

REPORT

B. J. Greenstein · H. A. Curran · J. M. Pandolfi

Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective

Accepted: 19 May 1998

Abstract In recent years, marine scientists have become increasingly alarmed over the decline of live coral cover throughout the Caribbean and tropical western Atlantic region. The Holocene and Pleistocene fossil record of coral reefs from this region potentially provides a wealth of long-term ecologic information with which to assess the historical record of changes in shallow water coral reef communities. Before fossil data can be applied to the modern reef system, critical problems involving fossil preservation must be addressed. Moreover, it must be demonstrated that the classic reef coral zonation patterns described in the early days of coral reef ecology, and upon which “healthy” versus “unhealthy” reefs are determined, are themselves representative of reefs that existed prior to any human influence. To address these issues, we have conducted systematic censuses of life and death assemblages on modern “healthy” patch reefs in the Florida reef tract that conform to the classic Caribbean model of reef coral zonation, and a patch reef in the Bahamas that is currently undergoing a transition in coral dominance that is part of a greater Caribbean-wide phenomenon. Results were compared to censuses of ancient reef assemblages preserved in Pleistocene limestones in close proximity to each modern reef. We have determined that the Pleistocene fossil record of coral reefs may be used to calibrate an ecological baseline with which to compare modern reef assemblages, and suggest that the current and rapid decline of *Acropora cervicornis* observed on a Bahamian patch reef may be a unique event that contrasts with the long-term persistence of this taxon during Pleistocene and Holocene time.

Key words *Acropora cervicornis* · Shifting baseline syndrome · Pleistocene fossil coral reef assemblages

Introduction

Over the last two decades, coral reefs have changed dramatically, particularly in the western North Atlantic – Caribbean province (Ginsburg 1994; Hughes 1994; Jackson 1997). Coral cover has declined, and has been replaced by fleshy macroalgae in most cases (de Ruyter van Stevenick and Bak 1986; Carpenter 1985; Hughes et al. 1987; Liddell and Ohlhorst 1986; Done 1992a; Wilkinson 1993). Although their relative importance and interrelatedness remain poorly understood, the causes for this transition include: hurricanes (Woodley et al. 1981; Rogers 1993), sea urchin mass mortality (Lessios 1988), coral diseases and coral bleaching (Brown and Ogden 1993; Glynn 1993; Littler and Littler 1996; Miller 1996), eutrophication (Tomascik and Sander 1987), sedimentation (Rogers 1990) and a variety of human-induced effects (Hughes 1994). The branching coral, *Acropora cervicornis*, particularly has suffered an extreme decrease in abundance throughout the Caribbean as a result of this confluence of factors (Hughes 1994).

While these transitions have alarmed the marine scientific community, the lack of long-term data on coral community composition has confounded attempts to determine whether these faunal replacements are natural components of long term ecological cycles or an unprecedented phenomenon resulting from primarily anthropogenic disturbances (e.g., Grigg and Dollar 1990; Brown 1997). As a result, frustration over the temporally limited view afforded by monitoring studies that rarely span a scientific career increasingly pervades the literature (e.g., Done 1992b; Jackson 1992; Hughes 1994; Bak and Nieuwland 1995).

Jackson (1992) suggested that the reef fossil record represents the exclusive database from which long term

B. J. Greenstein (✉)

Department of Geology, Cornell College, 600 First St. West, Mt. Vernon, Iowa 52314, USA.

H. A. Curran

Department of Geology, Smith College, Northampton, MA 01063, USA

J. M. Pandolfi

Paleobiology Department, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

(geological time scales) data on changes in coral community composition may be collected; similar coral communities and zonation patterns have prevailed for the past 600 ka in Barbados (Jackson 1992), and at least the past 125 ka in Papua, New Guinea (Pandolfi 1996). Ancient coral reef assemblages are preserved in Pleistocene and Holocene deposits exposed throughout the Caribbean region (e.g., Mesollela 1967; Mesollela et al. 1970; Geister 1980; White et al. 1984; White and Curran 1987, 1995; Macintyre 1988; White 1989; Johnson et al. 1995; Greenstein and Curran 1997; Greenstein et al. 1988). Moreover, much recent work has demonstrated that the excellent preservation exhibited by these deposits (Greenstein and Moffat 1996) has resulted in remarkable similarity of taxonomic composition and diversity between living shallow water reef coral associations and Pleistocene reef coral assemblages (Greenstein and Curran 1997; Greenstein et al. 1998). Given these observations, it seems obvious that the Pleistocene and Holocene fossil record of coral reefs is the only place to seek historical precedents for recent transitions observed today. Our purpose is to investigate whether the devastation of once thriving thickets of *Acropora cervicornis* and their subsequent replacement by colonies of *Porites porites* on a Bahamian patch reef has a preserved Pleistocene precedent.

Two significant problems must be overcome before any analysis of fossil data can be meaningfully applied to modern ecological issues:

1. Preservational bias, while corals can potentially produce spectacular fossil assemblages, coral reef sediments may not preserve ecologically significant events. The mass mortality of *Diadema antillarum* during 1983–84 was quickly erased from the sedimentary record, even though innumerable tests and spines of this animal were observed accumulating on surficial sediments (Greenstein 1989). Results of field experiments using the crown-of-thorns starfish, *Acanthaster planci*, suggested that preservation of starfish at outbreak proportions is tenuous in the sedimentary record of the Great Barrier Reef (Greenstein et al. 1995). Finally, the preservation potential of the fleshy macroalgae observed on Caribbean reefs today is very low (Kauffman and Fagerstrom 1993).
2. Shifting baseline syndrome, Jackson (1997) argued that the pioneering studies of modern reef ecology (e.g., Goreau 1959; Randall et al. 1961; Randall 1965) began after significant changes in coral reef ecosystems had already occurred. Against what standard, then, can current faunal and floral transitions be compared? Most reef ecologists accept, *a priori*, that coral community composition and patterns of zonation documented in the early days of coral reef ecology are “natural”. Jackson (1997) suggested that this assumption may be false, and he used written historical records to demonstrate that coastal Caribbean

ecosystems were severely degraded long before ecologists began to study them, primarily as a result of the very early decimation of marine megavertebate faunas by Western European colonial expansion. While not addressing the very early degradation of Caribbean reef ecosystems, concerns over a shifting baseline were also voiced by Precht (1990) and Woodley (1992), who suggest that the reef coral assemblages in Discovery Bay, Jamaica, from which the classic reef zonation patterns were described, had a unique storm disturbance history relative to most reefs in the Caribbean region.

In at least two areas of the Caribbean, the decline of live coral has been replaced by other species of coral rather than fleshy macroalgae. Replacement by corals has been observed in Belize (Aronson and Precht 1997) and the Bahamas (Curran et al. 1994), where dense thickets of *Acropora cervicornis* have been replaced by *Agaricia tenuifolia* and *Porites porites*, respectively. Because both *A. tenuifolia* and *P. porites* produce potentially preservable skeletons, the fossil record should yield some insight as to whether a historical precedent exists for either event. With this premise in mind, Aronson and Precht (1997) examined cores taken through the Holocene sediments accumulating on the Belize reef and concluded that no recognizable signals (abrupt changes in coral taxa, or evidence of an essentially monospecific death assemblage) of similar transitions were present, suggesting that the present drastic reduction of *A. cervicornis* has no precursor in the recent geological past (at least 3800 years; Aronson and Precht 1997). However, Jackson's (1997) concern about the degradation and subsequent change in reef coral communities owing to colonial activities could not be addressed by their core data.

Here, we pursue two objectives:

1. To determine whether the Pleistocene fossil record of Caribbean coral reefs provides an adequate ecological baseline with which to address a variety of current issues facing modern reef systems. To achieve this objective, we compared the taxonomic composition of modern Floridian patch reefs to that represented in Pleistocene reefs that were thriving long before any potential anthropogenic disturbance could have occurred. We chose modern reefs whose taxonomic composition conformed to early (pre-1980) descriptions (for example Ginsburg 1964; Multer 1977) of the majority of Caribbean patch reefs. If the Pleistocene deposits preserve community structure similar to that obtained from the modern reefs, then the shifting baseline syndrome is not an issue for reef coral communities conforming to pre-1980 descriptions. If the Pleistocene coral reef assemblages preserve community structure that is markedly different than that described for modern reefs, then the shifting baseline syndrome needs to be further explored. Our results suggest that concern

over the shifting baseline syndrome may be mitigated where a sufficient fossil record occurs.

2. To use data on coral reef community structure obtained from Pleistocene deposits to test the hypothesis that the currently observed widespread demise of *Acropora cervicornis* in the Caribbean and tropical Western Atlantic region is without a preserved precedent in Pleistocene time. To achieve this objective, we examined life and death assemblages on a Bahamian patch reef that has witnessed the complete die-off of once-dominant *Acropora cervicornis* and subsequent replacement by *Porites porites*, and compared our results to those obtained from a Pleistocene reef assemblage exposed approximately 2 km away on the island of San Salvador, Bahamas. Results suggest that the current transition observed in the Bahamas does not have a Pleistocene precedent preserved on San Salvador Island.

