PLIO-PLEISTOCENE EXTINCTIONS AND THE ORIGIN OF THE MODERN CARIBBEAN REEF-CORAL FAUNA

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ABSTRACT

Quantitative analyses of change in the Caribbean reef-coral fauna over the past 22 million years show that a major episode of accelerated faunal turnover occurred during the middle Pliocene to early Pleistocene (4-3 Ma). During turnover, origination and extinction rates of species were found to be equally and simultaneously high, and a relatively constant, “equilibrium” number of species was supported in the fauna. A second smaller episode of accelerated extinction occurred at 2-1 Ma, but was not accompanied by increased origination. Equilibrium was maintained during long periods of faunal stability before turnover (8-4 Ma), and a slightly lower equilibrium was maintained after the second extinction episode (1-0 Ma). As in species, high extinction rates are also detected in genera during the Plio-Pleistocene; however, unlike species, no new genera originated. More than 50°/0 of the genera that became extinct in the Caribbean still live today in the Indo-Pacific. Comparison of extinction rates between grass flat, shallow reef, and deep reef assemblages shows that grass flat corals were most susceptible to extinction. The observed patterns cannot be easily explained by any one environmental agent. However, close correspondence in timing with closure of the isthmus of Panama suggests that associated changes in oceanic circulation may have been at least partially responsible. Understanding long-term patterns of equilibrium and ecological balance will be important to modern reef conservation.

INTRODUCTION

Study of large-scale patterns in the fossil record suggests that tropical reef biotas are among the most vulnerable to extinction during times of extreme global environmental stress (Jablonski, 1991). Yet, little is known about long-term patterns of species extinctions and originations. For example, it remains unclear if and when episodes of accelerated species extinctions occurred in the Caribbean region over the past 50 million years. As a consequence, many questions of significance to modern reef conservation have yet to be addressed, including: (1) which external environmental agents have triggered regional extinction episodes in the geologic past, (2) how have reef communities recovered from such episodes, and (3) which members of reef communities have been most susceptible to extinction. Much of the reason for this lack of knowledge can be attributed to three factors which have hampered investigations of long-term evolutionary patterns in reef-corals: (1) inadequate systematic, (2) the poor resolution of age dates assigned to many fossil reef deposits, and (3) the lack of continuous fossil sequences and patchy distribution of reef deposits in time and space.

In the present paper, we report on preliminary research documenting patterns of extinction and origination in Neogene to Recent Caribbean reef-corals. To study these patterns, we have had to assemble a new compilation of stratigraphic ranges of Neogene to Recent Caribbean reef-coral species (Budd et al., in press). The new compilation differs from previous compilations (e.g., Frost, 1977) by using more up-to-date and consistent taxonomic methods, by including more Pliocene sites (15 Pliocene sites as opposed to six in Frost, 1977), and by using more refined age dates for many fossil deposits, Here we quantitatively analyze occurrences of species and genera in the compilation to identify periods of accelerated extinction and origination. We also evaluate changes in species richness over the past 22 million years. Because the localities in our data set are not evenly scattered through geologic time, we give special consideration to the problem of sampling bias. To determine if certain components of reef communities were more susceptible to extinction than others, we subdivide the data set into three habitat subgroups (grass flat, shallow reef, deep reef) and rerun the analyses. Finally, to assess possible causal agents for the observed patterns, we consider our results in light of reported patterns of regional environmental change.

MATERIAL AND METHODS

Our compilation consists of occurrences of 175 species and 49 genera (Budd et al., in press) (Fig. 1). It includes all recorded hermatypic taxa, except the families Oculinidae and Rhizangiidae which only variably contain zooxanthellae. The data consist of new occurrences from exposed Neogene siliciclastic sequences in the northern Dominican Republic (Saunders et al., 1986) and Costa Rica (Coates et al., 1992), as well as occurrences in the Bahamas Drilling Project cores. Also included are revised occurrences in faunal lists for 21 fossil sites scattered across the Caribbean region (Table 1). The sites comprise all known Caribbean reef assemblages, and consist of both carbonate and siliciclastic sections deposited in a range of near-shore to deeper forereef environments. Age dates for the localities have been estimated using published occurrences of microfossils within the same stratigraphic unit, interpreted relative to the Neogene time-scale of Berggren et al. (1985). Occurrences in the Recent were derived from a faunal list for the north coast of Jamaica (Wells and Lang, 1973), which we modified to include subsequent findings (e.g., Knowlton et al., 1992).

