

The Adequacy of the Fossil Record

Edited by
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The Completeness of the Pleistocene Fossil Record: Implications for Stratigraphic Adequacy

Benjamin J. Greenstein, John M. Pandolfi and H. Allen Curran

INTRODUCTION

Nearly three decades after Lawrence (1968) published work emphasizing the importance of understanding the information lost via taphonomic processes, the palaeontological community has underscored a major change in its perception of the fossil record by publishing this volume. The emphasis on adequacy in the fossil record caps a renaissance in taphonomic research that began at a symposium entitled 'The Positive Aspects of Taphonomy', held at the 1984 south-east regional meeting of the Geological Society of America in Lexington, Kentucky. The symposium was a catalyst for renewed field and laboratory investigations of experimental and actualistic taphonomy (see Donovan, 1991, and Allison and Briggs, 1991, for synthetic reviews). A unifying theme to this research is that actuopalaeontological ('palaeontology of the recent', see Schäfer, 1972) investigations allow for an understanding of processes affecting the preservation of organisms. Applying results of actuopalaeontological investigations to fossil material can therefore provide a great deal of palaeoenvironmental, palaeoecological and palaeobiological information applicable to palaeontological questions of varying scale.

Additionally, community ecologists and biologists are becoming increasingly aware that the fossil record is an exclusive and crucial database from

which to interpret long-term community patterns (Ricklefs, 1987; Jackson, 1992; Jackson *et al.*, 1996). During the last decade, palaeoecological studies in terrestrial (for example, Davis, 1986; Delcourt and Delcourt, 1991; Davis *et al.*, 1994; Reed, 1994; Coope, 1995) and marine (for example, Jackson, 1992; Buzas and Culver, 1994; Allmon *et al.*, 1996; Jackson *et al.*, 1996; Pandolfi, 1996) systems have demonstrated that the fossil record possesses a wealth of information applicable to current concerns of both global change and environmental perturbations on a local scale. Thus, taphonomic studies take on an additional objective: to assess the accuracy with which the recent past history of modern ecosystems is preserved. Our ongoing studies of modern and Pleistocene reef taphonomy (for example, Greenstein and Moffat, 1996; Greenstein and Curran, 1997; Greenstein and Pandolfi, 1997; Pandolfi and Greenstein, 1997a,b) have such an assessment as their overarching objective, and the results are particularly relevant to a variety of dilemmas presently facing community ecologists and marine resource managers alike.

The Pleistocene fossil record of coral reefs over the last million years is a particularly valuable repository for biological data because of its generally spectacular preservation, and also, with few exceptions, the same coral taxa that inhabit modern shallow-water reef environments are present in Pleistocene deposits. Although this is in part due to the young geological age of the interval, a great deal of qualitative (for example, Mesollela, 1967; Mesollela *et al.*, 1970; Chappell, 1974; White *et al.*, 1984; White and Curran, 1987, 1995; White, 1989; K.G. Johnson *et al.*, 1995; Hunter and Jones, 1996) and quantitative (Greenstein and Moffat, 1996; Pandolfi, 1996) data suggest spectacular preservation is common for reef coral assemblages accumulating during at least the last 600 Ka in both the Indo-Pacific and Caribbean provinces. The Caribbean shallow-water coral (and mollusc) faunas have undergone little speciation or extinction since faunal turnover ended roughly a million years ago (Potts, 1984; Allmon *et al.*, 1993; Jackson *et al.*, 1993; Budd *et al.*, 1994, 1996; Jackson, 1994a,b), despite intensifying cycles in climate and sea level throughout the Pleistocene. Thus, Pleistocene fossil coral reef deposits can potentially be used as a database with which to address a variety of issues facing reef ecologists and marine resource managers, whose frustration over the temporally myopic view afforded by monitoring studies that rarely span a scientific career increasingly pervades the literature (for example, Done, 1992; Jackson, 1992; Hughes, 1994a; Bak and Nieuwland, 1995). Two such issues explored in this chapter are an assessment of the response of coral reef communities to environmental perturbations, and the reliability of the Quaternary fossil record of reefs for observing patterns of community assembly over human and geological time scales.

Important ecological influences on coral reefs may operate on a variety of temporal and spatial scales (Porter and Meier, 1992), including decadal time

scales (Done, 1992; Bak and Nieuwland, 1995), and the need for long-term data sets has been recognized by a variety of workers (for example, Likens, 1987; D'Elia *et al.*, 1991; Jackson, 1992). Although the results of long-term (decadal scale) systematic monitoring studies of reef communities are becoming increasingly common (see, for example, case histories cited in Ginsburg, 1994), researchers generally acknowledge that patterns demonstrated to have recurred over 10, 20 and even 30 years (for example, Hughes, 1994a) may simply represent part of longer-term cycles that operate over geological time scales (Bak and Nieuwland, 1995), or at least over the multi-centennial scale common to the generation time and longevity of corals, the main structural component of reefs.

Given the great disparity between human time scales on the one hand and the time scale over which corals survive and global change occurs on the other, marine scientists are increasingly looking to the Holocene and Pleistocene fossil record of coral reefs to assess the impact of environmental perturbations on the reef ecosystem (Jackson, 1992; Jackson *et al.*, 1996). Jackson (1992) suggested that the reef fossil record represents the exclusive database from which responses of coral communities to global change may be gauged. For example, in Barbados, preliminary qualitative data from the Pleistocene raised reef terraces suggested that similar coral communities and zonation patterns have prevailed for the past 600 Ka (Jackson, 1992). In an overview of mollusc, reef coral and planktic foraminiferal communities, Jackson (1994a) found little correlation between the magnitude of environmental change, and subsequent ecological and evolutionary response during the Pleistocene. In a detailed study that examined geographic and temporal changes in community structure, Pandolfi (1996) found limited species membership in Indo-Pacific reef coral communities from 125 to 30 Ka. These studies give a very different picture of coral reef community structure and stability from that derived from traditional, small-scale ecological studies in the Recent.

Additionally, the Pleistocene record of fossil reefs provides ecologists and palaeoecologists with the opportunity to utilize studies such as those listed above to assess patterns of community assembly occurring over human and geological time scales. A central debate in community ecology concerns species membership in ecological communities, and there exists a spectrum of definitions of community that range from essentially random aggregations of species inhabiting a specific space (for example, Newell *et al.*, 1959; Johnson, 1972) to the concept of the community as a superorganism (for example, Whittaker, 1975; Kauffman and Scott, 1976). Jackson *et al.* (1996) used the fossil record of reefs over the last 10 Ma to explore the link between temporal scale and various perspectives on community membership. The Pleistocene record of fossil reefs provides ecologists and palaeoecologists with the opportunity to document patterns in coral reef community struc-

ture, and to compare community studies occurring over human and geological time scales.

Given the great potential of the Pleistocene fossil record of coral reef communities for addressing the issues listed above, an understanding of the taphonomic bias likely to affect reef coral assemblages preserved in Pleistocene strata is essential. Over the last few years, we have been comparing live and dead coral assemblages in modern environments in the Florida Keys and Bahamas to Pleistocene reef facies exposed in the Florida Keys and Bahama Archipelago to determine the accuracy with which the fossil record represents the taxonomic composition of a once-living coral community. Our main objective has been to determine the degree to which Pleistocene material has suffered taphonomic bias, and thus to inform community ecologists and marine managers as to whether the long-term view afforded by Pleistocene material is pertinent to the problems they are trying to address. In this chapter, we report on the results of this work, and conclude that the Pleistocene record of fossil coral reefs is an extraordinary and unique database with which to address a variety of issues in basic and applied palaeobiological research. We present here a series of three case studies of comparisons between reef coral life, death and fossil assemblages. Each case study is followed by a discussion of the specific results obtained. We end this chapter with a more general discussion of the adequacy of the Pleistocene fossil record of coral reefs.

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 was first applied to reef coral life and death assemblages in the Indo-Pacific. Greenstein and Pandolfi (1997) and Pandolfi and Greenstein (1997b) 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

The linear point intercept (LPI) method was used (Lucas and Seber, 1977) and transects were constructed at each site. In order to estimate cover for the widest range of coral growth forms and colony sizes adequately, transects were 40 m long (Mundy, 1991), each separated by 20–50 m. At 20 cm intervals along each transect, the transect intercept was observed. In 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 whether 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 reef facies exposed in the Florida Keys and at Great Inagua and San Salvador Islands, Bahamas. All of the Pleistocene reef facies examined accumulated during the Sangamon interglacial stage. Radiometric dates indicate that the Bahamian Pleistocene reefs on San Salvador and Great Inagua flourished between 119 and 131 Ka BP (Curran *et al.*, 1989; Chen *et al.*, 1991), while the reefs preserved in Pleistocene strata exposed in the Florida Keys flourished approximately 120–140 Ka ago (Harrison and Coniglio, 1985).