Materials and methods

Methods of data capture and analysis were essentially the same at all sites and locations, although the actual number of samples varied. The sampling protocol was developed by Pandolfi and Minchin (1995) and first applied to reef coral life and death assemblages in the Indo-Pacific. Greenstein and Pandolfi (1997) and Pandolfi and Greenstein (1997a) subsequently applied the sampling strategy to shallow and deep reef coral life and death assemblages, respectively, in the Florida Keys. We refer the reader to those studies for additional details.

Field methods

At all field localities, we used the linear point intercept (LPI) method (Lucas and Seber 1977) and constructed transects on living reefs and fossil assemblages. In order to estimate adequately cover for the widest range of coral growth forms and colony sizes, transects of 40 m length were used (Mundy 1991), each separated by 20–50 m. At 20 cm intervals along each transect, the transect intercept was noted. From the modern reef environments, the following data were recorded if the transect intercepted a coral: species, colony size, colony orientation, growth form, and whether the colony was alive or dead and whole or fragmented. The same data (with the obvious exception of whether the coral colony was alive or dead) were collected from transects laid across Pleistocene deposits.

In modern environments, we define the death assemblage as *in situ* dead coral material encountered along each transect and coral rubble accumulating adjacent to the reef framework. Dead coral colonies encountered along the transect were identified to the species level only if we could recognize them without breaking them open or peeling off any algae or other overgrowth. Bulk rubble samples composed of dead coral were taken at the 5, 15, 25 and 35 m marks of each transect. This methodology allowed us to sample adequately the death assemblage as defined here. Rubble samples were placed in a 5 mm mesh bag constrained by a 10 l bucket. Thus, coral species and growth form were recorded for each specimen > 5 mm in size that preserved morphology sufficient to permit identification. Taxonomic data obtained from the rubble samples were pooled with that obtained from dead corals encountered along each transect. Originally we estimated that four 10 l samples would provide us with approximately 200 specimens (data points): roughly comparable to the number of points censused along the transects for the live fauna.

In practice, where branching coral rubble dominated the substrate, collections often contained many more than 200 specimens. In addition, not all 200 points along the transects fell upon live coral. We were able to allow for the discrepancy in sample size between the two sampling techniques by standardizing the data before analyzing it (see later). The actual number of transects constructed at each site was determined by the size of the reef or fossil exposure. Individual sites are discussed.

Florida Keys—modern reefs

Eight transects were constructed on both Cannon Patch Reef and Horseshoe Reef, which occur in the “back reef” area of the Florida Keys Reef Tract (Fig. 1). Both reefs contain the general coral assemblages described by Ginsburg (1964) and Multer (1977) for patch reefs of the Florida Keys. Cannon Patch Reef is particularly dominated by large colonies of *Montastraea annularis* which form a massive framework within which carbonate sand is accumulating. Throughout this study, we use *M. annularis* to designate any of the sibling species recognized by Knowlton et al. (1992), although *M. faveolata* and *M. annularis* (*sensu stricto*) are the most common species of *Montastraea* present in the life, death and fossil assemblages described in this study. Horseshoe Reef, situated north of Cannon Patch Reef (Fig. 1) is dominated by a variety of corals with massive growth forms, particularly *Colpophyllia natans*, *Diploria strigosa*, and *Montastraea annularis*. Both reefs contain thickets of live *Acropora cervicornis*, and Horseshoe Reef also includes colonies

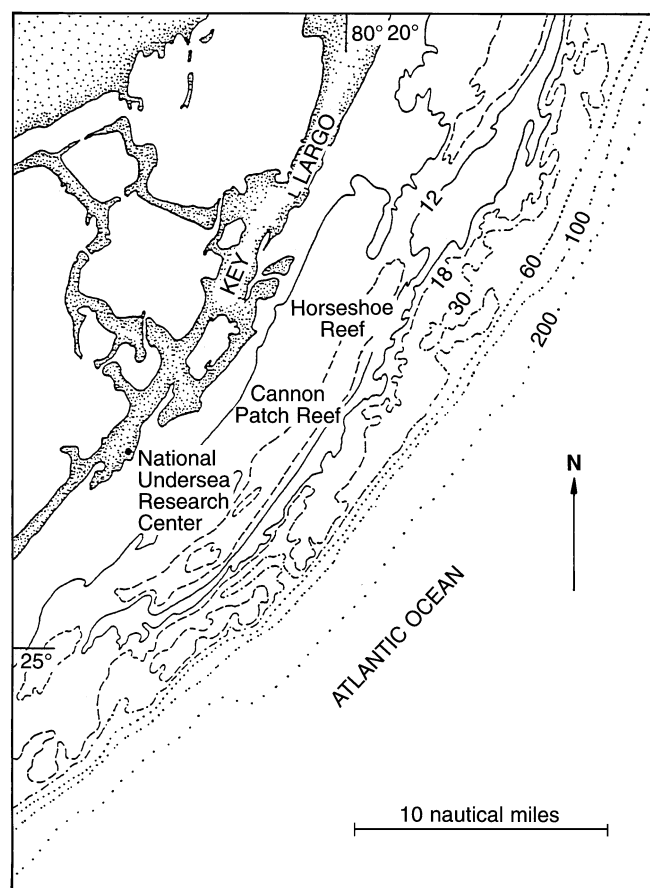


Fig. 1 Map of study area of modern reefs of the Florida reef tract. Operations were based at the National Undersea Research Center on Key Largo

of *Acropora palmata*. We chose these reefs because they exhibited apparently "healthy" living coral assemblages that closely matched those described for Floridian patch reefs by Ginsburg (1964) and Multer (1977).

Florida Keys–Pleistocene coral assemblage

We examined fossil reef coral assemblages from outcrops of the Key Largo Limestone exposed along Adam's Canal (Key Largo) and on Windley Key for comparison to the corresponding life and death assemblages currently accumulating offshore on Cannon Patch Reef and Horseshoe Reef (Fig. 2). There has been some debate as to the reef environment represented by the Key Largo Limestone. Stanley (1966) recognized that the *Montastraea* "annularis" – dominated coral assemblage exposed on Windley Key and along the Key Largo Waterway (now known as Adam's Canal) could represent either the shallow patch reefs or deep water West-Indian bank reefs described by Goreau (1959), and opted for the latter environment for the Key Largo Limestone. Hoffmeister and Multer (1968) agreed that the Pleistocene coral assemblage could reflect either environment, but preferred an interpretation as a shallow patch reef, pointing to stratigraphic constraints and, most importantly, the first description of the reef crest indicator species, *Acropora palmata*, at a similar stratigraphic level in cores obtained several miles east of the exposed *Montastraea* – dominated assemblages. Additional work by various researchers has supported the interpretation of shallow patch reef facies for the Key Largo limestone (for example, Dodd et al. 1973; Hodges 1980).

Line transects 40 m in length were placed along exposures of the Key Largo Limestone and intercepted the fossil reef over approximately a 2 m vertical interval in both Adam's Canal and Windley Key Quarry. At both locations, the transect intercepted *in situ* corals as well as coral rubble and carbonate sand that fills the interstices of the fossil reef complex, and thus our sampling regime represents an average of coral community composition over time. The coral reefs composing the Key Largo Limestone flourished between approximately 140–120 ka during the last interglacial (substage 5e of the marine oxygen isotope scale (see Harrison and Coniglio, 1985), thus the maximum amount of time represented by our sampling regime is

20 000 ka. However, the actual time span represented by these outcrops may be much shorter. Hubbard et al. (1990) determined that the average accretion rate for reefs dominated by *M. "annularis"* in Cane Bay, St. Croix, U. S. V. I. was 0.73 m/1000 y over the last 3–5 ka. Applying this rate to the thickness of the outcrop over which our transects were placed, allows an estimate of 2740 ka represented by our samples. Five transects were accommodated by the canal, while the quarry on Windley Key allowed space for only three transects. Transects from both localities were pooled, and compared with the data obtained from the patch reefs described already.

Bahamas–modern reef

Telephone Pole Reef, located in Fernandez Bay (Fig. 3), is a mid-shelf patch reef with a recent-past history that contrasts with the patch reefs we sampled in the Florida Keys. As recently as 1983, Telephone Pole reef was dominated by thickets of *A. cervicornis* set amidst larger heads of *Montastraea* "annularis" and other massive corals. For unknown reasons, colonies of *A. cervicornis* began to die off to the same extent witnessed on other Caribbean reefs. By 1992, the once-abundant thickets of *A. cervicornis* had been significantly replaced by *Porites porites* (Curran et al. 1994). Today, *A. cervicornis* has been entirely replaced by extensive colonies of *Porites porites*, and recent observation indicates that some of the *P. porites* colonies have begun to degrade (Curran, personal observation, January, 1998). The limited size of Telephone Pole Reef allowed for sampling of only four 40 m transects for modern life and death assemblages.

