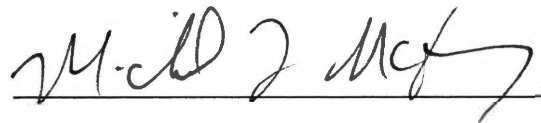


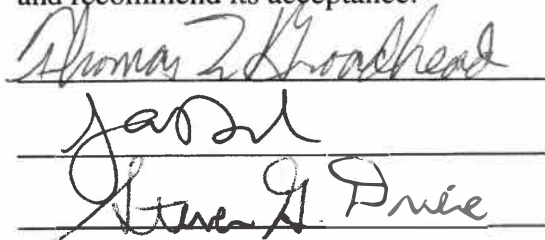
To the Graduate Council:

I am submitting herewith a dissertation written by William Gray Dean entitled "Relative Biodiversity Trends of the Cenozoic Caribbean Region: Investigations of Possible Causes and Issues of Scale using a Biostratigraphic Database of Corals, Echinoids, Bivalves, and Gastropods." I have examined the final paper copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geology.



Michael L. McKinney, Major Professor

We have read this dissertation
and recommend its acceptance:



Accepted for the Council:



Vice Provost and Dean of
Graduate Studies

Thesis
2003b
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**RELATIVE BIODIVERSITY TRENDS
OF THE CENOZOIC CARIBBEAN REGION:
Investigations of Possible Causes and Issues of Scale
using a Biostratigraphic Database of
Corals, Echinoids, Bivalves and Gastropods**

A Dissertation
Presented for the
Doctoral of Philosophy
Degree
University of Tennessee, Knoxville

William Gray Dean
December 2003

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ABSTRACT

The fossil record remains the primary tool to understand macro-evolutionary processes over time. Unfortunately, much debate has centered upon sampling biases that pervade the rock and fossil record. A relative metric is presented that reduces the effect of uneven distribution of fossils across time and space. The Diversity Index of Growth (DIG) metric measures relative change of biodiversity because it examines the four key parameters of biodiversity: New, Extinct, Stable and Total, as obtained from biostratigraphic data. In this study, DIG was utilized to examine biodiversity trends of a Cenozoic Caribbean database consisting of genus-level biostratigraphic occurrences of corals, echinoids, bivalves and gastropods. The results of this study indicate that the individual class-level trends observed from the database are consistent with previously interpreted trends of the four clades. Key features of the observed biodiversity trends of the Caribbean include three peaks of diversification, including increased biodiversity near the Paleocene-Eocene Thermal Maximum (PETM).

Marine invertebrate biodiversity appears to be linked to a variety of environmental processes, including volcanism and climate change. The timing of biodiversity increases corresponds to increases in sea-level and three major volcanic episodes in the Caribbean. The trends of the total biodiversity follow sea-level change, especially when sea-level data are reduced to relative change and compiled into time increments equal to the fossil data. The positive relationship between sea-level increases and biodiversification is observed at several spatial-temporal scales, and indicates that relative biotic diversity

change may be useful for following highstand facies or for sequence stratigraphy applications. Climate effects, as interpreted from isotopic data and terrestrial data, also suggest a potential agreement between climate, sea-level and biodiversity. Also investigated in this study are the effects of scale and hierarchy from temporal, spatial and taxonomic perspectives. Longer time intervals result in vastly different biodiversity trends than shorter time intervals over the same data set. Taxonomic hierarchy was investigated by comparing trends of species-level and genus-level biodiversity, and it was observed that similar biodiversity trends did not consistently cascade across taxonomic hierarchies. Also demonstrated in this study is the problem of comparing data of differing levels of spatial-temporal resolution. Not only do such comparisons stymie statistical correlations, but they can also yield conflicting interpretations of the causes of biodiversity.

A new metric is introduced to understand and quantify the relative degree of resolution achievable by a database. Sensitivity of Data (SOD) gives a measurement of the spatial, temporal, and observational extent over which the interpretations gleaned from a database are valid. In many instances, the potentially differing interpretations made from the same or similar data may be attributed to variation in the spatio-temporal sensitivity of the data, or the environmental processes to which they are compared. Thus SOD allows an evaluation of the temporal, spatial and therefore, hierarchical issues that affect interpretations of geologic data. Higher SOD values indicate finer-resolution data while lower SOD values indicate lower-resolution data. High SOD values are shown here in close agreement to isotopic or sea-level data that are sub-regional to basinal in scale. The

Caribbean database used here has a low SOD value and conforms better to regional to global scale data. I hypothesize that the sensitivity of the data contributes to the assignment of various environmental processes as higher or lower hierarchies that impart differential control to the biosphere. These higher- and lower-orders of processes likely may originate only because of variation in the quality and quantity of observations used to interpret past events. Thus, the relativity of time, data, and trends of the incomplete rock record suggest the need to investigate applications of relative metrics to not just the biostratigraphic data but to geologic data, as a whole.

TABLE OF CONTENTS

CHAPTER 1: PROLOGUE.....	1
INTRODUCTION.....	1
OVERVIEW.....	2
SUMMARY.....	10
CHAPTER 2: RELATIVE METRICS FOR ABSOLUTE PROBLEMS.....	12
ABSTRACT.....	12
INTRODUCTION.....	13
BACKGROUND.....	16
OBJECTIVES.....	24
MATERIALS.....	25
METHODS.....	29
RESULTS.....	34
DISCUSSION.....	45
CONCLUSIONS.....	47
CHAPTER 3: BIODIVERISTY TRENDS AND CAUSAL MECHANISMS.....	50
ABSTRACT.....	50
INTRODUCTION.....	50
BACKGROUND.....	54
MATERIALS AND METHODS.....	60
RESULTS.....	60
DISCUSSION.....	70
CONCLUSIONS.....	77
CHAPTER 4: UNDER THE INFLUENCE OF HIERARCHY AND SCALE.....	80
ABSTRACT.....	80
INTRODUCTION.....	81
BACKGROUND.....	85
MATERIALS.....	91
METHODS.....	91
RESULTS.....	95
DISCUSSION.....	112
CONCLUSIONS.....	118
CHAPTER 5: EPILOGUE.....	121
SUMMARY.....	121
IT'S ABOUT TIME... ..	127
FUTURE WORK.....	129
REFERENCES.....	131
WEB SOURCES:.....	139
APPENDIX.....	140
REFERENCES.....	162
WEB SOURCES:.....	163
VITA.....	164

LIST OF FIGURES

Figure 1. Biodiversity trends of Cenozoic molluscs from New Zealand.	18
Figure 2. The spatial scope of study.....	30
Figure 3. The Caribbean dataset as measured by absolute values..	35
Figure 4. Data from Sepkoski's Global Compendium viewed in terms of absolute values.	35
Figure 5. Correlation of regional biodiversity trends to global biodiversity trends.....	37
Figure 6. Biodiversity as observed by relative metrics..	37
Figure 7. Published carbon and oxygen isotope data from the western Atlantic Ocean..	40
Figure 8. The relationship between biodiversity and global sea level.	42
Figure 9. Regression of DIG values plotted versus length of time step.....	44
Figure 10. Regression of DIG versus length of time step with two "outliers" removed..	44
Figure 11. Relative biodiversity trends and major biotic, tectonic, and physical events that proximally cluster about the three DIG peaks.....	61
Figure 12. DIG values showing the differential trends of deep water versus shallow water fauna..	63
Figure 13. The various taxonomic groups are presented individually with their respective biodiversity trends.	63
Figure 14. Total genera biodiversity compared with explosive volcanic ash collected from ODP cores, Leg 165.	68
Figure 15. Ash fall rate compared to total DIG and sea-level.....	68
Figure 16. DIG signals of the total genera versus total species of the Caribbean database..	97
Figure 17. DIG signals of echinoid genera and species from the Caribbean database.. ..	97
Figure 18. DIG signals of gastropod genera and species from the Caribbean database..	98
Figure 19. DIG signals of coral genera and species from the Caribbean database.....	100

Figure 20. DIG values of coral species and genera from the Rio Cana stratigraphic section, northern Dominican Republic.....	100
Figure 21. The effect of varying temporal resolution upon data.....	102
Figure 22. DIG values of coral from the Rio Cana section plotted against the global sea level curve.....	105
Figure 23. DIG values of coral from the Rio Cana section (Fig. 22) plotted versus oxygen isotopes from the Caribbean (Reijmer et al., 2002).....	107
Figure 24. DIG values of foraminifera and ostracodes recovered from a well log in the Enriquillo Basin, southern Dominican Republic (Mann et al., 1999).....	108

CHAPTER 1: PROLOGUE

Introduction

Recent controversy has arisen regarding the value of fossil databases in determining true biodiversity trends (see *Paleobiology* 29(1)2003). Indeed, this is an unfortunate situation, because the fossil record, as represented by biostratigraphic databases, remains as the primary tool to understand biotic evolution (Jablonski, 1999). Much of this debate, however, is instigated by the vagaries of the rock record that produce unequal distributions of fossil “samples” across time and space (Jablonski et al., 2003). Though these sampling biases have been acknowledged for quite some time, (Koch, 1991), there are no clear means to correct them. Further, most techniques used to analyze biostratigraphic data are based upon absolute values either directly or they are highly controlled by dataset size. Other major factors affecting the potential quality of data extracted from the fossil record include variation in time intervals used to create time-series depiction of data. All of this has led some to speculate on the need to assess relative change of biodiversity rather than quantifying absolute change (Alroy, 2003). The focus of my personal research has been aimed directly at deriving and applying such a metric (Dean, 1997; Dean and McKinney, 2003).

The purpose of this dissertation is to quantify the relative changes in biodiversity over a time interval, and to compare these trends to major environmental gradients that may have affected biota. Additionally, I will examine the effect upon biostratigraphic information of variables such as temporal resolution, spatial coverage or hierarchical

constructs that bias interpretations of data. The focus of this research is on the Caribbean region, and the marine invertebrate groups of echinoids, corals, bivalves and gastropods during the Cenozoic Era. These four major biotic groups were chosen for their high-degree of preservation potential and their well-described taxonomy. A biostratigraphic database of genus-level citations (Appendix 1) was created from the ranges in time that these various organisms have been reported. Several other existing databases are also used in this research to examine finer-scale trends and biodiversity responses to environmental change. The following three chapters are organized, in style and content, as individual papers to be submitted to peer-review journals.

Overview

Chapter 2

In the first paper (Chapter 2) I address issues concerning the viability of interpretations from biostratigraphic data. Over the last 20 years, much controversy has surrounded paleobiologic interpretations made from fossil age ranges. The reasons for such controversy, in part, stem from the spatial averaging or extrapolation of regional data into global databases. Additionally, the coarse temporal resolution with which biostratigraphic data are often reported also incites debate. This effect is magnified too, when regional data are compiled into larger global databases. Thus the position has been made that global databases are not adequate tools for precise biologic interpretations due to the imprecision of temporal control (Vermeji and Leighton, 2003). Further, the disparities of rock and fossil preservation, an innate feature of the geologic record, leads

to further concerns of biased fossil samples, and thus, potentially biased interpretations of biodiversity (Smith et al., 2001; Smith 2003).

In Chapter 2, I address these concerns in several ways. First, I avoid the use of a global database and concentrate on the Caribbean region. Second, I attempt to minimize sampling biases through the use of the Diversity Index of Growth (DIG), a metric developed to depict the relative biodiversity trends of fauna over time. This metric differs from most standard approaches that either quantify the absolute biodiversity, or those that focus on the proportion of organisms that became extinct or speciated. These ‘traditional’ approaches to studying biodiversity, by their very design, are susceptible to variation in dataset size and thus are prone to sampling biases. Further, proportional extinction and speciation are not measuring true biodiversity, but rather, only a component of biodiversity. The problems inherent with these traditional approaches do instigate valid criticism. I maintain, however, that the criticism of specific analytical methodology should not be extended to the concept of biostratigraphic analyses, as a whole. This is because, even though sampling problems exist in the fossil record, examinations of relative change should reduce the artifacts incurred by sample size variation, which is the change in number of fossil citations between time intervals. Further, DIG considers biodiversity by considering extinction, speciation and stability and measures these variables together to produce a signal of diversity growth or decline. Not only is this metric more pertinent to biodiversity studies than traditional metrics because it measures relative change, but also, it makes use of all the potential parameters one can extract from biostratigraphic range data of fossils. In addition to DIG, Chapter 2

also examines another metric: Volatility. This metric I created by examining the proportion of biota that does not remain stable. Volatility is useful for understanding biotic change when speciation and extinction are equal and thus diversity remains the same.

The results from Chapter 2 indicate that marine invertebrate biota do respond to sea-level variation. Although this is an intuitive concept, it has not been easy to demonstrate with traditional metrics that are controlled by absolute values and thus potentially controlled by sampling biases. Thus, interpretations of my data depict relative biodiversity increases with sea-level increases. Although this could be the result of preferential bias caused by preservation and exposure of particular rock types associated with higher sea-level, it may also be a true depiction of biodiversity. The position that this database reflects true biodiversity can be made, because I demonstrate statistically that the trends of my data follow trends observed in another, independent and global database (e.g., Sepkoski's Compendium of Marine Genera). This suggests that either the rocks are biased consistently at global scales, or that true biodiversity trends are being observed. Furthermore, the agreement between databases indicates that the Caribbean Database used here may actually be following global-scale trends and not specific regional biotic response. The relative agreement, then, of my Caribbean database with key global events, such as a dramatic warming event 55 Ma, or with sea-level change, then suggests that global processes or events affect interpretations from regional-scale studies.

Chapter 3

This paper examines the connection between Caribbean biodiversity trends and global-scale processes. As was indicated from Chapter 2, the Caribbean database is in close agreement with global biostratigraphic data. Further, the trends of biodiversity track major global signals derived from isotopic data and sea-level change. In this paper, I examine the biodiversity change in context with the presumed factors that may cause sea-level variation, as well as with those that may be a product of sea-level change.

Major physical changes that are related to sea-level are tectonics, and climate. Although cause and effect among sea-level, tectonics and climate are equivocal, I attempt a comparison between these major environmental gradients and biodiversity signals as derived by DIG. It becomes apparent, however, that the scales and resolution of these various signals are not equivalent, which subsequently impedes rigorous correlation of these processes to one another. But, even at coarse scales (e.g. 5 – 15 my time intervals) and with circumstantial evidence there is a suggested relationship between tectonics and volcanism, sea-level and temperature with the DIG signals. Volcanic ash data from the Caribbean, along with other documented tectonic events, are temporally coeval with biodiversity increases both within the Caribbean, but also in the terrestrial realm as well. This suggests that climate change, caused perhaps by tectonic events, may be the common link between biotic response in the oceans and on land. This in turn may raise sea-level, through physical displacement of water (tectonics) and through warmer conditions. Evidence for this argument includes weathering of continents, geochemical signals, and the terrestrial floral responses as a result of climate change. These biotic

responses are proximally located in time and cluster about major volcanic events, both in the Caribbean and globally.

Unfortunately, the temporal scale of biostratigraphic data is not equivalent to the temporal scale of high-resolution Deep Sea Drilling Project (DSDP) or Ocean Drilling Project (ODP), and thus, statistical correlations would not be supportive. Further, global sea-level curves agree with these interpretations, but they too are at differing temporal and spatial scales of resolution. Thus, the arguments relating biodiversity, sea-level, climate and tectonics remain speculative, in the context of this paper. However, the conclusions and interpretations that I make are consistent in the context of other independent research. And these ultimately suggest that at large observational scales, tectonics control the subordinate processes, of climate, sea-level and biodiversity.

The soundness of the DIG metric is further tested, in Chapter 3. The DIG values of the separate biotic groups of corals, echinoids, bivalves and gastropods are compared to independent research, and indicate complete agreement between the biotic trends I have elucidated versus those proposed by other workers. Not only does this further validate the DIG method but it also adds support to the interpretations of causes of diversity change that I have proposed given that this metric appears to be an accurate tool. What is ultimately suggested, then, is the scale-dependence of data, and the subsequent interpretations one develops, which then leads to the final chapter of this dissertation.

Chapter 4

In this paper, my examination focuses upon issues of temporal and spatial scale of data that affect interpretations of biodiversity trends. To do this, I had to utilize several other sets of data not included in the first two papers. First, to demonstrate the effect of temporal resolution upon the inferred signals, I used a smaller set of coral biostratigraphic ranges that were reported in 1 million-year increments. I was subsequently able to broaden temporal resolution to both 2- and 6-million year increments to show that the uneven nature of geologic time intervals, especially with biostratigraphic range data, can have a dramatic effect upon the timing and magnitude of biodiversity trends. This I use as evidence as to why correlations between fine-scale data and coarse-scale data cannot be made. It also explains the less-than-perfect agreement of biodiversity “curves” as generated by DIG versus high-resolution isotopic data. Temporal offset is observed as the time intervals increase in length. These effects do not render biostratigraphic data useless, but, rather, mandate a better understanding of comparing data of vastly differing scales.

In order to show the close correspondence of biodiversity increase to sea-level increase, I had to reduce my spatial and temporal scope and focus on smaller sets of local- to basinal-scale data. Two sets of data for this analysis were available from the Dominican Republic. I used the coral biodiversity of a composite stratigraphic column and compared it first to a portion of the global sea-level curve and then to basinal isotopic data. In spite of the variation of spatial resolution between the global sea-level curve segment and the local coral DIG, there was good agreement. But the fine-scale

biodiversity trends had increases within a larger cycle of sea-level increase. When these stratigraphic data were compared to fine-scale isotopic data from the southern Bahamas Platform, however, better agreement between the two trends is observed. As a further test of DIG versus sea-level, and because an opportunity to compare equivalently-scaled biostratigraphic data and sea-level data was available, I utilized another set of data retrieved from a well-log in the southern Dominican Republic.

The data for this last comparison consisted of micro-fauna: ostracodes and foraminifera. These were used by the original authors to determine the precise age and position of the stratigraphic information with sea-level through paleoecologic reconstruction. Thus, the well-log data were correlated with sea-level, and I was, in this instance, able to retrieve both the DIG values and the sea-level data at exact temporal equivalence. This produced a very powerful example of biodiversity increase as a response to sea-level increase.

More importantly, this exercise was not a product of circular reasoning. The original authors of the data examined fossil type to infer habitat preference and water depth; the DIG method only examines numerical change of diversity and not actual type of organism. Thus, this result brings us full-circle to the very logical conclusion that marine biodiversity is related to sea-level, and that it actually increases as sea-level increases.

But, to further demonstrate that issues of spatial and temporal scale and variation of resolution between datasets hampers interpretations, I introduce yet another concept in which databases and their subsequent interpretations can be evaluated in terms of their effective scope.

To compare the spatial and temporal scope as well as observational resolution of databases, I propose a new metric termed the Sensitivity of Data (SOD). This metric allows individual datasets to be evaluated, as well as allowing comparison of other trends, such as sea-level or isotopic data, to biodiversity trends. Differences between the resolution and scope of data often lead to correlations that cannot be made and interpretations that conflict. To resolve this dilemma, I divide the number of taxa within a database by the study area, and then by the length of time the interval encompasses. This is then multiplied by the number of observations (time steps) and produces values that can be compared to other datasets to determine if the sensitivity of data is even within the same order of magnitude. The results of this exercise, when applied to the various datasets used in this research, do indeed indicate that lower SOD values are found in temporally large, spatially extensive datasets. Further, all other factors being equal, low SOD values are obtained with time-series data that have few intervals, versus those that are high-resolution and have numerous data points. This, in fact, helps to explain the lack of agreement between fine-scale data, such as sea-level, versus coarse-scale data, such as the Caribbean database I compiled. The SOD metric also explains why this database seems to reflect global as opposed to regional trends. The fine-scale data from the Dominican Republic, even though less-numerous in terms of taxa, actually were many orders of magnitude more sensitive than the Caribbean database. Thus, the fine-scale data with higher SOD values closely follow sea-level curves, which are usually drawn from high-resolution data. Even more importantly, this helps to explain disparities between various interpretations drawn from similar research.

Coarse-scale resolution of study will produce coarse-scale interpretations of causal mechanisms. This most likely is why my interpretation from the DIG signal of the Caribbean database resulted with an interpretation of large-scale process (sea-level and tectonics) as causal. Other researchers, focusing on narrow time intervals of the Cenozoic, have interpreted fine-scale (10^4 years) mechanisms, such as Milankovitch Cycles, for critical events during the temporal range of my study. The reason seems to be, then, due to the fine-scale resolution of their study which in turn produces a fine-scale time-series. Thus, I contend that much of our understanding and interpretation of biodiversity trends and the processes controlling them are primarily dependent upon the scale of study. This scale-dependence then is ultimately reduced into a hierarchy of environmental processes and responses that may only exist as an analytical concept rather than actual reality. Therefore, conflicting interpretations do not negate the result of one or the other, but instead are more indicative of the scale and resolution of the data. This is particularly important with the fossil record and biodiversity studies because often the resolution of fossil data is not as precise as the isotopic data to which we often compare. The problems of hierarchy, resolution and scale are illustrated in this chapter, with the SOD metric presented as a means to begin to understand the importance of these issues in interpreting data.

Summary

The problems of sampling and biases in the rock and fossil record can be minimized by the use of relative metrics. Thus, biostratigraphic data remain as viable tools for biodiversity study. Perhaps more insidious to our understanding of biological trends and

the processes that influence biodiversity is the scale-dependence of the questions we ask and the data we manipulate. Hierarchy and scale determine our interpretations of geological information; understanding how this occurs will likely improve our knowledge well beyond that of biodiversity. In the final chapter (5), as an Epilogue, I will synthesize the results of all three papers, and present several questions concerning our perception of knowledge, and suggest potential avenues for future work.

CHAPTER 2: RELATIVE METRICS FOR ABSOLUTE PROBLEMS

Abstract

Sampling of the fossil record has long been recognized as biased, due to biologic, geologic and human factors, which has led to controversy regarding the interpretations of most biodiversity studies. Much of the previous work has focused upon absolute values of fossil occurrences through time, whereas others have focused upon the proportion of extinct or new biota. Either of these approaches fails to minimize the effect of sample-size disparity between time intervals, regions, or biota, and therefore the subsequent interpretations are highly dependent upon the total number of organisms identified. This research takes another approach. Cenozoic Caribbean biodiversity trends of corals, echinoids, bivalves and gastropods are followed using a biostratigraphic database and a new metric that quantifies relative change. The metric termed Diversity Index of Growth (DIG) measures the relative change of biodiversity by using four key parameters that are readily extracted from biostratigraphic data: Total Taxa (T), New Taxa (N), Extinct Taxa (E), and Stable Taxa (S). Examining the relative diversity growth as it diverges from stability therefore reduces sampling problems incurred by quantifying absolute numbers. The results of this study indicate that: 1) the fossil record can be a viable tool for biodiversity study; 2) Caribbean biodiversity increased in three major peaks over the Cenozoic; and 3) that marine invertebrate biodiversity increases are linked to sea-level increases. Further biodiversity trends were consistent with carbon and oxygen isotopic signals, which suggest that these trends may be affected by similar environmental factors.

Introduction

The incomplete nature of the rock, and hence, the fossil record, has led to recent controversy regarding the value of interpretations gleaned from stratigraphic analyses of faunal occurrences (Jackson and Johnson, 2001; Smith et al., 2001; Alroy, 2003; Vermeij and Leighton, 2003; Smith 2003). Disparities caused by spatial-temporal variations in deposition, diagenesis and exposure of sedimentary rocks result in differential preservation of rock volume over time. This, in turn, leads to subsequent variation in the abundance and geographic distribution of the encased fossils (Raup, 1976; Smith et al., 2001, Peters and Foote, 2002). Biostratigraphic studies of the fossil record require the reduction of biotic occurrences into a time series, with which to examine macro-evolutionary trends over a defined period and geographic area. The variation of fossil distribution over time and space produces unequal-sized values of faunal occurrences between time intervals, as well as sampling regions, which then inhibits numerical comparisons between these intervals (Foote, 2003). This is because most biostratigraphic analyses utilize metrics based upon the absolute values of fossil occurrences, thus the variation in fossil distribution affects the measured result (Dean and McKinney, 2001; Alroy, 2003).

Further adding to the geologically-controlled size disparities discussed above are sampling biases, which also contribute to variation in the abundance of recovered and described fossils in time and space (Koch, 1991). These biases range from the differential taphonomy and diagenesis of individual specimens to the initial collection

and the final description and taxonomic assignment of fossils (Gingerich, 1985; Benton, 1995; Robeck et al., 2000). Concerns about the variability of fossil distribution and the subsequent biases have led some workers to speculate that the global databases may not be useful in terms of interpreting processes that control evolutionary trends (Jackson and Johnson, 2001). In fact, Vermeij and Leighton, (2003) express the concern that “global biodiversity is a meaningless concept” due in part, to sample-size disparities between taxa, rock and time (Peters and Foote, 2001, 2002; Foote, 2003; Crampton et al., 2003)).

The position that the fossil record, and hence biostratigraphic analyses of fossil data, has limited utility for global applications (Vermeij and Leighton, 2003) is quite unfortunate because the only means by which to unravel and attempt to understand biotic evolution on earth requires investigation of the fossil record, in spite of its shortcomings (Jablonski, 1999). Macro-evolutionary and paleoecologic studies often require the assembly of biostratigraphic databases from which to measure morphologic or diversity change over time (Benton, 1995; Peters and Foote, 2001). The construction of such datasets entails a defined resolution, both in terms of spatial scope as well as temporal precision (Robeck et al., 2000). Furthermore, some studies only focus on a specific taxonomic group or attempt to quantify the proportional extinction or speciation ratios of several distinct taxa, with the results ultimately being compared to inferred causes that are either biotic, physical or both (e.g., McKinney and Oyen, 1989; Edinger and Risk, 1994 ; Johnson et al., 1995, etc.). Biostratigraphic analyses, however, remain as a primary means by which to organize fossil data and to observe past biotic changes over time (Jablonski, 1999).

What does cause conflict with the presumed viability of biostratigraphic analyses,

however, is the manner in which we formulate questions, quantify the data, and our scope and resolution of study (Jackson and Johnson, 2001; Badgely, 2003; Miller, 2003).

In this study, I will show that a database can be constructed, and through the use of relative metrics, demonstrate that valuable information can indeed be extracted and interpreted. Because the rock and fossil record are incomplete, and any biostratigraphic database is but a subset of actual fossil distribution, then analyses that utilize absolute values are affected by size disparities between samples (Dean and McKinney, 2001; Alroy, 2003). Thus, I will utilize a method to compare and evaluate the data that examines relative change of fauna. Metrics that measure relative change of a biotic diversity allow a more uniform comparison to be made between uneven samples unlike absolute metrics that are controlled by dataset size.

The metric used for this study examines four key parameters easily extracted from biostratigraphic range data. For each time interval these are: the number of total taxa (T), the number of extinct taxa (E), the number of new originations (N) and the number of taxa that exist in the preceding and subsequent time intervals and are termed stable (S). The metric, Diversity Index of Growth (DIG), is normalized to database size, and measures the divergence from stability. Absolute metrics, as defined here, include biodiversity as measured by absolute values of faunal occurrences over time (e.g., Sepkoski's database; Benton's database) and proportional extinction and speciation (E/T and N/T). Proportional metrics only quantify a particular aspect of taxonomic dynamics, rather than utilizing the complete suite of identifiable parameters shown above.

Additionally, the values obtained by proportional metrics are highly controlled by dataset size (T), which because of the multiplicity of sampling biases discussed previously, does indeed vary between time, space and taxa. Thus the use of relative metrics (Alroy, 2003) should serve to reduce mathematical artifacts incurred from the myriad of biases apparent in the fossil record (Dean and McKinney, 2001).

Background

Sampling issues

That the fossil record is an incomplete sample of earth's biota (Koch, 1991) is no surprise. The vagaries of geologic processes suggest a wide variation in retrievable data (Peters and Foote, 2002). These processes range from initial depositional controls such as biostratigraphy, or preservational controls such as diagenesis, to the ultimate exposure and possible destruction of rocks. In fact, there seems to be a proportional relationship between estimated rock volume and fossil abundance (Sepkoski, 1975; Peters and Foote, 2001, 2002). Furthermore, facies preference of organisms also determines fossil abundance, and thus, the rock type sampled also influences the sample size (Smith et al., 2001). Additionally, biologic issues including taphonomic variables caused by such factors as mineralogy, skeletal design, and trophic level further exacerbate uneven distribution of observable fossils (Palmqvist, 1993; Smith et al., 2001; Badgely, 2003; Vermeji and Leighton, 2003). Certainly all of these factors reduce to an issue of sampling intensity, whereby the more voluminous portions of stratigraphy simply sample more individuals than do lesser volumes of rock (Raup, 1976; Peters and Foote, 2001, 2002; Smith et al., 2001). Likewise, younger rocks have endured lesser effects from

exposure, diagenesis and other physical, geological processes than have the older packages of rocks (Jablonski et al., 2003). The result is that younger rocks tend to provide a more complete sampling of the fossil record than do older rocks. This phenomenon has been termed the “Pull of the Recent” (Raup, 1972; Peters and Foote, 2002).

Recent study by Crampton et al. (2003) provides an excellent illustration of the effects of sampling intensity, possible facies control and apparent biodiversity trends in Cenozoic New Zealand (Fig. 1). This figure, suggests a strong relationship between rock outcrop area and the subsequent number of defined geologic formations. This in turn, imparts some control to the number of fossil collections which also become more numerous in younger versus older rocks. Certainly, then, more nearly complete sampling achieved from more numerous collection efforts results in larger sample-sizes. These artifacts, when viewed together (Fig. 1), suggest that interpreted biodiversity trends are dependent upon rock volume in addition to possible evolutionary processes. Thus, facies control on fossil distribution (Smith et al., 2001) is a plausible mechanism. What remains uncertain, however, are whether conditions that favor more complete rock preservation also favor increased biodiversity. These issues are the prime topics of this dissertation.

Temporal issues

The incomplete nature of the rock record and thus, variation in the duration geologic time-units, also causes inconsistencies. The compilation of biostratigraphic data results in the assignment of fossil information into time intervals, which are unequal in length

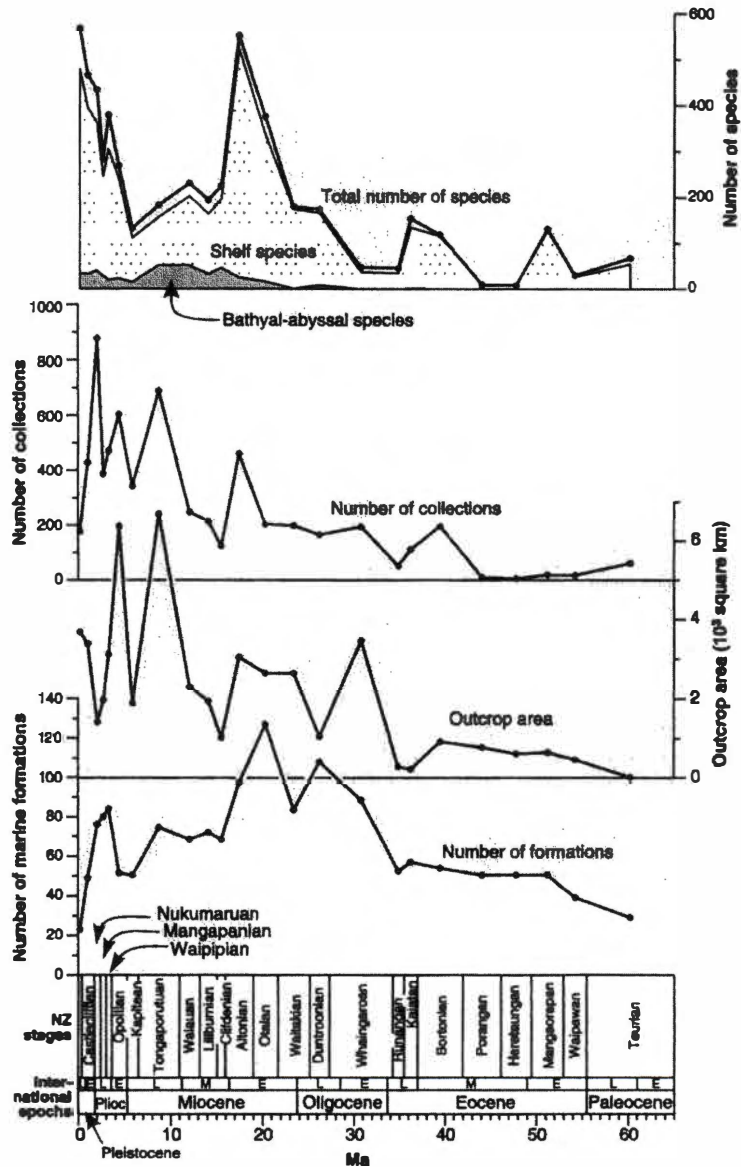


Figure 1. Biodiversity trends of Cenozoic molluscs from New Zealand. Apparent biodiversity trends, as calculated from absolute counts of taxa illustrate the relationship between occurrences of fossils and sampling. In this case, increased sampling results from increased exposure of rock outcrop area. Increases in rock volume, then, lead to increased number of formally described stratigraphic formations as well as more numerous collections of fossils from the field. Thus, the biodiversity increases observed may be related only to increased preservation and exposure of rock. Both of these factors (exposure and preservation) are possibly facies-controlled. Interestingly, however, the three major pulses of biodiversification at around 50 Ma, 35 Ma and 18 Ma are in general agreement with the results of this study. Figure modified from Crampton et al. (2003).

