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Appendix A

Additional information for the study of Pleistocene coral communities from Curaçao, Netherlands Antilles.

Abstract

This Appendix provides additional information for the study of Pleistocene coral communities from Curaçao. It is composed of a Methods section explaining one additional analysis: cluster analysis. It goes into some detail about the nature of the paleontological database from which the results of the published study are derived ("How good are the data?"). The Appendix goes into further detail about the basis for the coral taxonomy used in the study, including a list of species, figured examples of the different fossil forms of the *Montastraea "annularis"* species complex, and a table of species diversity for each sample. Further data are also given on species distribution patterns: two tables showing a list of species that occurred in only 1 or 2 (of 3) of the Pleistocene reef environments or 1 (of 2) of the sites per environment. Lastly a section on results from the cluster analyses, corroborates, in all cases, the results of the global non-metric multidimensional scaling ordinations presented in the original paper.

Keywords: community ecology, community structure, Quaternary, Pleistocene, paleoecology, coral, coral reefs, Caribbean

Research location: Curaçao, Dutch West Indies, 12° N and 68° W

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Methods

The main methods for sample design and data analysis used in the original paper and in this Supplement are illustrated in [Figure A1](#). One method used in the Supplement, and not explained in the original paper is the cluster analysis.

Cluster analysis. Cluster analysis provides a graphical display that attempts to group samples into clusters based on their similarity. Complete link clustering was performed on the ranked BC dissimilarity matrices, ensuring that the clustering obtained had exactly the same structure as that based on the original similarities. Since this is also the philosophy behind the ordination technique, results from ordination and clustering can be compared easily (Clarke and Warwick 1994).

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Can Quaternary reef coral assemblages be reliably studied on Caribbean raised reef terraces? How good is the Quaternary record of Caribbean reefs? A major concern in any paleoecological study is the quality of the data compared to that obtainable in studies of Recent communities. The data from this study are composed of fifty 40-m long transects, or about 2000 m of surveyed shallow reef habitats. Sampling curves of the cumulative number of Pleistocene species level off after a few transects within each environment ([Fig. A2](#)). Moreover, four lines of evidence suggest that our Pleistocene communities preserve significant amounts of ecological information from the original reefs.

1) We found the same diversity of reef coral species as that found in similar environments in the modern ([Table A1](#)). Thus, we have been able to identify most, if not all, of the coral species which lived in the three reef environments of the Pleistocene of Curaçao, and we are confident that no important components of the original reef coral communities have been lost during fossilization.

2) Species identifications could be made on closely related species which show subtle morphological differences. We were able to easily identify species from a number of different coral families. In addition, species within both the *Montastraea "annularis"* and *Montastraea "cavernosa"* species complexes could be differentiated, and an additional form within each complex was identified in the Pleistocene of Curaçao (see [Coral species and taxonomy](#)). Regardless of whether or not these new forms will survive rigorous morphometric analyses of corallite microstructure (Pandolfi *unpub. data*), or genetic analyses, our ability to identify them easily in the field as separate morphospecies speaks strongly for the quality of the Pleistocene data. Thus, the Pleistocene reef coral communities of Curaçao contain important ecological information at the species level.

3) The estimated length of time represented by our data is between 200 and 2350 years. This "time-averaging" (Johnson 1960) is advantageous for two reasons. First, corals commonly live many centuries or longer and it is appropriate to study community structure over at least a few generations (Cameron and Endean 1985). Secondly, the study of time-averaged assemblages, if not sampled over too long a time, can avoid the short-term effects of environmental noise, such as hurricanes and earthquakes. Although such events may be devastating in a short term, they may only result in minor fluctuations in community structure in the long term (Jackson 1991).

Two other groups of studies increase our overall confidence in our results. First, Mesoella (1967) documented patterns in the relative abundance of coral species, from the Pleistocene of Barbados that were similar to those reported for living reefs around Jamaica (Goreau 1959; Goreau and Wells 1967). Subsequent re-analysis of Mesoella's data suggests that these species distribution patterns persisted for over half a million years (Jackson 1992). The Pleistocene communities from Curaçao also show similar

abundance patterns to those existing on Caribbean reefs prior to the 1980's, when widespread degradation led to the collapse of many Caribbean reefs.

Second, taphonomic studies of the transition from a life to a death assemblage showed that modern life and death assemblages of Caribbean reef corals exhibit: 1) similar differentiation of reef coral communities with habitat; and 2) similar taxonomic diversity of reef coral species (Greenstein and Pandolfi 1997; Greenstein *et al.* 1998a; Pandolfi and Greenstein 1997). Moreover, the few comparative studies of life, death, and fossil assemblages show excellent agreement in taxonomic composition and diversity (Greenstein *et al.* 1998a,b). These studies, and the good agreement in diversity between modern and fossil reefs that we found in Curaçao ([Table A1](#)), indicate that ecological information appears to be well conserved in Quaternary fossil reef assemblages. This is in major contrast to Pleistocene terrestrial forest communities based on pollen. The relationship between abundance of pollen and abundance of original trees is uncertain (Bush 1995), and pollen may only represent taxa that made up as little as 5% of the original forest community (Terasmae 1973).