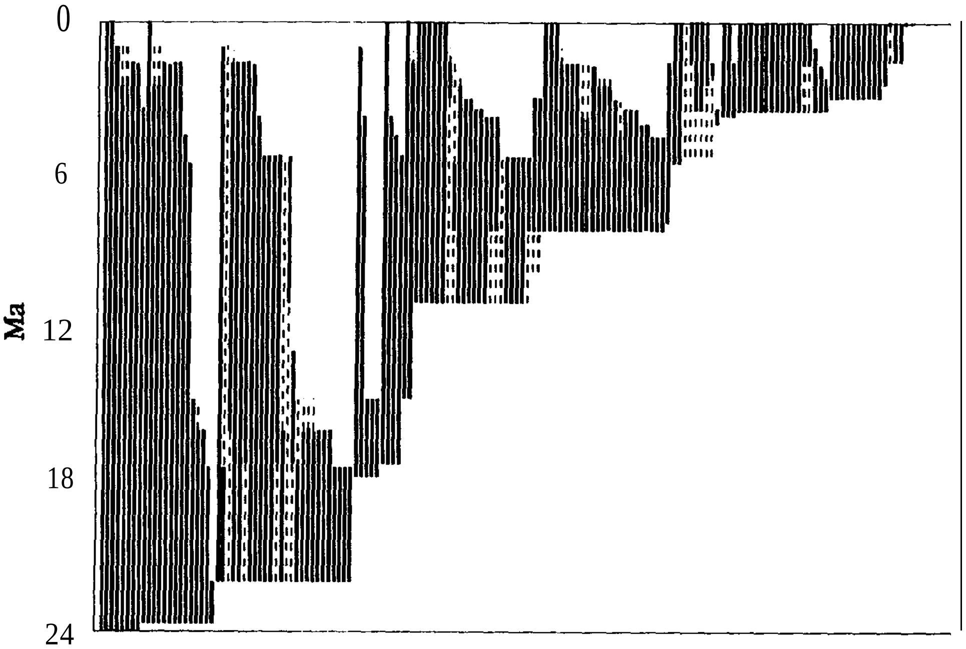

Figure 1. Stratigraphic ranges of all Caribbean reef-coral species over the past 24 million years. Dashed lines indicate occurrences in sites with uncertain age dates.

We identified species in newly collected material and revised faunal lists following a rigorous morphometric protocol designed to detect distinct morphologic entities through geologic time (Budd and Coates, 1992). In the protocol, cluster and canonical discriminant analyses are performed on 5-10 replicates per colony in well-preserved, large sample populations ($n > 10$). Preliminary tests on living material comparing these procedures with molecular methods have found >90% agreement between approaches. The results of analyses on well-preserved material were used to define a set of morphologic features which-served as a guide in the identification of less well-preserved material. Comparisons with similar taxa in the Mediterranean and Indo-Pacific regions indicate that almost all species in our compilation are restricted in geographic distribution to the Western Atlantic and Caribbean regions. Thus first and last occurrences recorded in the compilation represent true first and last occurrences for species.