(Alroy et al., 2001). This too, can lead to sampling biases because the long-duration time interval basically yields a more numerically rich sample than does a short-duration time interval. The result is a very irregular distribution of fossils in time and space (Smith et al., 2001). Such variation is not limited to the wide range of possible geological events or biological controls; it is compounded by human biases imparted to data collection, description, identification, and analyses, as well.

Human biases

The first of these human biases to affect our understanding of fossils lies within the collection phase (Jackson and Johnson, 2001). Humans are usually drawn to the large, conspicuous objects or those that are distinct. Moreover, this is limited to those organisms that have a greater degree of preservation (Badgley, 2003; Jablonski, 2003). Commonly, the collection and sampling only acknowledges those macro-individuals, which are usually members of higher trophic levels (Palmqvist, 1993), so that what is typically omitted are the primary producers and smaller-sized organisms. Therefore, initial observations and data retrieval are already biased, because many important biotic groups, such as algae, sea grasses or worms can be obscure and are not recognized at all in biostratigraphic compilations. Furthermore, some research is focused upon the study of a particular clade of organisms (e.g., Smith, 2000). Thus, although collection of that particular taxon may be robust, there may be disparity between the stratigraphic recognition of that group when compared to other clades that may exist in the very same rocks! For example, whereas coral reefs are obvious marine features, and their occurrences in time and space are well documented in the Caribbean, some echinoderms

disarticulate rapidly, and are not quite as obvious (Donovan, 2001). This leads to uneven levels of stratigraphic description between taxa.

Secondly, taxonomic assignment of samples may impart a new layer of bias to our data. The species concept, as applied to fossils, usually only distinguishes morphologic or skeletal differences. It may be quite impossible, at times, to distinguish in a fossil, especially infrequently occurring taxa, between morphologic differences caused by species-level differences or variation one may expect within a population of individuals (Gingerich, 1985). As a consequence, taxonomic assignment may be biased and the hierarchical levels uneven between different taxa. The evolutionary significance of a species from one particular group, such as humans, is not necessarily equivalent to a species of another distinct group, such as worms (Benton, 1995). This “taxonomic equivalence” between different groups may further diverge if we move to higher taxonomic units such as genera, families, classes or orders. Therefore, the systematic descriptions of each taxonomic level may not be equal units between biologic groups.

Analytical biases

A third component of human-incurred bias lies within the methods employed to examine the data once they are collected. While it is readily acknowledged that the fossil record, as a whole, is an incomplete sample, the creation of fossil databases induces additional biases caused by collection (Vermeji and Leighton, 2003). Therefore, the use of metrics that derive absolute values from an incomplete dataset is an utmost problem (Dean and McKinney, 2001; Alroy, 2003). Most macro-evolutionary analyses of the fossil record

utilize proportional extinction (E/T), origination (N/T) or turnover $(E+N)/T$ measurements. In such studies, the effect of unequal datasets between time and/or taxa is either ignored, or in some cases, the absolute numbers of fossil occurrences are “corrected” between time intervals through statistical manipulations such as rarefaction (Nehm, 2001; Smith, 2003). All of these options can have major effects upon interpretations of biodiversity trends, either by over- or under-estimating biotic abundance (rarefaction techniques), or by being controlled by an incomplete sample (absolute or proportional metrics).

First, biodiversity strictly means the number of different taxa existing over a defined period of time and space (Benton, 2001). Proportional extinction (E/T) or speciation (N/T) metrics are only considering one aspect of biologic diversity and do not take into account the alternative routes taxa may follow over time (Dean and McKinney, 2001). Some taxa are robust and neither speciate nor go extinct over particular time intervals, but remain extant (Rosenweig and McCord, 1991). Metrics aimed at determining biodiversity “trends” should examine more than just one parameter if we expect to understand the evolutionary direction of diversity increase, reduction, or stasis that taxa are moving towards over time.

Second, by not recognizing the effect of sample size disparity (Alroy et al., 2001), the conclusions drawn from measuring proportional speciation or extinction may fail to account for pronounced periods of favorable preservation or the effects of more taphonomically robust taxa (Peters and Foote, 2001; Smith, 2001). Sampling studies

have shown that high degrees of completeness in data are often correlated with high degrees of speciation or extinction (Foote and Sepkoski, 1999; Crampton et al., 2003), which suggests that the absolute values of fossil occurrences are dependent upon available rock volume (Fig. 1), which may be dependent upon facies (Smith, 2001). The retrieved absolute values subsequently affect the inferred biotic trends (Dean and McKinney, 2001). Indeed, proportional extinction (E/T), and origination (N/T), metrics are controlled by the denominator, (T). In turn, dataset size (T), is a result of sampling intensity caused by the many factors described above. Where such issues become paramount is when comparisons between different taxa or time intervals are attempted. The differences in habitat preference, skeletal design and hence, preservation potential between two or more biotic groups can be quite vast, and the numerous pathways of potential biases can have a large effect on the number of individuals sampled (Badgley, 2003). Thus, while the biases of the rock and fossil record have been acknowledged, there is no clear means by which to circumvent the effects these sampling variations may impart to analyses.

Third, critical assumptions of biodiversity must be made to mathematically address uneven sample sizes. It has long been recognized that sample size variation can affect the measured result when using absolute and proportional metrics (Koch, 1991). Therefore, some biostratigraphic studies include rarefaction of sample sets or employ other statistical means to adjust the samples for comparisons (Alroy, et al, 2001; Nehm, 2001). These manipulations, however, only alter the original sample data and may impart mathematical artifacts into an already uneven subset of information (Dean and

McKinney, 2001). Compressing or expanding the sample size, such as rarefaction techniques, has an effect of assuming a predictable variation of fossil occurrences between each time interval or between different taxa, and therefore this approach is fundamentally unsound. This is because the goal of biostratigraphic study is to understand the biodiversity changes between time intervals or between taxa. Making critical assumptions of the diversity of biota between time intervals does not improve our ability to evaluate the causes of uneven fossil distribution in time and space and hence understand the mechanisms of biodiversity.

It should be obvious, for the reasons stated above, that biostratigraphic data are skewed. Geologic controls notwithstanding, we have greater sampling intensity centered about: 1) more volumetric deposits, 2) younger deposits as well as, 3) more geographically/geologically favorable deposits (Peters and Foote, 2002; Crampton et al., 2003). The data are further unbalanced by preferential study of some biotic groups over others, and ultimately all this information categorized by an uneven system of description (Jackson and Johnson, 2001). Compounding matters are the analytical techniques used to quantify biodiversity, with most techniques only examining one facet of change, such as proportional extinction or speciation. Furthermore, most metrics of biodiversity either measure absolute values or proportional values, and these are highly controlled by dataset size. This in turn, often leads to statistical manipulation of the data, which ultimately provides little insight about biodiversity trends because critical assumptions of sample distribution can obscure the differences between biota and time that we seek to examine.

Objectives

This study focuses on the biodiversity of the Cenozoic Caribbean. As a smaller ocean body residing upon a highly tectonically active plate, many questions pertaining directly to this basin can be derived. The Caribbean's proximal location to North America has led to intense investigations from North American geologists and petroleum exploration. Therefore, it is likely that the resolution of data used for this study may be more robust versus fossil data from less-studied regions. Thus the ability to measure the fossil record and then to compare biodiversity trends to environmental change is greatly improved.

The position of this work is to employ a system of relative measurements to the data. Instead of extracting absolute values from the unequal fossil record, the relative change of fossil occurrences is measured. In fact, having an adequate understanding of the definition of biodiversity is paramount to developing a suitable means to quantify it (Benton, 2001). Biodiversity strictly means the number of particular taxa of concern over a defined period in time and space (Benton, 2001). Relative change is achieved, in this instance, by considering the variables that determine biodiversity and then normalizing the sample size to the total number of taxa identified in a time interval. Further, to elucidate diversification or decline, the value is measured as it diverges from stability, or no change. In this manner, the relative diversity growth or decline of a data set over time can be compared to the relative change of another dataset or timestep (Alroy, 2003). This method has been previously described as taxonomic flux (Dean, 1997; Dean and McKinney, 2001) and provides a means to measure a relative biotic diversification over

time, which thus allows for cross-taxon and cross-temporal comparisons without the major effects caused by dataset size variation.

Materials

The genus-level biostratigraphic database used for this project was compiled from various published sources and investigative groups (Appendix A). Two such working groups include the Panamanian Paleontological Project (PPP) and Neogene Marine Biota in Tropical America (NMITA) (Budd et al., 2001). Both of these groups focus on the last 25 million year history of the Caribbean, and both are still in progress. Fortunately, some data have been published from these studies, both in print and via the internet. The spatial-temporal coverage of the database is the Cenozoic Caribbean region. Given the inequities of the fossil record in general, much care is centered about consistency of data. The mechanics of database construction will be discussed below.

Temporal scope

In assembling a biostratigraphic database the desired temporal precision must first be determined. Although the highest resolution in time is usually desired (e.g., 1 million-year intervals or less), this is not necessarily how biostratigraphic ranges are reported. Often, coarse-scale assignments in time are all that are given (e.g., “Miocene” or “Oligocene”), which ultimately leads to the exclusion of such poorly constrained taxa from the database. For this study, sub-epoch to stage-level divisions were utilized to both: 1) provide the highest level of precision, and, 2) maintaining the vast majority of biostratigraphic occurrences. Thus, the Cenozoic epochs were divided into three

intervals (Upper, Middle and Lower), with the exception of the Paleocene, Oligocene and Pliocene, which were only divided into two intervals each (Upper and Lower). These divisions, although not official time units, are standard levels that are commonly used to document the stratigraphic ranges of biota. Biostratigraphic ranges reported in absolute time are converted to the resolution of sub-epoch to stage level. The net effect of this division produces time increments that shorten as we approach the Holocene (Table 1).

Because some classifications in age assignments and taxonomy have changed over time, the issue of continuity becomes relevant. For this study, the published datasets and citations admitted to the database only include those described, reviewed or revised after 1970. This provides taxonomic and temporal consistency of the data (Jackson and Johnson, 2001). Many boundaries and absolute ages have been improved recently, thus requiring that the stratigraphic occurrence be updated to account for timescale revisions. By defining some point in time when these fossils were first defined, or, when the data most recently reviewed, provides a better-constrained dataset versus one with taxonomic or temporal uncertainty. The use of only more modern data serves to create a database that reflects a more recent understanding of time, space and biota. Seeking to eliminate these biases is a first priority when obtaining data originating from numerous sources.

Biotic scope

The biotic scope of this research is also defined by the nature of the biostratigraphic information. Because the Caribbean is predominantly a carbonate reef and platform environment, the constructed dataset reflects this. It is further influenced by the personal

Table 1. Parameters of Caribbean Database.

Time (Ma)		65	60.5	56.5	50	38.6	35.4	29.3	23.3	16.3	10.4	5.2	3.4	1.6	0.01
Geologic Time		L. Pal	U. Pal	L. Eoc	M. Eoc	U. Eoc	L. Olig	U. Olig	L. Mio	M. Mio	U. Mio	L. Plio	U. Plio	Pleist.	Hol.
All	Total	7	10	36	52	62	72	90	111	209	279	299	301	258	144
	DIG	1	1	5	5	7	7	7	13	10	10	10	10	0.46	1.06
	E/T	0.14	0.00	0.19	0.26	0.41	0.20	0.23	0.45	0.16	0.07	0.07	0.17	0.47	0.00
	N/T	0.28	0.40	0.72	0.44	0.38	0.51	0.51	0.37	0.55	0.37	0.07	0.08	0.03	0.63
	(T-S)/T	0.28	0.40	0.86	0.59	0.51	0.69	0.50	0.47	0.61	0.41	0.19	0.23	0.48	0.63
Corals	Total	0	0	0	1	1	36	36	53	55	51	51	53	43	39
	DIG	0.00	0.00	0.00	1.00	1.00	2.00	1.00	1.28	1.00	1.00	1.04	0.85	0.93	1.00
	E/T	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.16	0.16	0.07	0.07	0.20	0.09	0.00
	N/T	0.00	0.00	0.00	1.00	0.00	1.00	0.23	0.32	0.16	0.09	0.07	0.07	0.02	0.00
	(T-S)/T	0.00	0.00	0.00	1.00	0.00	0.97	0.45	0.40	0.27	0.17	0.07	0.20	0.10	0.00
Echinoid	Total	7	10	36	43	47	29	19	22	14	10	9	13	8	5
	DIG	1	1	5	5	7	7	7	13	10	10	10	10	0.46	1.06
	E/T	0.14	0.00	0.19	0.27	0.40	0.48	0.11	0.41	0.35	0.10	0.22	0.38	0.38	0.00
	N/T	0.28	0.40	0.72	0.32	0.34	0.03	0.21	0.23	0.07	0.10	0.00	0.46	0.00	0.00
	(T-S)/T	0.28	0.40	0.86	0.57	0.57	0.51	0.26	0.54	0.35	0.20	0.22	0.53	0.38	0.00
Gastropod	Total	0	0	0	6	6	4	21	30	39	144	144	151	145	18
	DIG	0.00	0.00	0.00	5.00	0.78	1.00	2.36	2.36	2.57	1.50	1.07	0.97	0.14	1.05
	E/T	0.00	0.00	0.00	0.33	0.50	0.25	0.42	0.03	0.10	0.09	0.09	0.09	0.75	0.00
	N/T	0.00	0.00	0.00	1.00	0.33	0.25	0.85	0.60	0.70	0.43	0.13	0.07	0.01	0.05
	(T-S)/T	0.00	0.00	0.00	1.00	0.50	0.25	0.90	0.60	0.74	0.47	0.20	0.17	0.73	0.05
Bivalve	Total	0	0	0	2	8	4	4	6	41	74	88	84	64	18
	DIG	0.00	0.00	0.00	2.00	1.88	1.00	1.00	1.50	5.70	1.80	1.14	0.75	0.14	1.05
	E/T	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0	0.04	0.04	0.07	0.25	0.73	0.00
	N/T	0.00	0.00	0.00	1.00	0.75	0.00	0.00	0.33	0.85	0.47	0.14	0.04	0.01	0.05
	(T-S)/T	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.33	0.85	0.48	0.24	0.27	0.73	0.05

focus of individual researchers who usually examine only a particular fossil group such as corals or echinoids (e.g., Budd or Donovan). Included in this database, though, are four major marine invertebrate clades that exhibit good preservation, have robust taxonomic description and are considered to be major members of reef and platform communities. These groups are: scleractinian corals (both reef-forming zooxanthellate and non-reef azooxanthellate forms); gastropods and bivalves, and echinoids. Although these groups all share a common tropical environment they also have major differences in life modes and substrate preferences. This is especially evident with the bivalves that, as a group, have a large range of potential habitats. Thus, the utility of having a dataset of widely varied clades cannot be underestimated. Observing similarities or differences in diversity changes of such diverse groups may provide insight and distinction of physical environmental gradients (e.g., sea-level, tectonics, climate) that may be large in scale and effect, versus those gradients that may have only had effects upon limited portions of the marine biosphere (Jablonski, 1999).

The taxonomic focal level for this study is predominantly genus-level occurrences. This serves to reduce some taxonomic uncertainties associated with species-level descriptions. Included in this database, however, are some species-level ranges, which may provide detailed resolution towards fine-scale gradients and also allow for comparisons between the dynamics of taxonomic scale (Chapt. 4). Taxonomic assignments follow the most recently accepted systematics. For coral taxonomy, they follow the system of Budd et al. (1999), whereas for echinoids, Donovan, (1993) and molluscs are organized according to the system of Jackson et al., (1999).

Spatial scope

The spatial extent of the study is not limited to the Caribbean as it is currently configured. The influence of plate tectonics and changing environments over the 65+ million year history of this region necessitates a broader definition of the Western Tropical Atlantic. Carbonate production and reef communities were, in fact, highly active during the Eocene and Oligocene (Edinger and Risk, 1994; Johnson, 2001). Furthermore, eustatic sea-level rise during these periods flooded much of the US Coastal Plain (Summerhayes, 1986; Carter and McKinney, 1992). Thus, limestone deposits and reef members of what is now the Gulf Coastal Plain are considered for these geologic ages. Therefore, the database includes some citations from carbonate rocks in Georgia, Florida, Alabama, Mississippi, Louisiana and Texas, as well as the Atlantic provinces of Mexico (Fig. 2). The remaining stratigraphic ranges are from Caribbean regions of Central and South America, along with Caribbean islands.

Methods

To assess biotic diversity change as demonstrated by this database, the approach used here quantifies biodiversity as either a positive or negative divergence from stability. A means to quantify the relative change of biotic diversity within a biostratigraphic dataset has been previously proposed (Dean, 1997; Dean and McKinney, 2001). First, I define, as a system, the number of fossil occurrences in a particular time interval, and then allow three pathways that can be realized by this system. Two of these pathways, speciation



Figure 2. The spatial scope of study. Data collected for this research was drawn from faunal occurrences in the Western Tropical Atlantic from 65 Ma to present. Because the Caribbean Basin has not remained static and represents a remnant of the equatorial tropical seaway (Tethys), biostratigraphic ranges from Paleocene to Late Oligocene rocks in Gulf Coastal Plain, Atlantic Coastal Plain, along with the Atlantic Ocean Provinces in Mexico were included in the Caribbean Database. Also indicated in this figure are locations of select Ocean Drilling Program (ODP) cores discussed later in text.

and extinction are commonly understood. As would be expected, speciation or extinction of fauna indicates system growth or decline, respectively. However, a third possibility remains, namely, that of no net change, or system stability, when the biota neither becomes extinct nor speciate. Thus, the metric used here measures the relative divergence of system growth or decline as it deviates from system stability. To reduce the artifact of sample-size disparities, it is normalized to sample size. The equation used for this study has the following key parameters, which are terms easily extracted from any biostratigraphic range data. These are:

T = the total number of taxa in a particular time interval,

N = the number of new originations in that time interval,

E = the number of extinctions in the time interval,

S = the number which existed in both before and after a particular time interval.

The resulting equation used is:

$$(1) \quad (T-E+N+S)/[S+T(E+S)/(N+S)]$$

The use of this style of normalized metric reduces the mathematical biases inherent in metrics that assess absolute change, such as proportional extinction (E/T), or origination metrics (N/T). As simple two-term fractions, the value obtained by proportional extinction and origination metrics are highly controlled by dataset size (T). Because it is

readily apparent and acknowledged that the fossil record is indeed incomplete, and in fact any database created is subsequently only a subset of the fossil record, the use of absolute values such as taxic counts (e.g., Sepkoski's compendium) or partial diversity metrics (e.g., proportional extinction and origination) should be avoided (Dean and McKinney, 2001; Alroy, 2003). To lessen the effect of sample size variation, this metric is normalized to dataset size and provides a realistic result that can be interpreted in terms of expected biotic diversification or decline as the system diverges from stability (S), or 1. As measured by this metric, then, increase in biodiversification can proceed exponentially and includes all values above 1. Extinction, on the other hand, can only be 100 %, and thus can range from 1 to 0. Whereas this metric was initially described and labeled as "Taxonomic Flux", upon reflection, it seems that the actual measurements are an index of diversity growth or decline. Furthermore, "flux" implies a total value, whereas, this metric produces an index for comparison, not quantification of the total taxa moving from one time interval to the next one. Thus, for this dissertation, the metric is renamed as the Diversity Index of Growth (DIG).

A key aspect to this methodology is the recognition of system stability, i.e., no net change in the numerical size of the dataset, or 1. Thus, time periods in which no extinction or speciation occurs are measured as 1. Additionally, times of equal speciation and extinction are also reduced to 1, or no net change in diversity. To measure these moments of high turnover that result in no net change, a means to assess volatility is used. Because volatility, as defined here, is simply the opposite of stability (S), then proportional volatility can be measured by:

(2) $(T-S)/T$

The Caribbean database used in this study consists of 520 genera and approximately the same number of species. The range-through method of assuming a taxon's existence in time as defined by First Appearance Datums (FADs) and Last Appearance Datums (LADs) was observed (Kirchner and Weil, 2000). Taxa that have been identified at only one interval were also included. These taxa have been termed "singletons" and are often excluded from other biostratigraphic analyses as "noise" (Kirchner and Weil, 2000). In this study, however, a singleton would be considered as both a New Origination and as an Extinct member, and therefore the Diversity Index of Growth (DIG) metric would actually cancel out this effect. Singletons are not major contributors to the dataset, yet they are legitimate aspects of past biodiversity.

Statistical confidence, or error bars are not deemed appropriate for this study. Following the convention of Jackson and Budd (1996), it seems unreasonable to impose mathematical constraints upon the validity of stratigraphic data. Statistical confidence is valid for bulk sample studies, where standardized sample counts are achieved, or for comparing empirical measurements and trends to results produced by models. But these constraints are not applicable to biostratigraphic fossil data, because they have not been sampled in a standardized manner (Jackson and Johnson, 2001). As explained previously, the innate nature of incomplete sampling is a fact and feature of the rock and fossil record. To exclude or minimize data merely because of the unequal distribution of

rocks and fossils would mean a loss of important information. Further, the use of relative quantification (DIG) rather than absolute values of data is chosen primarily for the reduction of such artifacts caused by differentials between time, space and biota.

Results

As with the rock and fossil record, this database exhibits sampling biases ranging from the “pull-of-the-Recent” phenomenon to the duration of time intervals. Although these issues may impede the clarity of interpretations in absolute or proportional metrics, relative measures seem to actually overcome these biases. Further, only by understanding such disparities of sample size can we begin to truly understand the limitations of our analyses, and more importantly, obtain robust interpretations of biodiversity.

Relevance of database

A major aspect of the Caribbean database is the trend of increasing genus-level diversity, in terms of absolute numbers, as we approach the latest Holocene (Fig. 3). This effect, however, is not limited to this particular dataset. In fact, the benchmark genera-level marine database, created by Sepkoski (Foote, 2003) follows this very same trend (Jablonski et al., 2003) during the Cenozoic Era (Fig 4). Clearly, Figures 3 and 4 illustrate “pull-of-the-Recent” which is caused by better preservation and exposure of younger rocks that contribute to species-area effects (Peters and Foote, 2001, 2002). Both datasets when plotted together show good agreement with respect to one another

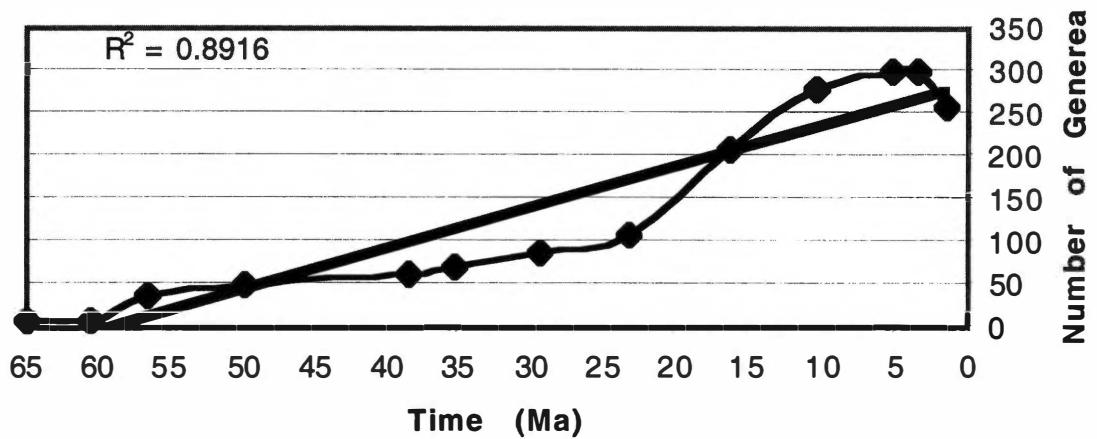


Figure 3. The Caribbean dataset as measured by absolute values. Note increase of genera as we approach the latest Holocene. Regression line has strong coefficient, which suggests “Pull of the Recent” effects. Compare this figure with Figure 4, which includes global data from Sepkoski’s Compendium of fossil marine genera.

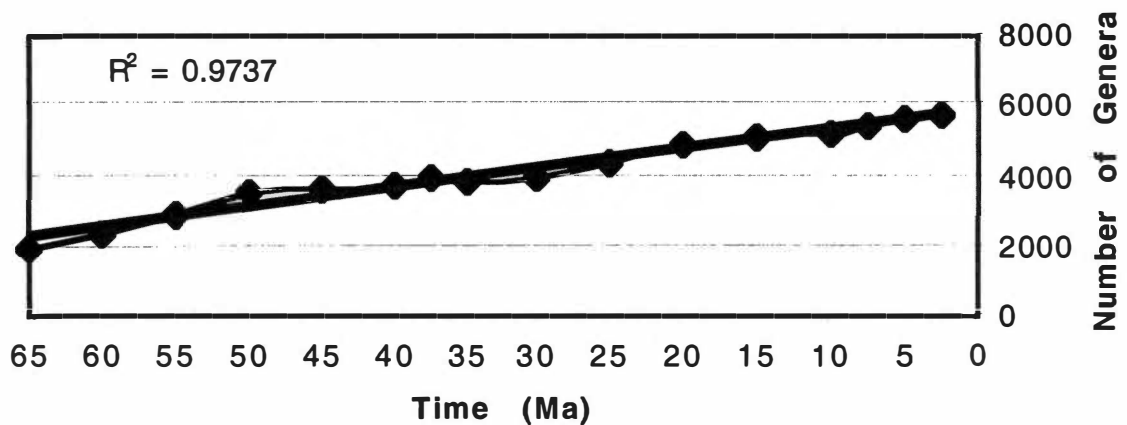


Figure 4. Data from Sepkoski's Global Compendium viewed in terms of absolute values. Note strong correlation of linear regression that indicates “Pull of the Recent” effects of absolute values. Data approximated from Foote (2002).

and have a very high r^2 value (Fig. 5). As a first test of these data, it is quite apparent that the compilation of Caribbean data is consistent with the trends of a numerically larger, and thus, seemingly more significant database. Sepkoski's database is global, in scale, and includes some 30,000 marine genera over the whole 540 million year duration of the Phanerozoic Eon. The Caribbean database used in this study, however, includes 520 genera drawn from only four clades of both a smaller study area and shorter era of geologic history. Of greater importance then, is the demonstration that the Caribbean database is following established trends and indeed is significant, in spite of biases inherent in the rock record, or even in the assembly of the database itself.

In fact, a major point of caution regarding the Caribbean database is the dearth of corals and mollusks from the Lower Paleocene through Lower Eocene (Table 1). During this interval, the database is composed of only echinoid data. While this alone may call into question the value of interpretations obtained over the early Cenozoic from this database, there are several lines of evidence that lend credence to this data. First, the construction of the database follows rigid protocols of temporal and taxonomic description. Absences of admitted fauna only reflect the adherence to stringent guidelines intended to produce a robust sample of the fossil record. Second, as described previously, the trends of this database are in excellent agreement with the Global Compendium (Figs. 3 – 5) that also depicts depressed taxonomic diversity in the early Cenozoic. Third, the biodiversity trends presented in this paper (Fig. 6) are also in excellent agreement with another Cenozoic global database (Dean and McKinney, 2001) that depicts mollusks as well as

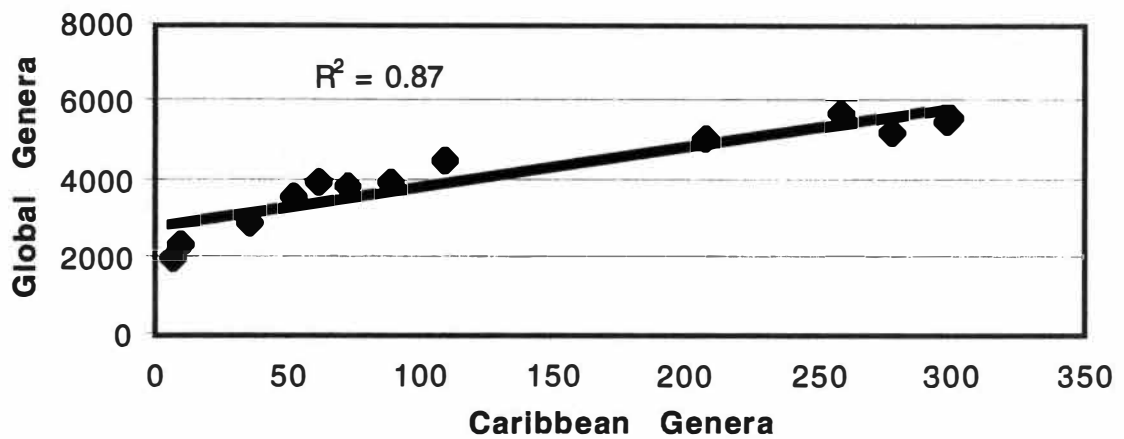


Figure 5. Correlation of regional biodiversity trends to global biodiversity trends. Data from Sepkoski's data (Fig. 4) and this study (Fig. 3) are plotted together. Note strong coefficient of regression that suggests that both datasets seem to follow the same trends.

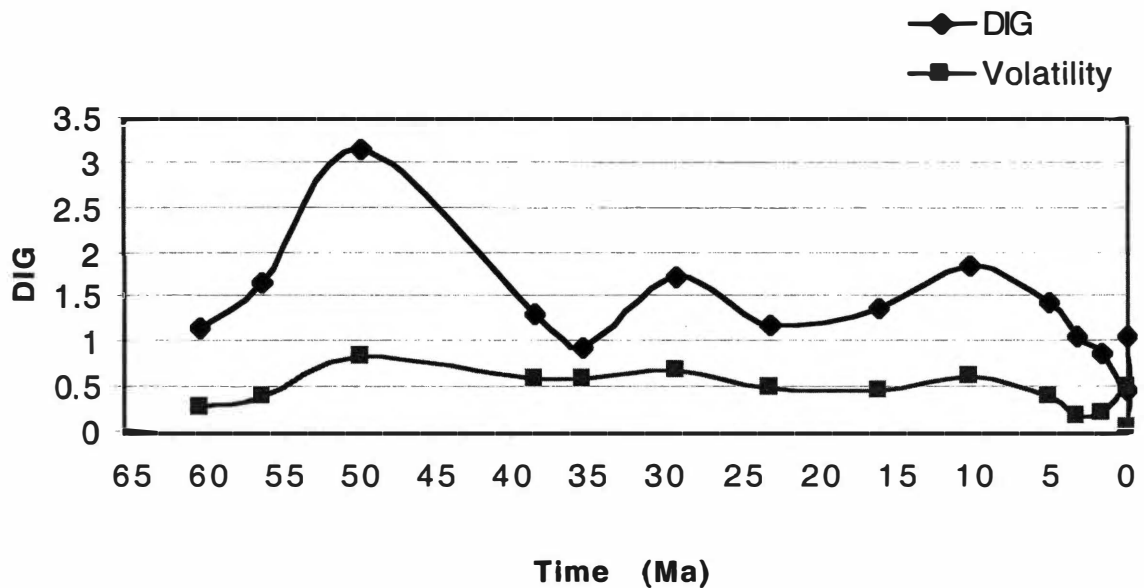


Figure 6. Biodiversity as observed by relative metrics. All values of DIG above 1 indicate diversification, values below 1 indicate diversity decline. Note, biodiversity coefficients decrease as we approach the Recent, and the highest values of diversification actually occurred at 50-55 Ma, with two other peaks at 30 Ma and 10 Ma. Volatility is also depicted on this graph, and it can only range from 0 to 1. Volatility also has a peak at 50-55 Ma, with two other peaks at 30 Ma and 10 Ma. Both methods indicate marine biodiversification has decreased from Mid-Eocene highs, and declines towards the present.

echinoid biodiversity. Fourth, the biodiversity trends presented here (Fig. 6), as well as those from earlier work (Dean and McKinney, 2001) are following the same trends of mollusk diversity (Fig. 1), as those from Cenozoic New Zealand (Crampton et al., 2003). Taken together, then, this indicates that the early Cenozoic biodiversity trends from the Caribbean database are accurate. Furthermore, had well-described mollusk or coral citations been readily available, it is likely the overall trends would remain similar.

