Changes in neogene Caribbean benthic community structure after closure of the Central America Seaway

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Changes in Neogene Caribbean benthic community structure after closure of the Central America Seaway

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

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by

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The Dissertation of Jill Suzanne Leonard-Pingel is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California, San Diego

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For Seth

Environments are not just containers, but are processes that change the content totally.

Marshall McLuhan

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Chapter 3 and 4 are being prepared for submission for publication with Jeremy Jackson as coauthor.

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ABSTRACT OF THE DISSERTATION

Changes in Neogene Caribbean benthic community structure after closure of the Central America Seaway

by

Jill Suzanne Leonard-Pingel

Doctor of Philosophy in Earth Sciences

University of California, San Diego, 2012

Professor Jeremy Jackson, Chair

The role that environmental forcing plays in driving macroevolution is a fundamental question in paleontology. To rigorously test the effect of environmental change on biology, independent paleoecological and paleoenvironmental data are necessary. Cases where these types of quantitative data have been generated are rare; consequently few paleobiologic studies have the rigor to address such questions. The work presented here uses quantitative ecological data on Caribbean bivalve assemblages dating back to 11 Ma to address the question of cause and effect with regard to environmental change, ecologic change, and biologic interactions.

Changes in the functional ecology of bivalve assemblages through time are linked to changes in Caribbean habitats. As coral reefs emerged as important habitats epifaunal bivalves became relatively more abundant constitutents of the bivalve assemblage. Likewise, as seagrass meadows became more common in the Caribbean, in conjunction with the emergence of coral reefs, bivalve diets diversified. Habitat also influenced biologic interactions. Predation intensity on bivalves increased in conjunction with the diversification of Caribbean habitats. Finally, throughout the Pliocene drilling among bivalve families remained constant, although drilling varies dramatically among bivalve taxa and is primarily related to life mode and habit. Thus, changes in the relative abundance of bivalves can also explain the observed differences in drilling intensity through time. As a whole, this research highlights the importance of environment in structuring communities and driving biological interactions. It also illustrates how the consequences of environmental perturbations may depend on cascades of ecological changes, with outcomes that are difficult to predict.

CHAPTER 1 – INTRODUCTION

One of the fundamental challenges facing modern paleontology is how to establish links between physical and biological change throughout Earth history. This question is not only essential for understanding the processes of macroevolution (Jablonski and Sepkoski 1996; Jablonski 1999, 2003; Vrba 2005; Jackson and Erwin 2006), but it is also important for making paleontology relevant at a time when society is asking science to define its application to global issues of sustainability and biodiversity loss. The new field of conservation paleobiology helps to provide baselines for pristine ecological conditions prior to human impacts and addresses similar questions about the influence of environmental change on biologic processes (Jackson et al 2001; Willis and Birks 2006; Dietl and Flessa 2011). Thus, paleontology now has two directions: looking back over Earth history to understand the processes that shape the biosphere, and looking forward to apply what we have learned from the past to be more informed about likely scenarios for the future. Questions of cause and effect are integral to both of these goals.

Identifying times of major environmental and biological change is one way to provide insight into cause and effect. Rigorous examination of changes in fossil communities in the context of independently documented, environmental change can ultimately lead to increased understanding of how the environment influences ecosystem structure and evolution (Knoll et al. 1996; Wing et al. 2005; O'Dea et al. 2007; Alegret et al. 2009; O'Dea and Jackson 2009; Smith and Jackson 2009). The fossil record of the Cenozoic is more easily interpretable than older sequences because of its generally superior preservation of biotas and greater similarity to the recent global biota (Sepkoski 1981). There are also several well-documented Cenozoic examples of large, environmental perturbations that resulted in major biological effects. These include the Paleogene-Eocene Thermal Maximum (PETM), the Messinian Salinity Crisis, and the closure of the Central American Seaway (CAS), which is the focus of my dissertation.

The PETM caused mass extinction of benthic foraminifera (Alegret et al. 2009, shifts in marine plankton assemblages (Crouch et al. 2001; Kelley 2002), and changes in terrestrial vertebrate and floral assemblages (Clyde and Gingerich 1998; Bowen et al. 2002; Wing et al. 2005; Jaramillo et al. 2010). The Messinian Salinity Crisis resulted in less dramatic and more regional biotic changes. There was little extinction of benthic marine fauna, as the Atlantic served as a refuge for many groups (Goubert et al. 2001; Néraudeau et al. 2001; Monegatti and Raffi 2010), but it is likely that this event impacted the diversity of some endemic Mediterranean fauna (Logan et al. 2004). It is interesting to note that ecological themes, like stepwise assemblage change, thresholds, and differential extinctions among taxonomic groups (Monegatti and Raffi 2010; Gibbs et al. 2012) are common in these investigations of biotic and environmental change. Nevertheless, we still lack fundamental understanding of the mechanisms and drivers of ecological change.

The closure of the Central American Seaway (CAS) and the separation of the Caribbean Sea from the Pacific Ocean around 3.5 Ma (Coates et al. 1992, 2004; Coates and Obando 1996; Bartoli et al. 2005) provides an ideal system to examine the effects of environmental change on community structure and evolution (Jackson et al.

1996). The lithologic and temporal framework is well established (Coates 1999; Coates et al. 1992, 2003, 2004, 2005; Coates and Obando 1996; McNeill et al. 2000) along with major changes in paleoenvironments and benthic communities. Caribbean salinity increased (Keigwin 1982; Cronin and Dowsett 1996; Haug et al. 2001; Steph et al. 2006a) and the mean annual range of temperature (MART), upwelling, and planktonic productivity in coastal environments all decreased (Teranes et al. 1996; Allmon 2001; Kirby and Jackson 2004; O'Dea et al. 2007) concurrent with final closure of the CAS. Closure also enhanced the Gulf Stream and increased North Atlantic thermohaline circulation (Steph et al. 2006b). Stable isotope records also indicate large-scale changes in the Pacific Ocean, notably a shoaling in the thermocline that could have influenced Walker circulation in the Pacific (Steph et al. 2006b).

There was also extensive taxonomic turnover associated with the closure of the CAS (Woodring 1966; Stanley and Campbell 1981; Petuch 1982; Stanley 1986; Vermeij and Petuch 1986; Allmon et al. 1993; Jackson et al. 1993; Collins 1999; Jackson et al. 1999), but the mechanisms underlying turnover are still unresolved. The three leading hypotheses are that turnover was caused by: 1) a decrease in planktonic productivity (Allmon 2001; Todd et al. 2002; O'Dea et al. 2007; O'Dea and Jackson 2009), 2) a decline in temperature associated with the intensification of northern hemisphere glaciation (Stanley and Campbell 1981; Stanley 1986;) or 3) shifts in the relative abundance of critical habitats including a striking increase in coral reefs and shallow water seagrass meadows (Johnson et al. 2007; Smith and Jackson 2009). Planktonic foraminifera from the open ocean also exhibit Pliocene faunal turnover

(Chaisson 2003; Sexton and Norris 2008). The Pacific foraminifera species *Truncorotalia truncatulinoides* is briefly found in the Caribbean around 2.5 Ma, approximately 500 kyr before its generally accepted global appearance at the Pleistocene boundary (Sexton and Norris 2008). It is unclear how and if changes in open ocean plankton are linked with changes in nearshore benthos, but the similarity in timing is interesting and thought provoking.

Interpretation is complicated by a 1-2 million year time lag after the onset of environmental change in the taxonomic turnover (origination and extinction) of several major animal taxa including corals, bryozoans, and gastropods (Budd and Johnson 1999; Jackson and Johnson 2000; O'Dea et al 2007; O'Dea and Jackson 2009). This time lag suggests a non-linear relationship between environmental change faunal turnover. Both the knowns (extensive previous research, large datasets, independent paleoenvionmental data) and the unknowns (causes of extinction, enigmatic time lag) provide an exceptional opportunity to study the complexities of paleoecological change.

My dissertation focuses on ecological changes in nearshore molluscan communities with the hopes of providing additional insight into the complicated nature of ecological change. Chapter two exploits shifts in the relative abundance of different trophic groups and life habits of bivalve mollusks to test competing hypotheses for the cause of community turnover over the past few million years. Both diet and the life habits are expected to be impacted by the environmental changes associated with the closure of the CAS. This chapter is in press in the journal *Paleobiology*.

Chapter three focuses on extrinsic controls on predator-prey interactions as determined by the incidence in drill holes made by gastropod predators in the shells of their bivalve prey. Biologic interactions are important drivers of macroevolution (Vermeij 1977, 1987; Bambach 1993; Jackson 1983; Steneck 1983), and their outcome can depend strongly on changes in the environment (Vermeij 1978; Hansen and Kelley 1995; Hoffmeister and Kowalewski 2001; Kelley and Hansen 2006) such as those associated with the closure of the CAS. I tested the hypothesis that the intensity of drilling predation should decrease as planktonic productivity decreased after isolation of the Caribbean from the Pacific (Vermeij 1987; Todd et al. 2002; Johnson et al. 2007). This chapter is being prepared for submission to the journal *Science*.

Chapter four focuses on the intrinsic characteristics of bivalve taxa that influence their susceptibility to predation. The theme of an arms race between predators and prey, especially shelled prey and their predators, pervades the evolutionary literature (Vermeij 1977, 1983; Dawkins and Krebs 1979; Bambach 1983). I compared predation rates among bivalve genera, as well as traits related to shell architecture and life habit, to test their importance for the vulnerability of different bivalves to drilling gastropod predation. This chapter will be submitted to a symposium volume celebrating 25 years of the Panama Paleontology Project to be published by the *Bulletin of Marine Science*.

Chapter five concludes the thesis with an assessment of the range of impacts of environmental change on macroevolution as illustrated by changes in the southwestern Caribbean over the past few million years. Taken as a whole, my dissertation research highlights the importance of being able to tease apart proximate and ultimate causes of paleoecologic changes. Throughout the dissertation, I provide evidence that changes in habitat drove changes in the molluscan community, but those changes in habitat were ultimately driven by large-scale oceanographic changes. This illustrates the non-linearity of biologic response to environmental perturbations, and provides an analogue for modern research on ecologic changes in response to anthropogenic perturbations.

Throughout the dissertation, my goal is to explore the complicated relationship between environmental change and macroevolution. My hope is that an analysis of molluscan ecological change during the Pliocene will both increase understanding of the macroevolutionary history of the Caribbean fauna, and also serve as an illustrative example of how ecological changes occur in the natural world.

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CHAPTER 2 – CHANGES IN BIVALVE FUNCTIONAL AND ASSEMBLAGE ECOLOGY IN RESPONSE TO ENVIRONMENTAL CHANGE IN THE CARIBBEAN NEOGENE

Abstract

We documented changes in the relative abundance of bivalve genera and functional groups in the southwest Caribbean over the past 11 Ma to determine their response to oceanographic changes associated with the closure of the Central American Seaway about 3.5 Ma. Quantitative bulk samples from 29 localities yielded 106,000 specimens in 145 genera. All genera were assigned to functional groups based on diet, relationship to the substrate, and mobility. Ordinations of assemblages based on quantitative data for functional groups demonstrated strong shifts in community structure, with a stark contrast between assemblages older than 5 Ma and those younger than 3.5 Ma. These changes are primarily due to an increase in the abundance of attached epifaunal bivalves (e.g., *Chama*, *Arcopsis*, and *Barbatia*) and a decrease in infaunal bivalves (e.g., *Varicorbula* and *Caryocorbula*). Taxa associated with seagrasses, including deposit feeding and chemosymbiotic bivalves (e.g., *Lucina*), also increased in relative abundance compared to suspension feeders. The composition of bivalve assemblages is correlated with percent carbonate content of sediments and percent of skeletal biomass that is coral. Our results strongly support the hypothesis that increases in the extent of coral reefs and *Thalassia* communities were important drivers of biologic turnover in Neogene Caribbean benthic communities.

Introduction

Environmental change has long been recognized as a major driver of macroevolutionary events (Jablonski 2003; Vrba 2005 and references therein), but there remain few unambiguous examples where environmental change can be linked directly to a biologic response in a mechanistically supported way (Jackson et al. 1996; Jackson and Erwin 2006). One reason is that paleontologists have traditionally been limited in their ability to make broad, ecological inferences from the fossil record because they have examined fossils out of their ecologic context (Jackson et al. 1999; McGhee et al. 2004). Recent work utilizing independently derived environmental and ecological data has increased understanding of many systems (Johnson et al 1995, O'Dea et al 2007, O'Dea and Jackson 2009, Smith and Jackson 2009, Bush and Brame 2010).

Here, we address the question of environmental cause and effect for changes in communities of bivalve molluscs during a regional extinction to better understand relationships among environment, ecology, and taxonomic turnover. We utilize information about the functional roles of bivalves, combined with the relative abundance of bivalves as a measure of success and dominance through time (McKinney et al. 1998; Vermeij and Herbert 2004; O'Dea et al. 2007). This approach helps to better understand how environmental change affected bivalve assemblages, the timing of these effects, the stability of bivalve assemblages, and the probable role that changes in the composition of functional groups played in taxonomic turnover.

The Plio-Pleistocene extinction of marine benthos in the Caribbean and Western Atlantic is well-documented (Woodring 1966; Stanley and Campbell 1981;

Stanley 1986; Vermeij and Petuch 1986), although the potential causes are still unresolved (Jackson et al. 1993; Allmon et al. 1993; Johnson et al. 1995, 2007; Petuch 1995; Budd and Johnson 1999; Todd et al. 2002; O'Dea et al. 2007; Landau et al. 2009; Smith and Jackson 2009; O'Dea and Jackson 2009). Nevertheless, there is general agreement that oceanographic changes associated with the final closure of the Central American Seaway (CAS) by the uplift of the Isthmus of Panama approximately 3.5 Ma (Coates et al. 1992, 2004; Coates and Obando 1996; Bartoli et al. 2005) were somehow responsible. Closure of the CAS resulted in increased salinity (Keigwin 1982; Cronin and Dowsett 1996; Haug et al. 2001), decreased seasonality as measured by decreased mean annual range of temperature (MART) (Teranes et al. 1996; O'Dea et al. 2007), and decreased upwelling and productivity across the Caribbean (Allmon 2001; Kirby and Jackson 2004; O'Dea et al. 2007). Speciation, extinction, relative abundance and life-history evolution of cupuladriid bryozoans and scallops in the SWC strongly implicates the collapse of productivity as the primary factor driving evolutionary change (O'Dea and Jackson 2009; Smith and Jackson 2009), but the cause(s) of turnover in other taxonomic groups has remained unclear because of a lack of information about ecology. This situation is complicated by a 1-2 Ma time lag, apparent in some taxonomic groups, but not in others, between the onset of environmental change and community turnover in the southwestern Caribbean and probably throughout the tropical Western Atlantic (Allmon et al. 1993; Budd and Johnson 1999; O'Dea et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009).

Most previous analyses emphasized originations and extinctions of benthic taxa that occurred around the time of closure of the CAS calculated on the basis of taxonomic occurrence (Woodring 1966; Stanley and Campbell 1981; Petuch 1982; Stanley 1986; Vermeij and Petuch 1986; Allmon et al. 1993; Jackson et al. 1993; Collins 1999; Jackson et al. 1999). Results demonstrate preferential extinction of Caribbean taxa that are now largely restricted to the eastern Pacific, although diversity did not decrease over time as a result of high origination rates (Allmon et al. 1993; Jackson et al. 1993; Jackson et al. 1999). However, these taxonomic analyses provide little insight into the ecological causes of faunal turnover.

Comparison of ecologic roles of taxa that survived the late Pliocene pulse in extinction versus those that became extinct strengthens ecological understanding of likely causes of extinction (Stanley 1986; Johnson et al. 1995; Budd and Johnson 1999; Todd et al. 2002; Johnson et al. 2007; Landau 2009; O'Dea and Jackson 2009; Smith and Jackson 2009). For example, corals experienced selective extinction of small, free-living taxa, while large, reef-building corals with massive and platy colony shapes preferentially survived (Johnson et al. 1995; Budd and Johnson 1999). In addition, suspension-feeding bivalves, predatory gastropods, and clonal free-living bryozoans have decreased proportionally through time (Todd et al. 2002; Johnson et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009). All of these studies suggest a strong ecological component to taxonomic turnover.