Bahamas–Pleistocene reef

The regressive stratigraphic sequence and fossil coral reef exposed in the abandoned quarry in Cockburn Town, San Salvador, Bahamas (Fig. 3), includes a coral rubblestone facies, composed predominantly of *Acropora cervicornis*, and a coralstone facies that contains abundant *in situ* *Acropora palmata*, *Montastraea* "annularis", and *Diploria strigosa*. These facies were defined by White et al. (1984) and

Fig. 2 Sample localities for the Key Largo Limestone exposed along Adam's Canal and in the Windley Key Quarry in the Florida Keys. Five transects were constructed along Adam's Canal, and three transects were constructed in the Windley Key Quarry (after Stanley 1966)

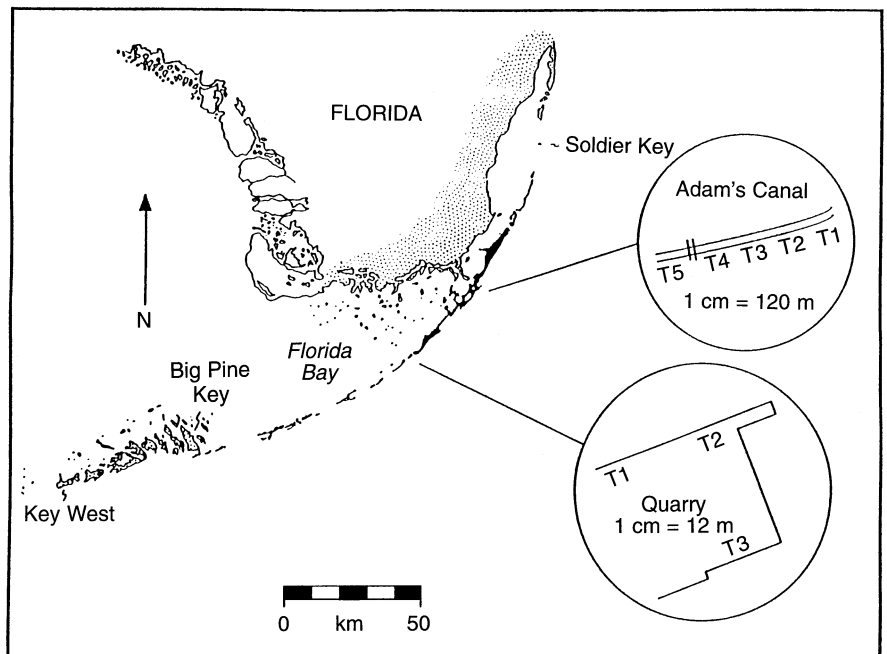
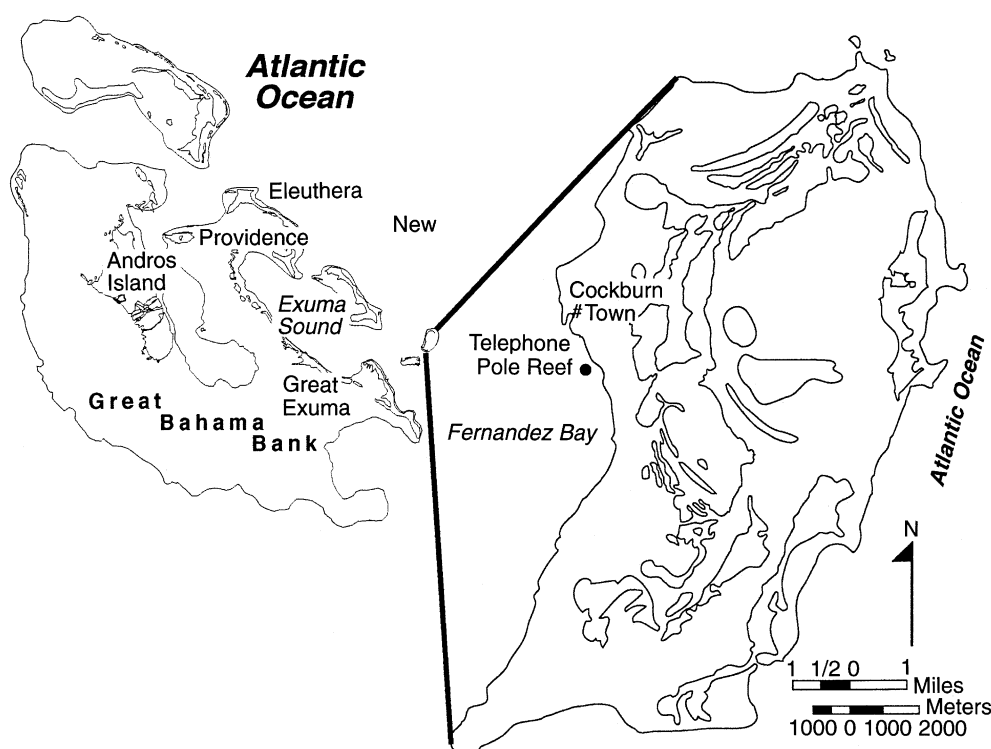


Fig. 3 Area of study, San Salvador Island, Bahamas. Telephone Pole Reef is located in Fernandez Bay, while the Cockburn Town fossil reef is located onshore at the north end of Fernandez Bay, in Cockburn Town



Curran and White (1985), who suggested that they represent back reef and reef tract environments, respectively, of a bank barrier reef complex. Our sampling protocol was essentially the same as that conducted on Key Largo; transects were placed across both facies, representing approximately 1.5 m of vertical exposure, and intercepted both *in situ* coral heads and material within the coral framework. Radiometric age dates obtained from 23 coral specimens obtained at various levels within the vertical exposure revealed that the corals composing the Cockburn Town fossil reef lived between 119–131 ka (Chen et al. 1991), yielding 12 ka represented by our samples. This fossil reef provides an excellent opportunity for a comparative taxonomic study because of its proximity to Telephone Pole Reef where *A. cervicornis* thickets and coral rubble provide modern examples of the ancient coral rubblestone facies described by White et al. (1984) and Curran and White (1985).

Sampling strategy

In order to achieve the stated objectives of this study, it was necessary to examine modern reefs that closely matched early ecological descriptions of presumed “healthy reefs” and compare them to reefs preserved in Pleistocene strata. The modern and Pleistocene reefs of the Florida Keys reef tract were selected for this purpose. Additionally, it was essential that we examined a living reef that had recently undergone a change in coral composition that included the disappearance of living *A. cervicornis*, and compared it to adjacent Pleistocene facies representing a similar environment. The modern patch reef in the Bahamas was particularly well suited for comparison to Pleistocene reef coral assemblages since the transition in coral dominance involved a potentially preservable taxon, *P. porites*, rather than essentially non-preserved macroalgae. Although its proximity to the living reef made the Cockburn Town fossil reef an excellent locality for our comparative study, White et al. (1984) and Curran and White (1985) interpreted the main portion of the Cockburn Town fossil reef as a bank barrier reef system; whereas, Telephone Pole Reef is a patch reef. We note, however, that both paleoecologi-

cal (primarily the coral fauna) and sedimentological (relationships between coral-bearing facies, shallow subtidal calcarenites and eolianites) characteristics as well as the presence of patch reefs in a portion of the outcrop (Chen et al., 1991) suggest that, while not an exact match, the reef exposed near Cockburn Town (and particularly the coral rubblestone facies) represents a depositional environment that is sufficiently similar to the modern reef for meaningful comparisons to be attempted.

We acknowledge that our sample of modern reefs is limited in size, but emphasize that to achieve the first objective of the study, it was essential that we chose reefs that matched pre-1980 descriptions of coral zonation, were in close geographic proximity to Pleistocene exposures, and reflected an environment of deposition similar to that preserved in Pleistocene strata. This effectively limited our survey to include the two patch reefs from the Florida reef tract described above. Had we randomly chosen a larger number of modern reefs for comparative study, our results would have highlighted the changes that have occurred on most reefs since 1980, as well as the differences between such reefs and those preserved in Pleistocene exposures. Potential localities for additional comparative studies exist elsewhere in the Caribbean [e.g., Curaao (Bak 1977; Pandolfi and Jackson, in review) and San Andrés (Geister 1980; Pandolfi and Jackson, unpub. data)]. To achieve the second objective of this study, it was necessary that we examine a modern reef that had recently witnessed a decline in live cover of *A. cervicornis*, was in close geographic proximity to Pleistocene exposures, and occurred in a depositional environment comparable to that preserved in adjacent Pleistocene strata. Telephone Pole Reef is the only modern patch reef on the leeward shelf adjacent to San Salvador Island that fulfills these prerequisites.