In modern environments, the death assemblage is defined as *in situ* dead coral material encountered along each transect and the dead coral rubble accumulating adjacent to the reef framework. It is assumed that this assemblage represents a reasonable proxy for the material that ultimately becomes a fossil assemblage. Dead coral colonies encountered along the transect were identified to the specific level only if they could be recognized without breaking them open or peeling off any algae or other overgrowth. Rubble composed of dead coral was sampled at the 5, 15, 25 and 35 m marks of each transect. This methodology allowed for adequate sampling of the death assemblage as defined above. Rubble samples were placed in a 5 mm mesh bag constrained by a 10 litre bucket. Thus, coral species and growth form were recorded for each specimen > 5 mm in size that preserved colony structure sufficiently to allow for an identification. Taxonomic data obtained from the rubble samples were pooled with data obtained from dead corals encountered along each transect.

Data Analyses

We constructed species sampling curves to investigate whether our methodology adequately accommodated the diversity present in the coral assemblages studied. Comparison of taxonomic composition was calculated using the Bray–Curtis dissimilarity coefficient (Bray and Curtis, 1957), which has been shown to be one of the most robust coefficients for the analysis of taxonomic composition data (Faith *et al.*, 1987). 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. This standardization equalizes the poten-

tial contributions of taxa to the overall dissimilarity in composition. Without standardization by taxon, the Bray–Curtis values are dominated by those taxa which attain high abundances (Faith *et al.*, 1987). 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), which has been shown to be one of the most effective methods available for the ordination of taxonomic composition data (Minchin, 1987). 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 stress values we obtained 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:

$$\text{species richness} = (S - 1) / (\log N)$$

where S = the number of species present in a sample and N = total number of specimens counted.

RESULTS

Case Study 1: Reef-Tract and Patch-Reef Environments of the Florida Keys and Pleistocene Analogues from Great Inagua Island, Bahamas

Modern life and death assemblages were systematically censused at two reef-tract sites (Little Carysfort Reef, R1; Grecian Dry Rocks, R2) and two patch-reef sites (Horseshoe Reef, P1; Cannon Patch Reef, P2) (Figure 4.1). The reef-tract and patch-reef sites were selected because they represent differing wave energy regimes and show the classic coral zonation described for the Caribbean (see, for example, Goreau, 1959; Geister, 1977). Eight LPI transects were laid down in each site; thus the modern data set comprises 64 samples

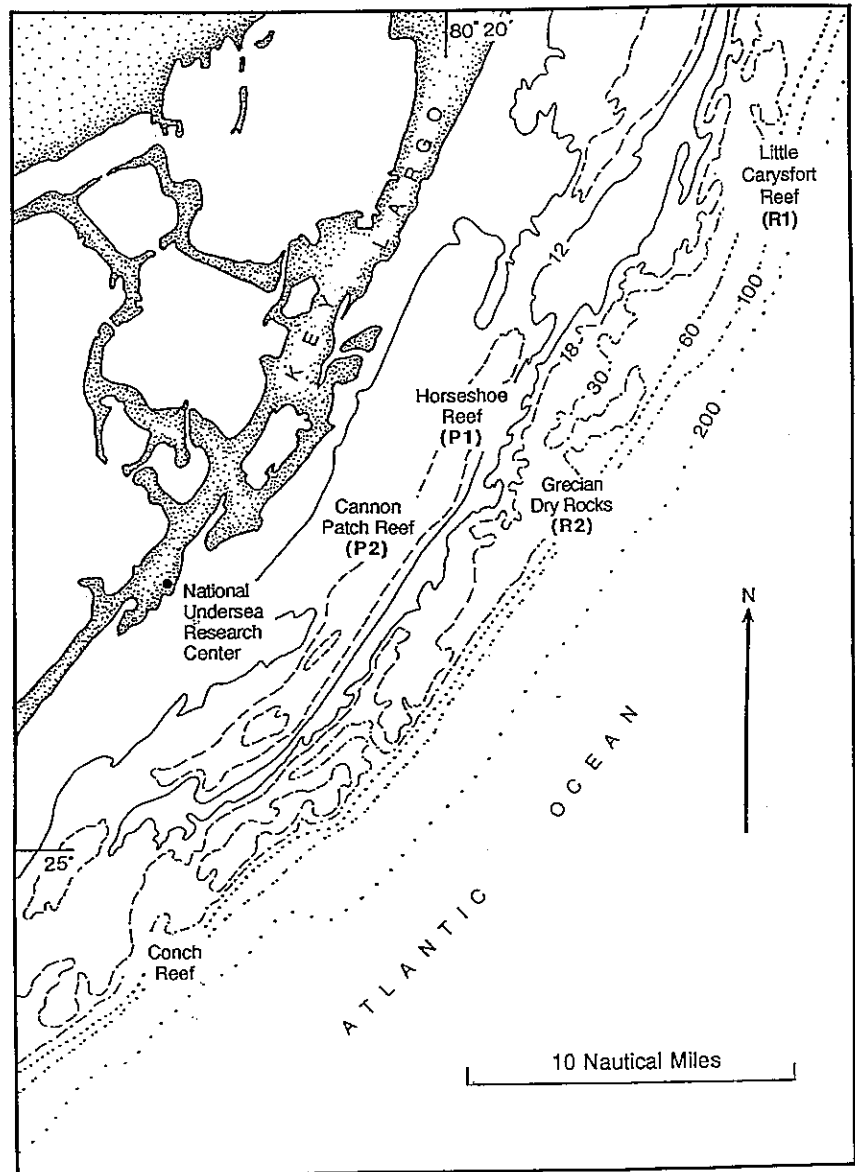


Figure 4.1 The study area of modern reefs of the Florida reef tract. Little Carysfort Reef (R1) and Grecian Dry Rocks (R2) represent high-energy reef-tract sites; Horseshoe Reef (P1) and Cannon Patch Reef (P2) represent lower-energy patch-reef sites

(8 transects \times 2 environments (reef tract and patch reef) \times 2 assemblages (life and death) \times 2 sites) and 30 reef coral species.

A spectacularly preserved exposure of fossil corals occurs on Devil's Point, along the south-west coast of Great Inagua Island, Bahamas (Figure 4.2). Radiometric dates indicate a Sangamon age for the reef (Chen *et al.*, 1991). White and Curran (1995) suggested that the remarkable preservation is the result of rapid burial of a once-living barrier-reef/patch-reef system following the Sangamon interglacial interval. Similar taphonomic circumstances have been invoked for reefs of the same age exposed on San Salvador Island, Bahamas (Greenstein and Moffat, 1996). Many of the fossil coral colonies are in growth position, and subsequent weathering has, in places, produced a highly three-dimensional fossil reef surface that, except for its location approximately 2 m above present sea level, is extremely similar to a modern reef framework/coral rubble assemblage. Thus, the same LPI methodology employed on the modern reefs was feasible. We laid a total of 14 transects on reef facies exposed on Devil's Point and followed the environmental interpretation of White and Curran (1995). Ten transects were constructed in the shallow reef tract, and an additional four transects were placed over patch-reef facies. The data from the Pleistocene facies thus comprise 14 samples and the same coral taxa present in the modern environments.

The cumulative number of species encountered in each sample is plotted for life and death assemblages at each site of the Florida reef tract in Figure 4.3. Eight samples were sufficient to account for coral diversity in life and death assemblages in the patch reef (Figure 4.3A). This was generally the case for life and death assemblages in the reef tract, although the number of species counted from the death assemblage sampled at Little Carysfort Reef did not level off prior to the eighth transect (Figure 4.3B). Differences in diversity values shown by the species sampling curves are generally not significant (see below). Plots of cumulative coral species diversity versus number of transects level off for the reef-tract facies from Great Inagua (Figure 4.4A), indicating that sampling is adequate to estimate species richness and compare taxonomic composition between fossil, life and death assemblages. Plots of cumulative coral species diversity versus number of transects level off only between the final two transects for the patch-reef facies from Great Inagua, yielding some uncertainty as to the adequacy of the sampling regime (Figure 4.4B).