Two complimentary hypotheses for the causes of community change have emerged from this research; (1) decrease in productivity (Allmon 2001; Todd et al. 2002; O'Dea et al. 2007; O'Dea and Jackson 2009) and (2) increased development of coral reefs and shallow-water seagrass meadows (Johnson et al. 2007; Smith and Jackson 2009). We tested these hypotheses through quantitative analyses of changes in bivalve ecology in relation to environmental change. First, decreases in planktonic productivity should be accompanied by a decrease in suspension-feeding bivalves, whose relative abundance closely reflects the level of planktonic primary productivity in a system (Birkeland 1987; Todd et al. 2002). In contrast, bivalves that depend less on a planktonic diet, such as deposit feeders or chemosymbiont bearing taxa, should increase in relative abundance. Secondly, an increase in reef environments should be accompanied by an increase in the abundance of epifaunal bivalves that live attached to hard substrates, and are often found in association with reefs (Stanley 1972; Waller 1993; Boyd 1998; Wilson 1998; Zuschin et al. 2000; Oliver and Holmes 2006). Likewise, an increase in abundance of seagrass meadows should be indicated by an increase in deposit feeding and chemosymbiotic bivalves (Jackson 1973; Johnson et al. 2007).

Previous research (Todd et al. 2002; Johnson et al. 2007) has addressed changes in molluscan ecology and inferred what observed ecological changes might mean about environmental changes in the Caribbean after the closure of the CAS. However, these studies have not used rigorous quantitative data to systematically examine changes in functional ecology for an entire taxonomic group, or independent measures of environmental change. Both Todd et al. (2002) and Johnson et al. (2007) infer changes in environment and habitat from changes in diet and diversity patterns, respectively. However, our results overwhelmingly demonstrate not only a change in bivalve life habits, but also provide evidence that these changes were directly influenced by changes in environment and benthic habitats.

Materials and Methods

We measured the abundance of bivalve genera from 193 bulk samples collected primarily from the Caribbean coasts of Panama and Costa Rica (Table 2.1, Fig. 2.1, and Fig. 2.2). These collections were made as part of the Panama Paleontology Project (PPP), and build on previous PPP studies of stratigraphy, age dating, paleoenvironments, and faunal composition (Coates et al. 1992, 2003, 2004, 2005; Collins 1993,1996; Collins et al. 1995,1996a,b; Aubry and Berggren 1999; Coates 1999a; Jackson et al. 1999; McNeill et al. 2000; O'Dea et al. 2007; Johnson et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009). Samples collected from a geographically constrained locality (e.g., a single outcrop or adjacent exposures that could be assigned to the same age and environment) were grouped into faunules (Jackson et al. 1999; O'Dea et al. 2007; Johnson et al. 2007; Smith and Jackson 2009). Faunules represent our best approximation of fossil communities, and help to overcome problems associated with small-scale sampling, which can under-estimate diversity (Ellingsen 2001; Shin and Ellingsen 2004). We recognize the likelihood of time averaging and environmental variability within faunules, although transport between contemporaneous environments is likely negligible (Kidwell and Bosence 1991). Time averaging may result in mixing of ecological signals, but it also increases the likelihood that a sample accurately represents an ancient community by dampening seasonal "boom and bust" and capturing rare taxa, ultimately providing a more complete picture of ancient bivalve assemblages (Kidwell and Flessa 1995; Kidwell 2001; 2002a).

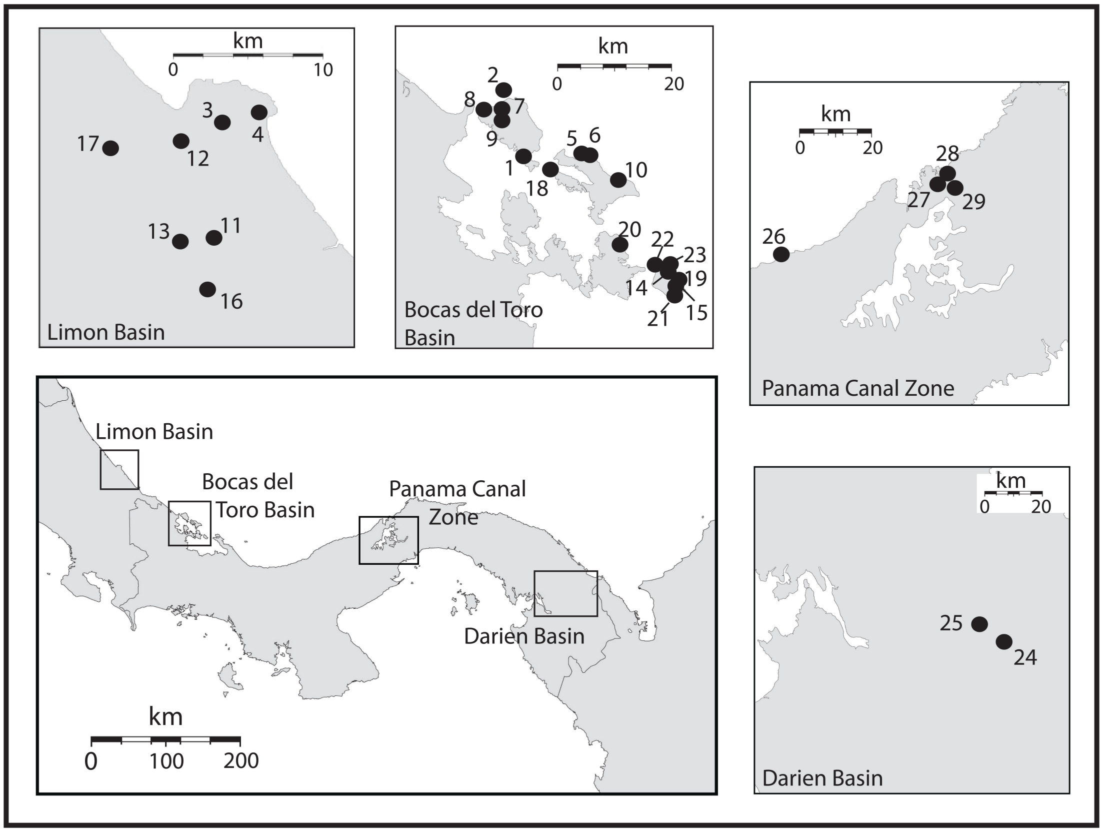

Figure 2.1: Map of Panama and eastern Costa Rica, with insets showing the four basins from which collections were taken; Limon basin, Costa Rica; Bocas del Toro basin, Panama; Panama Canal Zone, Panama; and Darien basin, Panama. Numbers correspond to faunules listed in Figure 2.2.

All faunules included in our analyses were deposited at an inferred paleodepth of $\leq$100 m and contained more than 100 bivalve specimens (Johnson et al. 2007). Bulk samples of approximately 10 kg were processed by repetitive freezing and thawing in Glauber's salt solution, which breaks down the consolidated sediment matrix while reducing damage to fragile fossil shells (Surlyk 1972). Samples were washed on a 2mm sieve that captures adults of all species. Smaller mesh sizes commonly contain juveniles that are difficult to identify; smaller shells are also more

Table 2.1: List of faunules including median age, number of bulk samples analyzed, number of identifiable bivalve valves sorted and counted, and the total number of genera identified. Faunule numbers correspond to numbers on Figures 2.1 and 2.2.

Faunule	Median Age (MA)	Number of Samples	Number of Valves	Number of Genera
Sand Dollar Hill[1]	11	3	1512	24
Isla Payardi[2]	9.6	9	3007	48
Mattress Factory[2]	9	2	1379	35
Rio Indio[2]	6.95	12	597	19
Rio Tupisa[2]	6.35	3	1045	43
Rio Chico N17[2]	6.35	5	4604	66
Cayo Agua: Punta Norte E[2]	4.25	7	1485	38
Cayo Agua: Punta Piedra Roja W[2]	4.25	11	10571	57
Cayo Agua: Punta Norte W[2]	4.25	10	3132	39
Isla Popa[2]	4.25	6	11018	38
Cayo Agua: Punta Nispero S[2]	3.55	4	1904	28
Isla Solarte[2]	3.55	5	3005	54
Santa Rita[2]	3.55	7	1186	54
Rio Vizcaya[2]	3.55	3	1639	37
Cayo Agua: Punta Tiburon - Punta Piedra[2]	3.55	6	1050	44
Cayo Agua: Punta Nispero W[2]	3.55	3	983	40
Quitaria[2]	3.5	1	476	26
Quebrada Chocolate[3]	3.1	1	7041	37
Bomba[2]	3.05	11	2310	44
Fish Hole[2]	2.6	4	321	64
Ground Creek Mud[2]	2.05	6	23971	29
Ground Creek Mangrove[2]	2.05	4	425	45
Ground Creek Porites[2]	2.05	9	2105	41
Wild Cane Key[2]	2.05	5	356	42
Wild Cane Reef[2]	2.05	7	273	33
Upper Lomas[2]	1.6	21	14545	59
Empalme[2]	1.6	7	3573	66
Swan Cay[2]	1.4	11	1300	41
Lennond[4]	0.125	10	1238	53
Total		**193**	**106,051**	**145**

[1] Age from personal communication with J. Todd
[2] Ages from Smith and Jackson 2009
[3] Age from Jackon et al. 1999
[4] Age inferred from stratigraphic position

likely to be transported out of their original habitat (Kidwell 2001, 2002b). Skeletal elements were sorted to class (O'Dea et al. 2007), and bivalves were then sorted to genus following the classification and nomenclature of Todd (2001a). A complete list of bivalve genera identified is available in the supporting online material. All identified valves were counted, using the protocol of Gilinsky and Bennington (1994), weighed to hundredths of a gram, and assigned to functional groups. We measured abundance using both counts and weights (as a proxy for biomass) in order to account for bias that could be caused by the accumulation of large numbers of small-bodied, weedy taxa that might be energetically less important than larger taxa which are numerically less abundant (Vermeij and Herbert 2004). Cleaning cleared most of the matrix from inside the shells, but residual sediment may have influenced weight measurements in some cases. Leaching of aragonite was also a minor concern, as shells were generally well preserved; in addition, leaching did not vary among samples.

Bivalve genera were assigned to functional groups based on their relationship to the substrate (epifaunal, infaunal, or semi-infaunal), diet (suspension feeder, deposit feeder, chemosymbiotic, or carnivore), and attachment (unattached, byssally attached, cemented, or variable), following the work of Stanley (1969, 1970, 1972, 1981), Thomas (1978a, 1978b), and Todd (2001b). We then calculated the similarity of the categorical variables (Gower distance) for each genus and ran a cluster analysis, resulting in the creation of a dendogram that grouped all the genera according to their functional similarity. We recognized 18 functional groups from the dendogram clusters (Table 2.2A). However, several of the groups were rare so we lumped them into eight composite groups (e.g., epifaunal cemented suspension feeder and epifaunal bysally-attached suspension feeder were combined to form epifaunal attached suspension feeder: Table 2.2B). Lumping yielded ordinations that were more easily interpreted, as the bivalves were not split into overly refined groups.

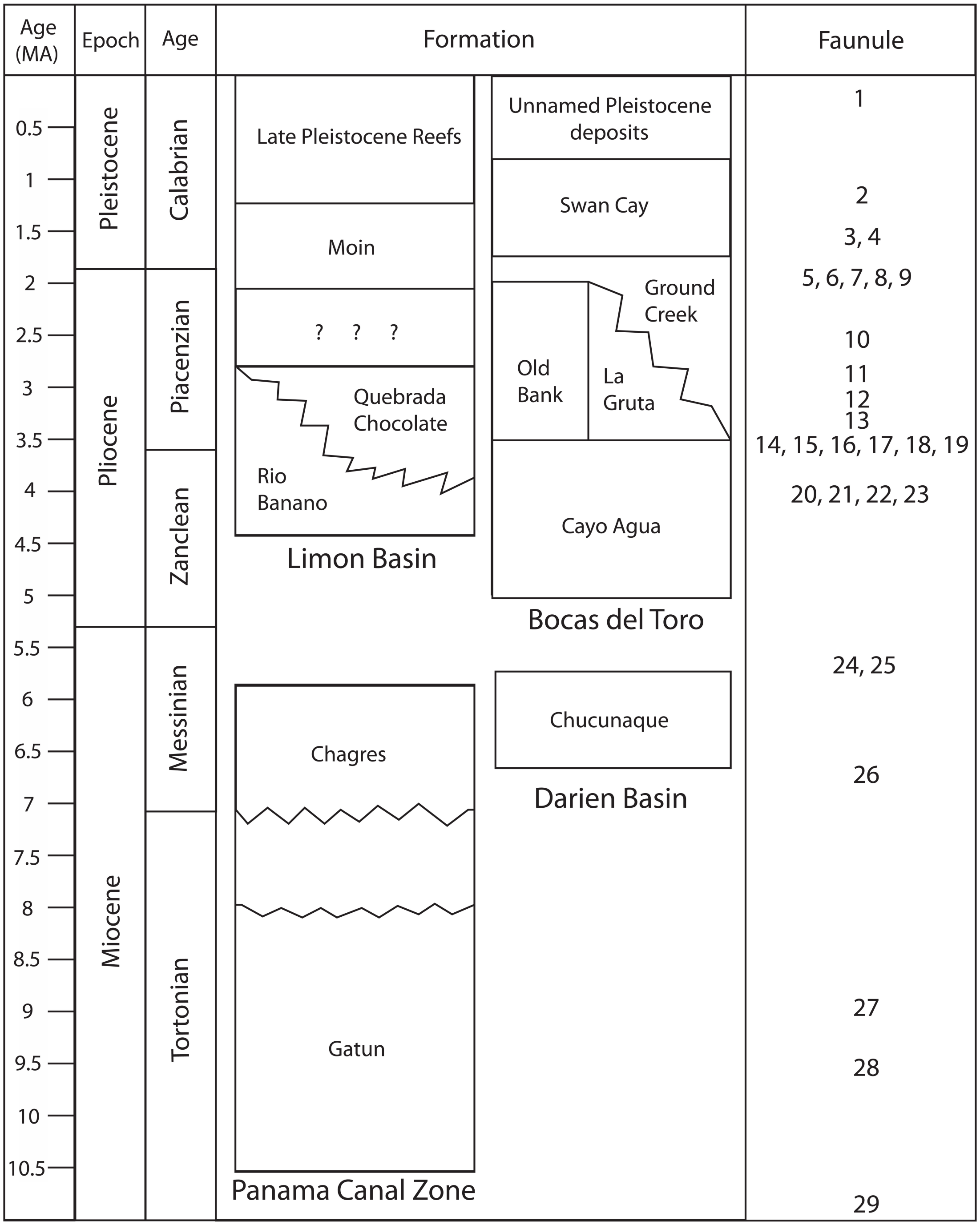

Figure 2.2: Stratigraphic occurrence of collections and faunules based on previous studies (Coates 1999b; Coates et al. 1992, 2004, 2005; McNeill et al. 2000).

Table 2.2: Bivalve functional groups identified by similarity analyses of the categorical values for each genus. (A) 18 groups identified from cluster analysis (B) simplified functional groups based on combinations of similar groups. Examples of common taxa within each functional group are also given.

Bivalve Functional Groups	**Common Genera**
A. Original Functional Groups	
Boring Suspension Feeder	*Gastrochaena*
Epifaunal Free-Living Mobile Suspension Feeder	*Limea*
Epifaunal Free-Living Swimming Suspension Feeder	*Amusium, Leopecten*
Epifaunal Immobile Unattached Suspension Feeder	*Musculus*
Epifaunal Bysally-Attached Mobile Suspension Feeder	*Ctenoides*
Epifaunal Bysally-Attached Suspension Feeder	*Arca, Spathochlamys*
Epifaunal Variably Attached Sedentary Suspension Feeder	*Argopecten*
Epifaunal Cemented Suspension Feeder	*Dendostrea, Chama*
Epifaunal Carnivore	*Cyclopecten*
Infaunal Free-Living Suspension Feeder	*Cardites, Gouldia, Macrocallista*
Infaunal Bysally-Attached Suspension Feeder	*Caryocorbula, Varicorbula*
Infaunal Chemosymbiotic Suspension Feeder	*Lucina, Phacoides*
Infaunal Carnivore	*Trigonulina*
Infaunal Subsurface Deposit Feeder	*Nucula, Saccella*
Infaunal Surface Deposit Feeder	*Merisca, Tellina*
Nestling Suspension Feeder	*Sheldonella*
Nestling Deposit Feeder	*Cumingia*
Semi-infaunal Suspension Feeder	*Chione, Anadara*
B. Simplified Functional Groups	
Epifaunal Free-Living Suspension Feeder	*Limea, Leopecten*
Epifaunal Attached Suspension Feeder	*Dendostrea, Spathochlamys, Barbatia*
Epifaunal Carnivore	*Cyclopecten*
Infaunal Chemosymbiotic Suspension Feeder	*Lucina, Phacoides*
Infaunal Suspension Feeder	*Caryocorbula, Macrocallista*
Infaunal Carnivore	*Trigonulina*
Infaunal Deposit Feeder	*Merisca, Nucula, Saccella*
Semi-infaunal Suspension Feeder	*Chione, Anadara*

Changes in bivalve assemblages through time were explored both ecologically and taxonomically. Changes in functional groups were examined by plotting the proportions of the eight functional groups as a time series, and by ordination analysis. Significance of time series was evaluated using weighted least squares regression. We also used Principal Components Analysis (PCA) to ordinate the faunules based on presence/absence data, counts, and weights of functional groups. As functional groups have low beta diversity among faunules (high overlap of present functional groups) we do not expect arch effects in the PCA. Taxonomic data were ordinated using both PCA and nonmetric multidimensional scaling (NMDS) following Bush and Brame (2010). PCA of generic data did not yield meaningful results, probably as a result of the arch effect (McCune and Grace 2002) and therefore only results of NMDS will be presented.