We cannot assume, however, that these data in Figures 3 and 4 unequivocally indicate more genus richness in near time versus deeper geologic time. Statistical regression of absolute values of genus membership versus time indicates that both the global data and the Caribbean data exhibit the artifact of “Pull-of-the-Recent”. In fact, the r^2 – values of both regressions indicate a very high degree of correlation between absolute value increase of genera diversity in near time. By using the Diversity Index of Growth (DIG), we can compensate for the inequities of dataset variation by avoiding the use of absolute metrics, and proportional extinction or speciation that are constrained by the absolute value of the dataset (Alroy, 2003; Miller, 2003). Indeed, this is a critical difference between biodiversity studies that utilize absolute metrics (Fig. 1) versus those based upon relative diversity change (Fig. 6). This in fact, may explain the difference in the magnitude of presumed biodiversity trends derived from Crampton et al. (2003) as opposed to those trends shown here. In this study, the *relative* increase in biodiversity is much greater in the lower Eocene (Fig. 6) than that of the *absolute* biodiversity change (Fig. 1), and the reverse is true as we approach the more fossil-rich recent. It is important

to note, then, that the magnitude of biodiversity change as seen in Figure 1 may be controlled by sampling intensity (as produced by available rock) whereas those controls are absent with relative metrics (Fig. 6).

Biodiversity trends

Comparison between the Caribbean DIG values (Fig. 6) and published global carbon and oxygen isotope curves (Fig. 7) of Zachos and others (2001) indicates good agreement between these two very independent sets of data and methodology. Both the DIG and oxygen isotope curves depict major diversity and temperature increases, respectively, around 52 Ma. This corresponds to a pronounced warming event, termed the Paleocene-Eocene Thermal Maximum (PETM) that has been documented in terrestrial as well as marine environments (Zachos et al., 2001). The agreement between DIG and ^{18}O curve is maintained until about 30 Ma, but resumes again after 10 Ma. The carbon isotopic curve also indicates relative agreement with the DIG values. Although there is some temporal offset, possibly caused by variation in resolution between both sets of data, each curve depicts three distinct “peaks”. Additionally, DIG indicates that Cenozoic diversity growth is not a monotonic increase, as would be observed from traditional methods using absolute values of fossil occurrences (Figs. 3, 4). Although biodiversity of marine genera did increase over the Cenozoic, DIG (Fig. 6) indicates that biodiversity proceeded as three evolutionary “pulses”. This suggests both the utility of the Caribbean database and also the ability to make important and unique biodiversity interpretations from fossil database compilations. In fact, biodiversity may be linked to major temperature change and the subsequent controls on sea-level (Jablonski, 1999; Dean and McKinney, 2001;

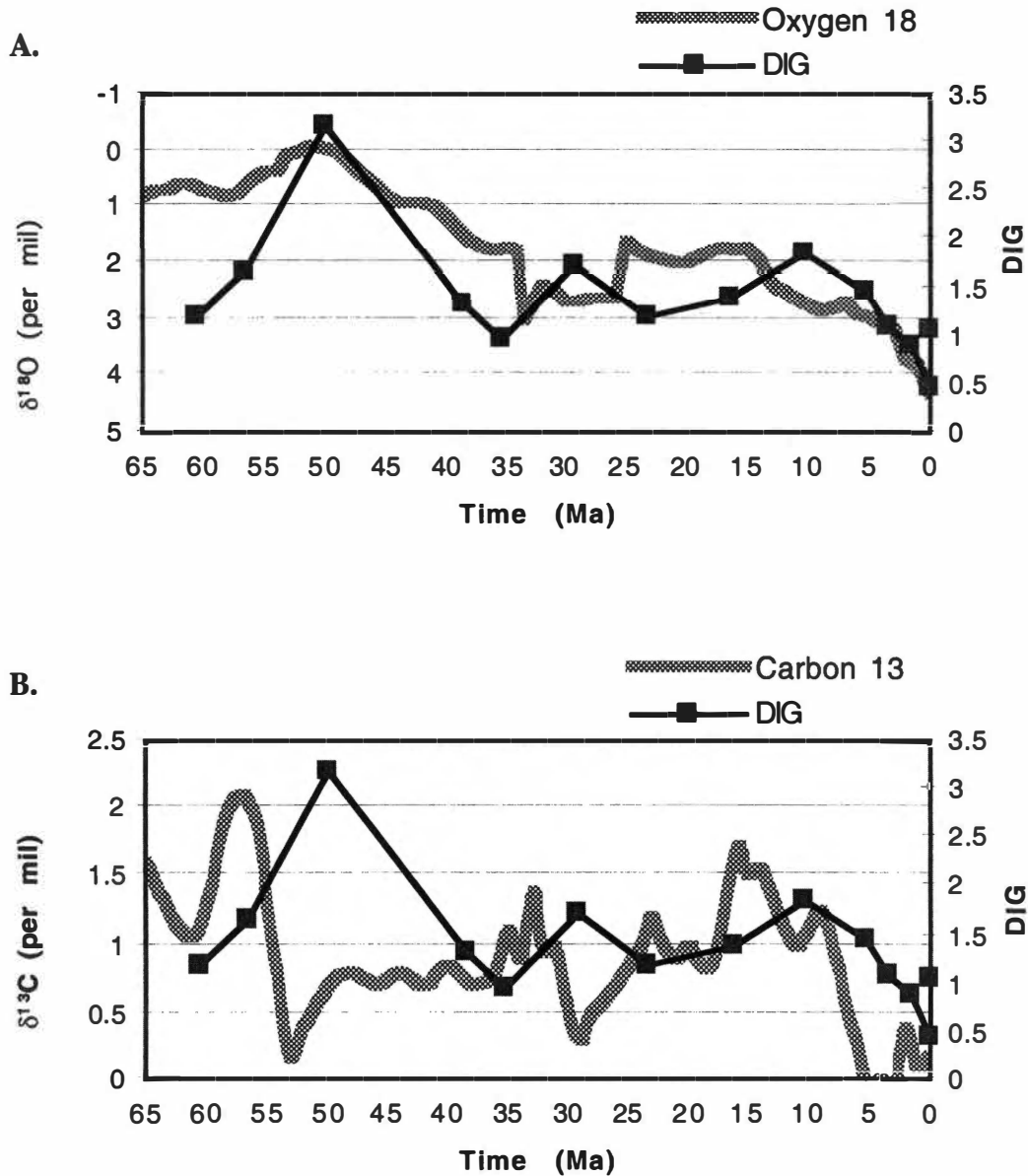


Figure 7. Published carbon and oxygen isotope data from the western Atlantic Ocean. Oxygen isotopes, 7a, indicate warming trends at 52 Ma, which likely increased sea level. Carbon isotopes, 7b, show a trend towards heavier carbon at this time, which may be caused by increased marine productivity. Note that smaller isotope excursions are also observed near 30 Ma and 10 Ma, which closely follows the DIG curve (Isotope data re-drawn from Zachos et al. (2001)).

Smith et al., 2001). The relationship of biodiversity to isotopic data (Fig. 7) has significant implications concerning biodiversity, climate and sea-level. It is commonly understood that decreased $\delta^{18}\text{O}$ values are linked to temperature increase that should result in higher-stand seas (Zachos, 2001). Carbon isotopes are often interpreted as indicators of marine productivity. The increased burial of organic carbon (^{12}C) from biotic consumption results in higher ratios of inorganic carbon (^{13}C) in the ocean system.

When DIG is compared to global eustatic sea-level curves (Fig. 8a), we can observe some similarities between biotic diversification events and sea-level trends. However, the temporal offset between highstand seas and diversity increases prevents exact comparison. The reasons are two-fold: 1) we are comparing data of vastly different levels of resolution, and, 2) DIG is a relative metric and the sea-level data are depicted as absolute values. To overcome this predicament and compile the sea-level data into equal time intervals like those of the fossil data, as well as to also capture the variation of sea-level, a simple method is used. First the area under the sea-level curve was calculated using the trapezoidal method. By using the time intervals dictated by the fossil data as boundaries, the sea-level data are then reduced to the same temporal resolution as the DIG data. In fact, this alone produces a very intriguing relationship between biodiversification and sea-level (Fig. 8b). As opposed to the high-resolution sea-level data that present a multitude of variation over time, the integral of sea-level depicts three major transgressions that closely match the three DIG peaks. Second, to present these

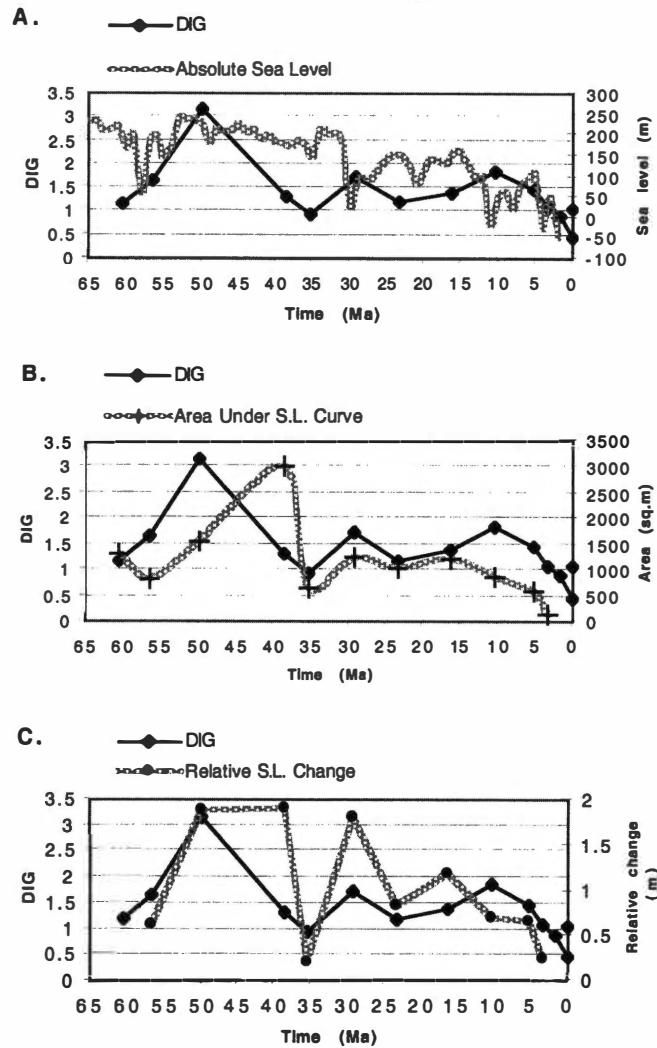


Figure 8. The relationship between biodiversity and global sea level. In 8a, DIG is compared to absolute sea-level. Because DIG is a relative metric, with temporal resolution that does not match that of the sea-level curve, measures to convert the sea-level to relative change are employed. In 8b, the area under the curve in 8a was calculated, and the boundaries used were those of the biostratigraphic time intervals. Equivalently-scaled data produces a sea-level curve that more closely matches the DIG signal, including three prominent “peaks” in close temporal proximity to the three biodiversity “peaks”. To depict sea-level as relative change, a co-efficient of area (8b) growth or decline was calculated in 8c. The relative change of sea-level is very similar to the relative change in biodiversity (Absolute sea-level data redrawn from Prothero, (1994)).

sea-level data as a relative change, we can calculate the co-efficient of the change in area between each interval.

The relative change of sea-level (Fig. 8c) results in a very close match between relative increases in sea-level and biodiversification trends. Thus, diversity growth, as evidenced by DIG, shows a pronounced increase in diversification values during periods of higher sea levels, which likely are product of more habitable, shallow marine area created by the flooding of land surfaces (Holland, 1995; Jablonski and Sepkoski, 1996; Jablonski, 1999; Smith et al., 2001). This position is supported by the oxygen and carbon isotopic curves that indicate increased temperature and productivity in close temporal proximity to biodiversity increase. Although it may seem intuitive that marine invertebrates would respond favorably to sea-level increase, such trends have not been clearly depicted with absolute metrics.

Rock versus time

Because we do not have accurate estimates available for preserved rock volume (Peters and Foote 2001, 2002), then the duration of time steps will be used here as a proxy. This, then, brings forward the issue of interval length and sample size. Regression of stage length versus sample size shows little if no correlation of DIG values (Fig 9). If the two “outliers” are removed from this plot, the r-value increases significantly (Fig. 10). But, those two outlying points are precisely the timing of the Paleocene-Eocene Thermal Maximum (PETM), which is a temperature excursion that has been interpreted from both terrestrial and marine data (Zachos et al., 2001) and is a critical aspect of both the

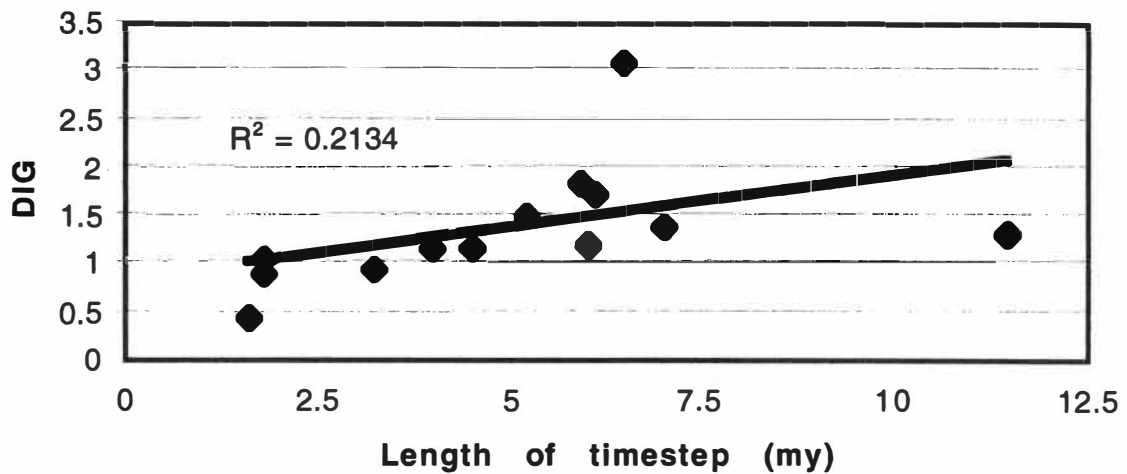


Figure 9. Regression of DIG values plotted versus length of time step. There seems to be a poor correlation between length of time interval and DIG value obtained. If time length serves as a proxy for rock volume, then this suggests that DIG is not highly controlled by sampling artifacts.

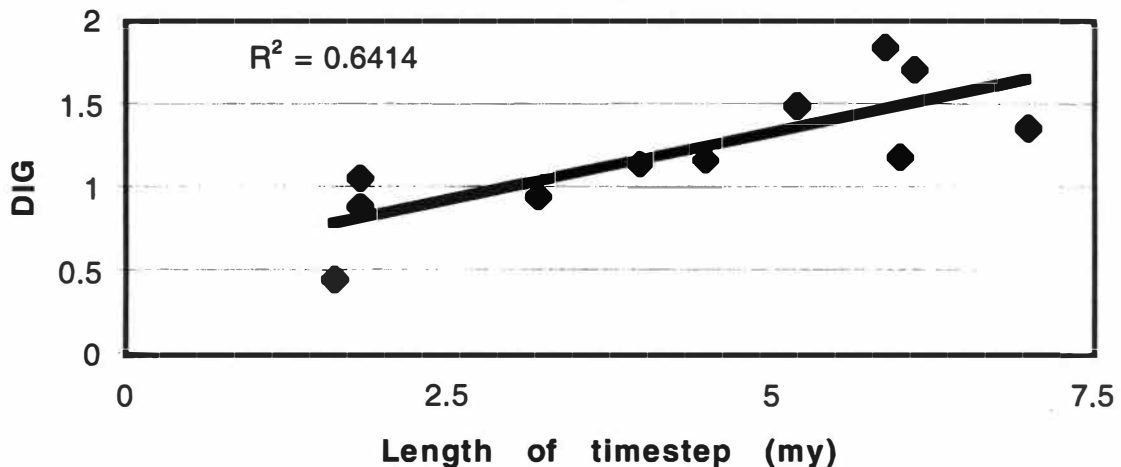


Figure 10. Regression of DIG versus length of time step with two "outliers" removed. R^2 factors increase significantly from Fig. 7, but, the two removed points are from the Eocene excursion, which is observed in a previous study (Dean and McKinney, 2001) and also captured by independent isotopic evidence. For these reasons, it is likely not valid to remove the two data points for this figure.

isotopic, DIG and sea-level curves (Figs. 5,6,7). That these data and methodology are able to capture such dynamics is pertinent to the study of fossil data and understanding the dynamics of biodiversity through time.

Discussion

A major concern regarding the comparison of marine diversity increase and high-stand seas lies with the influence of rock volume and sampling intensity (Raup, 1976; Peters and Foote, 2001, 2002). Given that higher stand seas would also likely produce increased shallow-marine areas, then, it could be argued that increased carbonate production during sea-level rise may, indeed, only provide an increased sample of fossils (Smith et al., 2001). It can be countered, however, that transgressive seas also emplace carbonate rock far onto terrestrial regions or onto islands that then may be preferentially destroyed by weathering processes (Smith et al., 2001). These two conflicting views do not consider the effect of high-stand seas in terms of biotic diversification (Jablonski and Sepkoski, 1996; Jablonski, 1999). Any topographic variation of the on-shore facies would provide a high degree of isolated marine populations. In a tectonically active region such as the Caribbean, the results of volcanism and uplift may be factors leading to topographic variation. Such environments may be favorable for species' adaptation, thus leading to allopatric speciation, and hence, observed biotic diversification.

Therefore, although the resultant interpretation regarding the effects of high-stand seas upon potential rock volume and sampling biases is far from unequivocal, the concomitant

shifts between DIG (Fig 6) carbon and isotope curves (Fig 7), and relative sea-level (Fig. 8), suggest a link between sea-level, temperature, productivity and biodiversity. This is further indicated by the fact that separate studies using the DIG method and global datasets (Dean 1997; Dean and McKinney, 2001) show similar trends regarding sea temperature and biodiversity increases at the Paleocene-Eocene Thermal Maximum (PETM) boundary, as well as moderate diversity increases, as we approach the latest Holocene. Moreover, the PETM excursion of carbon and oxygen isotopes has been observed in terrestrial data (Zachos et al, 2001), which suggests that the marine biotic diversification during high-stand seas is perhaps independent of rock volume and thus the preservational artifacts caused by transgressions (Smith et al., 2001). Further, two empirical studies of Mesozoic echinoids and ammonites also indicate biotic diversification during transgressions (Marchand and Thierry, 1997; Neraudeau et al., 1997).

In evaluating the overall trends of biodiversity in the Caribbean using DIG, the data depicted here (Fig. 6) do show a diversity increase from deep time to near time. Whereas the biotic diversity increase can be explained by the “pull-of-the-Recent” or by younger, less altered rocks (Jablonski et al., 2003), it is more difficult to reconcile the fact that DIG also captures critical events such as the PETM, which is not captured by absolute diversity values (Fig.3). Given the myriad of sampling biases that pervade the rock record, there is a large divergence in interpretation between data viewed in terms of absolute numbers (Fig. 3) versus using DIG (Fig 6). The interpretation made here suggests that indeed, absolute metrics may overestimate the rate of biodiversity growth

through time, as was suggested by Alroy and others (2001). The use of the volatility metric here (Fig. 6), as an opposite of stability (discussed above), does seem to bolster the view that much turnover was experienced near the PETM, perhaps caused by factors involving climate, sea-level, or, delayed recovery from the end-Cretaceous event.

In fact, the apparent trend of absolute diversity increase towards the latest Holocene may only be an artifact of decreased volatility at this time. Possible reasons for this volatility decline may be that this version of volatility is an absolute value, measuring turnover from 0 to 100%. Further, the decreasing duration of time intervals as we approach the present may not provide enough time for significant biotic change to be observed in this database. Thus, artifacts ranging from time length to Pull-of-the-Recent effects may possibly render metrics based upon absolute values useless for biostratigraphic time series. And, even though artifacts in sampling exist, DIG is a means to minimize or avoid those effects. Thus, in spite of the “Pull-of-the-Recent” and other sampling intensity issues that are present, the subsequent controls on observable (DIG) diversity growth index are not evident (Fig. 9).

Conclusions

The results of the genus-level biodiversity trends of the Cenozoic Caribbean database show many similarities to global dynamics from previous studies (Dean and McKinney, 2001). These include three “pulses” of evolutionary diversification. The first event occurred around 52 million years ago, followed by diversity decline. Subsequent biodiversification events occurred again at approximately 30 and 10 Ma. Furthermore,

the first and most pronounced biodiversification event of this study at 52 Ma coincides with the timing of the Paleocene-Eocene Thermal Maximum (PETM). This suggests that the major biodiversification at 52 Ma may be related to temperature increase, sea-level rise, or a combination of factors. An important aspect of this study is that the PETM event is not captured by absolute metrics. Relative diversity metrics such as DIG, however, seem to actually follow isotopic trends and do depict diversification at the PETM. Due to the unequal rock and fossil record, metrics measuring relative change of datasets are inherently a better method than those that ascertain absolute values. The DIG method here demonstrates that important biodiversity trends can indeed be interpreted from an incomplete fossil record. But, as a note of caution, Figure 8 illustrates the need for equal comparison between data. Relative metrics, such as DIG, must be compared to data, such as sea-level, which are presented in a relative form. Comparison of absolute data to relative data, or fine-scale resolution to coarse-scale resolution impedes accurate interpretations.

A common theme in biodiversity studies is the apparent trend of increasing diversity as we approach the latest Holocene. As indicated here, much of this may be an artifact of the Pull-of-the-Recent and the use of absolute values. Further, partial biodiversity metrics such as proportional extinction or speciation do not provide estimates of paleo-diversity. Figures 3 and 4 show excellent relationships between time and apparent diversity increases, however, the overall diversification observed by using relative metrics is much different (Fig. 6) than the monotonic increase observed by using absolute values of diversity (Figs. 3,4). The main divergence between these two methods is not

the aspect of increasing diversity, then, since both depict system growth. The DIG metric indicates that diversity increases in the Cenozoic Caribbean proceeded as three discrete “pulses”. Further, DIG produces relative agreement between sea-level (Fig. 8) isotopic data (Fig. 7) and diversity growth (Fig. 6), which suggests that actual biodiversity of marine organisms is related to temperature and sea-level. Diversity increase corresponding to sea-level increase, then, suggests that transgressions may provide increased shallow-water habitat that, in turn, may lead to biodiversification. This interpretation is supported by the observed shifts in ^{13}C data that indicate increased productivity coinciding with $\delta^{18}\text{O}$, sea-level and DIG curves.

CHAPTER 3: BIODIVERSITY TRENDS AND CAUSAL MECHANISMS

Abstract

The relative change of the biodiversity trends of Caribbean Cenozoic marine invertebrates are followed by using the Diversity Index of Growth (DIG). The individual biodiversity trends of each of the four groups (corals, echinoids, bivalves and gastropods) studied are consistent with diversity trends from independent data, which suggests that this approach is appropriate. Three major “pulses” of total biodiversification were observed at about 52 Ma, 30 Ma, and 12 Ma. These three biodiversification events are temporally proximal to major volcanic events in the Caribbean region as interpreted from ash deposits in deep ocean cores. Further, these biodiversification events may be linked to regional and global sea-level changes that occur coincident with the timing of global terrestrial biotic changes and climate events. At the scale of this study, this suggests that sea-level, climate and tectonics are major controls on marine biodiversification. The implications are that tectonics may be the driving process of sea-level and biodiversification, which is consistent with previous interpretations. Further, these results confirm the validity of using relative metrics to identify correlations between global and/or regional forcing functions and biotic responses.

Introduction

The last 65 million years of earth history have been replete with dynamic processes of tectonism, climate change and sea-level fluctuation. How these environmental changes

inter-relate to affect biodiversity is of utmost concern. The current high rate of anthropogenic CO₂ released into the atmosphere has dramatic implications for causing global warming, which may lead to major changes in climate, sea-level and biota. Because we cannot accurately predict the nature and type of climate change, and the subsequent effects in the present, the geologic record provides insight towards the physical and biological response to past rapid inputs of atmospheric carbon. Thus, the rocks themselves provide not only the key to the chemical and physical changes experienced by earth, but also, the fossil record contains answers to the biological response.

Although intensive research has focused specifically upon addressing issues between climate and tectonism, many questions between cause and effect remain. This is due, in part, to the intimate relationship between the atmosphere, lithosphere and biosphere that are chemically and physically reactive with one another. In fact, climatic processes that favor more extensive deposition (e.g., warmer climates and transgressions), thus more completeness of data, may often be the very same factors that physically and chemically weather and erode those deposits (Smith et al., 2001). Volcanic events that produce and release CO₂ often operate with coeval tectonic processes that subduct, uplift, deform or otherwise destroy or obscure physical evidence within rocks. Further, interactions between tectonically released gases and exposed rocks can lead to major changes in atmospheric chemistry, and hence, climate. Or, climate can be affected by changes in oceanic or atmospheric circulation as a result of tectonics. Additionally, climate effects, through weathering, erosion and deposition, may impart controls to tectonic rates, timing

and intensity through the subsidence of sedimentary basins, which may introduce silicic material (Rampino et al., 1979; Molnar and England, 1990; Raymo, 1994; Beck et al., 1995; Sigurdsson et al., 2000).

The invertebrate fauna, although likely responding to either or both climate and tectonics (Rampino et al., 1979), are certainly at the mercy of each of these processes. The ultimate deposition, preservation, and exposure of fossiliferous rock are dependent upon these very two environmental processes that we wish to track (Smith et al., 2001).

Further clouding our interpretations of geologic data are variations between the precision and resolution of the physical and biological systems investigated. Therefore, scaling issues and the timing of events become critical when developing hypotheses of cause and effect upon biostratigraphic databases, which usually have lower temporal resolution than isotope or sea level curves, or other high-resolution data (e.g., ODP and DSDP cores).

Fortunately, however, numerous chemical signatures of both climate and tectonics can be tracked and put into context with biostratigraphic information (Rampino et al., 1979; Bralower et al., 1997; Zachos et al., 2001). New information is emerging, such as volcanic ash or isotopic data from Ocean Drilling Project (ODP) cores, that when synthesized with biotic response, indicate close agreement between tectonic events, climate change and biodiversity trends over time (Bralower et al., 1997; Zachos et al., 2001; Thomas et al., 2003).

The Caribbean region provides an excellent example of the complex relationships between tectonics, climate and biodiversity trends. The Cenozoic history of this basin

and the associated fauna record a series of major environmental changes, from closure of the Tethys Seaway, a circum-equatorial ocean, to the subduction, obduction and thickening of oceanic crust. These tectonic activities are further complemented by intensive periods of volcanism, as evidenced by the formation of island arcs, a vast ignimbrite province in Mexico (Sigurdsson et al., 2000), as well as the Panamanian landbridge of Central America. Superimposed upon this tectonism is a climate regime of a “Greenhouse” Paleogene that transcends into an “Icehouse” Neogene (Zachos et al., 2001; Siesser, 1995). The results of such climate change, and tectonics, are variations in sea-level that affect not only sedimentary rock volume, but biotic habitat, as well. The proximal location of the Caribbean as an equatorial ocean is helpful in our understanding of marine biota because the warmer, dominantly shallow-marine conditions (<60 m) are favorable for carbonate production and the development of extensive reef systems. These reefs are highly productive marine communities that subsequently provide a large suite of organisms that are taphonomically robust and generally well-studied (Wood, 2001). Thus, the Caribbean provides a robust assortment of physical, chemical and biological signatures, from both a regional and global perspective, with which to address the evolution of the lithosphere, atmosphere and biosphere.

In this paper, my research will utilize the relative changes of biodiversity as measured by the Diversity Index of Growth (DIG) and compare faunal diversity within a marine invertebrate database to documented physical and chemical changes of the environment. This is simply because the use of DIG enables a relative perspective of biotic change, therefore, sampling artifacts and mathematical biases induced by dataset size variation do

not greatly hamper these interpretations (Dean and McKinney, 2001). In spite of both incompleteness and the temporal imprecision of fossil data, I will show that the cumulative effect of regional processes has global significance. Furthermore, this study will illustrate the close relationship among tectonics, climate and biotic diversity change in the shallow water marine fauna of the Caribbean region.

Background

Tectonics

The tectonic history of the Caribbean plate is complex and not completely understood. Although numerous tectonic events of the geologic past have been documented and described in the region, there remains much uncertainty regarding aspects of plate formation and precise movement over the last 80 million years. The formation of the plate has two main competing theories. The first theory postulates an in situ rift development that resulted in basaltic production. The second theory views the Caribbean Plate as a remnant portion of the Farallon Plate (Sinton et al., 1998; Mann, 1999). Most investigations of the Caribbean tectonic history, however, are in general agreement that the relative motions of the Caribbean produce distinct tectonic regimes of accretion, (subduction and obduction), lateral motions relative to the North and South American Plates as well as extensional features. Further, the thicker-than-average oceanic crust defines the Caribbean Plateau and along with numerous, documented volcanic events suggests a region closely tied to volcanism. The Deep Sea Drilling Project (DSDP) and the Ocean Drilling Project (ODP) have not only sampled many of these ocean floor

basalts, but investigators have also radiometrically dated the timing and estimated the magnitude and duration of tectonic events of the Caribbean (Sigurdsson et al., 2000).

The two competing theories of Caribbean Plate formation both involve vast outpourings of basalt to form the thick 15–30 km basalt plateau (Sinton et al., 1998). Although the in situ model of formation suggests that this mechanism was the product of extensional thinning as the North and South American Plates moved apart between 130 and 80 ma (Mann, 1999), the second model proposes the formation of the Caribbean Plate as a product of Pacific crust drifting over the Galapagos hotspot (Sinton et al., 1998; Mann, 1999; Revillon, 2000) and moving east towards the present location over time. It is this latter model that is generally favored because some trace-element associations suggest an undepleted mantle source, such as the Galapagos hotspot (Sinton et al., 1998). Both models also incorporate the apparent fact that the creation of the Caribbean Plate was pulsed, and is the result of at least three distinct and voluminous outpourings of rock, beginning with flood basalts around 80 Ma (Sinton et. al, 1998; Revillon, 2000) which are attributed to mantle plume activity from the hotspot. Another pronounced event of basaltic extrusion occurred again at about 76 Ma, possibly plume-related or from extensional thinning (Revillon, 2000), with the last major event at about 55 Ma, which has been attributed to crustal extension and thinning (Revillon, 2000). Certainly, for temporal scope of this study, it is the last event that is of primary concern.

Accretion of island arcs is occurring on the eastern margin of the plate, through subduction of Atlantic Ocean crust and the formation of the volcanic Greater and Lesser

Antilles. On the western margin, obduction and subduction are occurring as oceanic crust of the Nazca and Cocos plates are being subducted under Central America. Sinistral lateral motion between the Caribbean Plate and both the North and South American Plates suggests relative eastward movement of the plate (Sinton et al., 1998; Mann, 1999; Revillon, 2000). This continuing process of tectonic activity is observed today and core samples from ODP leg 165 indicate that at least three major pulses of explosive volcanism during the last 55 Ma have occurred. These events have not only been documented, but age-dated, as well (Mann, 1999; Sigurdsson et al., 2000).

Although the exact interactive roles of tectonics, volcanism, sedimentation and climate have been extensively debated (Rampino et al., 1979; Molnar and England, 1990; Sigurdsson et al., 2000; Wallmann, 2001) the effects of CO₂ upon climate are generally accepted (Zachos et al., 2001). Considering the contributions of volcanism and tectonics upon the global carbon budget (Shellito et al., 2003) as well as water volume, through physical displacement and climate change (Summerhayes, 1986; Wallmann, 2001), the nature and timing of tectonic activity will be synthesized here and examined in context of climate, sea-level and biodiversity trends.

Climate and sea level

The general trend of Cenozoic climate indicates a shift from early Paleogene “Greenhouse” conditions (Bralower, 1997; Zachos et al., 2001) to later Neogene “Icehouse” regimes (Salamy and Zachos, 1999; Spezzaferri et al., 2002). Climate trends have been determined from numerous, independent sources including the marine and

terrestrial fossil record, physical geologic deposition, and geochemical signatures (Prothero, 1994; Bestland, 1999; Lear et al., 2000; Harrington, 2001; Retallack, 2001; Zachos et al., 2001; Crouch et al., 2003; Thomas et al., 2003). The early Cenozoic climate is supported by evidence indicating highstand seas during these warmer periods and lowstand seas during the cooler periods (Zachos et al., 2001; Wallmann, 2001). Oxygen isotope data measured from foraminifera are generally accepted as a proxy for sea temperature (Shellito et al., 2003; Zachos et al., 2001), and these are further interpreted as indicators of sea level (Spezzaferri et al., 2002), with highstand seas corresponding to a depleted $\delta^{18}\text{O}$ signature, and lowstands correlating with “heavier” values.