Coral species and taxonomy

The 39 coral species identified in this study are listed in the Appendix. Seven transects were laid at each of two sites in each of the three ancient reef environments on the island ([Table A2](#)). We found 15 species in the WRC, 19 species in the WBR, and 21 species in the LRC; and for data collected along both the transects and the 1 hour search we found 30, 23, and 30 species, respectively ([Table A2](#)). In most instances preservation of corals along the chosen transects was excellent and identifications were made in the field. Where preservation was not satisfactory to identify corals to species in the field, they were collected and identified in the laboratory using microscopic analysis of corallite wall structure. In addition, a reference collection of each identified species was assembled which is now housed at the National Museum of Natural History of the Smithsonian Institution, Washington DC. Specimens could be identified to species in almost all cases, and all could be identified to genus. Inclusion of the few unidentified specimens made no difference to the results so they were excluded from the analyses presented.

The taxonomy of Neogene to Recent Caribbean corals has advanced significantly in the past 15 years, mainly through the efforts of Budd and colleagues (Budd *et al.* 1994) who used new morphometric data on corallite and colony characters to revise the fauna. All of these characters can be recognized in fossils, and the limited molecular data available support the separation of morphospecies (Lopez and Knowlton 1997; Knowlton *et al.* 1997). We have therefore followed their framework with three exceptions: *Colpophyllia*, the *Montastraea "annularis"* species complex (Knowlton *et al.* 1992) and the *Montastraea "cavernosa"* species complex.

Colpophyllia: We distinguished *C. amaranthus* by its almost cerioid (closely packed corallites with single mouths and shared walls) valley structure as opposed to the more meandroid (meandering valleys with multiple mouths) valleys of *C. natans* and *C. breviserialis*, rather than using colony size differences emphasized by Budd *et al.* (1994).

Montastraea "annularis" complex. Three different species have been recognized that show morphologic (Budd 1993), genetic (Knowlton *et al.* 1992), behavioral (Knowlton *et al.* 1997) and ecological (Van Veghel 1994) differentiation among growth forms: a massive form known as *Montastraea faveolata* with exert septa extending above the coenosteum, a columnar form known as *Montastraea annularis* (*sensu*

stricto) with prominent first order septa, and a massive to plate form with small knobs (the 'bumpy' species) known as *Montastraea franksii* with larger less regular corallites separated by larger distances than the other two species. We found even further morphologic differentiation in the Pleistocene assemblages of the Hato Unit of the Lower Terrace on Curaçao ([Fig. A3](#)). We recognized the massive, columnar and platy forms already assigned to the modern *Montastraea "annularis"* species complex, and an organ-pipe form which is now extinct (Pandolfi 1999; Pandolfi *et al.* in press). Thus, the analyses presented here include one more species from the *Montastraea "annularis"* species complex than that listed by Budd *et al.* (1994).

Montastraea "cavernosa" complex. We distinguished four presumptive sibling species in this group (one more than Budd *et al.* 1994), three of which match well the species and species characteristics they described.

In summary, our taxonomy for Pleistocene corals of Curaçao is based on the same criteria as those used for living and fossil species throughout the Caribbean, and includes the recent discovery of cryptic species complexes which can be readily distinguished in fossils. Thus, our level of taxonomic discrimination of Pleistocene corals is greater than for virtually all surveys of living reef coral communities in the Caribbean. Moreover, only two of the species we found in the Pleistocene of Curaçao are extinct today: *Pocillopora cf. palmata* and the organ-pipe growth form of the *Montastraea "annularis"* species complex (Geister 1977; Pandolfi 1999; Pandolfi *et al.* in press). Thus, this study examines an essentially modern fauna.

Species distribution patterns

Distribution of rare taxa. There were a number of species that occurred in only one of the reef environments, and a few that were absent from only one of the reef environments ([Table A3](#)). In the Pleistocene of Curaçao, 15 of 39 species occurred in only one of the three reef environments ([Table A3](#)), yet over 90% of the coral abundances came from just 4 or less of the coral species within each of the three environments. In the windward reef crest (WRC), there were a number of species encountered in the southern transects that were not encountered in the northern transects ([Table A4](#)). In the windward back reef (WBR), a number of species encountered in the northern transects were not encountered in the central transects ([Table A4](#)).