We examined the role of environmental factors as determinants of the composition of bivalve assemblages by using a multiple regression analysis where the response variable was an ordination axis of faunules and the independent variables described five independent environmental parameters including median depth, mean annual range in temperature (MART), mean percent carbonate, mean percent mud of sediments, and the mean percent of the biomass that was coral (Table 2.3). Paleo depths were estimated using benthic foraminifera (Collins 1993, 1999; Collins et al. 1995, 1996; Jackson et al. 1999), except in cases otherwise noted (see Table 2.3) where depth was inferred from the composition of the reef coral assemblage, or was indeterminable. MART was calculated from variation in zooid size of cheilostome bryozoans (O’Dea and Okamura 2000; O’Dea et al. 2007) in samples where cheilostome bryozoans were available. Percent carbonate of the sediment was determined by weighing ~100g of sediment from the < 2 mm size fraction before and after acid digestion. Percent mud was determined from a grain size analysis of the < 2mm size fraction (O’Dea et al. 2007). All biologic components were sorted into higher taxonomic groups, and the percent coral biomass is calculated as the weight of the coral fraction divided by the total weight of all biologic components. Stepwise AIC was used to select the final regression models.

Table 2.3: Environmental data for each faunule. Estimates of depths based upon benthic foraminifera were not available for Ground Creek *Porites*, Wild Cane Reef, and Lennond. In these cases, depth was estimated from the coral assemblage: Ground Creek *Porites* based upon a great abundance of *Porites porites* (Veron 2000); Wild Cane Reef based upon the presence of large, boulder-forming corals (Veron 2000); Lennond based upon abundant *Acropora cervicornis* (Hughes 1989; Pandolfi 1999).

Faunule	Median Age (MA)	Median Depth (m)	MART (degrees Celcius)	Percent Sediment - Carbonate	Percent Sediment - Mud	Percent Biologic Component - Coral
Sand Dollar Hill	11	-	6.18	20.24	8.6	0.43
Isla Payardi	9.6	27.5	6.18	25.73	47.9	0
Mattress Factory	9	28	6.18	24.55	35.3	0.25
Rio Indio	6.95	25	-	9.76	12.13	0.09
Rio Tupisa	6.35	100	6.65	15.28	41.2	0
Rio Chico N17	6.35	30	8.67	20.11	36.02	0
Cayo Agua: Punta Norte E	4.25	60	4.11	18.87	49.57	1.6
Cayo Agua: Punta Piedra Roja W	4.25	42	3.52	27.73	18.72	17.32
Cayo Agua: Punta Norte W	4.25	30	6.25	15.93	42.59	8.08
Isla Popa	4.25	50	6.65	19.77	56.69	0.02
Cayo Agua: Punta Nispero S	3.55	60	7.23	26.1	15.34	3
Isla Solarte	3.55	75	6.68	54.1	14.79	3.28
Santa Rita	3.55	30	5.73	44.4	28.88	5.86
Rio Vizcaya	3.55	12	-	31.66	15.47	0.19
Cayo Agua: Punta Tiburon	3.55	60	5.68	32.01	30.14	25.02
Cayo Agua: Punta Nispero W	3.55	60	7.23	26.1	33.85	1.56
Quitaria	3.5	30	3.13	20.83	20.19	2.67
Quebrada Chocolate	3.1	-	-	31.98	17.22	0.17
Bomba	3.05	30	3.13	68.96	29.78	1.65
Fish Hole	2.6	88	2.36	19.55	59.34	34.64
Ground Creek Mud	2.05	10	-	29.6	30.78	9.45
Ground Creek Mangrove	2.05	20	-	38.94	73.38	62.6
Ground Creek Porites	2.05	10	-	51.41	53.01	93.79
Wild Cane Key	2.05	30	4.19	45.76	33.11	52.62
Wild Cane Reef	2.05	25	4.19	56.4	28.29	67.05
Upper Lomas	1.6	75	2.82	43.28	21.33	35.7
Empalme	1.6	20	2.82	43.43	32.55	3.45
Swan Cay	1.4	100	3.22	63.49	20.9	15.74
Lennond	0.125	15	3.8	85.18	39.03	94.98

Results

We analyzed 29 faunules ranging in median age from 11 Ma to 0.125 Ma. The fossil record is most complete in the northwest of the sample area (Limon basin in Costa Rica and Bocas del Toro region in Panama; Fig. 2.1). The most noticeable gaps in the sequence are between 9 to 6.95 Ma and 6.35 to 4.25 Ma. Sampling is best between 4.25 – 1.6 Ma, when environmental changes associated with the closure of the CAS began (O'Dea et al. 2007).

Composition of Bivalve Assemblages Through Time. - Proportions of the eight functional groups varied greatly among faunules of the same age, obscuring simple univariate trends through time. Regression analyses of the proportions of the eight functional groups through time were marginally significant in only four of eight cases (Table 2.4). In contrast, Principal Components Analyses of faunules based upon counts and weights of functional groups clearly illustrate the overall changes in bivalve assemblages through time (Figs. 2.3 and 2.4). The first two principal components explain 86.6% of the total variability for counts and 90.7% for weights (Table 2.5). In both cases, PCA1 separates faunules dominated by epifaunal suspension feeders from faunules dominated by infaunal suspension feeders, whereas PCA2 primarily distinguishes faunules dominated by semi-infaunal suspension feeders from those dominated by infaunal suspension feeders. The ordination based on counts data also reveals a more subtle change in trophic structure along PCA1 between faunules with abundant deposit feeders and chemosymbiont-bearing bivalves versus faunules overwhelmingly dominated by suspension feeders. This separation is not apparent in ordinations based upon weights (Fig. 2.4). PCA 1 is positively correlated with age ($R^2 = 0.24$ $p < 0.01$) but not with depth, and PCA 2 is not significantly correlated with either age or depth (Table 2.6).

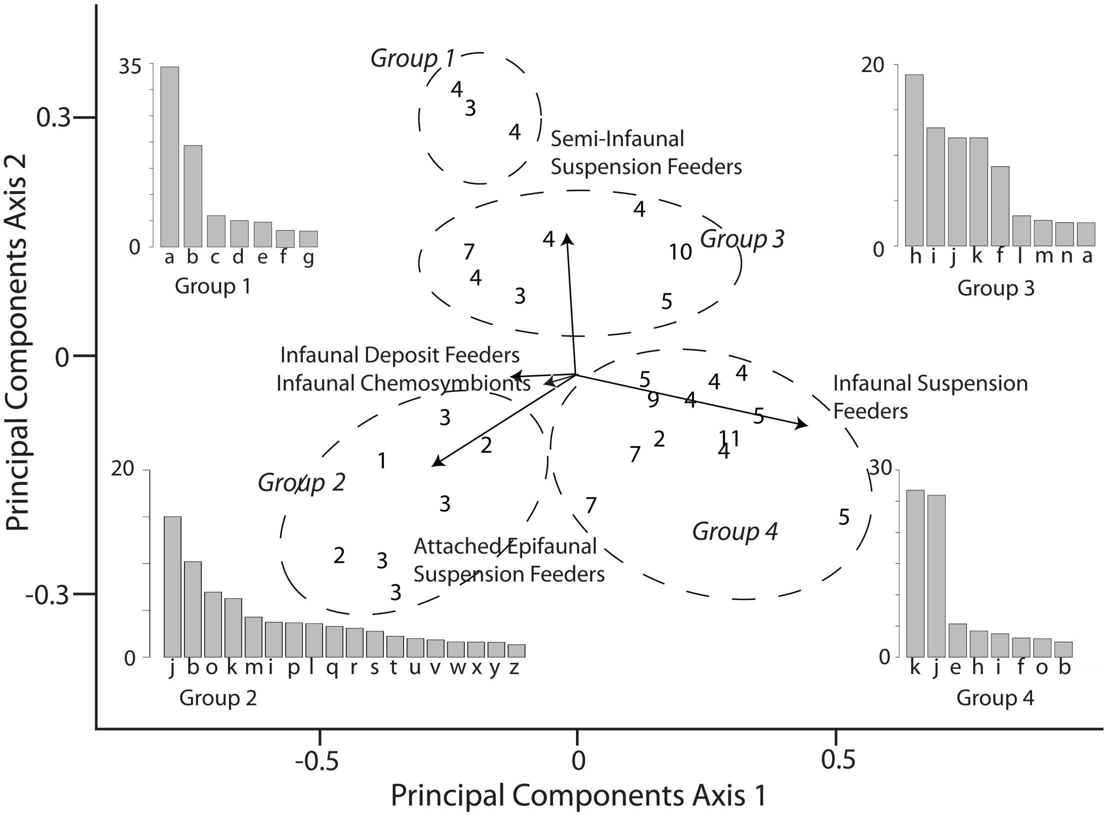

Figure 2.3: Principal Components Analysis of faunules based on counts of functional groups. Each arrow stands for a functional group and indicates the direction and relative importance (length of arrow) of that functional group in the PCA. Each number represents a faunule, and denotes the rough categorical age for that faunule (faunules between 0-1 Ma in age are denoted by a 1, faunules between 1-2 Ma are denoted by a 2, etc.). Faunules were assigned to one of four groups based on the ordination and confirmed by linear discriminant analysis. Bar plots illustrate the relative abundance of the genera that comprise 75% of the total numerical abundance of that group. Letters correspond to taxa illustrated in Figure 2.5 and are as follows, a, *Chione*, b, *Dendostrea*, c, *Nucula*, d, *Lucina*, e, *Macrocallista*, f, *Argopecten*, g, *Tagelus*, h, *Tucetona*, i, *Anadara*, j, *Caryocorbula*, k, *Varicorbula*, l, *Gouldia*, m, *Chama*, n, *Cardites*, o, *Saccella*, p, *Arcopsis*, q, *Barbatia*, r, *Limopsis*, s, *Plicatula*, t, *Phacoides*, u, *Pitar*, v, *Crassostrea*, w, *Arca*, x, *Spathochlamys*, y, *Crassinella*, z, *Varinucula.*

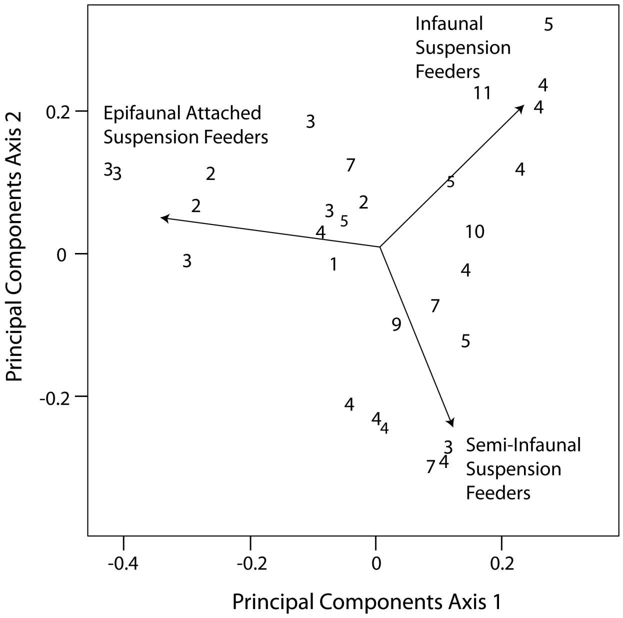

Figure 2.4: Principal Components Analysis of faunules based on weights (biomass) of the functional groups. Each number represents a faunule, and denotes the rough categorical age for that faunule as in Figure 2.3.

Ordinations based upon counts of functional groups revealed four groups of faunules (Fig. 2.3). The validity of these groups was strongly supported by a linear discriminant analysis, which correctly assigned faunules to their defined groups with a high degree of certainty (Group 1 – 100%, Group 2 - 100%, Group 3 - 86%, Group 4 - 92%). The four groups vary in taxonomic composition and community evenness as well as the relative abundance of functional groups. Group 4 contains most of the faunules older than 5 Ma. It is dominated by two corbulid taxa, *Varicorbula* (26.8%) and *Caryocorbula* (26%) that are characteristic of soft, muddy or sandy and sometimes harsh (e.g., brackish) environments (Anderson 1994; Lamprell et al. 1998), and are typical of the infaunal suspension feeders that characterize these older bivalve assemblages (Figs. 2.3 and 2.5; Table 2.7). In contrast, Group 2 contains the majority of faunules younger than 3.5 Ma. Group 2 has a much more even and diverse assemblage (Fig. 2.3). *Caryocorbula* is still the most abundant genus, comprising 15% of the numerical abundance; however, epifaunal taxa are also abundant, including several genera that attach to hard substrates and are often found in association with reef environments, including *Dendostrea, Chama, Arcopsis, Barbatia, Limposis,* and *Plicatula* (Stanley 1972; Waller 1993; Boyd 1998; Wilson 1998; Zuschin et al. 2000; Oliver and Holmes 2006) (Fig. 2.5). Group 2 also contains genera representing a diversity of diets; deposit feeders like *Saccella* and chemosymbiont-bearing bivalves like *Phacoides* are relatively common in this group (Fig. 2.5).

Group 1 is characterized by an overwhelming dominance of *Chione* (42.5%), and high trophic diversity, including common deposit feeders (*Nucula*) and chemosymbionts (*Lucina*) in addition to abundant suspension feeders. We interpret this assemblage as characteristic of a lagoonal seagrass environment (Jackson 1973; Johnson et al. 2007). Group 3 is dominated by suspension feeders, but differs from Group 4 in its high proportion of semi-infaunal taxa, such as *Tucetona* (18.9%) and *Anadara* (13%). Group 3 most likely represents a typical nearshore sandy environment (Boyd 1998).

In contrast to ordinations based on functional groups, ordinations of faunules based on generic abundance distinguished among faunules with regard to depth and age (Fig. 2.6; Table 2.6). NMDS dimension one is positively correlated with depth (R^2

= 0.21, $p < 0.05$) and NMDS dimension two is positively correlated with age ($R^2 = 0.37$, $p < 0.001$).

Table 2.4: Results of weighted lease squares regressions of the eight bivalve functional groups as a time series. Significant values are in bold.

Functional Group	Age
Epifaunal Free-living Suspension Feeder	**r = -0.42** **$R^2 = 0.27$** **$p < 0.01$**
Epifaunal Attached Suspension Feeder	**r = +0.44** **$R^2 = 0.19$** **$p < 0.05$**
Epifaunal Carnivore	r = +0.15 $R^2 = 0.02$ $p = 0.42$
Infaunal Chemosymbiotic	**r = +0.48** **$R^2 = 0.20$** **$p < 0.01$**
Infaunal Suspension Feeder	**r = -0.46** **$R^2 = 0.21$** **$p < 0.05$**
Infaunal Carnivore	r = +0.23 $R^2 = 0.05$ $p = 0.23$
Infaunal Deposit Feeder	r = +0.21 $R^2 = 0.009$ $p = 0.30$
Semi-Infaunal Suspension Feeder	r = -0.07 $R^2 = 0.005$ $p = 0.71$

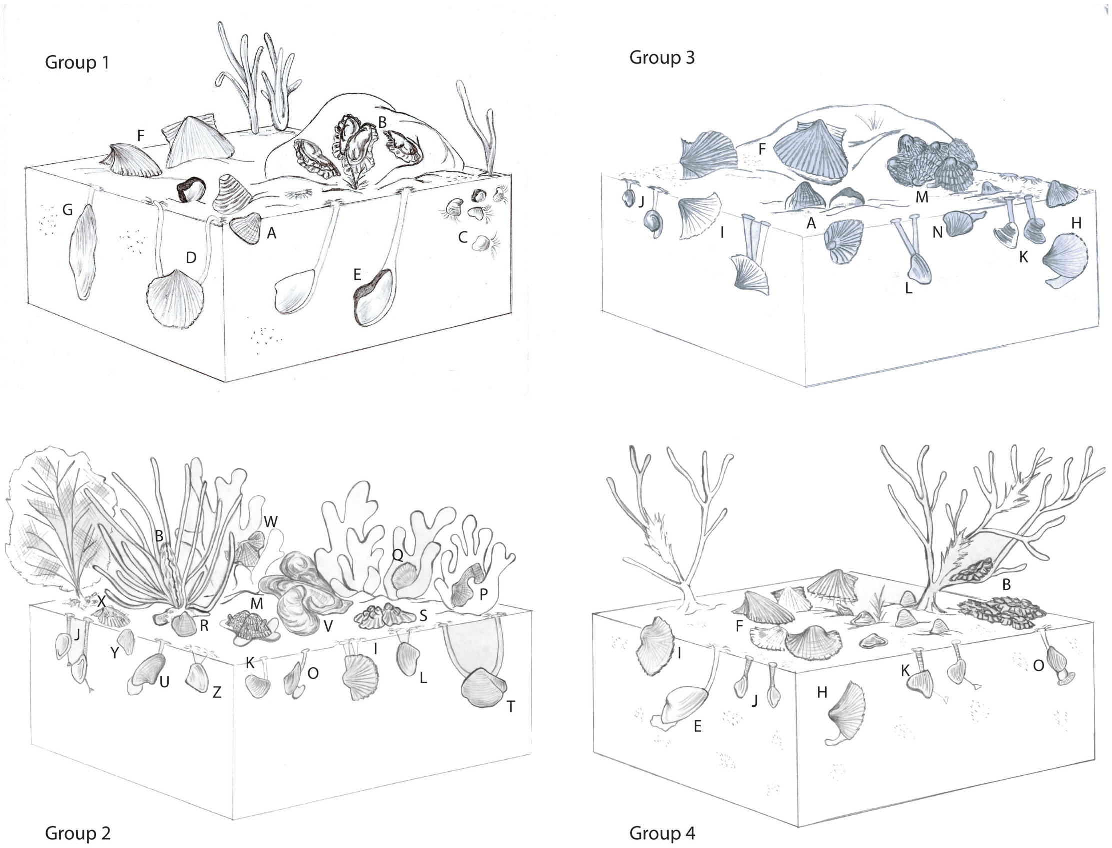

Figure 2.5: Life habits of the most common taxa in the four groups of faunules identified in Figure 2.3. Actual proportions are not represented. Letters correspond to taxa illustrated in Figure 2.3.

