REPORT

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

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

(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 (Pandolþ 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 Mo¤at 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 signiþcant 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 signiþcant events. The mass mortality of *Diadema antillarum* during 1983Ð84 was quickly erased from the sedimentary record, even though innumerable tests and spines of this animal were observed accumulating on surþcial sediments (Greenstein 1989). Results of þeld experiments using the crown-of-thorns starþsh, *Acanthaster planci*, suggested that preservation of starþsh at outbreak proportions is tenuous in the sedimentary record of the Great Barrier Reef (Greenstein et al. 1995). Finally, the preservation potential of the ßeshy macroalgae observed on Caribbean reefs today is very low (Kau¤man 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 signiþcant changes in coral reef ecosystems had already occurred. Against what standard, then, can current faunal and ßoral 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 Ónatural.Ó Jackson (1997) suggested that this assumption may be false, and he used written historical records to demonstrate that coastal Carib-

bean ecosystems were severely degraded long before ecologists began to study them, primarily as a result of the very early decimation of marine megavertebrate 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 ßeshy macroalgae. Replacement by corals has been observed in Belize (Aronson and Precht 1997) and the Bahamas (Curran et al. 1994), where dense

over the shifting baseline syndrome may be mitigated where a su¦cient 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-o¤ 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

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

Florida KeysÐPleistocene coral assemblage

We examined fossil reef coral assemblages from outcrops of the Key Largo Limestone exposed along AdamÕs Canal (Key Largo) and on Windley Key for comparison to the corresponding life and death assemblages currently accumulating o¤shore on Cannon Patch Reef and Horsehoe 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* ÒannularisÓ Ð dominated coral assemblage exposed on Windley Key and along the Key Largo Waterway (now known as AdamÕs 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. Ho¤meister and Multer (1968) agreed that the Pleistocene coral assemblage could reßect either environment, but preferred an interpretation as a shallow patch reef, pointing to stratigraphic constraints and, most importantly, the Þrst 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 AdamÕs Canal and Windley Key Quarry. At both locations, the transect intercepted *in situ* corals as well as coral rubble and carbonate sand that Þlls 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 ßourished between approximately 140Ð120 ka during the last interglacial (substage 5e of the marine oxygen isotope scale (see Harrison and Coniglio, 1985), thus the maximun 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.* ÒannularisÓ in Cane Bay, St. Croix, U. S. V. I. was 0.73 m/1000 y over the last 3Ð5 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.

