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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Ecology and environments of an extreme faunal turnover in topical American

Scallops

A Dissertation submitted in partial satisfaction of the requirements for the degree

Doctor of Philosophy

in

Earth Sciences

by

James Travis Smith

Committee in charge:

>Professor Jeremy Jackson, Chair
>Professor Phil Hastings
>Professor Lisa Levin
>Professor Richard Norris
>Professor Kaustuv Roy

2007

The Dissertation of James Travis Smith is approved, and it is acceptable in quality

and form for publication on microfilm:

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Chair

University of California, San Diego

2007

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Chapters 2, 3 and 4 have been prepared for submission for publication in the journal Paleobiology with Jeremy Jackson as my co-author in essentially the same form presented here. The dissertation author was the primary investigator and author of all three of these papers.

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PUBLICATIONS

O'Dea, A., H. Fortunato, J.T. Smith, L. D'Croz, K. Johnson, J. Todd and J.B.C. Jackson. 2006. Environmental change preceded Caribbean mass extinction by 2 million years. Proceedings, National Academy of Science (*In Press*).

Smith, J. Travis and Kaustuv Roy. 2006. Selectivity during background extinction: Plio-Pleistocene scallops in California. Paleobiology 32(3): 408-416.

Smith, J. Travis, J.B.C. Jackson, and H. Fortunato. 2006. Diversity and Abundance of tropical American scallops (Bivalvia: Pectinidae) from opposite sides of the Central American Isthmus. The Veliger 48(1): 26-45.

ABSTRACT OF THE DISSERTATION

Ecology and environments of an extreme faunal turnover in topical American

Scallops

by

James Travis Smith

Doctor of Philosophy in Earth Sciences

University of California, San Diego, 2007

Professor Jeremy Jackson, Chair

The relative importance of biotic interactions relative to environmental

forcing is a fundamental question in paleontology and evolutionary biology.

Predictive models generally focus on forcing entirely derived from either one or the

other of these two possible mechanisms. Testing the relative effects of these drivers

is difficult, and to date has not been carried out in a rigorous quantitative setting in

which ecology and environment can both be independently determined. The work

presented here uses the family Pectinidae, the scallops, from either side of the

Isthmus of Panama, extending back 12 Ma to address this question. Evolutionary

patterns of diversity, extinction and origination in scallops are similar to those

observed in bivalves as a whole, including a high level extinction 1 to 2 Myr after the

final closing of the Isthmus of Panama. However, evolutionary patterns varied

considerably among different ecological groups. Larval ecology of scallops evolved
in response to changing environments in the Caribbean in a manner predicted by
ecological models. Body size evolved in a manner predicted by competitive
interactions but was also highly constrained by life habit and life history of the taxa.

The overall evolutionary pattern of tropical American scallops was consistent
with the model of extinction derived from metapopulation theory that help to explain
the significant time delay in extinction patterns relative to environmental changes
within newly forming habitats in the Caribbean. Taken together, these results
indicate that both biotic interactions and environmental forcing had significant effects
on evolutionary patterns. Biotic effects were constrained within limits set by life
history and life habit, which evolved in response to the environment. Finally, the
success of applying metapopulation models and ecologically based models of larval
ecology indicates that scaling ecological models upwards provides much better
explanations of evolutionary patterns than predictions based on intrinsic
macroevolutionary characteristics.

CHAPTER 1 - INTRODUCTION

The relative effects of biotic interactions and environmental change on evolutionary patterns is a longstanding question in paleontology (Vermeij 1987; Jablonski and Sepkoski 1996; Jablonski 1999; Jackson and Erwin 2006). To provide insight into this difficult debate requires a rigorous use of the fossil record in a manner that allows quantitative comparisons of ecological and environmental characteristics (Jackson and Erwin 2006). The separation of the Caribbean from the Pacific by the Central American Isthmus around 3.5 Ma (Coates et al. 1992, 2004; Coates and Obando 1996; Bartoli et al. 2005) provides an ideal system within which to address these questions (Jackson et al. 1996). The formation of the isthmus divided what was once one continuous fauna into two distinct faunas (Woodring 1966; Jones and Hasson 1985). Subsequently, these newly divergent but closely related faunas were exposed to very different regimes of environmental change and today the systems are very different. This allows us to ask very specific questions about expected evolution in response to environmental change.

A major enigmatic feature of the evolutionary patterns in tropical America that I will address throughout this work is that much of the peak in rates of faunal turnover in the Caribbean, especially for gastropods and reef corals, occurred up to 2 Ma after the final closure of the Isthmus and associated major changes in environments (Budd and Johnson 1999; Jackson and Johnson 2000; O'Dea et al. 2006). The decrease in regional productivity in the Caribbean has been postulated as the primary cause of extinctions (Vermeij and Petuch 1986; Allmon 2001) and this

hypothesis is supported by major changes in abundance of different trophic groups

(Todd et al. 2002) and evidence for a regional drop in productivity in the Southwest

Caribbean (SWC) between 4-3 Ma (O'Dea et al. 2006). However, the changes in

biotic communities that have been observed (Todd et al. 2002; O'Dea et al. 2006) can

also be viewed as a potential source of evolutionary pressure in a model of evolution

driven by biotic interaction (Vermeij 1978; Dawkins and Krebs 1983).

Throughout the three main chapters of this dissertation I will focus primarily

on specific ecological models that can be applied to the topical American system and

how these help to better understand the observed evolutionary patterns. Two main

themes will arise in all three of these studies. The first is the fundamental question

"Does ecology matter?" (Jackson 1988). This can be asked in the pure context of

biological interactions (Vermeij 1978, 1987; Dawkins and Krebs 1979) or this idea

can be expanded to ask whether or not differing ecologies can give rise to differing

evolutionary patterns (Jackson 1974, 1988; Jablonski and Sepkoski 1996).

The second major theme is to assess the degree to which ecologically based

models can be scaled upward to explain larger scale evolutionary patterns. There has

been a tendency to treat evolutionary patterns completely separately from ecological

patterns (Jablonski et al. 1985; Jablonski 1986) despite evidence that

macroevolutionary processes are not decoupled from microevolutionary processes

(Maurer et al. 1992). This derives from the difficulties of comparing across scales of

time and space (Jackson 1992; Levin 1992, 1999; Jablonski and Sepkoski 1996;

Jackson and Erwin 2006). Classic ecological studies necessarily focus on small

geographic scales across time frames of days to several years. Paleontologists

studying evolutionary patterns rely on the fossil record, which can range from a single sample at one locality, to many localities spread across a wide geographic range and encompassing thousands to millions of years. The field of macroecology (Brown 1995) arose in part to allow ecologists to expand their range of consideration, but their still remains a disconnect between more ecological based models of evolution, which tend to incorporate aspects of ecological fitness and energy, and macroevolutionary models which often focus more on consequences of specific ecological traits. So as this theme carries through the following three chapters, I hope to provide insight into the need for this disconnect between these two scales of models.

In the second chapter I will describe the basic patterns of biodiversity, origination, and extinction of species of tropical American scallops. Scallops were chosen because of their relatively high diversity and abundance in our samples from throughout the region and their wide range of life habits that allow analyses of ecological effects. In addition, a great deal is known about the basic biology of economically valuable scallop species that facilitate inferences about the ecology of many extinct species. The focus of my study of the evolutionary patterns will be the degree to which patterns are consistent across the entire family in relation to observed patterns for Caribbean bivalves in general on varying temporal and spatial scales.

In the third chapter I will explore the evolution of larval ecologies in response to the changing environments. I have done this using estimates of egg size and larval duration obtained from morphological development of the larval shell. I have applied several ecological models that relate ecological fitness to differing environmental

conditions, as well as, predictions of macroevolutionary models. The patterns were analyzed within and among genera and I assessed the relative importance of within versus between species variability. Utilizing the wide range of life habits present in scallops, I also present analyses of ecological constraints on larval ecology

In the fourth chapter I present analyses of patterns of body size evolution. Models based on biotic interactions and environmental changes predict decreasing size towards the recent in the Caribbean, whereas models based on metapopulation theory, predict both larger or smaller sizes in the Caribbean depending on other life history and phylogenetic constraints. I have assessed how the patterns I observe support these models based on life habit and the life history data presented in the previous chapters.

The two threads I am hoping to follow are addressed throughout the three chapters. The question of the importance of ecology will be directly tested in all three studies utilizing life habit variability within scallops and their differential use of the environments we have sampled. Testing our ability to scale from ecological models to evolutionary patterns is the focus of the two studies presented in chapters three and four in which I specifically compare predictions of macroevolutionary and ecological models.

Literature Cited

Allmon, W.D. 2001. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology 166: 9-26.

Bartoli, G, M. Sarnthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schönberg, and D.W. Lea. 2005. Final closure of Panama and the onset of northern hemisphere glaciation. Earth and Planetary Science Letters 237: 33-44.

Brown, J.H. 1995. Macroecology. University of Chicago Press. 269 Pp.

Budd, A.F., and K.G. Johnson. 1999. Origination preceding extinction during late Cenozoic turnover of Caribbean reefs. Paleobiology 25: 188-200.

Coates, A.G., L.S. Collins, M-P. Aubry, and W.A. Berggren. 2004. The geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama arc with northwestern South America. Geological Society of America Bulletin 116: 1327-1344.

Coates, A.G. J.B.C. Jackson, L.S. Collins, T.M. Cronin, H.J. Dowsett, L.M. Bybell, P. Jung, and J.A. Obando. 1992. Closure of the Isthmus of Panama: Te near-shore marine record of Costa Rica and western Panama. Geological Society of America Bulletin 104: 814-828.

Coates, A.G., and J.A. Obando. 1996. The geologic evolution of the Central American isthmus. Pp. 21-56 *in* J.B.C. Jackson, A.F. Budd, and A.G. Coates (eds.), Evolution and Environment in Tropical America: University of Chicago Press, Chicago, Illinois.

Dawkins, R., and J.R. Krebs. 1979. Arms races between and within species. Proceedings, Royal Society of London B 205: 489-511.

Jablonski, D. 1986. Background and mass extinction: the alternation of macroevolutionary regimes. Science 231: 129-133.

——.1999. The future of the fossil record. Science 284: 2114-2116.

Jablonski, D., and J.J. Sepkoski. 1996. Paleobiology, community ecology, and scales of ecological pattern. Ecology 77: 1367-1378.

Jablonski, D., K.W. Flessa, and J.W. Valentine. 1985. Biogeography and paleobiology. Paleobiology 11: 75-90.

Jackson, J.B.C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. American naturalist 108: 541-560.

——. 1988. Does ecology matter? Paleobiology 14: 307-312.

——. 1992. Pleistocene perspective on coral reef community structure. American Zoologist. 32: 719-731.

Jackson, J. B. C., A. F. Budd, and J. M. Pandolfi. 1996. The shifting balance of natural communities. Pp. 89-122 in D. Jablonski, D. H. Erwin, and J. E. Lipps, eds. *Evolutionary Paleobiology*. University of Chicago Press.

Jackson, J.B.C., and D.H. Erwin. 2006. What can we learn about ecology and evolution from the fossil record? Trends in Ecology and Evolution 21: 322-328.

Jackson, J.B.C., and K.G. Johnson. 2000. Life in the last few million years. Paleobiology 26 (Supplement): 221-235.

Jones, D.S., and P.F. Hasson. 1985. History and development of the marine invertebrate faunas separated by the Central American Isthmus. Pp. 325-355 in F.G. Stehli and S.D. Webb, Eds. The Great American Biotic Interchange. Plenum Press. New York.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

——. 1999. Fragile dominion: complexity and the commons. Perseus Books, Reading, Massachusetts, 272 Pp.

Maurer, B.A., J.H. Brown, and R.D. Rusler. 1992. The micro and macro in body size evolution. Evolution 46: 939-953.

O'Dea, A., J.B.C. Jackson, H. Fortunato, J.T. Smith, L. D'Croz, K.G. Johnson, and J.A. Todd. 2006. Environmental change preceded Caribbean extinction by 2 million years. Proceedings National Academy of Sciences *In press.*

Todd, J.A., J.B.C. Jackson, K.G. Johnson, H.M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proceedings of the Royal Society of London, B 269: 571-577.

Vermeij, G.J. 1978. Biogeography and adaptation: Patterns of marine life. Harvard University Press, Cambridge, Massachusetts, 332 Pp.

——. 1987. Evolution and Escalation. Princeton University Press.

Woodring, W. P. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110: 425-433.

CHAPTER 2 – PATTERNS OF DIVERSITY AND EVOLUTION

Introduction

The isolation of the Atlantic from the Pacific Ocean by the Isthmus of Panama 3.5 Ma (Coates et al. 1992, 2004; Coates and Obando 1996; Bartoli et al. 2005) was associated with large changes in oceanographic conditions, high faunal turnover, and significant reorganization of the benthic communities in the Tropical Western Atlantic (TWA) between about 3.5 to 1.5 Ma (Jackson and Johnson 2000; Todd et al. 2002; O'Dea et al., 2006). Early studies were based largely on extinction of gastropods (Woodring 1966; Vermeij 1978; Petuch 1982; Jones and Hasson 1985; Vermeij and Petuch 1986), but more recent analyses have included bivalves (Stanley and Campbell 1981; Stanley 1986a; Jackson et al. 1993), reef corals (Budd and Johnson 1999), and bryozoans (Cheetham and Jackson 1996, 2000), all of which exhibit increased evolutionary turnover after 3.5 Ma. However, rates of origination and extinction vary greatly among different taxa, resulting in very strong faunal turnover in some taxa such as gastropods, reef corals, and erect bryozoans but not in other groups such as bivalves and encrusting bryozoans (Cheetham and Jackson 1996; Budd and Johnson 1999, Jackson and Johnson 2000; Todd et al. 2002). Moreover, greater focus on origination also revealed that molluscan diversity in the TWA had generally increased relative to the Tropical Eastern Pacific (TEP) (Allmon et al. 1993, 1996), contrary to earlier conclusions that Caribbean diversity had greatly decreased (Woodring 1966, Jones and Hasson 1985, Stanley and Campbell 1981, Vermeij and Petuch 1986).

Some of the most important ecological changes are only apparent through compilations of relative abundance instead of just lists of taxa (Todd et al. 2002). Predatory gastropods and suspension feeding bivalves declined significantly in abundance, but not in overall diversity, while reef dwelling gastropods became more abundant (Todd et al. 2002). In contrast, other ecological groups of mollusks remained relatively unchanged in abundance. These differences between ecological patterns based on relative abundance data versus those derived only from taxonomic lists raise questions about the methodology of paleontological research programs and emphasizes the importance of using abundance data in addition to diversity (McKinney et al. 1998, Jackson and Erwin 2006). However, abundance data can be highly affected by sampling biases, so that samples must be collected in a standardized and systematic fashion (Jackson et al. 1999; Jackson and Erwin 2006).

A major enigmatic feature of the TWA extinction is that much of the peak in rates of faunal turnover, especially for gastropods and reef corals, occurred up to 2 Ma after the final closure of the Isthmus and associated major changes in TWA environments (Budd and Johnson 1999; Jackson and Johnson 2000; O'Dea et al. 2006). High levels of extinction around the end of the Pliocene and Early Pleistocene have also been noted in faunas as far north as Florida (Stanley and Campbell 1981; Stanley 1986a, Petuch 1982, 1995; Allmon et al. 1993, 1996) and California (Stanley 1986b; Smith and Roy 2006). However, the relation of extinction patterns in these more northern faunas to the formation of the Isthmus is difficult to define, despite the temporal correlation. Allmon (2001) postulated that the major environmental cause of extinction in the TWA was a regional decrease in productivity. This hypothesis is

supported by major changes in abundance of different trophic groups (Todd et al. 2002) and evidence for a regional drop in productivity in the Southwest Caribbean (SWC) between 4-3 Ma (O'Dea et al. 2006).

In this chapter, I describe basic patterns of diversity, origination, and extinction, and apparent causes of faunal turnover for the highly diverse and abundant bivalve family Pectinidae (scallops) in the SWC and TEP over the past 12 Ma. The family Pectinidae is monophyletic (Waller 1978, 1984, 1991, 1993, 2006) yet exhibits a great variety of life habits and ecology that are useful to dissect how changes in the environment have affected the evolutionary expansion or decline of different functional groups. I also examined patterns of origination and extinction at different taxonomic levels as well as the correspondence between diversity and abundance on a sample-by-sample basis. Use of all the available information provides a much more complete and subtle understanding of evolution and environment than that based on taxon counting alone.

Materials and Methods

Quantitative samples of fossil scallops from Panama, Costa Rica, and Ecuador were obtained from 226 bulk samples supplemented by the more than 350 collections of specimens gleaned from outcrops by members of the Panama Paleontology Project (PPP) over the past 20 years. Paleontologists have studied all of the sedimentary basins included in my study since the 1920s so I have been able to build on their early collections and stratigraphic framework. Samples come from three regions: (1) the TEP, (2) central and eastern Panama (referred to here as "isthmian"), and (3) the Caribbean coast of western Panama and Costa Rica (Fig. 2.1). The most important
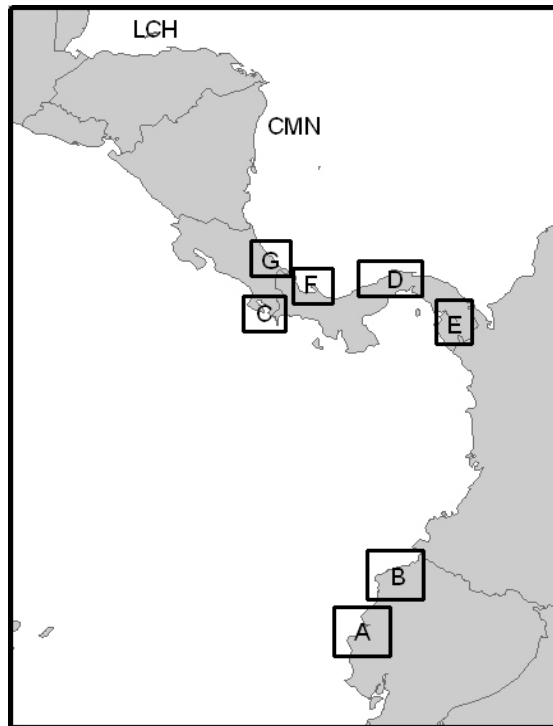
Figure 2.1. Map of sample areas. Boxed areas enclose the generalized basins described in the text; (A) Manabi, (B) Borbon, (C) Burica/Nicoya Peninsulas, (D) Canal Zone, (E) Chucanague, (F) Bocas del Toro and (G) Limon. Dredge samples were collected in two areas, (LCH) Los Cochinos, Honduras and (CMN) Cayos Moskitos, Nicaragua, where no fossils were sampled.

collections from the TEP are from the Borbon and Manabi basins in Ecuador (Pilsbry

and Olsson 1941; Olsson 1964; Hasson and Fischer 1986; Aalto and Miller 1999;

Landini et al. 2002; Cantalamessa et al. 2005; Collins et al. *In preparation*), the

Nicoya Peninsula in Costa Rica, and the Burica Peninsula in Panama (Olsson 1942;

Coates et al. 1992). Collections from the isthmian region that have both TEP and

TWA affinities include the classic formations from the Canal Zone (Woodring 1957-

1982; Collins et al. 1996b; Johnson and Kirby 2006), the north-central Coast of

Panama (Coates 1999), and the Darien region of Panama (Coates et al. 2004). The Caribbean region is the most extensively sampled and includes the Limon basin in northeastern Costa Rica (Olsson 1922; Collins et al. 1995; McNeill et al. 2000), and the Bocas del Toro basin in northwestern Panama (Olsson 1922; Collins 1993; Collins et al. 1995; Coates et al. 2003, 2005). Finally, dredge samples of recent scallops were obtained from the TEP and SWC as a baseline for comparison and calculation of Lyellian percentages for samples of fossils (Fig. 2.1; Smith et al. 2006).

Bulk samples were first sorted to class (bivalve, gastropod, coral, etc.). Scallops were picked and sorted from the bivalve fraction and identified to species following Waller (1969, 1984, 1991, 1993, 2006). Previously undescribed species were identified using open nomenclature pending more thorough taxonomic comparison with samples from outside the regions sampled. Appendix 1 lists all of the species found in this study. Individual samples were combined into faunules (Jackson et al. 1999; O'Dea et al. 2006) to obtain a more representative sample of the composition and diversity of the scallop fauna from different places, environments, and ages through time. A faunule represents a group of samples from a single outcrop or closely adjacent exposures that can be assigned with confidence to the same age and environment. Appendix 2 lists all of the faunules along with their age, environmental conditions, and diversity of scallops used in this study. These groupings do not reflect completely equivalent sampling in terms of range of environment or sampling intensity, but they provide larger sample sizes allowing statistical analysis of patterns within time bins.

Diversity was calculated as species richness (S), Shannon-Weiner Diversity (H), and estimates of species richness using the Chao1 and Chao2 equations (Chao 1984, 1987; Hayek and Buzas 1997; Foggo et al. 2003). Species richness was calculated using all of the different collections combined but H and the Chao indices were calculated using only occurrence data and H was calculated using only the quantitative data from bulk samples. Regional stratigraphic ranges were calculated for all species collected based on actual occurrence and range-through data within 1 Ma time bins to assess general trends in diversity. I also calculated extinction and origination rates through time based upon numbers of occurrences and per taxon rates.

Diversity in Space and Time

The fossil record of the past 12 Ma is much more complete for the SWC than the TEP (Coates et al. 1992; Figs. 2.2 and 2.3). Detailed sampling in the SWC has produced a reasonably complete record of scallop macroevolution, especially for the last 5 Ma. I sampled 14 faunules from the Late Pliocene and Pleistocene, 16 faunules from the Early Pliocene, and seven faunules from the Late Miocene. The most important gap in the record is for the Pleistocene younger than 1.4 Ma and the interval from about 4.3 to 7 Ma is relatively poorly sampled. The isthmian region includes 15 Late Miocene faunules and nothing from younger deposits including the Pleistocene deposits reported by Woodring (1957-1982). The record from the TEP includes a huge gap in sampling between 7.3 to 3.6 Ma. Seven faunules were sampled from the Late Miocene and seven faunules from the Late Pliocene to Early Pleistocene.
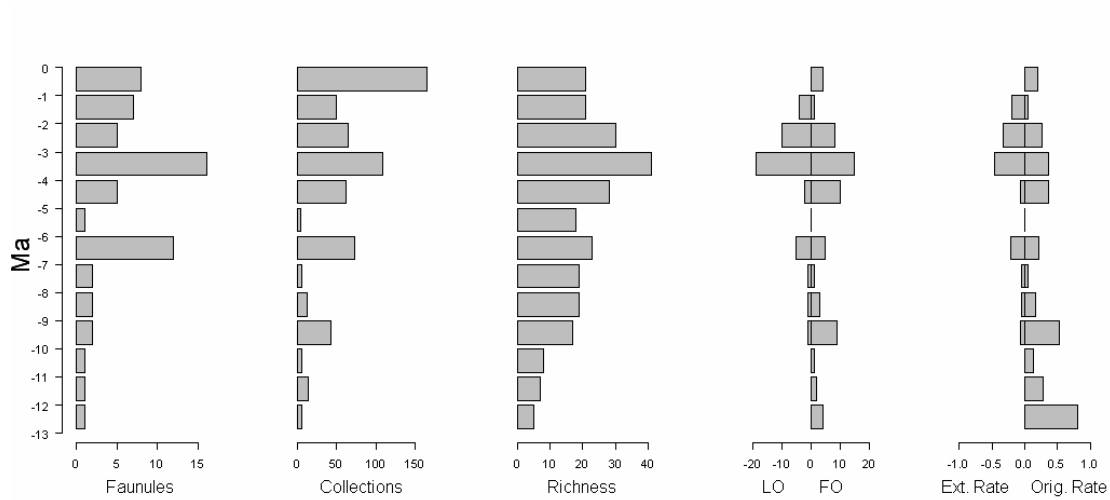
Figure 2.2. Caribbean sampling, species diversity, extinction and origination. Sampling is plotted as the number of faunules and collections. Species values are plotted as numbers of species for Richness, first occurrences (FO) and last occurrences (LO) and as per taxon rates for extinction and origination rates. All data were calculated in 1 Ma time bins.
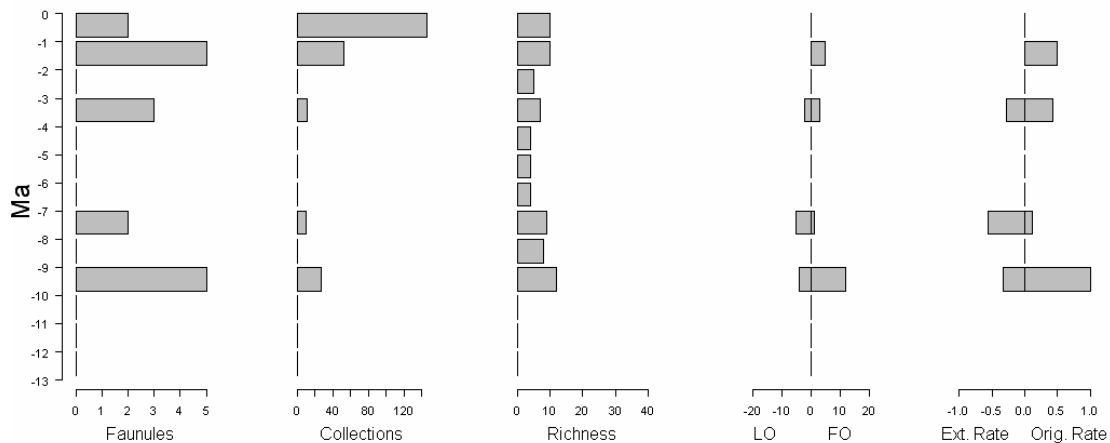
Figure 2.3. Eastern Pacific sampling, species diversity, extinction and origination. Values were calculated the same as in Figure 2.2.