Environmental Drivers of Community Change. - PCA1 based upon counts of functional groups was negatively correlated with both coral biomass ($R^2 = 0.35$, $p < 0.001$) and the carbonate content of the sediment ($R^2 = 0.30$, $p < 0.01$) (Fig. 2.7). Decrease in PCA1 correlates with an increase in the proportion of attached epifaunal life habits, as well as an increase in the proportion of deposit feeders and chemosymbionts (Fig. 2.3). PCA1 based on weights was also negatively correlated with percent coral, but not with carbonate ($R^2 = 0.37$, $p < 0.001$; $R^2 = 0.06$, $p = 0.104$, respectively). In contrast, the first dimension of the NMDS was positively correlated with depth ($R^2 = 0.21$, $p < 0.05$), whereas the second NMDS dimension was positively correlated with coral biomass ($R^2 = 0.58$, $p < 0.001$) and carbonate content of the sediment ($R^2 = 0.38$, $p < 0.001$) (Table 2.6).

Table 2.5: Variance explained by the first three principal component axes for each type of data used to ordinate the faunules by functional group.

Principal Components Analysis of Functional Groups

Data Used for Analysis	Percent Variance Explained			
	Component 1	**Component 2**	**Component 3**	**Component 1-**
Abundance Counts	63.1	23.5	9.47	96.07
Weights	52.9	37.8	5.75	96.45
Presence/Absence	50.8	30.6	13.7	95.1

Table 2.6: Results of regressions of ordination axes against age and environmental variables with a significant relationship to at least one ordination regression. Significant results are in bold.

	Age	**Depth**	**Percent Carbonate**	**Percent Coral**
PCA1	**r = -0.49** **$R^2 = 0.24$** **p < 0.01**	r = +0.13 $R^2 = 0.02$ p = 0.53	**r = -0.56** **$R^2 = 0.30$** **p < 0.01**	**r = -0.59** **$R^2 = 0.35$** **p < 0.001**
PCA2	r = -0.12 $R^2 = 0.02$ p = 0.52	r = -0.12 $R^2 = 0.08$ p = -0.16	r = -0.15 $R^2 = 0.02$ p = 0.45	r = -0.25 $R^2 = 0.06$ p = 0.18
NMDS1	r = +0.27 $R^2 = 0.07$ p = 0.16	**r = +0.46** **$R^2 = 0.21$** **p < 0.05**	r = +0.18 $R^2 = 0.03$ p = 0.36	r = +0.20 $R^2 = 0.03$ p = 0.30
NMDS2	**r = +0.61** **$R^2 = 0.37$** **p < 0.001**	r = -0.13 $R^2 = 0.02$ p = 0.52	**r = +0.62** **$R^2 = 0.38$** **p < 0.001**	**r = +0.76** **$R^2 = 0.58$** **p << 0.001**

Discussion and Conclusions

Bivalve assemblages from the southwestern Caribbean exhibit clear patterns of ecological and taxonomic change associated with the emergence of the Isthmus of Panama and final closure of the Central American Seaway 4-3 Ma. Analyses of functional groups reveal profound shifts in life habits and diets in response to changing environmental conditions whereas analyses of taxonomic composition more closely reflect changes in community membership over time with little comparatively ecological insight. In all cases, analyses based on quantitative abundance data more clearly elucidated ecological patterns that were not clearly apparent using simple occurrence data, as in previous studies (McKinney et al. 1998; Jackson et al. 1999). This reflects the low regional extinction and origination rates of bivalve species over the past 11 Ma (Todd et al. 2002; Smith and Jackson 2009).

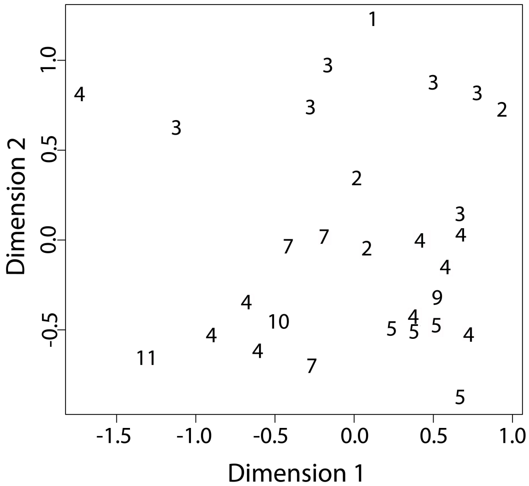

Figure 2.6: The first two dimensions of nonmetric multidimensional scaling performed on the generic abundance data. Each number represents a faunule, and denotes the rough categorical age for that faunule, as in Figure 2.3.

Counts and weights of individuals yield similar results, although ordinations based on counts revealed more fine-scale community changes (Figs. 2.3 and 2.4). This difference could be due to the differences in shell structure and morphology among functional groups. For example, many deposit-feeding bivalves have thin, delicate shells, and therefore changes in the abundance of deposit feeders may be less apparent in weight data. Although small taxa are not important contributors to the overall biomass they may still be important in structuring the overall community as agents of intense bioturbation or as prey.

Composition of Bivalve Assemblages Through Time. - The functional composition of bivalve assemblages changed greatly over time in terms of overall proportions of different trophic groups and life habits (Fig. 2.3). After final closure of the CAS around 3.5 Ma, with concomitant decline in seasonality, upwelling, and planktonic productivity (O'Dea et al. 2007), there is evidence for major changes in the functional composition of bivalve assemblages, which began before the peak in taxonomic turnover at 2 Ma (O'Dea et al. 2007). For example, many of the faunules in Groups 1 & 2 are older than 2 Ma (Fig. 2.3).

Most of the faunules younger than 3.5 Ma have a high proportion of epifaunal, attached taxa commonly associated with reef environments (Figs. 2.3 and 2.5). These younger faunules also display a greater variety in diet, with increased proportions of deposit feeders and chemosymbiotic bivalves relative to suspension feeders. Nevertheless, assemblages typical of older time periods persist after 3.5 Ma because muddy, soft bottom environments did not entirely disappear.

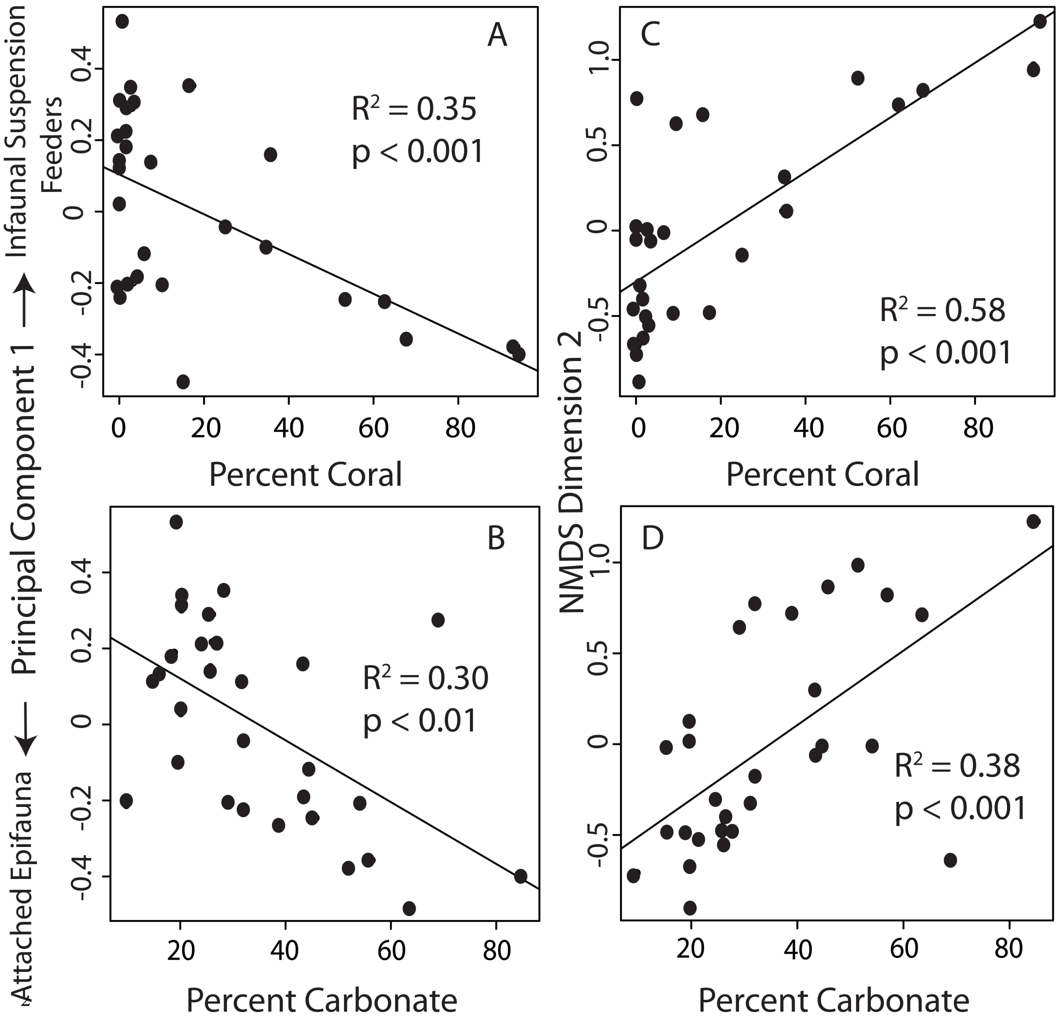

Figure 2.7: Percent coral biomass and carbonate content of sediment versus ordination results. The First Principal Component (PCA1) of the ordination based on count data for bivalve functional groups versus the (A) coral biomass ($R^2 = 0.35, p < 0.001$) and (B) carbonate content of sediment ($R^2 = 0.30, p < 0.01$). The second dimension of the NMDS plotted against (C) coral biomass ($R^2 = 0.58, p < 0.001$) and (D) carbonate content of the sediment ($R^2 = 0.38, p < 0.001$).

Taxonomic analysis strengthened understanding of the patterns based on functional groups. Typical infaunal suspension feeders, such as corbulids and venerids, numerically dominate the older faunules, whereas they are rivaled in

Table 2.7: Percentages of bivalve values belonging to each functional group for the assemblage groups defined in Figure 3.

	Percentage of Bivalve Shells			
Functional Group	**Group 1**	**Group 2**	**Group 3**	**Group 4**
Epifaunal Free-Living Suspension Feeder	0.45	2.36	4	2.64
Epifaunal Attached Suspension Feeder	15.94	41.25	17.56	11.81
Epifaunal Predatory Carnivore	0.53	0.45	0.99	0.55
Infaunal Chemosymbiotic Suspension Feeder	8.21	4.83	2.25	2.37
Infaunal Suspension Feeders	14.95	31.32	34.11	65.31
Infaunal Predatory Carnivore	0.3	0.1	0.16	0.12
Infaunal Deposit Feeder	14.46	12.49	4.84	5.53
Semi-infaunal Suspension Feeders	45.17	7.2	36.09	11.64

abundance by reef-associated taxa, including oysters, mussels, byssally attaching scallops, spondylids, and arks (Waller 1993; Boyd 1998; Wilson 1998; Zuschin et al. 2000; Oliver and Holmes 2006, Smith and Jackson 2009) in the younger faunules. This pattern is consistent with the striking increase in Caribbean reef development in the late Pliocene and Pleistocene (Johnson et al. 2007, 2008). The second dimension of the NMDS of faunules clearly reflects this shift in taxonomic makeup of bivalve assemblages. However, ordinations of faunules based on taxa are highly sensitive to comparatively small changes in depth that may obscure functional patterns (Fig. 2.6, Table 2.6; Jackson et al. 1999).

The shift in diets is subtler than for life habits, and requires a slightly different explanation. Deposit-feeding and chemosymbiotic bivalves are frequently associated with shallow-water seagrass communities (Jackson 1972,1973; Johnson et al. 2007). Seagrasses were present in the Caribbean since the Eocene when they were associated with free-living corals and bryozoans. However, these seagrass meadows occurred in deeper water and were dominated by a different genus of seagrass than the vast shallow-water meadows of the turtlegrass *Thalassia testudinum* that dominate the Caribbean today (Johnson et al. 1995, 2007; Cheetham and Jackson 1996; Cheetham et al. 2001). Several of the Cayo Agua faunules probably represent these deep-water seagrass beds, as evidenced by the abundance of free-living corals in these assemblages. The bivalves in these older seagrass systems are predominantly infaunal suspension feeders that are functionally similar to bivalves in muddy, soft-bottom habitats. Seagrass ecosystems shifted toward a more detritus-based trophic ecology after the closure of the CAS (Domning 2001), thereby providing more suitable habitat for deposit feeders (e.g., Nuculidae) and chemosymbiont-bearing bivalves (e.g., Lucinidae), which are relatively more abundant in younger faunules (Figs. 2.3 and 2.5).

Evolution and Environment. - Our results demonstrate a strong relationship between oceanographic change associated with the isolation of the Caribbean from the eastern Pacific and the taxonomic composition, structure, and function of shallow-water ecosystems in the southwestern Caribbean and are consistent with previous inferences based only on changes in faunal composition (Todd et al. 2002; Johnson et al. 2007). Simple environmental indicators, such as the percent carbonate and percent coral debris in sediments, are negatively correlated with the relative abundance of infaunal suspension feeders, but positively correlated with the relative abundance of attached epifaunal bivalves. Thus, to the extent that increased carbonate sediment and coral abundance are good proxies for increased development of coral reef tracts and seagrass meadows, our results strongly support the hypothesis that the increase in reefs and seagrasses in the late Pliocene and early Pleistocene was the major proximate factor in the functional turnover of bivalve assemblages.

Previous research has strongly supported the hypothesis that decrease in primary productivity was primarily responsible for changes in the relative abundance of different lineages of scallops and cupuladrid bryozoans (O'Dea and Jackson 2009; Smith and Jackson 2009), and of major taxa such as bivalves, gastropods, bryozoans, and corals (O'Dea et al. 2007). But this linkage is not well supported for changes in functional groups of bivalves, for which changes in habitats are more important than productivity per se. Rather, the decline in productivity facilitated the rise of coral reefs and shallow water seagrass meadows that, in turn, indirectly determined the success of different bivalve functional groups.

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CHAPTER 3 – ENVIRONMENTAL CHANGE DROVE RATES OF PREDATION IN CARIBBEAN NEOGENE MOLLUSCAN COMMUNITIES

Abstract

Rates of predation vary enormously throughout the fossil record for reasons that are poorly understood. We tested the hypothesis that the intensity of gastropod drill predation on bivalves should be positively correlated with planktonic productivity by comparing rates of predation before and after the collapse in Caribbean planktonic productivity due to isolation of the Caribbean from the Pacific approximately 4-3 MA. Contrary to expectation, predation intensity increased nearly two-fold because the drop in productivity resulted in a widespread increase in shallow-water coral reefs and seagrass meadows where drilling predation is much higher than in previously dominant soft-sediment environments. The consequences of environmental perturbations may depend as much upon the chain of ecological interactions set off by the new conditions as the magnitude of environmental change.

