxy for macroalgal biomass, was calculated as % *relative* macroalgal abundance (as approximated in Versions 1 and 2 of the AGRRA protocol) x macroalgal canopy height. Of the 75 species of fishes in the AGRRA belt transect list (see Appendix One, this volume), a total of 18 species of herbivores, both territorial and non-territorial, were analyzed (all acanthurids, scarids $\geq$5 cm, *Microspathodon chrysurus* (yellowtail damselfish) and black durgon (*Melichthys niger*). Free-swimming predators

and sedentary predators were classified as carnivores (all lutjanids, all serranids, and *Sphyraena barracuda*) for a total of 24 species. Fish densities (#/100 m^2) were calculated for each area for all 75 species and included all sightings except for scarids and haemulids where only the ≥ 5 cm sightings were used. Size information was used to calculate biomass for each fish species using the standardized conversion equations shown in Appendix Two (this volume).

Regional norms for different indicators were calculated by averaging reported survey values without weighting by the spatial extent of reefs or number of sites conducted within a given survey area. Several parameters were analyzed by students t-test and by 1-way and 2-way Analysis of Variance (ANOVA). The Plymouth Marine Laboratory's PRIMER software, Version 5 (Clarke and Gorley, 2001), was used to examine similarity among different indicators with either Bray Curtis similarity or two-dimensional multidimensional scaling (MDS) ordination.

To examine relationships between fish data and benthic habitat variables, regression analysis was used to analyze (1) mean herbivore density and mean macroalgal index for 17 assessments and (2) algal canopy height and density of the ≥ 25 cm corals. To examine the relationship of coral condition with respect to anthropogenic threats, survey areas were classified into one of three threat categories (high, medium, low) based on Bryant et al.'s (1998) global threat analysis (Table 1). The modeled threat layer of "overexploitation of marine resources," which is based primarily on proximity of a reef to coastal settlements, was used to examine relationships of fish density and biomass to presumed fishing pressure.

RESULTS

Results in the Synthesis differ somewhat from those reported in the individual papers in this volume due to differences in how sites were defined or stratified, in the selection criteria for calculating site means and, for stony corals, in the definition of old partial mortality (see Methods).

Sampling Effort

The characteristics of the sampling effort for the 20 assessments in this volume are summarized in Table 1. Each assessment is identified by its unique identification number (ID#) in both figures and tables. At least some deep (>5 m) habitats were assessed by all teams but shallow (≤ 5 m) reefs were examined extensively only in Andros (ID#2) and the Abrolhos, Brazil (ID#20). For this reason, most of the spatial comparisons in this synthesis are restricted to deep (>5 m) habitats. A detailed summary of the mean sampling effort for these deep sites in each assessment is given in Table 2.

Sampling size (as number of transects) versus standard error for live coral cover and coral density from four different areas of the western Atlantic [Virgin Islands (ID#13), Veracruz, Mexico (ID#6), Andros (ID#2), windward Netherlands Antilles (ID#14)] are shown in Figure 3. For both parameters, the error was reduced most substantially within the first six transects after which only small improvements were
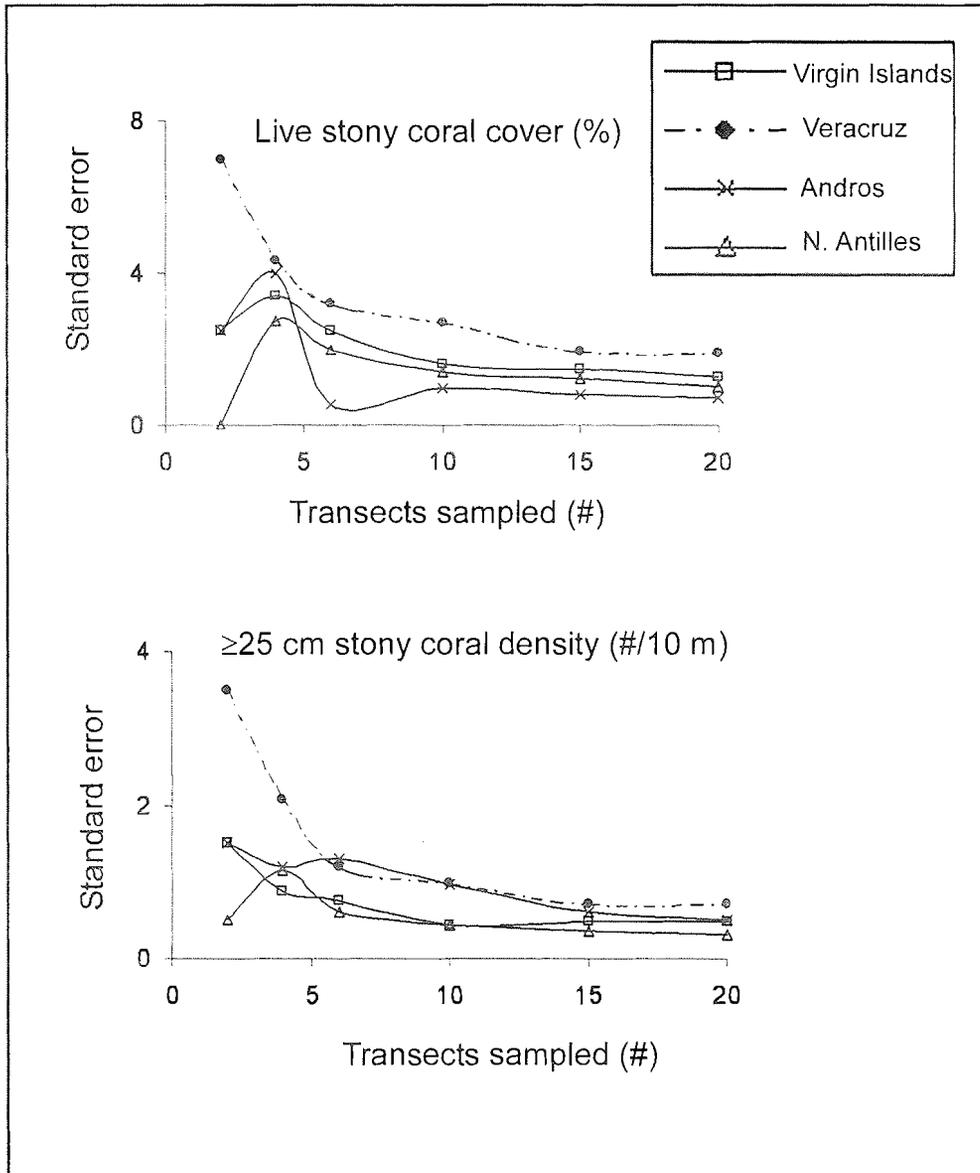
Figure 3. Sampling size (number of transects) versus standard error for four sites in different areas of the western Atlantic for live coral cover and coral density. For all parameters, the error is reduced most significantly within the first six transects, after which only small improvements are observed with increasing number of transects.

observed with increasing sample size. Figure 4 provides a summary of sampling size for several AGRRA benthic indicators versus standard error. When percent partial-colony mortality (recent and old) and coral diameter (as number of corals) were compared for four sites [Cayman (ID#12), Curaçao (ID#18), Belize (ID#10), and Andros (ID#2)], error was reduced most dramatically within the first 50 corals sampled. Algal relative abundance (macroalgae, crustose corallines and turfs) and macroalgal canopy height data were compared (as number of quadrats) for Veracruz, Abrolhos (ID# 20), Cayman, and Andros, with the standard error most reduced within the first 40 quadrats sampled.

In nearly all of the fish belt-transect surveys, an average of 600 m^2 was assessed at each site with the exceptions being Akuma/Xcalak (ID#8) and Curaçao (ID#18), each with less than 200 m^2. In both Mária la Gorda, Cuba (ID#11) and the Yucatan (ID#7), 50 x 2 m transects (a total of six per site) were used in accordance with an early version of the fish protocol, whereas 10 x 2 m transects (30/site) were employed in the small reefs of the Abrolhos (ID#20). The 14 remaining teams each performed 30 x 2 m transects (10/site).

Stony Corals

Composition and abundance. The 22,553 colonies sampled in the 20 surveys combined included 37 scleractinian and two hydrozoan species. The majority of these stony corals were assessed in deep (n=18,913 at >5 m) rather than shallow (n=3,640 at ≤5 m) sites. Of these, 1,122 colonies (5%) were surveyed in the Abrollos (ID#20), where the endemic Brazilian scleractinain, *Mussismilia braziliensis*, was the dominant coral. For the remaining corals in the wider Caribbean excepting Veracruz (ID#6) where they were not assessed, standing dead colonies constituted 13.5% of the colonies at shallow sites and 2.5% at deep sites.

The relative species composition, expressed as a percent of the total of corals (excluding all standing dead colonies and all the Brazilian corals) is shown in Figure 5A,B. Numerically the most abundant species in shallow reefs were *Acropora palmata* (27% of total), *Montastraea annularis* (19% of total), and *Porites* spp. (7% *P. astreoides*, 6% *P. porites* of total) (Fig. 5A). Live *Acropora palmata* was the dominant coral at 60% of all shallow reef-crest sites. Taxa that are usually dominant on shallow Caribbean reefs, such as *Agaricia tenuifolia* and *Millepora* spp. were less abundant in the AGRRA regional dataset. For shallow reefs, there was especially high between-survey species variability caused, in part, by differences in the type of shallow reef assessed (reef crest, back reef, patch reef-see individual papers in this volume and Table 1). The high number of *Acropora palmata* reflects the relatively large number (Table 1) of reef crests sites assessed off Andros (ID#2) where this coral was common. Live *Acropora palmata* was the dominant coral (>1/3 of coral population) at 17 of 23 shallow reef-crest sites summarized in this volume.

Deep reefs displayed less species variability among sites since most assessments were conducted in fore reefs [exceptions being bank reefs surveyed in the Flower Garden Banks, Gulf of Mexico (ID#5) and Mouchoir Bank in the windward Netherlands Antilles (ID#14); see Table 1 and papers in this volume]. *Montastraea* spp. dominated most deep
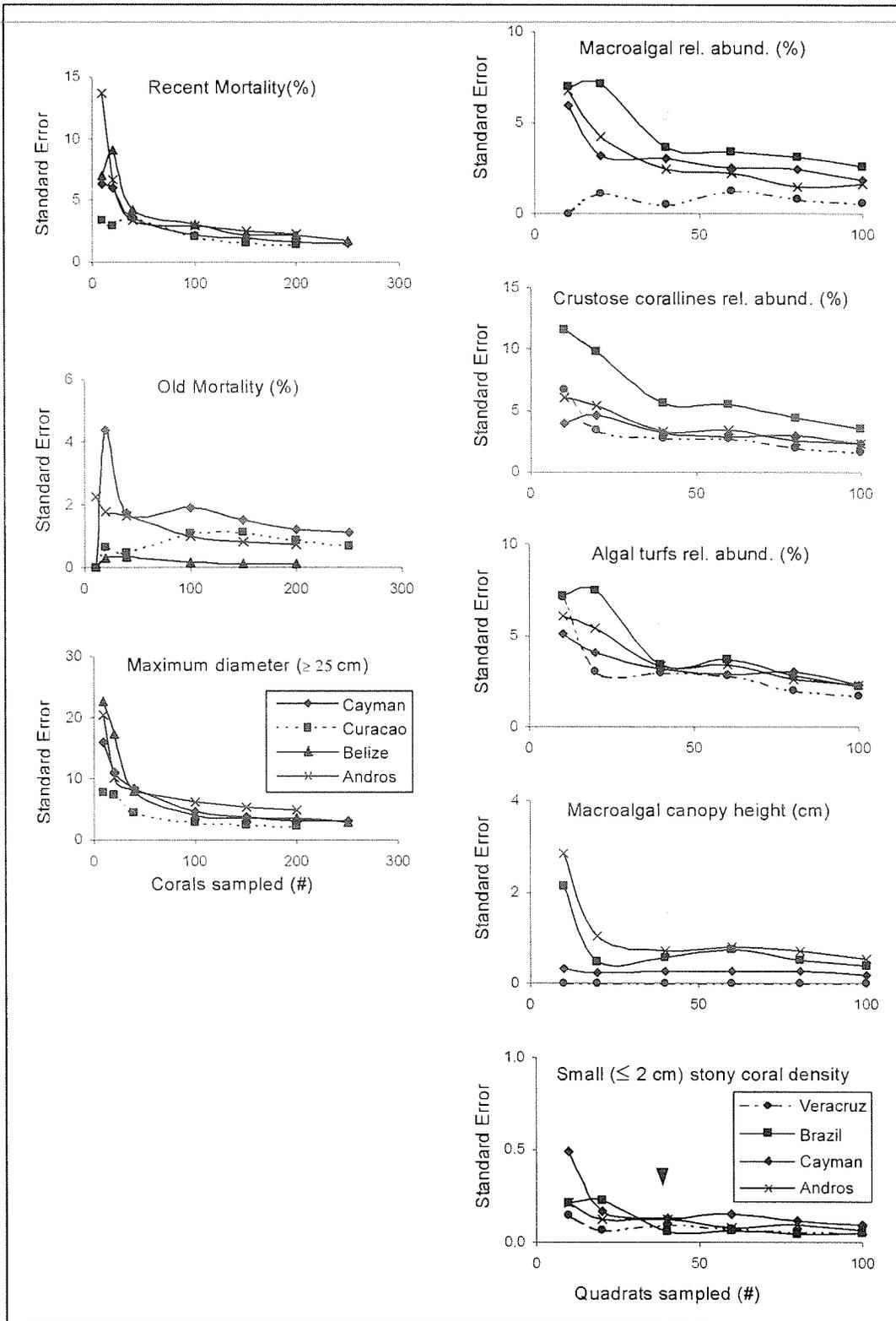
Figure 4. Sampling size (number of corals and quadrats) for several AGRRA benthic indicators versus standard error for four sites in different areas of the western Atlantic. For corals, error is reduced most dramatically within the first 50 corals sampled. For quadrats, the error is reduced most significantly within the first 40 quadrats sampled.
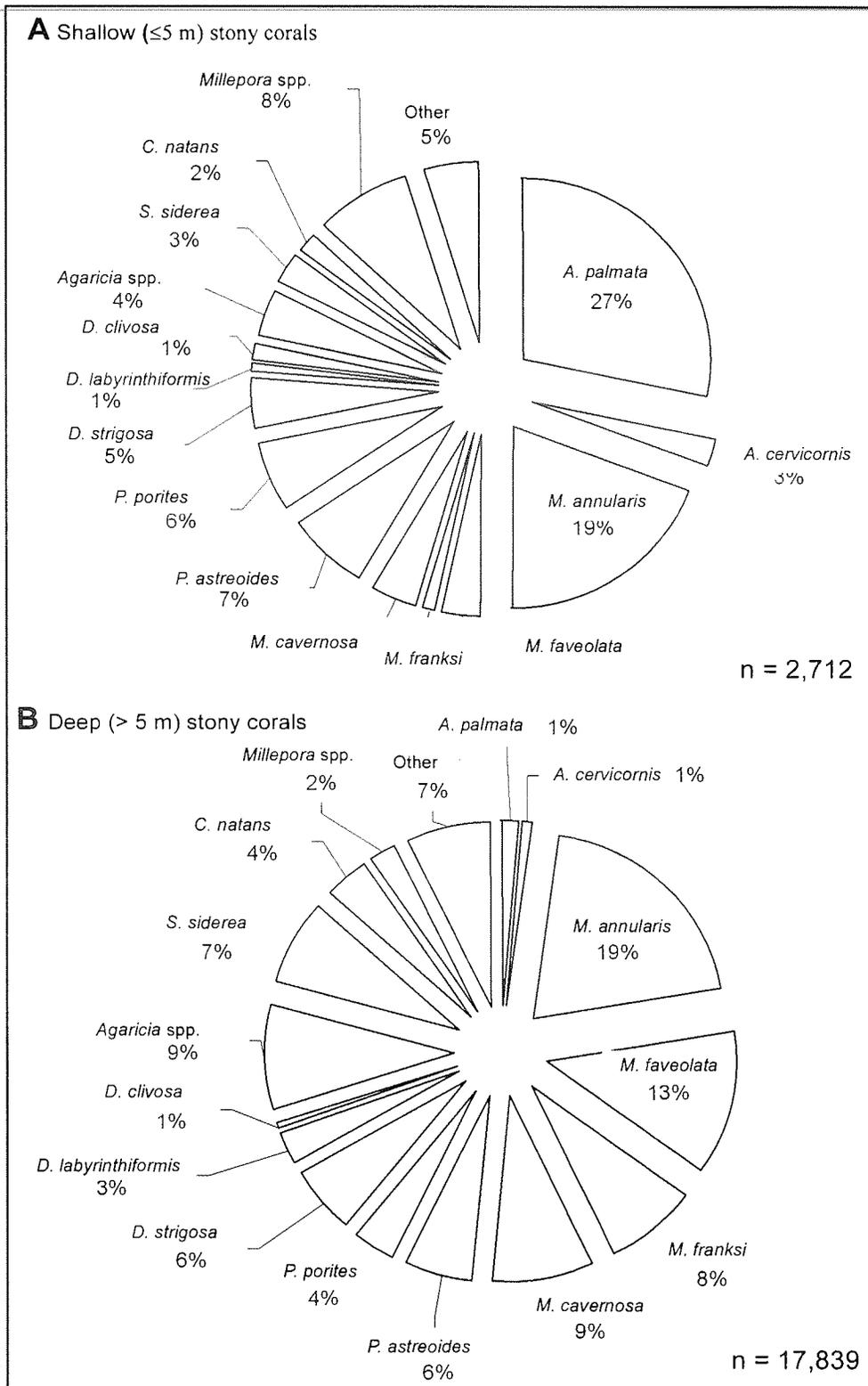
Figure 5. Composition of all stony corals (25 cm) from all assessments except Brazil (ID #20) combined for **(A)** shallow sites (5 m), and **(B)** deep sites (>5m). Includes only corals sampled within a maximum of 10 transects per site.

reef assemblages as follows: *M. annularis* (19% of total), *M. faveolata* (13% of total), *M. cavernosa* (9% of total) and *M. franksi* (8% of total). Other commonly observed taxa on fore reefs included *Agaricia* spp. (9% of total), *Siderastrea siderea* (7% of total), *Diploria strigosa* (6% of total), *Porites* spp. (*P. astreoides* 6%, *P. porites* 4% of total), and *Colpophyllia natans* (4% of total). *Acropora cervicornis*, a once-dominant fore-reef species, was rare. In the multidimensional scaling analysis based on mean species density in each assessment, outliers included Abaco (ID#1) and San Salvador (ID#3) in the Bahamas, the Flower Gardens (ID#5) andVeracruz, (ID#6) in the Gulf of Mexico, Costa Rica (ID#19), and the Abrolhos (ID#20). Cluster analysis revealed two clusters of high similarity (70% Bray Curtis similarity), shown in gray on the MDS ordination in Figure 6A. Yucatan (ID#7) and Akumal/Xcalak (ID#8; also in the Yucatan) were in the first cluster; the second cluster consisted of Andros (ID#2), Turks and Caicos (ID#4), Mária la Gorda (ID#11), the Cayman Islands (ID#12) and the Virgin Islands (ID#13).