Ordination of the Bray-Curtis matrix reveals that, within environments, the taxonomic composition of modern reef coral life and death assemblages, and that of Pleistocene fossil assemblages, is very similar (Figure 4.5). Moreover, the distinction between reef-tract samples and patch-reef samples obtained in modern environments is matched by a distinction between samples obtained from Pleistocene reef-tract and patch-reef facies. Finally, while the taxonomic composition of the Pleistocene patch-reef assemblages is

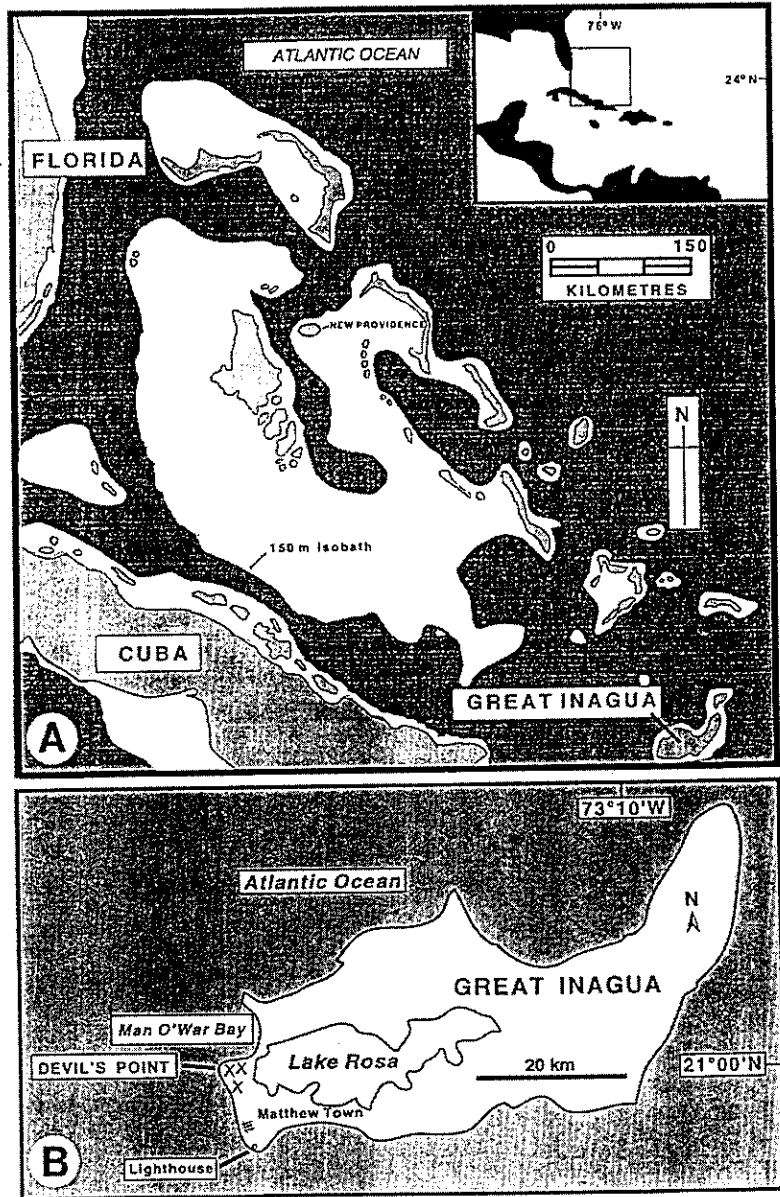


Figure 4.2 (A) Location of Great Inagua Island in the Bahama Archipelago. (B) Transects (marked by Xs) constructed on the fossil coral reef at Devil's Point. (After White and Curran, 1995)

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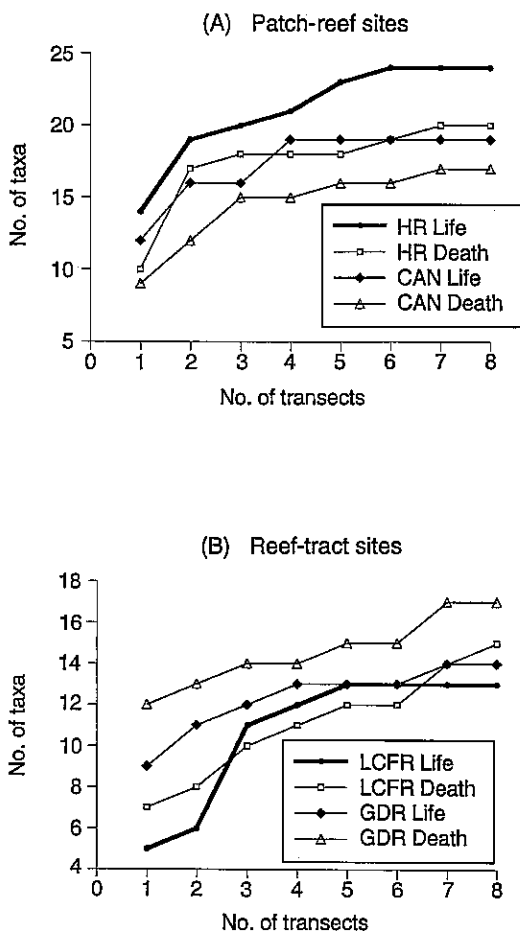


Figure 4.3 Cumulative diversity of reef coral species versus number of sampling intervals (transects) for life and death assemblages from (A) patch-reef and (B) reef-tract sites of the Florida reef tract. Each line is a plot proceeding from the first to the eighth transect. HR, Horseshoe Reef; CAN, Cannon Patch Reef; CFR, Little Carysfort Reef; GDR, Grecian Dry Rocks

similar to that of modern life and death assemblages within patch-reef environments, Pleistocene reef-tract assemblages are distinguished from the modern life and death assemblages of the Florida Keys.

Analysis of species richness revealed that no overall significant difference in diversity between life, death and fossil assemblages exists. However, the patch-reef life assemblage is more diverse than its dead counterpart, and the modern reef-tract death assemblage is more diverse than the reef-tract fossil assemblage preserved on Great Inagua (Figure 4.6).

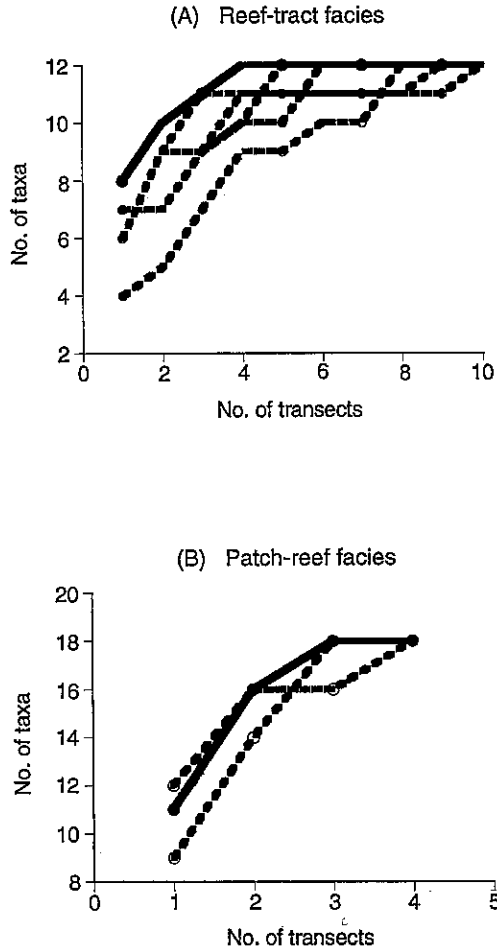


Figure 4.4 Cumulative diversity of reef coral species versus number of sampling intervals (transects) for Pleistocene reef coral assemblages exposed on Devil's Point, Great Inagua Island. (A) Reef-tract facies; (B) patch-reef facies. For each plot, the solid line is a curve proceeding from the first to the last transect. The dashed lines are plots of five random sequences of transects

Results of the ordination suggest that the community structure of modern patch reefs adjacent to Key Largo is accurately represented by analogous Pleistocene facies. Conversely, fossil reef-tract facies are less representative of their living counterparts. The fact that differences in the amount of ecological information preserved in the fossil assemblages exist between reef-tract and patch-reef environments indicates that taphonomic studies should be undertaken in a variety of modern reef environments, and the results applied

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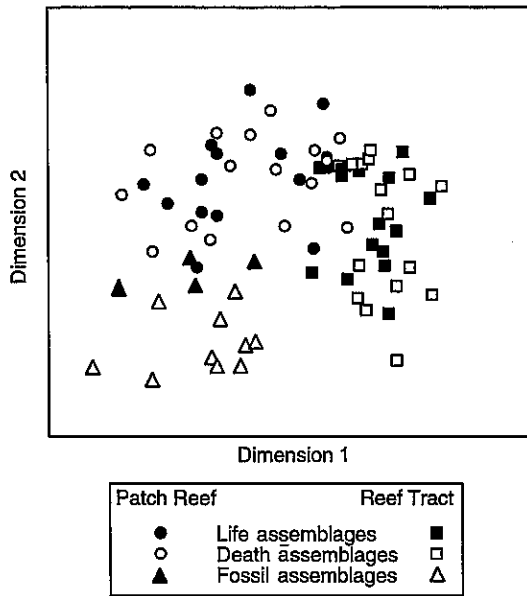