Changes in climate and ocean volume, whether tectonically induced or not, are thought to invoke major reorganization of ocean circulation patterns. Altering the transport of heat from equatorial regions to that of polar latitudes may have pronounced effects upon global climate regimes. Thus, even regional changes in bathymetry or ocean current patterns may have global significance (Thomas et al., 2003). Furthermore, climate response to tectonics may also be in the form of atmospheric chemistry change, as chemical weathering of uplifted and exposed rocks consumes CO_2 (Raymo and Ruddiman, 1992; Beck et al., 1995). Certainly, then, it follows that the additive effects of numerous regional changes may, indeed, produce a global response. Whether or not these processes are linked solely to tectonics or are controlled by other factors remains elusive, but it seems logical that the scale of study may dictate the interpreted result to some degree (Rahel, 1990) (see Chapter 4).

Major tectonic events of the Cenozoic that have been considered as forcing functions for climate include oceanic current change caused by the closure of the circum-equatorial Tethys seaway, first with the collision of India with Asia, then the closure of the Mediterranean Sea, and later with the formation of the isthmus of Panama (Harzhauser et al., 2002). Also pertinent to climate response is the episodic history of major volcanism (Rampino et al., 1979; Bralower et al., 1997; Sigurdsson et al., 2000) including not only that of the Caribbean province, but also from other regions such as the Columbia River Flood Basalts. Further tectonic influence may include the uplift and subduction along the Andean ranges (Rapela et al., 1988), Tibetan Plateau (Harzhauser et al., 2002) as well as inferred changes in both rifting and subduction rates (Rich et al., 1986). Response to these events has been correlated to the extensive development of polar ice sheets in the Late Paleogene to Neogene, which may have exacerbated climate change further by lowering sea levels as well as by increasing earth's albedo. The net result is a complex web of feedback mechanisms that potentially affect not only climate, but each other as well (Wallmann, 2001). Regardless, tectonically-induced changes in environmental regimes should result in biotic change that ultimately is captured by the fossil record (Rich et al., 1986).

Biotic trends

The response of the biosphere to Cenozoic environmental changes has been observed and described not only in the Caribbean, but globally as well. Many of these biotic events have been interpreted as direct products of climate change and sea level variation (Smith

et al., 2001). Diversity changes in Caribbean marine invertebrate taxonomic structure have been observed and described previously (Chapt. 2). These changes in diversity correspond closely to inferred changes in sea-level, as interpreted from oxygen isotope data. Independent research with the fossil record also depicts faunal turnover occurring at critical moments of both climate and sea-level changes, ranging from major events such as the Paleocene-Eocene Thermal Maximum (PETM) to finer-scale studies documenting glacio-eustatic changes of the Plio-Pleistocene (Prothero, 1994; Johnson et al., 1995; Bralower et al., 1997; Sigurdsson et al., 2000; Johnson, 2001; Spezzaferri et al., 2002; Klaus and Budd, 2003).

Evidence suggesting that global-scale events dominate the Caribbean fossil record lies within several independent sets of data. First, as has been shown previously, the Caribbean fossil data used in this study follow established, global trends (Chapt. 2). These trends indicate that an increase in global biotic diversification follows warmer, highstand seas (Dean and McKinney, 2001) and, in fact, those same trends are followed by the Caribbean dataset used here. Second, the timing of the sea-level changes corresponds to biotic events in the terrestrial realm (Rull, 2001; Zachos et al., 2001), such as the expansion of temperate grasslands or the advent of marine mammals (Prothero, 1994; Retallack, 2001). The close temporal proximity of terrestrial events to oceanic biotic events suggests the marine response is connected with global climate regimes. Furthermore, biotic reorganization of marine fauna is observed in distinct ocean basins and occurs at the same critical boundaries in time (Siesser, 1995; Salamy and Zachos,

1999). A summary of Cenozoic biotic, climatic and tectonic events of the both the Caribbean and whole earth is presented in Figure 11.

Materials and Methods

In this study, the trends of biotic diversification within the Cenozoic Caribbean region (as defined in chapter 2) will be examined utilizing the compilation of biostratigraphic ranges (Appendix 1). The dynamics of the database will be examined in terms of relative change utilizing the Diversity Index of Growth (DIG) metric discussed earlier (Chapt. 2). These trends will be compared to existing data from tectonic, climate and biotic research in order to ascertain the physical controls on biodiversity.

Results

Biotic response

The Caribbean dataset reflects biodiversity trends in relative agreement with both global oxygen and carbon isotope curves (Fig. 7). The biodiversity curves, in turn, compare reasonably well with Tertiary sea-level curves (Fig. 8a) that have been developed from sequence stratigraphy (Summerhayes, 1986; Prothero, 1994). This agreement between sea-level and DIG becomes much more apparent when sea-level variation is depicted at the same level of temporal resolution as biodiversity (Fig. 8b), and improves further when viewed as relative change (Fig. 8c). The data here suggest a relationship between inferred biotic diversity increase and sea-level increase.

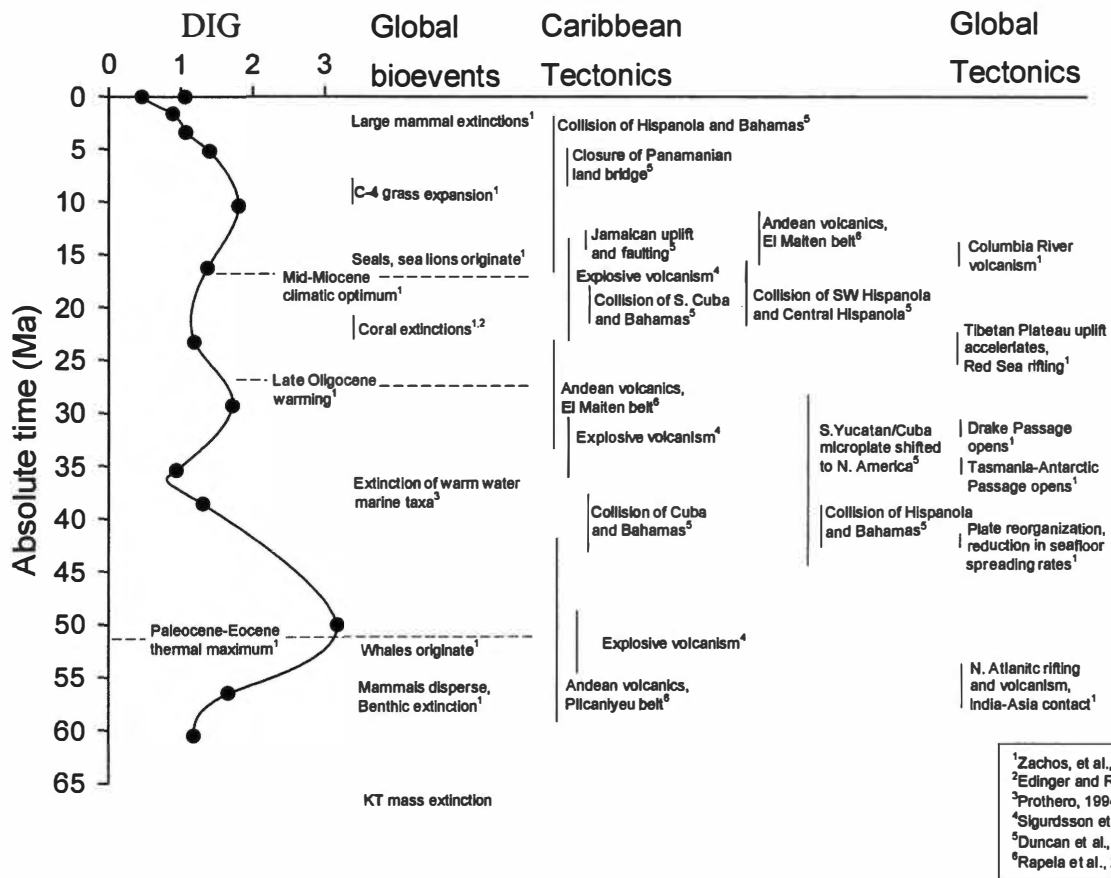


Figure 11. Relative biodiversity trends and major biotic, tectonic, and physical events that proximally cluster about the three DIG peaks. Sources cited within the figure.

As a first test of the control of sea-level upon biodiversity, a comparison between the DIG values of deep-water (> 60 m) and shallow-water (< 60 m) fauna is made. Whereas many definitions of deep- versus shallow-water exist, that of Lissner and others (1991) is pertinent to this study because their definition separates the more shallow reef-corals from the deeper-dwelling solitary (ahermatypic) corals, which are evaluated here. In addition, the study of Lissner and others (1991) indicates that this definition produces two distinct guilds of fauna that respond and recover from disturbances quite differently. By separating the deep-water fauna (ahermatypic corals; deep-water echinoids) from shallow-water fauna (hermatypic corals; some mollusks) in this dataset, we find that the DIG curve of the total Caribbean marine genera versus that of the shallow-water fauna is congruent (Fig. 12).

There are two, non-mutually exclusive possibilities for this observation. First, the majority of the data are shallow-water fauna. This is a reasonable assumption because the four clades followed for this study, namely, corals, gastropods, bivalves and echinoids (Fig. 13) are generally limited to relatively shallow-water settings. This has, in part, both physical and ecologic reasons. The ecosystem of hermatypic, reef-building corals is within the photic zone. Because reefs are focal points of the shallow-marine seascape, they attract a variety of diverse biota (Wood, 2001). As wave breaks, reefs also control nearshore (backreef) environments by decreasing water energy. Thus, the associated biota of coral ecosystems would also have the same general environmental needs as corals because the existence of reef structures play such a pivotal role. Furthermore,

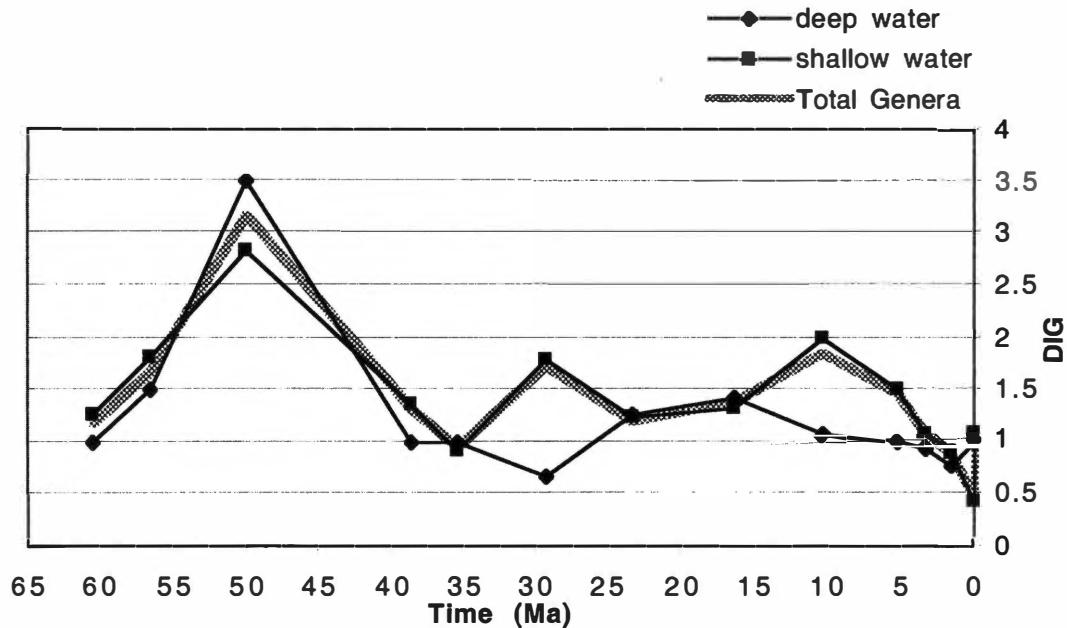


Figure 12. DIG values showing the differential trends of deep water versus shallow water fauna. Total genera DIG is presented with shaded line, shallow water genera represented by squares; deep-water by diamonds. Shallow water fauna, even as a subset of total data, closely follows the total DIG trend. This indicates that DIG may be a useful proxy for sea-level studies.

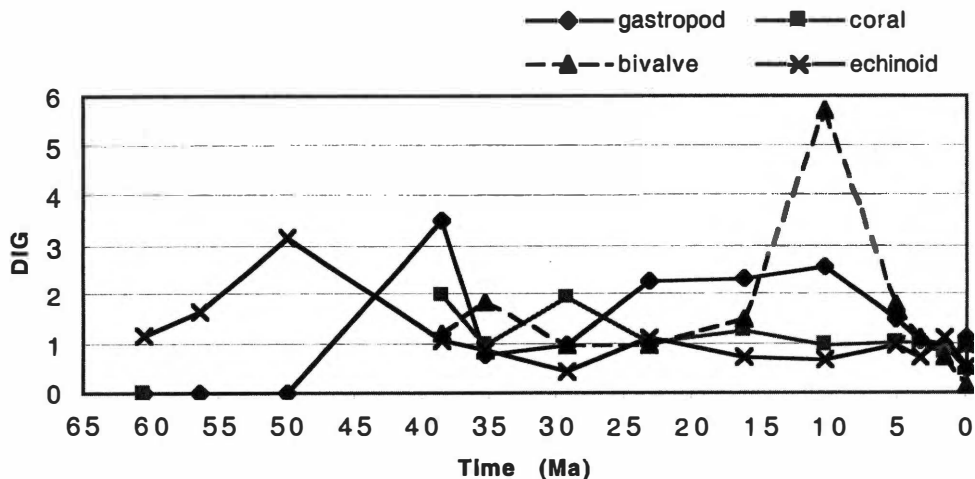


Figure 13. The various taxonomic groups are presented individually with their respective biodiversity trends. Gastropods are denoted by diamonds, corals by squares, bivalves by triangles and echinoids by +’s. The separate taxonomic groups follow different trends (discussed in text), which demonstrate that DIG values can be used to investigate biological trends, as well as facies trends (Fig. 12).

most marine productivity is focused in the shallow-water realm, where not only sunlight but nutrients, detritus and other organic material are abundant. Also, the shallow, warm marine waters are favorable for the secretion of calcium carbonate skeletons due to the decreased CaCO_3 solubility with increasing temperature. The effect of corals as a keystone fauna (Wood, 2001) is best depicted here in Figure 13, where only after the diversification of Caribbean coral genera at 35 – 29 Ma do the associated clades of bivalves and gastropods begin their diversification (Edinger and Risk, 1994). This is a logical result because most of these mollusks depend upon reef structures, indirectly or directly, as a nutrient source and to alter local water regimes. This not only provides the necessary habitat and substrate, but also attracts a variety of diverse organisms ranging from primary producers to higher trophic-level vertebrates.

The second possibility for the close relationship between the shallow-water fauna being closely linked to the total DIG signal is the likelihood that a preservational bias of shallow-water facies exists (Holland, 1995; Smith et al., 2001). Assuming that the DIG increases correspond to higher sea-level, and that many of the deposits are well inland of the present marine boundaries, then it is possible that major transgressions merely emplace rocks and their fossils in more favorable areas for study (Smith et al., 2001). This would exclude the deep-water facies and the associated rocks and fossils from the same degree of sampling as the shallow-water facies (Holland, 1995), which may explain the diversity decrease of deep-water (> 60 meters) fauna at around 30-35 Ma, and again at around 15 Ma (Fig 12). It is plausible, however, that much more information of deep-

water biota remains undiscovered in inundated areas unfavorable for study (Holland, 1995) or that inland deposits of deepwater facies have been eroded (Smith et al., 1999). The two possibilities presented explaining the close relationship between shallow-water fauna and the dynamics of the total database are not necessarily discrete, nor does the second one render fossil data unusable, especially for studies of sea-level and climate response. This is because climate, sea-level, and facies are linked. These factors subsequently converge to determine the extent and distribution of favorable ecologic habitat for marine invertebrates.

Although there is close agreement between shallow-water DIG and total genera DIG (Fig. 12), the biodiversity of the four taxonomic groups (Fig. 13) do not follow the exact trends as one another. Whereas this may be due, in part, to variables such as differential taphonomy or facies preference, as discussed above, answers may also lie within changes in bathymetry and ocean currents. This would not only affect larval dispersal patterns, but nutrient flux as well. The results of Figure 13 are consistent with previous interpretations of Caribbean corals that suggest biodiversity of reef-forming corals was greatest in the middle Oligocene (about 29 Ma), with declines in the Lower Miocene (23 Ma) and during the Plio-Pleistocene (Johnson, 2001; Edinger and Risk, 1994).

Trends of the other clades depicted in Figure 13 are also consistent with previous, independent research. Echinoids are shown here experiencing maximum relative diversification by the end Paleocene – early Eocene (55-50 Ma), with major diversity declines in the early Oligocene, the Miocene, and the Pliocene. This has been observed

in Tethyan echinoid biostratigraphy which also follows the same trends in terms of diversity changes and timing (McKinney and Oyen, 1989; McKinney et al., 1992). Gastropod diversity has also been interpreted similarly to trends depicted in Figure 13, with diversity increases during the Middle Eocene and Miocene (Roy, 1996; Harzhauser et al., 2002). Both authors attribute the diversity changes to the closure of the circum-equatorial Tethyan Region, beginning in the Eocene with the collision of the Indian subcontinent with Asia, and ending with the final closure of Panama at 3 Ma. The net effect of this closure would have been the fragmentation of larval dispersal pathways via planktonic vectors and the rise of regional endemism, which would produce new species. Indeed, it has been demonstrated that corals, gastropods and bivalves have had increasingly dissimilar affinities from Indo-Pacific stock from the Eocene to present (Edinger and Risk, 1994; Scheltema, 1995; Marko and Jackson, 2001; Harzhauser et al., 2002). Furthermore, bathymetric and ocean current change would have dramatic effects upon upwelling and nutrient flux, which could explain the differences between the timing of coral biodiversity response and the other three clades (Fig. 13).

Changes in upwelling and nutrient availability have an inverse response between corals and mollusks (Edinger and Risk, 1994). The gastropods and bivalves favor the nutrient-rich upwelling areas, whereas hermatypic corals, due to the presence photosymbiotic zooxanthellae, do not have this requirement. In fact, reef corals are at risk in nutrient-rich areas that promote detrimental algal encrustation on the reef structures (Aronson and Precht, 1997). Extensive phosphorite deposits of Miocene age have been documented in Florida, Cuba, Jamaica and Venezuela, which suggest upwelling off these coastlines

(Edinger and Risk, 1994). The timing of these deposits correspond to both coral diversity decrease and mollusk diversity increase (Fig. 13).

Tectonic relationships

Of particular interest to the present study is the episodic explosive volcanism in the Caribbean during the last 60 million years (Bralower et al., 1997; Sigurdsson et al., 2000). Leg 165 of the Ocean Drilling Program (ODP) obtained Caribbean seafloor cores containing distinct horizons of tephra deposits (Sigurdsson et al., 2000). The combined ash accumulation rates for two of these cores (998 & 999) are shown in Figures 14 and 15. This pronounced episodic volcanism does, in fact, compare reasonably well with the timing of DIG values, sea level and isotope curves (Fig. 7) presented in this paper. The source of volcanic ash recovered from the ODP cores is thought to be from the Chortis Block in Central America, and from the Sierra Madre Occidental province in Mexico, which contains the largest ignimbrite province in the world (Sigurdsson et al., 2000). Both of these potential source areas produced silicic material consistent with the material recovered in these ash layers. Furthermore, the timing of volcanic events in Central America and Mexico are contemporaneous with the age of the ash layers in these ODP cores. Additionally, each of the volcanic ash “peaks” roughly coincides with Pacific plate reorganization, in terms of direction or rate of movement (Sigurdsson et al., 2000). It is interesting to note that in both instances of sea-level or biodiversity increase (Figs. 14, 15) the onset of volcanism precedes the presumed sea-level or biodiversity response.

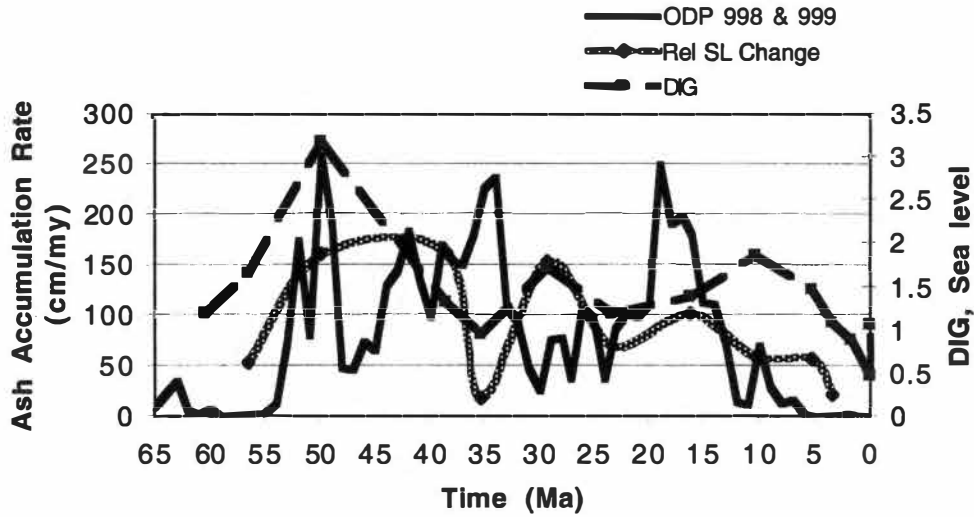


Figure 14. Total genera biodiversity compared with explosive volcanic ash collected from ODP cores, Leg 165. Volcanic rates are interpreted from increased accumulation of ash. Two cores (sites 998 and 999) are presented here, together, due to the lack of continuous signal at any one site. Volcanism is seen preceding biodiversity increases and relative sea-level change (Fig 8c), which may indicate tectonic control. (ODP data from Sigurdsson, et al. (2000)).

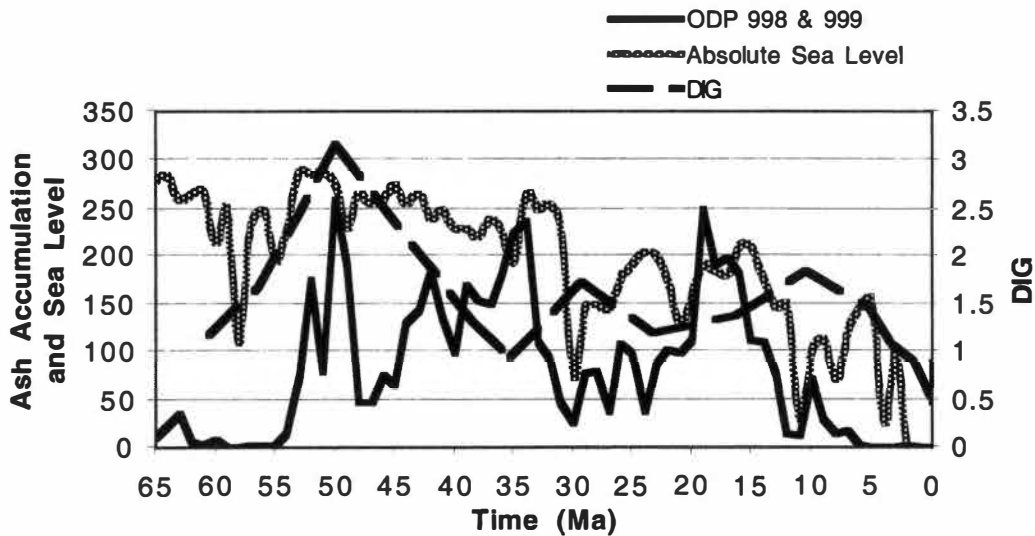


Figure 15. Ash fall rate compared to total DIG and sea-level. Ash fall data is the same from Fig. 14; absolute sea-level is the same as Fig. 8a. As with Fig 14, ash fall peaks precede sea-level increases and suggest tectonic control.

Although the ash accumulation data and Caribbean biostratigraphic data are both from the same region, it is necessary to reemphasize that the Caribbean DIG values seem to be following trends of a global, rather than regional scale (Chapt. 2). The close agreement, then, between regional tectonics and global dynamics would suggest a connection between Caribbean tectonism and global activity. The three major volcanic “peaks” seen in the ODP data (Figs. 14, 15) roughly coincide globally with notable tectonic activity. Furthermore, other global tectonic events of the Tertiary occur within the general timing of both the peak ash deposits and DIG increases (Fig. 11). These include the collision of the Indian subcontinent with Asia, beginning around 55 Ma (Harzhauser et al., 2002) and with the acceleration of thrusting and uplift at about 22 - 17 Ma (Raymo, 1994). Columbia River flood basalts also occurred near the most recent “peak” at about 15 Ma (Zachos et al., 2001). Work by Rapela and others (1988) documents three peaks of Andean volcanism (60-42 Ma; 33-23 Ma, and 16 –11 Ma) as subduction of the Pacific Plate under that of the South American Plate proceeded, apparently, in pulses. Sigurdsson and others (2000) further contribute to this list citing evidence for explosive volcanism in Central America from 45 –40 Ma and again at 35 –27 Ma. These authors also note that around 22 Ma, the East Pacific rise was subducted beneath the North American Plate, and other major Pacific Plate dynamics were occurring as the Farallon Plate was split into the Nazca and Cocos Plates. Indeed, large-scale tectonic activity is proximally focused near the timing of both presumed sea-level and biodiversity change (Rich et al., 1986) and is responsible for the interruption and closure of the circum-equatorial Tethys Sea (Harzhauser et al., 2002).

Discussion

The Caribbean biostratigraphic data presented here suggest a connection between apparent biodiversity, tectonics and sea-level. The relative agreement between tectonic events and biodiversity (Fig 11), as well as with sea-level (Figs. 14, 15) indicate that, at the very least, these processes operate in concert (Rich et al., 1986). And although correlation does not necessarily imply causation, it is tempting to speculate that indeed, tectonics may impart major control on sea-level, bathymetry and climate (Raymo and Ruddiman, 1992; Bralower et al., 1997; Sigurdsson et al., 2000; Zachos et al., 2001; Thomas et al., 2003), and thus biodiversity trends (Rich et al., 1986; Rampino and Caldeira, 1993). This control upon sea-level may be two-fold, i.e., as a direct displacement of water from sea-floor spreading as well as from climate change induced by volcanic gases. The link between tectonics, climate and sea-level has long been pondered (Chamberlin, 1899; Raymo, 1994; Bralower et al., 1997; Sigurdsson et al., 2000; Zachos et al., 2001). Although the relationships between tectonism and sea-level or climate and sea-level are generally accepted (Summerhayes, 1986; Wallman, 2001), separating the cause and effect between climate and tectonics (Bralower, 1997) has proven elusive, with the lack of temporal precision dampening these efforts. Whereas absolute values from paleontologic data have been applied as a means to unravel this quandary, the lack of robust temporal resolution, or the focus upon small-scale regions or lower taxonomic groups, hinders interpretations of large-scale processes. The use of a cross-taxonomic database examining relative taxonomic change, free from artifacts induced by absolute values (Dean and McKinney, 2001), begins to address this issue.

Biodiversity and sea-level

The biotic diversity increase observed during transgressions (Fig. 8) may be both real and apparent. It seems reasonable to expect more favorable habitats for shallow-marine organisms during transgressions that flood terrestrial surfaces (Holland, 1995; Smith et al., 2001). As postulated earlier (Chapter 2), it is quite logical to expect that biotic expansion occurs during highstand seas because new niches are available for exploitation, and that topographic variation of the former landscape may lead to fragmentation and isolation of populations. This, in turn, should favor speciation and observed taxonomic diversity growth, as has been observed in Mesozoic echinoids (Neraudeau et al., 1997) and Tertiary molluscs of New Zealand (Crampton et al., 2003). Furthermore, such fragmentation may be possible with minor fluctuations of a higher sea, which would accomplish the same effect of habitat partitioning. Reorganization of ocean currents and bathymetry, caused by tectonic processes, seems to have a major effect upon marine biodiversity trends, and in fact, previous studies have produced significant correlation coefficients between seafloor spreading rates and biodiversity (Rich et al., 1986). The excellent agreement between DIG values of the four clades (Fig. 13) with numerous independent investigations (discussed earlier) indicates that the interpreted biotic trends of diversity growth and decline are reasonable, if not accurate. Thus, biodiversity increase during these critical environmental times may, indeed, be real, in spite of preservational completeness caused by high-stand deposition (Holland, 1995, Smith et al., 2001).

As shown previously (Dean and McKinney, 2001), changes in absolute values of taxonomic occurrences are not equivalent to the relative changes in taxonomic diversity. Therefore, even if more numerous fossil occurrences are found in these highstand rock units, it is only the relative change of the dataset that affects DIG values. Of more importance, then, is the apparent relationship between DIG and sea-level, in general (Figs. 8, 14, 15). Even if DIG does not accurately reflect biodiversity trends, then, at the very least, highstand facies seem to be followed by this metric. Thus, the application of relative biostratigraphic change, specifically DIG, is quite relevant to studies addressing sea-level variation and the processes that control it. And, it would be quite difficult to interpret a geologic time-series of marine biotic dynamics without considering the effects of relative sea-level upon the distribution and density of fossils.

Controls on sea-level

Changes in sea level are generally linked to two mechanisms: climate and tectonics (Summerhayes, 1986). Most interpretations of oxygen isotope data link “lighter” values of $\delta^{18}\text{O}$ to warmer climates (Wallmann, 2001; Zachos et al., 2001). Furthermore, many workers interpret the resultant “curves” as indicators of sea level (Spezzaferri et al., 2002). Combined with the general acceptance of $\delta^{18}\text{O}$ data as a proxy for temperature is the role of tectonism affecting both climate and water volume (Summerhayes, 1986). Not only does the creation of new crust at mid ocean ridges produce topographic highs on the seafloor, but, the “fresh” new crust is volumetrically greater than older, cooler oceanic crust. Both of these mechanisms are thought to displace ocean water, thereby causing eustatic variations in sea-level.

The volatiles released from volcanic eruptions, especially CO₂, are considered to be primary greenhouse gases (Bralower et al., 1997; Zachos et al., 2001). Thus, tectonic events can both directly cause sea-level increases as well as affect climate, which in turn, may produce transgressions due to warmer conditions and regressions via glaciation. Further adding to the complexity are feedback cycles between weathering and climate. Weathering and erosion of continental crust, with subsequent deposition into basins, can displace ocean water, thus causing sea-level increases. Basinal subsidence, however, can negate this effect and can actually cause an observed sea-level fall (Summerhayes et al., 1986). Chemical weathering of exposed igneous rock may result in consumption of atmospheric CO₂, and hence cooling and possible glaciation, also leading to sea-level fall. Adding to this, some workers have also invoked weathering and deposition as a control on tectonics, through both the influence of subsiding basins as well as increasing the amount of material subducted (Sigurdsson et al., 2000). Regardless, various major tectonic events correlate with both biodiversity trends and climate proxies (Rich et al., 1986; Rampino and Caldeira, 1993). Although we are often at odds with a “chicken and egg” scenario between the cause and effect of weathering, climate and tectonics (Molnar and England, 1990) emerging geochemical evidence suggests that tectonic activity may actually precede sedimentary response, which supports the position taken here.

A recent high-resolution study of neodymium isotopes in fossil fish teeth from global ODP cores covering the Paleocene-Eocene Thermal Maximum (PETM) interval (Thomas et al., 2003) indicates that radiogenic values are highest in their Caribbean core (Leg 165,

Site 1001). Not only is the isotope value much more radiogenically enriched than corresponding Pacific Crust values, but such enrichment also indicates a weathering source of young volcanic rock (Thomas et al., 2003). Because their study was high-resolution they were able to show an initial enriched value that within several thousand years becomes less enriched and similar in isotopic value to the Pacific cores. Due to the short residence and mixing times of Nd in ocean systems (Thomas et al., 2003), their data therefore suggest that volcanism preceded the weathering of continental crust. The result of their study is in complete agreement with data used here indicating large-scale volcanic activity from the same location, and at the same point in time (Sigurdsson et al., 2000). The data shown in this paper (Figs. 14, 15) also indicate that Caribbean volcanism preceded both sea-level increase as well as biodiversity increase. Further, carbon isotope values measured from ODP core 1001 indicate a negative $\delta^{13}\text{C}$ excursion that tracks the shift between enriched Nd and less enriched values (Thomas et al., 2003). This corresponds with interpretations of increased marine productivity as a biotic response to the PETM (Siesser, 1995; Zachos et al., 2001). When one considers that the DIG values calculated for this present work also show a marked diversity increase during the PETM, then it seems reasonable to interpret tectonics as the control on climate, and on sea-level, either directly, or indirectly through climate effects. Thus, given these biodiversity increases that follow tectonics, we can interpret tectonics as a primary control on biodiversification, at the scale of observation used here. This is through sea-level and bathymetric change, as has been discussed previously, and perhaps, through the input of nutrient-rich material from volcanism, as well as that from the chemical weathering of terrestrial rocks (Salamy and Zachos, 1999; Crouch et al., 2003).