Small ($\leq$2 cm) coral density averaged 4/m^2 for the region with shallow reefs having fewer of these "recruits" (3.3/m^2) than deep reefs (4.4/m^2) (Tables 3A, 3B). By far the highest reported densities (9-15/m^2) for both shallow and deep reefs were in the Abrolhos (ID#20). On deep reefs, low densities (<2/m^2) were observed in the Flower Gardens (ID#5), Veracruz (ID#6), Akumal/Xcalak, (ID#8), and Mária la Gorda (ID#11) (Table 3B). Their species richness was also higher for deep ($\sum$=35 coral species) than for shallow ($\sum$=15 species) reefs, although this was partly a function of survey effort. Species composition of the recruits did not reflect the large ($\geq$25 cm) framework-builders present for the region as a whole. Brooders such as *Porites* spp. and *Agaricia* spp. dominated the assemblages with *Porites astreoides* being the most abundant species in both shallow and deep reefs. Broadcast spawners were far less common and the *Montastraea annularis* species complex only comprised ~2% of small corals observed overall. *Acropora palmata* (0.8% on shallow reefs) and *A. cervicornis* (0.2% on deep reefs) were both rare. An exception was *Siderastrea siderea*, for which the overall percentage of small corals was similar to, or greater than, adult abundance (3% versus 3% in shallow and 12% versus 7% in deep for $\leq$2 cm and $\geq$25 cm colonies, respectively).

Live cover and size. Live coral cover averaged 18% for shallow reefs with the highest (~38%) value reported for the reef crest sites on Andros (ID#2) and the lowest (~3%) for a patch reef in Costa Rica (ID#19) (Table 3A). On deep reefs, live coral cover ranged from 3% to 58%, averaging 26% for the region as a whole (Table 3B, Fig. 7A). The highest observed coral cover on deep reefs was in the Flower Gardens (ID#5). Four other assessments that are located in the southern-southeastern Caribbean [Los Roques (ID#16), Bonaire (ID#17), Curaçao (ID#18)) and St. Vincent (ID#15)] also had coral covers that exceeded the regional average (Table 3B). Apart from Curaçao (ID#18), Abrolhos (ID#20), and Costa Rica (ID #19), the density of large ($\geq$25 cm) colonies generally correlated with live coral cover for the other 15 survey areas (r^2= 0.8, p<0.001, n = 15, deep depths only). Shallow reefs had overall lower mean densities (~7.9/10m) than deep reefs (~9.3/10m) (Fig. 7B), although a significant correlation (r=0.7, p<0.01, n=13) existed between the shallow and deep coral densities for areas in which both depths were assessed. The density of large ($\geq$one meter maximum diameter) colonies of

A Stony coral species

B AGRRA fish species
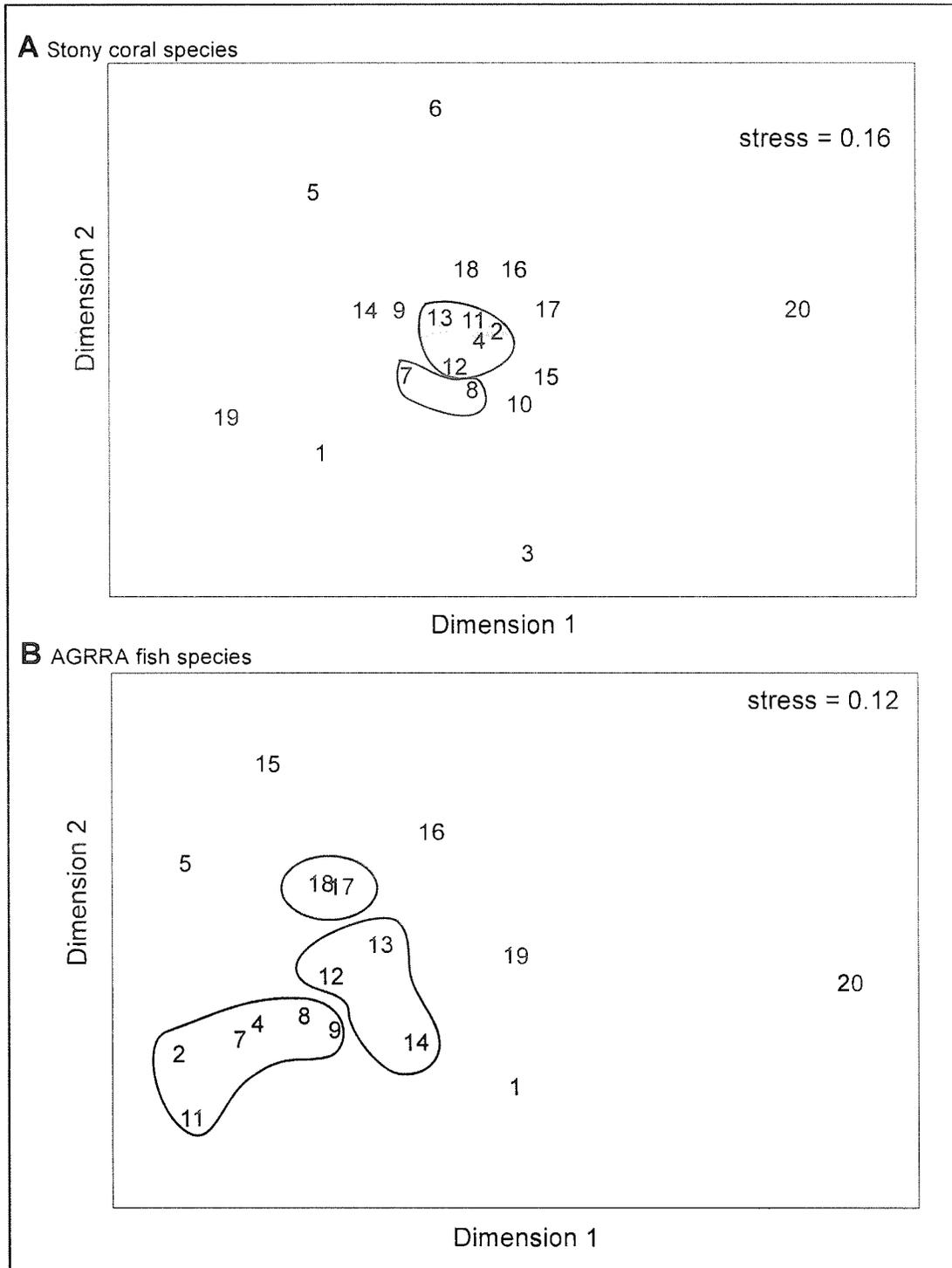
Figure 6. (A) MDS ordination of 20 survey areas (deep sites only) based mean species density for 20 most common large stony corals (=25 cm diameter). Groupings indicate Bray-Curtis similarity of 60% or more for all 20 surveys. **(B)** MDS ordination of 17 survey areas where fish were surveyed using belt transects (deep sites only). The clustering is based on mean species density for 40 most common species (excluding haemulids). See Table 1 for ID codes and text for discussion.
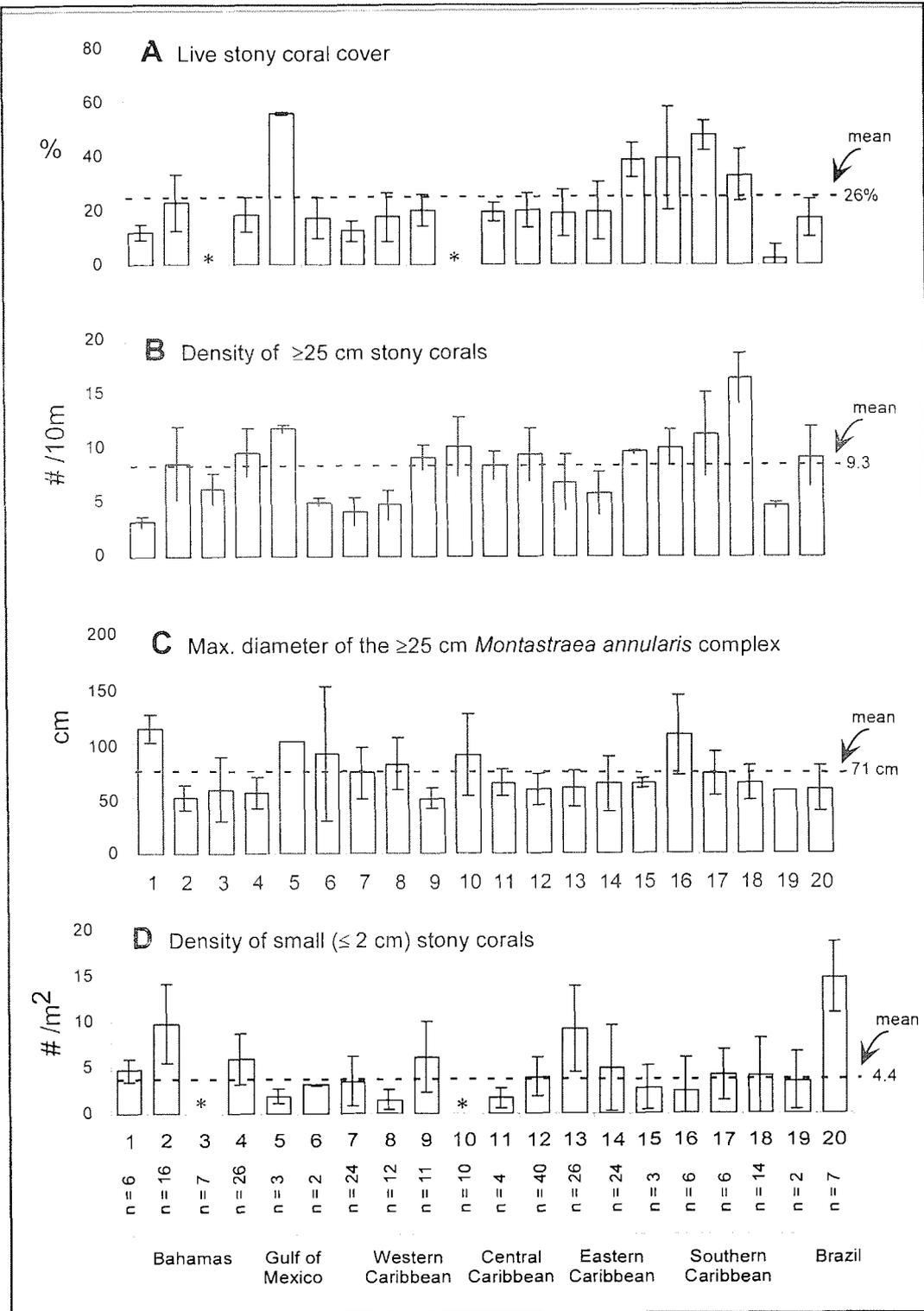
Figure 7. Comparison between means and standard deviation of deep sites for all 20 AGRRA assessments. **(A)** live coral cover; **(B)** coral density (number of ≥ 25 cm diameter corals/10m); **(C)** colony diameter of the *Montastraea annularis* complex, and **(D)** small (≤2 cm) coral density. The stars indicate a parameter that was not measured and the dashed line indicates the mean for all surveys. See Table 1 for ID codes.

Montastraea spp. at deep sites ranged from 0.01 to 3.1/10 m. Areas showing greatest densities were Flower Gardens, Bonaire, Los Roques, Curaçao, while areas with lowest densities were Brazil, Veracruz, Abaco, and Costa Rica.

Mean size (based on maximum colony diameter) for 17 of the 18 most common species of corals was generally larger in shallow sites (n=53) than in deep sites (n=249). The mean diameter for all 7,398 colonies of the *Montastraea annularis* complex of species (*M. annularis, M. faveolata* and *M. franksi)* averaged 71 cm for deep reefs in the region (Fig. 7C) with the largest colonies having been observed in Abaco (ID#1), Los Roques (ID#16) and the Flower Gardens (ID#5).

Deep sites with higher than average live coral cover and abundance generally had larger than average colony diameters for the *Montastraea annularis* species complex (especially Los Roques and the Flower Gardens). Exceptions included Abaco and Akumal/Xcalak (ID#8) which had above average sizes for this species complex and lower than average coral cover (about 13% and 20%, respectively), and Bonaire (ID#17) where coral cover was the second-highest recorded (~46%) but maximum colony diameter for the *M. annularis* complex was only "average" (Fig. 7A,C).

Size frequency distributions for five of the numerically-most-common taxa, *Montastraea annularis, M. faveolata, M. cavernosa, Siderastrea siderea,* and *Diploria strigosa* (all broadcast spawners; two being included in the above analysis), showed that most colonies were in the 30-40 cm size class (Fig. 8). *Acropora palmata* (another broadcaster) was most frequently observed in the 100-120 cm-size class. Brooding species (e.g., *Agaricia* spp. and *Porites* spp.) were predominantly distributed in smaller size classes. Overall, coral sizes were fairly similar across the region, with greatest variability evident on smaller spatial scales, particularly within sites. Areas thought to have more marginal conditions for coral growth showed consistently larger coral sizes of certain species as follows: Veracruz *(S. siderea, M. annularis)*; Abaco *(M. annularis, Colpophyllia natans)*; and Costa Rica *(D. strigosa)*.

Mortality. Recent partial mortality for the ≥25 cm colonies (expressed as the mean proportion (%) of the colony' surface area as seen from above) ranged from 0.1 to 27% across the 20 survey locations with a regional average of 4% for both shallow and deep reef types. High levels of recent mortality (~>15%) were observed on deep reefs in Andros (ID#2) and Yucatan (ID#7) (Fig. 9A) while the highest levels on shallow reefs occurred in Akumal/Xcalak (ID#8). Low recent mortalities (~<1%) were observed in Veracruz (ID#6), Bonaire (ID#17), and the Abrolhos (ID#20) for deep reefs (Fig. 9A) and in Veracruz, San Salvador (ID#3), and Cayman (ID#12) for shallow reefs. Recent mortality levels were not correlated between shallow and adjacent deep reefs within the same survey (Tables 3A, 3B).