Scallops were present in more than 95 % of all the samples both fossil and

recent, indicating that the species within this family utilize a very broad range of

environments comparable to bivalves as a whole. There were 83 species of Pectinidae

in my collections, 61 from the SWC, 18 from the TEP, and 3 that occur as fossils in both regions (Appendix 1). Species richness over the past 12 Ma was much more variable in the SWC than the TEP (Figs. 2.2, 2.3). SWC diversity increased from a low of 8 species in the Late Miocene to a high of 41 species in the Middle Pliocene (4 to 3 Ma) and then declined to 22 species today (Fig. 2.2). In contrast, diversity in the TEP was essentially unchanged over the same period, with the apparent decrease between 7 to 4 Ma due to a lack of samples for this interval so that the data are for range-through taxa only. Ten species occurred in the Late Miocene and Early Pliocene collections and 9-10 species in the Pleistocene to Recent (Fig. 2.3).

I constructed sampling curves for each time bin sampled to test for sampling bias, and compared numbers of species collected to the total known diversity represented by collected and range-through taxa combined. In the SWC (Fig. 2.4A), the most heavily sampled fossil time bin, as measured by total number of specimens, is the Middle Pliocene (4 to 3 Ma). A remarkable 40 of 41 total known taxa (98%) were recovered from this interval. Excluding the Early Pleistocene (1 to 2 Ma), the next four most heavily sampled time bins (10 to 9, 5 to 4, 3 to 2, and 7 to 6 Ma) contained between 82 - 92% recovery of species known to have been present. In contrast, the five most poorly sampled bins (6 to 5, 9 to 8, 8 to 7, 12 to 11, and 11 to 10 Ma) contained less than 50% of the species known to have occurred during those age intervals. The records for two bins must be addressed separately. The high recovery (80%) of the oldest bin (13 to 12 Ma) is an artifact of the first occurrence of all but a single Early Miocene species. Finally, the Early Pleistocene (2-1 Ma) bin is relatively well sampled (the third most specimens), but contained only 67 % of the

species known to have occurred in the SWC during this time. I attribute this low

recovery to the small number of faunules sampled (all from Swan Cay and
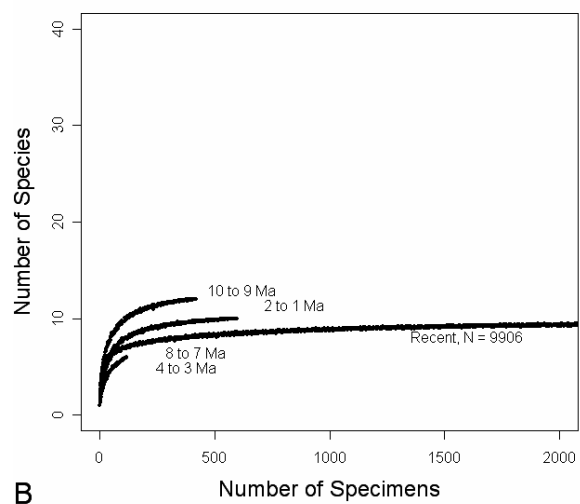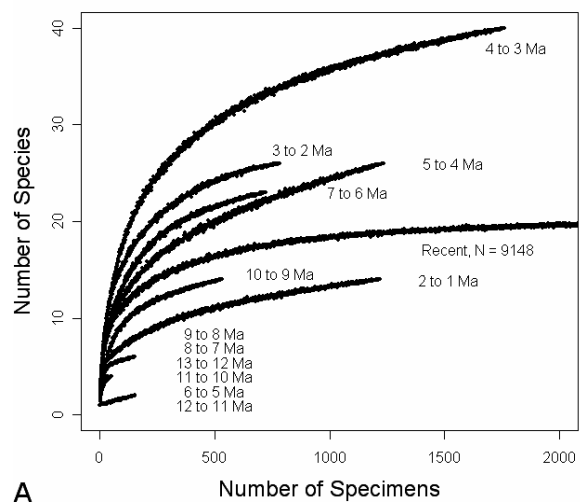
Figure 2.4. Collector's curves. Sampling effort for the time bins sampled in the Caribbean (A) and eastern Pacific (B). Axis was truncated at 2000 specimen, far less than the sampled level of the Recent time bins, to allow visual appraisal of the fossil time bins.
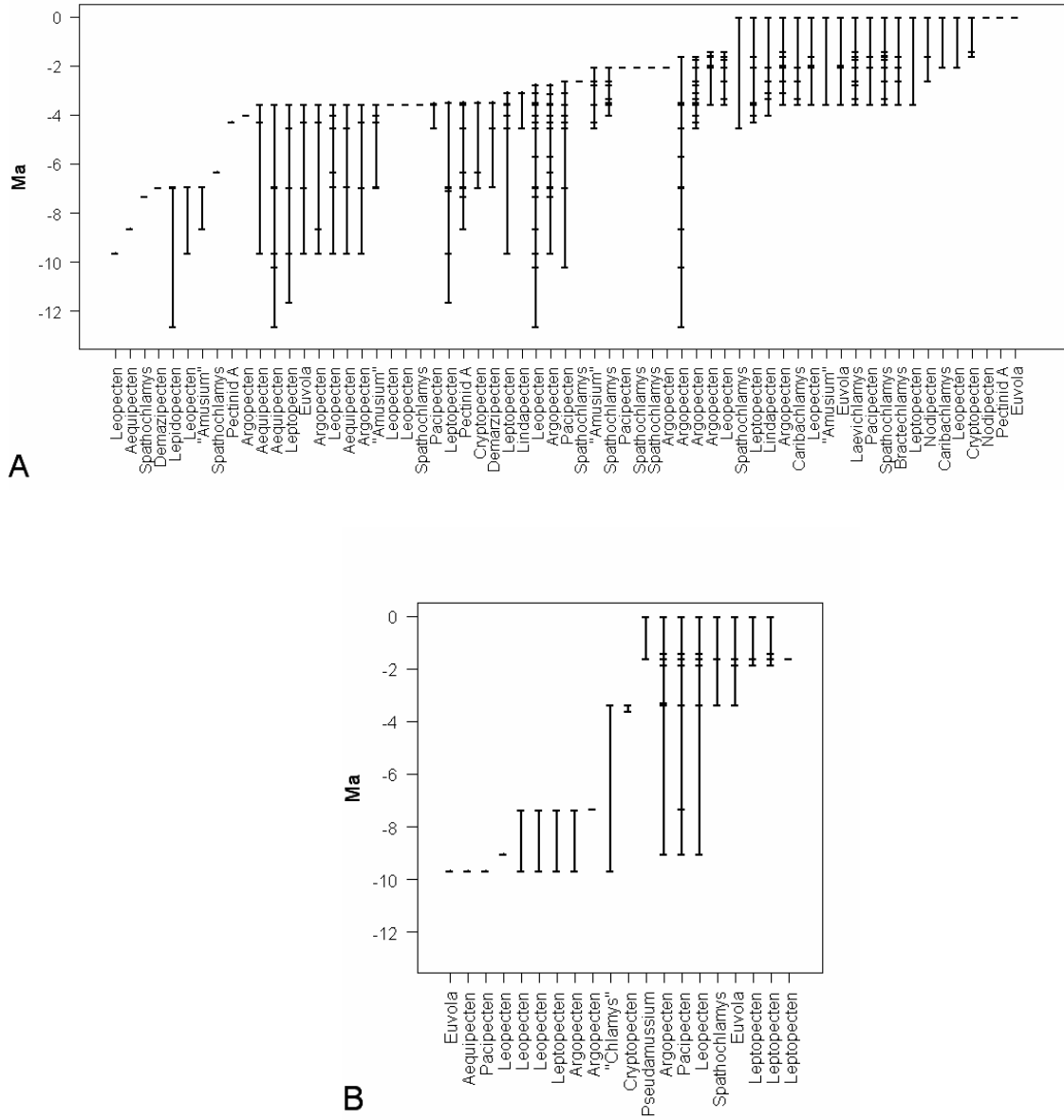
Figure 2.5. Stratigraphic ranges of tropical American scallops in the Caribbean (A) and eastern Pacific (B). Tick marks indicate actual stratigraphic occurrences. Ranges are labeled with the genus name for comparison with Table 1.

several faunules in the Limon basin) coupled with the increasing heterogeneity of

Caribbean environments at this time (O'Dea et al. 2006).

Sampling in the TEP was generally good (Figure 2.4B) despite the generally small number of specimens because of the greater homogeneity of TEP environments and relatively low numbers of species throughout the last 12 Ma. The stratigraphic ranges of all species in this study are depicted in Figure 2.5.

Origination, Extinction, and the Ecology of Faunal Turnover

The peaks in both origination and extinction in the SWC at 4 to 3 Ma coincide with the maximum diversity of scallop species. This is true for both the raw numbers of first and last occurrences (Fig. 2.2B) and for per taxon rates (Fig. 2.2C). In contrast, there is no obvious peak in origination or extinction in the TEP, although the 3 Ma gap in sampling may obscure a genuine peak in faunal turnover between 4 to 3 Ma (Fig. 2.3 B, C).

The overall patterns of diversity and evolution of scallops in the SWC correlate closely with those observed for bivalve genera and subgenera from the same region (Todd et al. 2002). There is a significant correlation between number of scallop species and bivalve genera and subgenera (Fig. 2.6A; $r^2 = 0.739$, P = 0.0003) and rates of extinction (Fig. 2.6B, $r^2 = 0.736$, P = 0.0004). The correlation between rates of origination for the 2 groups is only marginally significant (Fig. 2.6C; $r^2 = 0.324$, P = 0.0536).

Scallops exhibit a very wide range of life habits, including byssal attachment, free swimming, cementing and nestling on both level bottoms and hard substrata (Stanley 1970); although the two latter life habits were not observed in our samples from the SWC. Several genera exhibit a mixture of life habits. Most species of
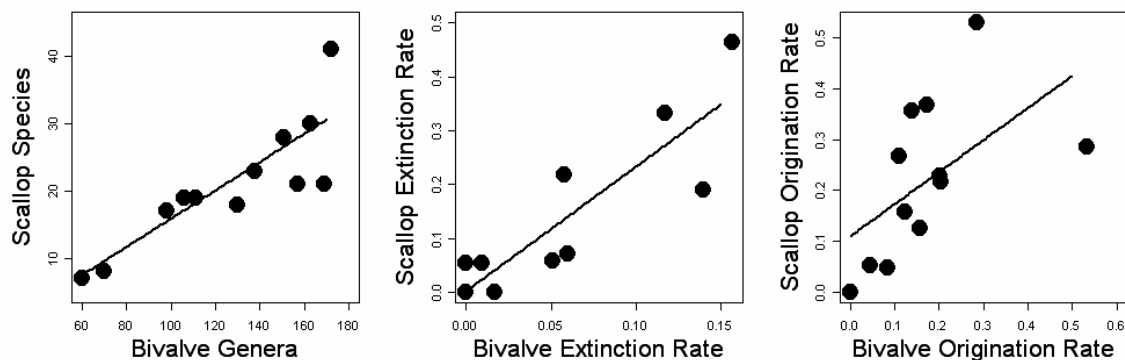
Figure 2.6. Comparison of taxonomic extinction rates. Plot compares the extinction rates for all bivalves (data from Todd et al. 2002) to the rates obtained in this study for scallop species. Individual points represent a 1 Ma time bin. There is a significant correlation between the calculated rates (see text).

scallops begin their juvenile benthic existence attached by byssal threads to small

hard substrata, but subsequently detach to become merely sedentary or strongly free-

swimming as adults (Stanley 1970; Waller 1984, 1991, 2006). However, species in

several genera, particularly those associated with coral reef and seagrass

environments, retain byssal attachment as adults. Life habits of most species are

readily apparent for fossil as well as living species from their shell morphology

(Stanley 1970), although the system breaks down for the genus *Leptopecten* that does

not fit the overall morphological pattern.

I exploited these ecological differences among scallops to examine the

ecological patterns associated with faunal turnover. All species were assigned to one

of four groups based on differences between the two most highly distinctive life

habits, (1) byssally attaching and (2) free swimming, and the two most abundant

genera with mixed life habits, (3) *Argopecten* (*sensu stricto*) excluding the

undescribed Pectinid Genus A (Smith et al. 2006), and (4) *Leptopecten* (plus

Pacipecten) that defy clear cut ecological separation. The four groups include 63 of the 82 scallop species (77 %) of the entire tropical American fauna sampled from the two oceans combined.

Byssally attaching scallops include species in the genera *Spathochlamys*, *Demarzipecten*, *Caribachlamys*, *Bractechlamys*, and *Laevichlamys*. *Spathochlamys* occurs in both the SWC and TEP, whereas the other byssally attaching genera are restricted to the Caribbean where they are overwhelmingly associated with coral reef environments. Free swimming species include all those traditionally assigned to the genus *Euvola* (Waller 1991). However, Waller (2006) has emended this group and species in this group are now assigned to two genera, *Leopecten* and *Euvola*. This groups also includes species traditionally considered *Amusium*, which Waller (1991) included in the genus *Euvola*. The two taxonomically defined groups are distinct ecologically and are diverse and abundant enough to justify separate analysis. *Argopecten* occurred in all environments sampled whereas *Leptopecten* were more narrowly distributed ecologically in the SWC. Recent *Leptopecten* in the TEP have been described as r-selected (Morton 1994), a life history pattern that appears to be unique among tropical American scallops.

The proportional diversity and abundance of the four groups in the SWC varied enormously over the last 13 Ma (Figure 2.7). I used proportions instead of absolute numbers of species and specimens to reduce the effects of sampling bias. The proportion of species richness through time was based on actual occurrences plus range through data (Fig. 2.7A). The most notable difference is in the byssally attaching group that was absent prior to 8 Ma except for one species from the
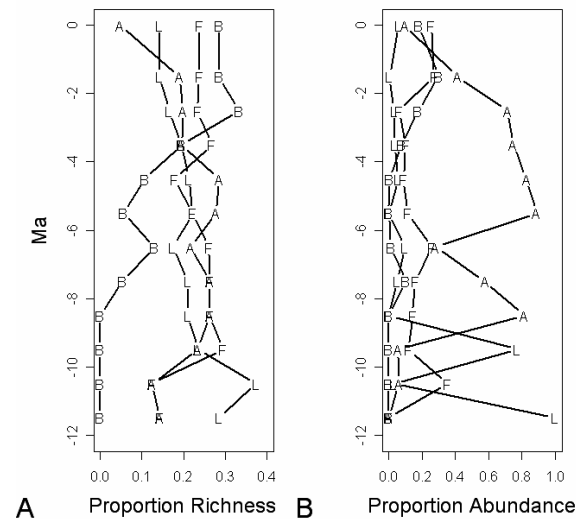
Figure 2.7. Proportions of richness and
abundance in the Caribbean. Proportion of
species richness and abundance is plotted for
byssally attaching (B), free swimming (F),
Argopecten (A) and Leptopecten (L) in 1 Ma
time bins. This data does not include all
species in the data set, so proportions do not
sum to 1 (see text).

reefal Emperador Limestone (16 to 18 Ma) that was not included in the analysis. The

proportion of byssally attaching species increased gradually to < 15 % from 8 to 4

Ma, after which diversity increased more rapidly until 2 Ma when byssally attaching

species became the most diverse group. *Argopecten* diversity increased to about 30 %

in the Early Pliocene, when it was the most diverse scallop genus, and then gradually

declined to only a single species. *Leptopecten* was the most diverse group 11- 10 Ma

but declined thereafter.

Patterns of proportional abundance for the four groups contrast markedly with

patterns of proportional diversity (Fig. 2.7B). Sampling is poorest before 8 Ma (Fig.

2.4A), so the highly erratic nature of the older portion of this plot is most likely due to

sampling bias. Afterwards, *Argopecten* was overwhelmingly the most abundant

group of scallops in the SWC before plummeting in the Late Pleistocene to Recent.

Byssally attaching species steadily increased in relative abundance after 4 Ma did not

become numerically dominant. Relative abundance of *Leptopecten* and free

swimming scallops varied much less after 8 Ma.
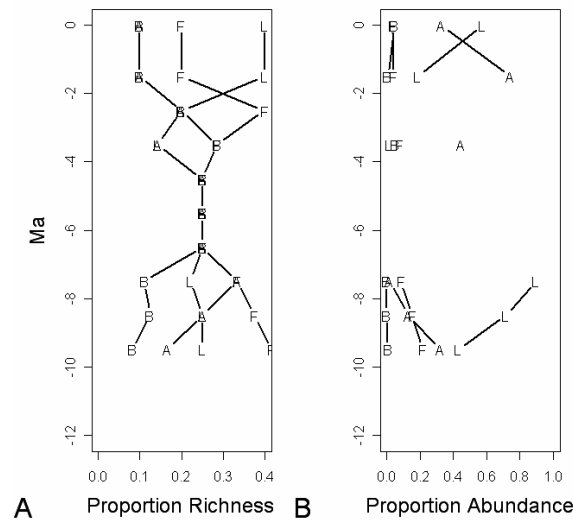
Figure 2.8. Proportions of richness and
abundance in the Pacific. Data is the same as
in Figure 2.7.

As for origination and extinction, patterns of proportional diversity and

abundance in the TEP are obscured by the 3 Ma gap in samples (Fig. 2.8B). There

are no samples prior to 9 Ma, between 7 and 3 Ma, and between 3 and 1 Ma.

Nevertheless, it is obvious that the patterns are strikingly different from the SWC

because *Leptopecten* or *Argopecten* are overwhelmingly dominant for the two well

sampled fossil horizons in the TEP as well as the Recent (Smith et al. 2006; Fig.

2.8B). In contrast, byssally attaching and free swimming species are both low in

diversity and numerically rare. The decline in diversity but not abundance of *Argopecten* in the SWC and TEP is similar to the pattern observed for this genus in California (Stump 1979; Smith and Roy 2006), the Gulf of Mexico, and the Atlantic coast of the Florida (Waller 1969).
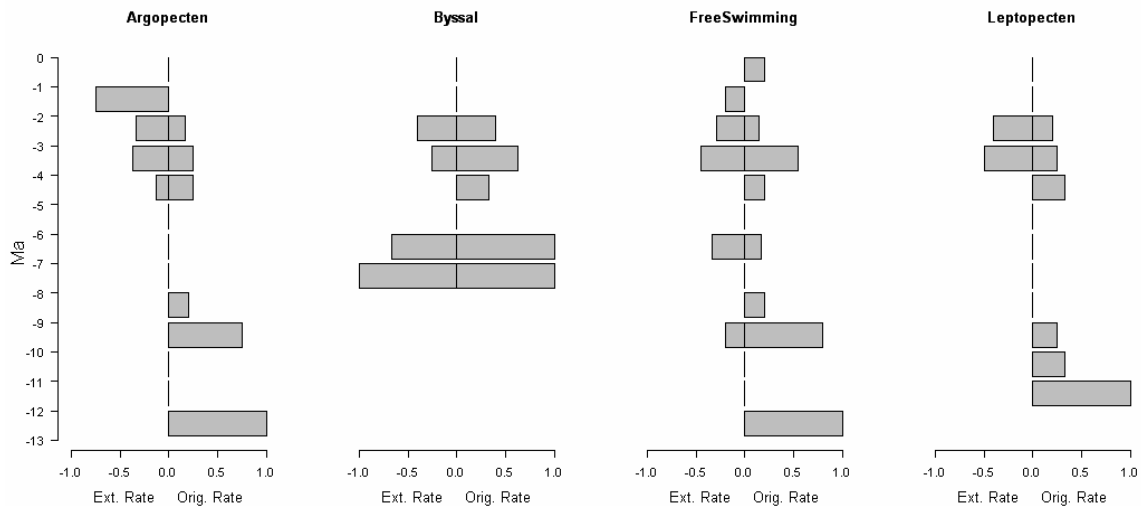
Figure 2.9. Extinction and origination rates of ecological groups. Evolutionary rates for the 4 ecological groups used in this study plotted in 1 Ma time bins.

Origination rates declined greatly over time for all groups except Leptopecten that remained low throughout the entire 12 Ma (Fig. 2.9). Focusing just on the last 5 Ma for which sampling is generally excellent, all four groups exhibit elevated evolutionary rates between 4 to 3 Ma, just as for the family as a whole (Fig. 2.2). However, the timing of peaks in extinction varies between the groups. *Argopecten* extinction rates peaked between 2 to 1 Ma, whereas rates for byssally attaching species peaked between 3 to 2 Ma, and rates for *Leptopecten* and free swimming species peaked 4 to 3 Ma. The earliest peaks in extinction for all four groups are artifacts of their first occurrence in our collections.

Local versus Regional Diversity and Geographic Heterochrony

Analyses of trends through time using 1 Ma bins ignore the very considerable spatial variability among local communities that we know are important in recent benthic communities (Jackson et al. 1999; Smith et al. 2006; O'Dea et al. 2006*s*). Therefore I compared patterns over time for faunules versus those based on 1 Ma bins to determine the magnitude of spatial variability in the SWC over time. Diversity of every faunule is invariably less than that for the 1 Ma bin that contains the faunule
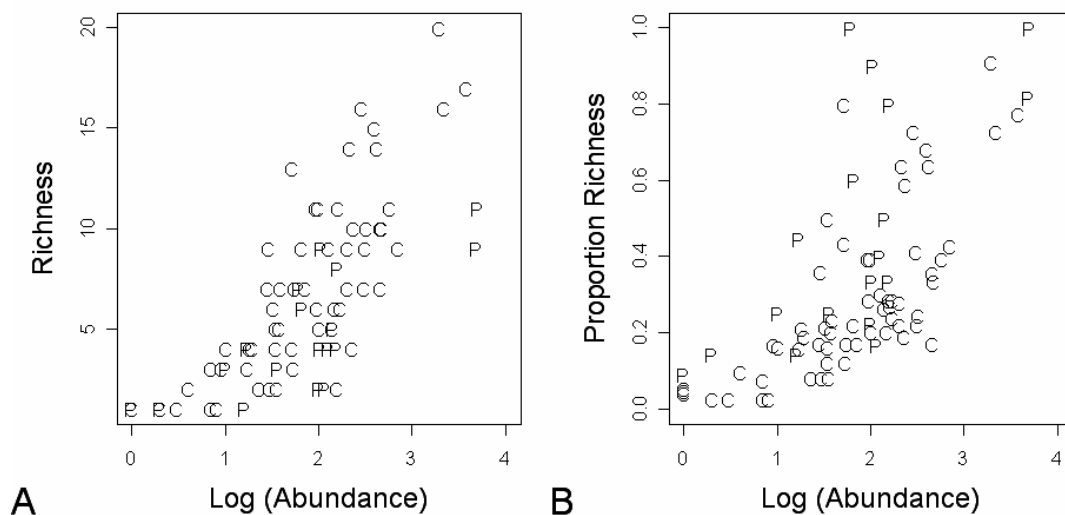
Figure 2.10. Effect of sampling intensity. Sampling effort, plotted as the Log of the total abundance in a faunule against the species richness (A) and proportion of total diversity recovered (B). C annotates a Caribbean faunule, P is eastern Pacific.

(Appendix 2). This is unsurprising because faunules comprise a much smaller sample than all of the faunules from an entire 1 Ma time bin, so that the differences in diversity may entirely reflect the differences in sample size. As expected, there is a clear relationship between species richness and sampling intensity among faunules with different numbers of specimens (Fig. 2.10A). However, plots of proportional

species richness (proportion of the richness in the time bin) versus numbers of specimens per faunule demonstrate that the relationship breaks down above approximately 100 specimens per faunule (Fig. 2.10B). This is because each faunule includes a much narrower range of environmental conditions and more closely approximates a local benthic community as recognized in the Recent than do all the samples from all the faunules in an entire 1 Ma time bin.

Diversity of faunules was plotted against time in the SWC using both species richness that incorporated all the data and the Shannon Diversity Index H that was based only on quantitative samples. The much higher species richness of Recent faunules (Fig. 2.11A) is due to the greater sampling intensity of dredge versus bulk samples. The dredges may also have sampled a wider range of bottom conditions than the fossil faunules. However, the differences between fossil and recent faunules are less for Shannon's H, for which some of the fossil faunules approach the diversity of the Recent (Fig. 2.11B). Excluding the Recent, there has only been a slight increase in diversity of faunules towards the recent (ANOVA, $F = 10.76$, $P = 0.0022$), despite the very large changes in regional diversity over the same time (Fig. 2.2).

Petuch (1982) proposed the idea of geographic heterochrony whereby relict and "modern" faunas could coexist temporally through the occupation of different habitats. If this is true, I should see faunules composed primarily or entirely of extant species co-occurring within the same 1 Ma age intervals with faunules dominated by extinct species. To assess this possibility I calculated Lyellian percentage for all the faunules using species occurrences and occurrences weighted by abundance.
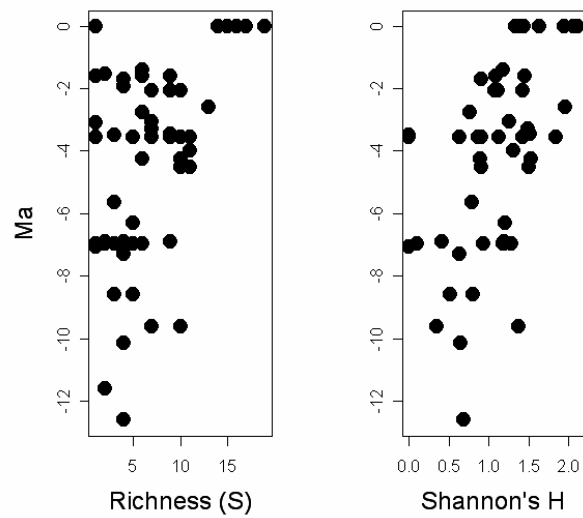
Figure 2.11. Diversity through time. Species richness and Shannon's H are plotted through time. Values were calculated by faunule. Richness includes all samples and H includes only the bulk samples we have obtained (see text).
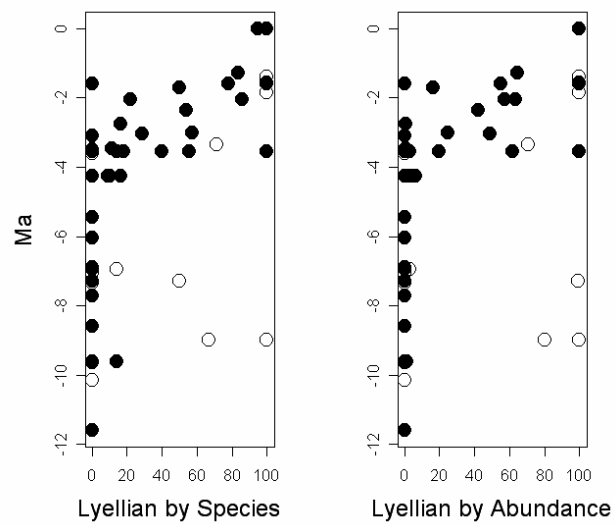
Figure 2.12. Lyellian percentages through time**.** Data are plotted by faunule using both species diversity and abundance.