Terrestrial response and climate

The link between tectonics, climate and sea-level has to be considered because the terrestrial biosphere was affected at the same critical points in time as the marine biosphere. The biotic response to the PETM is also evident with data of land mammals (Harrington, 2001) and tropical vegetation (Rull, 2000; Jaramillo, 2002) that show marked diversity increase at 55 Ma. The expansion of temperate grasslands is also temporally related to DIG biodiversity increases in the Miocene (Retallack, 2001; Zachos et al., 2001). Geochemical evidence for terrestrial response in terms of increased chemical weathering during the PETM has been demonstrated (Salamy and Zachos, 1999). Highly-weathered paleosols at the PETM boundary, grade into less-weathered paleosols at the Eocene-Oligocene boundary, presumably as a result of warmer, more humid climate regime changing to cooler and drier conditions (Bestland, 2000). This effect is apparent in the DIG curve that depicts a corresponding marine biodiversity increase and then decline from the Paleocene to Oligocene. Ocean chemistry response may add more support for this argument. The increasing silica content of the ocean at the PETM (Crouch et al., 2003) and towards Eocene-Oligocene boundary (Salamy and Zachos, 1999) has been interpreted as a marine response to continental weathering during warmer, wetter climates (Prothero, 1994).

Relevance to modern problems

An important implication from this study pertains to the current release of greenhouse gases into the atmosphere by anthropogenic activities. Estimates from geochemical

relationships of paleosols (Bestland, 2000) as well as from paleoclimate models (Shellito et al., 2003) indicate a higher concentration of CO₂ in the atmosphere during the PETM (up to 2000 ppm), than at present. Modern data suggest a rise of atmospheric CO₂ concentration from a pre-industrial level about 170 ppm to the current 360 ppm. Such rapid input of carbon over two hundred years is within the same order of magnitude of presumed increases at the PETM, which was only 220 thousand years in duration (Zachos et al., 2001; Thomas et al., 2003). Although it has been debated as to whether volcanic CO₂ is the sole greenhouse gas of concern at the PETM, or if rising marine temperatures released methane hydrates (Bralower et al., 1997) thus magnifying this effect, the data here suggest tectonics as the primary control of climate. It must be acknowledged, however, that many feedback cycles of weathering and consumption of CO₂, along with the ability of rocks, oceans and biota to sequester carbon, can obscure interpretations of cause and effect. Regardless, the dramatic response of marine and terrestrial biota to a short-lived climate excursion caused by rapid inputs of greenhouse gases to the atmosphere should be a primary concern.

Sedimentological constraints

A major issue regarding the interpretation of not only biodiversity, but of other signals from the stratigraphic record, is the dependence upon sedimentation. A point of caution raised by Sigurdsson and others (2000) reminds us that changes in climate may lead to changes in sedimentation rates and depositional area. Certainly, although it is readily apparent that weather patterns can have direct effects upon ash fall, this admonition is quite analogous to arguments discussed above concerning highstand preservational and

sampling artifacts of fossil data (Holland, 1995; Smith et al., 2001). Thus, what should be interpreted from these caveats is that many of our “signals”, be they geochemical, biotic or physical, are potentially controlled by the same processes we often wish to track: namely, climate and sea-level. The position of this paper is that DIG does indeed capture biodiversity trends, especially because the results of this study are in excellent agreement with previous work. But the similarity of the magnitude and timing of DIG, sea-level and isotopic curves raises two possibilities: 1) the data are correct and unbiased, or, 2) the sedimentary record is consistently biased by some uniform process. If the latter is true, then focus should be placed upon understanding why these signals are so temporally similar in an attempt to determine how tectonics, weather, climate and depositional variables affect geologic data.

Conclusions

Critical moments of Caribbean marine biodiversity increase or decline in the rock record graphically correlate with major global geologic processes. Whereas marine biodiversity growth seems to track sea-level, it also follows temporal trends observed in the terrestrial biosphere. The geological data retrieved from palynology, paleosols, and land fauna suggest that climate change may be the main control of terrestrial biodiversity. Whether or not climate change affects sea-level, or vice versa, remains debatable, but terrestrial weathering signatures and deposition of weathering product into the oceans seem to follow not only sea-level increase, but also, major episodes of tectonic activity. This suggests that climate is influenced by tectonic activity, and both, in turn, may have significant impact upon sea-level. Tectonic control on climate may be through direct

effects upon sea-level, or the creation of landmass that then alters oceanic and atmospheric currents and weather patterns. Volcanic degassing is likely a major contributor of CO₂ to the atmosphere, and subsequent warming may promote the release of other greenhouse gas sinks.

The net result is that marine biota respond to dramatic sea-level shifts, which ultimately are related to climate and tectonics. Relative biodiversity increases of total Caribbean marine genera are observed around 55 Ma, 30 Ma and 12 Ma. Furthermore, the biotic increases presented here follow similar peaks of both tectonic activity and sea-level rise. The DIG signal of the independent clades of echinoids, corals, gastropods and bivalves follows established trends. Although it is easy to view the marine biotic response as having been caused by major changes in relative sea-level, it is more difficult to reconcile eustatic variation as a control on continents. This is unless drastic reorganization of marine circulation patterns during transgressions controls climate or, that climate, as a response to tectonics, affects sea-level.

We can never escape the fact that sedimentary processes ultimately control the distribution of all sedimentary rocks, the observed fossil distribution, as well as the geochemical signatures of rocks and fossils. In turn, sedimentary processes are controlled by climate which affects both atmospheric and oceanic chemistry, along with circulation patterns. Even if DIG does not capture true biodiversity trends, this would be due to depositional controls affecting the quality of the rock and fossil record. It is important to note, then, that the same problems of uneven distribution that plague the

fossil record also affect any of the information (geochemical, etc.) recovered from the rock record. But, because it has been shown that the DIG values closely follow sea-level, then the signal we receive, if not one of biodiversity, is one of facies. Depending upon the scope of study, such information may prove equally viable. For what we ultimately see, then, is a signal from the rocks. Considering that the timing and magnitude of the DIG signal is consistent with vastly independent tectonic and isotopic data, as well as sea-level response, then, at the very least, the inferred signal remains as evidence of sea-level variation and may possibly be useful for sequence stratigraphy applications.

CHAPTER 4: UNDER THE INFLUENCE OF HIERARCHY AND SCALE

Abstract

The effects of taxonomic hierarchies and variant temporal and spatial scale are examined using a database of Caribbean Cenozoic marine invertebrates. The database was compiled from coral, echinoid, bivalve and gastropod fossil citations at the genus- and species-levels. Three additional sets of data were used to demonstrate the effect of temporal and spatial scales upon interpretations of biodiversity changes. Biotic trends of genus-level and species-level did not consistently cascade through taxonomic hierarchy, which is most likely indicative of differential preservation, collection, and description of fossils between the various groups. The effect of varying the length of time-intervals is tested by calculating biodiversity over different time increments. Variations in time length were observed to alter the biodiversity signals interpreted from the fossil record. Because the fossil record is characterized by uneven time-series, our work has demonstrated that much information gleaned from the fossil record may be affected by this inequity. The effects of spatial scale are demonstrated by comparing biotic trends within several local- to sub-regional scale datasets. All of these comparisons indicate that fine-scale (spatial, temporal, and hierarchical) data cannot be easily correlated with coarse-scale data. This has major implications for determining the cause-and-effect between physical processes and biotic response because quite often, the data derived and the data compared are at vastly different scales of resolution. This not only leads to variations in interpretations, but also impedes rigorous statistical correlations of data.

The variation between interpretations of data can be resolved if we understand that any interpretation is scale-dependent, and that different interpretations from the same dataset may be a result of this dependence upon scale. Effective correlations of data to presumed forcing functions can only be realized if there is a temporal equivalence of time intervals in a time-series analysis. Furthermore, the spatial extent of data is subject to the same limitations, therefore similar spatial resolution should be used during comparisons of multiple data sets. To help better understand the valid spatial-temporal extent of biostratigraphic and geologic data, a new metric was used. The Sensitivity of Data (SOD) quantifies the temporal range, spatial extent, number of data and the number of observation points to assign a value. SOD numbers have proved useful for comparing spatial-temporal scale data, determining which forcing function to use for valid correlations, and also for evaluating interpretations drawn from geologic databases.

Introduction

Issues of scale and resolution are critical factors that influence any interpretation from the rock and fossil record. This is especially true when comparing time-series data of entirely different physical processes to biotic diversity trends. The resolution between when the interpreted data (fossils) are initially deposited, and subsequently recovered, is at different levels of precision in both time and space. Global biostratigraphic data are often reported as “ranges” of biotic existence over geologic time, which usually are then grouped into epoch- to stage-level time increments (Table 1). Because these increments may be on the order of several million years in duration, the precision of biostratigraphic data often falls very short of trends from other physical processes, such as those of

isotopic data that have been generated from deep-sea cores, which may have a precision of several-thousand year increments or less. Trends of data that vary in temporal resolution are difficult to compare and correlate, much less rigorously test with statistics.

A major impediment that further affects geologic time-series data is the trend towards increasingly smaller packages of geologic time as we approach the present (Raup, 1972, 1976). This variation in resolution over time produces a time-series of intervals that are not temporally equivalent to one another, over the given range. This also impedes statistical testing because there is no control on maintaining a constant time increment by which we can evaluate change between intervals. Statistical confidence is only valid if standardized sampling is achieved (Jackson and Johnson, 2001). Because the fossil record is unbalanced with regard to fossil occurrences (Foote and Sepkoski, 1999; Alroy et al., 2001), and the intervals of time units are uneven, it is understandable that much controversy surrounds interpretations of cause and effect of biodiversity trends.

The influence of spatial scale adds further disparity to scientific understanding of physical and biological processes over time. Biostratigraphic information of fossil occurrences is, at the very least, a record of the local- to regional- scale existence of a particular organism in time (Willig, 2003). The extension of such small spatial-scale information to global compilations of biostratigraphic ranges can influence the inferred relevance of a particular group of organisms, or produce a temporal lag in the resulting biotic response with respect to the timing of some inferred environmental factor.

Furthermore, the idea of a “global” signal is often only the result of the homogenization

of many smaller spatial scales into a singular large-scale signal (Willig, 2003). Whereas comparisons among many regional-scale processes may provide insight towards biotic response to environmental change, it must be recognized, however, that the precision of our interpretations is diminished with increasing scales of observation. Thus, because of decreased observational resolution, the trends observed in “deeper” geologic time are more likely to resemble some perceived global signal versus those gleaned from “near” time.

The same problems of precision loss with expanded spatio-temporal scale can be extended to the levels of hierarchy imposed upon both fossils and the geologic record. Taxonomic groupings of organisms are a necessity when attempting to understand the relationship of biota to each other. But, large-scale observations of family- or class-level biodiversity trends (e.g., Benton, 1995) do not have the resolution to rigorously determine causal mechanisms (Badgley, 2003) of extinction events, for example, as would species- or genus-level, unless the causes are large in effect and globally synchronous. Furthermore, some of the inferred environmental factors that may affect marine biodiversity, such as sea-level variation, are also nested in hierarchical levels (Summerhayes, 1986). The observation that sea-level variation can be reduced to first-, second-, third-, fourth-order (etc.) sequences may be useful for understanding the various mechanisms affecting ocean volume. But again, the actual physical record of these changes is deposited within the scale of individual basins, which respond to local factors. In fact, the main differences between the higher-level, first- and second-order sequences and the lower third-, fourth-, fifth-order transgressive/regressive packages lie within the

areal extent of flooding and hence, the presumed mechanisms that cause this change (Plint et al., 1992). Generally, this refers to the scale of influence of the mechanisms that becomes progressively finer as we approach the present. However, this too is also a product of temporal resolution: fine-scale study produces fine-scale trends in both time and space.

Although scaling issues are critical to our understanding of biotic response to environmental factors that affect biodiversity, they do not necessarily render biostratigraphic information, whether local, regional, or global, useless (Alroy, 2003; Vermeji and Leighton, 2003). Rather, these scaling issues only set limits to the precision of the answers we seek (Rahel, 1990; Pandolfi, 2001). Global-scale biodiversity trends can only indicate large-scale physical processes or, perhaps, catastrophic events. Low-resolution biostratigraphic data, then, will likely never be highly correlated with fine-scale resolution data. At first glance this dilemma may seem to challenge the validity of biodiversity studies. But, in actuality, what this ultimately suggests then is that the precision of inquiry should be focused in order to ascertain the proper level of information realistically available (Badgley, 2003). Furthermore, issues of scale mandate an increased precision of how we report interpretations and their subsequent meaning in time and space. For example, grandiose interpretations of biotic evolution drawn from one taxon over a narrow time span or limited area (e.g., Gould's Bermudan land snails and punctuated equilibrium v. gradualism) cannot be extended to the entirety of the biosphere over the whole of the Phanerozoic. And neither can the interpretation of the mechanism of one mass extinction (e.g. the end-Cretaceous bolide impact) be extended to

another. Because we cannot change the precision of geologic data, we need to cautiously report not only the trends we see in our data, but indicate the spatial and temporal extent over which these interpretations are valid.

The purpose of this paper is to demonstrate the complex relationship of resolution and scaling issues to biostratigraphic data. I will compare several sets of marine invertebrate fossil data of the Cenozoic Caribbean to published sea-level and isotopic curves to show the influence of taxonomic, temporal and spatial-scale variation. Additionally, I will propose a method by which biostratigraphic databases can be compared and evaluated in an effort to determine their significance.

Background

A critical assumption of paleo-biodiversity studies is that they capture evolutionary trends (Vermeji and Leighton, 2003). Whether at the local, regional or global scale, biostratigraphic databases and their subsequent analyses attempt to depict diversity changes of organisms, usually over time. But, it must be emphasized, evolution proceeds at much smaller time scales than the biostratigraphic data can usually resolve. Although we can observe many spatial scales of biostratigraphic information, ranging from a single well-log to global compilations, evolution occurs at the population scale. Further, most biostratigraphic data exists, perhaps as genus- to family-level occurrences (e.g. Sepkoski, 1981; Benton, 1995), but evolutionary change proceeds strictly at the species-level (Benton, 2001).

Biodiversity, however, is driven by more than micro-evolutionary change of organisms. Physical geologic processes serve as forcing functions to disrupt and alter the composition of biota through environmental change and thus, extinction and speciation of taxa. The scale-dependent disparities between our data and the processes we attempt to understand (Levin, 1992) have caused recent controversy regarding the value of biostratigraphic macro-evolutionary study (e.g., *Paleobiology*, 29(1) 2003). Because evolution occurs only within species, and not higher taxa, and because it occurs within populations rather than being globally synchronous, it is pertinent to recognize that ecologists also must address scaling issues.

Modern ecology, does in fact, encounter similar problems of scale and resolution as does paleobiology. Whereas geologic biodiversity studies commonly attribute variation in fossil data to the vagaries of the rock record (Smith, et al, 2001; Badgley, 2003) or to disparity in temporal resolution, it is interesting to note that these same problems are apparent in data of existing community structure. In fact, variations in the temporal scales of observation can drastically change the interpretations of modern biotic dynamics. As Rahel (1990) points out, studies indicating community stability of coral-reef fish, which were interpreted as unstable in narrow time-scale studies, ultimately appeared stable over longer periods of time, and the reverse was observed for other fauna previously interpreted as stable over narrow time-frames. Further, Rahel (1990) also examines the effect of taxonomic hierarchy as a scale issue and shows that community stability can be observed even if the dynamics of individual species fluctuate. Rahel (1990) used an example of the absolute abundance of a marine polychaete, which varied

greatly over an 11 month period. But, however, the abundance ranking of this species remained constant when viewed in context of the community. As indicated by Levin (1992), the environmental gradients that control biotic dynamics, operate with different scales of spatial and temporal influence. To compound problems further, the diversity response of various species, or communities to the same environmental gradient is not uniform, either. Taken into context, then, we must assume that all of these scaling and resolutional issues are features of the biosphere and not merely geologic phenomena. And ultimately, at the heart of the matter, is that even in modern ecologic community study, numerical resolution, and hence, the interpretation of data, is a hierarchical feature (Rahel, 1990).

Although the sampling of modern communities is usually more robust in terms of completeness than of fossil communities (Badgley, 2003), there still remains an incompleteness of modern data (Rahel et al., 1984). This incompleteness may in turn, dictate the analytical methods used, which again, can yield vastly different interpretations from the same dataset (Rahel, 1990). All of this then brings forward the question of the relevance of the fossil record, and the inequities associated with the completeness of data or variable resolution (Badgley, 2003). Does this indicate that the fossil record and global database of stratigraphic ranges of organisms are worthless tools for macro-evolutionary study (Vermeji and Leighton, 2003)? Perhaps not, because in spite of the tremendous amount of variability in scale and resolution, analysis of the rock and fossil record does indeed produce “patterns”. Although scale-dependent they are the only means to decipher the cause of mechanisms that propagate and maintain patterns (Levin,

1992). What ultimately needs to be clarified, then, is the methodology used to determine these biologic patterns, whether in the modern communities (Rahel, 1990), or fossil communities (Pandolfi, 2001; Badgley, 2003). What we need to pursue are means to understand these patterns rather than actually cause them with our analytical tools. Only by understanding the processes behind these patterns, then, can we begin to understand the factors that affect biodiversity.

New efforts to address these issues are underway. Jackson and Johnson (2001) have suggested sampling protocols to produce uniform fossil sampling at regional scales. Bolstering this concept, Pandolfi (2001) has shown that just one extra hour of sampling at a fossil locality produces increased species abundance. Further, Pandolfi's study indicated similarity of abundance patterns between high-resolution taxonomic levels (e.g., species, genera) and lower-resolution levels (families, classes). Low-resolution taxonomic patterns are not always followed by the patterns from high-resolution data (Rahel, 1990). And Nehm (2001) demonstrated the negative effects of reverse-rarefaction upon the biodiversity interpretations of a highly-controlled sample of Caribbean gastropods. All of these recent studies suggest one clear theme: increased sampling and uniform analytic protocols are needed to compare regional biodiversity trends against one another (Jackson and Johnson, 2001; Alroy, 2003; Miller, 2003). Furthermore, these studies, taken in context, suggest there is no clear means to statistically evaluate and compare the interpretations of independent data sets.

The reasons for our inability to compare independent data are many-fold (Pandolfi, 2001; Jackson and Johnson, 2001). Aside from the issues of sampling, taxonomic hierarchy and resolution, as discussed above, a main factor in our understanding of past biodiversity is analytic (Alroy, 2003). In fact, having an adequate understanding of the definition of biodiversity is paramount to developing a suitable means to quantify it (Benton, 2001). Biodiversity strictly means the number of particular organisms of concern over a defined period in time and space. In quantifying this aspect, several different approaches have been used in paleobiology.

Absolute measures that involve taxon-counting of fossil occurrences over time intervals have been used (e.g., Sepkoski et al., 1981; Benton, 1995). This approach, while indeed quantifying the actual number of taxa, has been criticized, in part, because sampling artifacts caused by many factors (see Chapt. 2) can alter the number of fossil occurrences documented (Peters and Foote, 2001, 2002; Smith et al., 2001; Smith, 2003). Due to potential sampling biases that affect absolute abundances, other studies have focused upon proportional extinction and speciation ratios (Foote and Sepkoski, 1999; Kirchner and Weil, 2000; Foote, 2003) or stasis (Rosenweig and McCord, 1991) of paleobiodiversity. These approaches, although useful for understanding specific aspects of biotic change, are not diversity metrics because they are only measuring one aspect of biodiversity trends (Dean and McKinney, 2001).

As stated in Chapter 2, biodiversity trends, as seen through biostratigraphic data, are three-fold. Biota can become extinct, or new originations may appear, or there may be no

change in the existence of a particular taxon from one time interval to the next. A metric aimed at determining past biodiversity trends from a partial and incomplete fossil record should consider all these factors to determine how taxa respond over time. And a biodiversity metric should be normalized to reduce the effects of sample-size variation between time intervals, taxa, or datasets. Furthermore, the design of such a metric should make it equally applicable to modern ecologic problems, because these communities often suffer similar sampling biases as the fossil record. The Diversity Index of Growth (DIG), used in this and previous work (Chapts. 2,3; Dean and McKinney, 2001) is such a metric that examines all three factors of extinction, speciation and stability. To reduce artifacts of uneven sampling, it is normalized to dataset size and measures biodiversity as it diverges from stability. The form of DIG also allows it to be used with modern ecologic studies, which can thus provide insight between past and present biodiversity trends.

Previous analyses using this metric have revealed striking patterns. With a global scale database, it was demonstrated that marine invertebrate paleo-biodiversity trends were linked to ocean temperature (Dean and McKinney, 2001). In subsequent study (Chapts. 2, 3) even at regional scales, using a Caribbean database, global oxygen isotope and sea-level curves have patterns similar to the biodiversity trends elucidated by the DIG metric. Unfortunately, however, there were temporal lags (several million-year) between the peaks of diversity and highstand seas, and $\delta^{18}\text{O}$ excursions. These temporal lags are likely an issue of resolution because the fossil data are at a much more coarse-scale than are the isotopic or sea-level data. Not only does the variation between these different

signals present a less-than-perfect agreement between the patterns of physical processes versus that of biodiversity, but also, this precludes the ability to statistically correlate these different curves. With this present study, I will show how resolution and scale affect interpretation of these data. Thus, I will present equivalent data, in terms of resolution that indicate DIG and marine invertebrate biodiversity trends do, indeed, track major environmental factors, such as sea-level.

Materials

The data used for this study come from several existing compilations. All of the data are derived from marine invertebrate occurrences from the Caribbean Basin, but these reflect different spatial scales and temporal resolution. The data consist of: 1) The Caribbean compilation of genus- and species- level fossil occurrences (Appendix 1) as described in the previous two chapters; 2) The stratigraphic range data of Caribbean coral species (Johnson et al., 1995); 3) coral data from composite stratigraphic columns (Rio Cana section) of the northern Dominican Republic (<http://nmita.geology.uiowa.edu/faunal.htm-3/1/2003>); and also, 4) foraminifera and ostracode occurrences through a single well log in the southern Dominican Republic (Mann et al., 1999). These data will be compared to published sea level curves and isotopic data at various degrees of resolution.

Methods

I will assess the trends in biodiversity of these data by using the Diversity Index of Growth (DIG), as described previously (Dean, 1997; Dean and McKinney, 2001). This metric is able to assess all the potential dynamics (extinction, speciation or stability)

expected of organisms. Further, this is information that is readily retrievable from any biostratigraphic database.

The data of the Caribbean Database, used here and in the previous two chapters, is regional-scale information. Therefore, the range-through method of assuming a taxon's existence between the First Appearance Datum (FAD) and the Last Appearance Datum (LAD) was utilized (Kirchner and Weil, 2000). This is a common methodology that is valid for large regional- to global-scale compilations because it is highly unlikely that a genus or species would evolve, become extinct, and subsequently re-evolve at a later time. Gaps between appearances are more likely a result of uneven sampling or other biases, such as facies change. To a lesser degree, the concept of range-through was adapted for two other databases used in this work.

For the composite stratigraphic columns of the northern Dominican Republic (<http://nmita.geology.uiowa.edu/faunal.htm>), partial range-through was used. Because the sampling localities are unevenly spaced, and the sections themselves are composite, up-section traverses, I assumed a species existence between sample sites only at intervals that were 10 meters or less, apart. This assumption was used only to eliminate fluctuations in the DIG signal caused by fine-resolution variation in sampling or facies variability. These data are likely indicative of basin-scale response because the up-section sampling was not held in a constant location, but involved some 20 km² or more of area. Thus, for example, if a taxon was recorded at one sample site, then was absent in the next sample site, only 2 stratigraphic meters above the first, and then was recorded

again only 1 meter higher, it seems quite reasonable that that organism existed in this basin at the time of the middle sample. In most instances, the sample horizons were more closely spaced than ten meters.

In a similar fashion, partial range-through was used for the well core data of the Enriquillo Basin of the southern Dominican Republic (Mann et al., 1999). Unlike most biostratigraphic data available, this core produced highly-controlled samples of 10-meter increments. If a species of ostracode or foraminifera was defined at one interval, absent the next, and then described again, I assumed continuity between these two points. This assumption was only used if one 10-meter increment was missing. In both instances of these two sets of data, if the gap exceeded 10 meters, then, the taxon was considered as extirpated at last occurrence, and a new migrant in the next “new” appearance.

Finally, as a means to evaluate the individual sets of data used here, and to understand the limits of resolution unique to each dataset, I propose a new metric aimed at quantifying the spatial-temporal precision of a biostratigraphic database. The goal here is two-fold: 1) to understand the relevance and precision of interpretations drawn from a particular set of data, and; 2) to develop a means to compare the datasets, which usually are not equivalent in terms of size, spatial scope, or temporal coverage. This metric measures the sensitivity of data (SOD) and is a straightforward approach to express the range of validity a particular database exhibits. It assumes the following form:

$$(3) \quad (T/A/I) \times N$$

where,

T = Total number of taxa in the dataset

A = Spatial area (km²) of study

I = Increment of time range the study covers (my)

N = Number of time intervals or observations used for the time series

Such a metric should produce values that can be interpreted as a means to quantify the precision obtainable from a dataset. Lower values indicate a more coarse-scale resolution. These lower values would be caused by large spatial coverage, or long time ranges. Lower values would be likely observed with global-scale datasets. Higher values indicate more precision and are a product of fine-scale spatial coverage and/or narrow time frames. In both cases, increasing either the size of the dataset, in terms of taxa, or by having high-resolution time intervals would serve to increase the sensitivity of data, and hence, produce higher values. Interestingly, this measurement can be adapted for use with modern ecologic time-series study as well as for paleoecologic study. By incorporating a means to quantify databases, and the scope of study, SOD provides a means to determine if two vastly different biologic interpretations are even within the same scale of observation. Given that processes and patterns are scale dependent (Levin, 1992), then it seems pertinent to understand the limitation and range of validity a dataset can yield.

Results

The results of this study will be presented in the following manner. First, I will make a comparison of taxonomic hierarchy. The two sets of data used here include both genus- and species-level information. These will be compared to demonstrate the effects of taxonomic focus upon biodiversity interpretations. Second, I will present an examination of the effects of temporal resolution upon data. Due to the restrictions upon how fossil data are usually reported, only one dataset here allows this temporal comparison. Third, I will show how temporal resolution of data must agree with the temporal resolution of other geologic trends, if meaningful and significant correlations are to be made. To differing degrees, both the Dominican Republic datasets demonstrate this effect. And lastly, I will show how the Sensitivity of Data (SOD) can be used as a means to effectively evaluate the scope of resolution that each of these datasets exhibit.

Taxonomic comparison

The effect of taxonomic resolution upon observed biotic trends is often thought to be negligible at lower scales of resolution, but not necessarily so at higher levels of resolution (Rahel, 1990; Pandolfi, 2001). This has led to the use of higher-level taxa (genus-, family-level), to serve as a proxy for species-level biotic trends (Alroy, 2003), which are usually less well-described than the higher taxa. Comparisons between genus and species data for the biotic groups used in this study demonstrate that although biotic trends are similar between the taxonomic levels within the same database, the resulting patterns are not always equivalent or predictable.

First, as a generality, one would expect the lower taxonomic level (e.g., species) to be the driving signal of biodiversity trends within taxonomic hierarchy. This is because evolution is species-driven (Benton, 2001) and the systematic description of organisms organizes biota from numerous fine-scale groups to less-numerous coarse scales. Thus, biodiversity patterns should involve fine-scale patterns (species trends) that ultimately determine coarse-scale (genus and higher, trends) patterns. Often these biodiversity patterns within the various hierarchies are synonymous. Figure 16 compares the total genera versus total species DIG signal from the Caribbean dataset (Appendix 1, Chapt. 2,3). Although these are both calculated from the same data and at the same temporal resolution there are differences between the timing and magnitude of diversity change. Some of the variation in diversity patterns may be due to the variety of fossil organisms in this dataset, and that some of the described genera do not have accompanying species-level data. But Figure 16 indicates that, whereas similar broad-scale features may be shared by the two taxonomic levels, the patterns are not exact.

A closer match of biodiversity patterns is produced using the same biotic group (e.g., order, class), and comparing its species versus genera. Figure 17 shows the biodiversity trends of Caribbean echinoids. These are a close match in terms of diversity growth, decline and timing. The magnitude of biodiversity change is greater with species, but both taxonomic levels seem to be following similar trends. In Figure 18, the Caribbean gastropods, biodiversity growth is observed first at species-level, with a temporal lag between species and genera trends. Although from a strict evolutionary perspective we would expect biodiversity change to be at species-level prior to genus-level, the

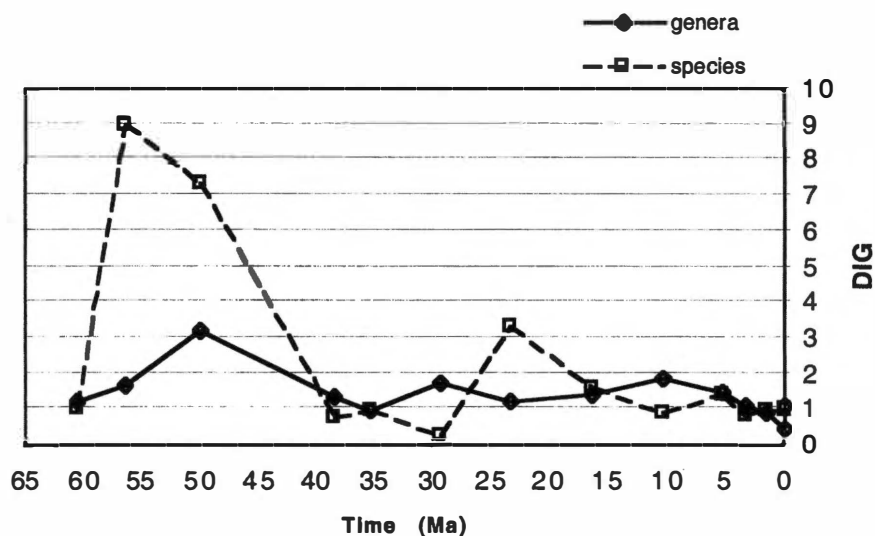


Figure 16. DIG signals of the total genera versus total species of the Caribbean database. The patterns between the species-level and genera-level biodiversity are not exact. Given that evolution is a species-level process and that taxonomic hierarchy organizes biota from species upward, we would expect for species diversity change to precede that of genera biodiversity trends. Given the temporal scale of this study, these curves should probably match. The disparity between species and genus-level trends indicates biases in taxonomic description as well as distributional biases within the database. Not all of the described genera in the database had accompanying species information.

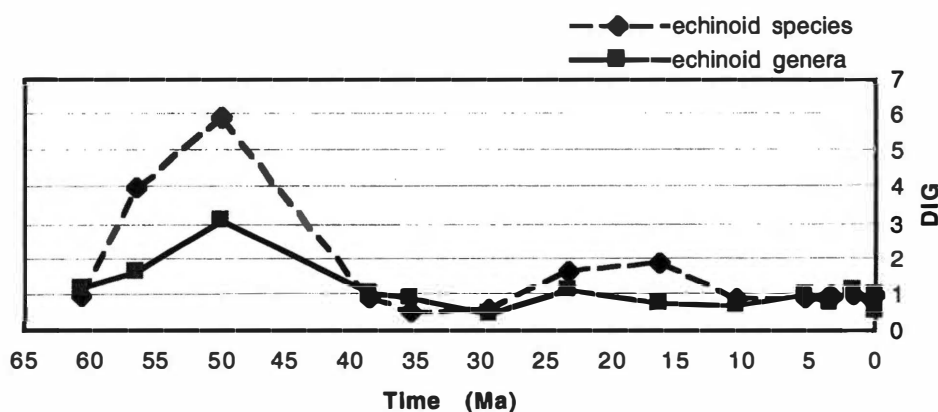


Figure 17. DIG signals of echinoid genera and species from the Caribbean database. Note the general agreement of biotic trends one would expect in a hierarchy: species, because they are more numerous than genera, have broader trends, which then determine the trend of the genus-level signals. This is likely because of excellent description of Caribbean echinoids taxonomically, temporally and spatially.