Old partial mortality (excluding the standing dead corals) averaged 22% for deep reefs and 27% for shallow reefs (Tables 3A. 3B). Deep reefs in the Flower Gardens (ID #5) and Veracruz (ID#6) had the lowest reported old mortality (~<10%) (Fig. 9B) while shallow reefs in the TCI (ID#4), Belize (ID 10), and the Virgin islands (ID#13) had the highest old mortalities (~>40%). Standing dead corals (expressed as a percentage of the total number of colonies assessed) were significanty more common (p<0.05, n=10 assessments) on shallow reefs (14%) than on deep reefs (4%) largely because of the
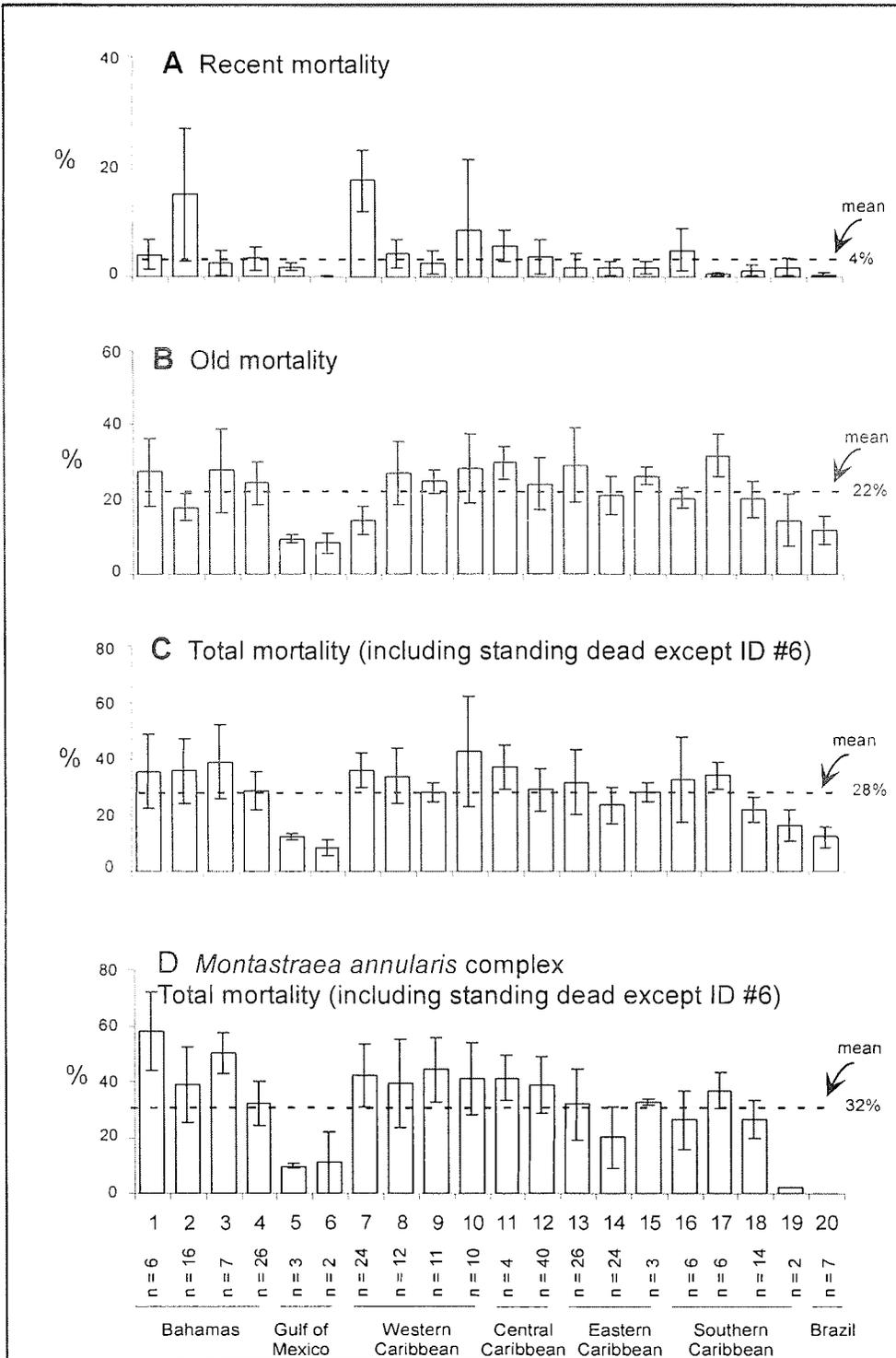
Figure 8. Comparison (as means and standard deviations) of the in deep (> 5 m) sites in all 20 AGRRA surveys: (**A**) recent partial colony mortality; (**B**) old partial colony mortality; (**C**) total partial colony mortality (including standing dead); (**D**) *Montastraea annularis* complex total partial colony mortality (including standing dead. The star indicates a parameter that was not measured and the dashed line indicates the mean for all surveys. See Table 1 for ID codes.
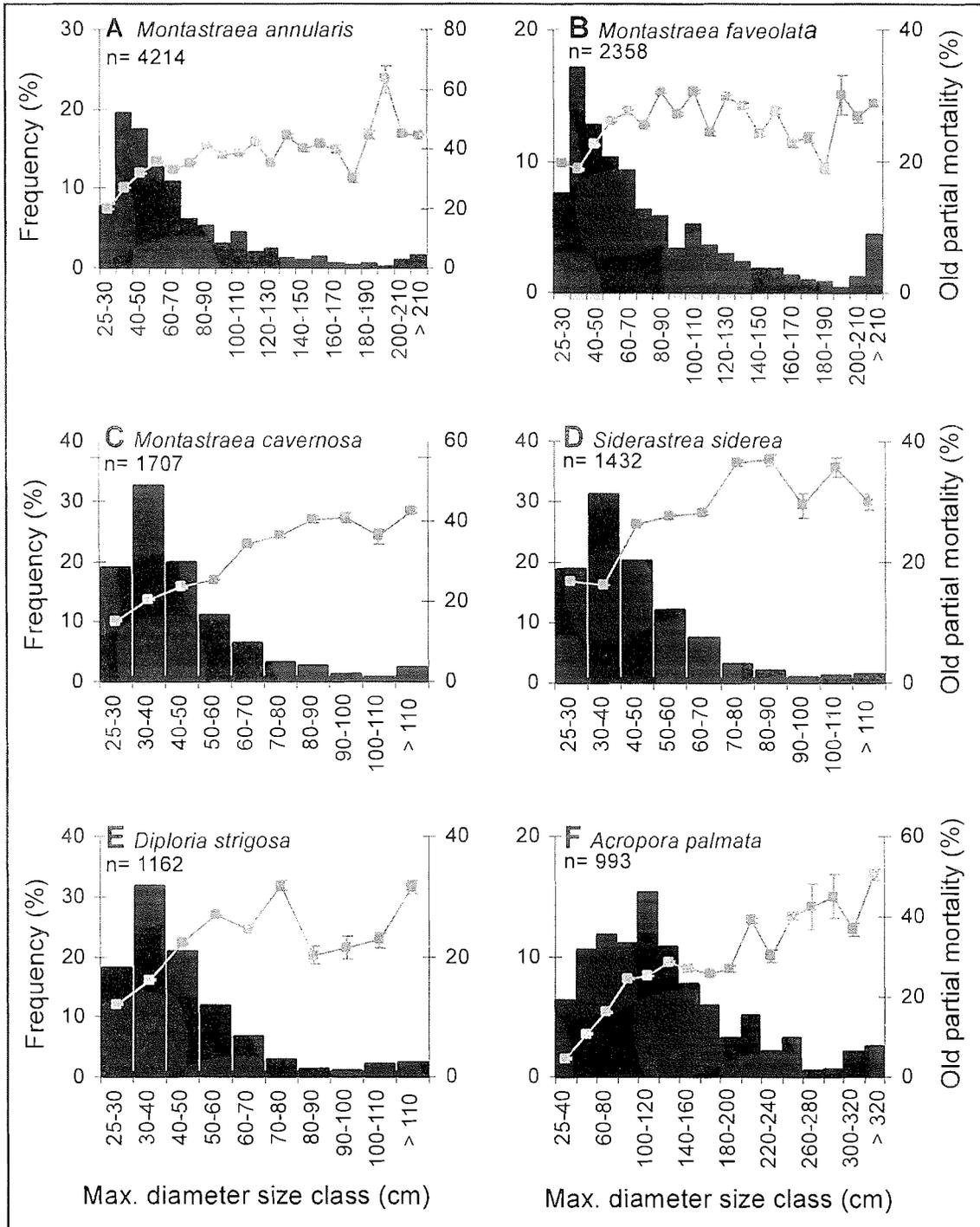
Figure 9. Size frequency distributions for six commonly observed coral species created by combining data (shallow and deep) from all assessments: **(A)** *Montastraea annularis;* **(B)** *Montastraea faveolata*; **(C)** *Montastraea cavernosa*; **(D)** *Siderastraea siderea*; (E) *Diploria strigosa*; and **(F)** *Acropora palmata*. Also plotted for each size class is partial old colony mortality, with the scale indicted on the second Y axis. Note the significant increase in partial mortality with increasing size, particularly within the smaller size classes, in each of these species.

abundance of dead colonies of *Acropora palmata*. Areas in which many of the shallow colonies were standing dead included Belize (ID#10) and San Salvador (ID#3) with 17% and 25% respectively, and Los Roques (ID#16) with 52% (Tables 3A, 3B). Total mortality (including colonies that were standing dead) averaged 28% of the colony surfaces in deep reefs (Fig. 9C), and 39% in the shallow reefs

Mortality levels (recent and old) varied dramatically among the individual coral taxa (Table 4). *Agaricia tenuifolia* had the highest recent partial mortality (>16% of colony surfaces affected) followed by *Montastraea franksi* (8%). *Agaricia tenuifolia* also had the highest old partial mortality (38%) followed by *M. annularis* (33%) (Table 4). Species with the largest number of standing dead colonies were *Acropora palmata* (32%), *Agaricia tenuifolia* (29%), and *Acropora cervicornis* (18%). On average, these three species had three times or more the amount of standing dead corals compared to the other species in which standing dead was recorded. Total mortality values in the *M. annularis* complex on the deep reefs (Fig. 9D) were greatest in Abaco (ID#1) and San Salvador (ID#3) and lowest in Costa Rica (ID#19).

For many of the taxa, smaller corals (~30 cm diameter) showed either no mortality or 100% mortality (i.e., they were completely dead), whereas larger corals (>60 cm diameter) most commonly displayed partial-colony mortality. Recent mortality showed no significant correlation with colony diameter; however, old mortality levels generally increased with increasing colony size through the smaller size classes. Thus increases in old mortality were most evident in the lower size classes up to the mode of the population, above which fluctuations were more apparent (Figure 8).

Disease, bleaching, overgrowth, and predation. Approximately 6% of the surveyed corals from all sites combined were infected with an identifiable disease. Signs of disease were observed in at least 20 coral species and, as illustrated in Table 4, many diseases were not species-specific but affected a variety of species. *Stephanocoenia intersepta* and *Acropora cervicornis* had the highest prevalence (21 and 13%, respectively) while the spatially dominant *M. annularis* species complex also had high occurrence of disease (~10%). The most commonly observed disease was white plague, followed by black-band, yellow-blotch (yellow-band), white-band, dark spots, and white pox (patchy necrosis) (Table 4). Black-band was most commonly observed in *M. franksi*, white plague in *M. faveolata* and *M. annularis*, white-band in *Acropora cervicornis* and *A. palmata*, and yellow-blotch in *M. annularis*. In some cases, the disease type was not identified or specified for several species with apparently high prevalences of disease (e.g., *A. cervicornis*, *S. intersepta*, *A. palmata*). Areas with the highest prevalence of disease included Andros (ID#2) and Akumal/Xcalak (ID#7), where 18% and 14%, respectively, of all deep (>5m) colonies were infected (Table 3B). These areas were assessed during August, 1998 and March, 1999. Prevalences of yellow-blotch were relatively more common in the southern Caribbean (e.g., in Curaçao, Bonaire, and Los Roques).

An average of 6% of the surveyed corals from all sites combined showed signs of bleaching, most often occurring as "partly bleached" or "pale". Four areas reported greater than 20% of colonies bleached (ID#s10, 13, 14 and 17), while only four areas had less than 2% bleached (ID#s 4, 12, 18 and 20). Differences in the amount of bleaching

and disease varied among taxa (Table 4). *Montastraea annularis* species complex (13-15% of colonies) and *Millepora complanata* (14%) exhibited the highest prevalence of bleaching. Bleaching was also often observed in *Diploria* spp., *Siderastrea siderea*, and *Acropora palmata*.

Macroalgal overgrowth was reported on an average of 4% of the colonies assessed for the entire region. Unusually high occurrences (>30% of all colonies) of macroalgal overgrowth were recorded in Lighthouse Atoll, Belize (ID#9) and Costa Rica (ID#19). However in 9 of the 17 deep surveys for which overgrowth was noted, fewer than 2% of the corals were affected. The percentage of colonies with evidence of tissue mortality due to fish bites was highly variable, being relatively high (≥10%) in Costa Rica, Lighthouse Atoll and the Virgin Islands (ID#13). Recent mortality caused by predation by snails (primarily *Coralliophila abbreviata*) or worms (*Hermodice carunculata*) was highest in shallow sites (e.g., Akumal/Xcalak (ID#8), Virgin Islands and Los Roques (ID#16)). Occurrences of damselfish algal gardens (as the percentage of affected colonies) were also highly variable, in part because of inconsistent reporting, but were recorded on an overall average of 6% of the corals. The highest occurrences (>40%) were at Lighthouse Atoll and Mária La Gorda (ID #11), while Costa Rica and the Turks and Caicos (ID #4) were the only assessments for which no damselfish algal gardens were reported (Tables 3A, 3B).

Algae and *Diadema*

Algal communities on deep reefs were composed, on average, of turf algae (48% relative abundance) with crustose coralline algae (29%) and macroalgae algae (23%) being relatively less abundant. Deep reefs with highest values for turf algae (>70%) included the Flower Gardens (ID#5) and the Abrolhos (ID#20) whereas those with the lowest (<21%) included Andros (ID#2), Cayman (ID#12) and St. Vincent (ID#15). Elevated (>35%) macroalgal relative abundances were found at three areas in the Bahamas (ID#1, 2, 3) and several areas in the central and eastern Caribbean (ID#s11-13, 15) (Fig. 10A). Macroalgal relative abundance was low (~5 %) in the Flower Gardens, windward Netherlands Antilles (ID#14) and Abrolhos and rare (<1 %) in Los Roques (ID#16). Shallow reefs (≤ 5 m) had similar algal compositions (turfs>crustoses> macroalgae), although between-site variability was considerably higher.

Macroalgal canopy heights were similar in deep (2.2 cm) and shallow (2.3 cm) reefs when averaged for the region. On deep reefs (Fig. 10B), the highest (>4 cm) canopy heights were recorded in Costa Rica (ID#19) and the Yucatan (ID#7), and the lowest (<1 cm) were in the Flower Gardens (ID#5) and Bonaire (ID#17). When macroalgal canopy height and relative abundance are considered together as a macroalgal index, there was a range of nearly 20-fold (Fig. 10C) between the lowest indices (<12) in Los Roques (ID#16) and the highest index (>200) in Andros (ID#2).

The range of values for the relative abundance of crustose coralline algae was moderate (~30%) for deep sites and in no cases exceeded 50% (Fig 10D). The macroalgal:crustose coralline ratios (not shown) averaged 1.1 (range 0.1 – 3.5) with Bonaire, Curaçao (ID#18), Los Roques, TCI (ID# 4), and the windward Netherlands Antilles (ID#14) all having relatively low (<0.6) ratios. A weak, non-significant
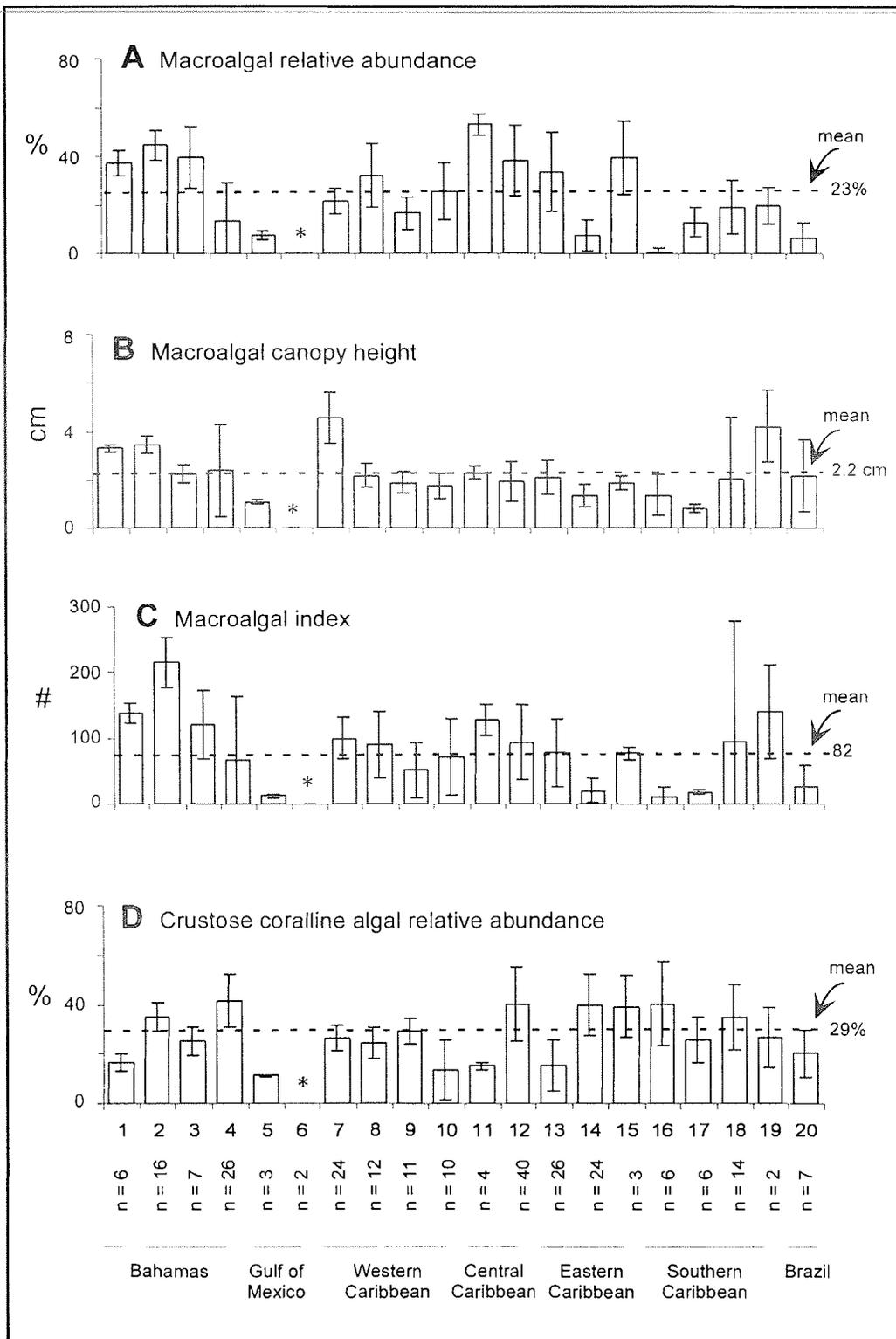
**Figure 10.** Comparison (as means and standard deviations) of algae in deep (> 5 m) sites in the 20 AGRRA areas: **(A)** relative abundance of macroalgae; **(B)** macroalgal canopy height; **(C)** macroalgal index, and **(D)** relative abundance of crustose coralline algae. The star indicates a parameter that was not measured and the dashed line indicates the mean for all surveys. See Table 1 for ID codes.

relationship was found between the percent live stony coral cover and the relative abundance of macroalgae (p=0.17, r^2=0.12). Statistically significant relationships were found between canopy height and both live coral cover (p<0.01, r^2=0.37) and large coral density (p<0.01, r^2=0.38) (Fig. 11). Canopy heights were also positively related to the density of *Siderastrea siderea* (p= 0.015, r^2=0.33) and negatively related to the density of *Colpophyllia natans* (p=0.03, r^2=0.29).

Densities of *Diadema antillarum*, both within and among surveys, were highly variable, with no individuals reported in about half (8/17) of the areas for which data are available (Table 1). Mean urchin density for all surveys reported in this volume was 2.9/100 m^2 with the highest densities (23/100 m^2) occurring in Costa Rica.

Fishes

A total of 71,102 fishes were sighted in belt transects consisting of 49,888 individuals in the deep sites and 21,214 in the shallow sites (Fig.12). Of these, a total of 10,073 (14%) were surveyed in Brazil (See Kikuchi et al., this volume). For the non-Brazil sites, the most abundant of the AGRRA families were acanthurids and scarids, followed by haemulids, lutjanids, pomacanthids, balistids, and serranids. The results of the multidimensional scaling (MDS) ordination based on mean AGRRA species abundance recorded at deep sites for the 17 belt-transect assessments is shown in Figure 6B. Areas with the least similarity in fish community structure [Abrolhos (ID#20), followed by Costa Rica (ID#19), Abaco (ID#1), Los Roques (ID#16), St. Vincent (ID#15), and the Flower Gardens (ID#5)] are mostly characterized by unusual environmental conditions. Cluster analysis revealed three groups, each with strong similarity (Bray-Curtis similarity of greater than 60%, areas shaded gray in Figure 6B), corresponding to areas in the southern Caribbean, parts of the Bahamas and the western and central Caribbean, and the central-eastern Caribbean regions, respectively.