Figure 4.5 Two-dimensional global non-metric multidimensional scaling (GNMDS) ordination of coral life and death assemblages from the Florida Keys and of fossil assemblages from Great Inagua Island, Bahamas. Points closest to one another represent samples (transects) that are more similar in taxonomic composition than points further away from one another. Samples obtained from the fossil assemblages are similar to samples obtained from the life and death assemblages occurring in modern patch-reef environments of the Florida Keys. Note also that the distinction between living reef-tract and patch-reef environments is tracked by both the death and fossil assemblages. The minimum stress value for the two-dimensional analysis was 0.20

to palaeoecological studies of their suspected Pleistocene analogues. We also acknowledge that the geographical difference between the Florida Keys and Great Inagua, Bahamas may be partially responsible for our results. Geographical differences notwithstanding, our results clearly indicate that the community structure of the Pleistocene assemblages reflects the well-documented distinction between reef-tract and patch-reef coral communities (see, for example, Goreau, 1959; Geister, 1977) that exists on modern Caribbean reefs. The change in taxonomic composition present along the environmental gradient between living reef-tract and patch-reef coral assemblages also occurs in the corresponding death and fossil assemblages. This observation corroborates the suggestion of White and Curran (1995) that the north to south transition between *Acropora*-dominated to *Montastrea*- (and *Diploria*-) dominated facies observed along the south-west coast of Great Inagua represents a transition between once-living bank-barrier (that is, reef-tract) and lagoonal patch-reef systems.

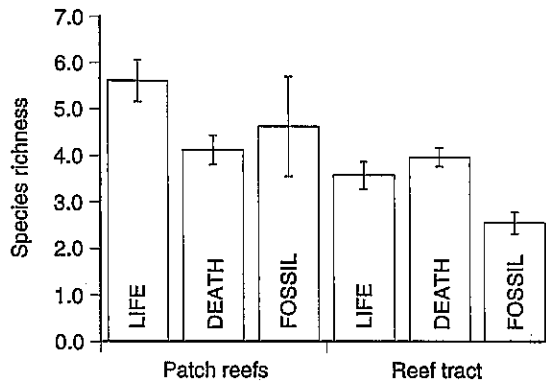


Figure 4.6 Species-richness values for modern life and death assemblages in reef-tract and patch-reef environments of the Florida Keys, and for Pleistocene fossil assemblages from reef-tract and patch-reef facies exposed on Devil's Point, Great Inagua Island. Calculations to the first decimal place are appropriate given the formula we utilized (see text for further discussion). Only the fossil assemblage composing the reef-tract facies shows a significant decrease in diversity, owing primarily to the paucity of milleporids and of a variety of taxa that are relatively rare (for example, *Porites furcata*, *Dichocoenia stokesii* and *Mycetophyllia danaana*; see Figure 4.7). Error bars are standard errors of the mean

The frequency distribution of the 25 most common coral species observed in the life and death assemblages in the Florida Keys and in the fossil assemblage on Great Inagua shows that coral colonies with branching growth forms predominate in the death assemblages, while massive colony growth forms predominate in the living and fossil assemblages (Figure 4.7A–C). This observation is more fully discussed later in the chapter. The diversity difference observed between life and death assemblages in the modern patch-reef is the result of the absence, in the death assemblage, of taxa that are rarely encountered alive (*Mycetophyllia lamarckiana*, *M. danaana* and *Dichocoenia stokesii*). Fossil reef-tract facies are less species-rich than their modern counterparts, primarily because of the paucity of milleporids, which are common components of the living reef tract, and secondarily because of the lack of a variety of taxa that are relatively rare on the living reef tract (for example, *Porites furcata*, *Dichocoenia stokesii* and *Mycetophyllia danaana* – compare Figure 4.7A–C). The lack of milleporids also accounts for the distinction between Pleistocene reef-tract facies and Holocene reef-tract life and death assemblages.

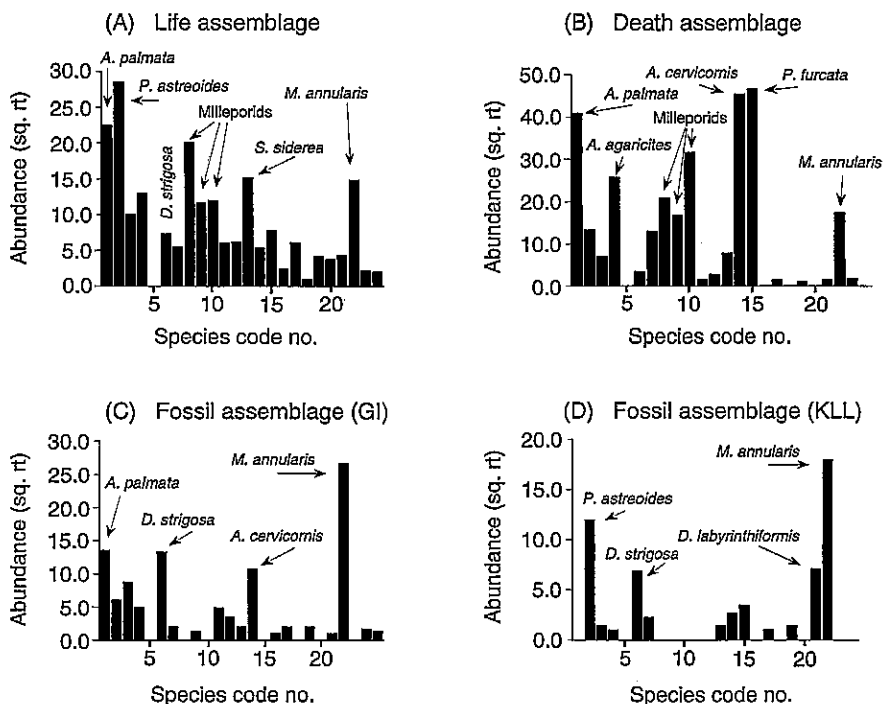


Figure 4.7 Frequency distribution of the 25 most common coral taxa in life (A) and death (B) assemblages of the Florida Keys, and in fossil assemblages preserved on Great Inagua Island (C) and in the Key Largo Limestone (D). GI = Great Inagua; KLL = Key Largo Limestone. Abundance data are transformed 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 colony growth forms in the life and fossil assemblages (for example, *Porites astreoides*, *Diploria strigosa*, *Siderastrea siderea* and *Montastrea annularis*). Species are coded on the x-axis as follows:

- | | |
|---------------------------------|--------------------------------------|
| 1. <i>Acropora palmata</i> | 14. <i>Acropora cervicornis</i> |
| 2. <i>Porites astreoides</i> | 15. <i>Porites furcata</i> |
| 3. <i>Porites porites</i> | 16. <i>Mycetophyllia lamarckiana</i> |
| 4. <i>Agaricia agaricites</i> | 17. <i>Montastrea cavernosa</i> |
| 5. <i>Millepora sp.</i> | 18. <i>Mycetophyllia danaana</i> |
| 6. <i>Diploria strigosa</i> | 19. <i>Colpophyllia natans</i> |
| 7. <i>Favia fragum</i> | 20. <i>Dichocoenia stokesii</i> |
| 8. <i>Millepora squarrosa</i> | 21. <i>Diploria labyrinthiformis</i> |
| 9. <i>Millepora complanata</i> | 22. <i>Montastrea annularis</i> |
| 10. <i>Millepora alcicornis</i> | 23. <i>Meandrina meandrites</i> |
| 11. <i>Diploria clivosa</i> | 24. <i>Solenastrea bournoni</i> |
| 12. <i>Siderastrea radians</i> | 25. <i>Solenastrea hyades</i> |
| 13. <i>Siderastrea siderea</i> | |