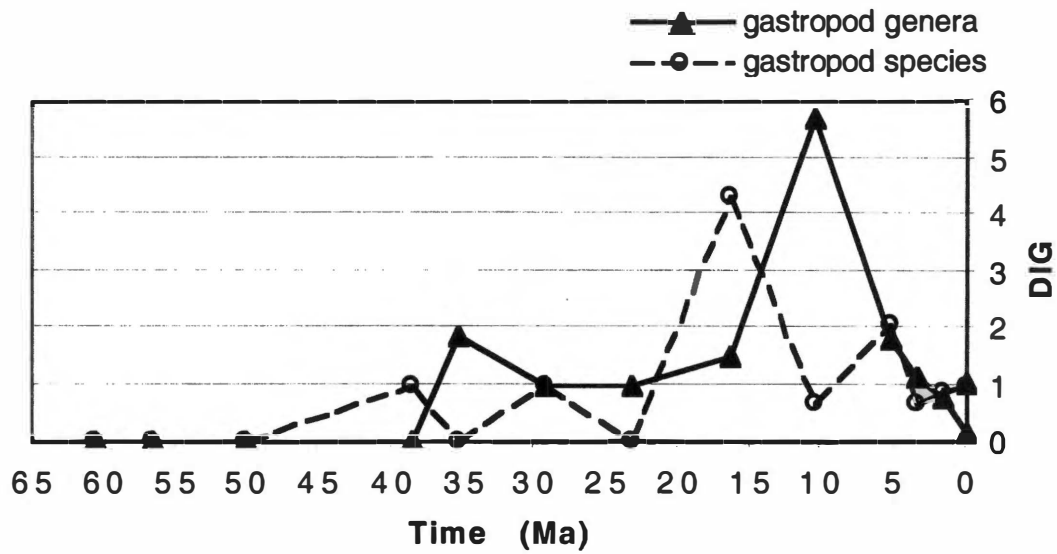


Figure 18. DIG signals of gastropod genera and species from the Caribbean database. As with Fig. 16, there is not a close agreement between trends as would be expected. This is likely the product of uneven sampling and description of fossils.

differential shifts over such large temporal resolution are not easy to explain. The reverse trend is evident in Figure 19, where the Caribbean coral biodiversification indicates change at the genus-level, before change at the species-level.

The reasons for these variations in signals are likely issues of resolution and sampling, in addition to biotic factors. While intensive field studies are currently underway in the Caribbean, there obviously remains much more work in terms of collection, identification and stratigraphic ranges of both species and genera. And, most often, higher-level taxa (genera) are more completely characterized in time and space than are lower-level taxa, such as species (Alroy, 2003). This effect becomes apparent when fine-scale study is attempted, such as that produced by data from Neogene Marine Biota of Tropical America (NMITA)(Budd et al., 2001). Coral data from the northern Dominican Republic have been collected from composite stratigraphic columns (<http://nmita.geology.uiowa.edu/faunal.htm>) that cover a 5 million year timespan, and the resultant DIG values are presented in Figure 20. The effect of having highly controlled sampling, taxonomy and stratigraphic ranges indicates that biodiversification trends cascade through taxonomic hierarchy (Rahel, 1990; Pandolfi, 2001; Alroy 2003). But it is imperative to note that as resolution expands spatially and temporally, the observed trends between taxonomic levels vary, and that these are not predictable (Figs. 16 - 19). And unfortunately, the fossil record, as whole, lacks the spatial and temporal controls seen in Figure 20.

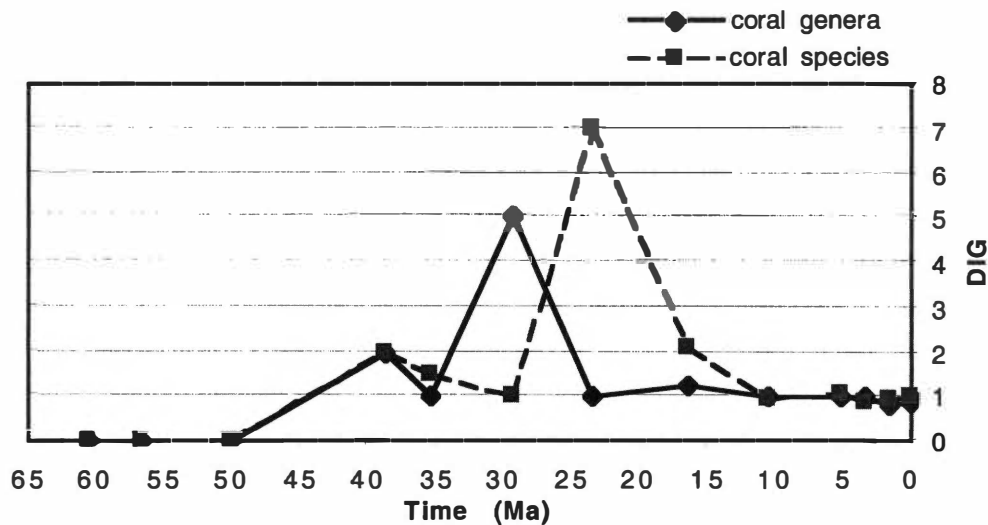


Figure 19. DIG signals of coral genera and species from the Caribbean database. Coral genera DIG should not precede species DIG. In all these depictions, (Figs. 16, 17, 18), the expected agreement between the taxonomic levels is not present. This casts doubt upon the assumption of higher-level clade biodiversity serving as a proxy for evolution, which by definition, occurs at species-level. Furthermore, it underscores the need for more uniform sampling and description protocols.

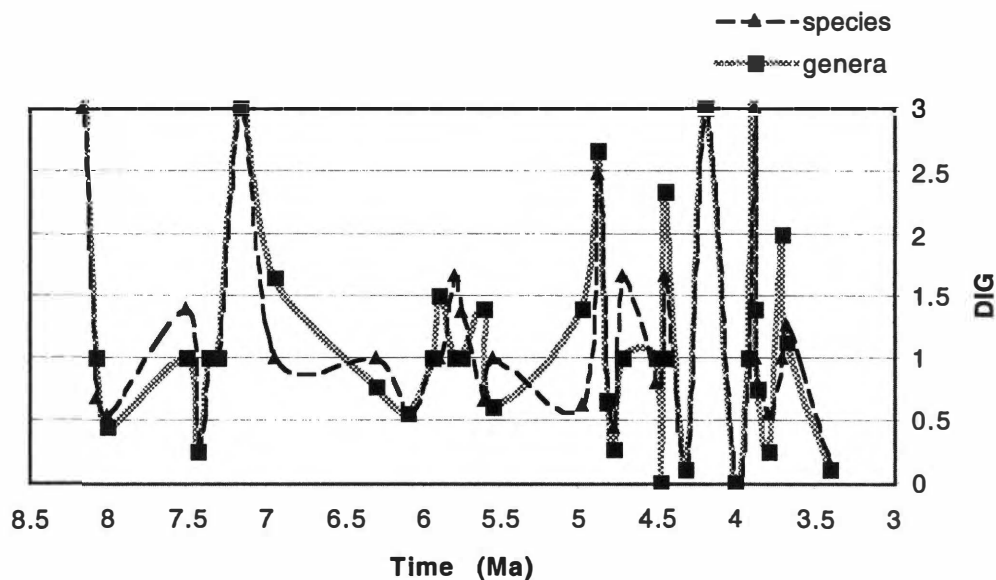


Figure 20. DIG values of coral species and genera from the Rio Cana stratigraphic section, northern Dominican Republic. This was compiled by NMITA (see text) and is indicative of stringent sampling protocols. Note the excellent agreement between species and genera trends of this dataset.

Temporal resolution

The variability of temporal resolution in the geologic record influences the patterns we derive from biostratigraphic data (Pandolfi, 2001). Temporal effects and the intensity of sampling affect interpretations from both paleontology and modern ecology (Rahel, 1990). Attempts to unravel the scale-dependence of community structure, past or present, are stymied by the fact that there is no clear delineation of scale by which measurement is optimum (Levin, 1992). In paleontologic data, we are often limited to the observational scale permitted by the rocks, which may vary between localities in terms of temporal extent. Thus, the actual exposures may produce deposits ranging from time-specific fossil assemblages to those that are time-averaged, with temporal uncertainty of at least 100,000 years. In the case of database compilations (e.g., this study), we are dependent upon the observational level used by previous research. Often the temporal resolution of reported data is fixed and does not allow for any investigation into temporal scale variability. Fortunately, one set of data used here of Caribbean coral biostratigraphic ranges (Johnson et al., 1995) does permit such comparison.

The 132 reef-forming coral species from Johnson and others (1995) are presented in ranges of 1 million-year increments over the past 24 million years. Whereas these data are included in the primary Caribbean dataset used for this thesis (Appendix 1), their depiction as a fine temporal scale subset allows presentation of the same data, only through differing levels of temporal observation. In Figure 21, these are shown at three scales of temporal observation: 1-million year intervals, 2-million year intervals and at 6-million year intervals. As would be predicted, increases in temporal scope produce lags

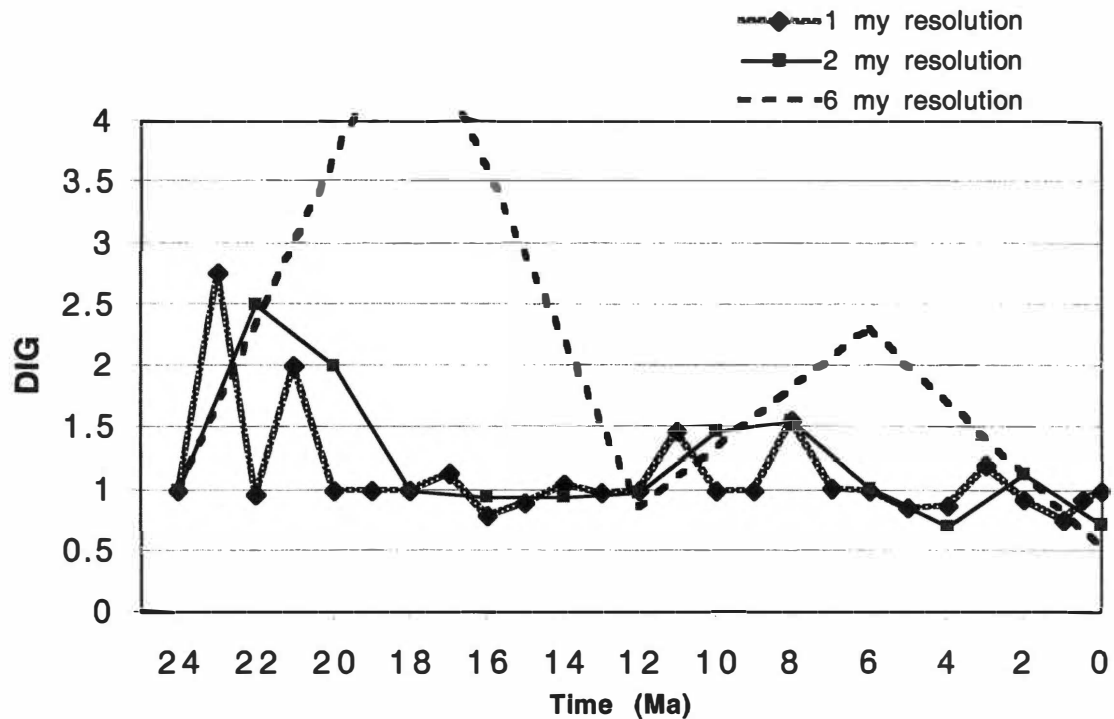


Figure 21. The effect of varying temporal resolution upon data. Here DIG values for the same set of coral data are presented at three different levels of temporal resolution (1 – my, 2 –my and 6 –my intervals). Note, that as the number of observations decreases, then so does the number of biodiversity changes. Further, temporal lags are increased with decreasing resolution. This has implications for time-series data over geologic time, which is an uneven grouping of time increments.

in the respective biodiversification trends, as resolution is broadened to coarser intervals. Although this is observed between the 1- and 2-million year intervals of resolution, the “observed” biodiversification is largest and most attenuated with the 6-million year interval. In terms of biodiversity growth or decline, the finer-scales (1 and 2 my intervals) capture more diversity swings than do the coarse scales (6 my). And although the 1- and 2-million year intervals are closer in temporal timing of diversity “peaks and valleys”, the observed patterns are not equivalent, nor are the dynamics of the 1-million year resolution totally captured by that of the 2-million year interval. Thus, even when the same data are presented at different observational scales, the resultant patterns vary. This has significant implications for geologic data, because, as discussed above, the geologic record is not uniform in terms of temporal resolution. Furthermore, many of the physical processes (sea level, climate change, etc.) that we wish to correlate to biodiversity trends are usually at different scales of observation from the fossil data.

Equivalence of data

Effective correlation of the causes of biodiversity trends requires more than the inference of particular environmental factors upon the biosphere - it requires that the data compared to one another be equivalent in observational scale. In macro-evolutionary studies using biostratigraphic information, this is often not the case. As discussed above, evidence and proxies of the various environmental and physical processes are retrieved independently at differing temporal scales. This problem is further compounded as the spatial-scale is broadened, which usually is met with a decrease in temporal, and sometimes taxonomic, resolution. In order to demonstrate the effect of comparing biotic data with equivalently-

scaled physical and chemical, geologic data, two narrowly-focused sets of data from the Dominican Republic are utilized.

The first set of data is from composite stratigraphic columns of the northern Dominican Republic, as reported by NMITA. This section follows the distribution of 70 coral species of the Late Miocene to Pliocene Rio Cana Section

(<http://nmita.geology.uiowa.edu/faunal.htm>). It is evident that there is some agreement between sea-level (Mann et al., 1999) variation and biodiversity trends (Fig. 22). This is particularly apparent between 6 Ma and 4 Ma, when a major rise in sea-level is tracked by numerous cycles of biodiversity change. But, if we are concerned that these two curves are not an exact fit, then several points need to be considered.

The sea-level curve used here is not local, rather, it is a global representation, and thus the spatial context is not equivalent to the regionally defined biostratigraphic data. The temporal resolution between these two curves is not equivalent, either. In fact, the stratigraphic data from NMITA bracketed the time intervals into six age ranges (8.3-7.5 Ma, 7.5 – 5.6 Ma, 5.6 – 4.5 Ma, 4.5 – 4 Ma, 4 – 3.7 Ma, and 3.7 – 3.4 Ma). For temporal assignment of the data, I assumed a constant sedimentation rate between each of the bracketed age ranges. Although the assumption of constant sedimentation rate is probably not valid, there is no other means to separate the sample localities and relate them to other time-series data such as sea-level. Given this, it is remarkable, indeed, that the biodiversity curve and sea-level curve are as close a match as is apparent.

Furthermore, most sea-level curves are generated by physical depositional evidence, as

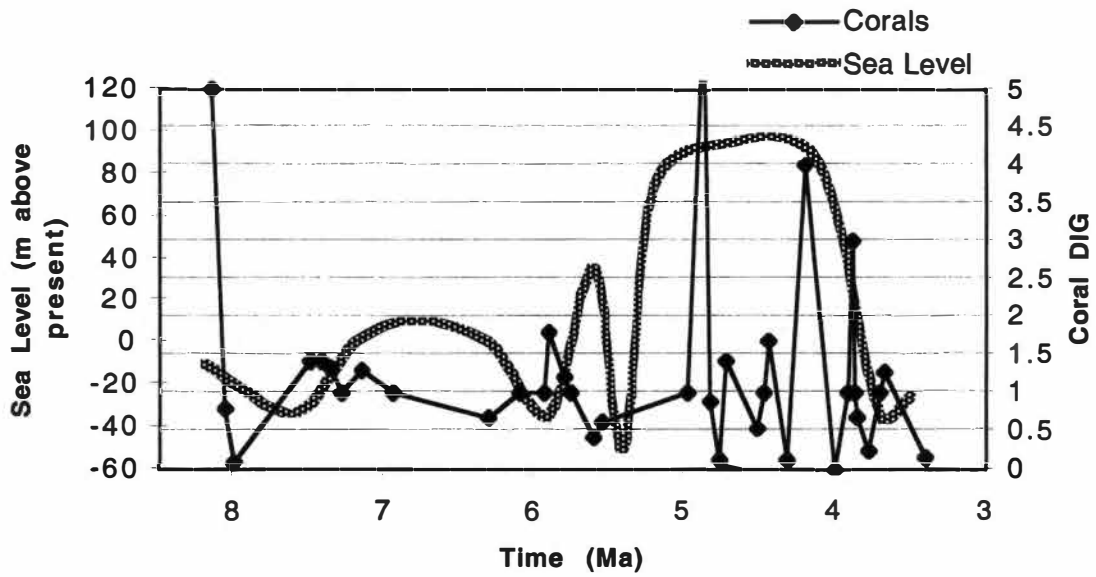


Figure 22. DIG values of coral from the Rio Cana section plotted against the global sea level curve. Note that there is a trend between biodiversity and sea level, but the resolution between these two signals is not equivalent either temporally or spatially. Thus there are higher frequency biodiversity swings between 5.5 Ma and 4 Ma, that are nested within an overall sea level increase.

well as with isotopic data as a proxy for ocean temperature. Therefore, at best, such a sea-level depiction is an average signal, not an exact representation, nor certainly is it site-specific. Thus, the sea-level curve is likely not an appropriate comparison.

For smaller spatial scales and temporal resolution such as the Rio Cana data (Fig. 22), then, finer-scale data must be compared. In Figure 23, oxygen isotopic data of the Ocean Drilling Project (Leg 165, Core 999) from the Caribbean Sea (Reijmer et al., 2002) are compared to the coral biodiversity seen in the Rio Cana section. Because the data are, 1) close in spatial proximity and, 2) more temporally equivalent, then a better agreement between both biodiversity and $\delta^{18}\text{O}$ data is achieved than with sea-level in Figure 22. In fact, temporal equivalence of data produces an even more dramatic effect in Figure 23. The data of Figure 24 are also from the Dominican Republic, but from the southern margin, and consists of foraminifera and ostracode biostratigraphy recovered from a well log in the Enriquillo Basin (Mann et al., 1999). Although the biota only consists of 40 species, the resolution of these data and their subsequent depiction relative to sea-level are powerful examples, nonetheless. This figure clearly indicates the intimate relationship of marine biodiversity to sea-level change, as would be predicted from both biological and geological perspectives (Holland, 1995; Smith et al., 2001).

A main feature of these data (Fig. 24) is that the microfossil assemblage enabled the authors (Mann et al., 1999) to correlate environmental facies of the rocks, and hence sea - level, with the environmental preferences of the biota. Not only were the authors able to

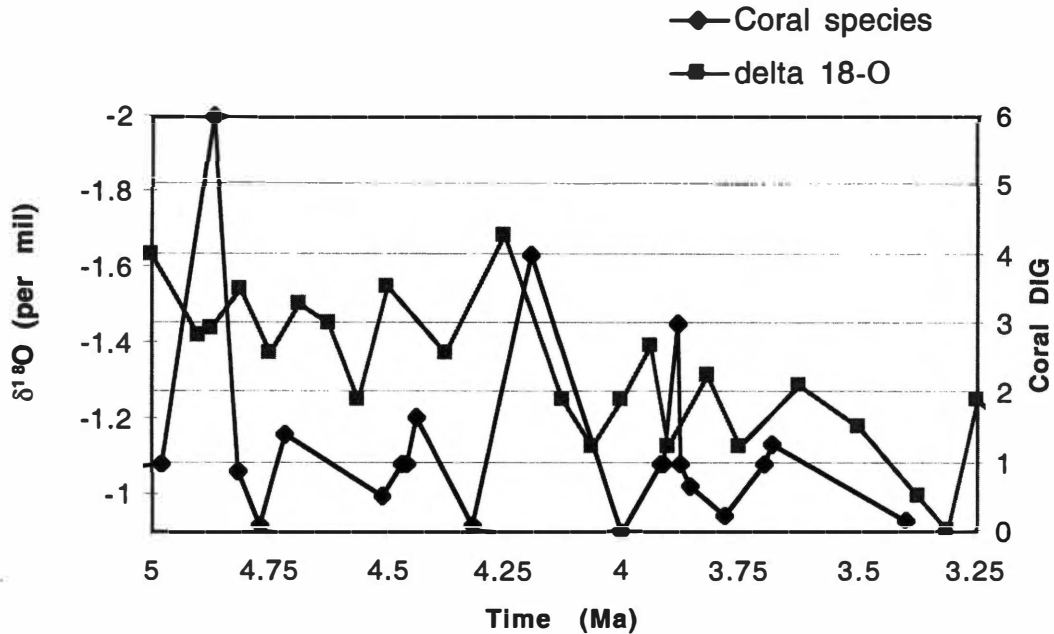


Figure 23. DIG values of coral from the Rio Cana section (Fig. 22) plotted versus oxygen isotopes from the Caribbean (Reijmer et al., 2002). The fine spatial and temporal resolution of the Rio Cana section mandate comparison to equivalently scaled data. The isotopic information from the Caribbean is both more spatially and temporally relevant to this data than is the global sea-level curve (Fig. 22), which is an average. While the curves are not an exact match, these are more closely fit than the curves in Figure 22. Note, exact time of the Rio Cana data was not given, only bracketed age ranges for certain points in the column. An average sedimentation rate was calculated between these data points, which may explain some disparity between the curves (e.g. at 3.9 Ma). Interestingly, this plot still produces a close fit between inferred sea-level increase (decreasing $\delta^{18}\text{O}$ values) and biodiversity increase.

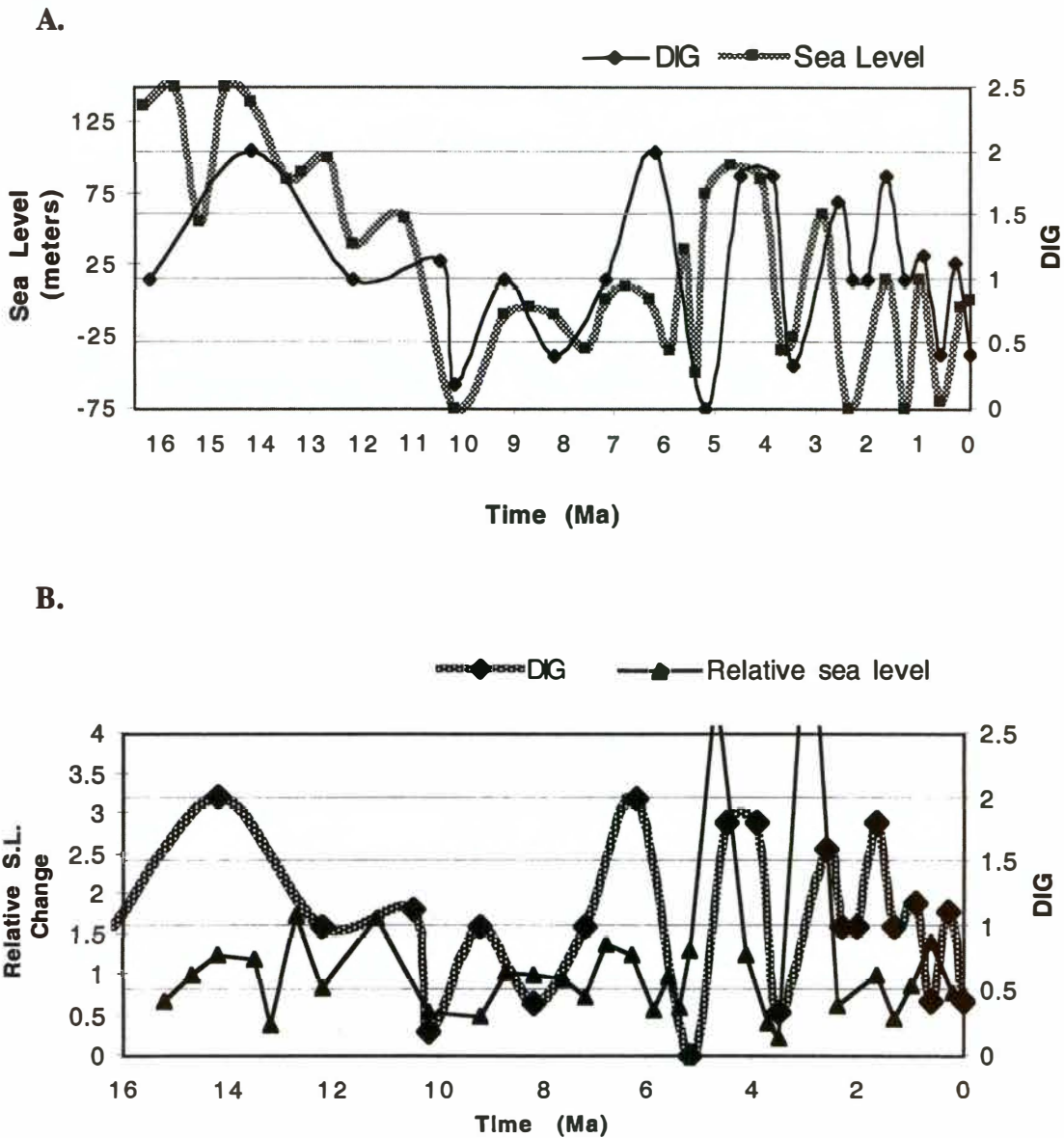


Figure 24. DIG values of foraminifera and ostracodes recovered from a well log in the Enriquillo Basin, southern Dominican Republic (Mann et al., 1999). The authors of the micro-fossil data had previously correlated the fossils to sea-level using paleoenvironmental interpretations. This allowed an equivalent plot between the timing of sea-level and the timing of fossil occurrences. The excellent agreement between sea-level and biodiversity in this instance is due to having both the environmental gradient (sea-level) and the biodiversity signal being equivalent in terms of temporal scale. Thus, even at a fine scales of resolution, the trends of biodiversity following sea-level are evident. In 24a, absolute sea-level is compared to DIG, in 24b, the relative change of sea-level (as calculated in Fig. 8) is compared to DIG.

correlate the facies with fossils, but they were also able to assign an equivalent age to both the well log and to the sea-level curve. Their divisions of time, however, although dependent upon the fossil type, were exclusive of the numeric density and relative biotic change, as measured by the Diversity Index of Growth (DIG). Therefore, the depiction of biodiversity following sea-level trends, as seen by DIG, is not circular reasoning to the data because it quantifies the dataset independently of paleoenvironmental interpretations of fauna. In fact, both methods seem to prove each other quite robust, which gives the DIG method validity in many applications. And ultimately, the use of these data demonstrates the importance of equivalently-scaled data when interpreting geologic data.

Sensitivity of data

An important outcome of this investigation is the need for consistency of data in terms of scale when making comparisons of, in this instance, environmental factors to biodiversity trends. Equally important is an understanding of the spatial-temporal scope of data when comparing interpretations drawn from independent sources. This problem has been acknowledged in both paleontology and modern ecology (Rahel, 1990; Levin 1992; Pandolfi, 2001; Badgley, 2003; Willig, 2003). Unfortunately, no clear-cut means have been proposed to address the problem of the differing scales between databases and scientific inquiries. Before we can begin to unravel this problem, however, we need a means to evaluate the disparity of scaling issues within data. For this I propose the Sensitivity of Data metric (SOD) that quantifies the biological, spatial, temporal, and observational extent of a database. This simply reduces to:

$$(4) \quad (T/A/I) \times N$$

where,

T = the number of taxa in the dataset

A = Spatial area (km²) of study

I = Million year increment of the time range the study covers

N = Number of intervals or observations of the time series

Estimates for area coverage of the four datasets are depicted with their respective values in Table 2. The number of taxa, and the number of observations are presented with respect to each figure in Table 3.

What SOD allows us, then, is a means to compare each dataset in terms of sensitivity or resolution. It should be no surprise that Figure 24, which has the best agreement between inferred forcing function and biota, has the highest SOD value (10⁻² Taxa/ km²/million year). This is in spite of the fact that it is numerically the smallest dataset, in terms of total taxa. Sensitivity of the Rio Cana section (Fig. 23) data is also robust (10⁻⁴ Taxa/ km²/million year), but the larger spatial coverage necessary to include the relevance of the Caribbean isotopic data decreased sensitivity by two orders of magnitude. When measured using only Dominican Republic area (Figs. 20, 22), the SOD value increases by several orders of magnitude. What is readily apparent, then, is the effect of both spatial coverage (Fig. 16) and temporal resolution (Fig. 21) upon SOD values. Although it is

Table 2. Areal coverage of three datasets.

Database locale	Source	Area (km ²)
Caribbean Sea	http://geography.about.com	2,515,900
Dominican Republic	http://graphicmaps.com	48,730
Enriquillo Basin (in D.R.)	Mann et al., (1999)	2,000

Table 3. Results of application of SOD to various databases utilized in this study.

Figure	Locale	Resolution Ma	Genera	Species	Interval 10 ⁻⁷ y	SOD Taxa/km ² /10 ⁻⁷ y
16	Caribbean		520		14	4.45 x 10 ⁻⁵
20, 22	Rio Cana		70		38	1.10 x 10 ⁻²
21	Caribbean corals	1		132	24	5.25 x 10 ⁻⁵
21	Caribbean corals	2		132	12	2.62 x 10 ⁻⁵
21	Caribbean corals	6		132	4	8.74 x 10 ⁻⁶
23	Rio Cana, Caribbean		70		38	2.15 x 10 ⁻⁴
24	Enriquillo Basin		40		22	2.71 x 10 ⁻²

easy to envision increasing spatial coverage as a means to decrease sensitivity of the data, the idea of resolutional control may not be quite as obvious. Figure 21 indicates that at some degrees of observational change (1 and 2 Ma), there is some disparity between SOD values and curves, even when the number of taxa and spatial extent are held constant. But this effect is magnified when viewed at coarse scales of resolution (6 Ma), which decreases the SOD an order of magnitude.

Though SOD can be a method for comparing datasets, it also can be used to strengthen interpretations of data. In comparisons of sea-level, for instance, versus that of biodiversity, it would be preferable to use signals that are comparable in scale, especially in area. However, the construction of sea-level curves is complex, and involves proprietary data not shared with most investigators. Further, the SOD metric would have to be modified to incorporate isotopic data points rather than the number of taxa. Most of the signals, however, such as sea-level curves or isotopic curves do have some spatial extent assigned to them, which may be larger than that of the biostratigraphic data. The resolution of such signals is generally increased by the fine-scale observations that elevate SOD through the number of data points (observations) used to construct the respective curves.

Discussion

There are many levels of scale-dependence within each biostratigraphic database that ultimately lead to variation in resolution. This transcends into different spatial, temporal, observational and taxonomic coverage that determine, in part, the extent of

interpretations that are achievable. Thus, the “paradox” that vastly different conclusions can be drawn from the same dataset (Rahel, 1990) can be resolved by understanding the limitations of the data, and more so, with that of the subsequent interpretations. Often these differing interpretations originate from comparisons with very different gradients or processes. At other times it is because of variation between the precision and resolution of the individual studies.

In Figure 7, the DIG values for the Caribbean dataset are plotted against oxygen isotope curves from Zachos and others (2001). In Chapter 2, the relationship between the isotope curve and DIG was interpreted as sea-level exerting a control on biodiversity. But, the original authors of the isotopic data (Zachos, et al., 2001) had a more focused study on the Paleocene-Eocene Thermal Excursion (PETM) that occurred at 52 million years ago. Their fine-scale study of foraminiferal isotopes from ODP cores produced high-resolution data that allowed them to correlate the PETM with Milankovitch cycles (100 Ka cycles). The reason for the disparity of interpretations, then between Zachos and others (2001) and this study, is likely an issue of precision and resolution of data. The final conclusion and context of any interpretation, then, being dependent upon the scale of the study (and data).

The Caribbean dataset has a calculated SOD in the range of 10^{-6} Taxa/ km²/million year. This is a very coarse level, especially when compared to high-resolution data (Fig. 24) that have values of 10^{-2} Taxa/ km²/million year. Certainly, the isotopic values from the ODP cores were based upon a high-level of observations, and over a much shorter period

of temporal coverage. Furthermore, the spatial extent of the core is limited and all these factors, if available for analysis, would produce a SOD-type value much more sensitive than that calculated for the Caribbean database. If we accept the hierarchical level of environmental factors that affect the biosphere (Rahel, 1990; Levin 1992; Pandolfi, 2001), then it is reasonable to assign a large-scale process, such as sea-level change to coarse-scale data, while at the same moment, assign fine-scale processes such as orbital variations, when the data are high-resolution. As put forth by Rahel (1990), such disparities between interpretations are no paradox, but rather, indicators of scale-dependence.

If we examine Figure 7 further, there are more explanations for the partial agreement of isotopic data and DIG. In the context of the exercises of this present work, some of the non-relationship between the curves can be explained by the non-equivalence of the data versus the environmental gradients with which we make comparisons. When data are equivalent, in terms of resolution and spatial coverage, as in Figures 23 and 24, biodiversity closely follows isotope curves and sea-level. Certainly, biotic response to sea-level is a reasonable and predictable association one would expect of marine fauna. The dynamics seen in Figure 7, however, are not exactly following the isotopic curve, most likely as a result of making scale-dependent comparisons between fine- and coarse-scale data. In fact, the resolution of isotopic data is usually at a precision that produces irregular oscillating patterns. The data used from Zachos and others (2001) were “smoothed” by a five-point running average; the isotopic data in Figure 23 (Reijmer et al., 2002), were smoothed by a fifteen-point running average by the source authors to

produce the “curves” presented in the respective papers. Therefore, the temporal resolution of isotopic data often exceeds that of biostratigraphic data. As shown in Figure 21, variation in temporal range produces differing signals that do not correlate, even from the same set of data.