Total AGRRA fish densities were nearly twice as high in shallow (85/100 m^2) as in deep (49/100 m^2) sites, mainly as a result of higher densities of haemulids and acanthurids in ≤5 m. For deep sites, comparisons among the 17 areas with comparable data records indicate that fish densities were highest in the Abrolhos (ID#20), followed by Los Roques (ID#16) and Curaçao (ID#18), while the lowest values were found off Andros (ID#2) (Fig. 13A). Herbivores dominated the deep fish assemblages (average of 35/100 m^2) at approximately six times the density of carnivores (average of 6/100 m^2) (Fig. 13B,C). Excluding data from the Abrolhos, total fish biomass (not shown) displayed a five-fold difference among surveys, ranging from 2,600 g/100 m^2 in Akumal/Xcalak (ID#8) to 12,640 g/100 m^2 in Los Roques. Using the Bryant et al (1998) *Reefs at Risk* overexploitation threat classification (see Table 1), total AGRRA fish biomass was 6,459 g/100 m^2 for the "high exploitation" reefs, 5,943 g/100 m^2 for reefs under "intermediate exploitation", and 6,846 g/100 m^2 for reefs experiencing "low exploitation". No significant difference in total fish biomass could be detected among the three different exploitation-threat categories using a 1-way ANOVA analysis.

Herbivores. Deep reefs in Abaco (ID#1), the Abrolhos (ID#20), and Los Roques (ID#16) all had higher than average densities of herbivorous fishes, whereas lower than
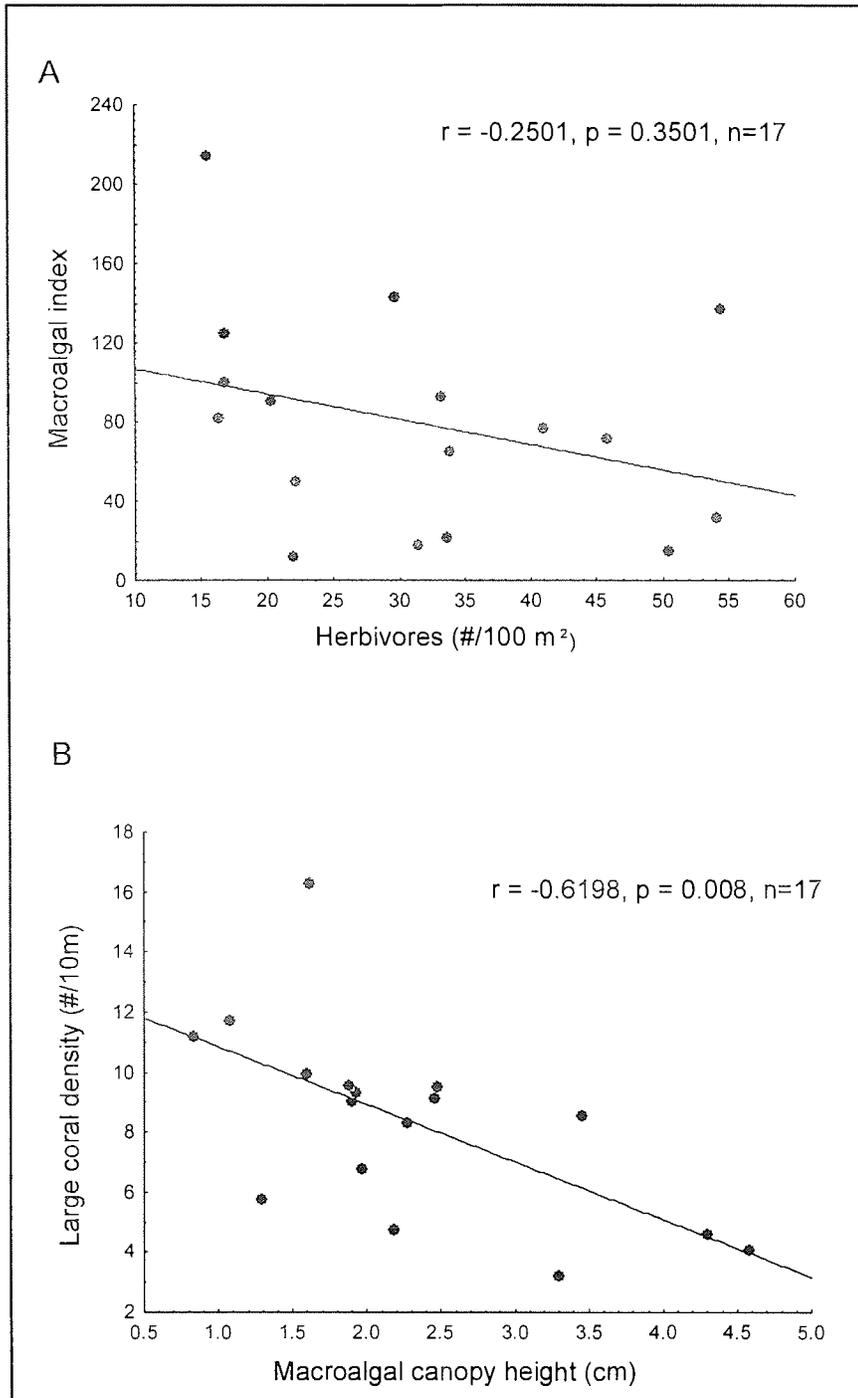
Figure 11. Regression plots of fish, coral, and algal indicators: **(A)** mean herbivore density (acanthurids, scarids ≥5 cm and *Microspathodon chrysurus)* and mean macroalgal index for 17 assessments; **(B)** algal canopy height and coral density (stony corals ≥25cm diameter/per transect).

A Shallow (≤5 m) AGRRA fishes

Serranidae
1%

Other
7%

Acanthuridae
29%

Scaridae
31%

Balistidae
0%

Chaetodontidae
1%

Pomacanthidae
0%

Lutjanidae
9%

Haemulidae
22%

n = 14,799

B Deep (> 5 m) AGRRA fishes

Other
7%

Serranidae
4%

Acanthuridae
27%

Scaridae
36%

Balistidae
3%

Chaetodontidae
4%

Haemulidae
10%

Pomacanthidae
2%

Lutjanidae
7%

n = 46,230
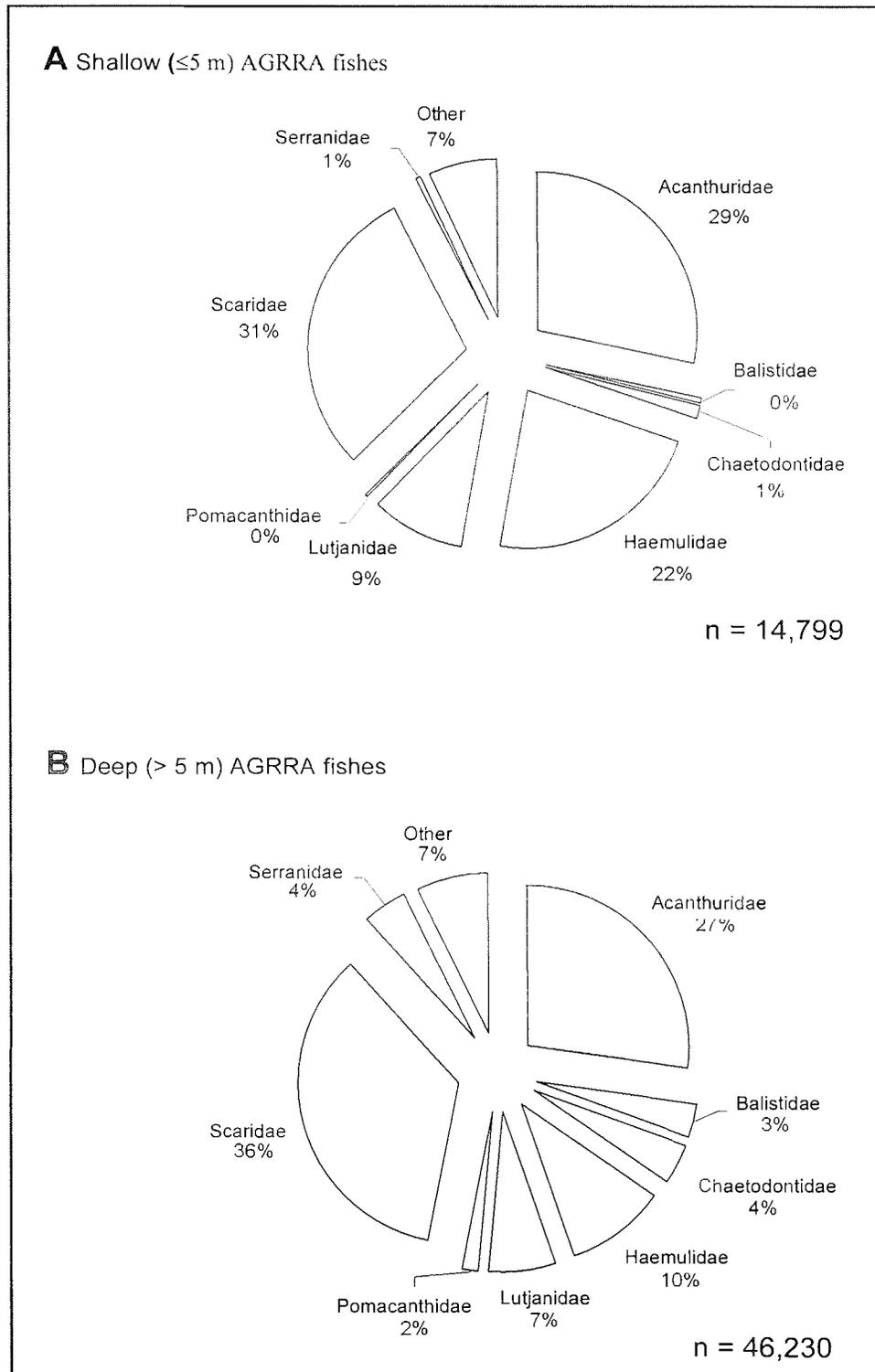
Figure 12. Composition of AGRRA fishes for major families for all assessments except Brazil (ID #20) combined for **(A)** shallow sites (≤5 m), and **(B)** deep sites (> 5m). Includes only fishes sampled within a maximum of 10 transects per site.
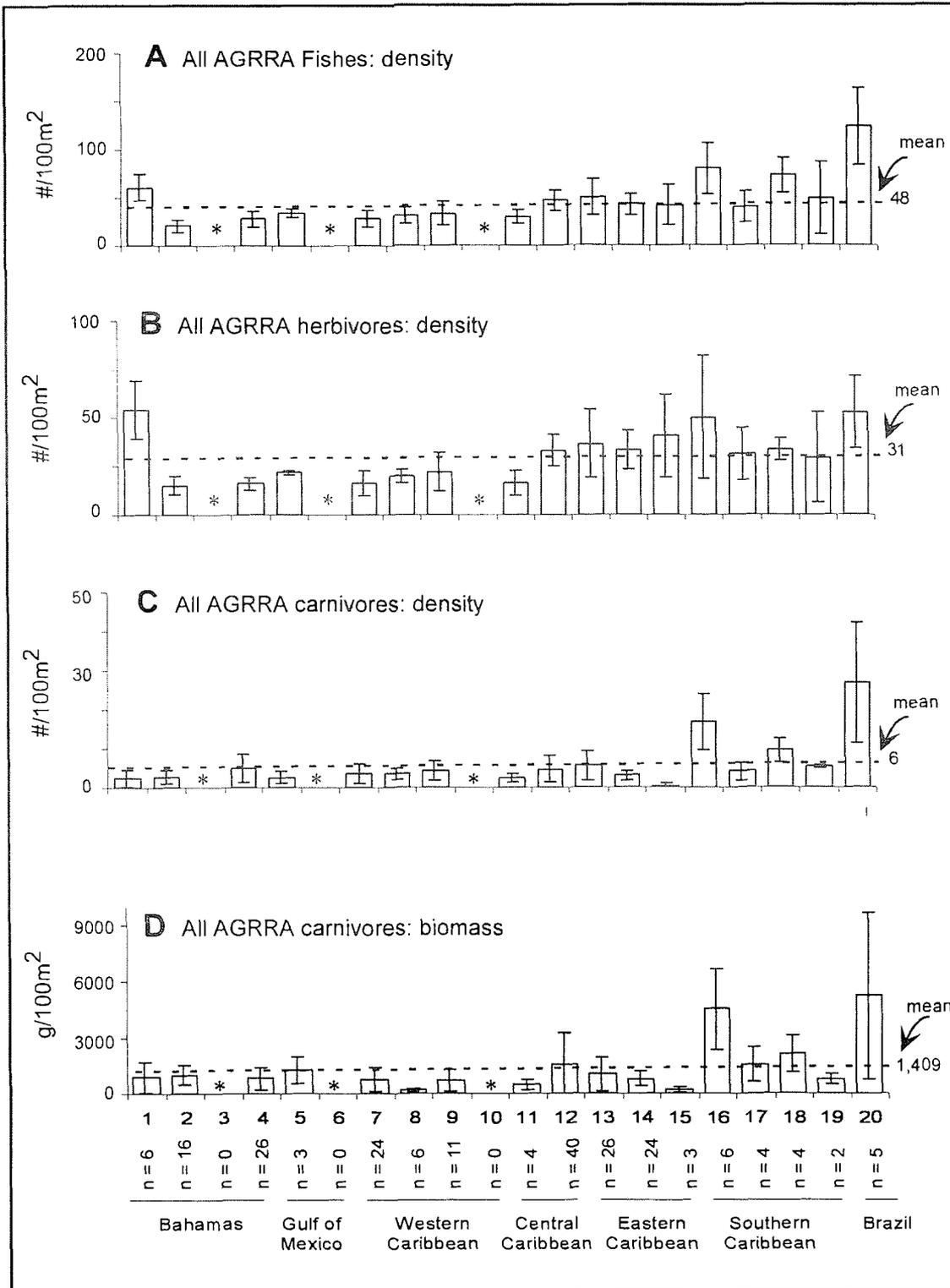
Figure 13. Comparison between means and standard deviation of deep sites (>5 m) for 17 AGRRA assessments: **(A)** all AGRRA fishes, **(B)** herbivorous fishes (acanthurids, scarids ≥5 cm and *Microspathodon chrysurus*); **(C)** carnivorous fishes (serranids, lutjanids, haemulids ≥5 cm). The star indicates a parameter that was not measured and the dashed line indicates the mean for all surveys.

average densities were found in Andros (ID#2), the Turks and Caicos (ID#4), Yucatan (ID#7), and Mária la Gorda (ID#11) (Fig. 13B). Herbivore biomass (not shown) ranged from a high of 7,484 g/100 m^2 in Costa Rica (ID#19) to a low of 1,508 g/100 m^2 in the Turks and Caicos). *Microspathodon chrysurus* (yellowtail damselfish) had a mean density of 2.2/100 m^2 with greatest numbers (>4/100 m^2) reported in Los Roques, Lighthouse Atoll (ID#9), and Costa Rica and the lowest (~0.1/100 m^2) in Andros. The density of acanthurids for all surveys combined averaged 11.8/100 m^2. Acanthurids were widespread throughout the region and all three species, *Acanthurus coeruleus* (blue tang), *A. chirurgus* (doctor fish) and *A. bahianus* (ocean surgeon), were present in all 17 areas surveyed. *A. coeruleus* was most abundant (averaging 5.7/100 m^2), with a high of 30.7/100 m^2 in Bonaire (ID#17), followed by *A. bahianus* (average = 5.3/100 m^2), which reached a high of 8.7/100 m^2 in the Virgin Islands. *Acanthurus chirurgus* was least abundant (average of 1.0/100 m^2) except for the Abrolhos where its density (13.7/100 m^2) was unusually high.

Scarids had a mean density of 13.7/100 m^2 and were most abundant in the eastern and southern Caribbean. The highest scarid densities (36.0/100 m^2), which occurred in Los Roques, were nearly five times those reported for Mária La Gorda) and Lighthouse Atoll (Fig. 14A). Parrotfish species composition was similar across the region except for the Abrolhos which contained a Brazilian endemic, *Scarus trispinosus* (greenlip parrotfish), not found elsewhere in the western Atlantic (Fig. 14A). *Scarus croicensis* (striped), *Sparisoma aurofrenatum* (redband), *Scarus taeniopterus* (princess), *Sparisoma viride* (stoplight) and *Scarus vetula* (queen) were the five most abundant parrotfish species overall, with mean densities of 3.8/100 m^2, 3.6/100 m^2, 3.1/100 m^2, 2.8/100 m^2, and 1.1/100 m^2, respectively. Large-sized parrotfishes, including *Scarus guacamaia* (rainbow), *Scarus coelestinus* (midnight), and *Scarus coeruleus* (blue), were observed only occasionally and were more common in the southern Caribbean than in other subregions.

Regression analysis showed no significant relationship (p>0.05, n=17) between macroalgal index and herbivore density at the scale of the entire region (Fig. 11A). Similarly, no significant relationships were found between herbivore density and any other algal indicator (e.g., macroalgal canopy height or relative abundance of macroalgae, turfs or crustose corallines). Regionally, total herbivore density or biomass showed no relationship with coral density or with such measures of habitat complexity as coral diameter or height, although significant relationships were found between individual scarid and acanthurid species. For example, densities of *S. vetula* (queen) and *S. taeniopterus* (princess) parrotfishes were positively related to live coral cover (r^2= 0.8, p<0.05, n=17; r^2= 0.6, p<0.05, n=17 respectively). The density of *A. chirurgus* (doctor fish) was negatively correlated to old partial mortality (r^2=-0.53, p<0.05, n=17) while that of *A. bahianus* (ocean surgeon) was negatively related to large coral density (r^2=-0.49, p<0.05, n=17).