There was a striking shift in Lyellian percentages in the SWC between 4 and 2 Ma regardless of whether abundance data were used (Fig. 2.12A, B, solid circles). However, faunules with Lyellian percentages close to zero persisted until 1.6 Ma while faunules with Lyellian percentages close to 100% occurred as early as 3.5 Ma. Faunules with intermediate Lyellian percentages were also common throughout this time. Thus geographic heterochrony was widespread throughout the SWC for 2 Ma. In contrast, the shift from low to high Lyellian percentages occurred between 7 to10 Ma in the TEP (Fig. 2.12A, B, open circles), and these differences are especially apparent for calculations weighted by abundance data.

Petuch postulated that relict faunas would occupy marginal environments. To test this idea, I compared the Lyellian percentages for faunules in the SWC during faunal turnover (4.5 to 1 Ma) to the percent carbonate in the sediment, mean annual range of temperature (MART), and water depth (Appendix 2; data from O'Dea et al. 2006). None of these variables was significantly correlated with Lyellian percentages despite their importance for explaining changes in overall community composition during this time (O'Dea et al. 2006).

Discussion and Conclusions

Patterns of scallop diversity have changed dramatically in the SWC over the past 12 Ma but not in the TEP. Total numbers of scallop species and their origination and extinction rates per million years in the SWC closely track their respective values for the entire bivalve fauna at the generic and subgeneric level (Fig. 2.6; Todd et al. 2002). All values peaked between 4 to 3 Ma as the barrier between the TEP and SWC

was finally sealed and oceanographic conditions changed from modern TEP conditions to those observed in the SWC today (Haug and Tiedemann 1998; Coates et al. 2004; Bartoli et al. 2005; O'Dea et al. 2006). However, the intensity of faunal turnover was nearly three times greater for scallop species than for bivalves as a whole, and none of the species in the SWC today originated more than 4.5 Ma.

The large stratigraphic gaps in the record from the TEP preclude detailed analysis but it is highly unlikely that species richness in the TEP exceeded their richness today. Interestingly, several of the species with first occurrences in the Late Pliocene of Ecuador have earlier fossil records in the Gulf of California or farther north along the outer coast of Baja California or in California (Moore 1984; Smith and Roy 2006). This pattern of northern species occurring in Ecuador during this time has been noted for fish and foraminifera (Landini et al. 2002). Moreover, unlike the SWC, three of the species alive today originated more than 9 Ma.

Three of the four main groups of scallops exhibited opposite patterns of success in the SWC and TEP as reflected in their proportional diversity and abundance (Figs. 2.7 and 2.8). *Leptopecten* was the most diverse and abundant genus in most samples from the TEP over the past 12 Ma but steadily declined in both diversity and abundance in the SWC. *Argopecten* diversity declined sharply in both oceans over the past 2 Ma as has been observed elsewhere in North America (Waller 1969; Smith and Roy 2006). *Argopecten* abundance remained high in the TEP but plummeted in the SWC in the last 2 to 3 Ma. The decline of *Argopecten* abundance is all the more striking because the genus comprised by far the most abundant group of

scallops in the SWC for the preceding 6 Ma. Byssally attaching species were never diverse or abundant in the TEP but have achieved spectacular success in the SWC.

By far the greatest increase in diversity in the SWC was for byssally attaching species (Fig. 2.7). Their increase is significantly correlated ($r^2 = 0.418$, $P = 0.059$) with an increased incidence of high carbonate environments (Appendix 2; O'Dea et al. 2006) and the widespread increase in the development of coral reefs since 4 Ma (Collins et al. 1996a; Johnson et al. 1995; Budd and Johnson 1999). Indeed, many byssally attaching species live attached to corals (Waller 1972, 1993). Although they also increased markedly in abundance, byssally attaching species never achieved the abundance characteristic of free-living species (Fig 2.7). In contrast, byssally attaching species were neither diverse nor abundant at any time in the TEP over the past 12 Ma (Fig. 2.8).

The persistence for 2 Myr of faunules of the same age but with widely divergent Lyellian percentages (Fig. 2.12) strongly supports Petuch's (1982) hypothesis of geographic heterochrony. However, I found no evidence that local communities with low Lyellian percentages were restricted to marginal environments based on measurements of MART, percent carbonate in sediments, and water depth. One possible explanation for a lack of environmental effect is that faunules were sampled on the wrong spatial and temporal scales relative to environmental variability, but this seems highly unlikely for two reasons. First, pervasive time averaging of sediments and fossils by bioturbation and other forms of disturbance should eliminate any fine scale differences in distributions in level bottom environments (Kidwell and Flessa 1996; Best and Kidwell 2000 a, b; Kidwell 2002).

Second, the scale and density of sampling was sufficient to identify strong relationships between benthic community composition and these same environmental parameters (O'Dea et al. 2006).

An entirely different possible explanation stems from metapopulation theory in relation to pervasive environmental change (Jackson et al. 1996; Hanski and Gilpin 1997). By this argument, species naturally exist in patches of high abundance in a landscape of low abundance or absence, and the persistence of the species depends on the number of patches occupied, the rate of colonization of new patches, and the rate of extinction in patches already occupied. Changes in these three parameters depend in turn upon the specific life history characteristics of the species in relation to their environment (Nee and May 1992; Tilman et al. 1994). Thus, species soon fated to go extinct may nevertheless persist in a declining frequency of patches until the last patch becomes extinct.

My data are in agreement with such a scenario (Fig. 2.12A, B). First, faunules within any 1 Ma interval typically include only a small fraction of the scallop species that existed during that interval. This was particularly true during the 4 to 3 Ma interval when no single faunule contained more than 13 of the 41 species that inhabited the SWC at that time. Overall differences in molluscan community composition was also extremely high among different faunules of the same age during this time (Fig. 16 in Jackson et al. 1999) Thus, differences in species composition between faunules were extremely high during this period of maximum faunal and environmental change, and these differences persisted, albeit at decreasing frequency, for 2 Ma. Moreover, some of the ill fated species were abundant until very

near the end as seen by the greater number of faunules with Lyellian percentages less than 30 to 40 % when relative abundance of species is included in the calculation (compare Fig. 2.12 B and A). Most importantly, there are very great differences in the life history characteristics of species that survived versus those that became extinct (Smith and Jackson *In preparation*) that are the very essence of the metapopulation model of extinction debt (Nee and May 1992; Tilman et al. 1994).

In summary, the extreme faunal turnover of scallops in the SWC has a strong ecological signature that is only apparent when the life habits of the different species and their abundance are fully taken into account. Moreover, and despite these considerable differences, the patterns of diversity, origination, and extinction for scallops are qualitatively very different from patterns for gastropods, reef corals, and erect bryozoans from the same region (Cheetham and Jackson 1996; Budd and Johnson 1999; Todd et al. 2002). Greater understanding of such major episodes of faunal turnover and extinction fundamentally depends upon exploiting such ecological differences to factor out the processes responsible.

Acknowledgements

Literature Cited

Aalto, K.R., and W. Miller III. 1999. Sedimentology of the Pliocene Upper Onzole Formation, and inner-trench slope succession in northwestern Ecuador. Journal of South American Earth Sciences 12: 69-85.

Allmon, W.D. 2001. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology 166: 9-26.

Allmon, W.D. Rosenberg, G. R.W. Portell, and K.S. Schindler. 1993. Diversity of Atlantic coastal plain mollusks since the Pliocene. Science 260: 1626-1629.

——.1996. Diversity of Pliocene-Recent mollusks in the western Atlantic: extinction, origination, and environmental change. Pp. 271-302 in J.B.C. Jackson, A.F. Budd, and A.G. Coates (eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago, Illinois.

Bartoli, G, M. Sarnthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schönberg, and D.W. Lea. 2005. Final closure of Panama and the onset of northern hemisphere glaciation. Earth and Planetary Science Letters 237: 33-44.

——. 2000a. Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings: I. Environmental variation in shell condition. Paleobiology 26: 80-102

Best, M. M. R. and Kidwell, S. M. 2000b. Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings: II. Effect of bivalve life-habits and shell types. Paleobiology 26:103-115.

Budd, A.F., and K.G. Johnson. 1999. Origination preceding extinction during late Cenozoic turnover of Caribbean reefs. Paleobiology 25: 188-200.

Cantalamessa, G., C. Di Celma, and L. Ragaini. 2005. Sequence stratigraphy of the Punta Ballena Member of the Jama Formation (Early Pleistocene, Ecuador): insights from integrated sedimentologic, taphonomic and paleoecologic analysis of molluscan shell concentrations. Palaeogeography, Palaeoclimatology, Palaeoecology 216: 1-25.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11: 265-270.

——. 1987. Estimating the population size for capture recapture data with unequal catchability. Biometrics 43: 783-791.

Cheetham, A. H. and J. B. C. Jackson. 1996. Speciation, extinction and the decline of arborescent growth in Neogene and Quaternary cheilostome Bryozoa of tropical America. Pages 205-233 in J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds. Evolution and environment in tropical America. University of Chicago Press.

Coates, A.G. 1999. Lithostratigraphy of the Neogene strata of the Caribbean coast from Limon, Costa Rica, to Colon, Panama. Bulletins of American Paleontology 357: 17: 37.

Coates, A.G. M.P. Aubry, W.A. Berggren, L.S. Collins, and M. Kunk. 2003. Early Neogene history of the Central American arc from Bocas del Toro, western Panama. Geological Society of America Bulletin 115: 271-287.

Coates, A.G., L.S. Collins, M-P. Aubry, and W.A. Berggren. 2004. The geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama arc with northwestern South America. Geological Society of America Bulletin 116: 1327-1344.

Coates, A.G. J.B.C. Jackson, L.S. Collins, T.M. Cronin, H.J. Dowsett, L.M. Bybell, P. Jung, and J.A. Obando. 1992. Closure of the Isthmus of Panama: Te near-shore marine record of Costa Rica and western Panama. Geological Society of America Bulletin 104: 814-828.

Coates, A.G., D.F. McNeill, M-P. Aubry, W.A. Berggren, and L.S. Collins. 2005. An introduction to the geology of the Bocas del Toro Archipelago, Panama. Caribbean Journal of Science 41: 374-391.

Coates, A.G., and J.A. Obando. 1996. The geologic evolution of the Central American isthmus. Pp. 21-56 *in* J.B.C. Jackson, A.F. Budd, and A.G. Coates (eds.), Evolution and Environment in Tropical America: University of Chicago Press, Chicago, Illinois.

Collins, L.S. 1993. Neogene paleoenvironments of the Bocas del Toro Basin, Panama. Journal of Paleontology 67: 699-710.

Collins, L.S. M-P. Aubry, W.A. Berggren, A.G. Coates, and M. Ordóñez A. In preparation. Regional correlation of Neogene sequences of coastal Ecuador and Central America. Stratigraphy.

Collins, L.S., A.F. Budd, and A.G. Coates. 1996a. Earliest evolution associated with closure of the Tropical American seaway. Proceedings of the National Academy of Science 93: 6069-6072.

Collins, L.S., A.G. Coates, W.A. Berggren, M-P. Aubry, and J. Zhang. 1996b. The late Miocene Panama isthmian strait. Geology 24: 687-690.

Collins, L.S., A.G. Coates, J.B.C. Jackson, and J.A. Obando. 1995. Timing and rates of emergence of the Limón and Bocas del Toro basins: Caribbean effects of Cocos Ridge subduction? Geological Society of America Special Paper 295: 263-289.

Foggo, A., M.J. Atrill, M.T. Frost, and A.A. Rowden. 2003. Estimating marine species richness: an evaluation of six extrapolative techniques. Marine Ecology Progress Series 248: 15-26.

Hanski, I. A. and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego.

Hasson, P.F., and A.G. Fischer. 1986. Observations on the Neogene of northwestern Ecuador. Micropaleontology 32: 32-42.

Haug, G.H., and R. Tiedemann. 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. Nature 393: 673-676.

Hayek, L.C., and M.A. Buzas. 1997. Surveying natural populations. Columbia University Press, New York. 563 Pps.

Jackson, J.B.C., and D.H. Erwin. 2006. What can we learn about ecology and evolution from the fossil record? Trends in Ecology and Evolution 21: 322-328.

Jackson, J.B.C., and K.G. Johnson. 2000. Life in the last few million years. Paleobiology 26 (Supplement): 221-235.

Jackson, J. B. C., A. F. Budd, and J. M. Pandolfi. 1996. The shifting balance of natural communities. Pp. 89-122 in D. Jablonski, D. H. Erwin, and J. E. Lipps, eds. *Evolutionary Paleobiology*. University of Chicago Press.

Jackson, J.B.C., P. Jung, A.G. Coates, and L.S. Collins. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. Science 260: 1624-1626.

Jackson, J.B.C., J.A. Todd, H. Fortunato, and P. Jung. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. Bulletins of American Paleontology 357: 193-230.

Johnson, K.G., A.F. Budd, and T.A. Stemann. 1995. Extinction selectivity and ecology of Neogene Caribbean reef corals. Paleobiology 21: 52-73.

Johnson, K.G., and M.X. Kirby. 2006. The Emperador Limestone rediscovered: Early Miocene corals from the Culebra Formation, Panama. Journal of Paleontology 80 283-293.

Jones, D.S., and P.F. Hasson. 1985. History and development of the marine invertebrate faunas separated by the Central American Isthmus. Pp. 325-355 in F.G. Stehli and S.D. Webb, Eds. The Great American Biotic Interchange. Plenum Press. New York.

Kidwell, S. M. 2002. Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. Geology 30:803-806.

Kidwell, S. M. and Flessa, K. W. 1996. The quality of the fossil record: Populations, species, and communities. Annual Reviews of Ecology and Systematics 26:269-299.

Landini, W., G. Bianucci, G. Carnevale, L. Ragaini, C. Sorbini, G. Valleri, M. Bisconti, G. Cantalamessa, and C. Di Celma. 2002. Canadian Journal of Earth Sciences 39: 27-41.

McKinney, F.K., S. Lidgard, J.J. Sepkoski Jr., and P.D. Taylor. 1998. Decoupled patterns of evolution and ecology in two post-paleozoic clades. Science 281: 807-809.

McNeill, D.F., A.G. Coates, A.F. Budd, and P.F. Borne. 2000. Integrated paleontologic and paleomagnetic stratigraphy of the upper Neogene deposits around Limon, Costa Rica: A coastal emergence record of the Central American Isthmus. Geological Society of America Bulletin 112: 963-981.

Moore, E.J. 1984. Tertiary marine pelecypods of California and Baja California: Propeamussiidae and Pectinidae. U.S. Geological Survey Professional Paper 1228-B: 112 Pp.

Morton, B. 1994. The biology and functional morphology of *Leptopecten latiauratus* (Conrad, 1837): an "opportunistic scallop". Veliger 37(1): 5-22.

Nee, S. and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61: 37-40.

O'Dea, A., J.B.C. Jackson, H. Fortunato, J.T. Smith, L. D'Croz, K.G. Johnson, and J.A. Todd. 2006. Environmental change preceded Caribbean extinction by 2 million years. Proceedings National Academy of Sciences *In press.*

Olsson, A.A. 1922. The Miocene of Northern Costa Rica. Bulletins of America Paleontology 9(39): 168 Pp.

——. 1942. Tertiary and Quaternary fossils from Burica Peninsula, Panama and Costa Rica. Bulletins of American Paleontology 27: 1-106.

——. 1964. Neogene Mollusks from northwestern Ecuador. 256 Pp. Paleontological Research Institution, Ithaca, New York.

Pilsbry, H.A., and A.A. Olsson. 1941. A Pliocene fauna from western Ecuador. Proceedings of the Academy of Natural Sciences, Philadelphia 93: 1-79.

Petuch, E.J. 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. Palaeogeography, Palaeoclimatology, Palaeoecology 37: 277-312.

——. 1995. Molluscan diversity in the Late Neogene of Florida: evidence for a two-staged mass extinction. Science 270: 275-277.

Smith, J.T., J.B.C. Jackson, and H. Fortunato. 2006. Diversity and abundance of tropical American Scallops (Bivalvia: Pectinidae) from opposite sides of the Central American Isthmus. The Veliger 48: 26-45.

Smith, J.T., and K. Roy. 2006. Selectivity during background extinction: Plio-Pleistocene scallops in California. Paleobiology 32: 408-416.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America Memoir 125: 296 pp.

——. 1986a. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the Western Atlantic bivalve fauna. Palaios 1: 17-36.

——. 1986b. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. Paleobiology 12: 89-110.

Stanley, S.M., and L.D. Campbell. 1981. Neogene mass extinctions of western Atlantic mollusks. Nature 293: 457-459.

Stump, T.E. 1979. The evolutionary biogeography of the West Mexican Pectinidae (Mollusca: Bivalvia). Ph.D. Thesis, U.C. Davis, 520 Pp.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65-66.

Todd, J.A., J.B.C. Jackson, K.G. Johnson, H.M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proceedings of the Royal Society of London, B 269: 571-577.

Vermeij, G.J. 1978. Biogeography and adaptation: Patterns of marine life. Harvard University Press, Cambridge, Massachusetts, 332 Pp.

Vermeij, G. J., and E. J. Petuch. 1986. Differential extinction in tropical American mollusks: endemism, architecture, and the Panama land bridge. Malacologia 27: 29-41.

Waller, T.R. 1969. The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with and emphasis on the Tertiary and Quaternary species of eastern North America. Journal of Paleontology 43 (supplement to No. 5): 125 Pp.

——. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). Philosophical Transactions of the Royal Society of London, B 284: 345-365.

——. 1984. The ctenolium of scallop shells: functional morphology of a key family-level character in the Pectinicaea (Mollusca: Bivalvia). Malacologia 25: 203-219.

——. 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). Pp 1 – 73 in S.E. Shumway (Ed.) Scallops: Biology, Ecology and Aquaculture. Elsevier, New York.

——. 1993. The evolution of "*Chlamys*" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific. American Malacological Bulletin 10: 195-249.

——. 2006. New phylogenies of the Pectinidae (Mollusca: Bivalvia): Reconciling morphological and molecular approaches. Pp 1 – 44 in S.E. Shumway (Ed.) Scallops: Biology, Ecology and Aquaculture (2nd edition). Elsevier, New York.

Woodring, W. P. 1957-1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. United States Geological Survey Professional Paper 306, Part A-E: 1-759.

——. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110: 425-433.

CHAPTER 3 – EVOLUTION OF LARVAL ECOLOGY

Introduction

The larval life history of marine organisms reflects trade-offs between parental investment, parental survival, and survival of the dispersive larval stage (Thorson 1950; Strathmann 1985; Pechenik 1999). Several models have been proposed to predict evolutionary differences in larval ecology in relation to environmental conditions (Roughgarden 1971; Vance 1973a, b; Holt and McPeek 1996; McEdward 1997; Levitan 2000) and, in turn, how differences in larval ecology may influence macroevolutionary patterns (Scheltema 1977; Jablonski and Lutz 1983; Jablonski 1986; Havenhand 1995; Pechenik 1999; Lessios et al. 2001). However, it remains to be seen to what extent the effects of selection predicted in ecologically based models may scale up in space and time to explain large-scale patterns predicted by the macroevolutionary models. Empirical studies addressing this question using living marine organisms are limited and most often focus on egg size (Rass 1941, 1986; Thorson 1950; Spight 1976; Thresher 1982; Lessios 1990; Jackson and Herrera 2000; Marko and Moran 2001; Moran 2004). Fewer studies have addressed larval duration (Victor 1986; Wellington and Victor 1989; Wellington and Robertson 2001; Wehrtmann and Albornoz 2002) and the only study to include several components of larval ecology in an environmental context is Wellington and Robertson (2001). Moreover, paleontological tests of large scale patterns in relation to life history theory have not been done for the same organisms in the same ecoregions as the biological studies so that no single study addresses all the issues in a consistent framework. To that end, I have undertaken to document the life history

evolution of tropical American scallops (Mollusca: Bivalvia: Pectinidae) across the developing Central American Isthmus over the past 12 million years in the context of modern life history theory. In this chapter, I address patterns of larval ecology across the Isthmus in light of well documented differences in environmental conditions between the two oceans to test the predictions of ecological and macroevolutionary models of larval evolution.

The uplift of the Central American Isthmus and the resulting environmental and faunal differences between the tropical eastern Pacific (TEP) and tropical western Atlantic (TWA) provide an ideal system to test the predictions of larval life history models (Lessios 1990; Jackson and Herrera 2000; Levitan 2000; Marko and Moran 2002; Moran 2004; O'Dea et al. 2004). The three primary environmental parameters affecting the predictions of ecologically based models are (1) food availability, which is a function of productivity; (2) temporal variability in oceanographic conditions and resources over daily, seasonal, and multidecadal time scales; and (3) spatial variability as measured principally by differences in habitats over varying spatial scales. On average, phytoplankton abundance, as measured by chlorophyll concentration, and temporal variability in factors such as temperature, nutrients, and productivity are much higher in the TEP than the TWA (Birkeland 1987; Beemis and Geary 1996; Teranes et al. 1996; D'Croz et al. 1991; D'Croz and Robertson 1997; D'Croz et al. 1999; Allmon 2001; O'Dea and Jackson 2002). In contrast, benthic habitats are more uniform in the TEP where seagrass meadows are entirely absent and there is very limited coral reef development (Jackson and D'Croz 1998).
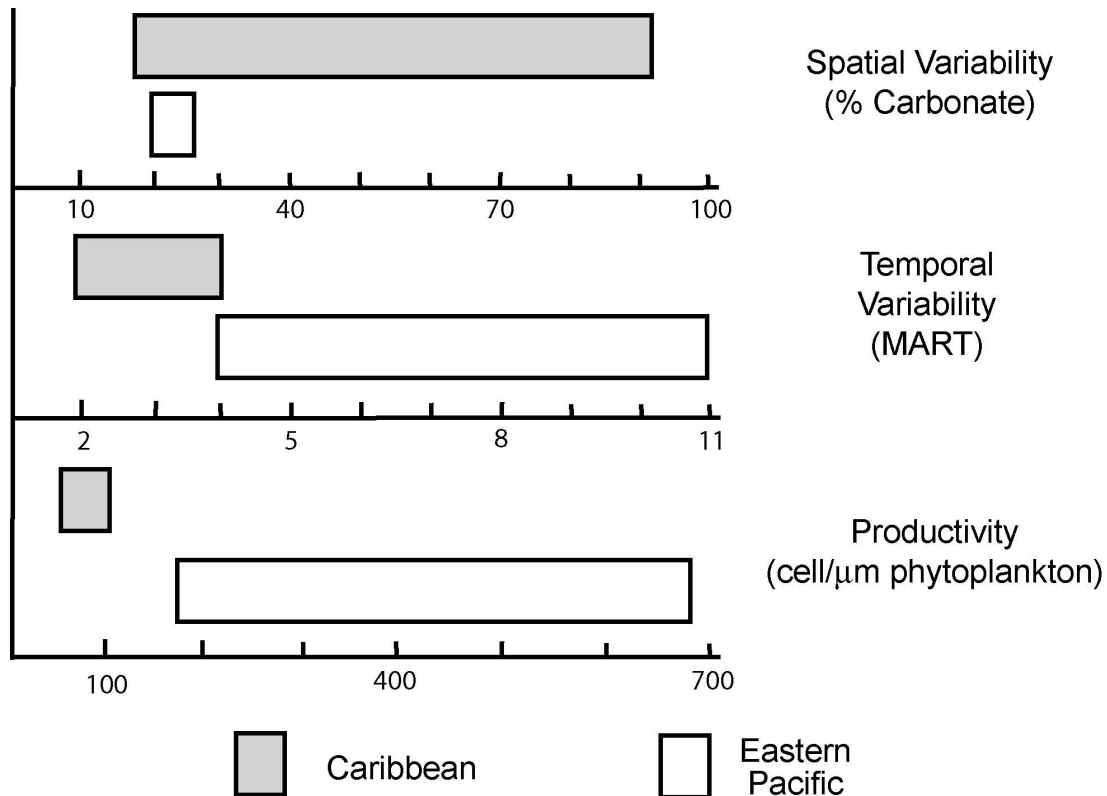
Figure 3.1. Graphical model of environmental variation on opposite sides of the Central American Isthmus. Data on phytoplankton concentration and mean annual range in temperature are average values of ranges observed at different sites within each ocean (D'Croz et al. 1991; D'Croz and Robertson 1997; D'Croz et al. 1999; O'Dea and Jackson 2002; O'Dea et al. 2006).

Environmental differences between the oceans are represented schematically

in Figure 3.1. The relations between any two of the three parameters are almost

certainly nonlinear and the set of conditions in either ocean represented three

dimensionally would be represented by a complex volume. Nevertheless, the model

captures the general differences between two very different environmental settings.

Values of MART and percent carbonate in sediments are from O'Dea and Jackson

(2002) and O'Dea et al. (2006) and of productivity from D'Croz and Robertson

(1997) and D'Croz et al. (1991, 1999). Spatial variability was calculated as the range

of percent carbonate measured in sediment samples in the samples (O'Dea et al.