Main Paper

The diversity and intensity of trophic interactions in the oceans have increased dramatically throughout the Phanerozoic due to escalating competition for food and space and innovations in feeding strategies and prey defense (Vermeij 1977, 1987; Bambach 1983, 1993; Jackson 1983; Steneck 1983). However, detailed mechanistic understanding of the determinants of changes in trophic interactions over shorter macroevolutionary timescales has remained elusive because trophic structure and the intensity of biological interactions also depend strongly on oceanographic conditions, habitat, taxonomic composition, and the earlier evolutionary histories of different biogeographic provinces (Vermeij 1978, Hansen and Kelley 1995, Hoffmeister and Kowalewski 2001, Kelley and Hansen 2006). For example, decreases in Caribbean planktonic primary productivity 4-3 MA associated with the rise of the Isthmus of Panama (Allmon 2001; Kirby and Jackson 2004; O'Dea et al. 2007) are hypothesized to have reduced rates of predation in Caribbean nearshore communities (Vermeij and Petuch, Vermeij 1989, Todd et al. 2002, Johnson et al. 2007) as well as causing major changes in community composition, life histories, and extinction (Woodring 1966; Vermeij and Petuch 1986; Johnson et al. 1995, 2007, 2008; O'Dea et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009).

We tested the hypothesized effects of decreased productivity on predation in the southwestern Caribbean by quantifying rates of gastropod drill predation for over 100,000 bivalve shells in 170 samples grouped into 28 marine faunules over the past 11 MA. All specimens were sorted to genus, counted, and assessed for the presence of gastropod drill holes. We then calculated the drilling intensity for each sample and faunule (Table 3.1) as well as for each bivalve genus (Table 3.2). For each faunule, we also calculated the ratio of predatory drilling gastropods to bivalve prey and the relative abundance of the two major drilling gastropod families (Muricidae and Naticidae).

The results overwhelmingly contradict the predictions of the productivity hypothesis. The percentage of drilled bivalves per faunule increases significantly towards the Recent, despite considerable scatter in the data. In contrast, the ratio of gastropod predators to bivalve prey remains unchanged over the entire interval (Fig. 3.1A & B). Regression of drilling through time within several bivalve families indicates no trends through time.

To try to explain these enigmatic results, we broke down our analyses by habitat to determine whether changes in the extent of different coastal environments were somehow responsible for the increase in predation. The geologically rapid decline in Caribbean planktonic productivity (O'Dea et al. 2007) was followed by a more gradual but pervasive increase in the extent of coral reefs and shallow-water seagrass meadows (Jackson et al. 1999; Domning 2001; Johnson et al. 2007, 2008). These biogenic ecosystems exhibit extremely high benthic primary production (Zieman and Wetzel 1980; Hatcher 1988, 1990; Gallegos et al. 1993) and contain bivalve assemblages that are strikingly different from those in soft-sediment environments (Jackson 1972, 1973; Todd et al. 2002; Johnson et al. 2007; Smith and Jackson 2009, Leonard-Pingel et al. 2012). In particular, hard substrata associated with reefs are dominated by epifaunal bivalves and their predominantly muricid gastropod predators, whereas seagrasses are commonly dominated by infaunal chemosymbiotic bivalves and their naticid gastropod predators. To test for habitat effects on predation, we classified the environment of each faunule as soft sediment or biogenic (Table 3.1) and calculated the median drilling rate for each. Predation rates for biogenic habitats were nearly double those for soft sediments (Fig. 3.2A). Moreover, bivalve genera characteristic of reefs and seagrasses (Table 3.2) experienced significantly higher predation rates than those characteristic of soft sediments (Fig. 3.2B). The percentage of drilled epifaunal bivalves characteristic of reef associated habitats and of drilled chemosymbiotic bivalves characteristic of seagrasses was 2 to 4 times higher than for infaunal bivalves characteristic of soft sediments (Fig. 3.2C & D). Gastropod predators varied in proportion to relative abundance of their prey. Epifaunal muricid gastropods increased relative to infaunal naticids along with the increase in biogenic habitats (Fig. 3.1C). Muricids were nearly 50% more abundant than naticids in biogenic habitats whereas naticids were nearly 5 times more abundant than muricids in soft sediments (Fig. 3.2E).

Our results do not negate the importance of the collapse in planktonic productivity for ecosystem structure and function (O'Dea et al. 2007), but it is necessary to distinguish between proximate and ultimate factors to unravel cause and effect (Mayr 1961, Didham et al. 2005; Leonard-Pingel et al. 2012). This is because the decline in planktonic productivity overwhelmingly changed coastal habitats throughout the region, and these differences in habitat determined the kinds of bivalves present and their susceptibility to predation. Our results provide an important macroevolutionary example of how changes in environmental conditions may influence the outcome of biological interactions in deep time, in ways analogous to the development of alternative community states in freshwater environments (Scheffer et al. 1993, Scheffer 2009) or for trophic cascades on newly isolated islands in tropical forests (Terborgh et al. 2001, Terborgh and Feeley 2010). The consequences of physical environmental change depend as much upon the cascading series of ecological interactions set off by the initial change in physical conditions as the magnitude of the physical changes per se.

Supplementary Online Material

Paleoenvironments.- Evidence for paleoenvironmental change during closure of the Central American Seaway (CAS) and formation of the Isthmus of Panama includes increased salinity (Keigwin 1982; Cronin and Dowsett 1996; Haug et al. 2001), decreased seasonality as measured by mean annual range in temperature (MART) (Teranes et al. 1996; O'Dea and Jackson 2002; O'Dea et al. 2007), and decreased upwelling and productivity based on growth rates of oysters and MART (Allmon 2001; Kirby and Jackson 2004; O'Dea et al 2007) in the Caribbean. Stratigraphy is from Coates (1999) and Coates et al. (1992, 2003, 2004, 2005) and McNeill et al. (2000). Additional paleoenvironmental evidence and documentation of faunal change include: water depths (Collins 1993, 1999; Collins et al 1995, 1996); sediments and relative abundance of major taxa (O'Dea et al. 2007); presence of reefs or shallow-water seagrasses (Coates 1999; Jackson et al 1999; Johnson et al. 2007, 2008; reef corals (Johnson et al 1995; Budd and Johnson 1999; Budd 2000; Johnson et al 2008); bryozoans (Cheetham and Jackson 1996; Cheetham et al 1999; Cheetham and Jackson 2001; O'Dea and Jackson 2009), and mollusks (Jackson et al. 1993, 1999;

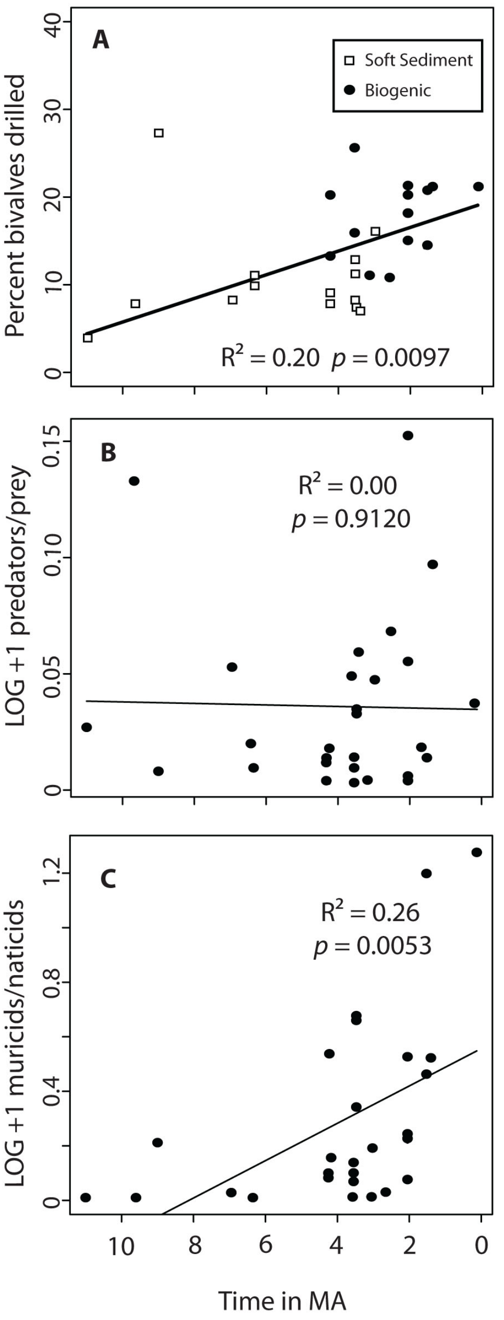
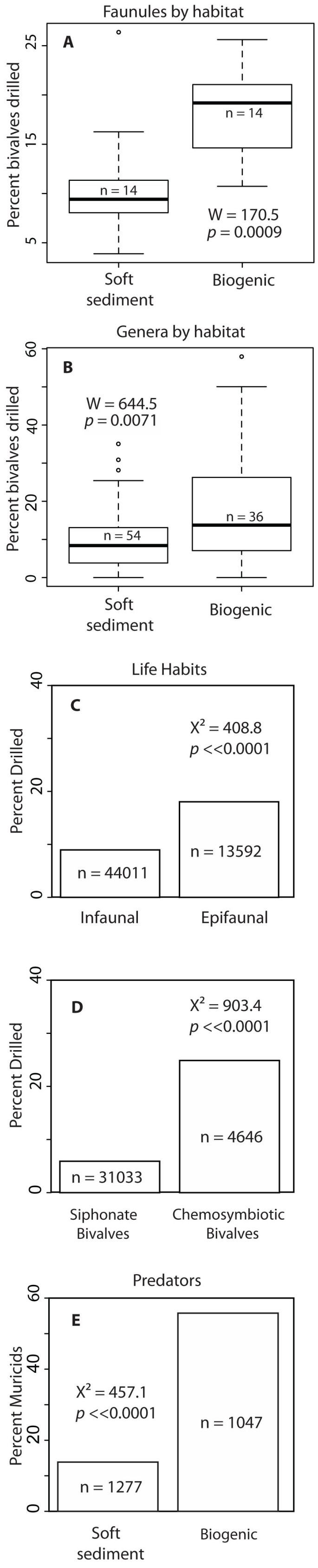


Figure 3.1: Changes in predation intensity on bivalves, the relative abundance of gastropod predators and bivalve prey, and the relative abundance of muricid to naticid gastropod predators in 28 faunules over the past 11 MA data were transformed as log (x + 1). A, Increase in percentage of bivalves drilled based on weighted least squares regression. Open squares indicate soft sediment habitats, and solid circles indicate biogenic habitats. B, The ratio of predatory drilling gastropods to bivalve prey does not change through time. C, The ratio of muricid gastropods to naticid gastropods increases significantly through time.

Figure 3.2: Differences in predation rates between habitats, bivalve functional groups, and relative abundance of gastropod predators over 11 MA. Comparisons are for shells from all 28 faunules combined. W values are from Wilcoxon Rank Sum tests and X^2 values are from Pearson's chi-square tests. A, Difference in median percentage of drilled bivalves between faunules from soft sediments versus faunules from biogenic habitats. B, Difference in median percentage of bivalves drilled between genera characteristic of soft sediments and biogenic habitats. C, Differences in predation upon infaunal and epifaunal bivalves. Numbers of shells shown in bars. D, Differences in predation upon siphonate bivalves and chemosymbiotic bivalves. E, Differences in relative abundance of common predatory gastropod families between soft sediment and biogenic habitats.


Faunules by habitat
A
Percent bivalves drilled
5
15
25
n = 14
n = 14
W = 170.5
$p = 0.0009$
Soft sediment
Biogenic
Genera by habitat
B
Percent bivalves drilled
0
20
40
60
W = 644.5
$p = 0.0071$
n = 54
n = 36
Soft sediment
Biogenic
Life Habits
C
Percent Drilled
0
20
40
$X^2 = 408.8$
$p << 0.0001$
n = 44011
n = 13592
Infaunal
Epifaunal
D
Percent Drilled
0
20
40
$X^2 = 903.4$
$p << 0.0001$
n = 31033
n = 4646
Siphonate Bivalves
Chemosymbiotic Bivalves
Predators
E
Percent Muricids
0
20
40
60
$X^2 = 457.1$
$p << 0.0001$
n = 1277
n = 1047
Soft sediment
Biogenic

Todd et al. 2002; Johnson et al. 2007; Smith and Jackson 2009; Leonard-Pingel et al., in press).

Materials and Methods. - We collected 176 bulk samples from the Caribbean coasts of Panama and Costa Rica. Samples from the same region, formations, and stratigraphic horizon were assigned to one of a total of 28 different faunules (Jackson et al. 1999; O'Dea et al. 2007; Johnson et al. 2007; Smith and Jackson 2009; Leonard-Pingel et al 2012). Faunules were assigned to one of four habitat types: reef, seagrass, mixed, or soft sediment based on lithologic descriptions, total faunual assemblages, and the % mud, and % carbonate in sediments (Coates 1999; Jackson et al 1999; O'Dea et al 2007, see Table 1).

Bulk samples were washed on a 2mm sieve and sorted to gross taxonomic groups. Bivalves were then sorted to genus following the nomenclature of Todd (2002), and valves were counted following the protocol of Gilinsky and Bennington (1994). Bivalves were examined for the presence of distinctive traces left by drilling gastropods (see Kitchell et al. 1981; Vermeij 1987; Kelley et al. 2001; Leighton 2002; Walker 2007); the number of valves displaying at least one successful drilling trace was then tallied (Kowalewski 2002).

Drilling intensity (see Kowaleski 2002) was calculated at the assemblage level for each sample and a median drilling intensity was then calculated for each faunule. For numerically abundant bivalve families (Arcidae, Corbulidae, Lucinidae, Osteridae, and Veneridae) drilling rates were calculated for each sample and a median drilling intensity for that family was calculated for each faunule. Drilling rates were calculated for the 90 bivalve genera with at least 25 valves in all samples (Table 3.2). Corbulid bivalves are small clams that live byssally attached to sediment grains just below the sediment surface and are abundant in the great majority of faunules. They also exhibit high rates of drilling predations throughout all 11 MA. We therefore excluded them from analysis of predation through time and for comparisons of drilling intensity between soft sediment and biogenic habitats. Drilling rates for genera include corbulid bivalves, because in this case the drilling signal of the corbulids would not influence or overwhelm the drilling signal from other genera. Linear regression of drilling rates through time including corbulids is not significant ($R^2 = 0.0925$, $p = 0.0637$).

Pearsons Chi-squared tests were used to test for significant differences in relative abundance of drilled and undrilled bivalve valves. Corbulids were removed for comparison of infaunal and epifaunal bivalves because of their anomalous life habit and scallops were removed from the epifaunal dataset because of their unique ability to move freely or swim. For comparison of drilling in chemosymbiotic and siphonate bivalves, the chemosymbiotic group includes all the lucinid bivalves; the siphonate group includes families of suspension-feeding or deposit-feeding bivalves with siphons long enough to facilitate relatively deep burrowing. The latter include members of the Noetiidae, Semelidae, Solecurtidae, Tellinidae, Thraciidae, and Veneridae.

Gastropods with a complete apex or aperture were counted, and naticid and muricid gastropods were identified and counted. A Pearson's Chi-squared test was performed to test the difference in relative abundance of each predator in soft sediment and biogenic habitats. The abundance of naticid and muricid gastropods as a percentage of total gastropods was calculated and linear regressions show that naticid gastropods significantly decrease through time ($R^2 = 0.5234$ $p = 1.36e\text{-}05$). On the other hand, muricid gastropods show an increasing trend through time, although this trend is not significant ($R^2 = 0.0501$ $p = 0.252$).

Table 3.1: Age, environmental data and abundance data for each faunule. Environmental data is available from O’Dea et al. (2007) and Leonard-Pingel et al. (2012).