We divided the total time period in the compilation into four sets of intervals of equal duration and made three calculations for each time interval: (1) extinction rate, the relative proportion of last occurrences in the interval; (2) origination rate, the relative proportion of first occurrences in the interval; (3) species richness, a count of the total number of species whose ranges extended through or terminated within the interval. Extinction and origination rates for each interval were calculated by dividing by species richness for the interval and by time. The intervals were respectively 1, 2, 3, and 4 million years in duration. In making the calculations, we attempted to account for two major sources of sampling bias: (1) unnecessarily long time intervals assigned to localities with poor stratigraphic resolution, and (2) uneven sampling resulting from some time intervals containing many *more* localities than others. To correct for poor resolution, we have weighted first and last occurrences relative to the duration assigned to the locality in which they took place, To correct for uneven sampling, nine species which occurred in only one locality were not used in the calculations. In addition, three localities with highly speculative age dates were also dropped. To evaluate the effects of sampling further, correlations were examined between each of the three calculated parameters (extinction rate, origination rate, and species richness) and number of localities for each time interval ("sampling intensity").

Changes in extinction and origination rates and species richness were then examined through geologic time (Figs, 2, 3). Observed periods of accelerated extinction and origination were confirmed using bootstrap resampling methods to establish statistical significance. Changes in fauna] composition were evaluated quantitatively by performing cluster analysis on presence-absence data for each locality. They were also examined qualitatively by studying patterns of survivorship (Fig. 4).

Finally, we compared susceptibility among three different habitat subgroups recognized using assemblages associated with different paleoenvironments in the Dominican Republic sequence. To identify these subgroups, cluster analysis was performed on occurrence data for all species collected in 18 different lithostratigraphic units showing little evidence of transport. The subgroups included: (1) a low diversity assemblage of free-living and branching colonies characteristic of reef-marginal grass flats; (2) a low diversity assemblage of mound-shaped and branching colonies characteristic of shallow (<10m) reef environments; and (3) a high diversity assemblage of mound-shaped, plate-shaped, branching, and free-living colonies

Table 1--- Twenty-one fossil sites whose faunal lists were used in the compilation. S = siliciclastic; C = carbonate; SB = soft bottom; SR = shallow reef; DF = deep forereef; MIX = transported; + = localities excluded in stratigraphic range charts and in calculations of origination and extinction rates.

Site	Absolute age	Environment
early to middle Miocene:		
1. Tampa Formation, Florida	22-23.7 Ma	S/SB,SR
2. Emperador Limestone, Panama	17.6-22 Ma	S/SR
3. Anguilla Formation, Anguilla	16.2-22 Ma	C/SB,SR
4. Chipola Formation, Florida	15-18 Ma	S/SB,SR
+5. providencia	15-22 Ma	C/SB,SR
6. Brasso and Tamana Formations, Trinidad	11.2-15 Ma	S/SB,SR
late Miocene to early Pliocene:		
7. Manzanilla Formation, Trinidad	5.3-I 1.2 Ma	S/SB,SR
+8, Lirio Limestone, Mona	5.3-11.2 Ma	C/SB,SR,DF
9. Buff Bay Formation, Jamaica	5.3-11.2 Ma	s/Mix
10. Imperial Formation, California	4.5-8 Ma	S/SB,SR
middle to late Pliocene:		
11. Bowden Formation, Jamaica	2-3.8 Ma	S/MIX
12. Pinecrest Sandstone, Florida	3-3.5 Ma	C/SB,SR
13. La Cruz Marl, Cuba	1.6-3.5 Ma	?C/SB,SR
14. Matanzas, Cuba	1-3.5 Ma	?C/SB,SR
15. Old Pera Beds, Jamaica	1.6-2.5 Ma	C/SB,SR
16. Caloosahatchee Formation, Florida	1.6-1.8 Ma	C/SB
early Pleistocene:		
17. Manchioneal Formation, Jamaica	1-1.6 Ma	C/SB,SR
18. Glades Formation, Florida	1-1.6 Ma	C/SB
late Pleistocene:		
19. Santo Domingo, Dominican Republic	100,000-500,000 yr	C/SB,SR
20. San Andrés	100,000-500,000 yr	C/SB,SR
21. Key Largo Limestone, Florida	100,000-500,000 yr	C/SB.SR

characteristic of deeper (> 10m) or more turbid reef environments. Extinction rates were calculated for each subgroup, and the resulting patterns compared (Fig. 5).