2006). The deposition of carbonate and the percent carbonate in the sediment are a

function of several environmental factors (Jackson and D'Croz 1998; Mutti and

Hallock 2003); thus the percent carbonate provides an integrated measure of varying

environmental conditions (Jackson and D'Croz 1998; O'Dea et al. 2006). In addition

to the three primary factors cited, the TEP today is cooler than the TWA (D'Croz and

Robertson 1997; Allmon 2001).

The geologic record indicates that the environmental conditions observed

today were established within less than 1 million years prior to and during the final

separation of the oceans 4 to 3 Ma (Coates et al. 1992, 2004; Haug and Tiedemann

1998; Bornmalm et al. 1999; Kameo and Sato 2000; Bartoli et al. 2005; O'Dea et al.

2006). Prior to that time, environmental conditions in the Caribbean were more

similar to conditions in the tropical eastern Pacific today (ibid).

A series of evolutionary models predicting differences in larval ecology based

on relative ecological fitness can be applied to this system. Vance (1973a, b)

constructed a fecundity-time model based on the assumption that egg size is

negatively correlated with the duration of larval life and time to feed in the plankton.

His model was the first to include environmental parameters other than temperature,

which had been the primary driving mechanism invoked by earlier studies (Rass

1941; Thorson 1950). Vance demonstrated that previous models based solely on

temperature were insufficient to explain the observed patterns and set the stage for

numerous subsequent studies that have expanded on Vance's work. He concluded

that only two extremes in the range of possible egg sizes and nutrition are evolutionarily stable. Large, lecithotrophic larvae that live primarily or entirely off their stored yolk should be favored in conditions of low food availability whereas small, feeding, planktotrophic larvae should be favored under conditions of abundant food or very high rates of predation in the plankton. Extrapolating to a comparison across the Isthmus, lecithotrophic larval types should predominate in the TWA and planktotrophic larvae in the TEP.

McEdward (1997) modified Vance's model to allow larger egg sizes beyond the limit of 100 percent nutrition to the growing larva. He also dropped the assumption of a difference in development time related to egg size and allowed for facultative feeding by planktotrophs. His model predicts that duration of planktotrophic development should increase with food availability but that facultative feeding should allow intermediate egg sizes to be evolutionarily stable. Again, extrapolating to the study region, egg size should be larger in the TWA and the duration of planktotrophic development should be longer in the TEP.

Levitan (2000) further modified the models of Vance and McEdward by including the assumption that size at metamorphosis is independent of egg size and that development time is nonlinearly proportional to egg size. As before, small eggs should predominate in areas of high productivity and larger eggs should be more common when larval mortality is high due to low food availability. However, Levitan's model also predicts that smaller eggs should be more common at higher temperatures in agreement with the earlier studies by Rass (1941) and Thorson (1950). Levitan interpreted this conflicting prediction as indicating temperature was

less important than nutrient availability. The first prediction agrees with McEdward

regarding the viability of intermediate egg sizes as opposed to just the two optimal

sizes predicted by Vance. Thus, we expect larger eggs in the TWA because

productivity is lower than the TEP.

Two additional models address the question of variation in planktonic

duration. Roughgarden (1971) proposed a model of selection for r and K phenotypes.

The model predicts that r-selected phenotypes will be favored in environments with

extreme seasonal variation or short growing periods (e.g., polar climates), whereas K-

selected phenotypes should be favored in environments with low seasonality or long

growing periods (e.g., tropics). For scallops, r-selected equates to small egg size

(same energy, more offspring) and possibly longer larval duration. Thus, r-selected

species should be favored in the TEP because of higher seasonality and possibly a

shorter growing period compared to the TWA.

Holt and McPeek (1996) developed a similar model based on the idea that

changes in fitness will affect the carrying capacity (K) for a population. They

assumed that dispersal is almost always down the fitness gradient. Populations are

largest at the point of highest fitness within the species range (where K is highest), so

the majority of dispersal is away from this point of optimal fitness towards conditions

of lower fitness (lower K). In conditions with low temporal variation but high spatial

variability, such as occurs in the TWA, the fitness drops rapidly from the optimal

point, so there will be selection for short larval durations (i.e. shorter dispersal

potential). In areas with higher temporal variability and lower spatial variability like

the TEP, the fitness gradient is very shallow, so there will be selection for longer

dispersal.

In summary (Table 3.1), the models of Vance, McEdward and Levitan predict

larger egg sizes in the TWA where productivity and temporal variability are lower but

spatial variability is higher than in the eastern Pacific (Fig. 3.1). Roughgarden's

model predicts more r-selection (smaller egg size and longer larval duration) in the

TEP and Holt and McPeek's model predicts shorter larval durations in the TWA.

Putting this all together, we expect to see larger egg sizes and shorter planktonic

larval duration in the TWA relative to the TEP.

Table 3.1. Summary of five larval life history models. All the models consistently
predict larger egg sizes in the Caribbean (C) and longer larval durations in the eastern
Pacific (EP). N/A indicates the model made no prediction for that variable. Levitan's
(2000) model makes contrasting predictions for egg size in relation to productivity
and temperature. The prediction shown is for productivity, determined by Levitan to
be the most important.

Model	Environmental Variable	Egg Size (PI)	Larval Duration (PII)
Vance, 1973	Productivity	C > EP	No Prediction
McEdward, 1997	Productivity	C > EP	No Prediction
Levitan, 2000	Productivity, Temperature	C > EP	No Prediction
Roughgarden, 1971	Seasonal Variability	C > EP	EP > C
Holt and McPeek, 1996	Spatial Variability	No Prediction	EP > C

The predictions of these models can be compared to models which focus on

the macroevolutionary implications of differing larval ecologies. Jablonski and Lutz

(1983) and Jablonski (1986) proposed a model in which lineages with shorter larval

durations (lecithotrophic taxa in their model) should have higher evolutionary rates

than lineages with longer larval durations (planktotrophic taxa). Their predictions were similar to those of Scheltema (1977) and Havenhand (1995) based on larval dispersal and Jackson (1974) based on physiological tolerance. The primary basis of the Jablonski models is that shorter larval durations should correlate with smaller geographic ranges and lower within-population connectivity. Both of these factors could lead to increased isolation of populations and therefore increased speciation and higher risk of extinction. Scallops in the TWA are twice as diverse as in the TEP today (Smith et al. 2006), and extinction and origination rates have been significantly higher in the TWA (Smith and Jackson *In preparation*). Thus, we can test whether evolution of shorter larval duration in response to changing environments, as predicted by ecologically based models, has led to increased evolutionary rates as predicted by macroevolutionary models.

The predictions outlined above are similar to those considered by most of the existing studies utilizing the Isthmus of Panama as a model system (Lessios 1990; Jackson and Herrera 1999; Marko and Moran 2000; Wellington and Robertson 2001; Moran 2004). Two fundamentally different approaches have been used for testing these predictions. The first approach is based upon the comparative phylogenetic method (Felsenstein 1985; Harvey and Pagel 1991) with the implicit assumption that phylogenetic constraint is the most important determinant of the larval ecology. The second approach is to treat each species as an independent evolutionary experiment assuming each has evolved independently in response to environmental conditions.

Phylogenetic studies employ two basic approaches. The first employs genera as the basic evolutionary unit and compares larval characteristics within each genus

between the oceans (Victor 1986; Victor and Wellington 1989; Jackson and Herrera 1998; O'Dea et al. 2004). The second is based on comparisons between the oceans of presumed sister (geminate) species assigned on the basis of molecular phylogenetic analyses of living species (Lessios 1990; Marko and Moran 2001; Wehrtmann and Albornoz 2002; Moran 2004). For example, Marko and Moran (2001) demonstrated a strong correlation between molecular divergence and differences in egg sizes between geminate species suggesting that egg size is phylogenetically constrained; and Jeffery and Emlet (2003) and Jeffery et al. (2003) obtained similar results for temnopleurid echinoids. However, Duda and Palumbi (1999) and Collin (2004) have independently shown that shifts from planktotrophic larvae to lecithotrophic larvae or direct development are not phylogenetically constrained within two different groups of gastropods, and more likely reflect physiological responses.

There are two potentially serious problems with both of these approaches. First, limitation of analysis to genera present in both oceans ignores the fact that the greatest response to contrasting oceanographic conditions is more likely to be found among taxa limited to just one of the two oceans because of differential extinction or origination. Among the scallops considered here, for example, the four genera restricted to the TWA represent the major macroevolutionary development in response to changing oceanographic conditions (Smith and Jackson *In preparation*). The second problem relates to the assumption that most genetically similar pairs of living species represent genuine sister (geminate) taxa, as in the studies of arcid bivalves from opposite sides of the Isthmus (Marko and Moran 2001; Marko 2002; Moran 2004). Marko (2002) reports dates of divergence for geminate pairs of arcid

species as old as 20 Ma, but this is extremely doubtful based on well established durations of bivalve species and the timing and rates of turnover of bivalve species measured directly in the fossil record (Stanley and Yang 1987; Roopnarine 1996; Smith and Jackson *In preparation*). Moreover, rates of extinction and faunal turnover for the past 10 Ma peaked just 2-1 Ma (Jackson et al. 1993; Allmon et al. 1996; Allmon 2001; Todd et al. 2002). Scallops in particular experienced 100% faunal turnover in the past 4.5 Ma indicating that most true sister species are extinct (Smith and Jackson *In preparation*). Thus, it is extremely unlikely that pairs of living species across the Isthmus are truly sister species unless the calculated times of divergence are only a few million years.

The second general approach to comparing life history patterns across the Isthmus is to assume each species is an independent evolutionary experiment and make a general comparison across the isthmus independent of phylogeny. Jackson and Herrera (1998) used this method in addition to a comparative approach based upon congeneric species, and obtained the same results regardless of method. Spight (1976) and Emlet et al. (1987) also used this approach to assess patterns within larger groups of marine invertebrates in other contexts. In this study, we will apply both a phylogenetic approach based on comparisons of congeneric species, as well as using species as independent evolutionary experiments.

Materials and Methods

Larval Shells

We measured the larval shells of 1615 specimens of scallops from dredge samples in the two oceans. These represented 50 species in 16 genera. PII

measurements were obtained for all larval shells but PI measurements were unambiguously discernable on only 481 specimens because of preservation; these included just 24 species in 12 genera. Mean PI and PII values for species are listed in Appendix 1. All specimens were cleaned ultrasonically in distilled water, rinsed in ethanol, and allowed to dry. Scanning electron microscope (SEM) images were obtained using an FEI Quanta 600 SEM at the Scripps Institution of Oceanography Analytical Facility. Images were made in the low-vacuum mode at a voltage of 20 Kv at magnifications of x 500 and x 1000. Each specimen was oriented with the hinge line horizontal within the chamber to minimize the possibility of length distortion. The images were measured using XT Docu 3.2 software by Soft Imaging Systems, which is distributed with the Quanta 600 SEM. Measurements were made from the most anterior to most posterior point on the PI and PII larval shells.

Taxonomy

Scallops are diverse in tropical American waters (Waller 1993; Smith et al. 2006; Smith and Jackson *In preparation*) and are an important group in fisheries worldwide (Waller 1991, 2006). As a result, there is a rich taxonomic and systematic literature as well as numerous investigations of larval development, nutrition, and ecology. Each scallop specimen obtained from the dredge samples was identified to species (Smith et al. 2006). Taxonomic placement within genera follows Waller (1969, 1986, 1991, 1993, 2006) and Judith Smith (1991). Waller's work is based on non-adaptive morphologic characters allowing consistent taxonomic identification between fossil and recent specimens. Generic assignments of species are strongly

supported by independent molecular studies (Matsumoto and Hayami 2000; Barruca et al. 2003).
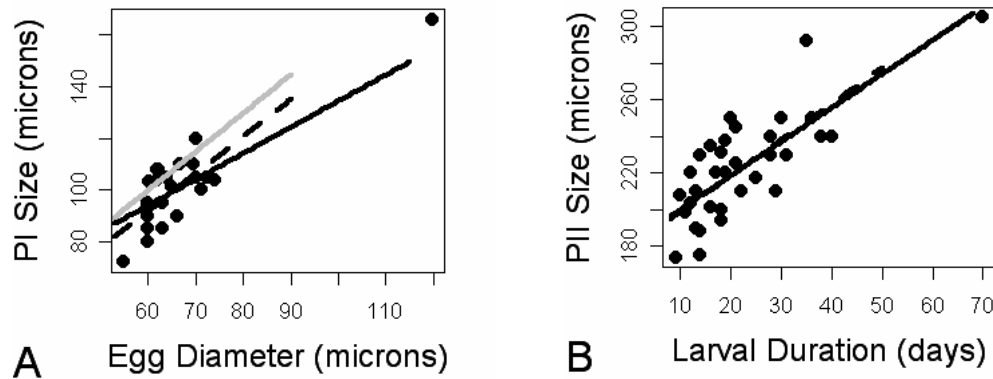

Figure 3.2. Correlation of PI and PII sizes with egg size and larval duration. Solid black lines represent the regression line including all data for PI (A) and PII (B) proxy analysis. The dashed line excludes the extreme point in both figures. The gray line in A represents the relationship obtained by Moran (2004). All correlations are significant (see text).

Morphologic Proxies for Larval Ecology

The larval development of scallops can be divided into 2 phases. The prodissoconch I (PI) is the first stage of larval shell growth up to the point at which the two shells completely enclose the growing organism (Waller 1991, 1993). Because of this physiological relationship, the PI is a good proxy for egg size (Waller 1993; Moran 2004). There is a significant correlation between PI size and egg size (Fig. 3.2A, $r^2 = 0.764$, $p < 0.0001$) illustrating the value of PI size a proxy for egg size. This data includes 24 species of scallops taken from the fisheries literature, summarized in Cragg and Crisp (1991). All data reported are shown in Figure 2 except values for experiments carried out in extreme and unnatural environmental conditions. Lecithotrophy has been reported for just two genera worldwide (Cragg

and Crisp 1991; Waller 1993): *Caribachlamys* in the Caribbean and *Equichlamys* in the Western Pacific. The latter of these is included in Figure 3.2A.

The data in Figure 3.2A are more variable than for arcid bivalves (Moran 2004) and the gastropod genus Conus (Kohn and Perron 1994). The greater variability for the scallops can be attributed to two factors. First, the data are derived from many studies and are often presented as the average egg diameter and PI size which confounds experimental error. Second, Moran's data are for parent-offspring comparisons, whereby egg sizes were compared to the PI shell on the parent. Thus, if egg size is heritable, this would decrease the variability in her analysis. Moran's results are included in Figure 3.2A (gray line). The overall slope is very similar to the slope we have observed excluding the lecithotrophic species (dashed line), but the intercept is slightly larger, suggesting that, on average, scallops have on smaller eggs than arcids.

The second stage of larval development is the prodissoconch II (PII). This reflects the period of larval shell growth from the end of the PI stage (marked by the PI/PII boundary on the larval shell) to metamorphosis. The size of this stage is a reflection of several factors, but in scallops, there is a significant and positive relationship between larval duration (time spent swimming in the plankton) and PII size (Fig. 3.2B, $r^2 = 0.598$, $p < 0.0001$). The plot includes experimental data for 33 species (summarized in Cragg and Crisp 1991) and reflects the same experimental error discussed above. The lecithotrophic genus *Equichlamys* is included in this analysis so that, as for PI, measurements of PII size provide a reliable proxy for both planktotrophic and lecithotrophic development.

There are several confounding environmental relationships that add to the variability in Figure 3.2B. Larval duration and settlement size are also negatively correlated with water temperature (Cragg and Crisp 1991). A significant positive relationship between growth rate and temperature also exists within species up to some taxon-dependent thermal optimum, beyond which growth rates drop rapidly to zero (Hodgson and Bourne 1988; Heaseman et al. 1996). For example, within one species, *Chlamys hastata,* individuals raised at lower temperatures matured more slowly than those reared at higher temperatures, spending more time in the plankton, but grew to significantly larger overall sizes (Hodgson and Bourne 1988). These observations add variability but still imply a general positive relationship between PII larval shell size and duration of free-swimming larval life among scallops, both within and between species. Therefore, we can use the overall size of the larval shell (PII) of scallops, which are preserved on shells of adult specimens, to obtain an estimate of the relative duration of larval life of the individual involved.

Results

Assumptions of the Life History Models

We plotted the relation between PI and PII size for all 481 specimens for which both measurements were available (Fig. 3.3) as an empirical test of the predicted negative to neutral relationship between egg size and larval duration based on the models (Table 1; Vance 1973a, b; McEdward 2000; Levitan 2000). Each point represents a PI and PII measurement from the same individual shell providing a comparison between PI and PII size within one individual. There is a significant
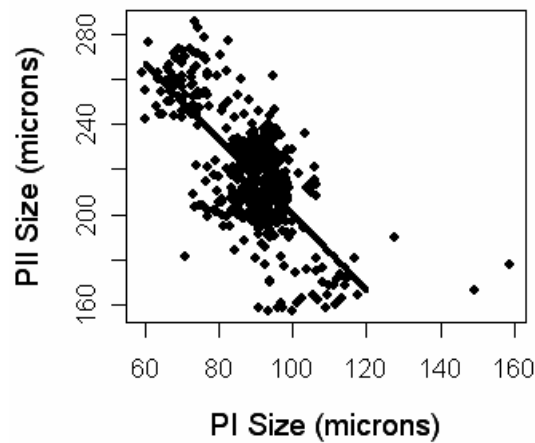
Figure 3.3.Relationship of PI and PII sizes.
Each point represents measurements from 1
specimen. The correlation between PI and
PII is significant excluding the 2
lecithotrophic specimens (the two points with
the largest PI sizes).

difference between the planktotrophic and lecithotrophic individuals (the 2 points

with the largest PI values). The wide range of variability among planktotrophic

individuals strongly supports the McEdward (1997) and Levitan (2000) models. The

relationship between egg size (PI) and larval duration (PII) in scallops is negative

and, excluding the lecithotrophic individuals, is linear ($r^2 = 0.487$, $p < 0.0001$). This

further supports McEdward's point that the models are good predictors up to the

threshold of lecithotrophy. Levitan's (2000) prediction that size at settlement is not

correlated with egg size is not supported by our data (Fig. 3.3) as well as by earlier

studies of scallops (Cragg and Crisp 1991; Heaseman et al. 1996); but it is supported

by the work of Kohn and Perron (1994) for the gastropod genus *Conus*. Data in

Figure 3.3 were combined into average values for the different scallop species in

Figure 3.4 with very similar results to Levitan's (2000) data for echinoderms. The

modal sizes are intermediate and very large egg sizes, which are inferred to be

lecithotrophic, are rare. The relationship between PI and PII size for planktotrophic

species is also still linear and significant ($r^2 = 0.401$, $p = 0.0009$).
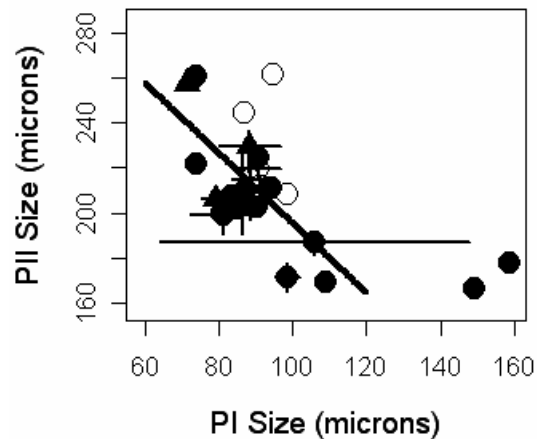

Figure 3.4. Correlation of PI and PII sizes averaged by species. Solid circles are Caribbean species, solid triangles eastern Pacific and open circles are extinct species. There is a significant correlation, excluding the two lecithotrophic species, as for Figure 3.3.

Most macroevolutionary studies make an implicit assumption that

intraspecific variation is insignificant relative to interspecific variation (Jablonski

1986; Stanley 1986; Budd and Johnson 1991; Maurer et al. 1992; Jablonski and Raup

1995; Jackson et al. 1996; Roopnarine 1996; Jablonski 1997; Smith and Roy 2006).

In these studies, for example, just one (or an average) measurement of shell size or

larval ecology was used for each species throughout its range. Many biogeographic

and macroecological studies are based on similar assumptions of constant characteristics throughout each species' range (Brown and Nicoletto 1991; Bhaud 1993; Roy et al. 2000; Roy and Martien 2001). To test for the relative effects of intra- and interspecific variation, we fit linear models to our entire data set. Across all of our data, species identity, generic membership and regional effects all explained significant amounts of variability for both PI and PII sizes (Table 3.2). A similar pattern is evident in both data sets. Species identity explained the greatest amount of variability, generic membership was intermediate, and regional effects, the lowest amount of variability.

Thus, interspecific variability is the dominant source of variation in our data, but there is a significant phylogenetic effect implied by the significance of generic membership. Intraspecific variability is significant, but accounts for a lower level of the total variation (40 – 45% relative to 75 -80% explained by species). We further explored these components of variability within individual species (Table 3.3). For PI size, we analyzed species that occurred in 2 or more faunules. Three of the 13 species showed significant within species variability. PII sizes were analyzed for species occurring in 3 or more faunules and 12 of the 25 species showed significant variability. Within species variation in PI size was always <10% of the total variability and PII size < 22% (Table 3.3); both of these results are consistent with the analysis of the entire fauna where interspecific variation accounted for >75% of the total variation.

Table 3.2. Results of linear fit models for
variation in PI and PII sizes.

PI Size

Group	F Statistic	r^2	p	N
Species	80.7	0.793	< 0.0001	24
Genus	139.6	0.761	< 0.0001	12
Faunule	20.18	0.444	< 0.0001	21

PII Size

Group	F Statistic	r^2	p	N
Species	101.2	0.753	< 0.0001	50
Genus	139.5	0.563	< 0.0001	16
Faunule	23.01	0.396	< 0.0001	49

We further tested the effect of within species variation on the overall patterns by comparing mean values for each faunule using mean values obtained for the whole species to mean values obtained using mean values for each species as measured in that faunule (i.e., including intraspecific variation). There was no significant difference in the overall patterns when within species variation was included (paired t-test: PI, t = 0.974, p = 0.3366; PII, t = -0.443, p = 0.6597). Thus, within species variability is a second order effect that should be incorporated when possible but is unlikely to significantly affect the overall results based on species alone (Table 3.2).

Table 3.3. Intraspecific variation. Results of linear fit models for species occurring in at least 2 (PI analyses) or 3 (PII analyses) faunules. The maximum, minimum and range are based on mean values for the faunules analyzed. The proportion of the total variation was calculated by dividing the range of the species by the total range observed in mean values of species. P-values in bold represent significant results.

PI size

Species	F	r²	p	N	Max	Min	Range	Prop.
"Amusium" laurenti	1.742	0.044	0.1201	7	97.83	92.36	5.47	0.027
Bractechlamys antillarum	0.673	-0.054	0.5810	4	111.55	105.75	5.8	0.028
Euvola perulus	0.494	-0.203	0.5551	2	94	86.3	7.7	0.038
Leopecten chazaliei	3.377	0.107	**0.0041**	7	99.25	87.17	12.08	0.059
L. coralliphila	5.357	0.555	0.0571	3	106.5	85.75	20.75	0.102
Leptopecten bavayi	1.032	0.016	0.4922	3	88.5	71	17.5	0.086
L. biolleyi	1.337	0.005	0.2517	2	72.6	70.72	1.88	0.009
L. sp. (cf. L. biolleyi)	0.009	-.043	0.9253	2	74.17	73.97	0.200	0.001
Lindapecten acanthodes	4.567	0.610	**0.0193**	8	111.75	92.5	19.25	0.094
Pectinid A lineolaris	0.882	-0.030	0.5034	5	90	82	8	0.039
Spathochlamys benedicti	2.518	0.200	**0.0251**	9	98.5	83	15.5	0.076
S. lowei	0.074	-0.115	0.7920	2	79.42	78.25	1.17	0.006
S. sp. 3	0.660	-0.085	0.5950	4	93.29	87.75	5.54	0.027

PII size

Species	F	r²	p	N	Max	Min	Range	Prop
"Amusium" bocasense	2.521	0.403	0.1689	5	264.5	234	30.5	0.150
"A." laurenti	2.74	0.068	**0.0152**	7	212.9	202.5	10.4	0.051
Argopecten costaricaensis	21.07	0.682	**<0.0001**	12	230.2	199.9	30.3	0.149
A. gibbus	7.206	0.414	**<0.0001**	8	219.0	186.5	32.54	0.160
A. levicostatus	6.353	0.425	**<0.0001**	9	244.3	200.8	43.5	0.213
A. sp. 1	3.692	0.473	0.1234	3	249.5	211.5	38	0.186

Table 3.3 (Cont.)

A. sp. 5	10.67	0.540	**<0.0001**	5	228.6	197.6	31	0.152
A. ventricosus	0.469	0.039	0.7580	3	246.5	215.5	31	0.152
Bractechlamys antillarum	1.737	0.112	0.1480	6	172	159.8	12.2	0.060
Euvola perulus	4.242	0.302	**0.0382**	3	257	224.7	32.3	0.159
Euvola sp. (cf. E. perulus)	4.351	0.572	0.1298	3	239	221.5	17.5	0.086
Laevichlamys multisquamata	3.425	0.421	0.0815	3	203.5	180.4	23.1	0.113
Leopecten chazaliei	12.77	0.342	**<0.0001**	9	231.1	197	34.1	0.167
L. coralliphila	2.385	0.264	0.0602	8	240.5	209.2	31.3	0.154
L. gatunensis	1.349	0.130	0.3774	4	256.8	239	17.8	0.087
Leptopecten bavayi	4.071	0.339	**<0.0042**	7	206.7	181.4	25.3	0.124
L. biolleyi	2.17	0.019	0.0933	4	274.5	253.3	21.2	0.104
L. sp. (cf. L. biolleyi)	1.099	0.005	0.3434	4	265.8	255.6	10.2	0.050
Lindapecten acanthodes	1.988	0.202	0.0565	10	193.5	162.4	31.1	0.153
Pacipecten linki	0.178	-0.904	0.9036	3	238.5	214.25	24.25	0.119
P. tumbezensis	4.198	0.286	**0.0178**	4	246.8	214	32.8	0.161
Pectinid A lineolaris	2.916	0.081	**0.0108**	7	205.3	193	12.3	0.060
Spathochlamys benedicti	4.175	0.223	**<0.0001**	14	215	192.7	22.3	0.109
S. lowei	18.34	0.553	**<0.0001**	3	226	203.4	22.6	0.111
S. sp. 3	0.766	-0.012	0.517	4	212	207.4	4.6	0.023

Differences in Life Histories across the Isthmus

Life histories of scallops are significantly different across the Isthmus today based upon PI and PII sizes for individual species. PI size is significantly larger in the TWA (Fig. 3.5A, t-test, t = 2.23, p = 0.0487), and PII size significantly smaller (Fig. 3.5B, t-test, t = -2.94, p = 0.0089), as predicted by the ecological models (Table 3.1).