Data analyses

From the Florida Keys, our data consist of 32 samples from modern environments (eight transects \times two assemblages, (live and dead), \times two reefs) and eight samples from Pleistocene exposures. From the

Bahamas, our data consist of 8 samples from modern environments (4 transects \times 2 assemblages) and 5 transects from Pleistocene outcrop. We constructed species sampling curves to investigate whether our methodology adequately accommodated the diversity present in the coral assemblages studied. We have shown, in various studies (e.g., Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997a; Greenstein and Curran 1997; Pandolfi 1996), that the methods of data analysis discussed are most appropriate for these data. Comparison of taxonomic composition was calculated using the Bray-Curtis dissimilarity coefficient (Bray and Curtis 1957), where dissimilarity values range from 0 (for a pair of samples with identical taxonomic composition) to 1 (for a pair of samples with no taxa in common). Abundance data were transformed to their square roots prior to the analysis, to reduce the influence of occasional large abundance values for some taxa (Field *et al.* 1982). In addition, the transformed abundance values for each taxon were standardized by the maximum attained by that taxon. The resulting Bray-Curtis matrix was subjected to an ordination technique that provided a visual summary of the pattern of dissimilarity values among the samples. The technique employed was global non-metric multidimensional scaling, or GNMDS (Kruskal 1964), where each sample is represented as a point in a coordinate space with a given number of dimensions. The distances between each pair of points are, as far as possible, in rank order with the corresponding dissimilarities in taxonomic composition; points that are close together on the resulting scatter plot represent transects with similar coral constituents. The degree to which the distances on the scatter plot depart from a perfect rank order fit is measured by a quantity known as "stress". The lower the stress value, the better the representation of the samples in the multidimensional space (stress values less than 0.2 generally result in interpretable results, Clarke and Warwick 1994). The obtained stress values decreased minimally after a two dimensional analysis.

Species richness patterns were compared between life, death, and fossil assemblages. To compute species richness, the number of species in each sample was counted and then corrected for sample size. Thus, species richness = $(S - 1)/(\log N)$, where S = the number of species present in a sample and N = total number of specimens counted.

Results

Florida Keys

The cumulative number of species encountered in each sample was plotted for life, death and fossil assemblages at each site examined on the Florida reef tract and in the Key Largo Limestone (Fig. 4). Eight samples were sufficient to account for coral diversity in life and death assemblages in the modern patch reefs (Fig. 4A). Six transects were sufficient to account for coral diversity in the Pleistocene facies exposed in the Key Largo Limestone (Fig. 4B). These results indicate that sampling is adequate to estimate species richness in the fossil assemblages and compare their taxonomic composition to that of the Holocene life and death assemblages occurring offshore.

Results of ordination reveal that samples from live patch reefs are, on the basis of their taxonomic composition, most similar to the samples from the fossil assemblages exposed in the Key Largo Limestone (Fig. 5). Analyses of species richness indicate that life assemblages in the patch reef are significantly

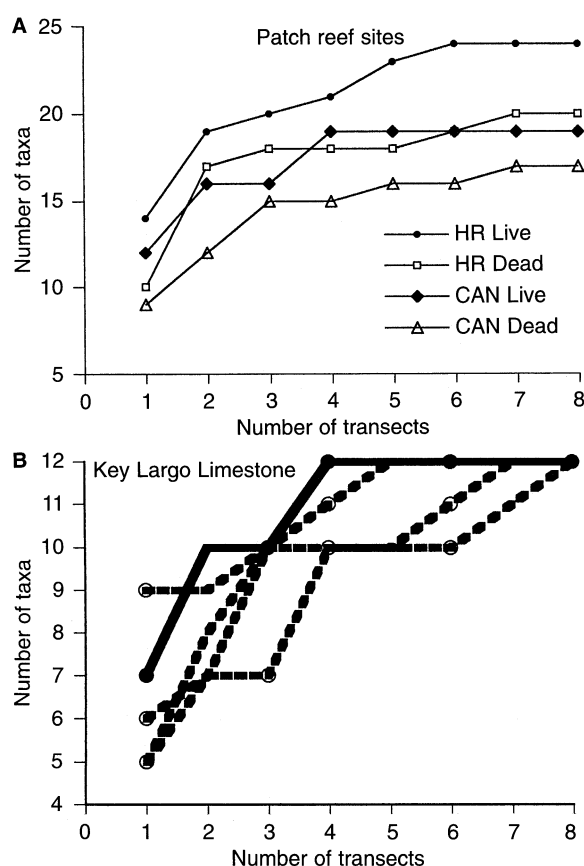


Fig. 4A, B Cumulative diversity of reef coral species versus number of sampling intervals (transects.) **A** Life and death assemblages for Horseshoe Reef (HR) and Cannon Patch Reef (CAN). Each line is a plot proceeding from the first through eighth transect. **B** Cumulative diversity of reef coral species versus number of sampling intervals (transects) from Pleistocene reef coral assemblages exposed along Adam's Canal and in the Windley Key Quarry in the Florida Keys. The solid line is a plot proceeding from the first transect sampled along Adam's Canal to the last transect sampled in Windley Key Quarry. The dashed lines are plots of five random sequences of transects

(ANOVA; $F_{(2,37)} = 14.20$; $P < 0.0005$) more diverse than either their dead or fossil counterparts (Fig. 6).

Bahamas

Species sampling curves indicate that four transects were insufficient to account for the full diversity of the life assemblage on Telephone Pole Reef (Fig. 7A). Sampling curves level off only between the final two transects for both the modern death assemblage and the fossil assemblage exposed in Cockburntown (Fig. 7B, C); we hesitate to claim adequate sampling based on these results.

Results of ordination reveal that samples from life, death, and fossil assemblages are clearly distinct from one another (Fig. 8). Moreover, the taxonomic composition of life assemblages is clearly less similar to that

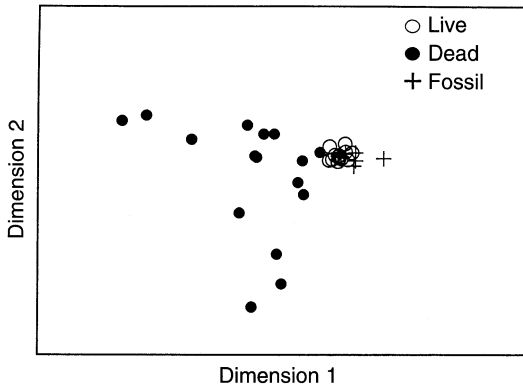


Fig. 5 Two-dimensional global nonmetric multidimensional scaling (GNMDS) ordination of coral life and death assemblages from two patch reefs in the Florida Keys, and fossil assemblages preserved in the Key Largo Limestone. Points closest to one another represent samples (transects) that are more similar in taxonomic composition than points farther away from one another. Note the extreme similarity between samples obtained from the fossil assemblages and those obtained from the living patch reefs. The minimum stress value for the two dimensional analysis was 0.17

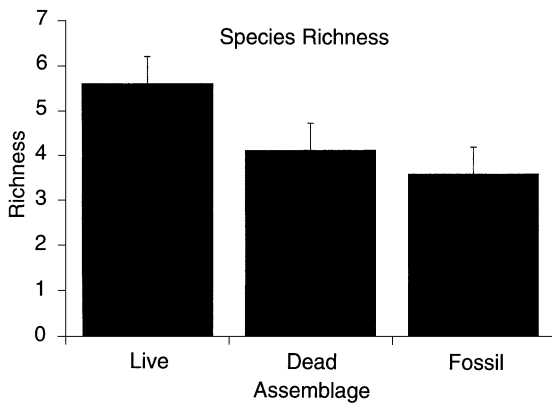


Fig. 6 Comparison of species richness between life, death and fossil assemblages of the Florida Keys. The patch reef life assemblage is more diverse than either the death or fossil assemblages. Error bars are standard errors of the mean, $n = 40$

of the fossil assemblages than to that of the death assemblages (Fig. 8). Analyses of species richness indicate that a significant (ANOVA; $F_{(2,10)} = 121.31$; $P < 0.0005$) decrease in species diversity occurs from life to death to fossil assemblages (Fig. 9).