RESULTS AND INTERPRETATIONS

In general, our results indicate that an episode of accelerated turnover followed by accelerated extinction occurred in the Caribbean reef-coral fauna between 4 Ma and 1 Ma. These events resulted in the replacement of a late Miocene to early Pliocene reef-coral fauna by a Pleistocene to Recent fauna. The Mio-Pliocene fauna was dominated by taxa such as Stylophora, Goniopora, and a suite of agariciid and poritid species which more closely resemble modem Pacific species than those of the modem Caribbean. Numerous free-living meandroid corals (Teleiophyllia, Thysanus, Trachyphyllia, Placocyathus) dominated Mio-Pliocene reef-associated grass flats. The modern Caribbean fauna (including Acropora palmata, Diploria strigosa, Porites astreoides, and the Montastraea annularis complex) originated during middle Pliocene to early Pleistocene time, as components of the Mio-Pliocene fauna became extinct, Five findings with regard to these patterns are particularly significant.

(1) Accelerated Plio-Pleistocene extinction and origination rates--- Examination of extinction and origination rate plots over time (Fig. 2) and results of bootstrap resampling tests indicate that extinction and origination rates were both

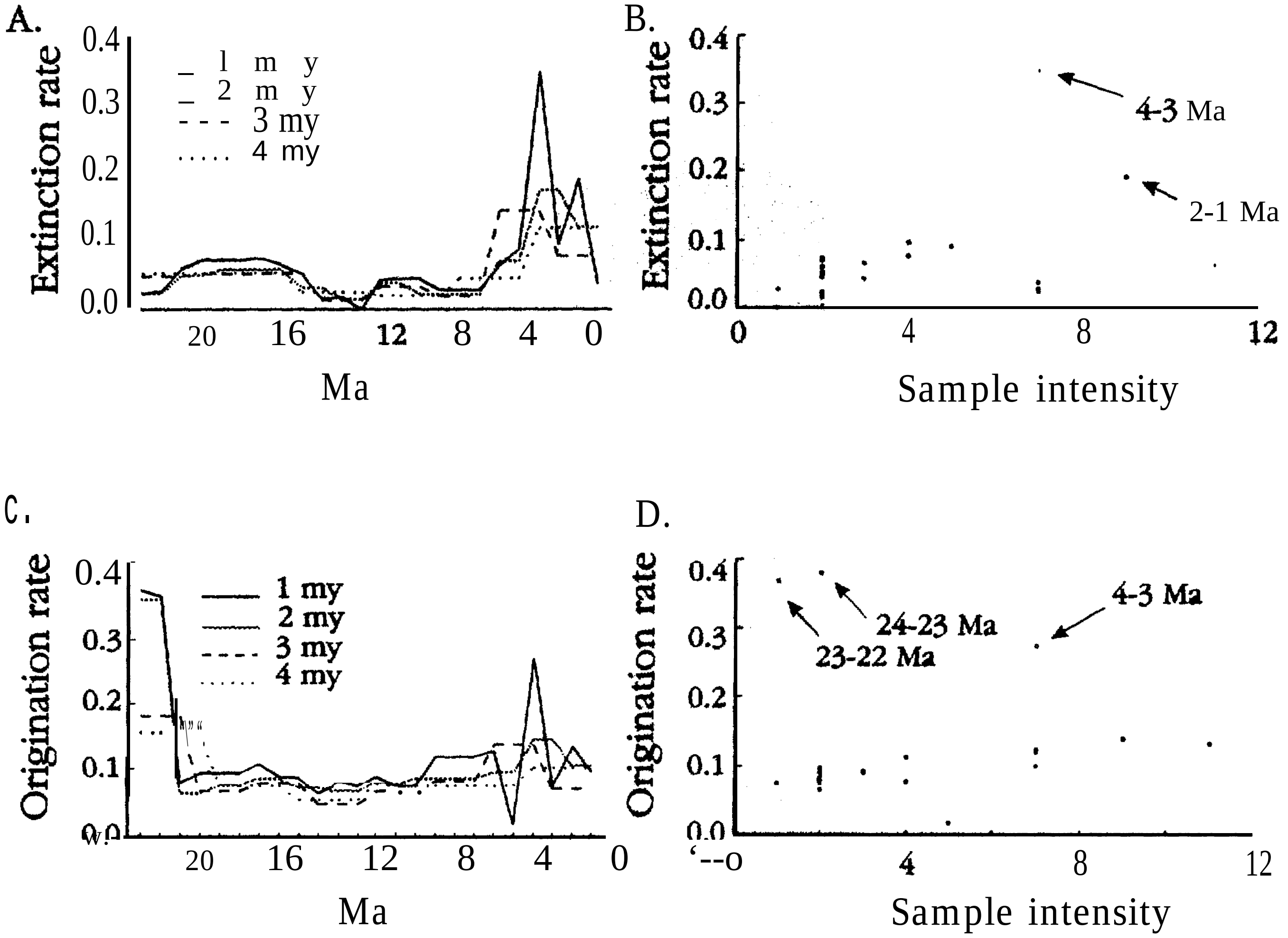

Figure 2. Evolutionary rates in Caribbean reef-coral species over the past 22 million years. Plots A and C show patterns calculated with interval durations of 1, 2, 3, and 4 million years. Plots B and D show the relationship between evolutionary rates and sampling intensity using 1 million year intervals. Each point represents one time interval.

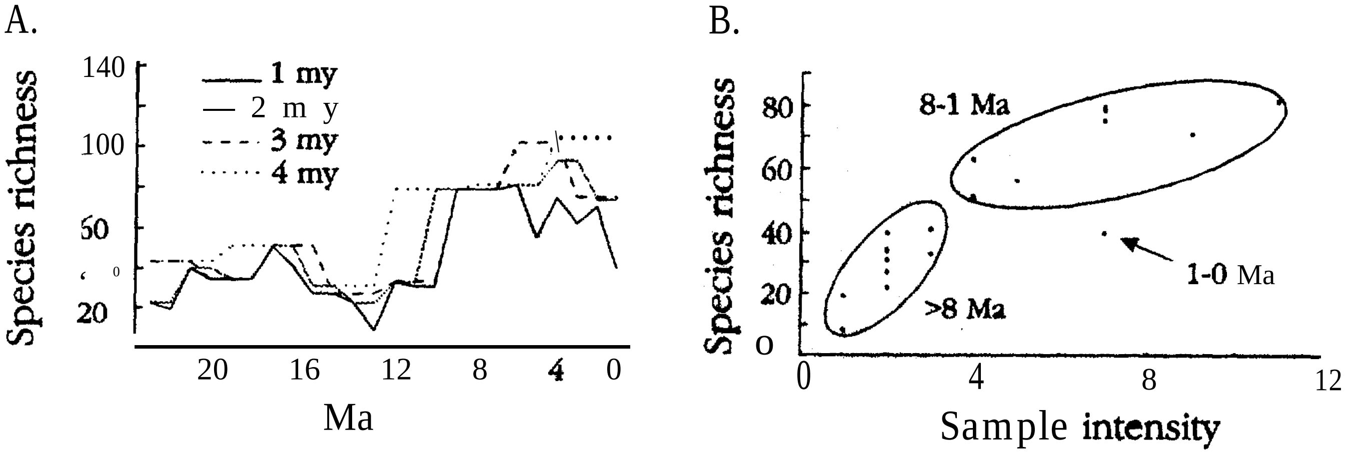

Figure 3. Species richness over the past 22 million years. Plot A shows pattern calculated using interval durations of 1, 2, 3, and 4 million years. Plot B shows the relationship between species richness and sampling intensity using 1 million year intervals. Each point represents one time interval.

accelerated between 4 Ma and 3 Ma, and that extinction rates alone were accelerated between 2 Ma and 1 Ma. Miocene background rates of extinction range between 0-8% per million years. Beginning approximately 4 Ma, extinction rates doubled, with extinction rates of 10 to possibly >35% per million years. Also at 4 Ma, origination rates rose. A smaller second wave of accelerated extinction with rates of up to 20% per million years followed later. Neither extinction nor origination rates are correlated with sampling intensity.