Faunule	# Samples	Age (MA)	Habitat	Depth (m)	MART (deg. C)	% Carbonate	% Mud	% Coral	# Bivalve Shells	Mean Drilling %	# Gastropods	# Muricids	# Naticids
Lennond	10	0.125	Mixed	15	3.8	85.18	39.03	94.98	1292	21.14	2680	55	3
Swan Cay	11	1.4	Reef	100	3.22	63.49	20.9	15.74	1327	21.06	3560	115	51
Empalme	6	1.6	Reef	20	2.82	43.43	32.55	3.45	3646	14.63	1994	74	5
Upper Lomas	21	1.6	Reef	75	2.82	43.28	21.33	35.7	14793	20.78	6204	158	83
Wild Cane Reef	7	2.05	Reef	25	4.19	56.4	28.29	67.05	278	15.05	1403	23	36
Wild Cane Key	4	2.05	Mixed	30	4.19	45.76	33.11	52.62	331	21.45	605	16	7
G. C. Porites	9	2.05	Reef	10	-	51.41	53.01	93.79	2119	18.15	1202	5	7
G. C. Porites	6	2.05	Seagrass	10	-	29.6	30.78	9.45	24476	20.29	1653	20	94
Fish Hole	4	2.6	Mixed	88	2.36	19.55	59.34	34.64	329	10.73	438	2	26
Bomba	10	3.05	Soft Sed.	30	3.13	68.96	29.78	1.65	2339	16.26	1503	7	128
Quebrada Chocolate	1	3.1	Reef	-	-	31.98	17.22	0.17	8438	11	509	15	27
Quitaria	1	3.5	Soft Sed.	30	3.13	20.83	20.19	2.67	478	7.11	630	1	34
Cayo Agua: Pt. Nispero W	3	3.55	Soft Sed.	60	7.23	26.1	33.85	1.56	989	11.34	402	2	13
Cayo Agua: Pt. Tiburon	4	3.55	Seagrass	60	5.68	32.01	30.14	25.02	998	16.24	200	6	5
Rio Vizcaya	3	3.55	Soft Sed.	12	-	31.66	15.47	0.19	1651	8.59	1155	13	56
Santa Rita	6	3.55	Soft Sed.	30	5.73	44.4	28.88	5.86	802	13.01	274	9	22
Isla Solarte	3	3.55	Soft Sed.	75	6.68	54.1	14.79	3.28	2626	8.35	2142	124	33
Cayo Agua: Pt. Nispero S	3	3.55	Seagrass	60	7.23	26.1	15.34	3	1922	25.62	132	7	2
Isla Popa	6	4.25	Soft Sed.	50	6.65	19.77	56.69	0.02	11067	9.16	141	6	33
Cayo Agua: Pt. Norte W	9	4.25	Seagrass	30	6.25	15.93	42.59	8.08	3887	13.31	637	45	18
Cayo Agua: Pt. Piedra Roja W	10	4.25	Seagrass	42	3.52	27.73	18.72	17.32	10616	20.23	1841	43	99
Cayo Agua: Pt. Norte E	7	4.25	Soft Sed.	60	4.11	18.87	49.57	1.6	1493	7.84	368	6	26
Rio Chico N17	4	6.35	Soft Sed.	30	8.67	20.11	36.02	0	5030	11	854	0	63
Rio Tupisa	3	6.35	Soft Sed.	100	6.65	15.28	41.2	0	1103	9.89	376	0	26
Rio Indio	11	6.95	Soft Sed.	25	-	9.76	12.13	0.09	601	9.67	202	3	35
Mattress Factory	2	9	Soft Sed.	28	6.18	24.55	35.3	0.25	1388	26.37	158	6	9
Isla Payardi	9	9.6	Soft Sed.	27.5	6.18	25.73	47.9	0	3184	8.05	3548	0	570
Sand Dollar Hill	3	11	Soft Sed.	-	6.18	20.24	8.6	0.43	1551	3.89	120	0	52

Table 3.2: The 90 bivalve genera with at least 25 valves represented in all samples. References for habitat are as follows. 1)Stanley 1970 2)Anderson 1992 3)Anderson 1994 4)Fortunato and Schafer 2009 5)Yonge 1946 6)Jackson 1973 7)Bitter-Soto 1999 8)Hauser and Oschmann 2007 9)Diaz et al. 1990 10)Zuschin 2001 11)Thomas 1975 12)Taylor 1968 13)Chinzei 1984 14)Haaker et al. 1988 15)Probert and Grove 1998 16)Rudnick et al. 1985 17)Keen 1971 18)Dando et al. 1985 19)Taylor and Reid 1984 20)Yonge 1969 21)Work 1969 22)Smith 2006 23)Morton 1980 24)Oliver 1981 25)Shumway and Parsons 2006 26)Yonge 1978 27)Pilsbry 1931 28)Simone and Wilkinson 2008 29)Slack-Smith 1998 30)Stasek 1961 31)Roopnarine 1996 32)Prezant 1998 33)Britton 1972 34)Olsson 1971 35)Hayward et al. 1997 36)Jones 1984 37)Coan 1984 38)Allen and Turner 1974 39)Thomas 1978 40)Allen and Sanders 1966 41)Urban and Campos 1994 42)Pires 1992 43)Allen 2004 44)Arnaud et al. 2001

Genus	Family	# of Valves	Valves/ 2	# Drilled Valves	Drilling Intensity	Habitat	Habitat References
Caryocorbula	Corbulidae	18526	9263	3247	35.05	Soft Sediment	1-4
Varicorbula	Corbulidae	16997	8498.5	2161	25.43	Soft Sediment	2-3,5
Chione	Veneridae	15317	7658.5	1780	23.24	Seagrass	6-8
Dendostrea	Ostreidae	5151	2575.5	332	12.89	Reef	9-10
Tucetona	Glycymerididae	4471	2235.5	568	25.41	Soft Sediment	11
Macrocallista	Veneridae	4405	2202.5	267	12.12	Soft Sediment	1
Anadara	Arcidae	3961	1980.5	250	12.62	Soft Sediment	1, 4, 12-13
Argopecten	Pectinidae	3765	1882.5	33	1.75	Soft Sediment	4, 14
Saccella	Nuculanidae	3064	1532	165	10.77	Soft Sediment	13, 15
Nucula	Nuculidae	2688	1344	144	10.71	Soft Sediment	1, 5, 15-16
Lucina	Lucinidae	2134	1067	137	12.84	Seagrass	1, 8
Gouldia	Veneridae	1982	991	230	23.21	Seagrass	8
Trigoniocardia	Cardiidae	1548	774	53	6.85	Soft Sediment	17
Myrtea	Lucinidae	1243	621.5	175	28.16	Soft Sediment	18
Tagelus	Solecurtidae	1240	620	14	2.26	Soft Sediment	1
Chama	Chamidae	1085	542.5	146	26.91	Reef	9-10, 19
Pitar	Veneridae	990	495	65	13.13	Soft Sediment	12-13
Cardites	Carditidae	908	454	87	19.16	Soft Sediment	20
Crassinella	Crassatellidae	878	439	86	19.59	Seagrass	8
Angulus	Tellinidae	853	426.5	28	6.57	Soft Sediment	13
Lirophora	Veneridae	839	419.5	44	10.49	Soft Sediment	1, 4
Barbatia	Arcidae	827	413.5	29	7.01	Reef	1, 9-10, 12, 19, 21
Arcopsis	Noetiidae	820	410	76	18.54	Reef	1, 9
Parvilucina	Lucinidae	787	393.5	197	50.06	Seagrass	6 ,8
Plicatula	Plicatulidae	753	376.5	130	34.53	Reef	9, 12, 19
Cyclopecten	Pectinidae	612	306	23	7.52	Soft Sediment	15
Ervilia	Semelidae	598	299	50	16.72	Seagrass	12
Spathochlamys	Pectinidae	582	291	4	1.37	Reef	12, 22
Merisca	Tellinidae	563	281.5	6	2.13	Soft Sediment	Based on the *Tellina* classification - still considered a subgenus in most classification regimes
Ostreola	Ostreidae	549	274.5	71	25.87	Reef	9, 12, 19
Leptopecten	Pectinidae	538	269	1	0.37	Reef/Hard Substrate	23
Eurytellina	Tellinidae	536	268	22	8.21	Soft Sediment	Based on the *Tellina* classification - still considered a subgenus in most classification regimes
Limopsis	Limopsodae	486	243	74	30.45	Reef/Hard Substrate	24
Leopecten	Pectinidae	482	241	2	0.83	Soft Sediment	25
Dimya	Dimyidae	359	179.5	104	57.94	Reef	26
Tellina	Tellinidae	332	166	12	7.23	Soft Sediment	1

Table 3.2 cont.

Genus	Family	# of Valves	Valves/ 2	# Drilled Valves	Drilling Intensity	Habitat	Habitat References
Trachycardium	Cardiidae	321	160.5	2	1.25	Seagrass	1
Lamelliconcha	Veneridae	302	151	19	12.58	Soft Sediment	12-13, 27
Anomia	Anomiidae	299	149.5	8	5.35	Reef	9
Arca	Arcidae	296	148	16	10.81	Reef	1, 9, 19, 21
Moerella	Tellinidae	285	142.5	44	30.88	Soft Sediment	15, 28
Arcinella	Chamidae	254	127	18	14.17	Reef	29
Hyotissa	Gryphaeidae	253	126.5	41	32.41	Reef	10,19
Noetia	Noetiidae	225	112.5	5	4.44	Soft Sediment	1
Laevicardium	Cardiidae	210	105	4	3.81	Soft Sediment	1, 13
Phacoides	Lucinidae	208	104	23	22.12	Seagrass	1
Crassostrea	Ostreidae	172	86	4	4.65	Reef, Hard Substratef	12
Pteria	Pteriidae	169	84.5	6	7.10	Reef	9, 12
Acila	Nuculidae	166	83	2	2.41	Soft Sediment	30
Acar	Arcidae	162	81	8	9.88	Reef	12, 19
Panchione	Veneridae	150	75	15	20.00	Soft Sediment	See references for *Lirophora*, 31
Varinucula	Nuculidae	128	64	4	6.25	Soft Sediment	15
Cardiomya	Cuspidariidae	119	59.5	2	3.36	Soft Sediment	33
Crenella	Mytilidae	119	59.5	6	10.08	Reef	19
Dosinia	Veneridae	117	58.5	5	8.55	Soft Sediment	1,13
Yoldia	Sareptidae	108	54	6	11.11	Soft Sediment	1, 16
Radiolucina	Lucinidae	106	53	18	33.96	Seagrass	See references for *Parvilucina*, 33
Costelloleda	Nuculanidae	102	51	2	3.92	Soft Sediment	34
Felaniella	Ungulinidae	100	50	9	18.00	Soft Sediment	35
Cyclinella	Veneridae	92	46	2	4.35	Soft Sediment	1
Elpidollina	Tellinidae	88	44	5	11.36	Soft Sediment	28
Strigilla	Tellinidae	85	42.5	3	7.06	Soft Sediment	1
Isognommon	Isognomonidae	77	38.5	4	10.39	Reef	9-10, 19, 21
Ventricolaria	Veneridae	73	36.5	6	16.44	Soft Sediment	36
Eucrassatella	Crassatellidae	72	36	5	13.89	Soft Sediment	37
Donax	Donacidae	72	36	0	0.00	Soft Sediment	1, 12
Pacipecten	Pectinidae	70	35	8	22.86	Reef/Hard Substrate	23
Trigonulina	Verticordiidae	70	35	4	11.43	Soft Sediment	38
Axinactis	Glycymerididae	65	32.5	3	9.23	Soft Sediment	11
Sheldonella	Noetiidae	61	30.5	6	19.67	Soft Sediment	39
Cumingia	Semelidae	61	30.5	4	13.11	Soft Sediment	1
Adrana	Nuculanidae	60	30	1	3.33	Soft Sediment	34
Spondylus	Propeamussiidae	60	30	4	13.33	Reef	9-10, 19
Amusium	Pectinidae	56	28	1	3.57	Soft Sediment	23
Anomalocardia	Veneridae	55	27.5	0	0.00	Soft Sediment	1
Ctenoides	Limidae	51	25.5	2	7.84	Reef	10
Abra	Semelidae	50	25	1	4.00	Soft Sediment	5, 40
Caribachlamys	Pectinidae	49	24.5	1	4.08	Reef	22
Semele	Semelidae	49	24.5	0	0.00	Soft Sediment	41
Codakia	Lucinidae	45	22.5	6	26.67	Seagrass	1, 6-7, 12
Aequipecten	Pectinidae	40	20	0	0.00	Seagrass	1

Table 3.2 cont.

Genus	Family	# of Valves	Valves/ 2	# Drilled Valves	Drilling Intensity	Habitat	Habitat References
Cavilinga	Lucinidae	39	19.5	9	46.15	Seagrass	See references for *Lucina, 33*
Lunarca	Arcidae	36	18	2	11.11	Soft Sediment	42
Flabellipecten	Pectinidae	36	18	0	0.00	Soft Sediment	25
Chionista	Veneridae	36	18	1	5.56	Seagrass	See references for *Chione,* 31
Americardia	Cardiidae	32	16	2	12.50	Soft Sediment	1
Limea	Limidae	29	14.5	3	20.69	Soft Sediment	43
Temblornia	Leptonidae	28	14	0	0.00	Symbiotic -in soft sediment burrows	17
Propeleda	Nuculanidae	27	13.5	1	7.41	Soft Sediment	44
Mulinia	Mactridae	26	13	1	7.69	Soft Sediment	1, 16

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CHAPTER 4 – DIFFERENTIAL PREDATION RATES AMONG BIVALVE GENERA

Introduction

Since Darwin (1859), predation has been recognized as a major driver of macroevolution. Coevolution between predators and prey has garnered special attention as a driver of community evolution and diversification (Dawkins and Krebs 1979; Vermeij 1977, 1983; Bambach 1983). Molluscan predator-prey interactions are particularly well suited to studies of predation through time because of their abundant fossil record and the potential for preservation of direct evidence of predation, especially traces such as drill holes and repair scars (Kowaleski 2002 and references therein). Researchers interested in coevolution have identified many traits of molluscan prey that they have defined as "anti-predatory." These traits may be related to shell architecture or to life mode (Vermeij 1977, 1983; Bambach 1983; Stanley 1988; Alexander and Dietl 2003). Here, I focus on bivalve molluscs and their anti-predatory modifications.

The architecture and composition of bivalve shells is often referred to in studies of molluscan predation. Thick, robust shells are thought to reduce the probability of a fatal attack by a crushing or drilling predator (Bertness and Cunningham 1981; Vermeij 1978, 1983; Palmer 1979; Kelley 1989; Harper and Skelton 1993; Smith and Jennings 2000; Alexander and Dietl 2003). Likewise, ornamentation on bivalve shells, such as spines, knobs, and crenulations of valve margins, is largely thought of as an adaptation to reduce predation (Stanley 1970; Logan 1974; Harper and Skelton 1993; Alexander and Dietl 2003). Finally, shell microstructure acts as a defense against predation; organic rich laminae within bivalve shells (also known as conchiolin) appear to inhibit drilling and shell breakage (Harper and Skelton 1993; Kardon 1998).

Some behaviors and life modes of molluscs are also adaptations to predation, such as the ability of many scallops to swim by jet propulsion to escape predators. Other epifaunal bivalves cement themselves to a hard substrate, ostensibly to reduce their vulnerability to predators by making themselves more difficult to manipulate (Harper 1991). Still other bivalves escape predation by boring into hard substrates, nestling, burrowing deeply or quickly into the sediment, or camouflaging themselves with sponges or other encrusting organisms (Stanley 1980; Vermeij 1983; Harper and Skelton 1993; Alexander and Dietl 2003).

These interpretations are compromised, however, because most previous studies of bivalve anti-predatory defenses are either based upon experimental manipulations of bivalve shells and predators (Harper 1991; Smith and Jennings 2000) or anecdotal. Here I utilize a large quantitative dataset with calculated drilling intensities, combined with data on shell architecture and life mode for each bivalve genus, to test proposed hypotheses about the relationships between shell architecture, life mode, and predation pressure. Specifically, I test the hypothesis that bivalves with smaller, weaker, and less ornamented shells should experience higher predation than their larger, stronger, and more highly ornamented counterparts. Secondly, I test the hypothesis that bivalve life habits and mobility influence their susceptibility to predation. Specifically, bivalves with the ability to escape predation, either by burrowing or moving freely (e.g. swimming), should experience lower predation rates than bivalves that are epifaunal or cannot move freely.