Cluster Analysis

Cluster analysis of the Bray-Curtis dissimilarity matrix provides an alternative graphical representation of the environmental differences in taxonomic composition among the reef coral assemblages and showed good agreement with both the GNMDS ordination and the ANOSIM results (see original paper).

In the combined cluster analysis (quantitative data set) of all transects from all environments, the dendrogram shows two major clusters ([Fig. A4](#)). The first major cluster has two components, one exclusively composed of WRC assemblages and the other predominantly composed of LRC assemblages. Some assemblages from the WRC are also found within the LRC cluster. The second major cluster is composed of almost exclusively WBR assemblages. Some assemblages from the LRC are also found within the WBR cluster ([Fig. A4](#)). It is clear that the LRC assemblages overlap with both the WRC and the WBR, but the latter two do not overlap.

Individual cluster analyses of transects from all three environments show very similar patterns in

taxonomic composition with respect to geographic position as did the GNMDS and the ANOSIM tests ([Fig. A5](#)).

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Appendix. List of reef coral (Scleractinia) species from the 125 ka Hato Unit, Lower Terrace, Curaçao.

Acropora cervicornis (Lamarck 1816)

Acropora palmata (Lamarck 1816)

Agaricia agaricites (Linneaus 1758)

Agaricia crassa (Verrill 1902)

Agaricia pusilla (Verrill 1902)

Colpophyllia amaranthus (Müller 1775)

Colpophyllia breviserialis (Milne Edwards and Haine 1849)

Colpophyllia natans (Müller 1775)

Dendrogyra cylindricus (Ehrenberg 1834)
Diploria clivosa (Ellis and Solander 1786)
Diploria labyrinthiformis (Linneaus 1758)
Diploria strigosa (Dana 1848)
Eusmilia fastigiata (Pallas 1766)
Favia fragum (Esper 1797)
Isophyllastrea rigida (Dana 1848)
Isophyllia sinuosa (Ellis and Solander 1786)
Madracis mirabilis (Duchassaing and Michelotti 1860)
Madracis decactis (Lyman 1859)
Manicina areolata (Linneaus 1758)
Meandrina meandrites (Linneaus 1767)
Millepora complanata (Linneaus)
Montastraea "cavernosa" sp. 1 (Linneaus 1767 - morph 1 of Budd et al 1994)
Montastraea "cavernosa" sp. 2 (Linneaus 1767 - morph 2 of Budd et al 1994)
Montastraea "cavernosa" sp. 3 (Linneaus 1767 - morph 3 of Budd et al 1994)
Montastraea "'cavernosa" sp. 4 (new species)
Montastraea annularis (sensu stricto) (Ellis and Solander 1786)
Montastraea faveolata (Ellis and Solander 1786)
Montastraea franksi (Gregory 1900)
organ-pipe *Montastraea* (new species)
sheet *Montastraea* (Ellis and Solander 1786)
Pocillopora cf. palmata (Palmer 1928)
Porites astreoides (Lamarck 1816)
Porites divaricata (Lesueur 1821)
Porites furcata (Lamarck 1816)
Porites porites (Pallas 1766)
Siderastrea radians (Pallas 1766)

Siderastrea siderea (Ellis and Solander 1786)

Solenastrea bourini (Milne Edwards and Haine 1849)

Stephanocoenia intersepta (Lamarck 1816)

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Colpophyllia: We distinguished *C. amaranthus* by its almost cerioid (closely packed corallites with single mouths and shared walls) valley structure as opposed to the more meandroid (meandering valleys with multiple mouths) valleys of *C. natans* and *C. breviserialis*, rather than using colony size differences emphasized by Budd *et al.* (1994).

Montastraea "annularis" complex. Three different species have been recognized that show morphologic (Budd 1993), genetic (Knowlton *et al.* 1992), behavioral (Knowlton *et al.* 1997) and ecological (Van Veghel 1994) differentiation among growth forms: a massive form known as *Montastraea faveolata* with exert septa extending above the coenosteum, a columnar form known as *Montastraea annularis* (*sensu*

stricto) with prominent first order septa, and a massive to plate form with small knobs (the 'bumpy' species) known as *Montastraea franksii* with larger less regular corallites separated by larger distances than the other two species. We found even further morphologic differentiation in the Pleistocene assemblages of the Hato Unit of the Lower Terrace on Curaçao ([Fig. A3](#)). We recognized the massive, columnar and platy forms already assigned to the modern *Montastraea "annularis"* species complex, and an organ-pipe form which is now extinct (Pandolfi 1999; Pandolfi *et al.* in press). Thus, the analyses presented here include one more species from the *Montastraea "annularis"* species complex than that listed by Budd *et al.* (1994).

Montastraea "cavernosa" complex. We distinguished four presumptive sibling species in this group (one more than Budd *et al.* 1994), three of which match well the species and species characteristics they described.