BahamasÐmodern 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*

Fig. 2 Sample localities for the Key Largo Limestone exposed along *AdamÕs Canal* and in the Windley Key *Quarry* in the Florida Keys. Five transects were constructed along AdamÕs Canal, and three transects were constructed in the Windley Key Quarry (after Stanley 1966)
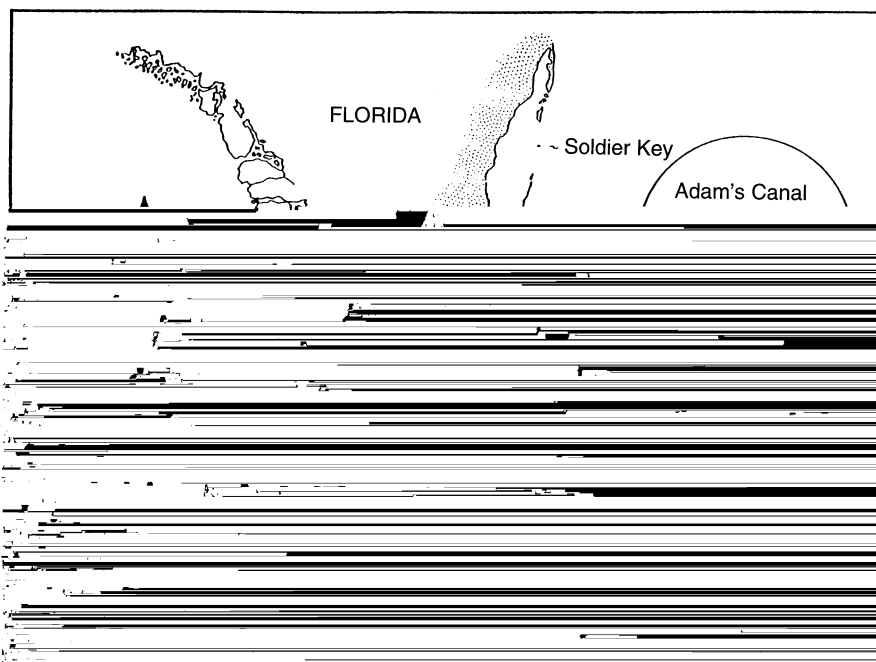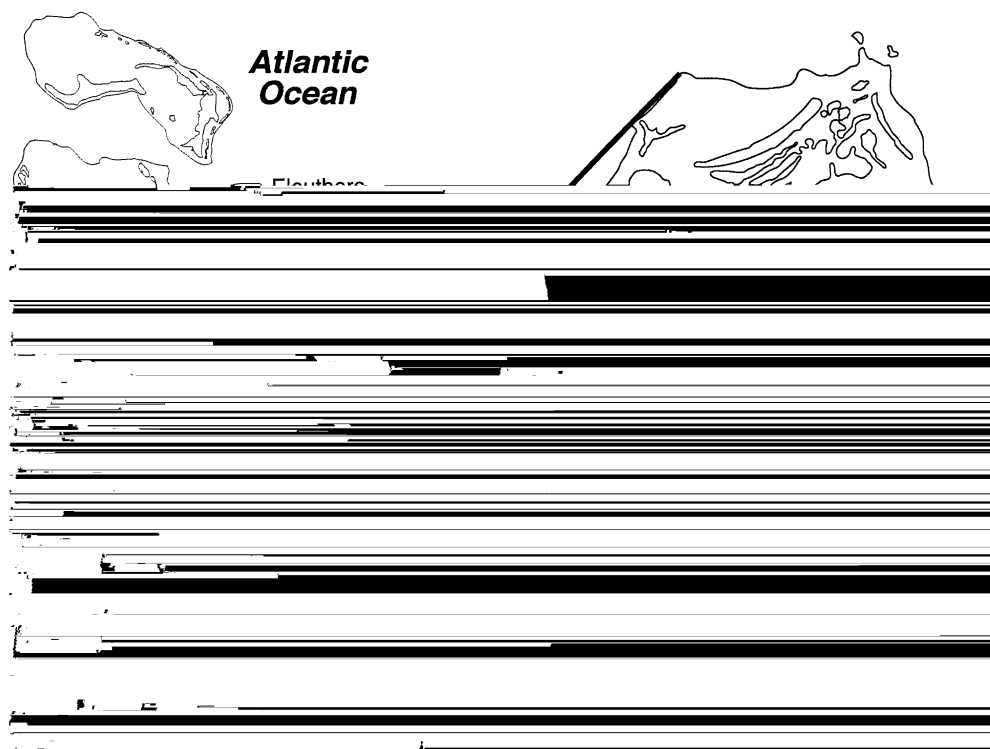
Fig. 3 Area of study, San Salvador Island, Bahamas. Telephone Pole Reef is located in Fernandez Bay, while the Cockburn Town fossil reef is located onshore at the north end of Fernandez Bay, in Cockburn Town

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 119Ð131 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 ðhealthy reefsÑand 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-preservable 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 su ¦ ciently 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 Þrst 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 reßected an environment of deposition similar to that preserved in Pleistocene strata. This e¤ectively 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 di¤erences 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; PandolÞ and Jackson, in review) and San Andres (Geister 1980; PandolÞ 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 fulÞlls these prerequisites.