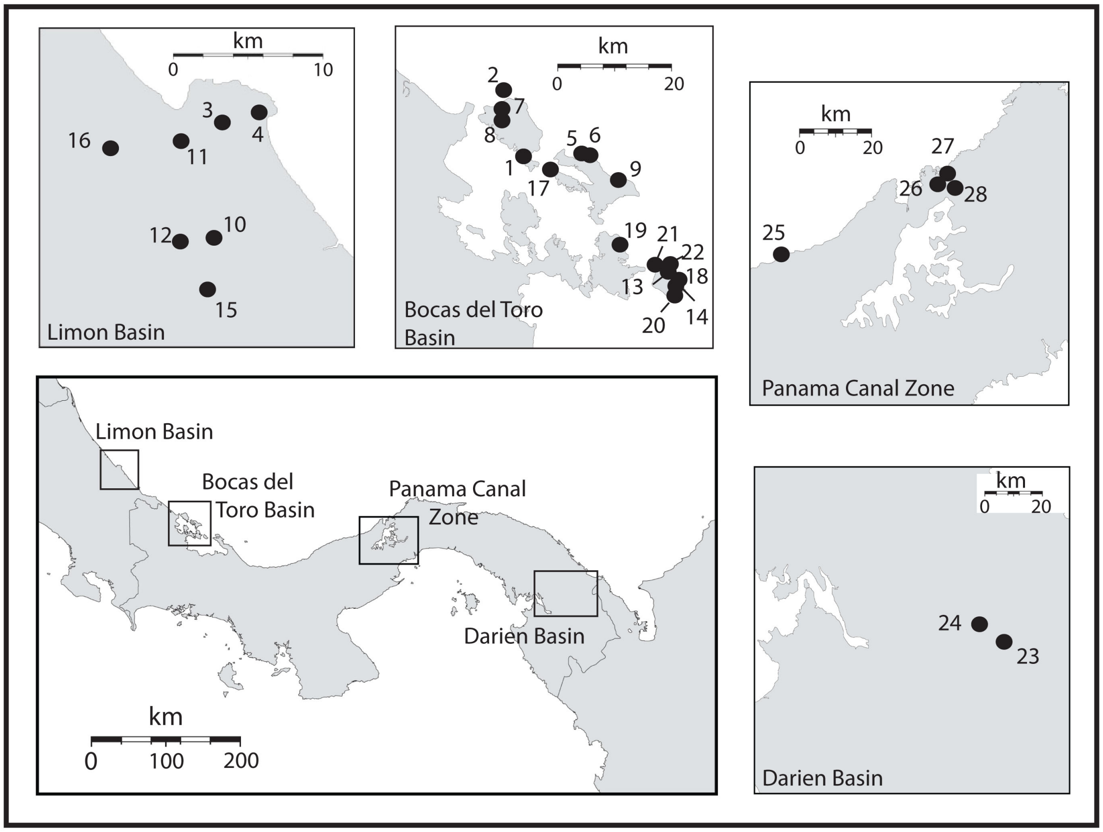

Figure 4.1: Map of Panama and eastern Costa Rica, with insets showing the four basins from which collections were taken; Limon basin, Costa Rica; Bocas del Toro basin, Panama; Panama Canal Zone, Panama; and Darien basin, Panama. Numbers correspond to faunules listed in Table 4.1.

Methods

I collected a total of 176 bulk samples from 28 fossil localities termed faunules (O'Dea et al. 2007; Smith and Jackson 2009; Leonard-Pingel et al. 2012) from four basins in northern Panama and eastern Costa Rica (Figure 4.1, Table 4.1). Bulk samples were processed and washed on a 2 mm sieve to remove fossil material from the rock matrix and fossils were sorted into gross taxonomic groups. Over 100,000 identifiable bivalves with a hinge and umbo (see Gilinsky and Bennington 1994) were sorted, counted, and identified to genus after Todd (2001). After bivalves were sorted, individual valves were examined for the presence of distinctive drilling traces left by predatory gastropods (see Kitchell et al. 1981; Vermeij 1987; Kelley et al. 2001; Leighton 2002; Walker 2007). The number of valves displaying at least one successful drilling trace was tallied (Kowalewski 2002), and the drilling intensity for each bivalve genus with at least 25 valves in all samples was calculated (Kowalewski 2002). Within each faunule, drilling intensity was calculated at the family level for numerically important bivalve families. The average shell weight (total weight of all shells/number of shells), ornamention (low, moderate, high), and depth of burial (epifaunal, semi-infaunal, surface infaunal, shallow infaunal, deep infaunal) were determined for each bivalve genus (Appendix 4.1).

Each variable related to shell architecture or life habit was examined in relation to drilling intensity. I used linear regression to examine the relationship between shell weight (a proxy for valve thickness) and drilling intensity. Kruskal-Wallis ANOVAs were used to test for significant differences among bivalve genera with different ornament and among different taxonomic groups.

Pearson's chi-squared tests were used to test for significant differences in relative abundance of drilled and undrilled bivalve valves for different shell sizes and different life habits and mobility. In the analyses of shell size and predation frequency genera were grouped as small (<10 mm) or large based on average adult lengths. Large venerids include members of the genera *Chione, Chionista, Chionopsis, Circumphalus, Cyclinella, Dosinia, Hysteroconcha, Lamelliconcha, Macrocallista,*

Table 4.1: List of bivalve genera providing drilling intensity, characters of shell architecture, and category of relationship to the substrate.

Faunule	Median Age (MA)	Number of Samples	# Bivalve Shells
Lennond (1)	0.125	10	1292
Swan Cay (2)	1.4	11	1327
Empalme (3)	1.6	6	3646
Upper Lomas (4)	1.6	21	14793
Wild Cane Reef (5)	2.05	7	278
Wild Cane Key (6)	2.05	4	331
Ground Creek Porites (7)	2.05	9	2119
Ground Creek Mud (8)	2.05	6	24476
Fish Hole (9)	2.6	4	329
Bomba (10)	3.05	10	2339
Quebrada Chocolate (11)	3.1	1	8438
Quitaria (12)	3.5	1	478
Cayo Agua: Punta Nispero W (13)	3.55	3	989
Cayo Agua: Punta Tiburon - Punta Piedra (14)	3.55	4	998
Rio Vizcaya (15)	3.55	3	1651
Santa Rita (16)	3.55	6	802
Isla Solarte (17)	3.55	3	2626
Cayo Agua: Punta Nispero S (18)	3.55	3	1922
Isla Popa (19)	4.25	6	11067
Cayo Agua: Punta Norte W (20)	4.25	9	3887
Cayo Agua: Punta Piedra Roja W (21)	4.25	10	10616
Cayo Agua: Punta Norte E (22)	4.25	7	1493
Rio Chico N17 (23)	6.35	4	5030
Rio Tupisa (24)	6.35	3	1103
Rio Indio (25)	6.95	11	601
Mattress Factory (26)	9	2	1388
Isla Payardi (27)	9.6	9	3184
Sand Dollar Hill (28)	11	3	1551
Total		**176**	**108754**

Panchione, Periglytpa, Pitar, Tivela, Transenella, and *Ventricolaria*. *Gouldia* is the only member of the small venerid group. Large lucinids include the genera *Anodontia, Cavilinga, Codakia, Ctena, Divalinga, Lucina, Lucinoma, Myrtea,* and *Phacoides*. Corbulids were removed for comparison of infaunal and epifaunal bivalves because of their anomalous life habit (byssal attachment to sediment grains just below the sediment surface), and their high abundance in most samples. Scallops were removed from the epifaunal dataset because of their unique ability to move freely or swim. At a more detailed level, Pearsons Chi-squared tests were run both with and without corbulids and scallops.

Principal Components Analysis was used to ordinate bivalve genera and families with regard to average shell weight, depth of burial, and mobility. Ornamentation was used in ordination of bivalve genera but not in ordination of bivalve families because it is not uniform within bivalve families. The first and second principal components of the ordinations were used in regression analysis against drilling rates.

Results

Linear regression of shell weight against drilling intensity was not significant. There is evidence, however, for higher drilling intensities in small genera compared with larger genera within families (Figure 4.2). Small venerids have a slightly higher, but statistically significant, drilling frequency than do larger venerids (Figure 4.2A, Table 4.2; $X^2 = 8.80$, $p = 0.0030$). Small lucinids experience drilling frequencies more than twice as high as their larger counterparts (Figure 4.2B, Table 4.2; $X^2 = 135.19$, $p \ll 0.0001$). Median drilling intensity differs significantly among bivalve genera with low, moderate, or high ornamentation, but the trend is the reverse of the hypothesized pattern (Figure 4.3, Table 4.2, $X^2 = 6.225$, $p = 0.045$). Remarkably, bivalve genera with high ornamentation experience significantly *higher* incidence of drilling than do bivalve genera with low ornamentation ($W = 271.5$, $p = 0.038$).

Relationship to the substrate strongly influences susceptibility of bivalves to predation. Predation intensity is twice as high in epifaunal bivalves as is in infaunal bivalves (Figure 4.4A, Table 4.2, $X^2 = 362.70$, $p << 0.0001$). Infaunal bivalves with the ability to burrow deeply into the sediment have significantly lower rates of predation than do bivalves that are shallow burrowers (Figure 4.4B, Table 4.2, including corbulids: $X^2 = 2017.77$, $p << 0.0001$; excluding corbulids: $X^2 = 23.95$, $p << 0.0001$). Likewise, epifaunal bivalves that are not cemented to the substrate experience predation rates that are half that of epifaunal bivalves that are cemented to the substrate (Figure 4.4C, including scallops: $X^2 = 330.43$, $p << 0.0001$, excluding scallops: $X^2 = 48.37$, $p << 0.0001$).

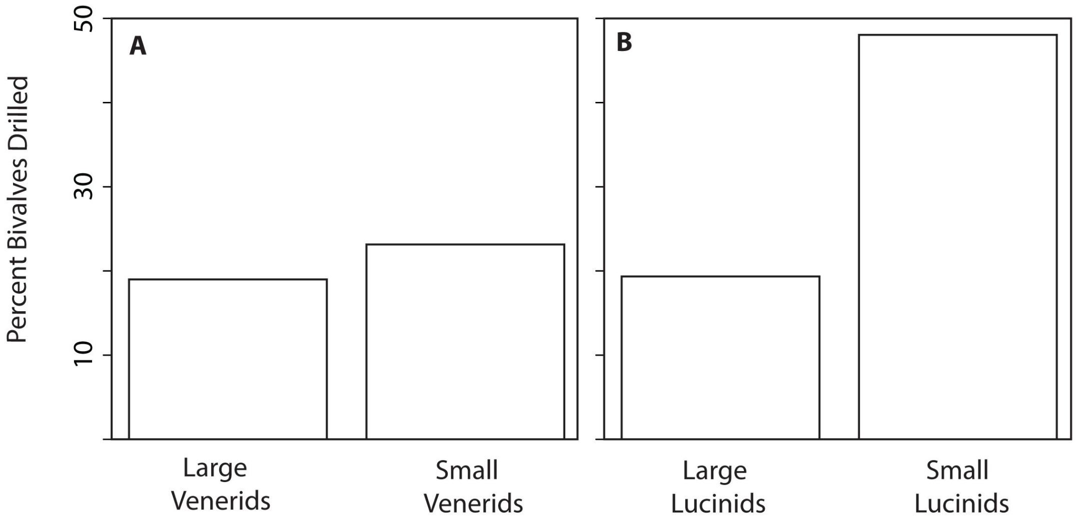

Figure 4.2: Difference in drilling intensity between large and small bivalves of the same family. A, Small venerids experience significantly higher drilling than do large venerids ($X^2 = 8.80$, $p = 0.0030$). B, Small lucinids experience much higher drilling than do large lucninds ($X^2 = 135.19$, $p << 0.0001$).

Taxonomic affinity also influences susceptibility to predation. Drilling intensities among numerically abundant bivalve families (Figure 4.5) differ significantly ($X^2 = 74.008$, $p = 7.792\text{e-}13$). Pectinidae (scallops) experience the lowest incidence of drilling with a median drilling intensity of only 0.87%. Several families with different life habits and shell architecture experience similar median drilling intensities (Figure 4.4). The families experiencing highest overall drilling intensity are Lucinidae (17.39%) and Corbulidae (21.7%). Corbulids are small, infaunal bivalves that live just beneath the sediment surface. Lucinids are much more variable in size and have well developed siphons which allow them to live well below the sediment surface. The high rate of drilling of lucinids reflects the predominance of small specimens and taxa.

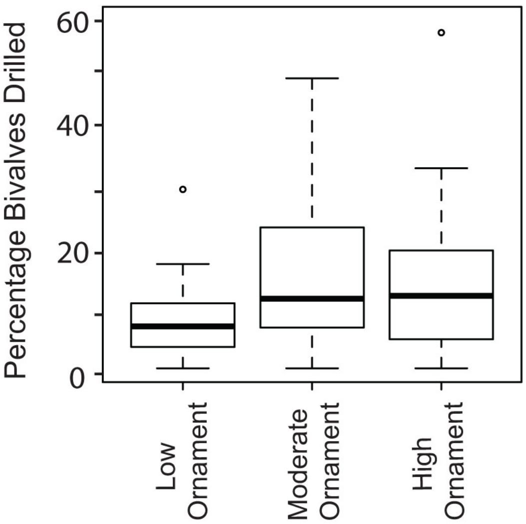

Figure 4.3: Drilling intensities for bivalve genera with low, moderate, and high shell ornamentation. Kruskal-Wallis ANOVA shows a significant difference among groups ($X^2 = 6.225$, $p = 0.045$).

Principal Components Analysis (PCA) of bivalve genera showed no pattern, but PCA of bivalve families revealed striking differences among families based on life habit (PCA 1) and mobility (PCA 2) (Figure 5.4). Regressions of PCA 1 and PCA 2 scores against median drilling rates for families were not significant ($R^2 = 0.07$, p = 0.48 and $R^2 = 0.32$, *p* = 0.11, respectively).

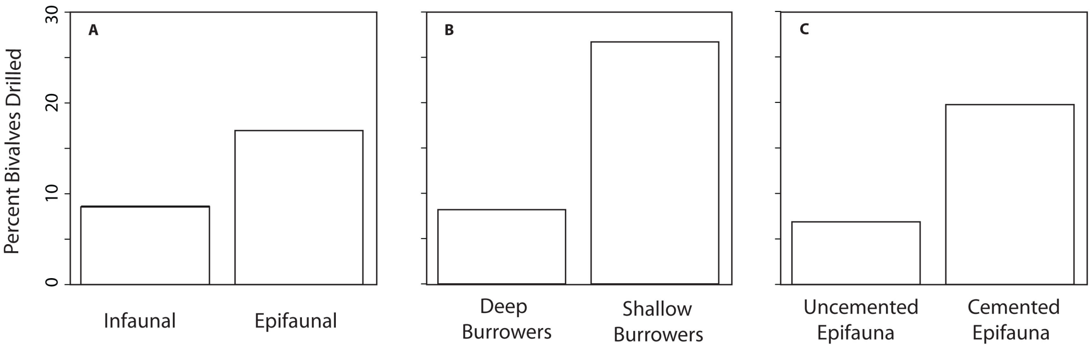

Figure 4.4: Differences in drilling between different life habits and mobilities of bivalves. A, The percentage of epifaunal bivalves drilled is twice that of infaunal bivalves ($X^2 = 362.70$, $p << 0.0001$). B, The percentage of surface and shallow burrowers drilled is more than three times higher than that of infaunal bivalves ($X^2 = 2017.77$, $p << 0.0001$). C, The percentage of drilling in cemented epifaunal bivalves is more than twice that of uncemented epifaunal bivalves ($X^2 = 330.43$, $p << 0.0001$).

Discussion

The apparent lack of a relation between average shell weight and predation intensity may reflect the overwhelming number of small valves in my collections. Shell thickness may only provide significant defense in cases of extreme shell thickening, such as very large oysters that were absent from my samples. It is also possible that shell thickness is not a deterrent to predatory drilling gastropods (Harper and Skelton 1993), or that average shell weight is not a good measure of shell thickness. In contrast, there is some evidence for an escape in size, as smaller genera within a family experience higher drilling intensities than larger genera (Figure 4.2), this may be especially true for bivalves with the potential to burrow deeply into the sediment, as larger individuals are able to burrow more deeply. Escape in size may also be more applicable to escape from predators that need to manipulate their prey in order to crush shells (Harper and Skelton 1993), whereas size may have little advantage is escaping drilling predators. Ornamentation was a surprisingly ineffective deterrent to predation. However, the role of ornament in reducing predation is ambiguous, with some experimental studies providing evidence of ornament as a successful deterrent to predation (Carter 1967; Logan 1974; Harper and Skelton 1993), while others do not support this claim (Vance 1978; Feifarek 1987). It is possible that in bivalve mollusks surface ornament is more closely related to burrowing (Stanley 1970).