Carnivores. The density of carnivorous fishes averaged 6.0/100 m^2 for the region and was similar in shallow and deep reefs. Lutjanids predominated the carnivore assemblages overall with nearly twice the densities of serranids. Proportionally more serranids occurred in deep reefs than in shallow, although the reverse was true for
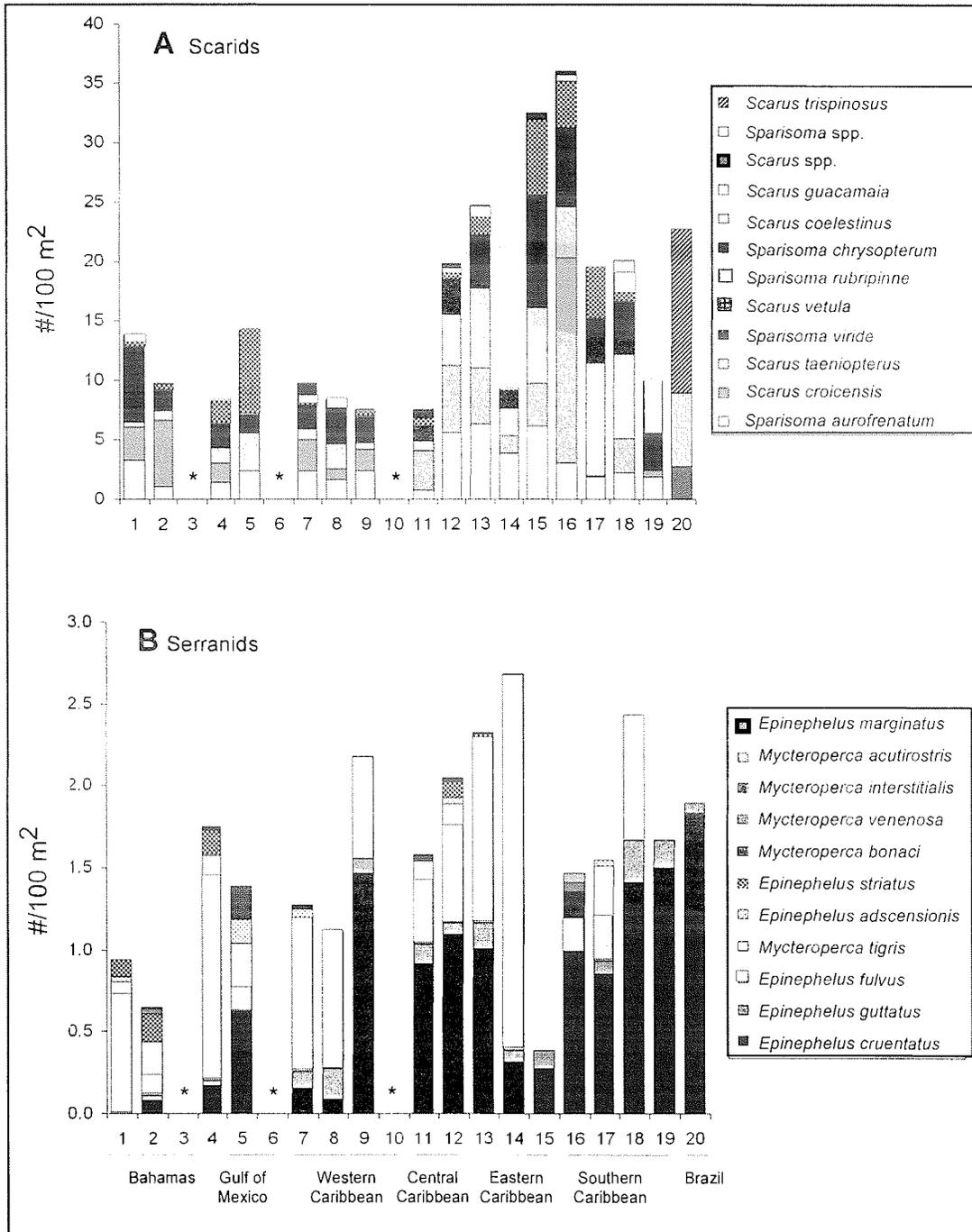
Figure 14. Stacked bar plot of fish family composition by survey (deep sites only) **(A)** scarid and **(B)** serranids. The star indicates a parameter that was not measured.

lutjanids. When comparisons are limited to the deep reefs (Fig. 13C), the areas with highest carnivore densities were the Abrolhos (ID#20) and Los Roques (ID#16), while the lowest were found in St. Vincent (ID#15) and Mária La Gorda (ID#11). Excluding the Abrolhos, carnivore biomass displayed a 40-fold difference across all other assessments, ranging from a low of 191 g/100 m^2 in Akumal/Xcalak (ID#8) to a high of 4,515 g/100 m^2 in Los Roques (Fig. 13D). No significant difference (p = 0.84, n = 3) was detected in total carnivore biomass between highly threatened reefs (~1,100 g/100 m^2) and either medium- (1,204 g/100 m^2) or low-threat reefs (~1,280 g/100 m^2).

The most abundant lutjanids were *Ocyurus chrysurus* (yellowtail snapper), *Lutjanus apodus* (schoolmaster snapper), and *L. mahogoni* (mahogany snapper) at densities of 1.6/100 m^2, 0.8/100 m^2, and 0.4/100 m^2, respectively. Densities of *Ocyurus chrysurus* recorded in the Abrolhos (ID#20) were one of the highest (~23.1/100 m^2) for any species. Serranids were present in all surveys at densities of less than 2/100 m^2 and were most abundant in the windward Netherlands Antilles (Fig. 14B). In all surveys, except Andros (ID#2) and the Abrolhos, smaller-bodied species including *Epinephelus cruentatus* (graysby), *E. guttatus* (red hind), *E. adscensionis* (rock hind), and *E. fulvus* (coney) dominated the grouper assemblages. The density of coneys decreased substantially in surveys conducted in the southern Caribbean where graysbys were proportionally more common (Fig. 14B). The most commonly seen large-bodied grouper was *Mycteroperca tigris* (tiger) with a mean abundance of 0.4/100 m^2. *Epinephelus striatus* (Nassau grouper) was rarely seen except in the Bahamas subregion with Andros having the highest density (0.2/100 m^2). Single [*E. marginatus* (dusky), *Mycteroperca rubra* (comb)] to no [*Epinephelus itajara* (goliath), *E.morio* (red), and *M. phenax* (scamp)] sightings were recorded in transects for a number of serranids on the AGRRA list. *Sphyraena barracuda* (great barracuda) was recorded in 10 of the 17 surveys, although usually at very low numbers (<0.2/100 m^2).

Index of Reef Health

To evaluate the overall condition of each survey on a relative scale, a preliminary biotic reef health index was developed for the deep (> 5 m) dataset utilizing 13 of the AGRRA indicators: live coral cover, large (≥25 cm) coral density, small coral density (Fig. 7D), maximum diameter of the *Montastraea annularis* complex , recent partial mortality, old partial mortality, total mortality (including standing dead), prevalence of coral diseases, macroalgal index, relative abundance of crustose coralline algae, *Diadema* density, herbivorous fish density, and carnivorous fish density. Only 17 areas could be analyzed because of missing [Veracruz (ID#6)] or incomparable [(San Salvador (ID#3) and Belize (ID#10), where fish were quantified in cylinders] fish data. A similarity matrix was calculated and analyzed using a Bray-Curtis similarity cluster dendrogram (Fig. 15). Three broad classes, distinguishable at the 70% similarity level, were labeled as "worse," "average," and "better" health categories. Only four areas fell into the "better" grouping: the Flower Gardens (ID#5), windward Netherland Antilles (ID#14), Los Roques (ID#16), and Bonaire (ID#17), each of which was characterized by low recent mortality, low prevalence of diseases, low macroalgal index, and relatively high fish densities. Seven areas fell into the "average" grouping and most of these had the majority of their
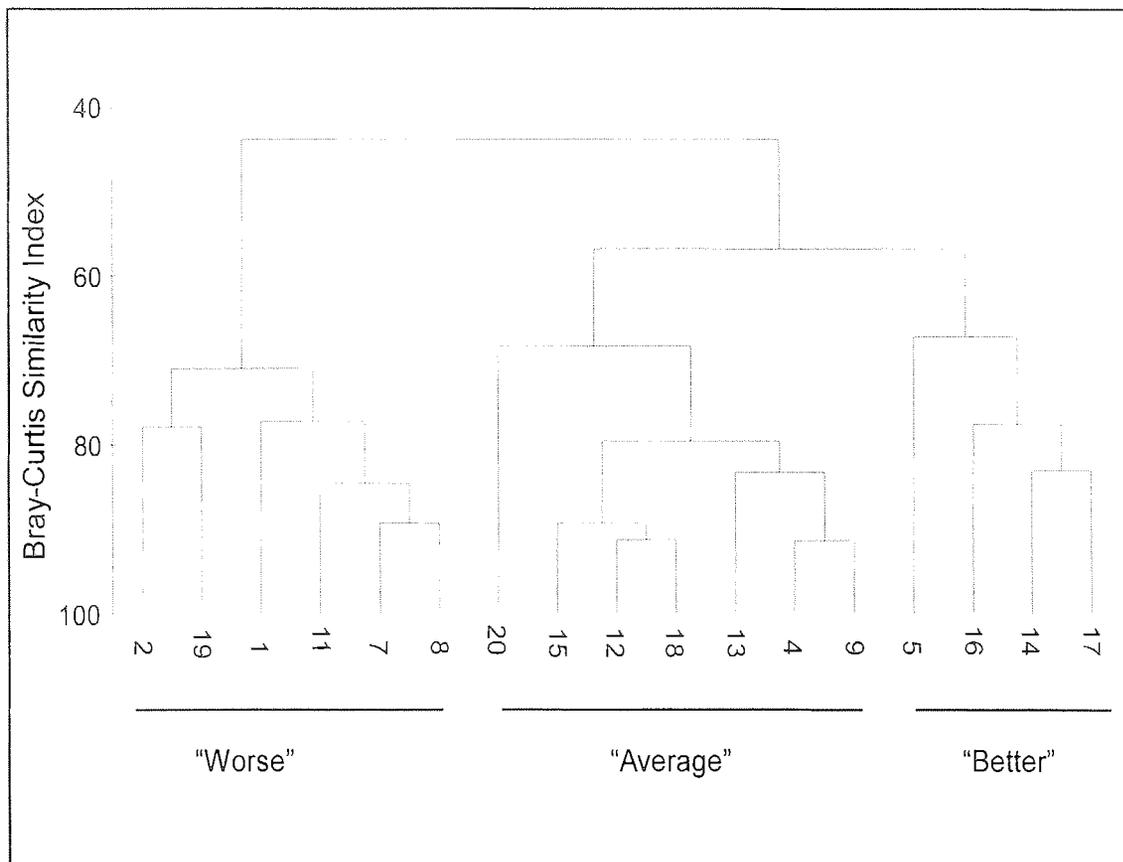
Figure 15. Bray Curtis similarity diagram of proposed reef health classification based on 13 AGRRA indicators. See Table 1 for ID codes and text for discussion.

indicators near the regional norms. Surveys in the most unfavorable class ("worse") were Abaco (ID#1), Andros (ID#2), Yucatan (ID#7), Akumal/Xcalak (ID#8), Mária La Gorda (ID#11), and Costa Rica (ID#19). These areas were generally typified as having high recent mortality, high prevalence of disease, moderate-to-high macroalgal index, and low fish densities.

DISCUSSION

Sampling Issues

Sampling effort. Differences in the sampling effort carried out for each AGRRA assessment resulted in part because of differences in the areal extent each team attempted to characterize as well as logistical sampling constraints (e.g., time, support, and accessibility). The fewest sites (two) were for the Flower Garden Banks (ID#5), which was also the deepest (~20 m) and furtherest offshore of the reef areas studied. The greatest effort was for the Cayman Islands (ID#12) where a total of 42 sites were assessed. Determining how much effort to allocate towards characterizing sites depends on the indicator and on its variance at different spatial scales. Results of the power analyses at the site scale suggest that, for a number of AGRRA benthic indicators, the greatest gain in terms of precision versus effort occurs within the first six transects which corresponds to roughly 60 corals and 40 quadrats. For the more specific indicators of rare species (i.e. abundance of large-bodied groupers, size frequency distribution of some corals), higher overall sampling would be necessary to get an adequate sample size to test significant differences.

The coefficients of variation (CV), defined as the standard deviation divided by the mean), for 12 of the AGRRA indicators at four spatial scales (deep sites only) are given in Table 5. For most indicators, the highest CV occurs at the smallest spatial scale (<0.1 km), however, there is still significant variation at the area and subregional scales (~1-100 km). This inverse relationship between CV and spatial scale suggests that in terms of sampling effort either slightly more effort should be allocated at the site scale (i.e., number of transects sampled per site) in comparison to the larger scales (i.e., number of sites sampled per area and number of areas sampled per subregion) and/or to observer training (see below). It also indicates that the size of the regional "signal" for some indicators (e.g., partial old mortality; herbivore fish abundance) is quite small but comparatively large for others (partial recent mortality, macroalgal canopy height, carnivore abundance).

Site selection and habitat classification. Considerable variance in AGRRA indicators at all but the smallest spatial scales can arise by sampling slightly different reef types. In this initial synthesis, only two categories of reefs were recognized (deep and shallow) and all sites in the deep category were used because the purpose was to compare the assessments presented in the volume. A majority of the deep sites were located on fore-reef slopes but some were located in other habitats. Habitat variation clearly has an influence on some AGRRA indicators (e.g., coral community composition, standing dead

coral) and these sites should be factored out in future comparisons. Reef slopes themselves can also have different morphologies that influence fish densities and other AGRRA parameters. For example, fore-reef slopes around the Turks and Caicos (ID#4) and on the leeward sides of Los Roques (ID#16) and Bonaire (ID#17) are characterized by sharp drops (walls) at depths of approximately 10m (the depth at which many surveys were undertaken). These "edges" tend to attract fishes at higher abundances compared to adjacent zones both shallower and deeper. Site selection and classification are even more critical for shallow-reefs where large differences in community coral composition, fish abundance, and algal parameters can occur across very small spatial scales (<100m). I have observed that reef habitats surrounded by areas of deep water (or similar sites with high relief surrounded by vast areas of no relief) will tend to attract fishes ("oasis effect") and have higher fish densities than areas wherein habitat is more evenly distributed. In the Abrolhos (ID#20), the unusually high fish densities are attributed, in part, to the shallowness and small size of the reefs. As the number of AGRRA assessments in the database grows, geomorphic and structural complexity characteristics should also be used to help classify reef types and design more representative sampling strategies for field assessments.

Methodology and observer bias. Observer bias is a potential contributor to variance in the benthic and fish data and needs to be addressed in any study that relies on more than a single observer to collect data. Many of the participants contributing to this synthesis had considerable experience with Caribbean reefs and, with few exceptions, one or more of the observers in each team had received formal training in the AGRRA protocols. Based on our workshop experiences, variance among observers who have undergone consistency training is small compared with the total variance at all spatial scales for any given indicator. When observers have not undergone such training, a number of the AGRRA indicators can be scored systematically in ways that lead to bias in the data. This is particularly true for fish where small differences in belt-transect width, length and swim time can lead to systematic differences in fish density estimates (Sale, 1998). Several of the surveys in this volume used different transect sizes or even different methods. Given the costs and time to collect AGRRA data, particularly from remote locations, it is recommended that the protocol be followed more closely in future field efforts and that more effort be spent on minimizing observer bias through consistency training of all observers with core AGRRA personnel.

Stony Corals

Community structure. A mean live stony coral cover of 26% for deep sites is considered fairly representative of the region during 1998-2000, although perhaps somewhat elevated since the most structurally complex sites were sometimes selectively targeted by AGRRA assessors. Historic baselines for coral cover do not exist in most areas, but a pre-1980 regional estimate based on available coral cover data was summarized by Gardner (2002) at between 40 and 50%. Thus Western Atlantic reefs have undergone significant losses over the past several decades yet despite many large-scale disturbances (e.g., the 1983-84 die-off of *Diadema antillarum,* numerous outbreaks of

disease and bleaching events) a fair amount of living coral remains. In some areas, however, and not reflected in these percentages, the original large corals that broadcast larvae have likely been replaced by smaller brooding species.

More substantial changes have probably occurred in the shallow (<5 m) reef crests and patch reefs where faster-growing acroporid corals once dominated (e.g., Goreau, 1959; Geister, 1977; Adey, 1978; Gladfelter, 1982). Results of the AGRRA assessments for the shallow reefs presented in this volume indicate an overall live coral cover of 18%; however, the small and spatially disproportionate sampling and high variability in reef types that were assessed preclude using this average as representative of the region. AGRRA assessments since 2000 have been directed specifically to more systematically sample shallow reefs.

For shallow and deep reef sites, the composition indicates typical species dominance patterns on western Atlantic reefs and reflects the amount of survey effort for a particular reef type. Coral species composition and abundance data for the 20 areas are influenced by: (1) environmental and/or biogeographic factors; (2) reef types that were assessed; and (3) their disturbance histories. One of the two clusters in the MDS analysis of the deep reefs is caused in part by the geographic location of its areas (ID#s 2, 4, 11, 12, 13) in the insular Caribbean (Fig. 6A). Outliers represent geographic extremes or areas that are currently marginal for reef growth. For example: Abaco (ID#1), the furthest north, is exposed to large Atlantic swells and to cooler water temperatures; Abrolhos (ID#20), the furthest south, is in a different biogeographical subregion and also experiences open ocean swells; both Costa Rica (ID#19) and Veracruz (ID#6) are heavily influenced by sediment runoff; and the Flower Gardens (ID#5), the deepest of the assayed reefs and somewhat isolated from other reef systems in the northwestern Gulf of Mexico, lack several common Caribbean scleractinian species (Roberts et al., 2002). The distinctiveness of the deep reefs in San Salvador (ID#3) (compared to other deep reefs) is thought to result from the way sites were grouped using the 5m cut off depth, which resulted in four "other" reef types being grouped with three reef-slope sites.

The abundance of "recruits" (estimated as small corals with diameters of ≤2 cm) is an important indication of a reef's potential for growth and for recovery after major disturbances. The total area sampled at each site (~2-3 m^2) was probably too small for these data to be highly reliable at the site scale. Patterns at the subregional level were not evident, but larger scale comparisons indicate that corals are currently recruiting most successfully in the Abrollhos (ID#20) and on the deep reefs in Andros (ID#2) and the Virgin Islands (ID#13). That the AGRRA data shows species composition of coral recruits often did not reflect the major coral-reef builders present is similar to other studies (e.g., Rogers et al., 1986).

Mortality. The AGRRA data support previous findings that show partial mortality differs among coral species and partially reflects the life history strategies and population dynamics of species and their susceptibility to various physical and biological factors (Bak and Luckhurst, 1980; Hughes and Jackson, 1980, 1985; Meesters et al., 1997). Large, long-lived broadcasting corals such as *Montastraea* spp. tend to exhibit higher amounts of partial tissue mortality while smaller, short-lived brooding species (e.g., some species of *Porites* and *Mycetophyllia)* tend to exhibit either complete mortality or no

mortality. For nearly all species, levels of old partial mortality increase with colony size (particularly in the early size classes) suggesting that corals are more likely to suffer severe, irreversible tissue damage the longer they live (e.g., Ginsburg et al., 2001). Since between-reef variability of mortality is strongly influenced by the species composition and sizes of the corals present in each reef (Bythell et al., 1993; Meesters et al., 1996), these variables should be considered when examining patterns at diverse spatial scales.