Extinction rates and origination rates were therefore accelerated, at least initially, over the same period of time. Consequently, whatever caused increased extinction did not inhibit simultaneous origination. This result argues against widespread, long-term environmental degradation as a possible initial extinction agent.

(2) Equilibrium number of species.-- Species richness appears to have been relatively high (-80-100) throughout most of the late Miocene to Pleistocene (8-1 Ma), and slight lower (40-60) in the late Pleistocene to Recent (1-O Ma) (Fig. 3). In time intervals older than 8 Ma, species richness is strongly correlated with sampling intensity; therefore, the low values shown for these intervals in Fig. 3a may be a result of reduced sampling. However, little correlation with sampling intensity or with time exists for samples younger than 8 Ma indicating that the observed temporal patterns (Fig. 3a) are less affected by sampling. Of these intervals, only the 1-O Ma interval appears less rich than would be predicted by sample density alone.

The observed constancy in species richness between 8-1 Ma indicates that an equilibrium number of species may have been maintained in the Caribbean reef coral fauna at least for much of the past 8 million years. This equilibrium persisted during times of relative faunal stability as well as during times of accelerated faunal turnover, Thus, on a large scale, reef communities appear to have retained ecological structure during Plio-Pleistocene reorganization. This result contrasts observations on smaller scales that reef communities are unstable, disturbed systems which never reach equilibrium over periods of tens of years (Cornell, 1978). Fossil reefs provide important tools for monitoring long-term biotic change.

(3) Stable taxonomic composition before and after turnover.-- Low extinction and origination rates (Fig. 2), as well as results of cluster analysis and survivorship data, indicate that the taxonomic composition of the Caribbean reef coral fauna was stable