Discussion

Classic patterns of coral zonation and a shifting ecologic baseline

Results of the ordination of samples from the Florida Keys (Fig. 5) suggest that the taxonomic composition of reef corals preserved in the Key Largo Limestone more accurately represents the assemblage of corals

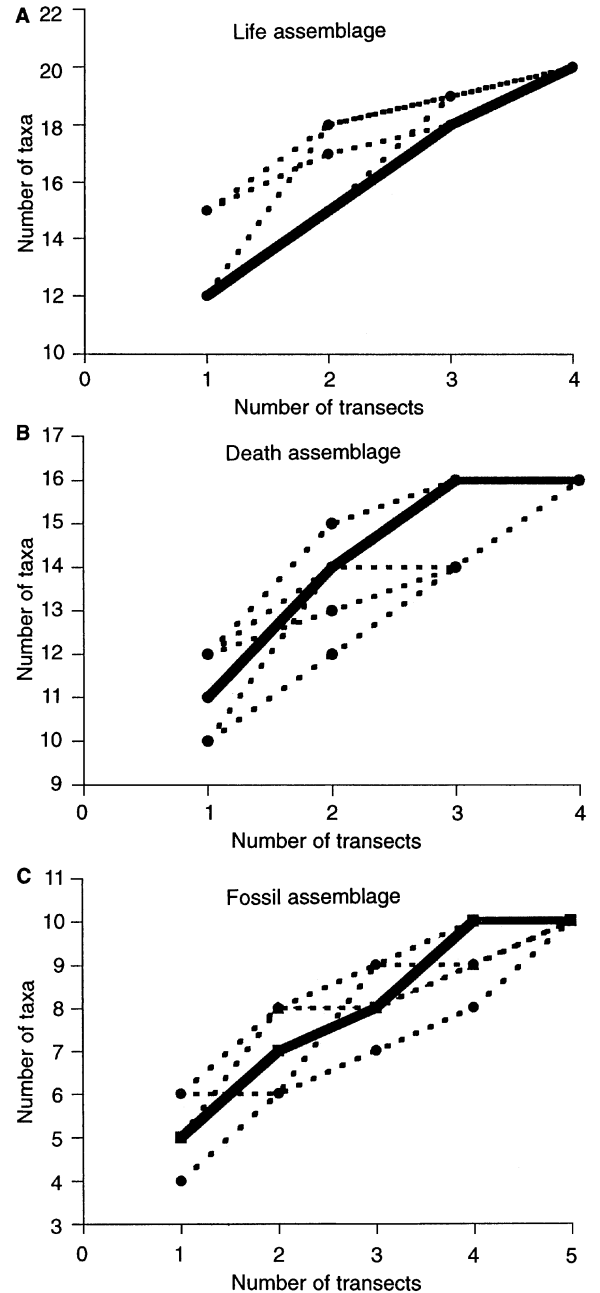


Fig. 7A–C Cumulative diversity of reef coral species versus number of sampling intervals (transects) from **A** live **B** dead and **C** fossil reef coral assemblages present on San Salvador. Four transects accommodated the diversity present in both death and fossil assemblages, but were insufficient to account for the diversity present on the living reef. For all sampling curves, the solid line is a plot proceeding from the first transect through last transect sampled for each assemblage; the dashed lines are plots of five random sequences of transects drawn from each assemblage

currently living in patch reefs offshore than the contemporary death assemblage. The fact that points representing samples from the living and fossil reef are virtually superimposed on one another indicates that taxonomic composition and relative abundance of the living and fossil patch reef are very comparable. The

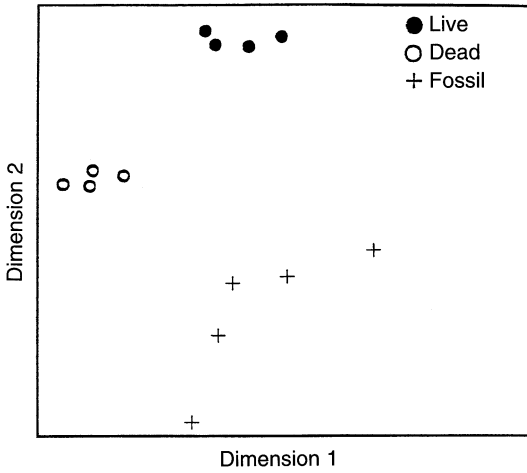


Fig. 8 Two-dimensional global nonmetric multidimensional scaling (GNMDS) ordination of coral life death and fossil assemblages from San Salvador, Bahamas. Points closest to one another represent samples (transects) that are more similar in taxonomic composition than points farther away from one another. Note that each assemblage occupies a distinct portion of ordination space. The minimum stress value for the two dimensional analysis was 0.09

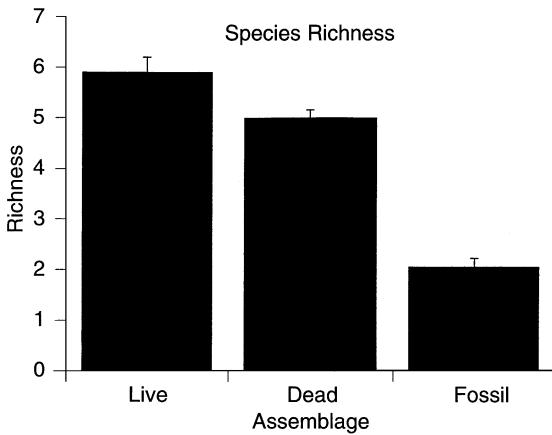
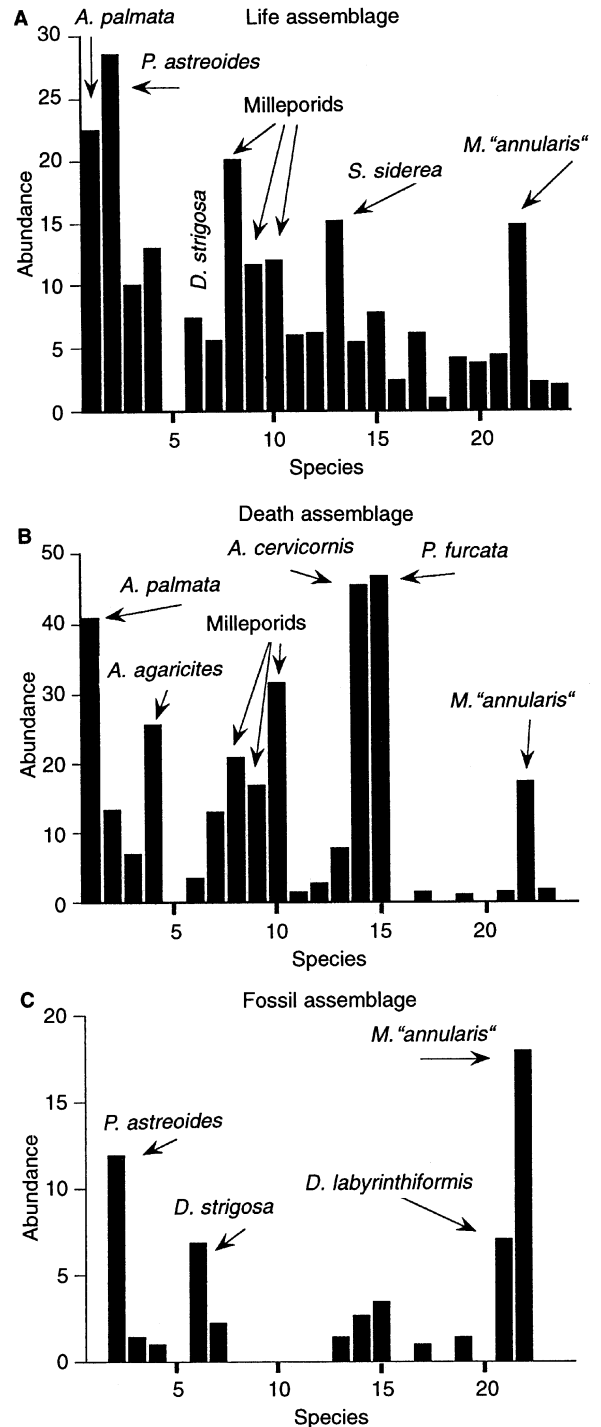


Fig. 9 Comparison of coral diversity between life, death and fossil assemblages on San Salvador as measured by species richness. Decreasing species richness values are the result of the lack of milleporids and coral taxa that are relatively rare on the living reef. Error bars are standard errors of the mean, $n = 13$

results are particularly striking given the amount of time potentially represented by our sampling protocol, and corroborate earlier studies suggesting that coral reef community patterns similar to those present on modern reefs persisted over geologically significant intervals of time (e.g., Mesollela 1967; Jackson 1992; Pandolfi 1996).

Life assemblages in the patch reefs of the Florida Keys are more diverse than either their dead or fossil counterparts owing primarily to the presence of corals that are relatively rare in the Florida reef tract (for example, *Mycetophyllia lamarckiana*, *M. danaana*, *Dichocoenia stokesii* and *Solenastrea bournoni*, Fig. 10).