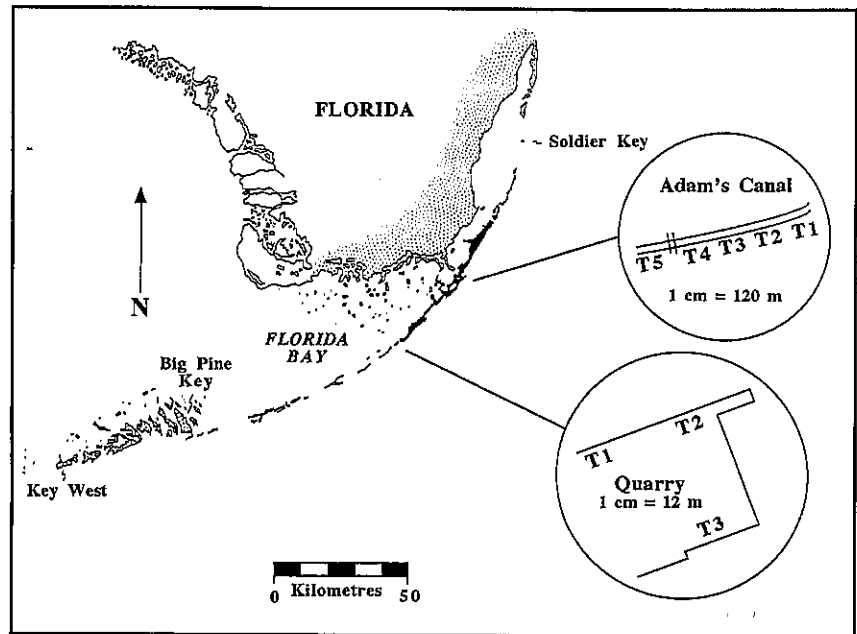


Figure 4.8 Sample localities for the Key Largo Limestone exposed along Adam's Canal and in the Windley Key Quarry in the Florida Keys. Five transects (T1–T5) were constructed along Adam's Canal, and three transects (T1–T3) were constructed in the Windley Key Quarry. (After Stanley, 1966)

Case Study 2: Reef-Tract and Patch-Reef Environments of the Florida Keys and Pleistocene Analogues from Key Largo, Florida

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 with the corresponding life and death assemblages currently accumulating offshore (Figure 4.8). There has been some debate as to the reef environment represented by the Key Largo Limestone. Stanley (1966) recognized that the *Montastrea 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 the interpretation of a shallow patch reef, pointing to stratigraphic constraints and, most importantly, the first description of the

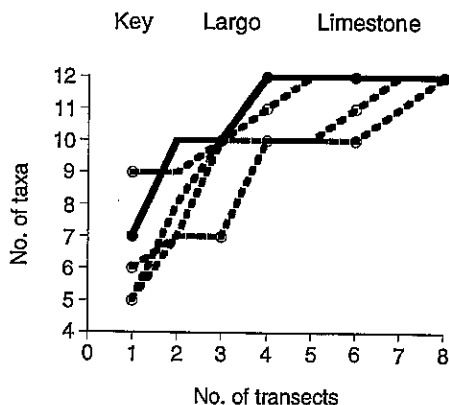


Figure 4.9 Cumulative diversity of reef coral species versus number of sampling intervals (transects) for Pleistocene reef coral assemblages exposed along Adam's Canal and in the Windley Key Quarry in the Florida Keys. The solid line is a plot proceeding from the first transect sampled along Adam's Canal to the last transect sampled in Windley Key Quarry. The dashed lines are plots of five random sequences of transects

reef-crest indicator species, *Acropora palmata*, at a similar stratigraphic level in cores obtained several miles east of the exposed *Montastrea*-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).

As with the exposures on Great Inagua, the outcrops allowed for LPI methodology. Five transects, each 40 m in length, were placed on vertical exposures of the Key Largo Limestone along the sides of Adam's Canal. Water in the quarry on Windley Key only allowed space for three transects. Data from transects from both localities were pooled, and compared with the data obtained from the reef-tract and patch-reef described above.

The cumulative number of species encountered on each transect has been plotted for the fossil assemblages preserved in the Key Largo Limestone exposed on Windley Key and along Adam's Canal (Figure 4.9). Six transects were sufficient to account for coral diversity in the Pleistocene facies, indicating that sampling is adequate to estimate species richness in the fossil assemblages and compare their taxonomic composition with that of the Holocene life and death assemblages occurring offshore.

Ordination of the Bray-Curtis matrix revealed different results from those obtained from Great Inagua. Comparison of the Key Largo Limestone with modern reef-tract and patch-reef environments (Figure 4.10) indicates that the fossil assemblages preserved on Key Largo and Windley Key are more similar to the life assemblages occurring offshore than they are to the death assemblages. Moreover, the fossil assemblages plot in close proximity to

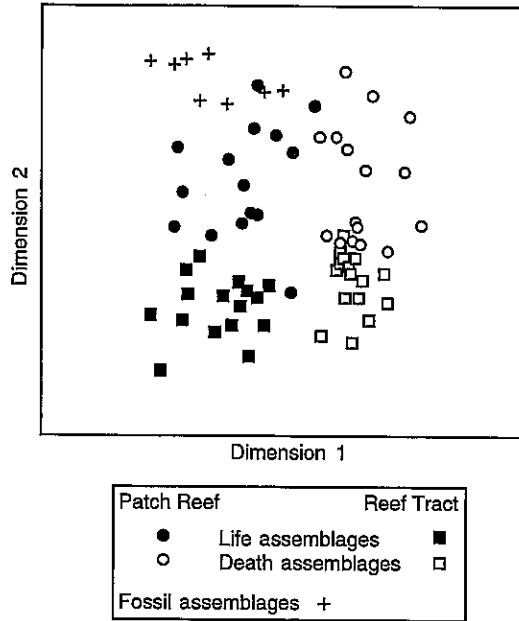


Figure 4.10 Two-dimensional global non-metric multidimensional scaling (GNMDS) ordination of coral life and death assemblages from the Florida Keys and of fossil assemblages preserved in the Key Largo Limestone. Note that samples obtained from the fossil assemblages are more similar to samples obtained from the living patch reef than they are to samples from the death assemblage present in either the reef-tract or patch-reef environment. The minimum stress value for the two-dimensional analysis was 0.17

patch-reef life assemblages, indicating that taxonomic composition and relative abundance of the living and fossil patch-reef are very comparable.

Analysis of species richness revealed no significant difference in diversity between life, death and fossil assemblages for the reef-tract localities and the Key Largo Limestone (Figure 4.11). Additionally, no significant difference in diversity between death assemblages sampled in patch-reef environments and the fossil assemblages was observed. Life assemblages in the patch-reef 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*; Figure 4.7D).

Results of the ordination (Figure 4.10) suggest that the taxonomic composition of reef corals preserved in the Key Largo Limestone more accurately represents the assemblage of corals currently living offshore (the patch-reefs, in particular) than the contemporary death assemblage. Although taphonomic analyses of the corals preserved in the Key Largo Limestone are

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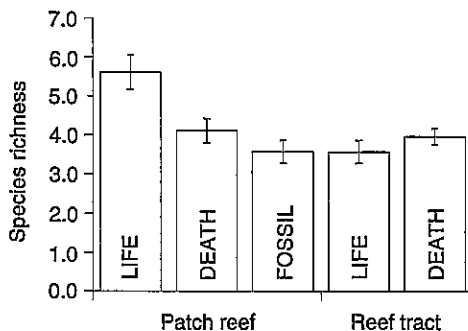


Figure 4.11 Species-richness values for life, death and fossil assemblages in reef-tract and patch-reef environments of the Florida Keys. Except for the modern patch-reef life assemblage, no significant differences in diversity exist. Error bars are standard errors of the mean

lacking, one would predict that such analyses would reveal spectacular preservation. This would be much like that anecdotally observed for the corals exposed on Great Inagua, and that demonstrated by Greenstein and Moffat (1996) for specimens of *Acropora palmata* and *A. cervicornis* preserved in a Pleistocene reef exposed on San Salvador, Bahamas (see below).

Case Study 3: Patch-Reef Environment in Fernandez Bay, and the Cockburn Town Fossil Reef, San Salvador, Bahamas

The Pleistocene reef exposed at Cockburn Town, San Salvador, Bahamas provides an excellent opportunity for a comparative taxonomic study because of its proximity to analogous modern reef environments (Figure 4.12). Here, a regressive sequence includes a coral rubblestone facies, composed predominantly of *Acropora cervicornis*, and a coralstone facies, which contains abundant *in situ* *Acropora palmata*. These facies have been interpreted to represent back-reef and reef-tract environments, respectively (White *et al.*, 1984). Telephone Pole Reef, located in Fernandez Bay, is a modern example of the coral rubblestone facies described by White *et al.* (1984), and is a mid-shelf patch reef that, in the past, was dominated by *A. cervicornis*. This branching coral has suffered a major decrease in abundance throughout the Caribbean region during the past two decades due to a combination of factors (see below). On Telephone Pole Reef, the once-abundant stands of *A. cervicornis* have been largely replaced by *Porites porites* (Curran *et al.*, 1994).