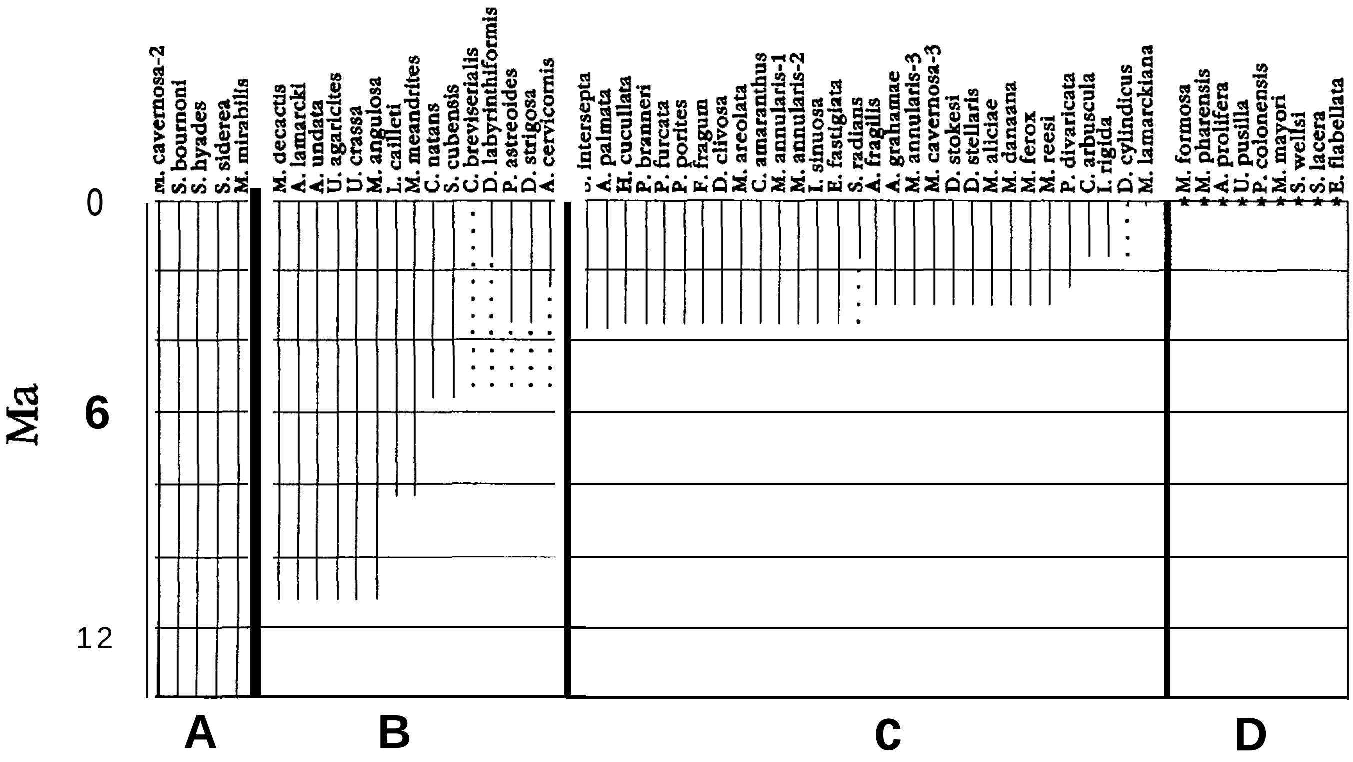

Figure 4. Stratigraphic ranges of species of modem Caribbean reef-corals. Dashed lines indicate occurrences in sites with uncertain age dates. Group “A”, species with originations before late Miocene time; group “B”, species with late Miocene to early Pliocene originations; group “C”, species with mid Pliocene to Pleistocene originations; group “D”, species with no reported fossil record.

for long periods of time before (8-4 Ma) and after (I-O Ma) after turnover. Of the 96 species that lived in the Caribbean during the late Miocene to early Pliocene, 78% became extinct during Plio-Pleistocene time. Of the 59 species currently living in the Caribbean, 51% originated during middle to late Pliocene time, and only 15% have no fossil record (Fig. 4).

Thus, faunal stability represents the norm in the long-term evolution of Caribbean reef communities, and continued throughout the glacial episodes and associated high frequency oscillations in temperature and sea level of the late Pleistocene (see also Jackson, 1992).

(4) Decrease in genera.-- Preliminary counts of genera in the compilation indicate that, during the period of accelerated turnover, 32% of the 38 genera that lived in the Caribbean during the Pliocene became extinct. Four subgenera and genera became globally extinct, and eight genera became extinct in the Caribbean region. The four taxa that became globally extinct (Teleiophyllia, Thysanus, Placocyathus, Antillia) were all free-living corals, common in reef-marginal grass flats. The eight genera that became regionally extinct include seven genera which occur today in the Indo-Pacific (Pocillopora, Gardineroseris, Pavona, Stylophora, Goniopora, Caulastrea, Trachyphyllia), and one genus which is currently restricted to Brazil (Mussismilia). Only two genera in the compilation (Dendrogyra, Mussismilia) have first occurrences after early Pliocene time; however, both of these genera are known in older Mediterranean deposits.