As seen in Figure 21, coarse-scale increments (6 Ma) do not produce the same pattern as fine scale increments (1 and 2 Ma, respectively). Unfortunately, the rock and fossil record exist as a combination of these variable increments, as we move from one unequal time interval to the next. The “pull of the Recent” effect (Raup, 1972) serves to create a time-series, in general, of coarse-scale that grades into fine-scale time intervals. To an unknown extent, the same is true with the spatial coverage of biostratigraphic data. The actual geographic ranges of the fossil data are uncertain for a studied region and this uncertainty is exacerbated by tectonic processes which can change the area of a region over time. Thus, the spatial coverage between factors such as “global” sea-level curves and regional biostratigraphic databases can be vastly different. Just as global biostratigraphic data are only homogenization of population- to regional-scale biotic dynamics (Vermeji and Leighton, 2003; Willig, 2003), so are regional to global curves of environmental or physical processes. Therefore, there is no real reason to expect data of markedly different scales and resolution to ever be highly correlated.

The reduction of fine-scale processes to coarse-scale global-scale depictions creates a hierarchy of gradients (Levin, 1992). These hierarchies cause problems of “curve-matching” and limit our understanding of the mechanisms of the patterns we observe.

Certainly, “global-scale” processes and “large-scale” gradients are only culminations of the net effect, and averaging of, the many fine-scaled, local events (Levin, 1992). The human-derived concept of organizing a hierarchy may originate from the limited observations available for some processes or certain time intervals (Levin, 1992). As shown by the SOD metric, increasing the number of time intervals (observations) greatly enhances the sensitivity of our data, and hence, the perceived scale of resolution. Thus decreasing the number of observations, or increasing spatial or temporal coverage, forces us into the realm of large-scale forcing functions and processes (gradients), such as tectonics, sea-level change or biodiversity trends, all of which are presumed to operate at long time intervals.

The perceived complexity of all these physical and biological processes intensifies due to the lack of complete understanding of the interactions between them. For example, sea-level variations have been organized into a hierarchy of first-, second-, third- (etc.) order sequences. At each level in the hierarchy, different causal mechanisms are assumed (Summerhayes, 1986; Plint et al., 1992). First-order sequences are attributed to changes in crustal volume as produced by the accretion and disintegration of supercontinents, as a result of tectonic processes at the scale of 100's of millions of years. Second-order cycles, operating at 10's to 100's of million years, are presumed to be caused by volumetric change of mid-ocean ridges as a result of changes in spreading rates. Third-order cycles are within 1 to 10 million year intervals, and are problematic in their causal mechanisms. The temporal cyclicity of these third-order sea-level changes is too long for climate-induced changes, which is on the order of 100,000's of years, yet too short for

sea-floor spreading rates. In addition, these are not globally correlated as with the other two higher-order sequences (Plint et al., 1992). The lower fourth- and fifth-order sequences are not global responses but are regional- to local- scale effects controlled by climate, tectonics, sedimentation and subsidence (Summerhayes, 1986; Plint et al., 1992).

The net effect is that all the various processes of orbital variation, climate, tectonics, local basinal response, and even biology ultimately interact to produce the presumed “larger-scale” pattern we infer. What is uncertain is how various processes operating at different temporal and spatial scales actually interact. At the present moment in space and time (i.e., now), all of the “hierarchies” of processes follow the same time scale and do interact. It is only after the fact, when we as observers, rather than participants, look back into past events and assign some level of importance to the various processes to create our hierarchies. As discussed previously, the scale, and thus rank of a particular process is determined, in part, by the number and quality of observations we have (Levin, 1992). And whereas such organizational hierarchies are critical to the human understanding of complex relationships, these very same hierarchies, which are dependent upon our observational resolution, also determine the patterns we interpret (Rahel, 1990). Thus, the “scale dependence” of processes and patterns (Rahel, 1990) is possibly a product of the lack of human understanding, which is hampered by our poor resolution of some events, in terms of observations.

All of this is significant to the fossil record and biodiversity patterns because, unless by unusual catastrophic circumstances (e.g., bolides), the resultant biodiversity trends

observed are probably caused by a multitude of factors, with any particular interpretation being controlled by the scale of study. The data presented in this and previous chapters suggest sea-level change, possibly from tectonic reasons, as a driving mechanism of Cenozoic Caribbean marine invertebrate biodiversity. But sea-level change is not a discrete process; it is the product of various other mechanisms that interact with one another to produce a general trend. Thus, there are likely numerous “causes” that can be considered as primary forcing functions for biodiversity. The main control upon our final interpretations, then, is that of observation and resolution, the quality of which determines the scale of influence we infer.

Conclusions

The hierarchical nature of the fossil record is scale-dependent, as are the physical processes that control biodiversity and evolution. This in turn leads to a multiplicity of causes for biotic trends observed in the fossil record, all of which may be valid at various scales of resolution. Determining the effect of scale-dependence is linked to the precision and resolution of our observations of the data. Fine-scale precision leads to interpretations of fine-scale causal mechanisms, with coarse-scale resolution producing large-scale patterns. The disparities between vastly differing interpretations of forcing functions upon biodiversity is most likely caused by the different levels of spatial, temporal, biological and observational resolution obtainable by individual biostratigraphic datasets, and the processes to which they are compared.

A major impediment in understanding the mechanisms that affect biodiversity trends, may lie with the variation in the resolution of data used in cause and effect correlations. In order to have a close agreement between presumed forcing functions and biodiversity, then the data compared should be equivalent in terms of resolution. The sensitivity of data (SOD) metric allows comparisons of fossil datasets for such equivalence.

Furthermore, this measurement begins to address the scale of influence a particular mechanism may impart to the biotic systems by quantifying the relative spatial-temporal sensitivity of the data. More importantly, this metric allows investigators a means to express the range of spatial, temporal, and biological extent over which interpretations of a particular biostratigraphic dataset are valid. In order to have meaningful comparisons between environmental gradients and biostratigraphic data, however, it would be beneficial to evaluate other time-series data with a similar system as SOD. This is simply because datasets can only be correlated if there is equivalently-scaled data.

The results of this study indicate that marine biodiversity follows sea-level variation. At fine-scale resolution, sea-level trends are closely matched by biodiversity changes; at coarser scales, this observation also seems valid, but the agreement between curves is less robust. Due to variation in data resolution, however, it is more difficult to correlate coarse-scale processes to one another. This problem is further exacerbated by temporal variability, and hence the sensitivity of biostratigraphic data within an unevenly distributed time-series.

The reduction of geologic and biologic processes into a hierarchy of scale is based upon the resolution and precision of our observations of data. The hierarchies subsequently created do not necessarily exist as natural divisions, but rather, as human-derived tools to understand complex processes and relationships. The assignment of interpretations of processes to higher or lower levels within a hierarchy is more indicative of the precision and resolution of our observations in time and space, rather than of the actual controls upon processes.

CHAPTER 5: EPILOGUE

Summary

Analysis of a database of fossil citations consisting of coral, echinoids, bivalves and gastropods indicates that Cenozoic Caribbean marine invertebrate biodiversity is linked to changes in sea-level. This effect is apparent at various spatial and temporal scales of observation. Although this may be an intuitive result, the vagaries of the rock and fossil record produce a time-series of data that is uneven in terms of fossil abundance between time-steps. Further, the sampling biases created from such unequal distribution of fossil occurrences has prevented unequivocal correlation of the relationship between biodiversity and sea-level. The main reason for the inability to link biodiversity to sea-level has most likely been analytical. Most biostratigraphic analyses of the fossil record rely upon metrics such as proportional extinction, proportional speciation or absolute values of the number of fossil occurrences. Any of these approaches, however, is affected by the sampling biases of the rock and fossil record.

Absolute metrics only quantify the number of organisms per unit time and, hence, are controlled by sampling artifacts. But proportional metrics, such as extinction or speciation, usually measure the number of fossils either becoming extinct (E) or speciation (N) over the total (T) number of fossils observed in a particular time intervals (e.g., E/T or N/T , respectively). Thus, these proportional metrics are also highly-controlled by dataset size, and therefore are also susceptible to sampling variation.

Furthermore, both extinction and speciation metrics are not measuring biodiversity, but rather, only one aspect of it.

As defined (Benton, 2001), biodiversity strictly means the number of particular taxa of concern over a given period of time and over a specified spatial area. Biodiversity trends include several potential pathways biota can follow over time. These are: 1) those that become extinct, (E), 2) those that speciate or are “new”, (N), 3) those which already exist and do not go extinct but remain stable, (S), and finally, 4) the total number of taxa for that time interval, (T). Thus, whereas proportional extinction and speciation are components of biodiversity trends, there are, indeed, other trends that biota can follow. To incorporate the total pathways biota can follow, and to correct for sampling biases caused by unequal distribution of fossil occurrences in time and space, a new metric is used.

The Diversity Index of Growth (DIG) was designed to quantitatively measure biodiversity as a relative divergence from stability. The key features of this metric are that it is normalized to dataset size (T), and it measures diversity as it diverges from the stable component (S). The form of this metric is as follows:

$$(T-E+N+S)/[S+T(E+S)/(N+S)]$$

The advantages of DIG are that it quantifies the relative change of biodiversity (Alroy, 2003) rather than being dependent solely upon dataset size. This reduces the artifacts

incurred by unequal distribution of fossils over time. Furthermore, it incorporates data that are easily extracted from biostratigraphic ranges of fossils, and includes key pathways that proportional extinction or speciation overlook. To quantify the volatility, a second metric, Volatility, (V) was developed, and is simply the opposite of stability. The form of this metric is as follows:

$$V = (T-S)/T$$

These two metrics, DIG and Volatility, are used in Chapters 2 – 4 to assess biodiversity, and to subsequently, attempt comparisons between major environmental processes and biodiversity trends. Graphical correlations between DIG and environmental proxies indicate a critical need: equal comparison of data. Most of these processes (sea-level, isotopes, etc.) are presented as absolute values. Furthermore, the resolution and precision of various “curves” are not uniform, either. Comparing DIG, which depicts relative change to curves showing absolute change, does not produce robust results simply because the comparisons are not equal. To compensate for this disparity between relative and absolute depictions of data, the relative change of sea-level was determined first by integrating the area under the sea-level curve and then by measuring the relative change of this area from one time interval to the next. This concept is useful for two reasons: 1) it incorporates the sea-level data into equal time increments as the fossil data; and, 2) it allows relative change of sea-level to be compared to relative change of biodiversity. Both of these factors produced much better agreement between sea-level and DIG (Chapt. 2).

The relationship among climate, tectonics, sea level and biodiversity trends are examined further in Chapter 3. Although a complex issue, (and one that incites much debate), the biodiversity trends of the Caribbean database suggest that sea-level and climate are influenced by tectonic activity, such as volcanism, and restructuring of continental landmasses. Other additional tectonic controls include bathymetric and ocean current changes. The conclusion that biodiversity is affected by such large-scale processes was drawn from the temporal occurrence of major explosive Caribbean-area volcanism which preceded biodiversity increases. Published studies also place these tectonic pulses before major terrestrial events and responses, such as climate change and chemical weathering (Sigurdsson et al., 2000; Thomas et al., 2003). In fact, the relationship between direct controls of biodiversity by tectonics is not made. Rather, sea-level imparts direct control to biodiversity, as a response to either tectonics, climate or both. This is, however, an issue of scale of causal mechanisms (Chapt. 4). The data depicted in Chapter 3 show three distinct biodiversity pulses, which are in agreement with three distinct sea-level rise pulses. These responses are in turn, preceded by three distinct explosive volcanic pulses in the Caribbean. The role of tectonism and biodiversity is expanded to global tectonic activity, because it was previously shown that the Caribbean database seems to be following global trends. The reasons for this broad, spatial-scale outlook are examined in Chapter 4.

In the last paper, I examine issues of spatial- and temporal-scale, as well as observational resolution with regards to not only biostratigraphic databases, but with presumed

gradients (i.e., tectonics, sea-level, etc.). Here, I show that the data we typically compare, are not equal. I do this by introducing another new metric, termed Sensitivity of Data (SOD) which assesses the temporal and spatial coverage one can expect from a particular database or inferred environmental gradient. Simply, this metric examines the following parameters:

T = the number of taxa in the dataset

A = Spatial area (km²) of study

I = Million year increment of the time range the study covers

N = Number of intervals or observations of the time series

And it assumes the following form:

$$(T/A/I) \times N$$

The values produced by this metric indicate which databases are broad in coverage, or less-sensitive to smaller-scale events (low values), versus those which have a more narrow spatial-temporal coverage and are sensitive to more local or large-scale events (high values). More importantly, it explains why correlations between cause and effect of biodiversity and presumed environmental gradients are not always robust. There are four factors (listed above) that influence sensitivity. Generally, biostratigraphic data are not equivalent in terms of the number of intervals (N) used in time-series when compared to high-resolution data. This effect was demonstrated in Chapter 2, when the calculations

of the area under the sea-level curve created boundaries of near-equal time increments comparable with those of the biostratigraphic data. This effect was also observed in a fine-scale resolution data series in Chapter 4, as well. In both instances, the relationship between DIG increases and sea-level increases are very close when both sets of data have near-equal time intervals. Additionally, issues of scale and resolution determine, to a large extent, the scale of interpretation of data. Coarse-scale (low SOD) databases will likely result in large-scale interpretations, whereas the reverse is true for fine-scale (high SOD) data. This has implications for not only how science interprets data, but also, how interpretations should be reported: with respect to the spatial-temporal coverage.

All of these scaling effects help contribute to a hierarchy of processes. In many cases, it is convenient to refer to some “large-scale” environmental process that may affect, for example, the biosphere. The creation of such hierarchies, however, is misleading, if not inaccurate. The scale of study, in part, controls the ultimate interpretation. The division of processes into large- and small-scale hierarchies is likely a product of the resolution of events, because it is unlikely that these are natural divisions. Rather, these hierarchies are created by humans as tools for understanding complex processes. In fact, the division of these geologic processes into separate hierarchies actually implies that they operate in a vacuum, devoid of interaction with other processes at various scales. This is patently untrue. Otherwise, then, we would only need to determine the cycles, and be content that a predictable and pre-determined course will be followed by some particular gradient. The result of centuries of earth science has shown, however, that the earth “systems” are not discrete entities, but rather, highly interactive systems with one another, regardless of

the scale of influence we, as human observers, assign. For example, early earth atmosphere was most likely changed from CO₂ rich to O₂ as a result of biotic photosynthesis. In our modern world, a similar but reverse process may be occurring as anthropogenic releases of CO₂ may be causing climate change. Thus, these various scaled “processes” do indeed react, and do not follow discrete trends.

It’s About Time...

Another major impediment discussed in Chapter 4 is the artifact of time. It is obvious that the resolution of past events decreases over longer intervals of time. This poor resolution, in turn, may often lead to the assignment of temporally distant events into larger-scaled hierarchies. The main reason, I propose, is due to the limited number of observations obtained from these distant events. Limited observations of more modern geologic processes (e.g., the imperceptively “slow” rates of tectonics) also forces assignment of such processes into larger-scale hierarchies

A definition of time, as constructed by the author, is that it is simply “change” to some particular system. To assess change, however, some reference must be assigned. This definition, in spite of being somewhat reference-bound in practice, may provide some philosophical insight, and is in fact, related to the seemingly disjunct topic of geologic biodiversity. This is because in order to perceive change, observations must be made. As shown in Chapter 4, altering the number of observations results in vastly different signals, even if these observations are based upon the same set of data. Ultimately, the change in frequency (or quality) of observations can lead to the assignment of processes

to various higher- or lower-order hierarchies. The system of hierarchies itself, may be problematic, as discussed in Chapter 4, but for this discussion, the change in frequency of observation may impart controls to the manner in which we depict time-series data.

Newtonian physics views time as a smooth, unbroken continuum. Although the work of Einstein calls into question this idea, relativistic behavior of time is typically not applied to geologic data. This discordance between theory and practice, then, could possibly be important in how we view, for example, the changes of biota over time. Generally, time-series data consist of some signal plotted versus time. The resulting 2-D graph, then, often assumes a waveform characteristic. Key questions pertaining to this phenomenon, then, are these signals reality, or are they caused by our analytical methods? Further, are these waveform-like signals only an artifact of the imposition of a rigid (and arbitrary) standard of time to a system that is, by some accounts, quite relative?

If one considers that the time-series depictions, such as those used in this study are indeed constructed from observations of past events, then we at the very least, have a graphical depiction that is in and of itself, real and tangible. But, as we move away, in time and space, from the point when these events actually happened, our observations decrease in frequency (and quality), and our graphical waves become distorted in terms of amplitude and wavelength. This has major implications, because the scenario just described is a common effect observed in wave dynamics, namely, the Doppler Effect. Whether or not there is such an effect upon actual time (although Einstein's Special Theory of Relativity

provides such a hint), or whether it is only in how we render data, the potential effects to alter our data and the inferred subsequent interpretations of them, should cause concern.

Geology, as a discipline, may be uniquely poised to address such questions. Not only does geology cover the vast expanses of rocks and fossils, but, by doing so, actually has tangible evidence of change. Thus the observations necessary to define time are contained in a 4.5 billion year record preserved in rocks. Furthermore, geology enjoys two separate systems of time, both relative (Geologic Time) and absolute (calibrated). The relationship of time to this study and the fossil record is likely the outcome of geologic time, in general. The natural divisions of geologic time are based upon the two critical factors seen here: biodiversity and facies change. Perhaps by comparing signals derived from both absolute and relative time systems, as well as factoring in the effects of decaying orbital variations, we may begin to assess the true nature of time.

Future Work

The results of this dissertation suggest several areas of which further study is warranted. Some major directions that can be taken in the future include the following:

- 1) Comparison of sea-level trends and biodiversity trends of various regions and time periods. A much more complete picture of the relationship of marine biota to sea-level may be achieved by examining trends from all of the Phanerozoic. Furthermore, comparison of trends between the terrestrial realm versus that of the marine environment may address questions between climate and biodiversity.

2) Integration of biodiversity trends with DIG to correlate stratigraphic sequences.

3) Using the metrics derived here (DIG, Volatility, SOD) as tools to observe and evaluate biodiversity changes over time in modern biotic systems. By having an equal methodology, then, comparisons between modern biodiversity problems and past biodiversity crises may be more effective. And certainly, relative change of biodiversity is important to modern ecology, because absolute counts of species or individuals in populations are unlikely.

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APPENDIX

Appendix. The Caribbean Database.

Order	Family	Genus	Species	Range	Water depth
Anthozoa		Goniopora	hilli	U. Olig - L. Mio	Shallow
			imperatoris	L. Mio - L. Plio	
			calhounensis	U. Mio - L. Plio	
		Alveopora	tampae	L. Plio	Shallow
		Asterosmilla	abnormalis	U. Mio - L. Plio	
			exarata	M. Eoc - U. Plio	
			profunda	M. Eoc - M. Mio	
			duncani	L. Mio	
			compressa	L. Mio	
	Guyniidae	Pourtalocyathus	hispidus	U. Mio - Hol	Deep
		Guynia	annulata	M. Mio - Hol	Deep
	Dendrophylliidae	Dendrophyllia	cornucopia	U. Mio - Hol	Deep
			Acropora	L. Olig - Hol	
		Actinacis		L. Olig - L. Mio	
		Agaricia		M. Mio - Pleist	Shallow
		Agathiphyllia		L. Olig - L. Mio	
		Alveopora		L. Olig - L. Mio	Shallow
		Antiguastrea		L. Olig - L. Mio	Shallow
		Antillia		L. Olig - U. Plio	Shallow
		Antillophyllia		L. Olig - U. Plio	
		Astreopora		L. Olig - L. Mio	
		Astrocoenia		L. Olig - L. Mio	Shallow
		Caulastrea		L. Olig - U. Plio	Shallow
		Cladocora		L. Olig - Hol	Shallow
		Colpophyllia		L. Olig - Hol	Shallow
		Cyathoseris		L. Olig - U. Olig	Shallow
		Dendogyra		Pleist - Hol	Shallow
		Dichocoenia		L. Olig - Hol	
		Diploria		L. Mio - Hol	Shallow
		Euphyllia		L. Olig - U. Olig	Shallow
		Favia		L. Olig - Hol	Shallow
		Favites		L. Olig - L. Mio	Shallow
		Galaxea		L. Olig - U. Mio	Shallow
		Gardineroseris		M. Mio - U. Plio	Shallow
		Goniastrea		L. Olig - L. Mio	Shallow
		Goniopora		L. Olig - U. Plio	Shallow
		Hydnophora		L. Olig - U. Olig	Shallow
		Isophyllia		L. Plio - Hol	Shallow
		Lamellastrea		L. Olig - U. Olig	Shallow
		Leptomussa		L. Olig - U. Olig	Shallow
		Leptoria		L. Olig - U. Olig	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Anthozoa		Leptoseris		L. Olig - Hol	Shallow
		Madracis		L. Olig - Hol	Shallow
		Manicina		U. Mio - Hol	Shallow
		Teleiophyllia		U. Mio - L. Plio	Shallow
		Meandrina		L. Olig - Hol	Shallow
		Placocyathus		M. Mio - U. Plio	Shallow
		Montastrea		L. Olig - Hol	Shallow
		Mussa		L. Plio - Hol	Shallow
		Mycetophyllia		L. Olig - U. Olig	
		Oculina		L. Olig - Hol	
		Pavona		L. Olig - U. Mio	Shallow
		Pironastrea		L. Olig - L. Mio	Shallow
		Pocillopora		M. Mio - U. Plio	Shallow
		Porites		L. Olig - Hol	Shallow
		Psammocora		L. Mio - U. Mio	Shallow
		Scolymia		L. Plio - Hol	Shallow
		Septatsrea		U. Mio - U. Plio	Deep
		Seriatopora		L. Mio - M. Mio	
		Siderastrea		L. Olig - Pleist	Shallow
		Solenastrea		M. Mio - Pleist	Shallow
		Stephanocoenia		U. Olig - Pleist	Shallow
		Stylangia		L. Olig - L. Mio	Shallow
		Stylocoeniella		L. Olig - U. Olig	Shallow
		Stylophora		L. Olig - U. Plio	
		Symphyllia		L. Mio	Shallow
		Syzygophyllia		L. Olig - U. Plio	Shallow
		Thysanus		L. Mio - U. Plio	Shallow
		Trochoseris		L. Olig - U. Olig	
		Turbinaria		L. Olig - U. Olig	
	Fungiacyathidae	Fungiacyathus	sp 1	L. Mio	Deep
	Rhizangidae	Septastrae	marylandica	M. Mio - Pleist	Deep
			altispina	U. Plio	
			americana	L. Plio - Hol	
	Oculinidae	Archohelia	limonensis	U. Plio	
	Caryophylliidae	Caryophyllia	communis	M. Mio	Deep
			antillarum	L. Mio - M. Mio	
		Antillocyanthus	maoensis	U. Mio - L. Plio	Deep
			alatus	U. Mio - L. Plio	
			cristatus	U. Mio - L. Plio	
			gracilis	U. Plio	
		Trochocyathus	chevalieri	U. Mio - U. Plio	Deep

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
			duncani	L. Plio	
			rawsonii	L. Mio	
		Ceratotrochus	duodecimcostatus	U. Mio	Deep
		Paracyathus	henekeni	M. Mio - L. Plio	Deep
			sinuosus	U. Mio - L. Plio	
			adetos	U. Plio	
			pulchellus	L. Plio - Hol	
			texanus	U. Eoc	
		Oxysmilia	pliocenica	U. Plio	Deep
		Deltocyathus	italicus	L. Mio - Hol	Deep
			Sp sensu	M. Mio	
		Stephanocyathus		M. Mio	Deep
		Asterosimilia	abnormalis	M. Mio	Deep
			exarata	U. Mio - U. Plio	
			profunda	U. Mio - U. Plio	
			duncani	L. Mio	
			compressa	L. Mio	
			irregularis	U. Plio	
			trinitatis	L. Mio	
			machapooriensis	L. Mio	
		Desmophyllum	Sp Sensu	M. Mio	Deep
	Turbinoliidae	Dominicotrochus	dominicensis	L. Mio - U. Mio	
		Sphenotrochus	senni	L. Mio - U. Plio	Deep
			trinitatis	L. Mio	
			brassensis	U. Mio - L. Plio	
			hancocki	U. Plio	
	Flabellidae	Flabellum	sensu	U. Mio	Deep
			sp1	M. Mio	
			sp2	M. Mio	
		Gardineria	minor	U. Plio - Hol	Deep
	Guyniidae	Guynia	annulata	L. Plio - Hol	Deep
		Stenocyathus	sensu	L. Mio	Deep
		Schizocyathus	fissilis	U. Plio - Hol	Deep
		Pourtalocyathus	hispidus	U. Mio - Hol	Deep
	Dendrophylliidae	Balanophyllia	pittieri	U. Plio	Deep
			grandis	Hol	
			Sp sensu	L. Mio - M. Mio	
		Dendrophyllia	cornucopia	U. Mio - Hol	Deep
			Sp sensu	L. Mio	
	Asrocoeniidae	Astrocoenia	incrustans	U. Olig - Hol	
		Stephanocoenia	intersepta	L. Mio - Hol	Shallow
			ducani	U. Olig - Hol	
			spongiformis	M. Mio - Hol	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
	Pocilloporidae	Stylophora	affinis	L. Mio - Hol	
			canalis	L. Mio - Hol	
			granulata	U. Olig - Hol	
			imperatoris	L. Mio - Hol	
			minor	U. Olig - Hol	
			monticulosa	L. Mio - Hol	
			panamensis	M. Mio - Hol	
			undata	M. Mio - Hol	
		Pocillopora	arnoldi	L. Mio - Hol	
			portoricensis	M. Mio - Hol	
		Madracis	decaseptata	M. Mio	
	Acroporidae	Acropora	panamensis	M. Mio - Hol	
			saludensis	U. Eoc	
		Astreopora	goethalsi	U. Olig - Hol	
	Agariciidae	Agaricia	lamarki	M. Mio - Hol	Shallow
			undata	M. Mio - Hol	
			crassa	L. Mio - Hol	
			machapooriensis	L. Mio - M. Mio	
			panamensis	L. Mio	
			pennyi	L. Mio - M. Mio	
			trinitatis	U. Olig - M. Mio	
		Leptoseris	anguillensis	L. Mio	
			gardeneri	L. Mio - Hol	
			glabra	M. Mio - Hol	
			walli	L. Mio - M. Mio	
	Sideastreidae	Psammocora	gasparillensis	L. Mio - M. Mio	Shallow
			trinitatis	L. Mio - Hol	
			conferta	U. Olig - L. Mio	
			mendenhalli	L. Mio - Hol	
			siderea	L. Mio - Hol	
			silecensis	L. Mio - M. Mio	
		Pironastrea	anguillensis	L. Mio - Hol	Shallow
	Poritidae	Porites (I)	anguillensis	U. Olig - L. Mio	Shallow
			astreoides	L. Mio - Hol	
			macdonaldi	U. Olig - L. Plio	
			portoricensis	U. Olig - Hol	
			trinitatis	L. Mio - M. Mio	
			waylandi	U. Olig - Hol	
		Porites (II)	baracoensis	U. Olig - Hol	Shallow
			chipolanum	L. Mio - M. Mio	
		Goniopora	calhounensis	L. Mio - M. Mio	Shallow
			hilli	U. Olig - Hol	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Cidaroida	Faviidae	Alveopora	imperatoris	U. Olig - Hol	Shallow
			panamensis	L. Mio	
			tampae	U. Olig - L. Mio	
			convivatoris	U. Mio - L. Plio	
		Favia	dominicensis	L. Mio - Hol	Shallow
		Diploria	zambensis	L. Mio - Hol	Shallow
		Thysanus	corbicula	L. Mio - Hol	Shallow
		Antiguastrea	cellulosa	U. Olig - M. Mio	Shallow
		Montastrea I	brevis	L. Mio - Hol	Shallow
			imperatoris	U. Olig - M. Mio	
			limbata	L. Mio - Hol	
			trinitatis	L. Mio - M. Mio	
		Montastrea II	canalis	L. Mio - Hol	Shallow
			cavernosa	U. Olig - Hol	
			cylindrica	L. Mio - Hol	
			endothecata	U. Eoc - Hol	
			tampaensis	L. Mio	
		Solenastrea	bournoni	U. Olig - Hol	Shallow
			hyades	L. Mio - Hol	
		Agathiphyllia	hilli	U. Olig - M. Mio	Shallow
	Trachyphylliidae	Trachyphyllia	bilobata	U. Olig - Hol	Shallow
		Antillophyllia	sawkinsi	L. Mio - Hol	Shallow
	Meandrinidae	Placocyathus	trinitatis	L. Mio - Hol	Shallow
			variabilis	L. Mio - Hol	
	Oculinidae	Dichocoenia	tuberosa	M. Mio - Hol	Shallow
		Galaxea	excelsa	L. Mio - Hol	Shallow
	Mussidae	Antillia	gregorii	L. Mio - Hol	Shallow
	Cidaridae	Histocidaris	sanchezi	L. Eoc - U. Eoc	Shallow
		Stereocidaris	"a"	M. Eoc - U. Eoc	Shallow
			"b"	U. Cret - L. Paleo	
		Cidaris	bermudezi	L. Mio - M. Mio	Shallow
			cubensis	U. Eoc	
			pratti	M. Eoc - U. Eoc	
			splendens	L. Paleo - L. Eoc	
		Calocidaris	palmeri	M. Mio	Shallow
		Tretocidaris	anguillensis	L. Mio	Shallow
		Palmerius	roberti	U. Eoc	Shallow
		Eucidaris	tribuloides	L. Plio - Hol	Shallow
			madrugensis	L. Mio - L. Plio	
		Prionocidaris	spinidentatus	L. Olig - Pleist	Shallow
			katherinae	M. Mio	
			clevei	M. Mio	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
		Prophyllacanthus	cookei loveni leoni eocenicus peloria	M. Mio - U. Mio M. Eoc - U. Olig U. Cret U. Eoc L. Olig - L. Mio	Shallow
		Phyllacanthus	Phyllacanthus mortoni carolinesis	M. Eoc - U. Eoc U. Eoc U. Eoc	Shallow
	Rhabdocidaridae	Fellius	foveatus	L. Eoc - M. Eoc	Shallow
	Psychocidaridae	Tylocidaris	bermudezi A macneili salina walcotti	M. Eoc - U. Eoc U. Cret L. Paleo U. Paleo - L. Eoc U. Paleo - L. Eoc	Shallow
Calycina	Acrosaleniididae	Heterosalenia		U. Cret	Shallow
		Salenia	tumidula	U. Paleo - L. Eoc	Shallow
Arbacioida	Arbaciidae	Coelopleurus			Shallow
			infulatus carolinensis	M. Eoc - U. Eoc M. Eoc - U. Eoc	
		Arbia			Shallow
			aldrichi	U. Olig	
		Lytechinus			Shallow
	Toxopneustidae		floralanus	U. Eoc	Shallow
Holactypoida	Holactypidae	Metholactypus		1	Deep
		Amblypygus			Deep
			americanus	L. Eoc - U. Eoc	
		Echinoneus	cyclostomus	Pleist - Hol	Deep
Cassiduloida	Nucleolitidae	Pygopistes		1	Deep
	Echinolampadidae	Echinolampas	clevei aldrichi alta altissima anguillae appendiculata brachytoma lycopersicus plateia stronglya paragoga tanypetalis hemisphericus umbrella	L. Eoc - M. Eoc L. Eoc - U. Eoc L. Eoc - M. Eoc L. Eoc - M. Eoc U. Olig M. Eoc - U. Eoc L. Eoc - M. Eoc L. Eoc - M. Eoc L. Eoc - M. Eoc L. Eoc - M. Eoc L. Eoc - M. Eoc U. Eoc - L. Olig L. Mio L. Mio	Deep Deep