In summary, our taxonomy for Pleistocene corals of Curaçao is based on the same criteria as those used for living and fossil species throughout the Caribbean, and includes the recent discovery of cryptic species complexes which can be readily distinguished in fossils. Thus, our level of taxonomic discrimination of Pleistocene corals is greater than for virtually all surveys of living reef coral communities in the Caribbean. Moreover, only two of the species we found in the Pleistocene of Curaçao are extinct today: *Pocillopora cf. palmata* and the organ-pipe growth form of the *Montastraea "annularis"* species complex (Geister 1977; Pandolfi 1999; Pandolfi *et al.* in press). Thus, this study examines an essentially modern fauna.

Species distribution patterns

Distribution of rare taxa. There were a number of species that occurred in only one of the reef environments, and a few that were absent from only one of the reef environments ([Table A3](#)). In the Pleistocene of Curaçao, 15 of 39 species occurred in only one of the three reef environments ([Table A3](#)), yet over 90% of the coral abundances came from just 4 or less of the coral species within each of the three environments. In the windward reef crest (WRC), there were a number of species encountered in the southern transects that were not encountered in the northern transects ([Table A4](#)). In the windward back reef (WBR), a number of species encountered in the northern transects were not encountered in the central transects ([Table A4](#)).

Cluster Analysis

Cluster analysis of the Bray-Curtis dissimilarity matrix provides an alternative graphical representation of the environmental differences in taxonomic composition among the reef coral assemblages and showed good agreement with both the GNMDS ordination and the ANOSIM results (see original paper).

In the combined cluster analysis (quantitative data set) of all transects from all environments, the dendrogram shows two major clusters ([Fig. A4](#)). The first major cluster has two components, one exclusively composed of WRC assemblages and the other predominantly composed of LRC assemblages. Some assemblages from the WRC are also found within the LRC cluster. The second major cluster is composed of almost exclusively WBR assemblages. Some assemblages from the LRC are also found within the WBR cluster ([Fig. A4](#)). It is clear that the LRC assemblages overlap with both the WRC and the WBR, but the latter two do not overlap.

Individual cluster analyses of transects from all three environments show very similar patterns in

taxonomic composition with respect to geographic position as did the GNMDS and the ANOSIM tests ([Fig. A5](#)).

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Appendix. List of reef coral (Scleractinia) species from the 125 ka Hato Unit, Lower Terrace, Curaçao.

Acropora cervicornis (Lamarck 1816)

Acropora palmata (Lamarck 1816)

Agaricia agaricites (Linneaus 1758)

Agaricia crassa (Verrill 1902)

Agaricia pusilla (Verrill 1902)

Colpophyllia amaranthus (Müller 1775)

Colpophyllia breviserialis (Milne Edwards and Haine 1849)

Colpophyllia natans (Müller 1775)

Dendrogyra cylindricus (Ehrenberg 1834)
Diploria clivosa (Ellis and Solander 1786)
Diploria labyrinthiformis (Linnaeus 1758)
Diploria strigosa (Dana 1848)
Eusmilia fastigiata (Pallas 1766)
Favia fragum (Esper 1797)
Isophyllastrea rigida (Dana 1848)
Isophyllia sinuosa (Ellis and Solander 1786)
Madracis mirabilis (Duchassaing and Michelotti 1860)
Madracis decactis (Lyman 1859)
Manicina areolata (Linnaeus 1758)
Meandrina meandrites (Linnaeus 1767)
Millepora complanata (Linnaeus)
Montastraea "cavernosa" sp. 1 (Linnaeus 1767 - morph 1 of Budd et al 1994)
Montastraea "cavernosa" sp. 2 (Linnaeus 1767 - morph 2 of Budd et al 1994)
Montastraea "cavernosa" sp. 3 (Linnaeus 1767 - morph 3 of Budd et al 1994)
Montastraea "'cavernosa" sp. 4 (new species)
Montastraea annularis (sensu stricto) (Ellis and Solander 1786)
Montastraea faveolata (Ellis and Solander 1786)
Montastraea franksi (Gregory 1900)
organ-pipe *Montastraea* (new species)
sheet *Montastraea* (Ellis and Solander 1786)
Pocillopora cf. palmata (Palmer 1928)
Porites astreoides (Lamarck 1816)
Porites divaricata (Lesueur 1821)
Porites furcata (Lamarck 1816)
Porites porites (Pallas 1766)
Siderastrea radians (Pallas 1766)

Siderastrea siderea (Ellis and Solander 1786)

Solenastrea bourini (Milne Edwards and Haine 1849)

Stephanocoenia intersepta (Lamarck 1816)

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John M. Pandolfi and Jeremy B. C. Jackson. 2001. Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. *Ecological Monographs* 71:49-67.

Appendices

**[Appendix A](#): Additional information for the study of Pleistocene coral communities from Curaçao.
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