Comparisons within genera the results are not significant although the trends are consistent with the pattern for total species (Fig. 3.6). Among genera which occur in both oceans, PII size was larger in the TEP than the TWA in 6 of 7 cases, but the differences were significant in only two cases (Fig. 3.6A). The results for a sign test of the frequency of pairs with larger PII
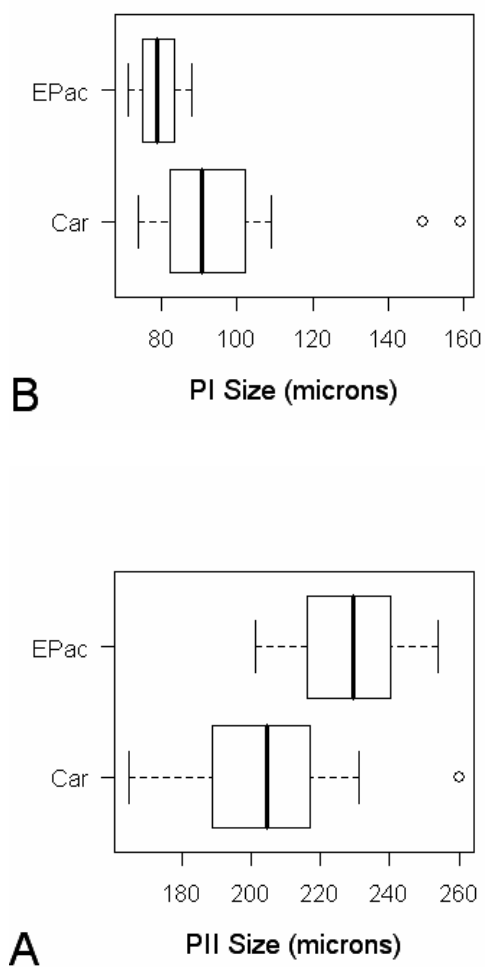

B   PI Size (microns)

A   PII Size (microns)

Figure 3.5. Comparison of the living faunas in the TEP and TWA. PI size is significantly smaller (A) and PII size significantly larger in the TEP (B).
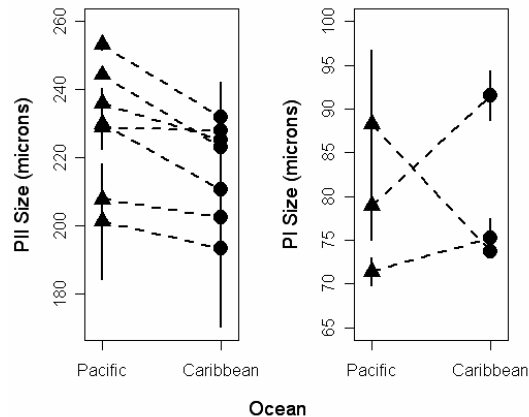
Figure 3.6. Within genus comparisons between the TEP and TWA. 6 of 7 genera have smaller PII sizes in the TWA, although only 2 of these are significant. 2 of 3 genera have larger PI sizes in the TWA.

size in the TEP are also insignificant because of small sample size. PI size was

significantly larger in the TWA for 2 of the 3 genera (Fig. 3.6B). Thus the trends are

consistent with those for total species but there are too few available comparisons to

test their significance. However, combining our PI data for three genera of scallops

with those for six genera of arcid bivalves (Moran 2004) yields a significant result

with 8 of 9 congeneric pairs having larger eggs in the TWA than the TEP (Sign Test,

$p = 0.039$). This result is consistent with those for egg size of echinoderms (Lessios

1990) and cheilostome bryozoans (Jackson and Herrera 2000).

Patterns through Time

Mean PI and PII values for TWA faunules are plotted against time in Figure

3.7 using the same faunules analyzed previously for patterns of diversity and faunal

turnover (Smith and Jackson *In preparation*). The striking shift towards smaller PII
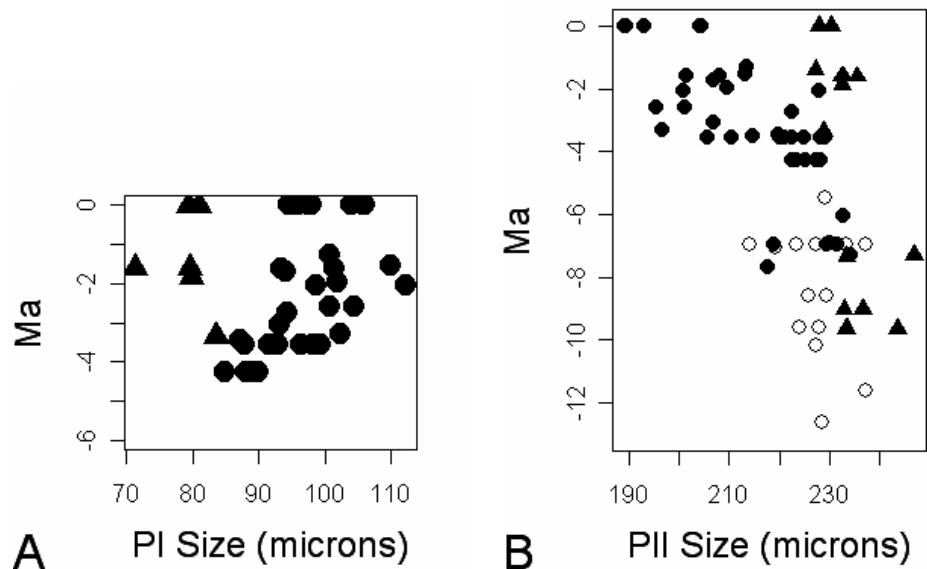
Figure 3.7. PI and PII size through time. Data are plotted by faunule (see text and Smith and Jackson *In preparation*). Solid triangles are TEP faunules, solid circles are TWA faunules and open circles are isthmian faunules. PII sizes decrease significantly in the TWA from 4 Ma to the Recent, PI sizes appear to increase in the TWA, but is biased by sampling (see text). PII sizes change very little in the TEP.

size and concurrent increase in variability coincides with the first occurrences of

many of the modern TWA species (Smith and Jackson *In preparation*). The pattern

for PI size appears to show a similar opposite pattern, but there are only four faunules

older than 4 Ma.

The origination times of modern species as a function of their PI and PII size

are plotted stratigraphically in Figure 3.8. The first occurrences of species with small

PII sizes occur at the same time as the shift towards faunules with smaller mean PII

sizes observed in Figure 3.7. Six of the seven species with the smallest PII shells
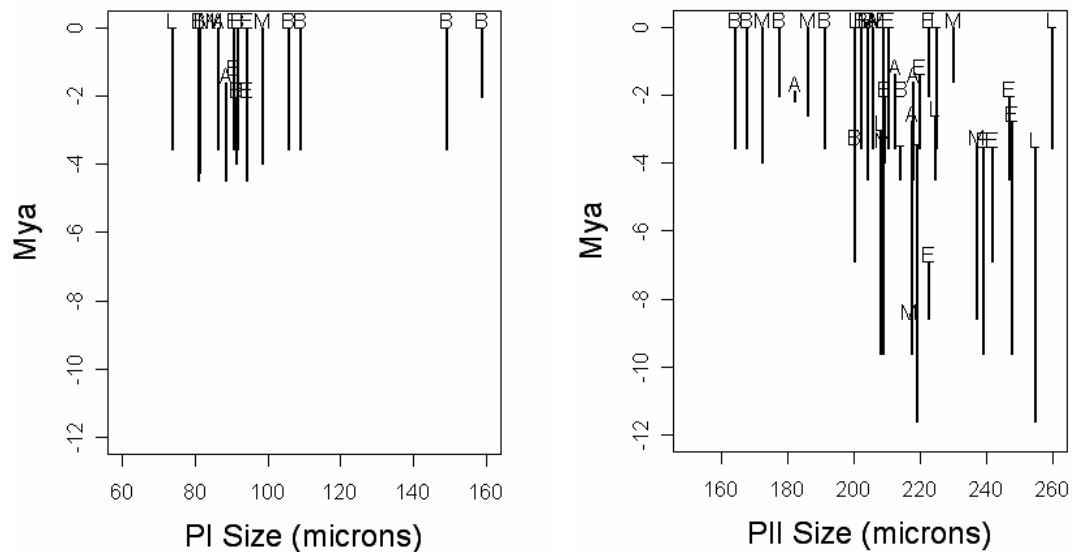
Figure 3.8. Stratigraphic ranges plotted against PI (A) and PII (B) sizes. Stratigraphic range data is from Smith and Jackson (*In preparation*). PI and PII sizes are from Appendix 1.

originated within the past 4 Ma and six are still extant. All of these are associated

with reef habitats and five of these live byssally attached to reef corals (Waller 1973,

1993). Four of these species are assigned to 3 genera which only occur in the

Caribbean, *Bractechlamys, Laevichlamys,* and *Caribachlamys*, the latter being the

only genus with lecithotrophic larval ecology.

Mean PI size for each faunule is significantly positively correlated with

percent carbonate in the sediment (Fig. 3.9A, r2 = 0.460, p < 0.0001) and negatively

correlated with the mean annual range of temperature (MART) (Fig. 3.9B, r2 = 0.271,

p = 0.0155). Mean PII values for faunules exhibit the opposite patterns. PII is

negatively correlated with percent carbonate (Fig. 3.10A, r2 = 0.464, p < 0.0001) and

marginally positively correlated with MART (fig. 3.10B, r2 = 0.242, p = 0.0528).
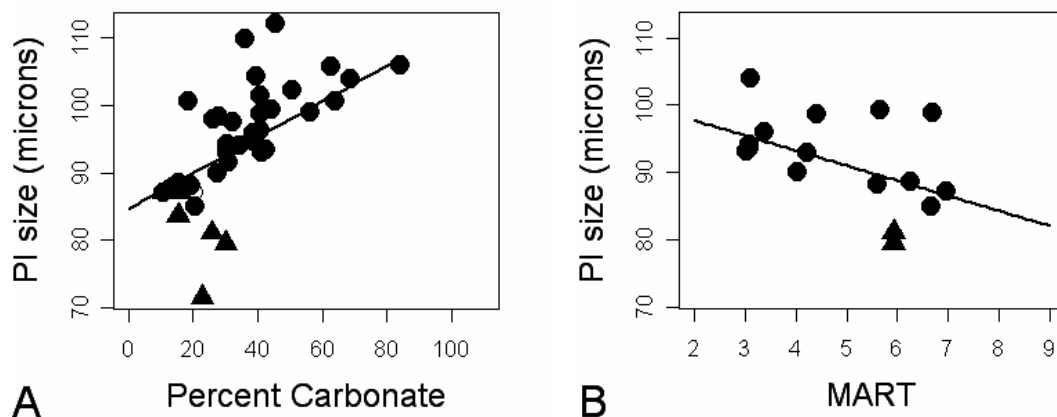
Figure 3.9. Correlation of PI sizes with environmental data. Values for percent carbonate (A) and MART (B) are from O'Dea et al. (*In Review*). Both correlation are significant, although only marginally in the case of MART (B).

The r-squared values are relatively low but the correlation between the environmental changes in the TWA and the evolution of novel life history patterns is clear. In addition, the six species with the smallest PII sizes (four of these six also have the largest PI shells observed) all appear for the first time in faunules with percent carbonate in excess of 40% (Smith and Jackson *In preparation*), a condition which does not occur in our samples prior to 3 to 4 Ma (O'Dea et al. 2006).

Surprisingly, there is no significant correlation between species durations as measured by stratigraphic range in our samples and dispersal potential as measured by PII size ($r^2 = 0.053$, $p = 0.1519$) as would be expected from the macroevolutionary models (Jablonski and Lutz 1983; Jablonski 1986). When living species, whose ranges are artificially truncated by the Recent, were excluded from the analysis the correlation was nearly significant and highly variable as seen by the low r-squared value ($r2 = 0.172$, $p = 0.06$). The difference in these two analyses is that the
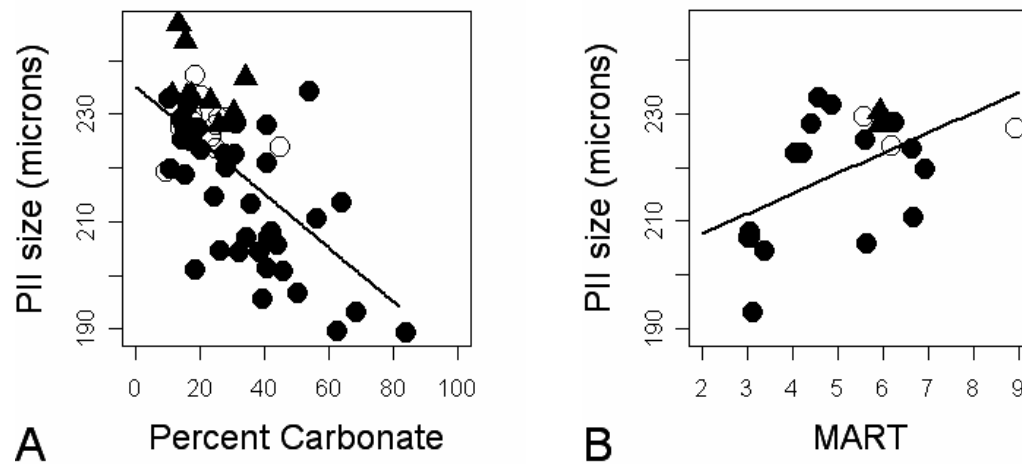
Figure 3.10. Correlation of PII sizes with environmental data. Data is same as for Figure 9. Both correlations are significant.

living species have long geologic ranges relative to small PII shells which is the

opposite of what is expected if truncated ranges were confounding the more inclusive

analysis.

I compared the sizes of larval shells of species that became extinct in the

TWA within the past 3.5 Ma with those of species living in the TWA and in the TEP

(Fig. 3.11) There was no significant difference between the PI sizes of the extinct

species versus species alive today in either ocean; although PI size was smaller for

recent species in the TEP compared to the TWA (Fig. 3.11A, t-test, t = 2.226, p =

0.0487). Living species in the TWA species have significantly smaller PII shells than

species in the TEP (Fig. 3.11B, t = 2.244, p = 0.0224) and species that became extinct

in the TWA (Fig. 3.11B, t = -2.799, p = 0.0044). However, there was no significant

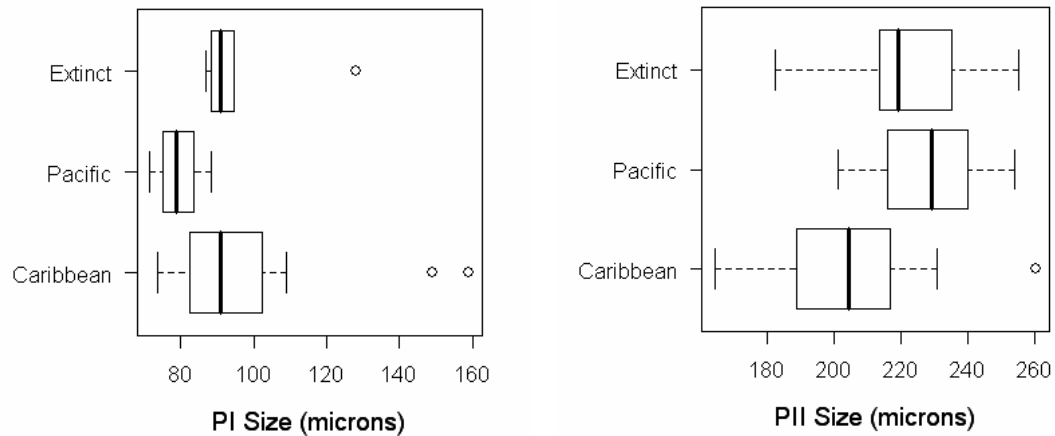difference between extinct and extant species in the TEP.

Figure 3.11. Comparison of PI and PII sizes for the Recent TEP and TWA faunas and the extinct species in the TWA. PI size is significantly smaller in the TEP, but there is no difference between the TWA living and extinct species (A). PII sizes are significantly smaller in the TWA, but there is no difference between the TEP and the extinct TWA species.

Discussion and Conclusions

The predictions of the life history models based on ecological fitness are well supported by differences in larval life histories of scallops and environmental characteristics across the Central American Isthmus today (Fig. 3.5), and by the overall evolutionary trends in life history evolution in the SWC over the past 10 Ma (Figs. 3.7, 3.8, 3.11). Moreover, there are clear and predictable functional relationships between these trends and the two environmental parameters, percent carbonate and MART (Figs. 3.9, 3.10), that best reflect the major changes in oceanographic conditions that transpired in the SWC 5 to 3 Ma as the Isthmus of Panama cut off circulation between the TEP and TWA (O'Dea et al. 2006). Predictions based primarily on energetic considerations (Vance 1973a, b; McEdward

1997; Levitan 2000) are as strongly supported as for those based on r- and K-selection theory in relation to spatial and temporal variations in habitats (Roughgarden 1971; Holt and McPeek 1996).

Smaller average egg size (PI size) and longer larval duration (PII size) in the TEP clearly reflect the high productivity and temporal variability but low spatial variability characteristic of the region. In contrast, larger average egg size and shorter larval durations in the TWA are a response to the low productivity and temporal variability coupled with extreme environmental heterogeneity of the Caribbean coast with its extensive localized patches of coral reefs and seagrass beds separated by great areas of level bottoms with high terriginous sedimentation and little reef or seagrass development. These patterns hold despite great differences among genera, species, and life habits and the considerable intraspecific variability characteristic of many common species (Table 3.2). However, these differences are much less apparent for comparisons between congeneric species from the different oceans (Fig. 3.6) because the numbers of comparisons are too small because of inadequate data.

The close fit between theoretical predictions based on life history did not scale up to predictable differences in macroevolutionary rates of lineages dominated by short- or long-distance dispersal (Jablonski and Lutz 1983; Jablonski 1986). Rather, new species originated disproportionately in relation to the advent of novel environments, in particular the expansion of oligotrophic coral reef and seagrass habitats that greatly increased in abundance after the isolation of the TWA and TEP 4 to 3 Ma (O'Dea et al. 2006; Smith and Jackson *In preparation*). Moreover, the historical context of the developing Isthmus provides strong support for the

importance of these environmental differences as the selective basis for the origin of new life history patterns because modern faunas in both oceans are derived from the same stock of species, many of which ranged throughout tropical American seas until the isthmian barrier was complete (Woodring 1966; Judith Smith 1991; Waller 1993; Jackson et al. 1993). High origination rates associated with short larval durations are consistent with the macroevolutionary models, but the lack of association between larval duration and extinction rates shows that ecological interactions play a much greater role.

Finally, the association of life history patterns with environmental change provides the critical link between metapopulation theory, extinction, and environmental change (Hanski and Gilpin 1997). Recent metapopulation models predict that environmental changes expressed as habitat loss may tip the balance in favor of species with one suite of life history characteristics compared to species with contrasting life histories (Nee and May 1992; Tillman et al. 1994; Jackson et al. 1996). The models were developed in the context of massive habitat loss due to human impacts but are just as applicable to major changes in habitats due to oceanographic change such as occurred in the TWA in relation to the formation of the Isthmus of Panama. Most importantly, the persistence of local populations dominated by species with the disadvantageous suite of life history characteristics side-by-side with patches dominated by species with advantageous characteristics (e.g., K- versus r-selected species) is consistent with the metapopulation models. But if the numbers of local populations occupied by the losing suite of species falls below some critical minimum threshold then the species should rapidly go extinct. This is exactly what

we observe for scallops in the SWC (Smith and Jackson *In preparation*) and that has been described elsewhere as geographical heterochrony - the discontinuous persistence over a broad area of faunal patches dominated by species of ancient or modern affinities (Petuch 1982). We conclude that natural selection of life history characteristics provides a much more powerful explanation for large-scale evolutionary patterns than more static models based on intrinsic evolutionary characteristics.

Acknowledgements

Literature Cited

Allmon, W.D. 2001. Nutrients, temperature, disturbance, and evolution; a model for the late Cenozoic marine record of the western Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology 166: 9-26.

Allmon, W.D., G. Rosenberg, R.W. Portell, and K.S. Schindler. 1996. Diversity of Pliocene-Recent mollusks in the western Atlantic: extinction, origination, and environmental change. Pp. 271-302 *in* J. B. C. Jackson, A. F. Budd & A. G. Coates, eds. Evolution and environment in tropical America. University of Chicago Press: Chicago, Illinois.

Barruca, M, E. Olmo, S. Schiaparelli, and A. Canapa. 2003. Molecular phylogeny of the family Pectinidae (Mollusca: Bivalvia) based on mitochondrial 16S and 12S rRNA genes. Molecular Phylogenetics and Evolution 31: 89-95.

Bemis, B.E., and D.H. Geary. 1996. The usefulness of bivalve stable isotope profiles as environmental indicators: Data from the eastern Pacific Ocean and the southern Caribbean. Palaios 11: 328-339.

Bhaud, M.R. 1993. Relationship between larval type and geographic range in marine species: complementary observations on gastropods. Oceanologica Acta 16: 191-198.

Birkeland, C. 1987. Nutrient availability as a major determinant of differences among coastal hard-substratum communities in different regions of the tropics. Pp. 43-98 *in* C. Birkeland, ed. Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological process, and productivity. UNESCO Report on Marine Science Vol. 46. UNESCO, Paris, France.

Bornmalm, L., J.G.V. Widmark, and B.A. Malmgren. 1999. Changes in circulation and trophic level in the Pliocene Caribbean Sea: Evidence from benthic foraminifer accumulation rates. Journal of Foraminiferal Research 29: 209-221.

Brown, J.H., and P.F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. American Naturalist 138: 1478-1512.

Budd, A.F., and K.G. Johnson. 1999. Origination preceding extinction during late Cenozoic turnover of Caribbean reefs. Paleobiology 25: 188-200.

Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung, and J. A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. Geological Society of America Bulletin 104: 814-828.

Coates, A.G., L.S. Collins, M. Aubry, and W.A. Berggren. 2004. The geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama Arc with northwestern South America. Geological Society of America Bulletin 116: 1327-1344.

Collin, R. 2004. Phylogenetic effects, the loss of complex characters, and the evolution of development in Calyptraeid gastropods. Evolution 58: 1488-1502.

Cragg, S.M., and D.J. Crisp. 1991. The biology of Scallop larvae. Pp. 75-132 *in* S. E. Shumway, ed. Scallops: Biology, ecology, and aquaculture. Elsevier Press, New York.

D'Croz, L., J.B. Del Rosario, and J.A. Gómez. 1991. Upwelling and phytoplankton in the Bay of Panama. Revista Biologia Tropical 39(2): 233-241.

D'Croz, L., and D.R. Robertson. 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. Pp. 2053-2058 *in* H.A. Lessios, and I.G. McIntyre, eds. Proc. 8th Inter. Coral Reef Symposium Vol. 2. Smithsonian Trop. Res. Inst., Balboa, Panama.

D'Croz, L., D.R. Robertson, and J.A. Martinez. 1999. Cross-shelf distribution of nutrients, plankton, and fish larvae in the San Blas Archipelago, Caribbean Panama. Revista Biologia Tropical 47(1-2): 203-215.

Duda, T.F. Jr., and S.R. Palumbi. 1999. Developmental shifts and species selection in gastropods. Proceedings National Academy of Science. 96: 10272-10277.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125: 1-15.

Hanski, I. A., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego.

Harvey, P.H., and M.D. Pagel. 1991. The Comparative method in evolutionary biology. 239 Pp. Oxford University Press.

Havenhand, J. N. 1995. Evolutionary ecology of larval types. Pp. 79-122 *in* McEdward, L.R., ed. Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, FL.

Heaseman, M.P., W.A. O'Connor, and A.W. Frazer. 1996. Ontogenetic changes in optimal rearing temperature for the commercial scallop, *Pecten fumatus* Reeve. Journal of Shellfish Research 15: 627-634.

Hodgson, C.A., and N. Bourne. 1988. Effect of temperature on larval development of the spiny scallop, *Chlamys hastata* Sowerby, with a note on metamorphosis. Journal of Shellfish Research 7: 349-357.

Holt, R.D., and M.A. McPeek. 1996. Chaotic population dynamics favors the evolution of dispersal. American Naturalist 148: 709-718.

Jablonski, D. 1986. Larval ecology and macroevolution in marine invertebrates. Bulletin of Marine Science 39: 565-587.

———. 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's rule. Nature 385: 250-252.

Jablonski, D., and R.A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biological Reviews 58: 21-89.

Jablonski, D., and D.M. Raup. 1995. Selectivity of End-Cretaceous marine bivalve extinctions. Science 268: 389-391. Jackson, J.B.C. 1974. Biogeographic consequences of eurytopy and stenotropy among marine bivalves and their evolutionary significance. American Naturalist 108 (962): 541-560.

Jackson, J.B.C., and J. D'Croz. 1998. The ocean divided. Pp. 38-71 *in* A.G. Coates, ed. Central America: A natural and cultural history, Yale University Press, New Haven, Connecticut.