The limited size of Telephone Pole Reef allowed for construction of a total of four 40 m transects over modern life and death assemblages, while five transects were accommodated by the quarry that exposes the Cockburn Town fossil reef. The sampling curves indicate that we have not yet sampled

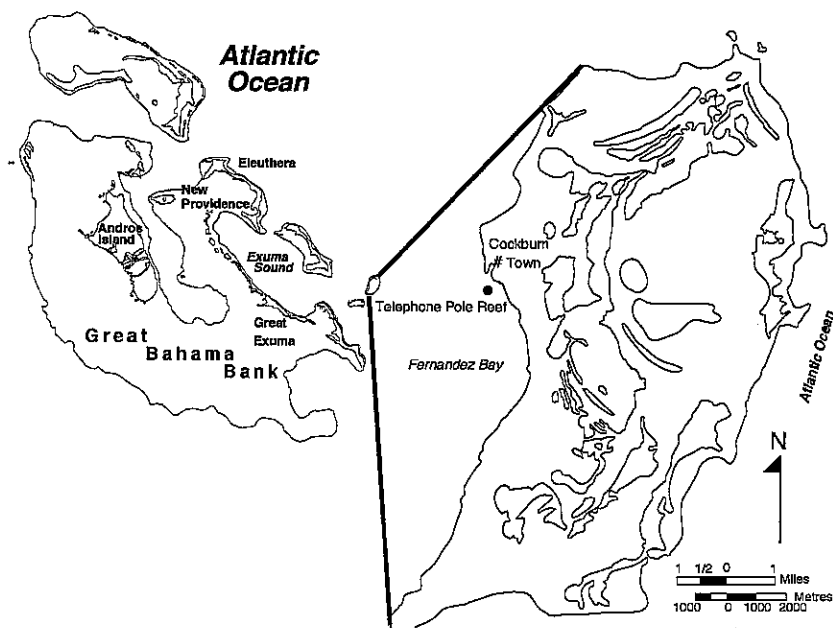


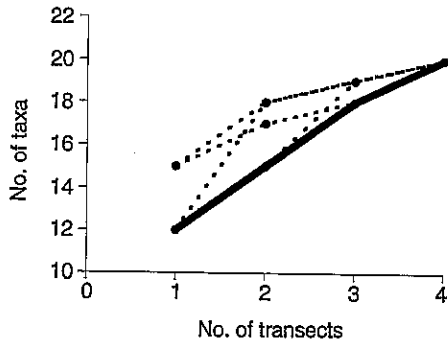
Figure 4.12 Area of study, San Salvador Island, Bahamas. Telephone Pole Reef is located in Fernandez Bay, while the Cockburn Town fossil reef is located onshore at the north end of Fernandez Bay, in Cockburn Town

in sufficient detail to account for the diversity of the life assemblage on Telephone Pole Reef (Figure 4.13A). In addition, sampling curves level off only between the final two transects for both the death and fossil assemblages (Figure 4.13B,C); we hesitate to claim adequate sampling based on these results.

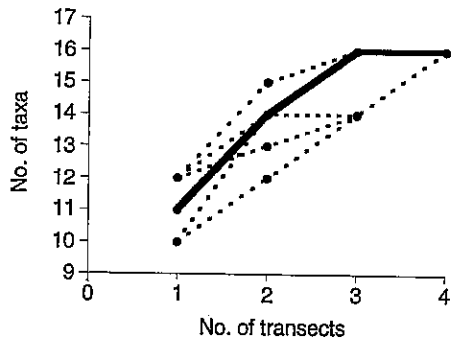
Results of ordination reveal a different pattern from those obtained in the previous surveys. Samples from life, death and fossil assemblages are clearly distinct from one another, in marked contrast to the ordination plots generated for the previous two case studies (Figure 4.14). Moreover, the taxonomic composition of life assemblages is clearly less similar to that of the fossil assemblages than to that of the death assemblages (Figure 4.14). Analyses of species richness indicate that a significant decrease in species diversity occurs from life to death to fossil assemblages (Figure 4.15).

The discrimination between the life assemblage and the death and fossil assemblages by the ordination technique is interpreted to be the result of the recent change in coral community structure on Telephone Pole Reef that is part of a Caribbean-wide phenomenon. Beginning at least as early as the 1980s, *Acropora cervicornis* has suffered an extreme decrease in abundance as

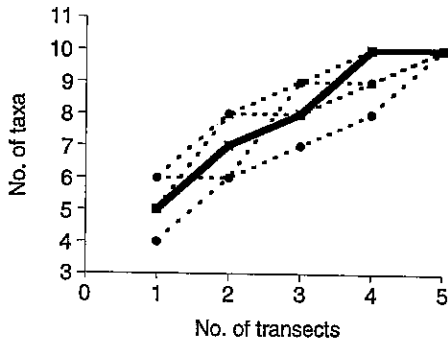
(A) Life assemblage



(B) Death assemblage



(C) Fossil assemblage



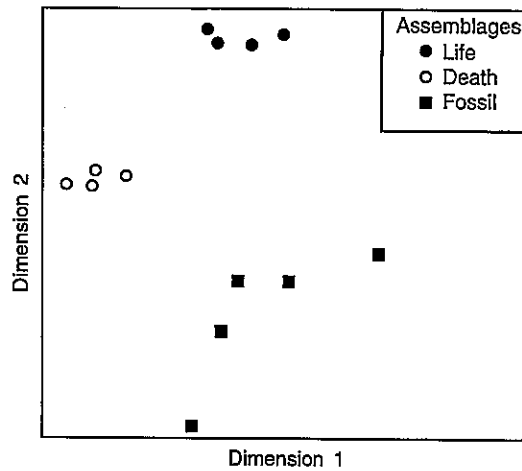


Figure 4.14 Two-dimensional global non-metric multidimensional scaling (GNMDS) ordination of coral life, death and fossil assemblages from San Salvador Island, Bahamas. Note the broad separation of each of the three assemblages. The minimum stress value for the two-dimensional analysis was 0.09

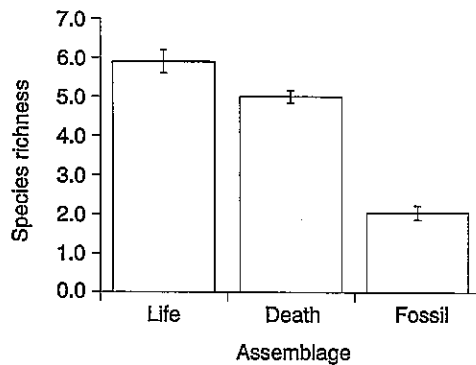


Figure 4.15 Species-richness values for life, death and fossil assemblages on San Salvador Island, Bahamas. Decreasing species-richness values are the result of the lack of milleporids and other taxa in the death and fossil assemblages that are relatively rare on the living reef. Error bars are standard errors of the mean

Figure 4.13 (opposite) Cumulative diversity of reef coral species versus number of sampling intervals (transects) from (A) life, (B) death and (C) fossil reef coral assemblages present on San Salvador Island, Bahamas. 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 to the last transect sampled for each assemblage. The dashed lines are plots of five random sequences of transects