The primary reason for the greater similarity of fossil assemblages to life assemblages instead of death assemblages in the Florida Keys is the prevalence of living and fossil massive coral colony growth forms (primarily *M. "annularis"* and *D. strigosa*) (Fig. 10). This growth form is relatively rare in the death assemblages surveyed on the Florida patch reefs, but common in both the life and fossil assemblages. The differential representation of this growth form in life/fossil versus death



assemblages has been discussed by Greenstein et al. 1998, Greenstein and Curran (1997) and Pandolfi and Greenstein (1997b) and will not be repeated here. In essence, massive colony growth forms are able to survive an extensive accumulation of a variety of physical, chemical and biological agents of degradation after they die. Thus, although they were present in the death assemblage, we were unable to identify them to the species level. The presence of massive coral colonies that could be identified to the level of species in the Key Largo Limestone suggests that rapid entombment of once-living reef communities has occurred. Several workers have outlined sedimentologic (e.g., White et al. 1984; White and Curran 1987; Curran et al. 1989; White 1989; White and Curran 1995) and taphonomic (for example, Greenstein and Moffat 1996) evidence for rapid burial of late Pleistocene bank-barrier and lagoonal reef systems of the Bahamas Archipelago, as shallow subtidal sands encroached on them in response to post-oxygen isotope Stage 5e regression. Although analyses of the way in which corals are preserved in the Key Largo limestone are lacking, one would predict that such analyses would reveal the rapid entombment reported in the studies cited.

Additionally, the taxonomic congruence exhibited by this analysis suggests to us that, at least for Floridian patch reefs, the classic patterns of coral zonation described by Ginsburg (1964) and Multer (1977) during the early days of “modern” coral reef ecology are consistent with those that existed long before Columbus’ time. We tend to agree with Jackson’s (1997) warning of a growing coral reef ecomanagement culture that is comparable to European “hedgerow ecologists” (Jackson 1997, p. S24) while hastening to point out that, for framework-building corals at least, the Pleistocene fossil record of coral reefs from the wider Caribbean presents marine scientists with a data base to test for a shifting ecological baseline. Analysis of this

data base can provide a clear frame of reference to marine resource managers as to what they are trying to manage or conserve. However, our results cannot be applied to other major constituents of the reefal community such as molluscs, sponges, soft corals and algae.

Changes in reef community structure

Although we acknowledge our limited sampling necessarily qualifies the results we obtained from our study sites in the Bahamas, they are strikingly different from those we obtained in Florida. In the former case, life and fossil assemblages are clearly least similar to each other in terms of the coral taxa they contain (Fig. 8). We interpret this observation to be the result of the recent change from an *Acropora cervicornis* - dominated assemblage to a *Porites porites* - dominated assemblage on Telephone Pole Reef (Fig. 11). The previous *A. cervicornis* - dominated community is now manifested in the death assemblage (Fig. 11B), while *P. porites* is abundant only in the life assemblage (Fig. 11A). Additionally, the paucity of milleporids in either the death or fossil assemblage relative to the life assemblage further segregates life assemblage samples from those obtained from the fossil and death assemblages (compare Figures 11A-C).

The decrease in species richness from live to dead to fossil assemblage results from the absence of the three milleporids we distinguished in our surveys (*Millepora complanata*, *M. squarrosa* and *M. alcicornis*) as well as taxa that are rare in the life assemblage (e.g. *Diploria clivosa*, *Montastraea cavernosa*, *Meandrina meandrites*, and *Dendrogyra cylindrus*).

To test our hypothesis with respect to the decline of *A. cervicornis*, we removed this taxon from the data set and re-ran the GNMDS ordination (Fig. 12). Samples from live, dead, and fossil assemblages are more closely comparable, although the degree of similarity between live and fossil assemblages is less than that obtained from the Florida Keys. These results indicate the importance of *A. cervicornis* in producing the distinction between the life, death and fossil assemblages examined on San Salvador.

Lack of a Pleistocene precedent for the demise of *A. cervicornis* in the Bahamas

The Pleistocene assemblage exposed on San Salvador apparently fails to reflect accurately the life assemblage currently in place on Telephone Pole Reef, while the Key Largo Limestone apparently reflects modern patch reef life assemblages of the Florida Keys much more closely. We suggest that we have obtained this result because the demise of *A. cervicornis* in the Bahamas and subsequent replacement by another coral species is without a Pleistocene precedent recorded in

Fig. 10A–C Histogram of the frequency distribution of the 25 most common coral taxa in **A** life, **B** death and **C** fossil assemblages of the Florida Keys. Abundance data are transformed to square roots. Note the relatively high abundance of branching coral growth forms in the death assemblage (for example, *Acropora palmata*, *A. cervicornis* and *Porites furcata*) and massive coral growth forms in the life and fossil assemblages (for example, *Porites astreoides*, *Diploria strigosa*, *Siderastrea siderea* and *Montastraea “annularis”*). For this and the following histogram, data codes (x-axis) are as follows: 1. *Acropora palmata* 2. *Porites astreoides* 3. *Porites porites* 4. *Agaricia agaricites* 5. *Millepora* sp. 6. *Diploria strigosa* 7. *Favia fragum* 8. *Millepora squarrosa* 9. *Millepora complanata* 10. *Millepora alcicornis* 11. *Diploria clivosa* 12. *Siderastrea radians* 13. *Siderastrea siderea* 14. *Acropora cervicornis* 15. *Porites furcata* 16. *Mycetophyllia lamarckiana* 17. *Montastraea cavernosa* 18. *Mycetophyllia danaana* 19. *Colpophyllia natans* 20. *Dichocoenia stokesii* 21. *Diploria labyrinthiformis* 22. *Montastraea “annularis”* 23. *Meandrina meandrites* 24. *Solenastrea bournoni* 25. *Solenastrea hyades*.

Note that the code for *Montastraea “annularis”* includes colony growth forms now recognized as sibling species

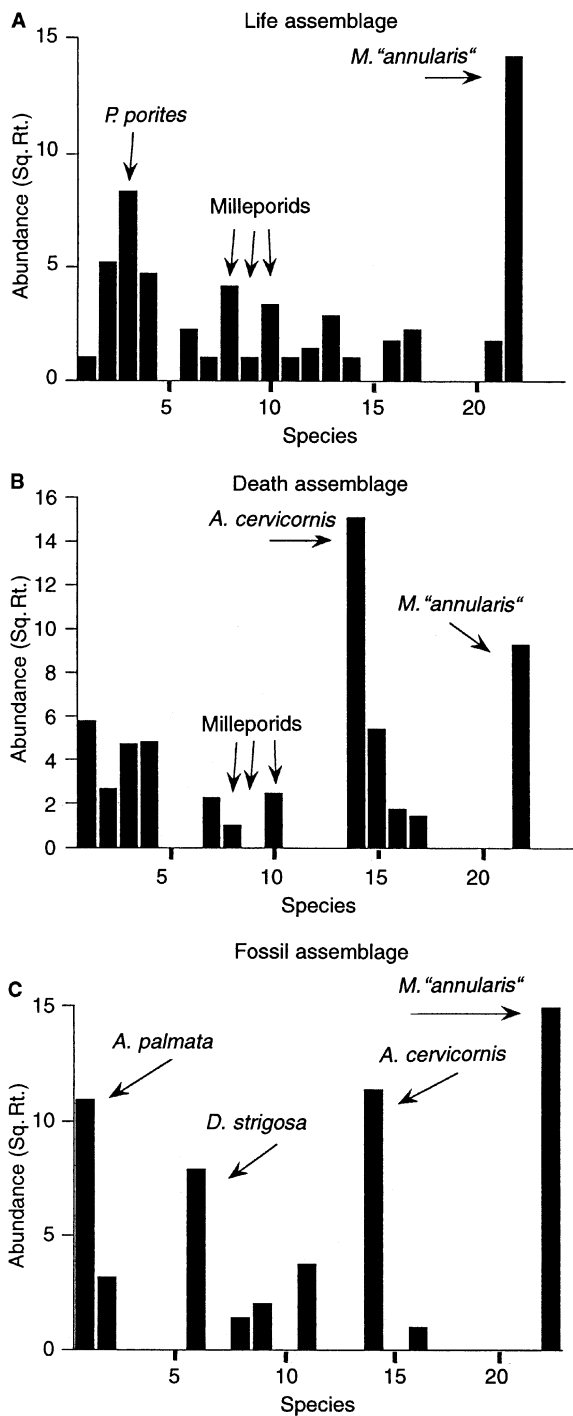


Fig. 11A–C Histogram of the frequency distribution of common coral taxa in **A** life **B** death and **C** fossil assemblages preserved on San Salvador. Abundance data are transformed to square roots. Note the relatively high abundance of *Porites porites*, milleporids and *Montastraea "annularis"* in the life assemblage. The death assemblage comprises *Acropora cervicornis*, *A. palmata*, and lower abundances of *M. "annularis"*

the assemblages preserved on San Salvador. Recall that we purposely chose modern patch reefs for our surveys in the Florida reef tract that conformed to early descriptions of patch reefs in that region. It is compelling