The mortality signal is also a function of how long the corals remain within the "recent" state before transitioning to the "old" state and finally to unidentifiable substrate or rubble. This rate of transformation is strongly influenced by sedimentation, bioerosion, and overgrowth all of which vary both spatially and temporally. Given these influences and geographic variations in the prevalence of disease and bleaching events, hurricanes and other disturbances in 1998-2000, it is not surprising that levels of recent partial mortality (along with the amount of standing dead coral) were highly variable at nearly all examined spatial scales (0.1-1000 km). In contrast, old partial mortality showed much lower variation at larger spatial scales (>~0.1 km) suggesting similar processes were affecting this indicator for the entire region.

A useful distinction can be made between background mortality of stony corals caused by chronic stressors and acute mortality caused by intermittent major disturbances (see also Steneck and Lang, this volume). Some inferences can be made about each of these sources given the range of environmental conditions that affected the reefs sampled in this volume. Chronic or background coral tissue damage and mortality can result from a variety of low-intensity stressors including predation, disease, bioerosion, sedimentation, competition and abiotic perturbations (Meesters et al., 1996, 1997). Many instances of partial mortality are small and within the abilities of corals to regenerate new tissue; however, above certain sizes (~10cm^2), dead skeletal areas tend to become overgrown or eroded by other organisms (Meesters et al., 1996; Clark, 1997). Under increasingly severe chronic conditions, especially for species with slow rates of regeneration (e.g., most massive corals), there will be increases in partial mortality followed by decreases in size structure, increases in the number of physiologically distinct colonies, and finally shifts in the species assemblages. Abaco (ID#1) and Costa Rica (ID#19) are two of the most chronically stressed reef areas assessed in this volume. The deep Abaco reefs had the highest levels of total mortality for the *M. annularis* complex (Fig. 9) coupled with the lowest densities of large (>1m) colonies (Table 3B). Costa Rica had proportionally more colonies of *Siderastraea*, which is well-known for its high tolerance of sediment stress (Cortés and Risk, 1985) than any of the other 19 areas, but relatively low levels of total partial mortality for the *M. annularis* complex and of partial old mortality for all stony corals. These patterns underscore that differences in partial mortality are influenced by the species composition of corals present and coral size and should be considered together when examining patterns at various spatial scales.

Establishing a present-day baseline for background coral mortality allows us to distinguish the magnitude of mortality following severe disturbance events such as disease epizootics, bleaching, or hurricanes. Based on the AGRRA data presented in this volume, our current best estimate of background (chronic) partial mortality on reefs can be approximated from the regional averages of <4% for recent mortality and <22% for old mortality. However, a more accurate estimate of chronic mortality is achieved by

removing those areas known to have been recently impacted by severe disturbance events (e.g., ID#s 1,2,3,7,8,10). This results in an estimate of <2% for recent mortality and <21% for old mortality. Associating a time frame with these recent and old mortality signals would allow us to make an inference about the *rates of mortality*. Assuming the recent morality signature (i.e., raised calices around corallite, unless calices have been removed by parrotfishes) remains visible for approximately one year, present-day rates of annual turnover ("cumulative partial mortality") might be on the order of 2%, excluding any regeneration of soft tissues. By extension, this would imply that old mortality signatures remain visible for approximately a decade, after which coral skeletons are no longer identifiable. Although these values appear to represent a reasonable upper limit of background mortality to expect on reefs today, it is unknown how this estimate compares to historic background levels when chronic stresses may have been quite different. Hughes and Connell (1999) argue that rates of coral mortality can be naturally quite high even in the absence of major disturbance events, thus historic mortality levels may not be drastically different from those observed today. If so, this would imply that 30-50 years ago a regional average of 2% recent and ~20% old mortality may have existed, and that decreases in live coral cover may be more a function of changes in the rates of coral regeneration and recruitment rather than of changes in the rates of coral mortality.

Coral tissue damage that results in large lesions or even complete colony mortality often results from major disturbance events (e.g., disease eipzooitics, bleaching, hurricanes). Shortly after the disturbance, this type of acute mortality is reflected mainly in high values for recent mortality and standing dead. For example, high levels of recent mortality were related to the presence of certain coral diseases at the subregional and local scales (Table 4B) including black-band disease (Andros, Kramer et al., this volume), white plague (Akumal/Xcalak, Steneck and Lang, this volume) and yellow-blotch disease (Curaçao, Bruckner and Bruckner, this volume). Mass mortality events often affect corals regardless of size but certain species are more susceptible than others. For this reason, species-specific levels of recent mortality are probably a more reliable way of examining spatial and temporal variation in disturbance events.

The amount of standing dead coral, often overlooked in current monitoring methods, is an excellent indicator for hindcasting past disturbance events possibly exceeding a decade (provided no major hurricanes have directly affected the area in the meantime and if rates of overgrowth and bioerosion are not too high). Reliablity in counting and identifying standing dead massive corals to the genus or species level depends on how much time has passed since the disturbance event and how much effort an observer puts into exposing and identifying their skeletons. The highest occurrences of standing dead coral on deep reefs were reported from Belize (ID#10) and San Salvador (ID#3), two areas strongly influenced by the 1998 ENSO (see two papers by Peckol et al., this volume). As the reefs examined included some deeper patch-reef and back-reef communities, how much this signal represents the ENSO disturbance history versus differences in reef type from those in most of the other assessments is unclear. In general, the standing dead signature is more dramatic on shallow reefs where dead *Acropora palmata* are easily identified and can persist upright for decades, particularly if they become encrusted with crustose coralline algae which makes the skeletons less susceptible to bioerosion (personal observations).

Diseases and bleaching. AGRRA data indicate that diseases were present throughout most of the wider Caribbean region in 1998-2000 with very few areas exhibiting no occurrences, not even on reefs removed from close human influence. These data are consistent with numerous reports suggesting that the prevalence, extent and type of diseases in Caribbean stony corals continue to increase (Richardson, 1998; Green and Bruckner, 2000; Wheaton et al., 2001). An unexpected observation from the AGRRA surveys was the high prevalence of disease in the *Montastraea annularis* complex observed on some of the deep reefs, particularly given their relatively remote locations (e.g., Cayman, Kievman et al, this volume; Andros, Kramer et al, this volume; Virgin Islands, Nemeth et al, this volume).

Outbreaks of disease (or epizootics) nearly always resulted in high spatial variability at the community and individual level and differentially affected species. On the regional scale, all size classes of corals were affected by diseases. However, on some local scales, size effects were evident. For example, higher prevalences of yellow-blotch disease were correlated with larger (>0.5 m) coral sizes in Curaçao (Bruckner and Bruckner, this volume). Spatial patterns of disease occurrence on Andros suggested that at least some diseases may be highly contagious or spread rapidly and easily. Some of the deep reefs with high prevalences of diseases, for example, of white plague and black-band off Andros (Kramer et al., this volume) and of yellow-blotch off Curaçao (Bruckner and Bruckner, this volume), also had high coral densities and complex reef structures dominated by the *M. annularis* species complex and may be more susceptible to rapid spread of a disease because of the close proximity of colonies. However, no diseases were observed on the well-developed reefs in the Flower Gardens (Pattengill et al., this volume) (although noted to exist in low amounts outside of transects) suggesting that: (1) some regions may be less exposed to diseases; (2) other stressors such as bleaching make corals particularly susceptible to diseases that are present on most reefs; and/or (3) some coral genotypes may be more resistant to diseases that others.

The AGRRA data suggest a strong linkage between bleaching-related mortality and infectious diseases which could be due to increased pathogen activity and/or sensitivity of corals to their effects during periods of elevated sea surface temperatures. Recent mortality in areas that had been affected by mass bleaching during the 1998 ENSO event was closely associated with the presence of black-band disease in Andros (Kramer et al., this volume) and white plague in Andros (ibid.) and the Yucatan (Ruiz et al., this volume; Steneck and Lang, this volume). However, these relationships are somewhat confounded since not all disease outbreaks are tied to temperature and because the impact of a disease will vary based on how long it lasts and how fast it spreads. Increased water temperatures have been related to elevated prevalence of five coral diseases (bacterial bleaching, black-band disease, white plague, aspergillosis and dark spots disease) (reviewed by Harvell et al., 1999; Rosenberg and Ben-Haim, 2002; see also Porter, 2001). Clumped distributions observed in the AGGRA surveys mentioned previously, may be due both to the intrinsic intensity of the disease and local patterns of increased sea surface temperature similar to a post-bleaching-related outbreak of black-band disease in Florida (Kuta and Richardson, 1996), whereas "normal background diseases" observed at the local scale on many of the other AGRRA surveys may have a

more random distribution pattern similar to that reported by Edmunds (1991). It is still unclear if bleaching causes corals to be more susceptible to opportunistic pathogens, and/or if pathogens normally present exacerbate levels of bleaching and bleaching related mortality. The relationships among disease, bleaching and mortality, and the temporal and spatial scales in which these processes are operating, will influence whether the effects of these events are transient or lethal (e.g., Kramer and Kramer, 2002).

Condition of keystone corals. The AGRRA data provide further information concerning the regional decline of *Acropora* (Aronson and Precht, 2001), which is particularly evident for *A. palmata* as standing dead signatures in several locations (e.g., Los Roques, Villamizar et al., this volume; Tobago Cays, Dechamps et al., this volume). *Acropora palmata* still predominates species composition on many shallow reefs in the region although the proportion of dead-to-living colonies varies dramatically on the local scale. Surprisingly large stands of live *A. palmata* were found off Andros, Bahamas (Kramer et al., this volume) and, more recently, on the southwestern coast of Cuba (AGRRA database, unpublished data). In contrast, *Acropora cervicornis* was present on many of the deep reefs that were assessed, but was very sparse with no thickets or haystacks even remotely resembling the stands reported from Jamaica (Goreau, 1959), Bonaire (van Duyl, 1982) and Florida (Dustan and Halas, 1987) as recently as the late 1970's to early 1980's. The fragile nature of branches of *A. cervicornis* allows it to be broken down to rubble soon after death; thus the likelihood of observing standing dead colonies is substantially lower than for other species. *Acropora cervicornis* rubble can persist for several decades (Shinn et al., in press) however, and was noted in several areas (e.g., Cayman, Curaçao).

Significant gaps still exist in our understanding of the geographical distribution and condition of acroporids. For some areas (Bonaire, Curaçao, Cayman, Mária la Gorda, Costa Rica) shallow reef crests are of limited spatial extent and thus were not sampled. Elsewhere (Yucatan, Belize, San Salvador, Turks and Caicos, and the Virgin Islands), the extensive reef crests were not assessed because of inaccessibility or high wave energy. Greater sampling of shallow reef-crest habitats within the wider Caribbean should be a priority since so little region-wide information is currently available. Nevertheless, the historic range does not appear to be reduced or lost in either acroporid species although occurrence and abundance data suggest range reductions have occurred at the local scale. The presence of acroporid recruits was higher than expected in some areas (e.g., Andros, Cayman) and the existence of a few localized healthy populations of *Acropora palmata* is encouraging. However, very few *A. cervicornis* recruits were observed (Virgin Islands, Nemeth, this volume; Netherlands Antilles, Klomp et al., this volume) and there were few signs of significant reestablishment of/recolonization by this species.

Four species within the *Montastraea* family (*Montastraea annularis, M. faveolata, M. franksi* and *M. cavernosa)* numerically accounted for about half (~50%) of the frame-building corals on the deep reefs assessed in this volume except for Abrolhos where the endemic *Mussismilia braziliensis* predominated (Kikuchi et al., this volume). The density (as numbers/10 m) and sizes of *Montastraea* colonies can be used to indicate the stability of environmental conditions (e.g. Done, 1995) as well as infer characteristics

of mortality, regeneration, and recruitment (e.g., Bak and Meesters, 1998). High densities of large (>~1 m) colonies are indicative of environmentally stable "old growth" conditions (e.g., the Flower Gardens, Bonaire, Los Roques, and Curaçao). In contrast, the lowest densities are found in areas that are marginal for reef growth (e.g., Abaco, Costa Rica). Smaller colonies (<30 cm) are less likely to have partial mortality but more likely to experience complete mortality, and thus may be a more sensitive indicator of environmental growth conditions. In current versions of the AGRRA protocol all corals equal to, or greater than, 10 cm maximum diameter are now sampled.

High recent mortality coupled with the disease outbreaks described above were observed in the *Montastraea annularis* species complex at several areas during 1999-2000. Because of their slow rates of tissue growth (Hubbard and Scaturo, 1985), colonies with large injuries from fast-spreading diseases (e.g., white plague) have a high likelihood of impaired skeletal growth (Hughes and Jackson, 1985) or diminished reproductive output (Szmant and Gasman, 1990) and some may not recover at all. Given the importance of the *M. annularis* complex as the current and historic principal framebuilder of intermediate-depth reefs, these large, and perhaps unprecedented, disease and bleaching impacts are cause for great concern. Improving our understanding of its dynamics (reproduction, settlement, mortality) and exploring any cases (genotypic, geographic, habitat, depth-dependent) of resistance and/or resilience to these impacts as may occur naturally should help better direct management strategies towards their persistence and recovery.

Fishes

Community structure. Fish community structure at any given locality can be attributed to a wide range of factors including environmental conditions, habitat complexity, and fishing and management regulations. Other factors such as predator-prey interactions (Hixon, 1991), larval supply and recruitment (Cowen, 2000), history of disturbance (Syms and Jones, 2000), quality and intactness of adjacent habitats (e.g., Munday, 2002), and natural biogeographic variation within species may also contribute to the overall variance in fish community structure. Most of the AGRRA species are found throughout the western Atlantic with the exception of the Abrolhos. Some species are known to be much more common in certain areas than others. For example, Nassau grouper are much more prevalent in the Bahamas than in other parts of the Caribbean. However, when combined into a carnivore index, these species differences become less distinct because there may well be other carnivore species present to fill the niche occupied by one that is not present.

Herbivore species composition and sizes were remarkably consistent across surveys. That herbivore densities were more variable, with consistently higher numbers in the eastern and southern Caribbean and lower numbers in the Bahamas, Gulf of Mexico, Mária la Gorda (ID#11) and western Caribbean (Fig. 13B), may be partially related to geomorphic factors discussed above.

Several significant relationships (positive and negative) between habitat variables and the abundance of individual fish species were observed and need to be explored in more detail before conclusions can be drawn regarding their significance. However, that

coral size, density, and partial mortality were not directly related to overall fish density (or biomass) nor with herbivore or carnivore indicators at the scale of the entire region suggests that some tropical fish-habitat relationships identified at smaller scales (e.g., Luckhurst and Luckhurst, 1978; Lindquist and Gilligan, 1986; Nemeth et al., this volume) do not hold at larger spatial scales. One possible reason for the lack of a relationship at the regional scale is that guilds of fishes are utilizing the best available habitat within each of the assessment areas even though the habitats may be quite different from one area to another. Habitat quality in itself may not be the limiting factor determining fish abundance, but other factors such as larval supply, recruitment, and trophic predator-prey relationships may be more important. Clearly definitions of habitat quality vary and may include other measures not included in this analysis such as percentage of *A. palmata* (shallow), percentage of *M. faveolata* (deep), or independent measures of rugosity. Since 2000, the newer version of the AGRRA protocols incorporates an independent measure of substrate rugosity which, in the future, will help to classify reefs based on relief and to better test relationships between structural complexity and other benthic, algal, and fish variables.

Overfishing. Differences in fish community structure that can be either directly or indirectly linked to human fishing have been documented in numerous studies (e.g. Roberts, 1991, 1995). While areas that now receive higher protection from fishing [Flower Gardens (ID#5), Los Roques (ID#16), Cayman (ID#12), and Bonaire (ID#17)] displayed slightly higher total biomass than areas with little protection (e.g., the Bahamas and western Caribbean), the difference was not significant. Since in some areas sites were surveyed within and outside of protected areas (e.g., Abaco (ID#1), Cayman (ID#12), Virgin Islands (ID#13), a more rigorous analysis would require assigning levels of protection at the site scale. However, assigning AGRRA sites with an unbiased estimate of protection from fisher-related mortality across the entire Caribbean is difficult because of the wide range of management and harvesting practices in place. An unbiased measure of total fish extraction, broken down by species and area (preferably at a fine spatial scale), is needed before fish density and biomass patterns related to fishing can be examined robustly at large spatial scales.

Results of the 1-way ANOVA analysis using Bryant et al.'s (1998) "overexploitation threat index" show no clear pattern for total biomasss or herbivore biomass or carnivore biomass and can be interpreted to suggest several possibilities. For example, the modeling of overexploitation threat may not accurately portray fishing pressures on reefs. In fact, this is likely since the threat index is based on a global-level analysis using a reef's proximity to coastal settlements which vary greatly in size and in the proportion of people that harvest reef fishes. Not factored in the index as other factors that can influence fish populations are habitat quality, adjacent habitat availability (shelf area), and levels of management. It is also likely that AGRRA *total* fish density (and biomass) data are not very sensitive to the type of fishing pressure common at many of the areas assessed in this volume because they are heavily weighted by herbivorous fishes which, except for some large parrotfish such as *Scarus guacamaia*, are seldom heavily targeted. One of the most widely discussed examples in which nearly all reef fishes are harvested is Jamaica (e.g., Koslow et al., 1994). Indeed, during AGRRA assessments

conducted along the north coast of Jamaica in August 2000, total biomass (<1,500 g/100 m^2), herbivore biomass (<1000 g/100 m^2) and carnivore biomasss (<150 g/100 m^2) were all significantly lower than had been found at any of the areas in this synthesis (Klomp et al., in press). It would appear that the herbivore (and total fish) density (and biomass) indicators are only strongly affected by intensive overfishing, and that a regional signal associated with more selective targeted fishing may be more difficult to detect.

Carnivore density (as well as size and biomasses) is considered a more sensitive indicator of the type of fishing pressure occurring at many of the areas in this synthesis. As discussed earlier, the high densities (and biomass) reported in the Abrolhos (ID#20) are thought to arise primarily from differences in both habitat type and assessment methodology. For the remaining areas, spatial patterns are apparent and suggest that portions of the western (ID#s7-9) and eastern (ID#s13-15) Caribbean are consistently low in carnivore densities while portions of the southern Caribbean (ID#s16-18) are consistently high. The overall low number of sightings for larger-bodied groupers and snappers (<~1/100 m^2) as a whole suggests the entire region is overfished for many of these more heavily targeted species. Interestingly, the Bahamas subregion in particular Andros (ID#2), has a much higher proportion of large-bodied groupers (*E. striatus, M. tigris, M. venenosa*) to smaller-bodied species (*E. cruentatus, E. guttatus, E. fulvus*) than the rest of the region. The Bahamas subregion as a whole may have the least exploited grouper populations in the western Atlantic, an observation also supported by the large number of active grouper spawning aggregations (Sadovy, 1999).