Data analyses

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

Bahamas, our data consist of 8 samples from modern environments (4 transects] 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 Pandolþ 1997; Pandolþ and Greenstein 1997a; Greenstein and Curran 1997; Pandolþ 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 coe¦cient (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 inßuence 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 þt is measured by a quantity known as ÒstressÓ 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.

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 þrst through eighth transect. **B** Cumulative diversity of reef coral species versus number of sampling intervals (transects) from Pleistocene reef coral assemblages exposed along AdamÕs Canal and in the Windley Key Quarry in the Florida Keys. The solid line is a plot proceeding from the þrst transect sampled along AdamÕs Canal to the last transect sampled in Windley Key Quarry. The dashed lines are plots of þve random sequences of transects

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 su¦cient to account for coral diversity in life and death assemblages in the modern patch reefs (Fig. 4A). Six transects were su¦cient 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 o¤shore.

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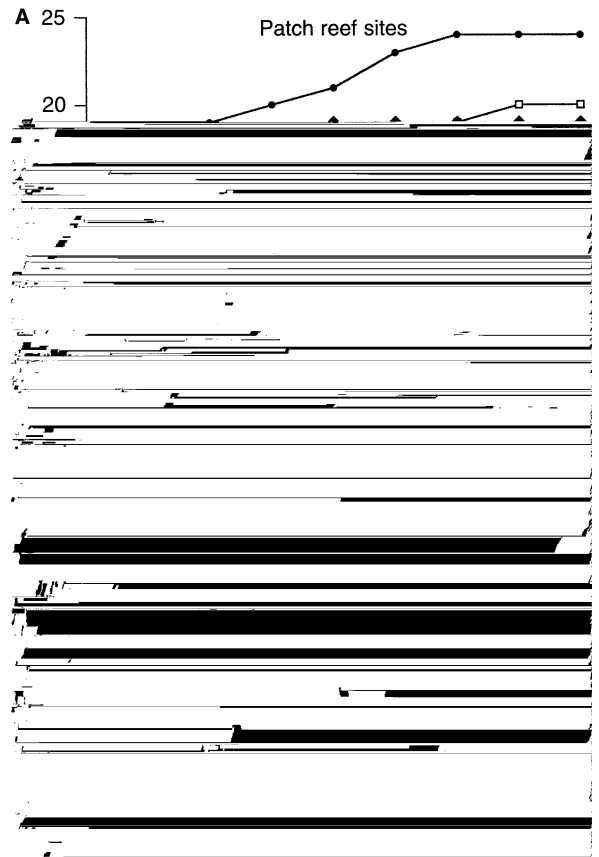
(ANOVA; $F_{(2, 37)} = 14.20$; $P < 0.0005$) more diverse than either their dead or fossil counterparts (Fig. 6).

Bahamas

Species sampling curves indicate that four transects were insu¦cient to account for the full diversity of the life assemblage on Telephone Pole Reef (Fig. 7A). Sampling curves level o¤ only between the þnal 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
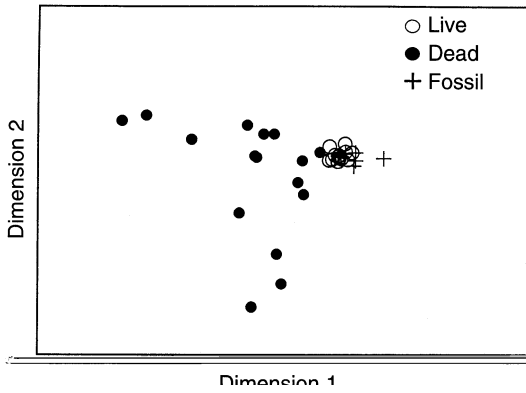
Fig. 5 Two-dimensional global nonmetric multidimensional scaling (GNMDS) ordination of coral life and death assemblages from two patch reefs in the Florida Keys, and fossil assemblages preserved in the Key Largo Limestone. Points closest to one another represent samples (transects) that are more similar 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
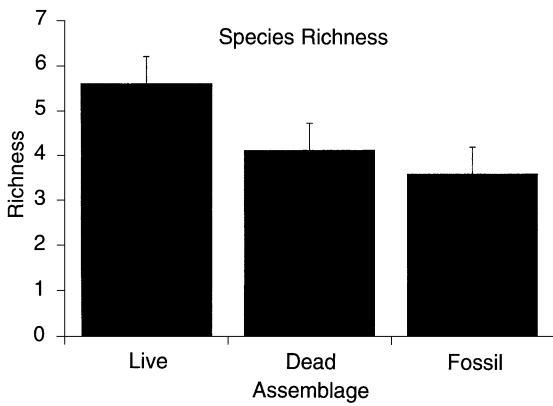