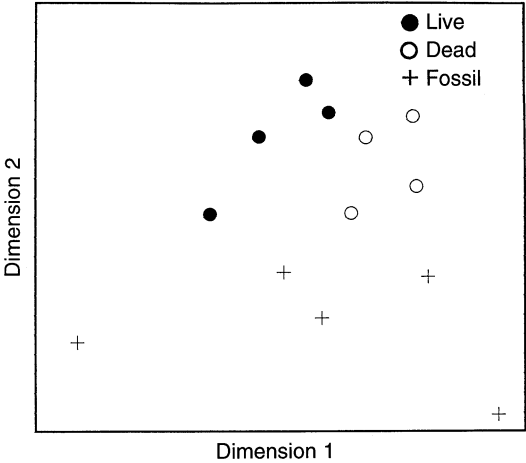


Fig. 12 Two-dimensional global nonmetric multidimensional scaling (GNMDS) ordination of coral life, death and fossil assemblages from San Salvador, Bahamas, with *Acropora cervicornis* removed from the data set. Points closest to one another represent samples (transects) that are more similar in taxonomic composition than points farther away from one another. Note that the three assemblages are more similar than those presented in Fig. 8. The minimum stress value for the two-dimensional analysis was 0.02

that these “healthy” reef communities were reflected by the fossil assemblages in the Florida Keys, whereas the present *Porites*-dominated community on Telephone Pole Reef is not reflected by the fossil assemblage exposed on San Salvador. Moreover, it is sobering to consider that the modern reefs we selected in Florida no longer represent the majority of typical Caribbean and tropical Western Atlantic patch reefs, given the rapidity with which *A. cervicornis* - dominated communities have been altered in the region. From this we can only conclude that, although the *A. cervicornis*-dominated coral association persisted during Pleistocene climatic fluctuations, it is apparently vulnerable to the array of perturbations currently being inflicted on it.

However, we must qualify this conclusion by acknowledging the possibility that the geologically rapid entombment of the reef exposed near Cockburn Town represents a “snapshot” comprising the minimum amount of time over which the reef accreted, and thus only one of a series of many possible states of coral dominance are preserved. It seems likely to us that rapid transitions in coral community composition similar to those observed presently in the Caribbean region would be preserved somewhere had they occurred. However, reef communities that existed during Pleistocene sea level high stands are preserved in similar depositional sequences and exposed throughout the Caribbean and tropical western Atlantic region. They have been examined in Barbados (Mesollella 1967; Jackson 1992; Pandolfi and Jackson unpublished data), Jamaica (Larsen 1983), San Andrés (Geister 1980; Pandolfi and Jackson unpublished data), Grand Cayman (Hunter and Jones 1996), San Salvador (White et al.

1984; Curran and White 1985), Great Inagua (White and Curran 1995; Greenstein and Curran 1997) and Curaçao (Bak 1977; Pandolfi and Jackson in review). These exposures consistently preserve coral assemblages and zonation patterns that are strikingly similar to those described in the early days of modern reef ecology. We therefore submit that the transitions observed today are without recorded historical precedent during the interval of Pleistocene time recorded in the exposures we studied. We acknowledge that throughout most of the region, corals are dying and being replaced by algae rather than by organisms with potentially preservable skeletons. We do not expect however, that similar coral community structure will occur immediately after a reef has been overgrown by algae, and thus changes in coral community composition should be preserved even when the new reef dominant is not. Clearly additional comparisons of modern reefs in a variety of states to fossil reefs are needed to understand modern perturbations more fully, but we submit that the results presented here serve to provide a framework for future comparative analyses of modern and ancient coral reef community structure.

Conclusions

Systematic censuses of life and death assemblages were conducted on "healthy" modern patch reefs in the Florida reef tract that conform to the classic Caribbean model of reef coral zonation, and a patch reef in the Bahamas that is currently undergoing a transition in coral dominance that is part of a western North Atlantic – Caribbean-wide phenomenon. Results were compared to censuses of ancient reef assemblages preserved in Pleistocene limestones in close proximity to each modern reef. We have determined that the Pleistocene fossil record of coral reefs may be used to calibrate an ecological baseline with which to compare modern reef assemblages. Specifically, we have documented that the living patch reefs of the Florida Keys are representative of patch reefs that flourished prior to any human influence in that area. Additionally, we suggest that the current and rapid decline of *Acropora cervicornis* observed on a Bahamian patch reef may be a unique perturbation that contrasts with the long-term persistence of this taxon during Pleistocene and Holocene time. Although the results of our species sampling curves dictate that our results from the Bahamas must be considered preliminary, primarily owing to relatively small sample size, we offer the following specific conclusions:

1. The taxonomic composition of the fossil coral assemblage preserved in the Key Largo Limestone is very comparable to the living patch reefs currently thriving offshore because of the excellent preservation of corals with massive colony growth forms.
2. Because of the similarity in taxonomic composition between modern patch reefs and preserved Pleistocene reef assemblages, early descriptions of the ecology of reef corals from Florida patch reefs are also indicative of reefs that flourished long before shallow reef ecosystems had begun to be degraded by human activities. In this case, concern over shifting base line syndrome is mitigated for the corals by the fossil record. Thus the fossil record provides a powerful tool for understanding the degree to which shifting baseline affects our capacity to evaluate modern reef degradation. This result cannot be generalized to include the non-coral components of reef systems.
3. Based on the assemblage of corals they contain, the life and fossil assemblages in the Bahamas are more dissimilar to one another than either is to the contemporary coral death assemblage. This result is in stark contrast to the results we report from the Florida Keys, and is a consequence of a recent transition to a *Porites porites* - dominated coral assemblage from an *Acropora cervicornis* - dominated assemblage on the living reef.
4. Although further study of Pleistocene reef facies is needed, the current Caribbean – wide reduction in abundance of *Acropora cervicornis* apparently is without a Pleistocene precedent within the exposures examined.

Acknowledgements Field work in the Florida Keys was entirely supported by two grants from the National Undersea Research Center (UNCW 9612, 9613) awarded to B. Greenstein and John Pandolfi (Smithsonian Institution). We acknowledge the facilities and staff of the center on Key Largo, especially Dr. Steven Miller, for a variety of efforts on our behalf. Logistical support on San Salvador Island was provided by the Bahamian Field Station. Additional financial support to Greenstein and Curran from Smith College and to Pandolfi from the Smithsonian Tropical Research Institute is gratefully acknowledged. The following students, all from Smith College, served as field assistants in the Florida Keys: Tatiana Bertsch, Elizabeth Gardiner and Lora Harris. In the Bahamas, Lora Harris, Kathryn Jermann, Sara Rosenzweig and Sarah Smalheer served as field assistants. Russell Kelley (Coral Sea Imagery) served as a field assistant in the Florida Keys.

References

- Aronson RB, Precht WF (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23:326–346
- Bak RPM (1977) Coral reefs and their zonation in Netherlands Antilles. *Stud in Geol (Tulsa)* 4 Reef and related carbonates; ecology and sedimentology: 3–16
- Bak RPM, Nieuwland G (1995) Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. *Bul Mar Sci* 56:609–619
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Brown BE (1997) Disturbances to reefs in recent times. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, NY, pp 354–379