Jackson, J.B.C., and A.H. Herrera Cubilla. 2000. Adaptation and Constraint as determinants of zooid and ovicell size among encrusting Ascophoran Cheilostome Bryozoa from opposite sides of the Isthmus of Panama. Pp. 249-258 *in* A. Herrera Cubilla and J.B.C. Jackson, eds. Proceedings of the 11th International Bryozoology Association Conference, Smithsonian Tropical Research Institute, Balboa, Panama.

Jackson, J. B. C., A. F. Budd, and J. M. Pandolfi. 1996. The shifting balance of natural communities. Pp. 89-122 *in* D. Jablonski, D. H. Erwin, and J. E. Lipps, eds. *Evolutionary Paleobiology*. University of Chicago Press.

Jackson, J. B. C., P. Jung, A. G. Coates, and L. S. Collins. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. Science 260: 1624-1625.

Jackson, J. B. C., P. Jung, and H. Fortunato. 1996. Paciphilia revisited: transisthmian evolution of the *Strombina* group (Gastropoda: Columbellidae). Pp. 234-270 *in* J. B. C. Jackson, A. F. Budd & A. G. Coates, eds. Evolution and environment in tropical America. Univ. of Chicago Press: Chicago, Illinois.

Jeffery, C.H., and R.B. Emlet. 2003. Macroevolutionary consequences of developmental mode in temnopleurid echinoids from the Tertiary of Southern Australia. Evolution 57: 1031-1048.

Jeffery, C.H., R.B. Emlet and D.T.J. Littlewood. 2003. Phylogeny and evolution of developmental modes in temnopleurid echinoids. Molecular Phylogenetics and Evolution 28: 99-118.

Kameo, K., and T. Sato. 2000. Biogeography of Neogene calcareous nannofossils in the Caribbean and the eastern equatorial Pacific – floral response to the emergence of the Isthmus of Panama. Marine Micropaleontology 39: 201-218.

Keigwin, D. Jr. 1982. Isotopic paleoceanography of the Caribbean and eastern Pacific uplift in the Late Neogene time. Science 217: 350-353.

Kohn, A.J., and F.E. Perron. 1994. Life history and biogeography. 106 Pps. Oxford University Press, New York.

Lessios, H. A. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from two sides of the Isthmus of Panama. Am. Nat. 135: 1-13.

Lessios, H.A., B.D. Kessing, and J.S. Pearse. 2001. Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. Evolution 55(5): 955-975.

Levitan, D.R. 2000. Optimal egg size in marine invertebrates: Theory and phylogenetic analysis of the critical relationship between egg size and development time. American Naturalist 156(2): 175-192.

Lockwood, J. L., T. M. Brooks, and M. L. McKinney. 2000. Taxonomic homogenization of the global avifauna. Animal Conservation 3:27–35.

Marko, P.B. 2002. Fossil calibration of molecular clocks and the divergence times of geminate species pairs separated by the Isthmus of Panama. Molecular Biology and Evolution 19: 2005-2021.

Marko, P.B., and A.L. Moran. 2001. Correlated evolutionary divergence of egg size and a mitochondrial protein across the Isthmus of Panama. Evolution 56: 1303-1309

Matsumoto, M., and I. Hayami. 2000. Phylogenetic analysis of the family Pectinidae (Bivalvia) based on mitochondrial cytochrome c oxidase subunit 1. Journal of Molluscan Studies 66: 477-488.

Maurer, B.A., J.H. Brown, and R.D. Rusler. 1992. The micro and macro in body size evolution. Evolution 46: 939-953.

McEdward, L.R. 1997. Reproductive strategies of marine benthic invertebrates revisited: facultative feeding by planktotrophic larvae. American Naturalist 150: 48-72.

McKinney, M. L. 1995. Extinction selectivity among lower taxa: gradational patterns and rarefaction error in extinction estimates. Paleobiology 21:300–313.

———. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495–516.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14:450–453.

Moran, A.L. 2004. Egg size evolution in tropical American arcid bivalves: the comparative method and the fossil record. Evolution 58: 2718-2733.

Mutti, M., and P. Hallock. 2003. Carbonate systems along nutrient gradients: some sedimentological and geochemical constraints. International Journal of Earth Sciences 92: 465-475.

Nee, S. and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61: 37-40.

O'Dea, A., and J.B.C. Jackson. 2002. Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. Palaeogeography, Palaeoclimatology, Palaeoecology 185: 77-94.

O'Dea, A., A. Herrera-Cubilla, H. Fortunato, and J.B.C. Jackson. 2004. Life history variation in cupuladriid bryozoans from either side of the Isthmus of Panama. Marine Ecology Progress Series 280: 145-161.

O'Dea, A., J.B.C. Jackson, H. Fortunato, J.T. Smith, L. D'Croz, K.G. Johnson, and J.A. Todd. *In Review*. Environmental change preceded Caribbean extinction by 2 million years. Proceedings, National Academy of Science.

Pechenik, J.A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Marine Ecology Progress Series 177: 269-297.

Petuch, E.J. 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. Palaeogeography, Palaeoclimatology, Palaeoecology 37: 277-312.

Rass, T.S. 1941. Geographic parallelisms in morphology and development of teleost fish of northern seas. MOIP, Moscow.

———.1986. Biogeographic rule of inverse relation between egg size and environmental temperature in poikilothermous animals. Trudy IOAN 116: 152-168.

Roopnarine, P.D. 1996. Systematics, biogeography and extinction of Chionine bivalves (Bivalvia: Veneridae) in Tropical America: Early Oligocene to Recent. Malacologia 38: 103-142.

Roughgarden, J. 1971. Density-dependent natural selection. Ecology 52(3): 453-468.

Roy, K., and K.K. Martien. 2001. Latitudinal distribution of body size in north-eastern Pacific marine bivalves. Journal of Biogeography 28: 485-493.

Roy, K., D. Jablonski, and K.K. Martien. 2000. Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. Proceedings, National Academy of Science 97: 13150-13155.

Scheltema, R.S. 1977. Dispersal of marine invertebrate organisms: Paleobiogeographic implications. Pp 73- 108 *in* Kaufman, E.G. and J.E. Hazel eds. Concepts and methods of biostratigraphy. Dowden, Hutchinson and Ross, Inc. Stroudsburg, PA.

Smith, J.T., J.B.C. Jackson, and H. Fortunato. 2006. Diversity and abundance of tropical American Scallops (Bivalvia: Pectinidae) from opposite sides of the Central American Isthmus. Veliger 48: 26-45.

Smith, J.T., and K. Roy. 2006. Selectivity during background extinction: Plio-Pleistocene scallops in California. Paleobiology 32: 408-416.

Smith, Judith.T. 1991. Cenozoic giant pectinids from California and the Tertiary Caribbean province: *Lyropecten*, "*Macrochlamis*", *Vertipecten*, and *Nodipecten* species. U. S. Geological Survey Professional. Paper 1391: 155 pp.

Spight, T.M. 1976. Ecology of hatching size for marine snails. Oecologia 24: 283-294.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America Memoir 125: 296 pp.

——. 1986. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. Paleobiology 12: 89-110.

Stanley, S.M., and X. Yang. 1987. Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. Paleobiology 13: 113-139.

Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16: 339-361.

Teranes, J.L., D.H. Geary, and B.E. Bemis. 1996. The oxygen isotope record of seasonality in Neogene bivalves from the Central American Isthmus. Pp. 105-129 *in* J. B. C. Jackson, A. F. Budd & A. G. Coates, eds. Evolution and environment in tropical America. Univ. of Chicago Press: Chicago, Illinois.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews, Cambridge Philosophical Society 1- 45.

Thresher, R.E. 1982. Interoceanic differences in the reproduction of coral-reef fishes. Science 218: 70-72.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65-66.

Todd, J.A., J.B.C. Jackson, K.G. Johnson, H.M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proceedings of the Royal Society of London, B 269: 571-577.

Vance, R.R. 1973a. On reproductive strategies in marine benthic invertebrates. American Naturalist 107: 339-352.

———.1973b. More on reproductive strategies in marine benthic invertebrates. Am. Nat. 107: 353-361.

Victor, B.C. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Marine Biology 90: 317-326.

Waller, T.R. 1969. The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the Tertiary and Quaternary species of Eastern North America. Paleontological Society Memoir 3: 1 – 125.

———. 1973. The habits and habitats of some Bermudian marine mollusks. Nautilus 87: 31-52.

———. 1986. A new genus and species of scallop (Bivalvia: Pectinidae) from off Somalia, and the definition of a new tribe Decatopectinini. Nautilus 100: 39-46.

———. 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). Pp 1-73 *in* S. E. Shumway, ed. Scallops: biology, ecology and aquaculture. Elsevier: New York, New York.

———. 1993. The evolution of "*Chlamys*" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific. American Malacological Bulletin 10: 195-249.

———. 2006. New phylogenies of the Pectinidae (Mollusca: Bivalvia): Reconciling morphological and molecular approaches. Pp 1 – 44 in S.E. Shumway (Ed.) Scallops: Biology, Ecology and Aquaculture (2nd edition). Elsevier, New York.

Wehrtmann, I.S., and L. Albornoz. 2002. Evidence of different reproductive traits in the transisthmian sister species, *Alpheus saxidomus* and *A. simus* (Decapoda, Caridea, Alpheidae): description of the first postembryonic stage. Marine Biology 140: 605-612.

Wellington, G.M., and D.R. Robertson. 2001. Variation in larval life-history traits among reef fishes across the Isthmus of Panama. Marine Biology 138: 11-22.

Wellington, G.M., and B.C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology 101: 557-567.

Woodring, W. P. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110: 425-433.

CHAPTER 4 – EVOLUTION AND CONSTRAINT OF BODY SIZE

Introduction

The environmental changes associated with the formation of the Isthmus of Panama coincided with major faunal reorganization of benthic communities in the Tropical Western Atlantic (TWA) (Jackson et al. 1993, 1999; O'Dea et al. *In press*). These changes, environmental and biotic, have been cited as driving mechanisms for the patterns of morphologic evolution that have been observed in TWA faunas (Vermeij 1978, 1987; Roopnarine 1996; Johnson et al. 1995; Jackson et al. 1996; Anderson 2001). The general biologic model pioneered by Geerat Vermeij (1978) is that higher levels of predation in the TEP should lead to larger sizes in the TEP and that loss of predators in the TWA should have relaxed selection for large size about 4 Ma. This scenario has been supported by evidence of a decrease in predatory gastropods in the Caribbean (Todd et al. 2002). In addition, reduced nutrients in the Caribbean have also been postulated to lead to smaller sizes in the Caribbean (Allmon 1992; Jackson et al. 1996; Roopnarine 1996; Anderson 2001). However, none of these questions have been addressed in a rigorous ecological context which includes life history data and environmental control across multiple life habits.

Tropical American scallops show a remarkable 100% turnover of species in the past 4.5 Ma (Smith and Jackson *In preparation a*). Smith and Jackson (*In preparation a*) argue that the idea of extinction debt from metapopulation theory (Nee and May 1992; Tilman et al. 1994; Stone et al. 1996; Hanski and Gilpin 1997) provides a plausible explanation for the observed evolutionary patterns. The extinction debt model is based on colonization and extinction within a changing

patchwork landscape. Smith and Jackson (*In preparation b*) also found significant evolutionary changes in the larval ecology of the tropical American scallops that support a metapopulation model of extinction. Data for Neogene Caribbean corals and other mollusks are also consistent with the model (Petuch 1982; Jackson et al. 1996).

Colonization potential is an important component of any metapopulation model of extinction (Nee and May 1992; Stone et al. 1996). Previous studies suggest that larger body sized organisms are more successful colonizers (Roy et al. 2002). Smith and Roy (2006) found patterns of size selective extinction in scallops in the Neogene of California that were interpreted to support this pattern, with large species preferentially surviving.

Thus, the ecological literature provides an alternative model to those purely based on productivity and size-selective predation. In a system where nutrient availability is the driving mechanism of size selectivity, we expect to see evolution towards smaller sizes in the Caribbean, as is observed in venerid (Roopnarine 1996) and corbulid (Anderson 2001) bivalves. If biotic interactions, particularly predation, are the driving mechanism as postulated by Vermeij (1978, 1987) then we also expect smaller sizes in the Caribbean. However, if an extinction debt model applies, we would expect selection for greater colonization ability. Egg size has increased in Caribbean scallops in relation to decreased productivity and increased spatial environmental heterogeneity associated with the development of coral reefs (Smith and Jackson *In preparation b*). Successful colonization of changing habitat space requires sufficient high fecundity rates (Roy et al. 2002). However, since size

correlates with energy available for reproduction in invertebrates (Strathmann 1985; Jablonski 1996; Roy et al. 2002), the observed shift towards larger eggs coupled with smaller size would imply a decrease in fecundity. Therefore, in an extinction debt scenario, a consideration of fecundity and colonization potential suggests that larger size would be selected to compensate for increased egg size.

I will address these predictions using the tropical American scallops by addressing three questions. (1) What are the general trends in body size of tropical American species? (2) Is there evidence of size selective extinctions within genera or across all species? (3) Is there a relationship between life history and body size?

Materials and Methods

Data were obtained from specimens collected by the Panama Paleontology Project (PPP) over the past 15 years. Locality and stratigraphic data is outlined in Smith and Jackson (*In preparation* a, b). Every complete specimen was measured from most anterior to most posterior point, and ventral to dorsal (Fig. 4.1). The size was computed as the geometric mean of these measurements following standard methods used in the literature (e.g. Jablonski and Raup 1995; Smith and Roy 2006). In addition, the aspect ratio was calculated for each specimen. Stanley (1970) showed for scallops that measurements of umbonal angle and auricle symmetry (Fig. 4.1) can be used to make inferences regarding life habit. The exception in Stanley's system were species in the genus *Leptopecten*, which we are treating separately. The aspect ratio incorporates aspects of both these measurements (Fig. 4.1) and was more
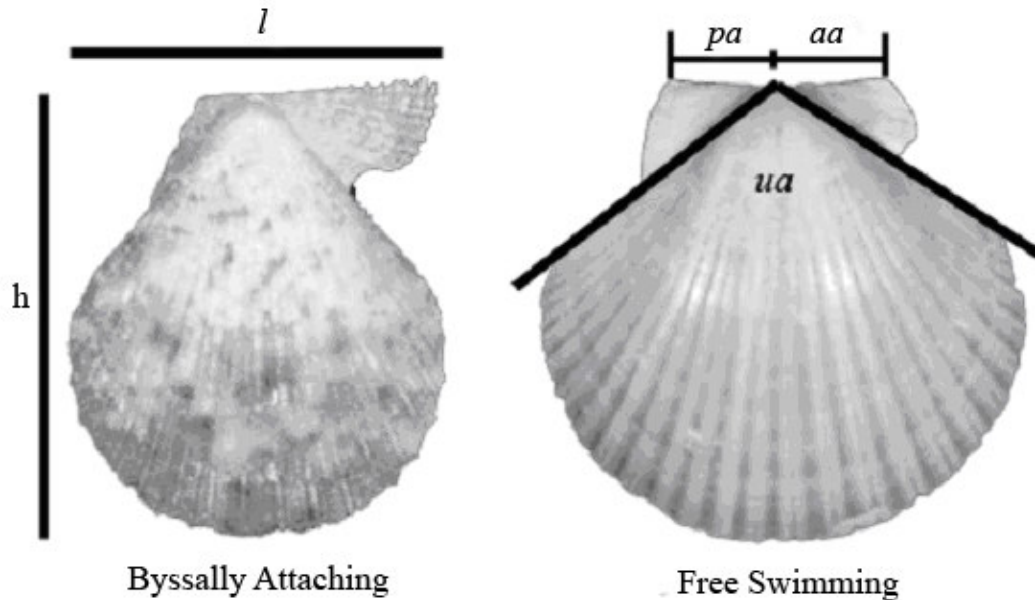
Figure 4.1. Size and shape measurements of scallops. For this study we measured length (*l*) and height (*h*) shown on the byssally attaching species. Size was computed as the geometric mean of these two measurements (see text). We calculated the aspect ratio as *l/h*. Stanley (1970) used umbonal angle (*ua*) and the auricle symmetry (*pa/aa*), depicted on the free swimming species, as a morphologic determinant of life habit. Aspect ratio can was more consistently measured in our data and captures elements of both of these measurements (see text).

consistently recovered from our specimens. I used my estimate of aspect ratio to

make more refined life history determinations than in our previous work (Smith and

Jackson *In preparation a, b*). Measurements were collected for 72 of the 83 species

in my collections and the values are summarized in Appendix 1.

Median values of size and aspect ratio were calculated for each species, based

on all measurements obtained for that species, and each faunule in my data using 1

measurement for each species occurring in that faunule. In addition, for each faunule

I have measurements of percent carbonate and mean annual range of temperature

(MART) as estimates of environmental conditions (Appendix 2; see O'Dea et al.

2006; Smith and Jackson *In preparation a* for a summary) and for each species I have

estimates of egg size and larval duration, as measured by the prodissoconch I and II

(PI and PII) shell sizes (Appendix 1; Smith and Jackson *In preparation b*).

I compared the size distributions of extinct and living faunas in the tropical

eastern Pacific (TEP) and the southwestern Caribbean (SWC). Size selectivity was

also tested within genera and ecological groups. My ecological groupings in general

follow Smith and Jackson (*In preparation a, b*). Species were classified as free

swimming or byssally attaching based on our measurements of aspect ratio and three

genera were analyzed as distinct ecological groups, *Argopecten*, *Leptopecten* and

Pacipecten. Argopecten are diverse and abundant in tropical America and have

distinct evolutionary patterns to the other groupings (Smith and Jackson *In*
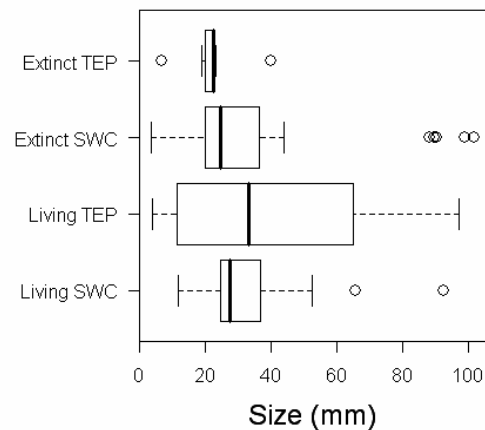
Figure 4.2. Size distributions for living
and extinct scallop species in the tropical
eastern Pacific (TEP) and southwestern
Caribbean (SWC). There is no
significant difference in any of the size
distributions.

preparation a). *Leptopecten* and *Pacipecten* do not fit cleanly into Stanley's (1970)

morphologic classification scheme. I previously treated these two genera together

(Smith and Jackson *In preparation a, b*), but in this paper it was apparent they show very different patterns and warranted separate treatment. I then compared the PI and PII values obtained for each species to body size to assess patterns of ecological constraint within ecological groups and across the whole fauna. As a more quantitative measure of life habit, I compared body size to aspect ratio and finally, I analyzed the patterns of aspect ratio through time using data for faunules.

Results

There was no significant difference in body size between the TEP and SWC, or between living and extinct species in either ocean (Fig. 4.2, ANOVA, F = 1.089, p
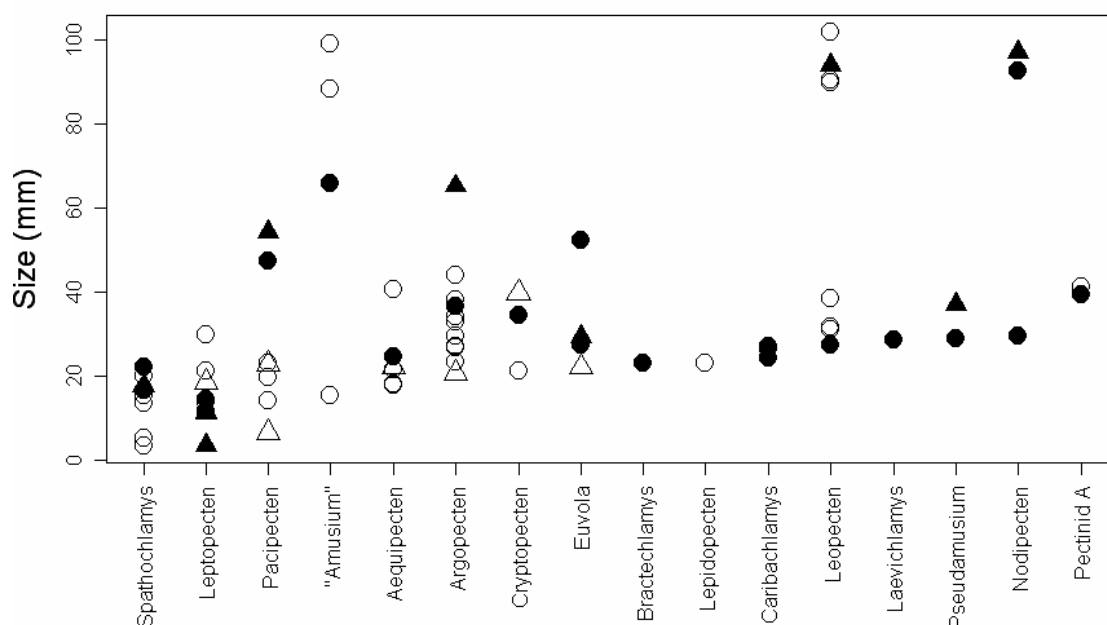
Figure 4.3. Within genus comparisons of body size of tropical American scallops. Triangles are TEP species, circles SWC species and open points represent extinct species.

= 0.3006). This is not unexpected in that the range of sizes is similar in all 4 groups; the exception being the extinct TEP where we do not see any very large species. There was also no evidence for size selection within scallop genera, contrary to results for California scallops (Fig. 4.3; Smith and Roy 2006) that were more consistent with previous work on the taxonomic structure of extinction selectivity (McKinney 1995, 1997; Lockwood et al. 2002). I made pairwise comparisons of species within each genus. Six of 13 living species in the SWC (Fig. 4.3, solid circles) were larger than the median for the genus and 6 were smaller. In the TEP, 5 of 9 living species (Fig. 4.3, solid triangles) were larger than the median and 3 were smaller. Extinct species in Figure 2 are annotated by open points. None of these pairwise comparisons were significant (sign test, $p > 0.05$). Pairwise comparison between oceans also failed to produce a significant result; in 6 of 10 comparisons the TEP species was larger than congeneric SWC species.

I have previously found differences in the evolutionary patterns of biodiversity between ecological groups of scallops (Smith and Jackson *In preparation a*) so I compared the sizes of species within ecological groups. Extant byssally attaching species were significantly larger than extinct byssally attaching species (Fig. 4.4, Mann-Whitney, $p = 0.0292$) and extant *Leptopecten* were significantly smaller than extinct species (Fig. 4.4, Mann-Whitney, $p = 0.0318$). There were no significant differences between extinct and living species in the other ecological groupings (Fig. 4.4, Mann-Whitney, $p > 0.05$), including living and extinct TEP species as well as the SWC species. Sample size was small in most cases so the significant results obtained appear to be robust. Living species within each of the 5

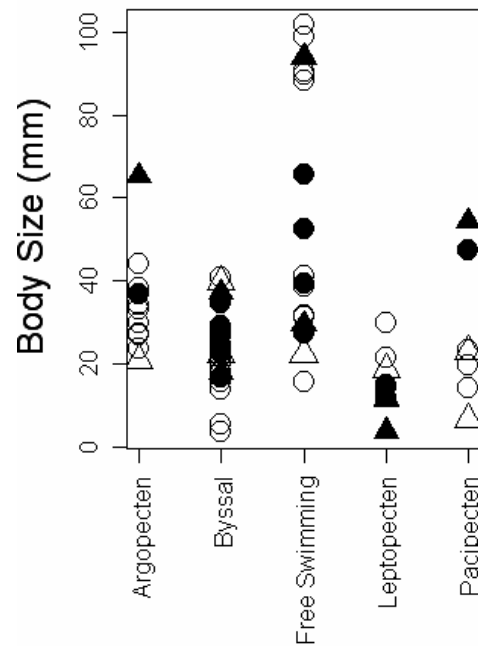groups are larger in the TEP relative to the SWC in just 4 of 8 pairwise comparisons, which is not significant.

Figure 4.4. Comparison of body size within ecological groupings. Ecological groups follow Smith and Jackson (*In preparation a*) except as noted in the text and Table 1. Extant byssally attaching species (solid points) are significantly larger than extinct species (open points). Extant *Leptopecten* species are significantly smaller than extinct species. The other groups show no significant pattern between living and extinct species. Pairwise comparisons between oceans within groups showed no significant patterns.
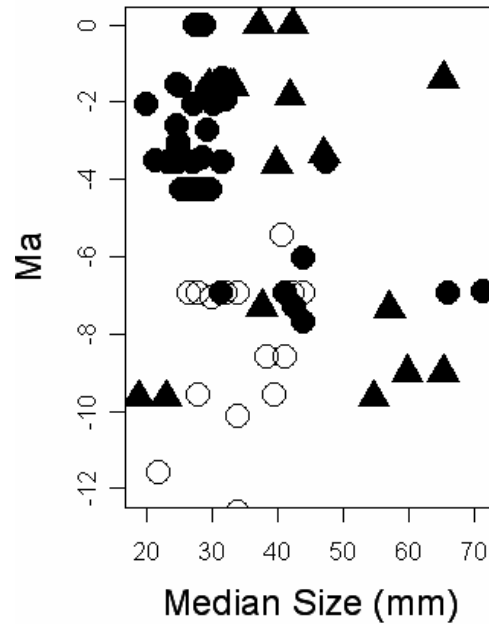
Figure 4.5. Median size of faunules through time. Triangles are TEP, solid circles Caribbean and open circles "isthmian" following Smith and Jackson (*In preparation a, b*). There is a significant trend through time and a significant difference between TEP and SWC faunules that are younger than 4 Ma (see text).