Fig. 6 Comparison of species richness between life, death and fossil assemblages of the Florida Keys. The patch reef life assemblage is more diverse than either the death or fossil assemblages. Error bars are standard errors of the mean, $n = 40$

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

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 accurate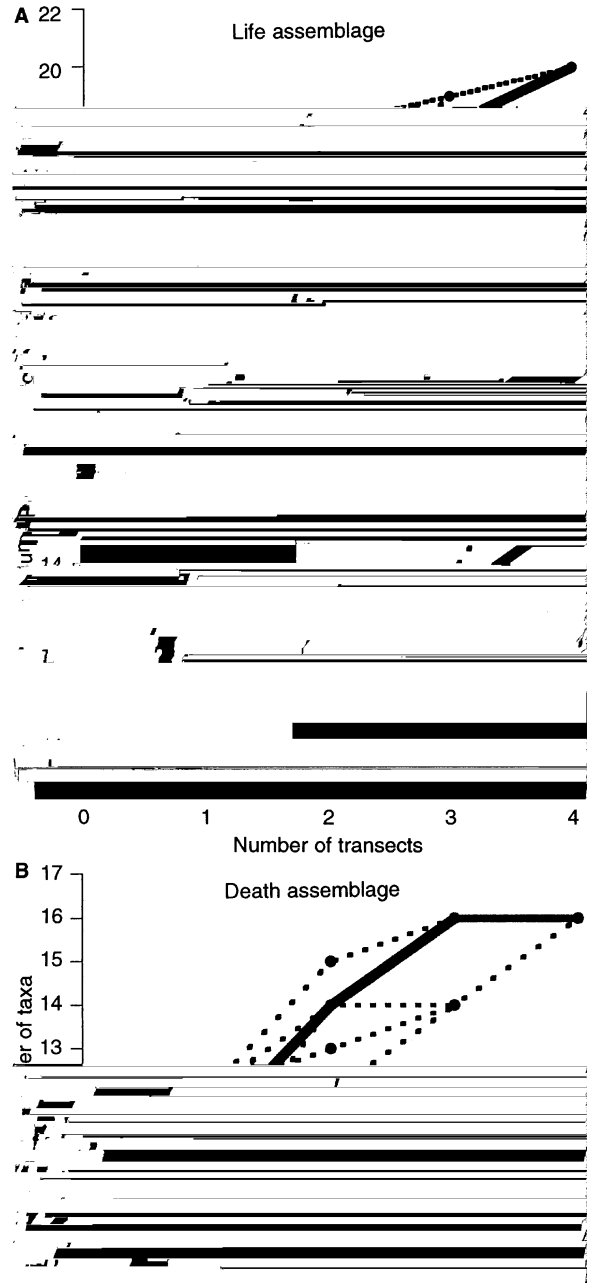ly represents the assemblage of corals currently living in patch reefs oﬀshore than the contemporary death assemblage. The fact that points representing samples from the living and fossil reef are virtually superimposed on one another indicates that taxonomic composition and relative abundance of the living and fossil patch reef are very comparable. The
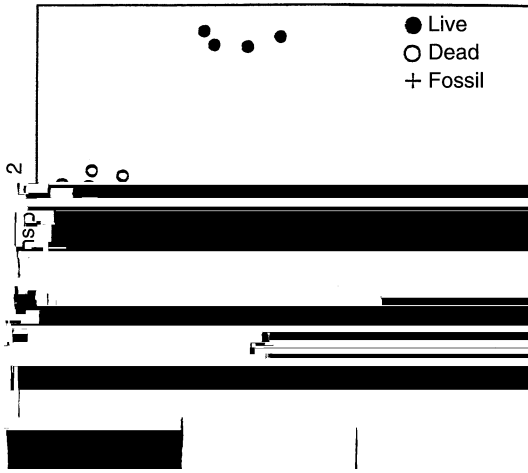
Fig. 8 Two-dimensional global nonmetric multidimensional scaling (GNMDS) ordination of coral life death and fossil assemblages from San Salvador, Bahamas. Points closest to one another represent samples (transects) that are more similar in taxonomic composition