The lack of a significant relationship between carnivore density (or biomass) and overexploitation threat can be explained in part to the way this threat was modeled and in part also to the observation that the assessment areas probably do not represent a full gradient between "pristine" (unfished) and extremely overfished. In addition, the fish AGRRA belt transects are not considered the ideal size for quantifying the larger, solitary carnivores that are targeted by light-to-moderate fishing intensities. The narrow width and small areal coverage per site (600 m^2) can often result in observers missing cryptic and/or shy serranids and lutjanids that are present on the reef. Statistical power is low because of the overall low number of observations. Fish biomass reports based on Bohnsack-Bannerot cylinders are generally lower than those derived from belt transects, although, to my knowledge, no systematic comparison has been conducted. In addition, the large length-class intervals used by the observers reduce the power of the methodology to detect small differences in fish size. Ideally, belt transect data should be considered in conjunction with the Roving Diver sighting frequency data, as suggested by Schmitt et al. (2002).

Although not examined in this synthesis, many of the individual papers in this volume include sighting frequencies derived from Roving Diver surveys. Based on species accumulation curves for three sites, Nemeth et al. (this volume) determined that a minimum of six Roving Diver surveys (or greater than seven hours search time) would be needed to approximate the actual species diversity in the deep St. Croix reefs. However, much less time would be required to determine the presence and qualitative density of the 75 or so AGRRA species which could also be used to improve our ability to distinguish light-to-moderate levels of fishing pressure.

Algae and herbivory. The lack of any significant relationship between algal index and herbivore density/biomass in our data are somewhat in contrast to those of Williams and Polunin (2001) who reported that herbivore biomass showed a significant negative correlation with macroalgal cover and a positive correlation to cropped substrate in five localities across the wider Caribbean. Differences in the assessment techniques for quantifying algal cover are thought to be responsible for these different results. The AGRRA technique scores algal abundance and canopy heights in areas where there is at least 80% algal cover and does not record the absolute abundance of macroaglae for the entire hard substrata of a reef. In fact, the inverse relationship between live stony coral cover and macroalgal canopy height that is evident in the AGRRA data supports the notion that macroalgal canopy height may be a function of the available hard substratum. Many algal species are unpalatable for fishes and canopy heights may only correlate with herbivorous fish density at relatively low abundances where algal choices are limited. However, these results also suggest that there are probably other factors (e.g., environmental conditions limiting algal growth) contributing to each of these signals at the regional scale. Densities of *Diadema antillarum* were low at nearly all surveys except for Costa Rica and thus probably do not exert a strong influence over algal assemblages at this time.

Reef Health

That three groupings resulted from the similarity analysis (Fig. 15) was somewhat surprising since the indices employed have ecological functions spaning a range from the individual-to-community-to-ecosystem levels (Table 6). In part, the high degree of similarity within the groups (>70%) arises because several indicators reinforced one another (e.g., inverse relationship between coral cover/density and macroalgal index as discussed earlier). Clearly, the choice of indicators had strong bearing on the outcome of this type of similarity analysis. Indicators that displayed the highest large-scale variation (e.g., recent mortality, carnivore density) had more influence on the groupings than those that had minimal large-scale variation (e.g., old partial mortality, colony diameter) (Table 5). None of the areas in the "better" category had experienced severe damage to its stony corals from the 1998 ENSO event although high percentages of mottled and pale colonies were seen in both Bonaire (ID#17) and the windward Netherlands Antilles (ID#14) at the time of their assessment (February, 1999 and December 1999, respectively). In contrast, four of the six assessments in the "worse" category were strongly influenced by this event as was Belize (ID#10) (see Peckol et al., this volume). However, the other two survey areas in the worse category [Costa Rica (ID#19) and Abaco (ID#1)] are subject to high chronic stresses, as reflected mainly in their low coral density, low coral cover, and high macroalgal index. Most of the areas in the "worse" category also had subnormal densities of carnivores while those in the "better" category had above-normal densities.

Patterns observed in the overall state of the region and inferred causes (natural versus anthropogenic) for these patterns have begun to emerge from this preliminary analysis. It was expected that coral reefs remote from human population centers might be more intact and in better condition than those adjacent to population centers where there is a higher potential for exposure to pollution, overfishing, nutrient enrichment,

sedimentation, recreational diving, and anchor damage. Results from this synthesis suggest such may not be the case. Often more remote reefs showed as much, if not more, evidence of reef degradation than reefs closer to human coastal development. For example: Andros (ID#2) had high recent partial mortality of corals, high macroalgal index, and few fish; Anegada and Guana in the British Virgin Islands (ID#13) had high prevalences of coral disease; at Los Roques (ID#16), *A. palmata* in the shallow barrier was nearly 100% standing dead; and in Mouchoir Bank, Turks and Caicos Island (ID#4), macroalgal abundance was high. Fringing reefs on some highly populated islands [i.e., Bonaire (ID#17), windward Netherlands Antilles (ID#14)] seem to have avoided sea surface temperature "hotspots" while remote reefs in the Bahamas [(i.e., Andros, San Salvador (ID#3)] did not.

The observations that remote reefs are in poor shape does not imply that human actions are not influencing reef condition; this has been demonstrated conclusively by numerous studies (e.g., Ginsburg, 1994). Rather, it suggests that the driving forces influencing reef condition across the region are complex and probably involve multiple sources operating over several spatial and temporal scales. Regional (e.g., *Diadema* dieoff, some coral diseases) and subregional (ENSO-driven bleaching and associated diseases) stressors superimposed on localized states (e.g., reef development, degree of overfishing, disturbance history, abiotic conditions), and the degree to which reefs have ecologically adapted to these states over the past several decades, is a more plausible explanation for the current patterns. It also implies that human "proximity" now has a global reach, given atmospheric build-ups and transport of pollutants. The driving forces of western Atlantic reef degradation are operating at large spatial scales and management efforts should be directed towards these same regional scales.

A critical issue that has practical consequences on the outcome of any reef health assessment relates to the benchmark used for the rankings. In this preliminary analysis, departures from ecologic norms were used as the principal criteria for judging health. However, departures from normality are not necessarily unhealthy since natural reef ecosystems are expected to experience routinely disturbance events such as hurricanes (Rogers, 1993). A more meaningful measure of reef health may thus be resilience (Holling, 1973) but there is significant debate with respect to the time scales necessary to gauge reef resilience (Done et al., 1996). Evaluating reef condition based principally on ecologic criteria without regard to other criteria (e.g., socioeconomic, abiotic parameters) leads to its own bias. For example, a heavily managed reef can be ecologically subnormal but may be judged healthy if it fulfils a designated purpose. Thus, while the intent here was to examine patterns of normality and classify survey areas based on their broad groupings, applying judgmental health labels to these groupings is probably premature.

One criticism to the AGRRA approach is that indicators and values are largely based on what we know about the functioning of coral reefs today rather than the type of pristine natural reefs that may have existed in the past. What represents a "normal" or even "healthy" reef today may well be "degraded" with respect to an earlier baseline (Jackson, 1997). Recognizing that ecological baselines have shifted (Jackson, 1997, 2001; Greenstein et al., 1998), the value of making multiple observations across multiple spatial scales that can approximate the average state for the region today is still very high. The initial AGRRA norms synthesized in this volume can now be used as yardsticks to

evaluate reef condition like those for human health (e.g., blood pressure, infant mortality, prevalence of heart disease, life expectancy). In addition, these observations can be used with certain limitations within the hypothesis-testing framework (Underwood, 2000). The results presented in this synthesis, and in the papers of this volume, represent a preliminary analysis of a large amount of data. As additional AGRRA assessments are undertaken, the regional norms will shift to become more representative of the region, particularly for shallow reefs. In addition, more powerful analyses will be possible as our classification and stratification of reef types improves and as more species-specific indices are incorporated into the dataset.

CONCLUSIONS

- A mean live coral cover of 26% in the deep sites suggests significant losses have occurred over the past several decades but that substantial amounts of coral remain.
- Significant bleaching-induced mortality associated with the 1998 ENSO event was most apparent in the western Caribbean and Bahamas subregions.
- Linkages between infectious diseases, bleaching, and recent mortality were evident and are thought to be a result of increased pathogen activity and sensitivity of corals to disease and mortality during periods of elevated sea surface temperatures.
- Coral and fish community species composition across the entire region were most strongly influenced by environmental and biogeographic factors.
- AGRRA data provides further evidence on the regional decline of acroporids, although some moderate occurrences of *A. palmata* were identified and the historic range does not appear to be reduced or lost in either species.
- Large and perhaps unprecedented disease and bleaching impacts on the *M. annularis* species complex were documented by many of the AGRRA surveys. Given the importance of *Montastraea* as the current and historic principal frame builder of reef slopes, this decline is cause for great concern.
- The overall low number of sightings for larger-bodied groupers and snappers ($<\sim 1/100$ m^2) as a whole suggests the entire region is overfished for many of these more heavily targeted species.
- Herbivore density (or biomass) and macroalgal index were not related at the scale of the entire region suggesting that there are probably other factors (availability of substrate, abiotic factors) contributing to each of these signals.
- More remote reefs showed as much evidence of reef degradation as reefs more proximal to human coastal development.
- Driving forces influencing present-day reef condition across the region are complex, and probably involve multiple sources operating over several spatial and temporal scales.

ACKNOWLEDGMENTS

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Table 1. Summary site information for the 20 AGRRA assessments in this volume.

ID#	AGRRA Region	Survey Area	Date(s)	Modeled Threat Index[1] Combined	Over-exploitation	Benthic Shallow (≤5 m)	Benthic Deep (>5 m)	Benthic Total	Fish Shallow (≤5 m)	Fish Deep (>5 m)	Fish Total	Sampling unit (m)²	Shallow (≤5 m) Reef crest	Back reef	Patch reef	Other	Deep (>5 m) Reef slope	Bank reef	Other	Other Diadema density (#/100 m²)
1	Bahamas	Abaco, Bahamas	Aug., 1999	H	H	2	6	8	2	6	8	30 x 2	1	1			6			0
2	Bahamas	Andros, Bahamas	Aug., 1998	M	M	15	16	31	15	16	31	30 x 2	15				16			0.6 ± 1.2
3	Bahamas	San Salvador, Bahamas	June, 1998	M	L	4	7	11	4	7	11	7.5		2	2		3	4		---
4	Bahamas	Turks & Caicos Islands	Aug., 1999	M	L	2	26	28	2	26	28	30 x 2		1	1		24	2		0
5	Gulf of Mexico	Flower Garden Banks, USA	Nov., 1999	L	L	0	2	2	0	2	2	30 x 2						2		1.1 ± 0.4
6	Gulf of Mexico	Veracruz, Mexico	July, 1999	H	H	3	3	6	----	----	----	----					3	3		---
7	Western Caribbean	Yucatan, Mexico	June - Sept., 1999	M	L	0	24	24	0	24	24	50 x 2					24			0
8	Western Caribbean	Akumal/Xcalak, Mexico	March, 1999	M	L	2	12	14	0	6	6	30 x 2			2		12			0.2 ± 0.9
9	Western Caribbean	Lighthouse Atoll, Belize	July - Oct., 1999	M	L	0	11	11	0	11	11	30 x 2					11			0
10	Western Caribbean	Belize	May, 1999	M	L	3	10	13	3	10	13	7.5			3		5	5		---
11	Central Caribbean	Mária La Gorda, Cuba	July, 1999	M	M	0	4	4	0	4	4	50 x 2					4			1.8 ± 1.9
12	Central Caribbean	Cayman Islands	June, 1999, & June, 2000	M	M	2	40	42	2	40	42	30 x 2	1			1	39		1	0.2 ± 1.4
13	Eastern Caribbean	Virgin Islands	July, 1999 – Aug., 2000	H	H	4	26	30	4	23	27	30 x 2				4	23	2	1	2.6 ± 5
14	Eastern Caribbean	Windward Netherlands Antilles	Dec., 1999	M	L	0	24	24	0	24	24	30 x 2					21	3		0
15	Eastern Caribbean	Grenadines, St. Vincent	June, 1999	M	M	2	3	5	2	3	5	30 x 2	2				3			2.4 ± 3
16	Southern Caribbean	Los Roques, Venezuela	Oct., 1999	L	L	7	6	13	7	6	13	30 x 2	4	1	2		6			5.5 ± 10.8
17	Southern Caribbean	Bonaire	Feb., 1999	M	M	0	6	6	0	4	4	30 x 2					6			0
18	Southern Caribbean	Curaçao	Aug., 1998 & Jan., 2000	H	H	0	14	14	0	4	4	30 x 2					14			0
19	Southern Caribbean	Costa Rica	Oct., 1999	H	M	1	2	3	1	2	3	30 x 2				1	1		1	23 ± 33
20	Brazilian	Abrolhos, Brazil	Feb.-April, 2000	M	L	6	7	13	6	5	11	30 x 2					6		7	0
Total						53	249	302	48	223	276		23	4	10	16	221	9	19	2.3 ± 5.6

[1]The threat index (H=high, M=medium, L=low) for each area is based on model outputs from Bryant et al.'s (1998) global *Reefs at Risk* classification.
[2]30 x 2 = 30 m long x 2 m wide belt transects; 50 x 2 = 50 m long x 2 m wide belt transects; 7.5 = 7.5 m radius cylinders

Table 2. Summary of mean sampling effort in deep sites for each assessment.

ID#	Mean depth (m)	Mean sampling effort/site in deep (> 5m) sites (for a maximum of 10 transects)				
		Benthic component (#)			Fish component-belt transects	
		Transects	Corals	Quadrats	#	Area (m²)
1	8	10.0	32	42	10.0	600
2	10	9.9	84	43	9.9	596
3	9	9.3	58	42	---	---
4	14	9.6	91	48	9.8	591
5	21	10.0	118	48	10.0	600
6	10.5	10.0	50	41	---	---
7	10.5	9.6	40	48	6.0	600
8	13	9.2	45	43	3.0	180
9	7.5	9.2	83	45	10.0	600
10	10	10.0	100	19	---	---
11	7.5	10.0	84	43	6.0	600
12	10.5	9.6	90	48	9.7	582
13	10.5	9.8	66	47	10.0	600
14	13	9.5	55	40	10.0	600
15	10.5	10.0	96	49	10.0	600
16	10	5.8	56	18	9.8	590
17	10	8.0	95	32	9.8	585
18	13.5	8.4	138	19	3.3	195
19	6.5	10.0	47	48	10.0	600
20	6	9.6	88	48	10.0	600

Table 3. Summary of means and standard deviations for selected benthic AGRRA indicators for the 20 assessments (for a maximum of 10 transects/site).