Despite the lack of consistent differences between TEP, SWC and the extinct species, there is a significant trend towards smaller size towards the Recent when data are plotted by faunule, although the fit of the model is very low (Fig. 4.5, Linear Fit Model, $F = 9.052$, $r^2 = 0.09$, $p = 0.0036$). Faunules in the Caribbean contain a much smaller percentage of the total species present in the region compared to the TEP (Smith and Jackson *In preparation a*) and the significant result obtained with this

analysis is the result of, on average, smaller sizes within SWC faunules in younger (<

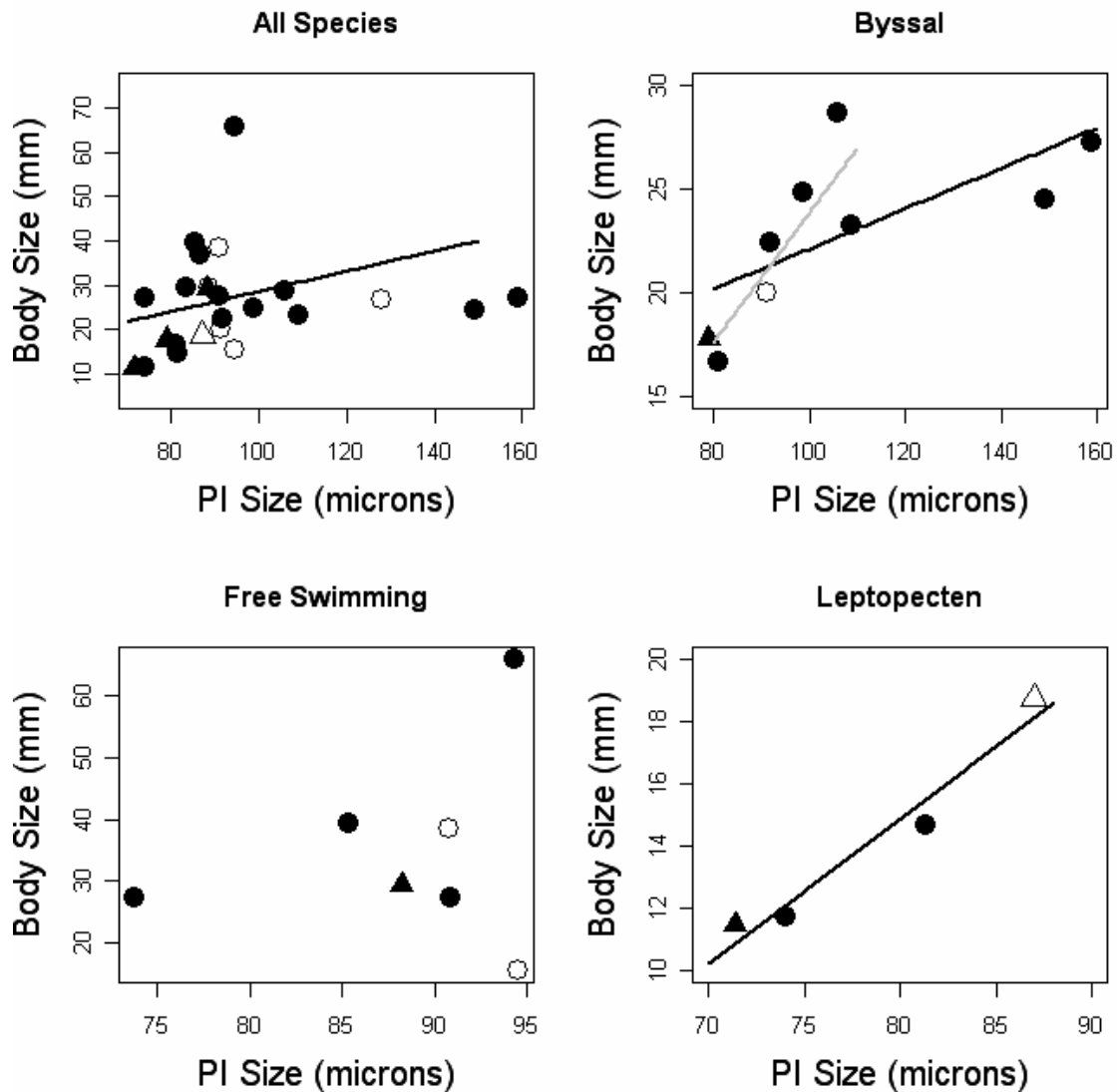4 Ma) faunules (t-test, t = -3.268, p = 0.0114).

Figure 4.6. Comparison of PI size with body size. There is a significant, but variable correlation across the entire fauna. The correlation within byssally attaching species and *Leptopecten* is also significant. There is no significant correlation within free swimming species.

The extinction debt model implies changes in life history, and previous work

has shown significant changes in PI and PII sizes, proxies for egg size and larval

duration (Smith and Jackson *In preparation b*). I compared the size distributions to

the PI and PII sizes from our previous work. There is a significant, but highly

variable relationship between PI size and maximum size across all species (Fig. 4.6, r^2

= 0.203, p = 0.0022). Results varied within the 3 ecological groups for which I had

sufficient data. There was no significant relationship between PI size and body size

in Free Swimming species (Fig. 4.6, r^2 = 0.141, p = 0.871) but there was a significant

correlation within *Leptopecten* (Fig. 4.6, r2 = 0.957, p = 0.0219) and byssally

attaching species (Fig. 4.6, r2 = 0.465, p = 0.0432). The results within byssally

attaching species is a better fit when lecithotrophic species are excluded (Fig. 4.6,

gray line, r2 = 0.742, p = 0.0028). There was no significant relationship between PII

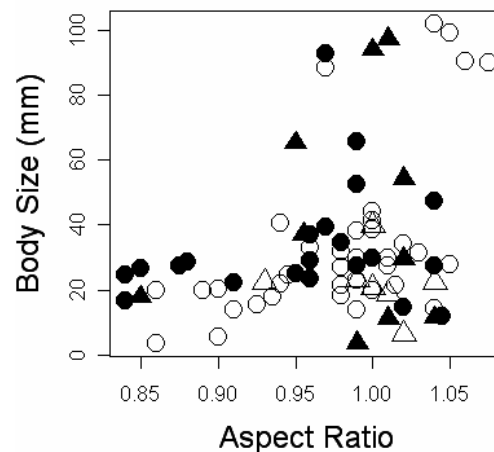size and maximum size within ecological groups or across the entire fauna.

Figure 4.7. Relationship between aspect
ratio and body size. There is no
significant correlation, but there appears
to be an upper limit of body size for
byssally attaching species (species with
and aspect ratio < 0.95).

The above results are potentially confounded because I am treating ecological groups and groups defined by taxonomy equally. I therefore refined the groups by using aspect ratio to provide a more quantitative approach to life habit. There is no significant relationship between body size and aspect ratio when compared among species (Fig. 4.7). However, there appears to be an upper size limit of about 30 mm for byssally attaching species with low aspect ratios.   This observation is consistent with the idea that there is an upper size limit for byssally attaching species, above which the strength of attachment is not sufficient, and our data show this relationship (Stanley 1970, 1972).
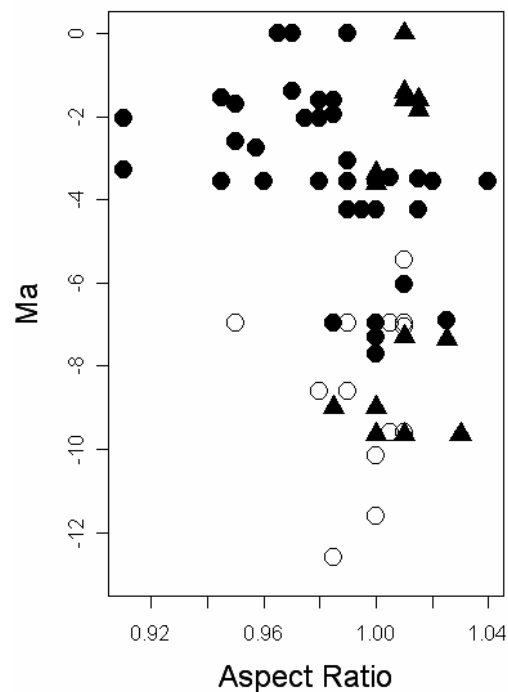

Figure 4.8. Proportion of byssally attaching species in faunules through time. Median values of aspect ratio are shown by faunule. Symbols are same as for Fig. 4.

I plotted aspect ratios through time using faunules (Fig. 4.8). There is a significant increase in variation starting around 3.5 Ma. Based on the observed relationship between life habit and body size, this clearly reflects the origination of byssally attaching species after 3.5 Ma (Smith and Jackson *In preparation a*) and is similar to the patterns of environmental change observed over the same period of time (O'Dea et al. *In press*). Byssally attaching species exhibited the largest diversity increase in the Caribbean and occur primarily within high carbonate reef environments (Smith and Jackson *In preparation a*). This pattern is clearly apparent in the strong correlations between median aspect ratio for each faunule and their environments (data from O'Dea et al. *In press*; Smith and Jackson *In preparation a*). There is a significant correlation with the percent carbonate in the sediment (Fig. 4.9A, $r^2 = 0.324$, $p < 0.0001$) and with the MART (Fig. 4.9B, $r^2 = 0.398$, $p < 0.0001$).
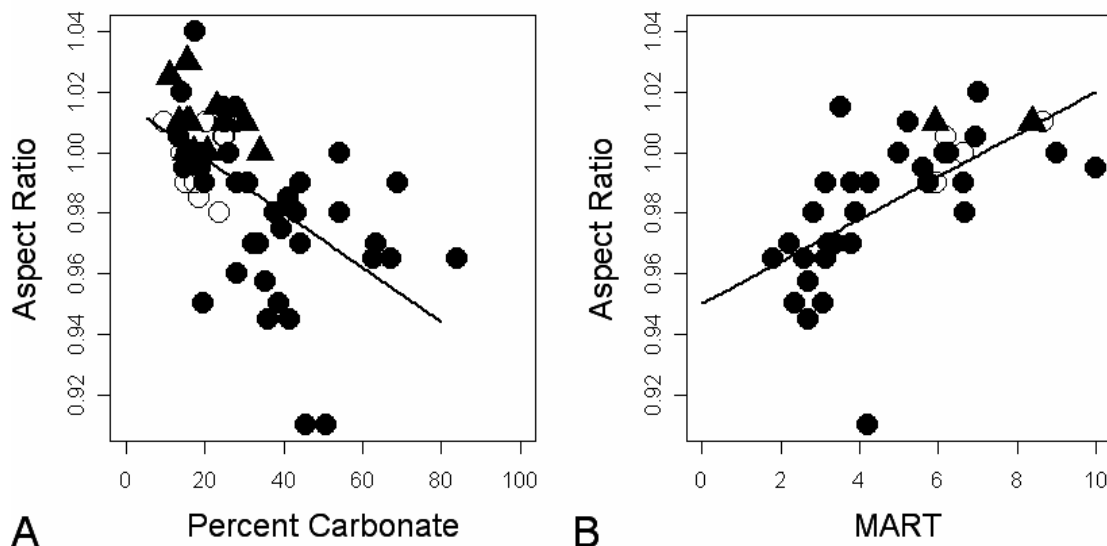

Figure 4.9. Relationship of aspect ratio to percent carbonate (A) and MART (B). The proportion of byssally attaching species in each faunule, as measured by the median aspect ratio, is significantly correlated with both environmental measures (see text).

Discussion and Conclusions

In contrast with previous work, I have found no systematic pattern of body size evolution or a relationship between body size and extinction susceptibility. Rather, my results indicate a complex interplay between life history ecology, life habits, and changing environments. Despite the lack of significant overall trends, I do see a pattern of decreasing size in the SWC when the patterns are analyzed at the faunule level (Fig. 4.5). The divergence of these results with that of previous work in the region may reflect the much wider range of life habits exhibited by scallop species relative to the venerids, corbulids and strombids analyzed by Roopnarine (1996), Anderson (2001) and Jackson et al. (1996) respectively. This interpretation is further supported by the highly varied but significant size selectivity I have observed within the ecological groups. My results are similar to those for Cretaceous bivalves that showed no evidence of significant size selective extinction (Jablonski and Raup 1995).

There is a significant relationship between PI size, a proxy for egg size and body size (Figs. 4.6). Egg sizes of marine invertebrates in the SWC evolved in response to environmental change (Lessios 1990; Levitan 2000; Marko and Moran 2001; Moran 2004; Smith and Jackson *In preparation b*). Byssally attaching species appear to have an upper size limit (Fig. 4.7). However, these species are also adapted to low nutrient, spatially variable reef environments that has resulted in the evolution of large eggs and short larval durations (Smith and Jackson *In preparation b*). Thus, evolution of body sizes among byssally attaching species has been constrained by life habit and life history, but within these constraints, surviving species are significantly

larger than extinct species. In contrast, *Leptopecten* species have been described as r-selected (Morton 1994). Species of *Leptopecten* have small egg sizes and long larval durations (Smith and Jackson *In preparation b*) and smaller species have preferentially survived. Together these two groups illustrate a tight constraint in the evolution of body size in relationship to egg size (Fig. 4.8).

Finally, my data do not support a general model of decreased size in relation to either decreasing nutrients or predation. Rather a much better explanation of my results involves a more complex interplay of life history traits and the environment within a framework of metapopulation theory. The reef associated byssally attaching species evolved in a low nutrient, spatially heterogeneous environment. Life history adaptations to this environment include large egg sizes and short larval durations, a condition I observe in these species (Smith and Jackson *In preparation b*). However, if we apply an extinction debt model from the metapopulation literature (Nee and May 1992; Tilman et al. 1994; Stone et al. 1996), we also expect to see selection for colonization ability and higher, or at least maintained, fecundity rates. Within these constraints, maintenance of colonization potential should strongly select for larger body size (Strathmann 1985; Roy et al. 2002), which is what I have observed for byssally attaching species among which larger species have preferentially survived. The larger sizes were also related to increased egg sizes (Fig. 4.6) suggesting there was selection to maintain or increase fecundity rates. In contrast, r-selected species in the genus *Leptopecten* show the exact opposite trend, with selection for smaller body size and smaller egg sizes, but this produces the same result with regard to fecundity (Fig. 4.6).

Body size exhibits highly complex relationships with all aspects of ecology (Peters 1983) and my results are no exception. However, trends can be revealed when the patterns are analyzed within distinct ecological groups. This has revealed a complex interaction between body size, ecological interactions and the environment. Ecological interactions, the ability to colonize changing habitats, and competitive ability to maintain populations in those patches have all played an important role in the evolution of body size of tropical American scallops. It is important to account for ecological characteristics of species to understand their evolutionary responses to changing physical and biotic environments.

Acknowledgements

Literature Cited

Allmon, W.D. 1992. Role of temperature and nutrients in extinction of turritelline gastropods: Cenozoic of the northwestern Atlantic and northeastern Pacific. Palaeogeography, Palaeoclimatology, Palaeoecology 92: 41-54.

Anderson, L.C. 2001. Temporal and geographic size trends in Neogene Corbulidae (Bivalvia) of tropical America: using environmental sensitivity to decipher causes of morphologic trends. Palaeogeography, Palaeoclimatology, Palaeoecology 166: 101-120.

Hanski, I. A. and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego.

Jablonski, D. 1996. Body size and macroevolution. Pp. 256–289 *in* D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. Evolutionary paleobiology. University of Chicago Press, Chicago.

Jackson, J.B.C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. American naturalist 108: 541-560.

Jackson, J. B. C., A. F. Budd, and J. M. Pandolfi. 1996. The shifting balance of natural communities. Pp. 89-122 *in* D. Jablonski, D. H. Erwin, and J. E. Lipps, eds. Evolutionary Paleobiolog*y*. University of Chicago Press.

Jackson, J. B. C., P. Jung, A. G. Coates, and L. S. Collins. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. Science 260: 1624-1625.

Jackson, J.B.C., P. Jung, and H. Fortunato. 1996. Paciphilia revisited: transisthmian evolution of the *Strombina* group (Gastropoda: Columbellidae). Pp. 234-270 *in* J.B.C. Jackson, A.F. Budd, and A.G. Coates, eds. Evolution and environment in tropical America. University of Chicago Press.

Jackson, J.B.C., J.A. Todd, H. Fortunato, and P. Jung. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. Bulletins of American Paleontology 357: 193-230.

Johnson, K.G., A.F. Budd, and T.A. Stemann. 1995. Extinction selectivity and ecology of Neogene Caribbean reef corals. Paleobiology 21: 52-73.

Lessios, H. A. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from two sides of the Isthmus of Panama. Am. Nat. 135: 1-13.

Levitan, D.R. 2000. Optimal egg size in marine invertebrates: Theory and phylogenetic analysis of the critical relationship between egg size and development time. American Naturalist 156(2): 175-192.

Lockwood, R. 2005. Body size, extinction events, and the early Cenozoic record of venerid bivalves: a new role for recoveries? Paleobiology 31:578–590.

Marko, P.B., and A.L. Moran. 2001. Correlated evolutionary divergence of egg size and a mitochondrial protein across the Isthmus of Panama. Evolution 56: 1303-1309

McKinney, F.K., S. Lidgard, J.J. Sepkoski Jr., and P.D. Taylor. 1998. Decoupled patterns of evolution and ecology in two post-Paleozoic clades. Science 281: 807-809.

McKinney, M. L. 1995. Extinction selectivity among lower taxa: gradational patterns and rarefaction error in extinction estimates. Paleobiology 21:300–313.

———. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495–516.

Moran, A.L. 2004. Egg size evolution in tropical American arcid bivalves: the comparative method and the fossil record. Evolution 58: 2718-2733.

Morton, B. 1994. The biology and functional morphology of *Leptopecten latiauratus* (Conrad, 1837): an "opportunistic scallop". Veliger 37(1): 5-22.

Nee, S. and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61: 37-40.

O'Dea, A., J.B.C. Jackson, H. Fortunato, J.T. Smith, L. D'Croz, K.G. Johnson, and J.A. Todd. *In Press*. Environmental change preceded Caribbean extinction by 2 million years. Proceedings, National Academy of Science.

Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press, New York. 329 Pps.

Petuch, E.J. 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. Palaeogeography, Palaeoclimatology, Palaeoecology 37: 277-312.

Roopnarine, P.D. 1996. Systematics, biogeography and extinction of Chionine bivalves (Bivalvia: Veneridae) in Tropical America: Early Oligocene to Recent. Malacologia 38: 103-142.

Roy, K., D. Jablonski, and J. W. Valentine. 2002. Body size and invasion success in marine bivalves. Ecology Letters 5:163–167.

Smith, J.T., and J.B.C. Jackson. *In preparation a*. Ecological change during extreme faunal turnover of tropical American scallops.

———. *In preparation b*. Evolutionary divergence in larval ecology across the Central American Isthmus.

Smith, J.T., and K. Roy. 2006. Selectivity during background extinction: Plio-Pleistocene scallops in California. Paleobiology 32: 408-416.

Smith, J.T., J.B.C. Jackson, and H. Fortunato. 2006. Diversity and abundance of tropical American Scallops (Bivalvia: Pectinidae) from opposite sides of the Central American Isthmus. Veliger 48: 26-45.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America Memoir 125: 296 pp.

———. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. Journal of Paleontology 46: 165-212.

Stone, L., E. Eilam, A. Abelson, and M. Ilan. 1996. Modeling coral reef biodiversity and habitat destruction. Marine Ecology Progress Series 134: 299-302.

Strathmann, R.R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16: 339-361.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65-66.

Todd, J.A., J.B.C. Jackson, K.G. Johnson, H.M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proceedings of the Royal Society of London, B 269: 571-577.

Vermeij, G.J. 1978. Biogeography and adaptation: Patterns of marine life. Harvard University Press, Cambridge, Massachusetts, 332 Pp.

——. 1987. Evolution and Escalation. Princeton University Press.

Waller, T.R. 1984. The ctenolium of scallop shells: functional morphology of a key family-level character in the Pectinicaea (Mollusca: Bivalvia). Malacologia 25: 203-219.

CHAPTER 5 – CONCLUSION

Ecology does matter! However, my results do not support a model based solely on either biotic interactions or response to environmental change driving evolutionary patterns. Rather, there is a complex interplay between constraints of life habit, larval ecology and size in relation to the environment. Life history characteristics related to larval ecology evolved in response to changing environmental conditions, with novel larval ecologies originating in the newly developing reef environments in the Caribbean. These environments favored specific life habits and selection for other ecological characteristics, based on biotic interactions, were constrained by the life habits and larval ecologies dominant in these environments.

One of the most striking observations to arise from my analyses of diversity was the persistence for several Myr of relict faunas contemporaneous with more or less modern faunas (Fig. 2.12). This strongly supported the idea of geographic heterochrony proposed by Petuch (1982). However, my results did not indicate that these relict faunas inhabited marginal environments as predicted. This pattern instead was consistent with metapopulation ecology. This was further supported by the observation that no single fauna contained all of the species occurring within a given time bin, including the recent. The environment in the Caribbean became more variable after the formation of the Isthmus (O'Dea et al. 2006) and within the newly forming patchy habitat; faunas persisted, colonized and went extinct. From metapopulation theory, the idea of extinction debt (Nee and May 1992; Tilman et al.

1994) provided a possible mechanism for the delayed extinction patterns relative to the closing of the Isthmus.

The application of metapopulation models was expanded on in my analyses of larval ecology and body size. Invoking an extinction debt model implies changes in life history ecology. I observed highly selective patterns of evolution which supported this. Around 3.5 Ma byssally attaching species diversity increased, particularly species associated with reef environments. These species has larval ecologies specifically adapted to reef environments, large eggs and short larval durations (Fig. 3.9, 3.10). However, in an extinction debt scenario, fecundity and an ability to colonize or compete within the existing patch are important. Egg size was significantly correlated with body size within ecological groups (Fig. 4.6), so in addition to increasing egg size, an adaptation to low nutrient environments, the surviving byssally species were significantly larger than extinct species (Fig. 4.4), suggesting selection for higher fecundity rates. However, the maximum size of these species was constrained by their byssally attaching life habit (Fig. 4.7), so patterns of size selectivity were only apparent when ecology was taken into account. In addition, these species has the shortest larval durations of all species in this study, indicating adaptation for short larval dispersal.

The complex relationship between ecological characteristics can be summarized utilizing a principle component analysis of the 4 main traits I observed; PI size (egg size), PII size (larval duration), aspect ratio and body size. The results show the 4 main observations from my results (Fig. 5.1). First, we can see the nearly
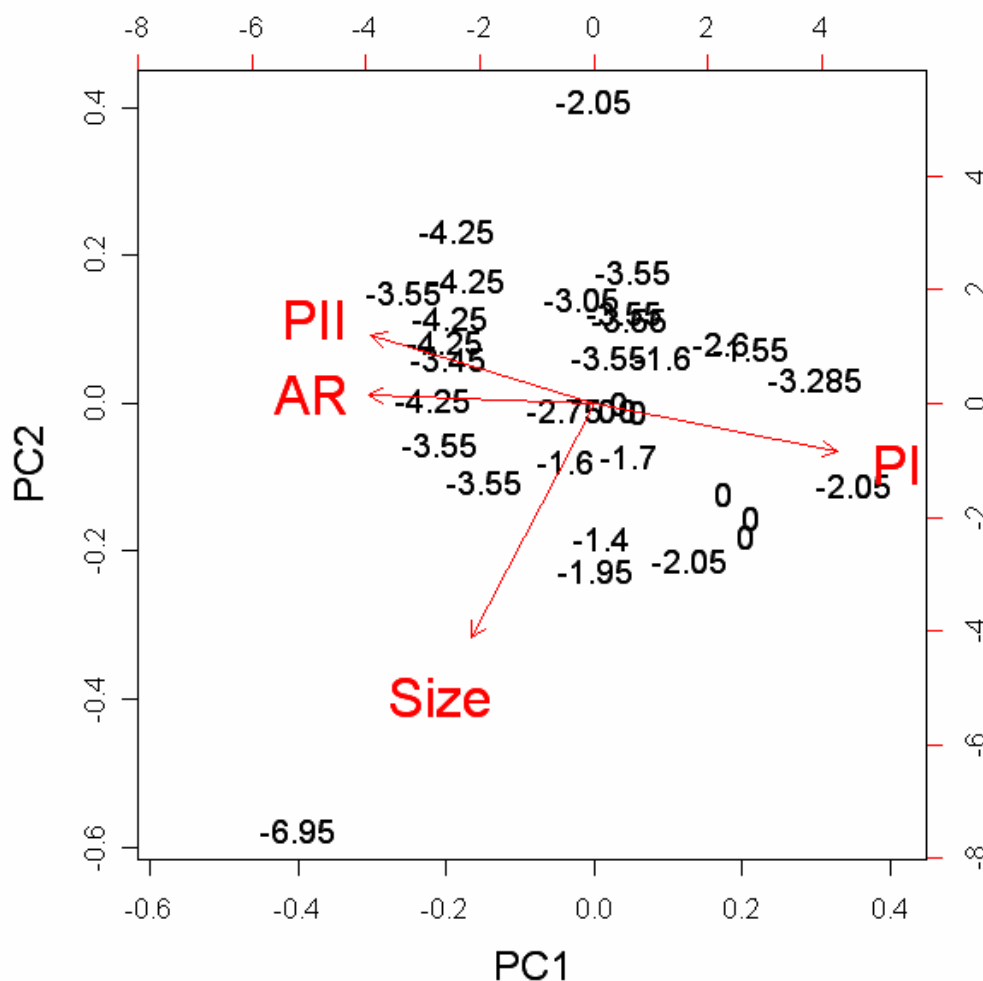
Figure 5.1. Principle component analysis of ecology. Faunules were analyzed using median aspect ration (AR), median PI, median PII and median size based on the values for species occurring in each faunule. Faunules are denoted by their age in Ma.

linear relationship between PI and PII size by the opposite weightings of these two measurements, similar to what I observed in chapter 3 (Fig. 3.3, 3.4). Second, aspect ratio (AR) weighs almost same as PII (opposite of PI) along both axes. This is not surprising in that one of the dominant evolutionary feature I have observed is the development of large egg sizes (PI) in byssally attaching species (low AR). The third is that we can observe the complex interaction of body size with the other three

characteristics and note that size weights more along PC2 than PC1. This could be

interpreted to indicate a stronger effect of environmentally driven selection, which

acts on egg size (Fig. 3.9), larval duration (Fig. 3.10) and life habit (Fig. 4.9).