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
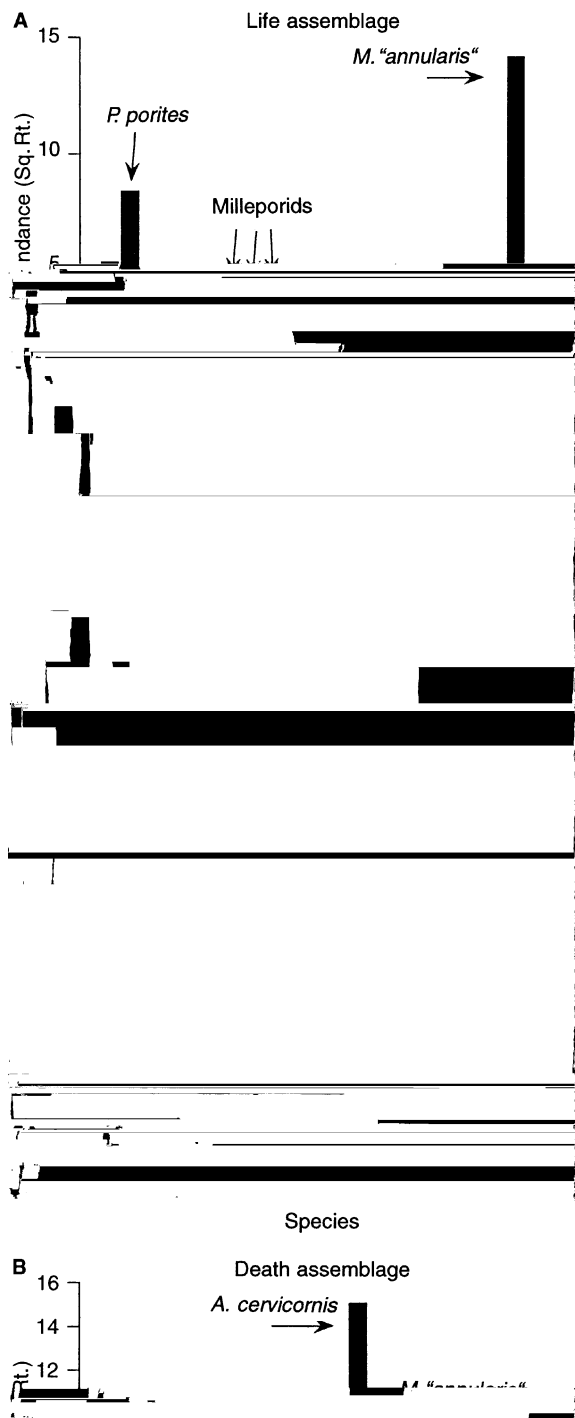
A

Life assemblage

15

M. "annularis"

P. porites

10

Milleporids

Abundance (Sq. Rt.)