ID#	Mean depth (m)	≥25 cm stony corals (#)	Live stony coral cover (25%)	Stony coral density ≥25 cm corals (#/10 m)	Stony coral density <2 cm corals (#/m²)	Partial-colony mortality (%) Recent	Partial-colony mortality (%) Old	Stony corals (%) Standing dead	Bleached	Diseased	Algal overgrowth	Fish bites	Snails/Worms	Damselfish gardens
A. Shallow (≤5 m) sites														
1	4	109	18.5 ± 10.6	5.8 ± 2.3	4.5 ± 1.3	2.0 ± 8.3	24.1 ± 30.6	11.0	0.9	2.8	---	---	---	---
2	1	1275	37.8 ± 16.7	10.0 ± 3.2	2.5 ± 1.3	4.4 ± 11.7	21.6 ± 25.4	8.3	14.3	5.9	4.2	5.1	8.5	2.2
3	4	165	---	5.5 ± 2.2	---	0.8 ± 3.8	28.8 ± 28.7	15.2	1.8	1.2	0.6	---	---	---
4	3	137	9.5 ± 2.6	7.5 ± 2.0	2.3 ± 2.7	1.3 ± 7.7	42.3 ± 34.6	24.8	0	4.4	---	---	---	---
5	---[1]	---	---	---	---	---	---	---	---	---	---	---	---	---
6	4.5	137	18.7 ± 9.3	6.0 ± 2.8	1.0 ± 0.7	0.4 ± 2.9	6.9 ± 11.8	---	5.8	0	35.8	1.5	---	---
7	---	---	---	---	---	---	---	---	---	---	---	---	---	---
8	2	134	19.2 ± 11.8	7.5 ± 2.4	2.7 ± 3.3	26.9 ± 22.9	37.8 ± 23.3	6.0	10.4	13.4	0	6.7	27.6	0
9	---	---	---	---	---	---	---	---	---	---	---	---	---	---
10	4	292	---	11.1 ± 5.7	---	3.4 ± 10.5	43.1 ± 31.4	17.1	20.2	1	1.4	---	---	---
11	---	---	---	---	---	---	---	---	---	---	---	---	---	---
12	3.5	104	19.3 ± 6.1	5.8 ± 2.4	4.5 ± 3.3	0.5 ± 3.3	16.9 ± 22.7	---	0	4.8	0	0	3.8	1.0
13	4.5	248	14.0 ± 7.2	8.0 ± 3.3	4.2 ± 2.7	3.6 ± 5.3	44.8 ± 33.9	1.6	28.6	2.8	37.1	17.3	25.8	2.0
14	---	---	---	---	---	---	---	---	---	---	---	---	---	---
15	3.5	160	29.5 ± 5.7	8.3 ± 1.4	3.1 ± 2.9	1.9 ± 7.2	22.1 ± 21.5	6.3	2.5	0	0.6	0.6	18.1	1.3
16	2.5	332	14.6 ± 12.4	8.1 ± 4.0	1.3 ± 2.0	5.4 ± 9.8	21.1 ± 25.3	52.1	3.6	0.9	2.1	1.2	21.4	0.6
17	---	---	---	---	---	---	---	---	---	---	---	---	---	---
18	---	---	---	---	---	---	---	---	---	---	---	---	---	---
19	2	44	3.4 ± 1.0	6.1 ± 2.7	0.3	1.3 ± 6.3	28.0 ± 26.1	6.8	4.5	6.8	40.9	11.4	0	4.5
20	4	503	10.6 ± 5.4	12.4 ± 6.0	9.4 ± 2.4	0.1 ± 0.9	18.3 ± 21.9	0	0.4	0	---	---	---	---
Mean	*3.2*	*280*	*17.7 ± 9.5*	*7.9 ± 2.2*	*3.3 ± 2.5*	*4 ± 7.1*	*27.4 ± 11.6*	*14.9*	*7.2*	*3.4*	*12.3*	*5.5*	*15.0*	*1.7*
B. Deep (>5 m) sites														
1	8	194	13.5 ± 10.1	3.7 ± 1.7	4.7 ± 1.2	4.4 ± 12.4	26.1 ± 28.7	6.2	14.9	1.0	8.2	---	---	1.0
2	10	1347	25.0 ± 14.3	10.1 ± 4.8	9.7 ± 4.2	16.5 ± 29.9	17.9 ± 24.3	4.1	8.5	17.7	7.9	0.1	0.1	2.9
3	9	406	---	6.9 ± 2.7	---	2.9 ± 8.8	29.5 ± 29.7	11.6	3.2	0.5	1.5	1.7	0.2	1.2
4	14	2362	19.1 ± 8.7	10.2 ± 3.7	5.9 ± 2.7	3.3 ± 11.8	24.2 ± 25.2	1.1	0.3	5.4	---	---	---	---
5	21	235	57.8 ± 13.1	12.4 ± 2.8	1.9 ± 0.8	1.8 ± 6.1	9.5 ± 16.4	1.3	3.4	0	3.4	7.2	---	1.3
6	10.5	151	22.2 ± 13.0	6.9 ± 3.4	3.1 ± 0.1	0.1 ± 1.1	8.2 ± 13.6	---	2.6	0	35.1	---	---	---
7	10.5	951	14.5 ± 6.9	5.3 ± 2.3	3.5 ± 2.7	17.8 ± 19.9	14.5 ± 16.4	5.6	10.4	13.9	---	---	---	1.7
8	13	541	20.9 ± 13.1	6.1 ± 2.4	1.7 ± 1.1	5.0 ± 12.0	26.3 ± 25.9	4.1	11.1	3.7	0.4	3.9		9.4
9	7.5	909	21.1 ± 9.9	9.6 ± 2.5	61 ± 3.8	2.9 ± 9.0	24.8 ± 24.7	0.4	10.0	3.5	31.7	10.5	8.6	40.9
10	10	1004	---	11 ± 5	---	6.3 ± 18.0	29.9 ± 29.9	11.8	17.6	1.9	1.1	---	---	---
11	7.5	334	20.2 ± 5.1	9.1 ± 2.6	1.7 ± 1.1	5.5 ± 12.8	29.4 ± 28.1	1.8	5.4	4.8	1.2	---	---	47.6
12	10.5	3617	20.5 ± 9.1	10.2 ± 4.2	3.9 ± 2.1	4.2 ± 13.2	24.0 ± 25.1	1.1	1.4	5.3	0.3	0.4	0.2	2.5
13	10.5	1723	22.3 ± 12.1	8.9 ± 4.4	9.1 ± 4.6	1.5 ± 5.6	29.8 ± 29.6	1.0	26.8	6.2	8.6	8.0	1.2	5.2
14	13	1309	21.4 ± 12.7	6.5 ± 3.2	4.9 ± 4.6	1.4 ± 7.7	20.8 ± 24.8	0.8	26.5	1.4	0.2	0.4	0.4	1.3
15	10.5	288	39.1 ± 9.8	10.4 ± 2.9	2.8 ± 2.4	1.6 ± 5.7	26.2 ± 25.6	0.3	11.8	4.2	3.8	1.4	1.0	17.4
16	10	335	41.6 ± 2.2	10.4 ± 3.2	2.5 ± 3.5	4.1 ± 10.1	20.0 ± 18.8	6.6	4.2	3.0	1.2	3.6	2.1	14.3
17	10	570	46.5 ± 13.3	13.3 ± 4.1	4.2 ± 2.7	0.7 ± 2.5	31.3 ± 27.5	2.3	27.2	5.3	1.1	6.5	0.4	13.3
18	13.5	1925	35.2 ± 11.9	17.9 ± 5.3	4.0 ± 4.1	1.1 ± 3.6	20.0 ± 20.4	0.5	0.1	10.4	0.8	1.5	0.7	3.5
19	6.5	93	2.5 ± 1.1	5.4 ± 1.8	3.5 ± 3.1	1.8 ± 7.1	14.3 ± 18.5	---	9.7	9.7	22.6	2.2	---	---
20	6	619	20.5 ± 9.9	11.5 ± 4.6	14.6 ± 3.8	0.4 ± 3.9	11.3 ± 18.6	0	2.9	0	---	---	---	0.3
Mean	*10.6*	*945.7*	*25.8 ± 13.3*	*9.3 ± 3.3*	*4.4 ± 3.4*	*4.2 ± 4.7*	*21.9 ± 7.2*	*3.5*	*9.9*	*4.9*	*7.6*	*3.6*	*1.5*	*1.5*

--- = no data

Table 4. Comparison of recent and old partial-colony mortality, incidence of standing dead, bleaching, and disease for the 20 most common stony coral species or taxa (all colonies ≥25 cm in diameter), for a maximum of 10 transects/site.

| Coral species or taxon | Stony corals (#) | Partial-colony mortality (%) | | Standing dead | Bleached | Stony corals (%) (not including standing dead) | | | | | | |
		Recent	Old (minus standing dead)			Total	BBD	WBD	WP	YBD	Other	Unknown
Montastraea annularis	4220	6.9	33.3	1.9	15.3	9.7	1.0		6.0	2.3	0.3	0.1
Montastraea faveolata	2368	5.5	24.2	0.4	12.5	9.4	1.0		6.3	1.2	0.8	
Montastraea cavernosa	1727	3.1	23.5	1.2	10.0	1.7	0.6		0.4	0.1	0.6	
Siderastrea siderea	1465	2.5	22.4	0.4	11.9	4.4	0.8				2.7	
Montastraea franksi	1397	8.4	19.2	0.6	14.0	10.2	3.7		3.7	1.6	1.2	0.1
Porites astreoides	1211	2.1	11.7	0.5	4.8	2.5					2.5	
Diploria strigosa	1195	4.3	19.6	2.8	11.1	2.8	0.5		1.5	0.3	0.3	0.2
Agaricia sp.	1170	3.1	22.6	0.8	4.1	3.4	0.1		2.2		0.7	0.3
Acropora palmata	1465	3.8	24.3	32.2	10.0	9.1		2.4			1.0	5.6
Mussismilia braziliensis	871	0.1	15.0	0.0	1.0	0.0						
Porites porites	869	3.8	26.8	2.1	2.7	2.0					2.0	
Colpophyllia natans	760	3.2	19.5	1.7	4.6	4.4	1.5		1.9		1.1	
Diploria labrynthiformis	501	5.8	19.4	1.6	10.3	3.2	0.6		1.4	0.2	1.0	
Agaricia agaracites	376	2.6	18.9	0.3	3.5	3.5	0.3		2.9	0.3		
Millepora sp.	333	0.5	15.4	3.6	0.6	0.6					0.6	
Millepora complanata	267	4.6	20.6	5.6	14.3	0.4	0.4					
Acropora cervicornis	277	7.3	23.5	18.4	6.6	12.8		12.4			0.4	
Agaricia tenuifolia	308	16.5	38.0	29.2	4.1	0.9						0.9
Stephanocoenia intersepta	207	1.6	29.4	0.5	5.3	21.4	1.5			0.5	19.4	
Meandrina meandrites	155	4.5	15.0	0.0	1.9	5.8	1.3		2.6			
Total (N); Mean (others)	**21,142**	**4.5**	**22.1**	**5.2**	**7.4**	**5.4**						

[1]BBD = black-band disease; WBD = white-band disease; WP = white plague; YBD = yellow-blotch (=yellow-band) disease; Other = dark spots, white pox (=patchy necrosis), etc.

Table 5. Comparison of the coefficient of variation (standard deviation divided by the mean) for 12 AGRRA indicators in the deep sites (>5 m) at four spatial scales.

AGRRA Indicator	Coefficient of Variation (%)			
	within Transects (~0-0.01 km)	within Site/ between Transects (~0.01-0.1 km)	within Assessment/ between Sites ~(1-100 km)	between Assessments (~100-1000 km)
Live coral cover (%)	---	37	34	49
Density of ≥25 cm stony corals (#)	---	37	23	38
Maximum diameter of the *M. annularis* complex (cm)	44	36	33	28
Recent partial-colony mortality (%)	122	138	78	116
Old partial-colony mortality (- standing dead) (%)	100	50	26	30
Total mortality (including standing dead) (%)	93	44	28	33
Relative abundance macroalgae (%)	76	56	56	58
Macro canopy height (cm)	41	38	36	87
Relative abundance crustose coralline algae (%)	64	46	33	57
Total AGRRA fish density (#/100 m^2)	---	46	40	54
AGRRA herbivore density (#/100 m^2)	---	49	36	40
AGRRA carnivore density (#/100 m^2)	---	104	57	106

Table 6. Summary of 15 AGRRA indicators that were used to develop a preliminary biotic health index showing major characteristics of each for the surveys synthesized in this volume.

| AGRRA indicator	Ecological relevance	Spatial scale variation S = Small (<1 km) I = Interm. (1-100 km) L = Large (100-1000km)	Approximate temporal signature S = Short (< 2yrs) I = Interm.(2-10 yrs) L = Long (>10 yrs)	Stress type Indicator: Acute/chronic	Qualitative relationship	This volume		
						Regional		End-members:
						Average (Norm)	Endpoints	Lowest Highest
Live stony coral cover (%)	Community	L	S-L	Either	Low=unfavorable High = favorable	26	3 – 56	Costa Rica Flower Gardens
Large coral density (# ≥25 cm)/10 m	Community	S, L	I to L (include standing dead)	Chronic	Low = unfavorable High = favorable	9	4-18	Abaco Curaçao
Maximum diameter of *M. annularis* complex (cm)	Individual Community	S	I to L	Chronic	High = favorable Low = unfavorable	71	49 – 115	Lighthouse Atoll Los Roques
Recent partial-colony mortality (%)	Individual Ecosystem	S	S	Acute	Low = favorable High = unfavorable	4	1 - 18	Veracruz Yucatan
Old partial-colony mortality (–standing dead) (%)	Individual Ecosystem	S	I	Chronic	Low = favorable High = unfavorable	22	8 - 31	Veracruz Bonaire
Standing dead corals (%)	Individual Ecosystem	S	S-L	Either	Low = favorable High = unfavorable	4	0 - 12	St. Vincent Belize
Diseased corals (%)	Individual	S	S	Acute	Low = favorable High = unfavorable	5	0 - 18	Flower Gardens Andros
Bleached corals (%)	Individual		S	Acute	Low = favorable High = unfavorable	10	0 - 27	Curaçao Bonaire
Small corals (# ≤ 2 cm/m²)	Ecosystem		S	Either	Low = unfavorable High = favorable	4	2 - 15	Yucatan Abrolhos
Macroalgal index	Community Ecosystem		S, I	Chronic	Low = favorable High = unfavorable	82	12 - 215	Flower Gardens Andros
Relative abundance of crustose coralline algae (%)	Community	L	S, I	Chronic	Low= unfavorable High = favorable	29	11 - 42	Flower Gardens Turks & Caicos
Diadema density (#/100 m²)	Community		S-I	Either	Low = unfavorable High = favorable	2	0 – 23	SEVERAL Costa Rica
Total AGRRA fish density (#/100 m²)	Community	L	I	Chronic	Low = unfavorable High = favorable	49	21 – 123	Andros Abrolhos
AGRRA herbivore density (#/100 m²)	Community Ecosystem	S	I	Chronic	Low = unfavorable High = favorable	31	15 - -54	Andros Abaco
AGRRA carnivore density (#/100 m²)	Community Ecosystem	S, L	S	Either	Low = unfavorable High = favorable	6	0.4 – 26	St. Vincent Abrolhos
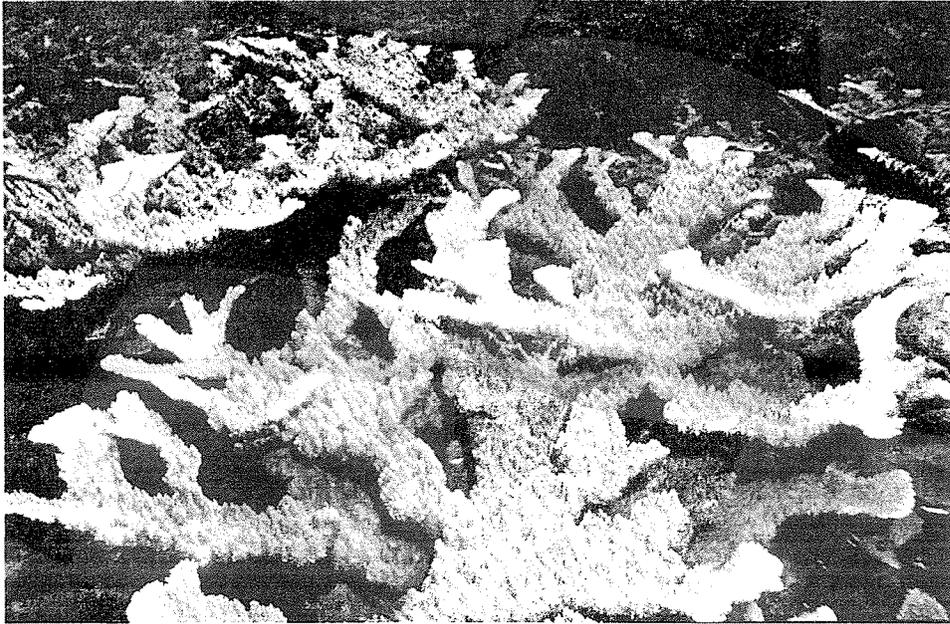
Plate 2A. Historically, many of the shallow crests of ocean-facing Caribbean reefs looked much like this luxuriant thicket of *Acropora palmata*. Beginning in the early 1970's, colonies of *A. palmata* and of *A. cervicornis* began to die from the effects of what has become known as white-band disease. (Photo Robert N. Ginsburg)

Plate 2B. The decline of acroporids has been so pervasive in the last three decades that numerous reef crests are now little more than vast cemeteries of dead coral. Many large dead acroporids are still "standing" in growth position (as shown here). AGRRA surveys have revealed a number of healthy reefs off Andros (this volume) and Cuba (subsequent assessments) where live acroporids are locally abundant. (Photo Robert S. Steneck)
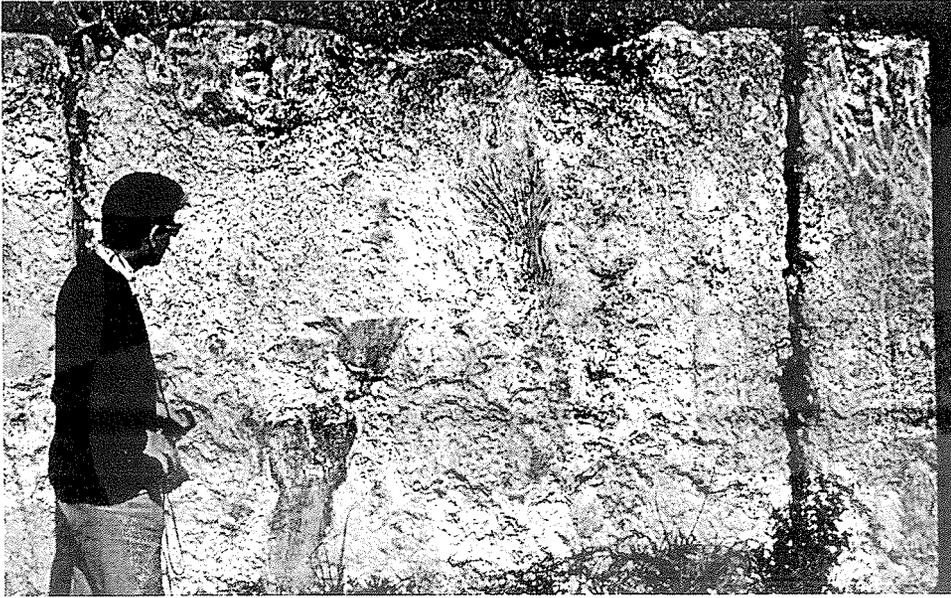
Plate 3A. How much coral is in a coral reef limestone? The wall above in an abandoned quarry, now a State Park on Windley Key, Florida, shows a section of a Late Pleistocene reef limestone, *ca.* 125,000 years old. Measurements of the total area of coral that is visible to the naked eye within a five block area gave an average of 39% . Only the larger massive coral skeletons are in growth position, and most coral is fragmented. Including the smaller fragments and sand-sized grains of coral would increase the total to nearly 50% for this patch reef community. (Photo Robert N. Ginsburg)
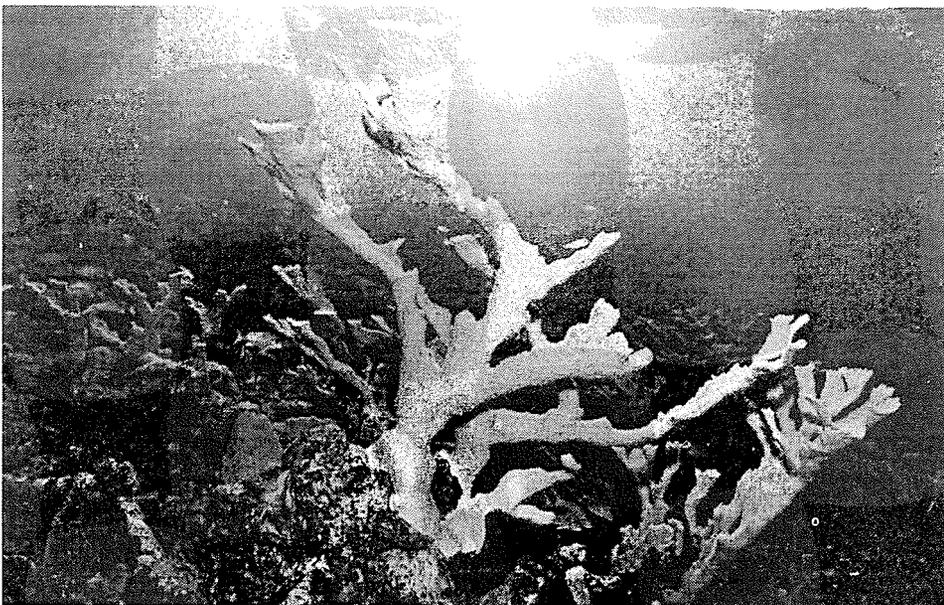

Plate 3B. AGRRA indicators can be used to provide norms of reef condition, like the value of calibrating the geological record of a coral community exemplified 3A. As additional AGRRA assessments are undertaken, the regional norms will become more representative of the region thus moving towards the development of a regional baseline of *current* coral reef health. The combination of both past and current temporal perspectives is key in understanding how to preserve coral reefs for future generations. (Photo Bernhard Riegl)