Finally, the values in Figure 5.1 are plotted by faunule, and the points are represented

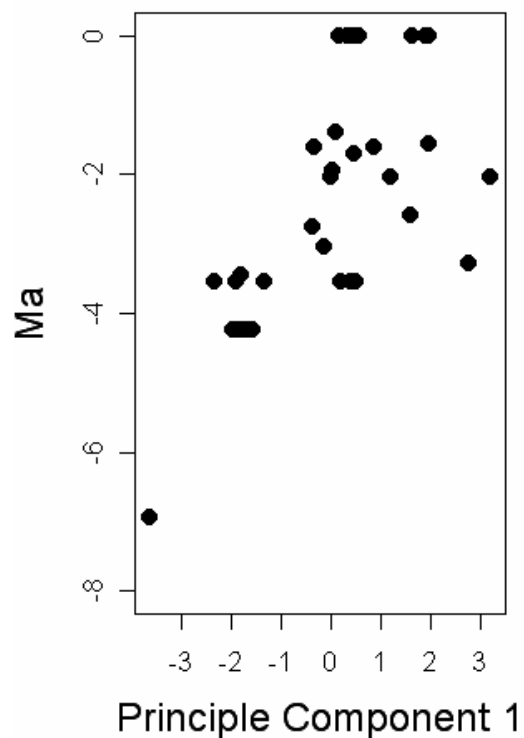by the age of the faunule. We can observe that younger faunules generally score

Figure 5.2. Values of principle component
1 for faunules plotted against age of the
faunule.

higher along PC1. This can be observed graphically by plotting PC1 versus age of

the faunule (Fig. 5.2). Sampling is poor prior to 5 Ma, but a general trend to larger

PC1 scores is clearly apparent.

I assessed the overall relationship between ecology and environment by plotting PC1 against the percent carbonate and mean annual range of temperature (MART) for each faunule. There is a significant correlation between the overall ecology score as measured by PC1 and both percent carbonate (Fig. 5.3A, $r^2 = 0.411$, $p < 0.0001$) and MART (Fig. 5.3B, $r^2 = 0.478$, $p < 0.0001$).
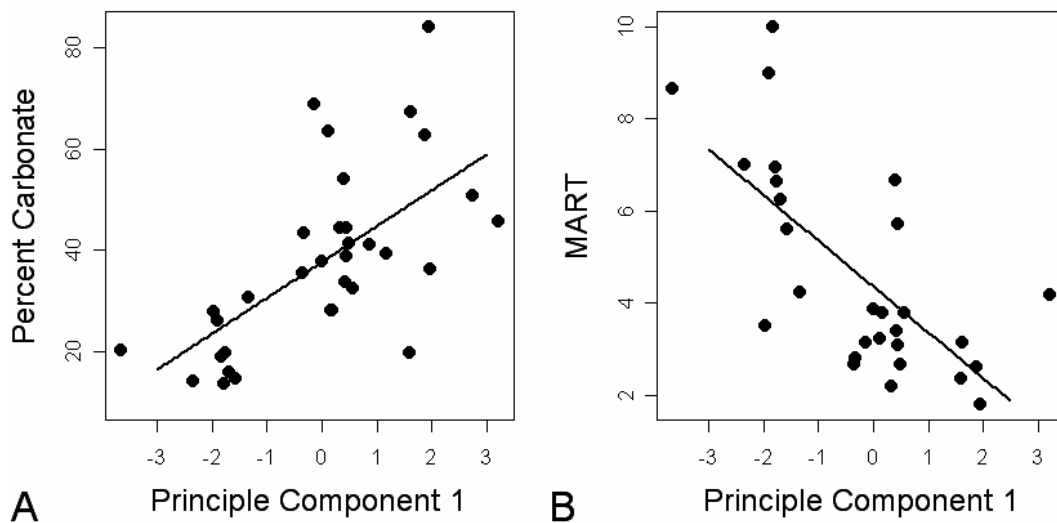

Figure 5.3. Ecology and Environment. Correlation of ecology, as measured by principle component 1 for each faunule compared to percent carbonate (A) and MART (B). Both correlations are significant (see text).

To summarize my opinion of the second major theme that I have tried to follow, scaling of ecological models upwards provided far better predictions of evolutionary patterns than those made by macroevolutionary models. This was clearly illustrated in my studies of larval ecology and body size. The complex relationships between life history characteristics and the constraints on these characteristics related to ecology makes generalizing across large groups difficult.

Taken together, my results illustrate why the debate of biotic versus environmental factors is so difficult. The environment is clearly driving evolutionary patterns (Fig. 5.3), this is almost certainly true the case in the observed patterns of larval ecology. My analyses of body size could be interpreted to support biotic interactions in that there is selection occurring to maintain higher fecundity rates, which must relate to competition, but the relationship between size and larval ecology indicates there is constraint within which selection due to biotic interactions is occurring. Applied to this question, the answer, as if often the case, is more likely that they are both important and worse, from an analytical point of view, they interact in a way that assigning relative importance to one or the other is at best extremely difficult.

Finally, the patterns in this study have been dominated by the effects of relatively few species. These species originated with novel life histories in the newly developing environments in the Caribbean. These species are characterized by several traits that could be interpreted as making them more prone to extinction than other species. They are relatively rare in comparison to non-reef species as indicated by the disconnect I observe between proportions of diversity and abundance (Fig. 2.3, 2.4.). They have larger eggs, and although they also show evolution toward larger sizes, this most likely equates to lower fecundity rates than the smaller egged species. In addition, despite lack of support in my data for the model proposed by Jablonski and Lutz (1983), these species had very short larval durations which could also be interpreted as leading to higher extinction risk in the face of large scale habitat loss. If these characteristics are common adaptations to life in oligotrophic reef

environments, it is then less surprising that reef habitats are often cited as being

biodiversity hotspots (Roberts et al. 2002).

In conclusion, the effects of ecology cannot be overlooked by paleontologists

and evolutionary biologists. This requires knowledge of not only ecological

characteristics, but a fundamental understanding of the environmental context in

which the ecologies have evolved. The Panama Paleontology Project has provided

me and others with an incredible framework within which to address very specific

evolutionary questions. My work has provided answers for only one family of

bivalves in tropical America. While it is my hope that these results are robust, work

with other groups, mollusk or other, must be undertaken for comparison before we

can really understand the consequences of extreme environmental changes as we have

observed in the Caribbean.

Literature Cited

Jablonski, D., and R.A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biological Reviews 58: 21-89.

Nee, S. and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61: 37-40.

O'Dea, A., J.B.C. Jackson, H. Fortunato, J.T. Smith, L. D'Croz, K.G. Johnson, and J.A. Todd. 2006. Environmental change preceded Caribbean extinction by 2 million years. Proceedings National Academy of Sciences *In press.*

Petuch, E.J. 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. Palaeogeography, Palaeoclimatology, Palaeoecology 37: 277-312.

Roberts, C.M., C.J. McClean, J.E.N. Veron, J.P. Hawkins, G.R. Allen, D.E. McAllister, C.G. Mittermeier, F.J. Schueler, M. Spalding, F. Wells, C. Vynne, and T.B. Werner. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295: 1280-1284.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65-66.

List of species with first (FO) and last occurrences (LO), PI and PII sizes, maximum body size, aspect ratio (AR) and ecological grouping. A value of *n/a* for the (+/-) indicates only 1 measurement was obtained.

Species	Fauna	FO (Ma)	LO (Ma)	PI Size (+/-)	PII Size (+/-)	Max Size (mm)	AR	Ecological Group[a]
"Amusium" bocasense (Olsson, 1922)	TWA	4.5	2.05	94.5 (*n/a*)	247.2 (7.8)	15.62[b]	0.93	Free Swimming
"A." laurenti (Gmelin, 1791)	TWA	3.55	Recent	94.4 (0.7)	210.6 (1.6)	65.79	0.99	Free Swimming
"A." sp. 2	TWA	8.6	6.9	-	233 (*n/a*)	88.22	0.97	Free Swimming
"A." toulae (Brown and Pilsbry, 1913)	TWA	6.95	3.55	-	242 (*n/a*)	98.95	1.05	Free Swimming
"Chlamys" onzola (Olsson, 1964)	TEP	9.65	3.35	-	-	-	-	Byssal
Aequipecten canalis (Brown and Pilsbry, 1913)	TWA	18	3.55	-	-	21.68	0.94	Mixed[a]

A. plurinomis (Pilsbry and Johnson, 1917)	TWA	12.6	3.55	-	209 (*n/a*)	40.71	0.94	Mixed[a]
A. sp. 3	TWA	9.6	3.55	-	-	24.58	0.95	Mixed[a]
A. sp. 4	TWA	8.6	8.6	-	217 (*n/a*)	18.11	0.98	Mixed[a]
A. sua (Olsson, 1964)	TEP	9.65	9.65	-	-	22.3	0.93	Mixed[a]
Argopecten costaricaensis (Olsson, 1922)	TWA	4.5	1.6	88.5 (4.9)	218.3 (2.6)	29.7	0.99	Argopecten
A. gibbus (Linnaeus, 1758)	TWA	3.55	Recent	86.6 (5.6)	206 (4.0)	36.83	0.96	Argopecten
A. levicostatus (Toula, 1909)	TWA	9.6	2.75	-	217.7 (3.5)	43.91	1	Argopecten
A. nerterus (Woodring, 1982)	TWA	9.6	3.55	-	-	38.25	0.99	Argopecten
A. sp. A	TEP	7.3	7.3	-	-	20.86	1	Argopecten

A. sp. 1	Both	9.65	3.55	-	219.1 (12.4)	23.59	0.96	Argopecten
A. sp. 4	TWA	2.05	2.05	-	182.5 (3.1)	33.1	0.96	Argopecten
A. sp. 5	TWA	3.55	1.4	128 (38.4)	212.8 (4.5)	26.93	0.98	Argopecten
A. sp. 8	TWA	4	4	-	-	34.14	1.02	Argopecten
A. uselmae (Pilsbry and Johnson, 1917)	TWA	12.6	1.6	-	-	27.29	1.01	Argopecten
A. ventricosus (Sowerby II, 1842)	TEP	9	Recent	-	229.9 (4.4)	65.2	0.95	Argopecten
Bractechlamys antillarum (Recluz, 1853)	TWA	3.55	Recent	109.0 (1.9)	167.8 (2.4)	23.22	0.96	Byssal
Caribachlamys imbricata (Gmelin, 1791)	TWA	2.05	Recent	159 (*n/a*)	177.8 (2.3)	27.23	0.88	Byssal
C. sentis (Reeve, 1853)	TWA	3.55	Recent	149.3 (*n/a*)	164.4 (3.7)	24.54	0.84	Byssal

Cryptopecten cactaceus (Dall, 1898)	TWA	6.95	3.45	-	-	21.44	0.98	Mixed[a]
C. phrygium (Dall, 1886)	TWA	1.6	Recent	-	230.5 (*n/a*)	34.49	0.98	Mixed[a]
C. woodringi (Olsson, 1964)	TEP	3.6	3.35	-	-	39.84	1	Mixed[a]
Demarzipecten sp. 1	TWA	6.9	3.45	-	200.5 (*n/a*)	-	-	Byssal
D. sp. 2	TWA	6.95	6.95	-	-	-	-	Byssal
Euvola gordus (Olsson, 1964)	TEP	9.65	9.65	-	-	22.23	1.04	Free Swimming
E. perulus (Olsson, 1961)	TEP	3.35	Recent	88.3 (8.4)	228.8 (6.2)	29.43	1.02	Free Swimming
E. sp. (cf. E. perulus)	TWA	-	Recent	73.8(*n/a*)	230.9 (5.2)	27.34	1.04	Free Swimming
E. reliquus (Brown and Pilsbry, 1913)	TWA	9.6	3.55	-	-	27.77	1.05	Free Swimming

E. ziczac (Linnaeus, 1758)	TWA	3.55	Recent	-	209 (*n/a*)	52.41	0.99	Free Swimming
Laevichlamys multisquamata (Dunker, 1864)	TWA	3.55	Recent	106.1 (42.1)	191.3 (4.1)	28.69	0.88	Byssal
L. antiguensis (Brown, 1913)	TWA	9.6	9.6	-	-	89.79	1.08	Free Swimming
L. catianus (Weisbord, 1964)	TWA	9.6	3.55	-	239.5 (12.0)	31.29	1.03	Free Swimming
L. chazaliei (Dautzenberg, 1900)	TWA	3.55	Recent	90.9 (0.7)	223.1 (1.6)	27.46	0.99	Free Swimming
L. coralliphila (Olsson, 1922)	TWA	3.55	1.4	90.8 (6.0)	220.3 (3.4)	38.52	1	Free Swimming
L. gatunensis (Toula, 1909)	Both	12.6	2.75	-	247.9 (8.2)	101.75	1.04	Free Swimming
L. macdonaldi (Olsson, 1922)	Both	9.6	6.9	-	-	90.46	1.06	Free Swimming
L. marquerensis (Durham, 1950)	TEP	9	9	-	-	-	-	Free Swimming

L. sericeus (Hinds, 1845)	TEP	9	Recent	-	244.3 (*n/a*)	93.85	1	Free Swimming
L. sp. (cf. L. sericeus)	TWA	2.05	Recent	-	-	-	-	Free Swimming
L. sp. 4	TWA	3.55	3.55	-	-	31.7	0.98	Free Swimming
L. sp. 5	TWA	3.55	3.55	-	-	-	-	Free Swimming
Lepidopecten scissuratus (Dall, 1898)	TWA	12.6	6.9	-	-	23.24	0.96	Mixed[a]
Leptopecten bavayi (Dautzenberg, 1900)	TWA	4.25	Recent	81.4 (9.1)	200.4 (3.5)	14.68	1.02	Leptopecten
L. biolleyi (Hertlein and Strong, 1946)	TEP	1.85	Recent	71.4 (1.5)	253.8 (1.7)	11.46	1.04	Leptopecten
L. sp. (cf. L. biolleyi)	TWA	3.55	Recent	74.0 (1.7)	260.4 (3.1)	11.74	1.05	Leptopecten
L. cracens (Olsson, 1964)	TEP	9.65	7.35	87 (*n/a*)	233.3 (8.6)	18.72	1.01	Leptopecten

Species								
L. ecnomius (Woodring, 1982)	TWA	11.6	3.45	-	219.3 (9.8)	29.87	1.01	Leptopecten
L. euterpes (Berry, 1957)	TEP	1.6	Recent	-	-	3.67	0.99	Leptopecten
L. sp. 2	TWA	9.6	3.05	-	208.5 (7.9)	21.37	1.02	Leptopecten
L. sp. 4	TWA	11.6	3.55	-	255 (*n/a*)	13.97	0.99	Leptopecten
L. velero (Hertlein, 1935)	TEP	1.85	Recent	-	224.5 (10.7)	11.36	1.01	Leptopecten
Lindapecten acanthodes (Dall, 1925)[c]	TWA	4	Recent	98.6 (3.5)	172.5 (3.3)	24.81	0.95	Mixed[a]
L. sp. 1 [c]	TWA	4.5	3.05	-	-	17.8	0.94	Mixed[a]
Nodipecten arthriticus (Reeve, 1853)	TEP	1.6	Recent	-	201.3 (17.0)	97.12	1.01	Mixed
N. sp. (cf. N. arthriticus)	TWA	-	Recent	83.3 (*n/a*)	207.3 (*n/a*)	29.63	1	Mixed

N. nodosus (Linnaeus, 1758)	TWA	2.6	Recent	-	182.2 (31.9)	92.71	0.97	Mixed
Pacipecten linki (Dall, 1926)	TWA	3.55	Recent	-	225.0 (17.2)	47.32	1.04	Leptopecten
P. maturensis (Maury, 1925)	TWA	4.5	2.6	-	225.0 (14.9)	23.15	0.99	Leptopecten
P. sp. A	TEP	9.65	9.65	-	-	6.59	1.02	Leptopecten
P. sp. 1	TWA	4.5	3.5	-	214.3 (6.4)	14.22	1.04	Leptopecten
P. sp. 3	TWA	2.05	2.05	-	-	19.68	1	Leptopecten
P. tumbezensis (d'Orbigny, 1846)	TEP	9	Recent	-	235.9 (4.5)	54.26	1.02	Leptopecten
Pectinid A lineolaris (Lamarck, 1819)	TWA	-	Recent	85.4 (1.8)	204.1 (1.2)	39.45	0.97	Mixed
P. A. mimyum (Woodring, 1982)	TWA	8.6	3.45	-	237.3 (0.5)	41.16	1	Mixed

P. A. sol (Brown and Pilsbry, 1913)	TWA	4.25	4.25	-	-	-	-	Mixed
Pseudamusium (Peplum) fasciculatum (Hinds, 1845)	TEP	1.6	Recent	-	-	37.06	0.96	Mixed[a]
P. (P.) sp. (cf. P. (P.) fasciculatum	TWA	-	Recent	-	-	28.93	0.96	Mixed[a]
Spathochlamys benedicti (Verrill and Bush, 1897)	TWA	3.55	Recent	91.7 (2.8)	202.6 (1.2)	22.38	0.91	Byssal
S. lowei (Hertlein, 1935)	TEP	3.35	Recent	79.0 (3.9)	207.8 (4.2)	17.78	0.85	Byssal
S. sp. 1	TWA	6.3	6.3	-	-	19.97	0.86	Byssal
S. sp. 2	TWA	2.6	2.6	-	-	3.58	0.86	Byssal
S. sp. 3	TWA	4	2.05	91.3 (3.0)	209.4 (2.5)	20	0.89	Byssal

S. sp. 4	TWA	7.3	7.3	-	-	20.08	0.90	Byssal
S. sp. 5	TWA	3.55	3.55	-	-	5.47	0.90	Byssal
S. sp. 6	TWA	2.05	2.05	-	-	15.57	0.93	Byssal
S. sp. 7	TWA	2.05	2.05	-	214.5 (*n/a*)	13.76	0.91	Byssal
S. vestalis (Reeve, 1853)	TWA	4.5	Recent	81 (*n/a*)	204.4 (7.1)	16.71	0.84	Byssal

[a] Ecological groups listed are those used in chapter 2. In chapter 3, these species were defined as byssally attaching using the purely morphologic scheme described in the text.

[b] Measurements for this species were only obtained from juvenile specimens. Exclusion of this species did not change the results presented in chapter 4.

[c] Species in the genus Lindapecten were grouped with the genus Aequipecten in Chapter 4.

APPENDIX 2

List of faunules used in this study with age estimate, mean percent carbonate,
estimates of MART, species richness and Shannon's H.

Caribbean Faunules	Basin	Median Age (Ma) (+/-)	S_{obs}	H	% CO3	MART
Bahia Almirante	Panama	Recent	15	1.95	28.06	3.80
Bocas del Toro	Panama	Recent	20	1.63	33.58	3.39
Cayos Moskitos	Nicaragua	Recent	14	1.44	84.15	1.80
Gulfo de los Moskitos	Panama	Recent	16	1.4	44.29	2.20
Laguna Chiriqui	Panama	Recent	17	1.33	35.24	3.80
Los Cochinos	Honduras	Recent	16	2.06	62.83	2.60
San Blas	Panama	Recent	14	2.11	67.37	3.13
Swan Cay	Bocas del Toro	1.4 (0.6)	6	1.19	63.49	3.22
Cangrejos Creek	Limon	1.55 (0.05)	2	-	36.1	-
Empalme	Limon	1.6 (0.1)	6	1.08	41.07	-
Cerro Mocho	Limon	1.6 (0.1)	1	-	-	-
Upper Lomas del Mar	Limon	1.6 (0.1)	9	1.45	43.28	2.82
Lower Lomas del Mar	Limon	1.7 (0.2)	4	0.91	38.83	3.08
Pueblo Nuevo	Limon	1.95 (0.15)	4	-	-	-
NW Escudo de Veraguas	Bocas del Toro	2.0 (0.1)	9	1.12	37.66	3.88
Wild Cane Key	Bocas del Toro	2.05 (0.15)	7	1.42	45.76	4.19
Ground Creek	Bocas del Toro	2.05 (0.15)	10	1.07	39.40	-
Fish Hole	Bocas del Toro	2.6 (0.4)	13	1.96	19.55	2.36
NC Escudo de Veraguas	Bocas del Toro	2.75 (0.85)	6	0.77	35.44	2.68
Bomba	Limon	3.05 (0.15)	7	1.26	68.96	3.13
Old Bank	Bocas del Toro	3.3 (0.3)	7	1.49	50.68	-
Bruno Bluff	Bocas del Toro	3.45 (0.15)	9	1.51	13.52	6.95

Quitaria	Limon	3.5 (0.1)	3	-	24.53	-
Isla Solarte	Bocas del Toro	3.55 (0.05)	7	0.88	54.10	6.68
Santa Rita	Limon	3.55 (0.05)	9	1.84	44.40	5.73
Cayo Agua: Punta Nispero South	Bocas del Toro	3.55 (0.05)	9	0.91	31.18	7.23
Cayo Agua: Punta Nispero West	Bocas del Toro	3.55 (0.05)	7	1.43	14.04	-
Cayo Agua: Punta Tiburon	Bocas del Toro	3.55 (0.05)	10	1.13	30.73	4.23
SE Escudo de Veraguas	Bocas del Toro	3.55 (0.05)	5	0.64	28.10	-
NE Escudo de Veraguas	Bocas del Toro	3.55 (0.05)	11	0.86	41.40	2.68
Rio Bananito	Limon	3.55 (0.05)	1	-	-	-
Rio Vizcaya	Limon	3.55 (0.05)	1	-	17.34	-
Cayo Agua: Punta Norte East	Bocas del Toro	4.25 (0.75)	11	1.51	18.87	4.11
Cayo Agua: Piedra Roja	Bocas del Toro	4.25 (0.75)	11	1.31	27.73	3.52
Cayo Agua: Punta Norte West	Bocas del Toro	4.25 (0.75)	10	0.91	15.93	6.25
Isla Popa	Bocas del Toro	4.25 (0.75)	10	1.53	19.77	6.65
Cayo Zapatilla	Bocas del Toro	4.25 (0.75)	6	0.90	14.61	5.62
Shark Hole Point	Bocas del Toro	5.65 (0.05)	3	0.8	14.25	5.22
South Valiente West	Bocas del Toro	6.29 (0.97)	5	1.21	18.22	6.16
Finger Island	Bocas del Toro	6.9 (1.3)	2	0.41	16.55	6.17
Plaintain Cay	Bocas del Toro	6.9 (1.3)	2	-	-	-
Patterson Cay	Bocas del Toro	6.9 (1.3)	2	-	-	-
Playa Lorenzo	Bocas del Toro	6.9 (1.3)	4	-	-	-
Toro Cay	Bocas del Toro	7.3 (1.3)	4	0.64	54.17	-
Rio Tuba	Limon	7.7 (0.5)			-	-

Isthmian Faunules	Basin	Median Age (Ma) (+/-)	S_{obs}	H	% CO3	MART
Gatun	Canal	6.0 (2.5)	9	1.2	28.27	-

Rio Tupisa	Chucanague	6.35 (0.75)	5	1.19	15.28	6.65
Rio Chico N17	Chucanague	6.35 (0.75)	7	0.94	20.11	8.67
Rio Icuanati	Chucanague	6.95 (1.35)	4	1.18	24.88	-
Rio Tuquesa	Chucanague	6.95 (1.35)	6	1.29	17.48	-
Yaviza	Chucanague	6.95 (1.35)	2	-	-	-
Rio Indio	North Coast	6.95 (1.35)	3	0.1	18.47	-
Rio Chucanague	Chucanague	7.05 (1.25)	1	-	9.46	-
Rio Calzones	North Coast	8.25 (2.95)	4	0.8	15.02	4.57
Miguel de la Borda	North Coast	8.6 (1.8)	3	0.52	23.57	-
Mattress Factory	Canal	9.0 (0.4)	10	1.37	24.55	6.18
Isla Payardi	Canal	9.6 (1.3)	7	0.35	25.15	-
Rio Tuira	Chucanague	10.15 (0.75)	4	0.64	14.22	-
Martin Luther King	Canal	11.6 (0.2)	2	-	-	-
Rio Chico N11	Chucanague	12.6 (0.1)	4	0.68	18.36	-

Eastern Pacific Faunules	Basin	Median Age (Ma) (+/-)	S_{obs}	H	% CO_3	MART
Gulf of Chiriqui	Panama	Recent	11	1.72	25.92	5.92
Gulf of Panama	Panama	Recent	8	1.3	30.26	5.92
Tablazo	Manabi	1.4 (0.4)	5	1.08	15.36	-
Armuelles	Burica	1.6 (0.1)	9	-	-	-
Nicoya	Nicoya	1.6 (0.1)	8	-	-	-
Punta Canoa	Manabi	1.6 (0.6)	4	0.54	23.00	-
Gulfo Dulce	Burica	1.85 (0.35)	6	-	-	-
Calle Esmeralda	Borbon	3.35 (0.25)	7	1.24	15.39	-
Rio Camarones: Onzole	Borbon	3.6 (0.4)	1	-	20.62	-
Jama	Manabi	7.3 (1.3)	2	-	13.36	-

Favio Alfaro	Manabi	7.35 (1.35)	4	0.5	11.13	-
Palma Royal	Borbon	9 (0.4)	3	0.53	34.01	-
Punta Verde: Onzole	Borbon	9 (0.4)	3	-	-	-
Cueva de Angostura	Borbon	9.65 (1.25)	4	0.66	15.54	-
Punta Verde: Angostura	Borbon	9.65 (1.25)	4	0.67	17.11	-
Rio Cayapas	Borbon	9.65 (1.25)	2	0.12	16.10	-