Species

B

16

14

12

Death assemblage

A. cervicornis

M. "annularis"

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"

● Live
○ Dead
+ Fossil

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

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 ree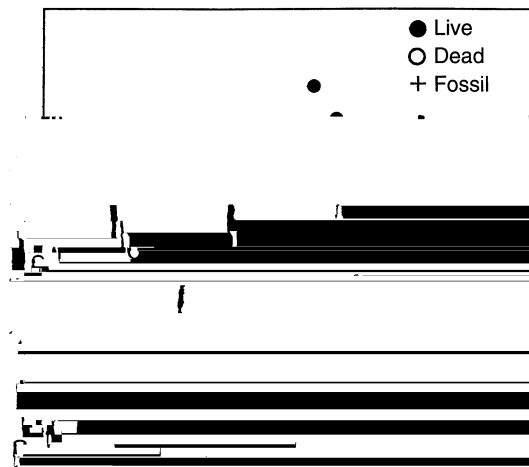fs in that region. It is compelling that these "healthy" reef communities were reflected by the fossil assemblages in the Florida Keys, whereas the present *Porites*-dominated community on Telephone Pole Reef is not reflected by the fossil assemblage exposed on San Salvador. Moreover, it is sobering 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.

1984; Curran and White 1985), Great Inagua (White and Curran 1995; Greenstein and Curran 1997) and Curaçao (Bak 1977; Pandolþ 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

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 herbiovores. 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: Th230/U234 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 Þeld 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 signiÞcance. 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 Pleisotcene. 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, PandolÞ 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, PandolÞ JM, Moran PJ (1995) Taphonomy of crown-of-thorns starÞsh: Implications for the recognition of ancient population explosions. Coral Reefs 14:91–97

Greenstein BJ, PandolÞ 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 I: 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, Scaturo 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, Guzman HM (1992) Sibling speciens of *Montastrea annularis*, coral bleaching, and the coral climate record. Science 255:330–333

Kruskal JB (1964) Multidimensional scaling by optimizing goodness of Þt to a nonmetric hypothesis. Psychometrika 29:1–27

Larsen DC (1983) Depositional facies and diagenetic fabrics in the

Multer HG (1977) Field guide to some carbonate rock environ-
ments: 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 22:152ﬁ176

Pandolﬁ JM, Minchin PR (1995) A comparison of taxonomic com-
position and diversity between reef coral life and death assem-
blages in Madang Lagoon, Papua New Guinea. Palaeoecol
Palaeoclimatol Palaeoceanogr 119:321ﬁ341

Pandolﬁ JM, Greenstein BJ (1997a) Preservation of community
structure in death assemblages of deep water Caribbean reef
corals. Limnol Oceanogr 42:1505ﬁ1516

Pandolﬁ JM, Greenstein BJ (1997b) Taphonomic alteration of reef
corals: e¤ects of reef environment and coral growth form. I: The
Great Barrier Reef. Palaios 12:27ﬁ42

Precht WF (1990) Geologic and ecologic perspectives of cata-
strophic storms and disturbance on coral reefs: lessons from
Discorvery Bay, Jamaica. Geol Soc Am Abstr w Progr 22:A331

Randall JE (1965) Grazing e¤ect on sea grasses by herbivorous reef
ﬁshes in the West Indies. Ecology 46:255ﬁ260

Randall JE, Schroeder RE, Starck WA Jr (1961) Notes on the
biology of *Diadema antillarum*. Carib J Sci 4:421ﬁ433

Rogers CS (1990) Responses of coral reefs and reef organisms to
sedimentation. Mar Ecol Prog Ser 62:185ﬁ202

Rogers CS (1993) Hurricanes and coral reefs: the intermediate dis-
turbance hypothesis revisited. Coral Reefs 12:127ﬁ137

Stanley SM (1966) Paleoecology and diagenesis of Key Largo Lime-
stone, Florida Am Ass Petrol Geol Bull 50:1927ﬁ1947

Tomascik T, Sander F (1987) E¤ects of eutrophication on reef-
building corals. II. Structure of scleractinian coral communities
on fringing reefs, Barbados, West Indies. Mar Biol 94:53ﬁ75