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth		
Spatangoida	Cassidulidae	Eurhodia	cartaginsis	L. Mio	Shallow		
			rugosa	M. Eoc - U. Eoc			
			holmesi	M. Eoc			
			matleyi	M. Eoc - U. Eoc			
			trojana	U. Eoc - L. Olig			
			patelliformis	U. Eoc - L. Olig			
		Rhyncholampas		L. Eoc - M. Mio	Shallow		
			matleyi	L. Eoc - M. Eoc			
			alabamensis	M. Eoc - U. Eoc			
			antillarum	L. Eoc - M. Eoc			
			conradi	U. Eoc			
			carolinensis	M. Eoc			
			ellipticus	L. Eoc - M. Eoc			
			ericsoni	U. Eoc - L. Olig			
			georgiensis	U. Eoc - L. Olig			
			gouldii	L. Olig - U. Olig			
			parallelus	L. Eoc - M. Eoc			
			Santeelampas			Shallow	
				oviformis			M. Eoc
			Cassidulus	U. Eoc		Deep	
		Rhynchopygus	L. Eoc	Deep			
		Gitolampas	georgiensis	L. Paleo			
	Hemiasteroidae	Hemiaster	herrerae	U. Cret	Deep		
			madrugensis	U. Cret			
			muscovensis	L. Paleo			
			parastatus	U. Paleo - L. Eoc			
			siboneyensis	U. Cret			
			gonzalezmunoz	U. Cret			
			Paleopneustidae	Pericosmus			Shallow
						stehlini	
	giganteus	U. Olig - L. Mio					
	depressus	U. Olig - L. Mio					
	marroquinensis	U. Olig - L. Mio					
	valenzuelai	L. Mio					
	atolladosae	U. Eoc					
	rojasi	U. Eoc					
	zanoletti	U. Eoc					
blanquizalensis	U. Olig - L. Mio						
camagueyanus	U. Olig - L. Mio						
mortenseni	U. Olig - L. Mio						
cubanus	U. Eoc						
roigi	L. Mio						

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
	Schizasteridae	Schizaster	beckeri	L. Eoc - M. Mio	Deep
			gigas	L. Olig	
			subcylindricus	M. Eoc - U. Eoc	
			altissimus	L. Eoc - M. Mio	
			bathypetalus	L. Eoc - M. Eoc	
			dumblei	L. Eoc - U. Eoc	
			hexagonalis	L. Eoc - M. Eoc	
			doederleini	L. Eoc - M. Eoc	
			pentagonalis	L. Plio	
			camagueyensis	M. Eoc	
			cartagensis	U. Eoc	
			cubitabellae	U. Olig - L. Mio	
			delgadoi	U. Eoc	
			gerthi	L. Mio - M. Mio	
			llagunoi	U. Cret	
			munozi	U. Eoc	
			ocalanus	U. Olig - L. Mio	
			guirensis	U. Eoc - L. Olig	
			riveroi	L. Mio	
			salutis	L. Mio	
			neuvitasensis	U. Eoc	
			rojasi	U. Eoc	
			santanai	U. Olig - L. Mio	
		Ditremaster		M. Eoc - U. Eoc	Deep
			beckeri	U. Eoc	
		Agassizia		L. Eoc - L. Mio	Deep
			avilensis	U. Olig - L. Mio	
			clevei	L. Eoc - L. Mio	
			alveari	L. Mio	
			inflata	L. Eoc - U. Eoc	
			lamberti	U. Eoc - L. Olig	
			mossomi	U. Olig	
		Aguayoaster		M. Eoc	Deep
			aquayoi	M. Eoc	
		Caribbaster	dyscritus	L. Eoc - M. Eoc	Deep
			loveni	L. Eoc - U. Eoc	
		Lambertona	lamberti	L. Eoc	Deep
		Linthia		U. Cret - U. Eoc	Deep
			alabamensis	L. Paleo	
			gonzalezmunoz	U. Cret	
			elevatus	U. Cret	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
			alta	U. Cret	
			trechmanni	L. Eoc	
		Prenaster	parvus	U. Eoc	Deep
		Cyclaster	jacksoni	U. Eoc	Deep
			sanchezi	U. Eoc	
			brodermanni	U. Eoc	
			palmeri	U. Eoc	
			drewryensis	U. Eoc - L. Olig	
		Holaster	cinctus	U. Paleo - L. Eoc	Deep
		Paraster	armiger	U. Eoc - L. Olig	Deep
			americanus	L. Olig	
	Micrasteridae	Habanaster		U. Eoc	Deep
			sanchezi	U. Eoc	
	Brissidae	Brissus	cabrerai	U. Eoc	Deep
			unicolor	L. Eoc - M. Eoc	
			camagueyensis	U. Eoc	
			caobaense	M. Eoc	
			durhami	M. Eoc - U. Eoc	
			minutus	U. Olig - L. Mio	
		Brissopsis	aguayoi	U. Olig - L. Mio	Deep
			biarritzensis	U. Eoc	
			blanpiedi	L. Olig	
			jimenoi	L. Mio - M. Mio	
			steinhatchee	U. Eoc - L. Olig	
		Eupatagus	alatus	L. Eoc - U. Eoc	Deep
			antillarum	L. Eoc - L. Olig	
			attenuatus	M. Eoc - U. Eoc	
			clevei	U. Eoc - M. Mio	
			defectus	L. Eoc - M. Eoc	
			gardnerae	U. Eoc	
			hildae	L. Olig - U. Olig	
			stefaninii	U. Eoc	
			ingens	M. Eoc - U. Eoc	
			ocalanus	U. Eoc - L. Olig	
			santanae	U. Olig - L. Mio	
			sanchezi	L. Mio	
			siboneyensis	U. Eoc	
			turibacoensis	U. Eoc	
			mortenseni	U. Olig - L. Mio	
		Macropneustes	armadilloensis	U. Eoc	Deep
			altus	L. Eoc - M. Eoc	
			angustus	L. Eoc - M. Eoc	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Phymosomatoida	Asterostomatidae	Meoma Plagiobrissus	parvus	L. Eoc - M. Eoc	Deep
			mortoni	U. Eoc - L. Olig	
			sp 1	L. Eoc - M. Eoc	Deep
			antigua	M. Eoc	
			curvus	U. Eoc - L. Olig	
			dixie	U. Eoc - L. Olig	
			loveni	L. Eoc - M. Eoc	
			abruptus	L. Eoc - M. Eoc	
			elevatus	L. Eoc - M. Eoc	
			latus	L. Eoc - M. Eoc	
			perplexus	L. Eoc - M. Eoc	
			robustus	L. Eoc - M. Eoc	
			pawsoni	L. Eoc - M. Eoc	
		Asterostoma	excentricum	L. Eoc - M. Eoc	Shallow
			dickersoni	M. Eoc	
			irregularis	M. Eoc	
			subcircularis	M. Eoc	
			vaughani	L. Eoc	
		Antillaster	arnoldi	L. Eoc - M. Mio	Shallow
			longipetalus	L. Eoc - M. Eoc	
			fernandezi	U. Olig - L. Mio	
			albeari	M. Eoc - U. Eoc	
			lamberti	U. Mio	
		Brissopsis	jimenoi	L. Plio - U. Plio	Shallow
		Brissopatagus	alabamensis	U. Eoc	
		Lovenia		L. Mio	
		Echinocardium	peloria	L. Eoc - M. Eoc	
		Phymosoma	multiaporus	L. Eoc - M. Eoc	
		Tiadechinus	chondra	L. Eoc - M. Eoc	
		Trochalosoma ?		M. Eoc	
		Dixieus	dixie	U. Eoc	
		Phymotaxis	mansfieldi	U. Olig	
		Arbacia		Hol	
Temnopleuroida	Temnopleuridae	Brochopleurus	pretiosus	U. Eoc	Shallow
			simplex	L. Eoc - M. Eoc	Shallow
		Gagara	chickasawhay	U. Olig	
Oligopygoida		Oligopygus	mossomi	U. Olig	
			salis	U. Paleo - L. Eoc	
			wetherbyi	L. Eoc - L. Olig	
			jamaicensis	L. Eoc - M. Eoc	
			cubensis	U. Eoc	
			haldemani	U. Eoc - L. Olig	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth	
Echinoida Clypeasteroida	clypeasteridae	Haimea	collignoni	U. Eoc	Shallow	
			phelani	U. Eoc - L. Olig		
			rotundus	M. Eoc		
			10 sp	L. Eoc - U. Eoc		
			alvarezi	U. Eoc - L. Olig		
			alta	M. Eoc - U. Eoc		
			ovumserpentis	M. Eoc - U. Eoc		
		Echinometra		U. Plio	Shallow	
		Clypeaster	rogersi	L. Olig - U. Olig	Shallow	
			rosaceus	U. Plio - Hol		
			cotteau	U. Eoc - L. Olig		
			maoadentroensis	L. Plio		
			oxybaphon	U. Olig		
			caudatus	L. Plio		
			santee	U. Paleo - L. Eoc		
	Fibularidae	Fibularia	alabamensis	U. Eoc	Shallow	
			jacksoni	L. Eoc - U. Eoc		
			texana	M. Eoc		
			vaughni	U. Eoc - L. Olig		
			ellipticus	L. Eoc - M. Eoc		
		Echinocyamus	bisexus	M. Eoc - U. Eoc	Shallow	
			parvus	M. Eoc - U. Eoc		
			meridionalis	M. Eoc		
			huxleyanus	M. Eoc		
	Neolaganidae	Neolaganum	dalli	L. Eoc - M. Eoc	Shallow	
			durhami	U. Eoc - L. Olig		
			acunai	M. Eoc - U. Eoc		
		Cubanaster	"x"	M. Eoc - U. Eoc	Shallow	
		Wythella	eldridgei	U. Eoc - L. Olig	Shallow	
		Weisbordella	cubae	M. Eoc - L. Olig	Shallow	
			absicata	U. Eoc		
			johnsoni	U. Eoc - L. Olig		
		Mellitidae	Encope	sverdrupi	U. Plio - Pleist	Shallow
				aberrans	U. Mio - Hol	
				Mellita	L. Mio	
			Periarchus	floridanus	L. Olig	Shallow
Protosutellidae		lyelli	M. Eoc - U. Eoc	Shallow		
		pileussinesis	U. Eoc			
		floridana	U. Eoc - L. Olig			
	Durhamella	ocalana	U. Eoc - L. Olig	Shallow		
	Mortonella	quinquefaria	U. Eoc - L. Olig	Shallow		
		Abertella	L. Mio - L. Plio	Shallow		

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Disasteroidea	Holasteridae	Protoscutella	conradi	M. Eoc	Shallow
			plana	M. Eoc	
			mississippiensis	M. Eoc	
			pentagonium	M. Eoc	
			toumeyi	M. Eoc	
		Cardiaster	palmeri	U. Cret	Shallow
			cubensis	U. Cret	
			leonensis	U. Cret	
		Echinocorys	ovalis	U. Paleol - L. Eoc	Shallow
			ovatus	U. Cret	
Meso	Urechinidae	Sancheaster	habanensis	M. Eoc	Shallow
	Bursidae	Bursa (Colubrellina)		M. Mio - U. Mio	
	Cymatiidae	Distorsio (Rhysema)		M. Mio	
	Ovulidae	Simnia (Calpurna)		M. Mio - L. Plio	Shallow
	Xenophoridae	Xenophora		M. Mio - Hol	Shallow
	Hipponicidae	Cheilea		M. Mio - L. Plio	Shallow
		Hipponix		U. Eoc	
	Aclidae	Aclis		M. Mio	
	Epitoniidae	Epitonium		M. Mio	Shallow
		Cylindriscala		Hol	Shallow
Meso	Modulidae	Scalina		M. Eoc - Hol	Shallow
		Modulus		U. Olig - Hol	Shallow
		Psammodulus		M. Mio	Shallow
		Seguenzia		M. Mio	Shallow
	Litiopidae	Alaba		M. Mio - Hol	Shallow
	Mathildidae	Mathilda		M. Mio	Shallow
	Vitrinellidae	Teinostoma		L. Mio - M. Mio	Shallow
		Vitrinella		M. Mio	Shallow
		Cyclostremiscus(Ponocyclus)		M. Mio	Shallow
		Solariorbis		M. Eoc - M. Mio	Shallow
Meso	Smaragdiinae	Didianema		M. Mio	Shallow
		Smaragdia		M. Mio	
	Turritellidae	Turritella		U. Olig - Pleist	Shallow
		Vermicularia		L. Mio - Pleist	Shallow
	Olividae	Springvaleia	leroyi	L. Plio	Shallow
		Dactylidella		L. Plio - Pleist	Shallow
		Oliva		M. Mio - Pleist	Shallow
		Olivella		U. Mio - U. Plio	Shallow
		Niteoiva		M. Mio - Pleist	Shallow
		Minioliva		M. Mio - Pleist	Shallow
		Macgintiella		U. Mio - Pleist	Shallow
Neo		Ancilla		U. Mio - U. Plio	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Neo-	Buccinidae	Agaronia		M. Mio - Pleist	Shallow
		Cymatophos		M. Mio - U. Plio	Shallow
		Antillophos		M. Mio - Pleist	Shallow
		Solenosteira		M. Mio - U. Plio	Shallow
		Metula		U. Mio - U. Plio	Shallow
		Amarophos		U. Mio	Shallow
		Hindsia		U. Mio - L. Plio	Shallow
		Pisania (Celatoconus)		Hol	Shallow
		roycei		Pleist	
	Obtortionidae	Alabina		M. Mio - Pleist	Shallow
Neo	Nassaridae	Nassarius		U. Olig - Pleist	Shallow
Neo	Conidae	Conus		U. Olig - Hol	Shallow
Meso	Terebridae	Strioterebrum		M. Mio - Pleist	Shallow
		Panaterebra		M. Mio - U. Mio	Shallow
		Oreoterebra		M. Mio - U. Plio	Shallow
		Polinices		L. Mio - Hol	Shallow
		Stigmaulax		M. Mio - Hol	Shallow
		Naticarius		M. Mio - Pleist	Shallow
		Glossaulax		M. Mio - U. Mio	Shallow
		Natica		U. Mio - Pleist	Shallow
		Tectonatica		M. Mio	Shallow
		Sinum		M. Mio - Pleist	Shallow
Meso			polandi	Pleist	
		Smaragdia			Shallow
Neo	Cancellariidae		edentula	Pleist	
		Cancellaria		L. Mio - Pleist	Shallow
			guppyi	U. Mio	
			mauryae	U. Mio	
			juncta	U. Mio	
			harrisi	U. Mio - L. Plio	
			rowelli	L. Mio - M. Mio	
			inquilinus	L. Plio	
			gabbiana	L. Mio - M. Mio	
			epistomifera	L. Mio - L. Plio	
			bajonensis	U. Mio	
			pectilis	L. Plio	
			miranda	U. Mio	
			lopezana	L. Mio - M. Mio	
		Aphera	islacolonis	L. Mio - L. Plio	Shallow
		Perplicaria	canae	U. Mio	Shallow
		Trigonostoma	gurabis	U. Mio	Shallow
		Axelella	emblema	L. Mio - M. Mio	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Neo	Columbellidae	Agatrix	losquemadica	U. Mio - L. Plio	Shallow
		Admetula	zalayana	L. Plio	Shallow
		Strombina		M. Mio - U. Mio	Shallow
		Sincola		M. Mio - U. Plio	Shallow
		Sinaxila		L. Plio - U. Plio	Shallow
		Mitrella		U. Mio - Pleist	Shallow
		Lirastrombina		U. Mio - Pleist	Shallow
		Costoanachis		M. Mio - Pleist	Shallow
		Strombinophos		U. Mio - Pleist	Shallow
		Anachis		U. Mio - Pleist	Shallow
		Parvanachis		U. Plio - Pleist	Shallow
		Cosmioconcha		U. Mio - Pleist	Shallow
Neo	Marginellidae	Volvarina		U. Mio - Pleist	Shallow
		Prunum		U. Mio - Pleist	Shallow
		Persicula		M. Mio - Pleist	Shallow
		Dentimargo		U. Mio - U. Plio	Shallow
		Marginella		U. Mio - Pleist	Shallow
			formosa	Pleist	
		Granulina		U. Plio - Pleist	Shallow
		Granula		U. Plio - Pleist	Shallow
Cephalaspidea	Acteonidae	Ovulactaeon	aldrichi	M. Eoc	Shallow
		Acteocina		M. Mio - Pleist	
Cephalaspidea	Cylichnidae	Cylichnella		M. Mio - U. Plio	Shallow
		Cylichna		M. Eoc - U. Olig	Shallow
	Caecidae	caecid		M. Mio - Pleist	Shallow
Neo	Turridae	Polystira		M. Mio - Pleist	Shallow
		Agladrillia		M. Mio - Pleist	Shallow
		turrid		U. Mio - Pleist	Shallow
		Hindsiclava		M. Mio - Pleist	Shallow
		Clathrodrillia		M. Mio - Pleist	Shallow
		Ithycythara		M. Mio - Pleist	Shallow
		Knefastia		L. Plio - Pleist	Shallow
		Glyphostoma		U. Mio - Pleist	Shallow
		Carinodrillia		U. Mio - Pleist	Shallow
		Syntomodrillia		U. Mio - Pleist	Shallow
		Kurtziella		U. Mio - Pleist	Shallow
		Crassispira		M. Mio - Pleist	Shallow
		Compsodrillia		U. Mio - Pleist	Shallow
		Scobinella		U. Mio - Pleist	Shallow
		Fusiturricula		U. Mio - Pleist	Shallow
		Miraclathurella		M. Mio - Pleist	Shallow
		Bellaspira		U. Mio - Pleist	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Meso	Architectonicidae	Thelecythara	compsa	U. Plio - Pleist	Shallow
		Architectonica		L. Mio - Pleist	Shallow
		Pseudotorinia		U. Mio - Pleist	Shallow
		Heliacus		U. Mio - Pleist	Shallow
Meso	Strombidae	Strombus		10 M. Mio - Pleist	Shallow
	Siliquariidae	Siliquaria		U. Plio - Pleist	
	Pyramidellidae	turbonilline		M. Mio - Pleist	
		Eulimella		U. Plio - Pleist	
pyramidelline		M. Mio - Pleist			
Eulimastoma		U. Mio - Pleist			
Neo		Ondina	L. Plio - Pleist		
	Volutidae	Voluta	U. Mio - Pleist	Shallow	
	Ringiculidae	Ringicula	U. Mio - Pleist	Shallow	
	Vermetidae	Petalconchus	L. Mio - Pleist	Shallow	
Serpulorbis		M. Mio - Pleist	Shallow		
Neo	Mitridae	Mitra	U. Mio - Pleist	Shallow	
			Pleist		
		Subcancilla	M. Mio - Pleist		
		Retusidae	Volvulella	M. Mio - Pleist	Shallow
Sulcoretusa	U. Mio - Pleist		Shallow		
	Rissoinidae	Crepticacella	M. Mio	Shallow	
		Rissoina	M. Eoc	Shallow	
	Rissoidae	rissoine	U. Mio - Pleist		
		Alvania	U. Mio - Pleist		
Meso	Calyptraeidae	Rissoa	M. Mio		
		Crucibulum	L. Mio - Hol	Shallow	
		Calyptraea	L. Mio - Pleist	Shallow	
		Crepidula	M. Mio - U. Plio	Shallow	
		Cypraeidae	Luria	U. Plio - Pleist	Shallow
			Macrocypraea	U. Plio - Pleist	Shallow
	cypraeid		M. Mio - Pleist	Shallow	
	Cuvierinidae	Cavolinia	L. Plio - Pleist	Shallow	
		Diacria	L. Plio - Pleist	Shallow	
		Styliola	U. Mio - Pleist	Shallow	
	Cephalaspidea	Bullidae	Bulla	L. Plio - Pleist	Shallow
		Eulimidae	eulimid	M. Mio - Pleist	
	Meso		Cassidae	Niso	M. Mio - Pleist
Sconsia		U. Mio - Hol		Shallow	
Bathygalea		U. Mio		Shallow	
Cassis		L. Plio - Pleist		Shallow	
Phalium		L. Plio - Pleist		Shallow	
		Morum	macgintyi	Pleist	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth	
Archaeo	Limacinidae	Limacina		U. Mio - Pleist		
		Teinostoma		M. Mio - Pleist		
	Adeorbidae	Solariorbis		M. Mio - Pleist		
		Meioceras		L. Mio - U. Plio		
	Caecidae	Caecum		L. Mio - M. Mio	Shallow	
	Triphoridae	triphorid		U. Mio - Pleist	Shallow	
		Cyclostremiscus		M. Mio - Pleist		
	Skeneidae	Diodora		U. Olig - Hol	Shallow	
	Fissurellidae	Hemitoma		M. Mio - Hol	Shallow	
		Fissurella		M. Mio - Hol		
Neo	Personidae	Distorsio		M. Mio - Pleist	Shallow	
	Fasciariidae	Latrius		U. Mio - Pleist	Shallow	
		Fasciolaria		M. Mio - Pleist	Shallow	
Meso	Tonnidae	Malea		M. Mio - Pleist	Shallow	
Meso	Cerithiidae	Bittium		U. Olig - L. Plio	Shallow	
		Rhinoclavis		U. Mio - U. Plio	Shallow	
		Alabina		M. Mio - Hol	Shallow	
		Alaba		U. Olig	Shallow	
		Cerithium		U. Olig	Shallow	
	Archaeo	Trochidae	Microgaza		M. Mio - Hol	Shallow
			Calliostoma		U. Olig - Hol	Shallow
			Euchelus		L. Plio - Pleist	Shallow
			Solariella		L. Plio - Pleist	Shallow
	Neo	Epitoniidae	Epitonium		M. Mio - Pleist	
Coralliophilidae		Coralliophila		U. Mio - Pleist	Shallow	
Cerithiopsidae		Cerithiopsis		U. Mio - Pleist		
Terebridae		Terebra		U. Mio - U. Plio		
	Arene		U. Plio - Pleist			
Archaeo	Turbinidae	Tricolia		U. Mio - U. Plio	Shallow	
		Homalopoma		U. Mio	Shallow	
		Liotia		M. Mio - U. Mio	Shallow	
		Neritina (Nereina)		L. Mio - Hol	Shallow	
		Turbo		U. Olig	Shallow	
Meso	Ficidae	Ficus		M. Mio - L. Plio	Shallow	
		Solenosteira		U. Olig		
	Barleeidae	Barleeia		L. Plio - Pleist	Shallow	
		Balcis		U. Mio - Pleist		
	Eulimidae	Eulima		M. Mio - Hol		
		Niso		U. Mio - U. Plio		
		Atys		L. Plio - U. Plio		
	Haminoeidae	Haustellum		M. Mio - Pleist	Shallow	
	X- Neo	Muricidae	typhine		M. Mio - Pleist	

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
		Dicathais	handgenae	U. Plio	
		Eupleura		M. Mio - U. Plio	
		Murex		L. Mio - Pleist	Shallow
			annieae	Pleist	
			messorius	L. Mio - L. Plio	
			pennae	L. Mio	
			adelosus	U. Mio - L. Plio	
			macgintyi	Pleist	
		Chicoreus	cornurectus	M. Mio - L. Plio	Shallow
			dujardinoides	L. Mio	
			corrigendum	L. Mio	
			cosmani	U. Mio	
			clausii	L. Plio	
			enigmaticus	U. Mio	
			infrequens	L. Mio	
			pomatus	U. Mio - L. Plio	
			pomum	L. Mio - Pleist	
			compactus	U. Mio	
			domingensis	U. Mio - Hol	
			articulatus	M. Mio - Hol	
			formosus	M. Mio	
			amplius	U. Mio	
			yaquensis	U. Mio	
			eumekes	U. Mio	
		Pterynotus	phyllopterus	L. Plio - Hol	Shallow
			aliculus	L. Plio	
			neotripteris	U. Mio - L. Plio	
			mirificus	U. Mio - L. Plio	
		Poirieria	dominicensis	L. Plio	Shallow
			gabbi	L. Plio	
			collata	L. Plio - Pleist	
		Aspella	castor	L. Plio - Hol	Shallow
		Dermomurex	olssoni	U. Mio - L. Plio	Shallow
			granulatus	L. Plio	
			cracentis	L. Plio	
			pterynoides	U. Mio - L. Plio	
			portelli	L. Olig	
		Attiliosa	aldridgei	U. Mio - Hol	Shallow
		Hexagonus	oxytata	Pleist	
		Tritonalia	graceae	Pleist	
		Muricidea	mansfieldi	Pleist	
		Murexiella		U. Olig - Pleist	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Neo			hidalgoi	L. Plio - Hol	
			macgintyi	U. Plio - Hol	
			textilis	L. Mio - M. Mio	
		Muricopsis	praepauxillus	U. Mio - L. Plio	Shallow
			quisqueyensis	U. Mio	
		Murexsul	mimicus	U. Mio	
		Favartia	zalaya	U. Mio	Shallow
			germainae	U. Mio - Hol	
		Acanthotrophon	striatus	U. Mio	Shallow
		Typhis	sowerbii	U. Mio - Hol	Shallow
			obesus	L. Mio - L. Plio	
			alatus	U. Mio	
		Siphonochellus	expansus	L. Plio - Hol	Shallow
			cercadicus	L. Plio - U. Plio	
			apheles	L. Mio	
		Pterotyphis	spinirectus	L. Plio	Shallow
			pinnatus	L. Plio - Hol	
		Thais	triangularis	L. Plio - Hol	Shallow
			trinitatensis	U. Mio - Hol	
			santodomingensis	U. Mio - L. Plio	
		Spinidrupa	quadridentata	U. Mio - U. Plio	Shallow
			radwini	U. Mio - L. Plio	
			demissa	L. Plio	
		Urosalpinx	denticulatus	U. Mio	Shallow
		Cymia	henekeni	L. Mio	Shallow
			marcanoi	U. Mio	
		Vitularia	dominicana	L. Plio	Shallow
		Pteropurpura		U. Mio - Hol	Shallow
Meso	Potamididae	Batillaria		U. Olig	Shallow
		Potamides		U. Olig	Shallow
		Pyrazisinus		U. Olig	Shallow
Meso	Fossaridae	Fossarus		U. Olig	Shallow
Neo	Melongiidae	Melongena		U. Olig - Pleist	Shallow
		Busycon		U. Plio - Hol	Shallow
		Sinistrofulgur		U. Plio - Pleist	Shallow
Neo	Harpidae	Harpa		U. Olig	Shallow
Archaeo	Acmaeidae	Acmaea		M. Eoc - U. Eoc	Shallow
Anaspidea	Akeridae	Akera		U. Olig	Shallow
Notospidea	Tylodinidae	Umbraculum		U. Eoc	Shallow
Neo	Fusidae	Fusinus		Pleist	Shallow
			watermani	Pleist	Shallow
Stylommatophora	Polygyridae	Praticolella	prisca	M. Mio	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Order	Crassatellidae	Crassinella		M. Mio - Pleist	Shallow
		Eucrassatella		M. Mio - U. Plio	Shallow
	Corbulidae	Caryocorbula		M. Mio - Pleist	Shallow
		Varicorbula		U. Mio - Pleist	Shallow
		Bothrocorbula		M. Mio - Pleist	Shallow
Arcoida	Arcidae	Rasia		M. Mio - Pleist	Shallow
		Cunearca		M. Mio - Pleist	Shallow
		Anadara		U. Mio - U. Plio	Shallow
		Barbatia		L. Plio - Pleist	Shallow
		Acar		L. Plio - Pleist	Shallow
		Lunarca		L. Plio	Shallow
		Arca		M. Mio	Shallow
Arcoida	Glycymerididae	Tucetona		U. Eoc - Pleist	Shallow
		Glycymerella		U. Mio - Pleist	Shallow
		Glycymerus		U. Eoc	Shallow
	Semelidae	Ervilia		M. Mio - U. Plio	Shallow
		Abra		U. Mio - U. Plio	Shallow
Ostreoida	Pectinidae	Semele		M. Mio - U. Plio	Shallow
		Argopecten	ocalanum	U. Mio - Pleist	Shallow
		Leptopecten		M. Mio - U. Plio	Shallow
		Chlamys		U. Eoc - U. Plio	Shallow
		Flabellipecten		M. Mio - Pleist	Shallow
		Spathochlamys		L. Plio - Pleist	Shallow
		Amusium		M. Eoc - U. Eoc	Shallow
		Pecten		M. Mio	Shallow
Veneroida	Veneridae	Lirophora		U. Mio - Pleist	Shallow
		Macrocallista		M. Mio - Pleist	Shallow
		Gouldia		U. Mio - Pleist	Shallow
		Chione		U. Eoc - Pleist	Shallow
		Chionopsis		M. Mio - Pleist	Shallow
		Lamelliconcha		M. Mio - Pleist	Shallow
		Dosinia		U. Mio - Pleist	Shallow
		Pitar		L. Plio - Pleist	Shallow
		Transennella		U. Mio - Pleist	Shallow
		Mercenaria		M. Mio - Pleist	Shallow
	Lucinidae	Parvilucina		U. Mio - Pleist	Shallow
		Lucinisca		U. Mio - Pleist	Shallow
		Myrtea		U. Mio - U. Plio	Shallow
		Lucinoma		Pleist	Shallow
		Linga		M. Mio - U. Plio	Shallow
		Pleurolucina		U. Mio - L. Plio	Shallow
		Lepilucina		L. Plio	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Mytiloida	Nuculanidae	Saccella		M. Mio - Pleist	Shallow
		Jupiteria		L. Plio - Pleist	Shallow
	Nuculidae	Nucula		U. Mio - U. Plio	Shallow
		Lamellinucula		L. Plio - Pleist	Shallow
		Leionucula		L. Plio - Pleist	Shallow
		Acila		U. Mio	Shallow
	Cardiidae	Agnocardia	cinderellae	L. Plio	Shallow
		Acrosterigma	linguatigris	U. Mio	Shallow
		Americardia	media	U. Mio - Hol	Shallow
			guppyi	U. Mio - Hol	
		Trigoniocardia	haitensis	U. Mio	Shallow
			cercadica	U. Mio - Pleist	
			sambaica	U. Mio - L. Plio	
			marcanoi	U. Mio	
			leptopleura	U. Mio	
			maturensis	U. Mio - L. Plio	
			aminensis	L. Mio - M. Mio	
			mela joensis	L. Plio	
		Nemocardium	islahispaniolae	U. Mio - L. Plio	Shallow
			gurabicum	U. Mio	
		Laevicardium	laevigatum	U. Mio - Hol	Shallow
			vitellinum	U. Mio - Hol	
			venustulum	U. Mio - L. Plio	
		cardid		M. Mio - U. Plio	Shallow
		Laevicardium		M. Mio - U. Plio	Shallow
		Trachycardium	flexicostatum	U. Mio	Shallow
			lingualeonis	U. Mio - L. Plio	
			dominicense	L. Mio	
			tintinnabularum	L. Mio - U. Mio	
			bowdenense	L. Plio - Pleist	
			dominicanum	U. Mio	
	Chamidae	Chama		U. Mio - Pleist	Shallow
		Arcinella		M. Mio - U. Plio	Shallow
	Gryphaeidae	Hytissa		M. Mio - Pleist	Shallow
	Kelliellidae	Alveinus		M. Mio - L. Plio	Shallow
		Kelliella		L. Plio - U. Plio	Shallow
	Propeamussiidae	Cyclopecten		M. Mio - Pleist	Shallow
	Mytilidae	Crenella		M. Mio - Pleist	Shallow
		Lithophaga		U. Eoc - U. Plio	Shallow
	Dimyidae	Dimya		L. Plio - Pleist	Shallow
	Plicatulidae	Plicatula		L. Plio - Pleist	Shallow
	Carditidae	carditesine		M. Mio - Pleist	Shallow

Appendix. Continued.

Order	Family	Genus	Species	Range	Water depth
Ostreoida	Cardiniidae	Tellidorella		U. Mio - U. Plio	Shallow
	Tellinidae	Moerella		U. Mio - L. Plio	Shallow
		Eurytellina		M. Mio - Pleist	Shallow
		Tellina		U. Mio - U. Plio	Shallow
		Angulus		M. Mio - Pleist	Shallow
		Phyllodina		L. Plio - Pleist	Shallow
		Merisca		U. Plio	Shallow
	Noetiidae	Noetia		M. Mio - U. Plio	Shallow
		Arcopsis		L. Plio - Pleist	Shallow
		Eontia		L. Plio - Pleist	Shallow
	Limopsidae	Limopsis		U. Plio - Pleist	Shallow
		Pectunculina		U. Mio - U. Plio	Shallow
	Anomiidae	Anomia		U. Mio - Pleist	Shallow
	Verticordiidae	Trigonulina		U. Mio - Pleist	Shallow
	Mactridae	Mulinia		M. Mio - Pleist	Shallow
	Spondylidae	Spondylus		U. Mio - Pleist	Shallow
	Ostreidae	Crassostrea		M. Mio - Pleist	Shallow
		Ostreola		U. Mio - Pleist	Shallow
		Dendostrea		U. Mio - Pleist	Shallow
		Ostrea		M. Eoc - U. Eoc	Shallow
		Yoldia		U. Mio - Pleist	Shallow
	Solecurtidae	Tangelus		U. Plio - Pleist	Shallow
	Cuspidariidae	Cardiomya		U. Mio - Pleist	Shallow
	Pinnidae	Atrina		M. Mio - U. Mio	Shallow
Pterioida	Malleidae	Nayadina	ocalensis	U. Eoc	Shallow

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