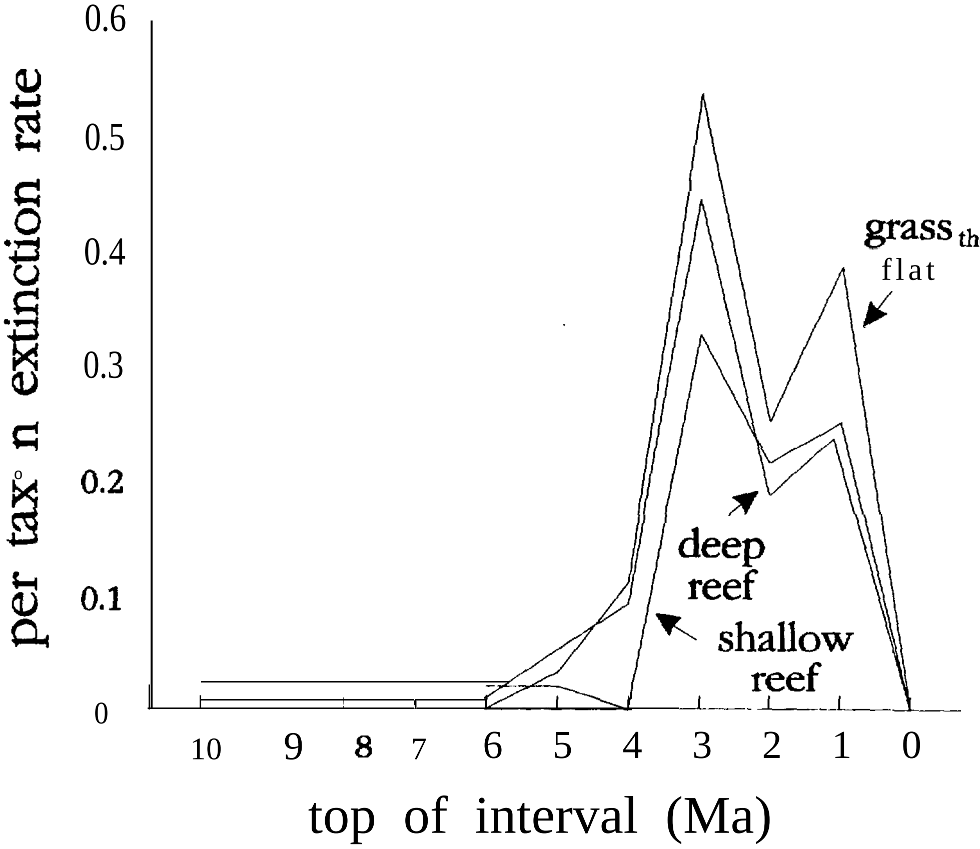

Figure 5. Extinction rates for species characteristic of grass flat, shallow reef, and deep reef communities.

Thus, it appears that although many genera became at least regionally extinct during Plio-Pleistocene time, no new genera arose. Even though species richness remained the same throughout turnover, the number of genera in the reef-coral fauna of the modem Caribbean is considerably less than during early Pliocene time.

(5) High susceptibility to extinction in grass flat corals--- Examination of plots of extinction rates (Fig. 5) for the three habitat subgroups (grass flat, shallow reef, deep reef) shows that all three groups experienced accelerated rates at 4-3 Ma and 2-1 Ma. The grass flat subgroup was most heavily impacted, with extinction rates of 30-50% per million years. The other subgroups were slightly less affected, especially during the second extinction wave.

Therefore, whatever caused increased rates of turnover and subsequent extinction, its most potent effects were felt in soft bottom environments with communities characterized by small, short-lived, free-living species. Taxa with large colony sizes were less likely to become extinct.

DISCUSSION AND CONCLUSIONS

The fact that Plio-Pleistocene turnover and extinctions have also been reported in Caribbean molluscs (Stanley, 1986) and bryozoans (A.H. Cheetham, pers. comm. 1993), but not in Indo-Pacific reef-corals (Veron and Kelley, 1988), suggests that regional abiotic factors may have been ultimately responsible for the observed turnover and subsequent extinction in corals. However, to date, our attempts to relate the findings to possible external causal agents have not yielded clear answers. Since Indo-Pacific corals did not experience turnover or extinction, the observed Caribbean turnover does not appear to have been caused by global changes in sea level. Also, the fact that faunal stability prevailed throughout the high frequency temperature and sea level oscillations of late Pleistocene time argues against sea level or temperature being primary causal agents.