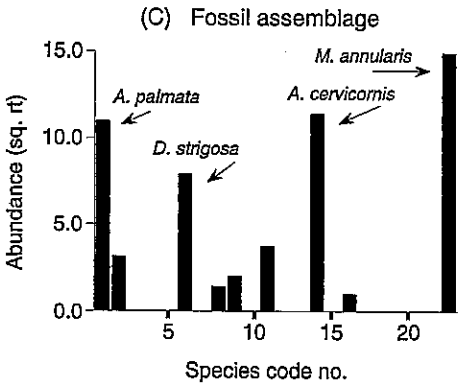
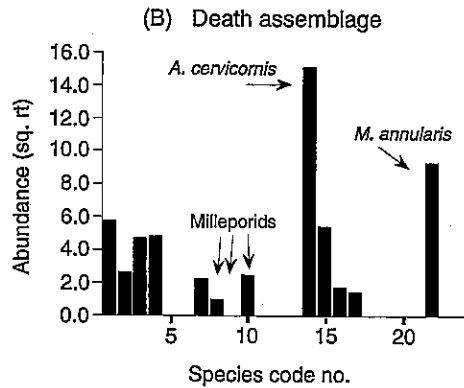
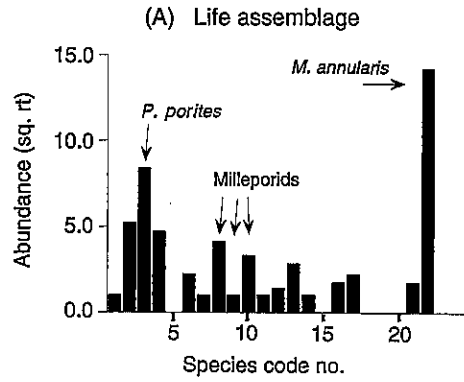
a result of a confluence of factors including hurricanes (Woodley *et al.*, 1981), spread of macroalgae consequent on sea urchin mass mortality (Lessios, 1988), coral diseases and coral bleaching (Brown and Ogden, 1993; Littler and Littler, 1996; Miller, 1996), and a variety of human-induced effects (Hughes, 1994b). On Telephone Pole Reef, *A. cervicornis* has been replaced by large colonies of *Porites porites*. The previous *A. cervicornis*-dominated community is now manifested in the death assemblage (Figure 4.16B), while *P. porites* is abundant only in the life assemblage (Figure 4.16A). Additionally, the paucity of milleporids in both the death and fossil assemblages relative to the life assemblage further segregates life assemblage samples from those obtained from the fossil and death assemblages (compare Figures 4.16A–C). Susceptibility of these hydrozoans to the variety of physical, biological and chemical processes that tend to destroy potential fossil material was also suggested by the results obtained for the first two case studies reported here (compare Figures 4.7A–D), and possibly implicates phylogenetic differences between hydrozoan skeletal microstructure and scleractinian skeletal microstructure as a source of difference in the preservation potential of these taxa. The decrease in species richness from life to death to fossil assemblage results from the absence of the three milleporids distinguished in the surveys (*Millepora complanata*, *M. squarrosa* and *M. alcicornis*) as well as of taxa that are rare in the life assemblage (for example, *Diploria clivosa*, *Montastrea cavernosa* and *Meandrina meandrites*; Figure 4.16). Finally, the greater similarity between life and fossil assemblages is primarily the result of the presence, in high abundance, of massive colonies of *Montastrea annularis*. The presence of

Figure 4.16 (opposite) *Frequency distribution of common coral taxa in (A) life, (B) death and (C) fossil assemblages preserved on San Salvador Island, Bahamas. Abundance data are transformed to square roots. Note the relatively high abundance of Porites porites, milleporids and Montastrea annularis in the life assemblage. The death assemblage comprises Acropora cervicornis, A. palmata and lower abundances of M. annularis. Species are coded on the x-axis as follows:*

- | | |
|---------------------------------|--------------------------------------|
| 1. <i>Acropora palmata</i> | 14. <i>Acropora cervicornis</i> |
| 2. <i>Porites astreoides</i> | 15. <i>Porites furcata</i> |
| 3. <i>Porites porites</i> | 16. <i>Mycetophyllia lamarckiana</i> |
| 4. <i>Agaricia agaricites</i> | 17. <i>Montastrea cavernosa</i> |
| 5. <i>Millepora sp.</i> | 18. <i>Mycetophyllia danaana</i> |
| 6. <i>Diploria strigosa</i> | 19. <i>Colpophyllia natans</i> |
| 7. <i>Favia fragum</i> | 20. <i>Dichocoenia stokesii</i> |
| 8. <i>Millepora squarrosa</i> | 21. <i>Diploria labyrinthiformis</i> |
| 9. <i>Millepora complanata</i> | 22. <i>Montastrea annularis</i> |
| 10. <i>Millepora alcicornis</i> | |
| 11. <i>Diploria clivosa</i> | |
| 12. <i>Siderastrea radians</i> | |
| 13. <i>Siderastrea siderea</i> | |

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recognizable massive colony growth forms in both life and fossil assemblages pervades this study, and is the result of a combination of taphonomic factors and sampling methodology. We elaborate on this statement in the following section.

DISCUSSION

An implicit assumption in the application of palaeoecological studies of Pleistocene reef communities to a variety of current ecological issues is some degree of congruence between fossil assemblages and their living predecessors. Studies of taphonomic processes in modern marine environments have dealt almost exclusively with the transition from life to death assemblages, primarily with molluscan skeletal remains (a great deal of this work is synthesized by Kidwell and Bosence, 1991), foraminifera (Martin and Wright, 1988) and, more recently, with reef corals (Pandolfi and Minchin, 1995; Greenstein and Moffat, 1996; Greenstein and Pandolfi, 1997; Pandolfi and Greenstein, 1997b). The death assemblage is viewed as an intermediate point during the transition from biosphere to lithosphere. The ecological information removed during the transition from the life assemblage to the death assemblage by a variety of physical and biological processes is collectively referred to as 'taphonomic bias'. Most authors assume that taphonomic bias evident in the death assemblage will, at best, simply be transferred to the fossil assemblage or, worse (from the standpoint of 'adequacy'), be augmented by subsequent processes during the later biostratigraphic and diagenetic intervals. Examination of living, dead and analogous fossil assemblages in the former case might indicate a decrease in similarity in community structure and a change in diversity between the life and death assemblage, but no continuing differences when death and fossil assemblages are compared. The results of the latter case might reveal decreasing similarity of community structure and changes in diversity through each transition. The case studies we report here have allowed us to test these assumptions, and are thus unique in that they take actuopalaeontological investigations of life and death assemblages one step further, to include investigations of attendant Pleistocene facies composed of essentially the same coral taxa – the 'next step back' into the ancient. We have obtained surprising results: for the life and death assemblages accumulating in the Florida reef-tract and Fernandez Bay, San Salvador, taphonomic bias in the death assemblage has not translated to the fossil assemblage in a stepwise process. Rather, differences in the degree to which fossil assemblages reflect the community structure of life versus death assemblages exist between the Florida Keys and the Bahamas, and between reef-tract and patch-reef environments within the Florida Keys reef system. Thus, the death assemblage is

not necessarily the predictor of what might become fossilized, and the assumption that a progression from life to death to fossil assemblage exists in all reef environments should be reconsidered.

Degradation and Coral Identification

The primary reason for the greater similarity of fossil assemblages preserved in the Key Largo Limestone (case study 2) to life assemblages instead of death assemblages in the Florida Keys is the prevalence of living and fossil massive coral colony growth forms (primarily *Montastrea annularis* and *Diploria strigosa*) (Figure 4.7A,B,D). This growth form is relatively rare in the death assemblages surveyed on the Florida reef-tract, but common in both the life and fossil assemblages. The differential representation of this growth form in life and fossil assemblages versus death assemblages is the result of three major factors.

The first factor is that large, massive colony growth forms, which cement directly on to the reef framework, suffer degradation by physical, biological and chemical processes disproportionately to branching and free-living colony growth forms. In a study of the effect of growth form and environment on the preservation potential of reef-building corals on the Great Barrier Reef (Pandolfi and Greenstein, 1997a), we demonstrated that massive colony growth forms in the death assemblage showed consistently higher levels of degradation than did branching and free-living growth forms. Because they possess more robust skeletons than their branching counterparts, massive coral colonies are able to survive for longer intervals of time in the taphonomically active zone (TAZ; see Davies *et al.*, 1989). They thus accumulate a variety of physical, chemical and biological agents of degradation that serve to obscure the details of the colony surface sufficiently to prevent discrimination between species. However, branching and free-living growth forms are more rapidly reduced to essentially unrecognizable grains of carbonate sand; when present in the death assemblage, they are found in less degraded condition because the skeleton does not survive long enough to accumulate extensive features of degradation. This fact influenced the results of our systematic comparisons between life and death assemblages accumulating in shallow (2 and 6 m) and deep (20 and 30 m) reefs of the Florida reef tract (Greenstein and Pandolfi, 1997, and Pandolfi and Greenstein, 1997b, respectively). We demonstrated a striking growth form bias in all depths and reef zones: branching coral growth forms are over-represented in the death assemblage, while massive colony growth forms are over-represented in the life assemblage. We refer the reader to these studies for a more detailed discussion of the nature and effect of this bias.

The second factor involves a combination of our sampling protocol and the

way in which fossil corals present themselves in outcrop. First, the rubble samples obtained in modern environments were biased towards those taxa and growth forms not cemented directly on to the reef framework (that is, many branching coral species). Perhaps more importantly, our transect methodology included no way of identifying *in situ* massive coral colonies whose surficial degradation precluded accurate specific identification. When encountered, these surfaces were recorded as 'hard substrate'. Massive colonies preserved as fossils may readily be split open and identification can be accomplished by studying their internal microstructure. In fact, vertical outcrops present at all Pleistocene localities often presented massive colonies broken along the plane of the outcrop. If it had been logistically feasible to split open all the degraded massive colony growth forms that were encountered under water, we inevitably would have identified to the species level many more massive colonies in the death assemblages than we did using the present methodology, and the growth form bias would not have been as severe. However, even though our sample size of massive coral growth forms would have increased by breaking corals open, we cannot be sure whether increased identification would have resulted in greater representation in the death assemblages of the same massive coral species found in the life assemblages. In any event, the fossil assemblage, where coral microstructure is readily available for study, is more similar to the original life assemblage than the present death assemblage as we measured it.