- Brown BE, Ogden JC (1993) Coral bleaching. *Sci Am* 268:64–70
- Carpenter RC (1985) Sea urchin mass mortalities: effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. *Proc 5th Int Coral Reef Cong, Tahiti* 4:53–60
- Chen JH, Curran HA, White B, Wasserburg GJ (1991) Precise chronology of the interglacial period: $\text{Th}^{230}/\text{U}^{234}$ data from fossil coral reefs in the Bahamas. *Geol Soc Am Bul* 103:82–97
- Clarke KR, Warwick RM (1994) Change in marine communities: An approach to statistical analysis and interpretation. National Environment Research Council, UK, 144 pp
- Curran HA, White B (1985) The Cockburntown Fossil Coral Reef. In: Curran HA (ed) Pleistocene and Holocene carbonate environments on San Salvador Island, Bahamas – Guidebook for Geological Society of America, Orlando annual meeting field trip, CCFL Bahamian Field Station, Ft. Lauderdale, Florida, pp 95–120
- Curran HA, White B, Chen JH, Wasserburg GJ (1989) Comparative morphologic analysis and geochronology for the development and decline of two Pleistocene coral reefs, San Salvador and Great Inagua Islands. In: Mylroie J (ed) *Proc 4th Symp Geol Bahamas*. Bahamian Field Station, San Salvador, pp 107–117
- Curran HA, Smith DP, Meigs LC, Pufall AE, Greer ML (1994) The health and short-term change of two coral patch reefs, Fernandez Bay, San Salvador Island, Bahamas. In: Ginsburg RN (ed) *Proc Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*, 1993, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida, pp 147–153
- de Ruyter van Stevenick ED, Bak RPM (1986) Changes in abundance of coral reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar Ecol Prog Ser* 34:87–94
- Dodd JR, Hattin DE, Liebe RM (1973) Possible living analog of the Pleistocene Key Largo reefs of Florida. *Geol Soc Am Bul.* 84:3995–4000
- Done TJ (1992a) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132
- Done TJ (1992b) Constancy and change in some Great Barrier Reef coral communities. *Am Zool* 32:655–662
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Geister J (1980) Calm-water reefs and rough-water reefs of the Caribbean Pleistocene. *Acta Palaeont Polon* 25:541–556
- Ginsburg RN (ed) (1964) South Florida Carbonate Sediments, Geological Society of America Annual Meeting, Guidebook for Field Trip 1:72 pp
- Ginsburg RN (ed) (1994) Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History, 1993. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida
- Glynn PW (1993) Coral reef bleaching: Ecological perspectives. *Coral Reefs* 12:1–17
- Goreau TF (1959) The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40:67–90
- Greenstein BJ (1989) Mass mortality of the West-Indian echinoid *Diadema antillarum* (Echinodermata: Echinoidea): A natural experiment in taphonomy. *Palaios* 4:487–492
- Greenstein BJ, Moffat HA (1996) Comparative taphonomy of Holocene and Pleistocene corals, San Salvador, Bahamas. *Palaios* 11:57–63
- Greenstein BJ, Pandolfi JM (1997) Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: Implications for the Quaternary record of coral reefs. *Bul Mar Sci* 19:39–59
- Greenstein BJ, Pandolfi JM, Moran PJ (1995) Taphonomy of crown-of-thorns starfish: Implications for the recognition of ancient population explosions. *Coral Reefs* 14:91–97
- Greenstein BJ, Pandolfi JM, Curran HA (1998) The completeness of the Pleistocene fossil record: Implications for stratigraphic adequacy. In: Donovan SK (ed) *The adequacy of the fossil record*. John Wiley and Sons, London, pp 75–109
- Greenstein BJ, Curran HA (1997) How much ecological information is preserved in fossil reefs and how reliable is it? *Proc 8th Int Coral Reef Symp, Panama City, Panama* 1:417–422
- Grigg RW, Dollar SJ (1990) Natural and anthropogenic disturbances on coral reefs. In: Dubinsky (ed) *Ecosystems of the world* 25: Coral reefs. Elsevier, Amsterdam, pp 439–452
- Harrison RS, Coniglio M (1985) Origin of the Pleistocene Key Largo Limestone, Florida Keys. *Bull Can Petrol Geol* 33:350–358
- Hodges LT (1980) Coral size and relationships of the Key Largo Limestone. *Proc 3rd Int Coral Reef Symp* 3:347–353
- Hoffmeister JE, Multer, HG (1968) Geology and origin of the Florida Keys. *Geol Soc Am Bull* 79:1487–1502
- Hubbard DK, Miller AI, Scaturro D (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U. S. Virgin Islands): Applications to the nature of reef systems in the fossil record. *J Sed Petrol* 60:335–360
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes TP, Reed DC, Boyle MJ (1987) Herbivory on coral reefs: Community structure following mass mortalities of sea urchins. *J Exp Mar Biol Ecol* 113:39–59
- Hunter IG, Jones B (1996) Coral associations of the Pleistocene Ironshore Formation, Grand Cayman. *Coral Reefs* 15:249–267
- Jackson JBC (1992) Pleistocene perspectives on coral reef community structure. *Am Zool* 32:719–731
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16 (suppl): S23–S32
- Johnson KG, Budd A, Stenmann TA (1995) Extinction selectivity and ecology of Neogene Caribbean reef corals. *Paleobiology* 21:52–73
- Kauffman EG, Fagerstrom JA (1993) The Phanerozoic evolution of reef diversity. In: Ricklefs RE, Schluter D (eds) *Species diversity in ecological communities: Historical and geographical perspectives*. University of Chicago Press, Chicago, pp 315–329
- Knowlton N, Weil E, Weigt LA, Guzmán HM (1992) Sibling species of *Montastrea annularis*, coral bleaching, and the coral climate record. *Science* 255:330–333
- Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1–27
- Larsen DC (1983) Depositional facies and diagenetic fabrics in the Late Pleistocene Falmouth Formation of Jamaica. Unpubl MS Thesis, University of Oklahoma, Norman, Oklahoma
- Liddell WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *J Exp Mar Biol Ecol* 95:271–278
- Lessios HA (1988) Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Ann Rev Ecol Syst* 19:371–393
- Littler MM, Littler DS (1996) Black band disease in the South Pacific. *Coral Reefs* 15:20
- Lucas HA, Seber GAF (1977) Estimating coverage and particle density using the line intercept method. *Biometrika* 64:618–622
- Macintyre IG (1988) Modern coral reefs of western Atlantic: New geological perspective. *Am Ass Petrol Geol Bul* 72:1360–1369
- Mesollela KJ (1967) Zonation of uplifted Pleistocene coral reefs on Barbados, West Indies. *Science* 156:638–640
- Mesollela KJ, Sealy HA, Matthews RK (1970) Facies geometries within Pleistocene reefs of Barbados, West Indies. *Am Ass Petrol Geol Bull* 54:1899–1917
- Miller I (1996) Black band disease on the Great Barrier Reef. *Coral Reefs* 15:58
- Minchin PR (1987) An evaluation of relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107

- Multer HG (1977) Field guide to some carbonate rock environments: Florida Keys and Western Bahamas. Kendall Hunt, Iowa, 415 pp
- Mundy C (1991) A critical evaluation of the line intercept transect methodology for surveying sessile coral reef benthos. Masters Thesis. University of Queensland, Australia
- Pandolfi JM (1996) Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea. Constancy during global change. *Paleobiology* 22: 152–176
- Pandolfi JM, Minchin PR (1995) A comparison of taxonomic composition and diversity between reef coral life and death assemblages in Madang Lagoon, Papua New Guinea. *Palaeoecol Palaeoclimatol Palaeoceanogr* 119: 321–341
- Pandolfi JM, Greenstein BJ (1997a) Preservation of community structure in death assemblages of deep water Caribbean reef corals. *Limnol Oceanogr* 42: 1505–1516
- Pandolfi JM, Greenstein BJ (1997b) Taphonomic alteration of reef corals: effects of reef environment and coral growth form. I: The Great Barrier Reef. *Palaios* 12: 27–42
- Precht WF (1990) Geologic and ecologic perspectives of catastrophic storms and disturbance on coral reefs: lessons from Discovery Bay, Jamaica. *Geol Soc Am Abstr w Progr* 22: A331
- Randall JE (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46: 255–260
- Randall JE, Schroeder RE, Starck WA Jr (1961) Notes on the biology of *Diadema antillarum*. *Carib J Sci* 4: 421–433
- Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Mar Ecol Prog Ser* 62: 185–202
- Rogers CS (1993) Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12: 127–137
- Stanley SM (1966) Paleocology and diagenesis of Key Largo Limestone, Florida. *Am Ass Petrol Geol Bull* 50: 1927–1947
- Tomascik T, Sander F (1987) Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar Biol* 94: 53–75
- White B (1989) Field guide to the Sue Point fossil coral reef, San Salvador Island, Bahamas. In: Mylroie JE (ed) *Proc 4th Symp Geol Bahamas, Bahamian Field Station, San Salvador*, pp 353–365
- White B, Curran HA (1987) Coral reef to eolianite transition in the Pleistocene rocks of Great Inagua, Bahamas. In: Curran HA (ed) *Proc 3rd Symp Geol Bahamas, CCFL Bahamian Field Station, Ft. Lauderdale, Florida*, pp 165–179
- White B, Curran HA (1995) Entombment and preservation of Sargamonian coral reefs during glacioeustatic sea-level fall, Great Inagua Island, Bahamas. In: Curran HA, White B (eds) *Terrestrial and shallow marine geology of the Bahamas and Bermuda*. *Geol Soc Am Spec Pap* 300, Boulder, Colorado, pp 51–61
- White B, Kurkij KA, Curran HA (1984) A shallowing-upward sequence in Pleistocene coral reef and associated facies, San Salvador, Bahamas. In: Teeter JW (ed) *Proc 2nd Symp Geol Bahamas, CCFL Bahamian Field Station, Ft. Lauderdale, Florida*, pp 53–70
- Wilkinson CR (1993) Coral reefs of the world are facing widespread devastation: can we prevent this through sustainable management practices? *Proc 7th Int Coral Reef Symp, Guam* 1: 11–21
- Woodley JD (1992) The incidence of hurricanes on the north coast of Jamaica since 1870: Are the classic reef descriptions atypical? *Hydrobiologia* 247: 133–138
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Hoffman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney ML, Rylaarsdam KW, Tunnicliffe BJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl AR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749–755