The third factor involves the preservation history of the fossil reefs we examined. In addition to preserving microstructure that was readily available for study, the majority of fossil corals with massive growth forms could be identified on the basis of their surficial structures. This was particularly true on both Great Inagua and San Salvador Islands, where much of the original three-dimensional reef framework is exposed. The presence, in the fossil assemblages, of massive coral colonies that could be identified to the level of species suggests that rapid entombment of once-living reef communities has occurred. Several workers have outlined sedimentological (for example, White *et al.*, 1984; White and Curran, 1987, 1995; Curran *et al.*, 1989; White, 1989) and taphonomic (for example, Greenstein and Moffat, 1996) evidence for rapid burial of late Pleistocene bank-barrier and lagoonal reef systems of the Bahama Archipelago, perhaps as shallow subtidal sands encroached on them in response to the post-Sangamon regression. No such data are available for the Key Largo Limestone. For the Bahamian facies at least, we suggest that our results reflect the rapid entombment of once-living reef systems during the post-Sangamon regression. Thus, live and dead corals were buried concurrently, and a death assemblage as we define it (*in situ* dead coral as well as coral rubble accumulating adjacent to the reef framework) was essentially 'skipped' in the process. The observed similarity in taxonomic composition between the *Montastrea*-dominated facies preser-

ved on Great Inagua and modern life and death assemblages in the Florida reef system (case study 1) also supports this interpretation.

Constancy and Change in Reef Community Structure

Zonation in distribution patterns of coral species has been well documented for Caribbean reefs in modern environments (Goreau, 1959) and their Pleistocene analogues (Mesolléla, 1967; Geister, 1977; Jackson, 1992; Jackson *et al.*, 1996). Our results suggest specifically that the distinction between reef-tract and patch-reef coral community structure is indeed preserved in fossil assemblages. However, does this mean that temporal patterns in reef community structure preserved within a particular reef facies over tens to hundreds of thousands of years (see Jackson, 1992, 1994a; Pandolfi, 1996) have been archived in Pleistocene strata? Our results from San Salvador, where a patch-reef currently undergoing a transition in community structure was compared with its Pleistocene analogue, might yield insight into the limits of the 'adequacy' of Pleistocene coral reef deposits.

As mentioned above, Telephone Pole Reef is currently undergoing a transition from an *Acropora cervicornis*-dominated coral assemblage to an assemblage with abundant *Porites porites*. The distinction between life, death and fossil assemblage samples by ordination (Figure 4.14) is primarily the result of the abundant stands of *P. porites* currently inhabiting the reef (Figure 4.16A), and, secondarily, the presence of hydrozoans. *Porites* is much less abundant in the death and fossil assemblages (Figure 4.16B,C). The death assemblage contains the once-abundant stands of *A. cervicornis* that are now extremely rare in the life assemblage and are also abundant in the fossil assemblage. Although insufficient sampling necessarily qualifies our results, they are strikingly different from those we obtained in the previous two case studies, and there are two alternative hypotheses that explain the apparent failure of the Pleistocene assemblage exposed on San Salvador to reflect the life assemblage accurately.

First, the demise of *A. cervicornis* in the Bahamas and Caribbean, and subsequent replacement by another coral species (on Telephone Pole Reef, *P. porites*), is without historical precedent. In Belize, the once-abundant stands of *A. cervicornis* have been replaced by *Agaricia agaricites* (Aronson, 1996; Aronson and Plotnick, in press). Careful examination of cores taken through the reef sedimentary record in Belize revealed no recognizable signals (abrupt changes in coral taxa or taphonomic evidence of an essentially monospecific death assemblage) of similar transitions, suggesting that the present drastic reduction of *A. cervicornis* has no precursor in the recent geological past (at least 3800 years; Aronson, 1996). In the Florida Keys, we purposely chose for our surveys modern reefs that conformed to earlier

(pre-1980) descriptions (for example, Multer, 1977) of the majority of the reef-tract reefs (for example, abundant live *Acropora palmata* in the shallowest zones, grading to more diverse, deeper assemblages of living *Porites astreoides*, *Montastrea annularis* and *Diploria strigosa*). It is compelling that these 'healthy' reef communities were reflected by the fossil assemblages in the Florida Keys and Great Inagua, 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 the rapidity with which communities dominated by *A. cervicornis* have been altered. From this we can only conclude that the persistence of this coral association during Pleistocene climatic fluctuations (Mesollela, 1967; Jackson, 1992) is not an artefact of taphonomic bias.

An alternative hypothesis is that rapid changes in coral dominance within a community commonly occur, but the fossil record has not been studied in sufficient detail to observe these temporally short-term fluctuations in reef community structure. Short-term studies of living coral reefs have recorded fluctuations of dominant species at virtually all spatial scales, ranging from metre quadrats (for example, Hughes *et al.*, 1987; Bak and Nieuwland, 1995) through individual reefs (for example, Porter *et al.*, 1981; Woodley *et al.*, 1981) to entire provinces (for example, Lessios, 1988). Moreover, short-term fluctuations may be a prerequisite for long-term stability (Chesson and Huntly, 1989) and, thus, produce the type of long-term persistence of coral communities documented by Mesollela (1967), Jackson (1992) and Pandolfi (1996). With the tremendous age resolution now available for Quaternary reef deposits, it is possible to collect detailed information at much shorter time scales than previously thought. On the basis of our results here, we encourage short-term fossil studies as a complement to previous palaeoecological studies at larger time scales.

Adequacy of the Quaternary Fossil Record of Coral Reef Communities

Our results suggest that, for the Pleistocene strata we have examined, the stepwise transition from life to death to fossil assemblage cannot be assumed. Fossil assemblages may preserve modern life and death assemblages (case study 1), life assemblages (case study 2) or death assemblages (case study 3). Since the amount of taphonomic bias can be different in different reef environments, it becomes imperative to assess the amount occurring by conducting taphonomic analyses in each modern environment that is to be studied as a fossil assemblage. Based on the results of the three case studies we conclude that, with a synthesis of taphonomic studies in modern reef environments, the Quaternary record of fossil reefs becomes an extraordi-

Peninsula, Papua New Guinea. Pandolfi (1996) showed that similar associations of reef coral species reassembled repeatedly through time, suggesting limited species membership. Jackson (1992) suggested that a similar pattern might exist throughout the past 500 000 years in Barbados. We believe our taphonomic work clearly shows that preservation bias is minimal for Quaternary fossil reefs. Moreover, in combination with attendant taphonomic analyses in appropriate modern environments, the Quaternary record of fossil reefs provides ecologists and palaeoecologists with a rich and reliable data resource to compare patterns of community assembly occurring over multiple time scales, both human and geological. However, we stress the importance of examining preservational attributes in palaeoecological studies, especially those which purport to examine the recent past history of modern ecosystems. This is especially true from our studies, since different reef environments responded differently in their preservational attributes.

Sequence stratigraphic controls on reef preservation

The life and death assemblages present adjacent to Key Largo have been accumulating during the Holocene transgression (Lidz and Shinn, 1991). Those preserved on Great Inagua and elsewhere in the Bahamas were buried during a late Pleistocene regression (White and Curran, 1995). Our analysis of Pleistocene fossil assemblages, combined with the previous work of Greenstein and Pandolfi (1997) and Pandolfi and Greenstein (1997b), suggests stratigraphic sequence (transgressive versus regressive) may be a first-order mechanism for determining preservational style of fossil reef systems. Specifically, regressive reefs might be more likely to be preserved by a rapid burial event as shallow subtidal sand and beach deposits encroach on them during a relative lowering of sea level. In contrast, transgressive reefs may be less prone to catastrophic burial and thus, if preserved at all, may exhibit poorer preservation than their regressive counterparts. We suggest that further taphonomic research on ancient reef communities be conducted in tandem with analyses of the sequence stratigraphic context in which the assemblages occur. This approach will allow palaeontologists to understand the implications of pristine versus highly degraded fossil coral material accumulated in the geological past, when the abundance and diversity of organisms that serve to degrade coral material may have been very different from those in Pleistocene or modern time.

ACKNOWLEDGEMENTS

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