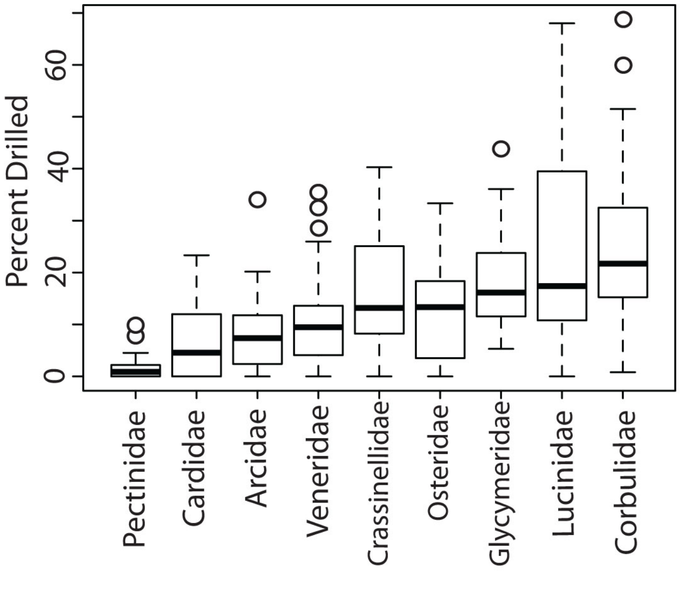

Figure 4.5: Bivalve genera grouped by taxonomic affinity (families) are significantly different ($X^2 = 74.008$, $p = 7.792e-13$).

Table 4.2: Table of percent drilling, statistical tests used, and p-values for comparisons between different shell architecture characteristics, life habits, and mobility of bivalves.

Comparison	Percent Drilled	Test	*P*-values
Large Venerids	18.99	Pearsons' Chi-square	$p = 0.0030$
Small Venerids	23.15		
Large Lucinids	19.35	Pearson's Chi-square	$p << 0.0001$
Small Lucinids	48.04		
Low Ornament	7.32	Kruskal-Wallis ANOVA	$p = 0.045$
Moderate Ornamnet	12.00		
High Ornament	12.50		
Infaunal Bivalves	8.19	Pearson's Chi-square	$p <<0.0001$
Epifuanal Bivalves	26.70		
Deep Infauna	8.19	Pearson's Chi-square	$p <<0.0001$
Shallow Infauna - with corbulids	26.77		
Deep Infauna	8.19	Pearson's Chi-square	$p <<0.0001$
Shallow Infauna - no corbulids	15.95		
Uncemented Epifauna - with scallops	6.88	Pearson's Chi-square	$p <<0.0001$
Cemented Epifauna	19.76		
Uncemented Epifauna - no scallops	12.75	Pearson's Chi-square	$p <<0.0001$
Cemented Epifauna	19.76		

Life habit is a very important determinant of bivalve susceptibility to predation. Deep burrowers are drilled less frequently than shallow burrowers and surface-dwelling infauna. This protection appears to extend even to burrowing naticid predators. Scallops, which have the ability to actively swim when disturbed by predators, have a much lower incidence of predation than any other groups of epifaunal or infaunal bivalves in our sample. In contrast, cemented epifaunal bivalves suffer much higher predation. This may reflect two factors. First, cementation, which acts as a deterrent to some predators (Harper and Skeleton 1993; Alexander and Dietl 2003), may not deter drilling gastropods (Harper and Skeleton 1993). Second, cemented epifaunal bivalves are often found in reef habitats. My work on drilling and habitat has provided strong evidence for high predation in reef environments (Chapter 3).

Bivalve families differ greatly in their overall susceptibility to drilling predators. While many single characters appear to provide little information about drilling intensity (e.g. shell thickness and ornamentation), differences in drilling among higher taxa are strikingly clear. These results make intuitive sense. Scallops (Pectinidae), which have crenulated shells and an ability to actively escape predators, are rarely preyed upon by drilling gastropods, whereas small bivalves that live right beneath the sediment surface, such as Corbulidae, experience high predation. Taxonomy accounts for many factors at once, including ornamentation, life habit, and mobility, and shell microstructure.

In contrast to these clear taxonomic differences, ordination of genera and families in terms of shell weight, ornamentation, depth of burial, and mobility failed to reveal any patterns in relation to drilling intensity suggesting that additional factors such as shell microstructure and bivalve behavior may play an important role. Differences among habitats may also be important. For example, Lucinidae and Veneridae are grouped close together in Figure 4.6 but differ strikingly in predation rates. However, lucinids predominate in seagrass habitats where drilling rates are more than double those in unvegetated soft sediments where venerids are most abundant. Susceptibility to predation based on habitat may therefore be difficult to tease apart from susceptibility inherent in bivalves based on shell architecture, behavior, and taxonomy.

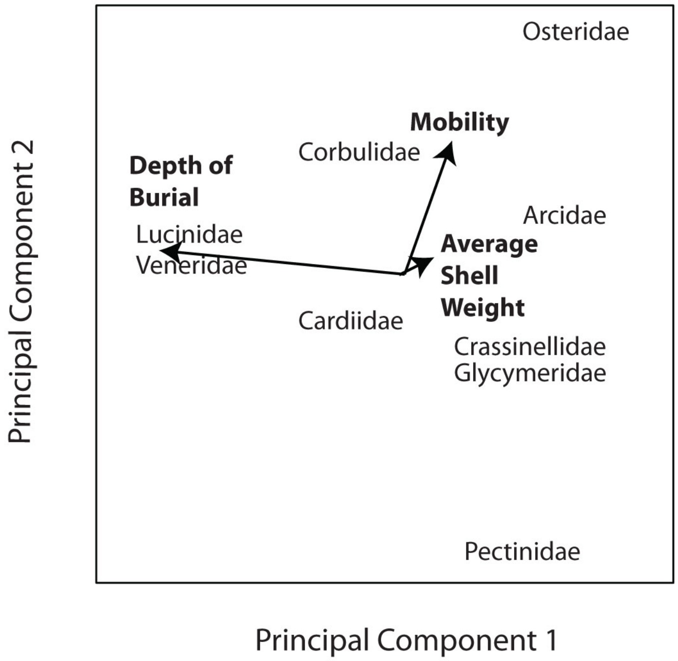

Figure 4.6: Principal Component Analysis of bivalve families based on average shell weight, life habit, and mobility.

Conclusions

Several traits of bivalve genera are related to drilling intensity in ways previously hypothesized whereas others are not. Shell size, life habit, and mobility strongly influence susceptibility of bivalves to drilling predators whereas shell thickness and ornamentation do not. Taxonomic affinity integrates the influence of different characters and provides a useful signature of susceptibility to predation that is intuitive and informative. Nevertheless, variability within families is high (Figure 4.4) due to variations in predation intensity based on environmental influences such as habitat type.

Acknowledgements

I would like to thank Mui Ho for her assistance with the laboratory work. This chapter has been prepared for submission for publication with Jeremy Jackson as my co-author in essentially the same form presented here. The dissertation author was the primary investigator and author of this paper.

Appendix 4.1

Genus	Family	# of Valves	Drilling Intensity	Average Shell Weight	Ornament	Depth	Mobility
Caryocorbula	Corbulidae	18526	35.05	0.01	Moderate	surface infaunal	bysally attached
Varicorbula	Corbulidae	16997	25.43	0.02	Moderate	surface infaunal	bysally attached
Saccella	Nuculanidae	3064	10.77	0.01	Moderate	surface infaunal	free living
Nucula	Nuculidae	2688	10.71	0.01	Low	surface infaunal	free living
Gouldia	Veneridae	1982	23.21	0.01	Moderate	surface infaunal	free living
Parvilucina	Lucinidae	787	50.06	0.00	Moderate	surface infaunal	free living
Ervilia	Semelidae	598	16.72	0.01	Low	surface infaunal	free living
Moerella	Tellinidae	285	30.88	0.01	Low	surface infaunal	free living
Cardiomya	Cuspidariidae	119	3.36	0.00	Moderate	surface infaunal	free living
Radiolucina	Lucinidae	106	33.96	0.01	Moderate	surface infaunal	free living
Costelloleda	Nuculanidae	102	3.92	0.01	Moderate	surface infaunal	free living
Trigonulina	Verticordiidae	70	11.43	0.00	Moderate	surface infaunal	free living
Adrana	Nuculanidae	60	3.33	0.02	Moderate	surface infaunal	free living
Abra	Semelidae	50	4.00	0.00	Low	surface infaunal	free living
Lunarca	Arcidae	36	11.11	0.01	High	surface infaunal	variable
Propeleda	Nuculanidae	27	7.41	0.02	Moderate	surface infaunal	free living
Trigoniocardia	Cardiidae	1548	6.85	0.03	High	shallow infaunal	free living
Pitar	Veneridae	990	13.13	0.02	Moderate	shallow infaunal	free living
Cardites	Carditidae	908	19.16	0.06	High	shallow infaunal	free living
Lirophora	Veneridae	839	10.49	0.06	High	shallow infaunal	free living
Trachycardium	Cardiidae	321	1.25	0.18	High	shallow infaunal	free living
Lamelliconcha	Veneridae	302	12.58	0.02	Moderate	shallow infaunal	free living
Laevicardium	Cardiidae	210	3.81	0.06	Low	shallow infaunal	free living
Acila	Nuculidae	166	2.41	0.14	Moderate	shallow infaunal	free living
Panchione	Veneridae	150	20.00	0.06	High	shallow infaunal	free living

Genus	Family	# of Valves	Drilling Intensity	Average Shell Weight	Ornament	Depth	Mobility
Varinucula	Nuculidae	128	6.25	0.05	Moderate	shallow infaunal	free living
Dosinia	Veneridae	117	8.55	0.25	Moderate	shallow infaunal	free living
Cyclinella	Veneridae	92	4.35	0.05	Low	shallow infaunal	free living
Ventricolaria	Veneridae	73	16.44	0.15	Moderate	shallow infaunal	free living
Sheldonella	Noetiidae	61	19.67	0.01	High	shallow infaunal	bysally attached
Chionista	Veneridae	36	5.56	0.08	High	shallow infaunal	free living
Americardia	Cardiidae	32	12.50	0.16	High	shallow infaunal	free living
Temblornia	Leptonidae	28	0.00	0.01	Low	shallow infaunal	variable
Chione	Veneridae	15317	23.24	0.12	High	semi infaunal	free living
Tucetona	Glycymerididae	4471	25.41	0.09	High	semi infaunal	free living
Anadara	Arcidae	3961	12.62	0.19	High	semi infaunal	bysally attached
Crassinella	Crassatellidae	878	19.59	0.00	Moderate	semi infaunal	free living
Noetia	Noetiidae	225	4.44	0.17	High	semi infaunal	bysally attached
Yoldia	Sareptidae	108	11.11	0.01	Low	semi infaunal	free living
Eucrassatella	Crassatellidae	72	13.89	0.46	Moderate	semi infaunal	free living
Axinactis	Glycymerididae	65	9.23	0.75	High	semi infaunal	free living
Dendostrea	Ostreidae	5151	12.89	0.10	High	epifaunal	cemented
Argopecten	Pectinidae	3765	1.75	0.08	High	epifaunal	free living
Chama	Chamidae	1085	26.91	0.06	High	epifaunal	cemented
Barbatia	Arcidae	827	7.01	0.03	Moderate	epifaunal	bysally attached
Arcopsis	Noetiidae	820	18.54	0.01	High	epifaunal	bysally attached
Plicatula	Plicatulidae	753	34.53	0.06	High	epifaunal	cemented
Cyclopecten	Pectinidae	612	7.52	0.00	Low	epifaunal	free living
Spathochlamys	Pectinidae	582	1.37	0.02	High	epifaunal	bysally attached
Ostreola	Ostreidae	549	25.87	0.12	High	epifaunal	cemented
Leptopecten	Pectinidae	538	0.37	0.03	High	epifaunal	bysally attached
Limopsis	Limopsodae	486	30.45	0.01	Moderate	epifaunal	bysally attached

Genus	Family	# of Valves	Drilling Intensity	Average Shell Weight	Ornament	Depth	Mobility
Leopecten	Pectinidae	482	0.83	0.05	Low	epifaunal	free living
Dimya	Dimyidae	359	57.94	0.04	High	epifaunal	cemented
Anomia	Anomiidae	299	5.35	0.03	High	epifaunal	cemented
Arca	Arcidae	296	10.81	0.10	High	epifaunal	bysally attached
Arcinella	Chamidae	254	14.17	0.13	High	epifaunal	cemented
Hyotissa	Gryphaeidae	253	32.41	0.26	High	epifaunal	cemented
Crassostrea	Ostreidae	172	4.65	1.65	High	epifaunal	cemented
Pteria	Pteriidae	169	7.10	0.03	Low	epifaunal	bysally attached
Acar	Arcidae	162	9.88	0.03	High	epifaunal	bysally attached
Crenella	Mytilidae	119	10.08	0.01	Moderate	epifaunal	bysally attached
Isognommon	Isognomonidae	77	10.39	0.25	Low	epifaunal	bysally attached
Pacipecten	Pectinidae	70	22.86	0.01	High	epifaunal	bysally attached
Spondylus	Propeamussiidae	60	13.33	0.46	High	epifaunal	cemented
Amusium	Pectinidae	56	3.57	0.56	Low	epifaunal	free living
Ctenoides	Limidae	51	7.84	0.03	Moderate	epifaunal	bysally attached
Caribachlamys	Pectinidae	49	4.08	0.10	High	epifaunal	bysally attached
Aequipecten	Pectinidae	40	0.00	0.13	High	epifaunal	bysally attached
Flabellipecten	Pectinidae	36	0.00	0.06	High	epifaunal	free living
Limea	Limidae	29	20.69	0.00	High	epifaunal	free living
Macrocallista	Veneridae	4405	12.12	0.05	Low	deep infaunal	free living
Lucina	Lucinidae	2134	12.84	0.06	Moderate	deep infaunal	free living
Myrtea	Lucinidae	1243	28.16	0.01	Moderate	deep infaunal	free living
Tagelus	Solecurtidae	1240	2.26	0.02	Low	deep infaunal	free living
Angulus	Tellinidae	853	6.57	0.01	Low	deep infaunal	free living
Merisca	Tellinidae	563	2.13	0.01	Moderate	deep infaunal	free living
Eurytellina	Tellinidae	536	8.21	0.07	Moderate	deep infaunal	free living
Tellina	Tellinidae	332	7.23	0.01	Low	deep infaunal	free living
Phacoides	Lucinidae	208	22.12	0.04	Moderate	deep infaunal	free living

Genus	Family	# of Valves	Drilling Intensity	Average Shell Weight	Ornament	Depth	Mobility
Felaniella	Ungulinidae	100	18.00	0.03	Low	deep infaunal	free living
Elpidollina	Tellinidae	88	11.36	0.02	Low	deep infaunal	free living
Strigilla	Tellinidae	85	7.06	0.01	Moderate	deep infaunal	free living
Donax	Donacidae	72	0.00	0.06	Low	deep infaunal	free living
Cumingia	Semelidae	61	13.11	0.01	Low	deep infaunal	free living
Anomalocardia	Veneridae	55	0.00	0.07	Moderate	deep infaunal	free living
Semele	Semelidae	49	0.00	0.04	Low	deep infaunal	free living
Codakia	Lucinidae	45	26.67	0.13	Moderate	deep infaunal	free living
Cavilinga	Lucinidae	39	46.15	0.00	Moderate	deep infaunal	free living
Mulinia	Mactridae	26	7.69	0.02	Low	deep infaunal	free living

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CHAPTER 5 – CONCLUSIONS

The persistent theme throughout my dissertation research is the importance of environmental change in driving evolution. For this, the distinction between proximate and ultimate factors is fundamental to analyzing why change occurs. Biological systems are inherently complex, and cause and effect are ensnarled in a web of evolution, environment, physiology, and ecology (Mayr 1961). Understanding of both proximate and ultimate drivers of change informs us about the processes that were important in shaping earth's biosphere, and provides essential evolutionary context to study current ecosystem change.

The ultimate driver of Caribbean ecosystem change was the sharp decrease in planktonic productivity concurrent with the closure of the Central American Seaway (CAS). This regional oceanographic change allowed for the propogation of new, biogenic coral reef and seagrass meadow habitats (Johnson et al 2007; O'Dea et al 2007) that in turn drove changes in nearshore molluscan benthic assemblages. Dramatic shifts occurred in the relative abundance of bivalve functional groups with regard to both life habit and diet (Figures 2.3 and 2.5). Gastropod assemblages also changed as illustrated by the shift in the dominant drilling predator from Naticidae in the older gastropod assemblages to Muricidae in younger assemblages (Figure 3.1C).

Biological interactions echoed the cascading changes in environments and faunual assemblages. Bivalves living in biogenic habitats experienced much higher predation intensity than bivalves in soft sediments, leading to higher overall predation intensities in molluscan communities as these habitats propogated. In addition, a strong shift in the preponderance of different bivalve life habitats resulted in more potential prey being available to epifaunal drilling predators. Together, these differences resulted in significantly higher predation after the closure of the CAS. However, these changes did not appear to affect macroevolutionary patterns, as drilling intensities within families did not significantly change through time.

Previous work has shown spatial heterogenity of different environments after the closure of the CAS (O'Dea et al 2007). Results of my analyses reinforce this idea of environmental patchiness. Although trends in bivalve functional groups through time are significant, there is high variability among faunules of the same age, probably due to differences in environment and habitat (Figure 5.1). For example, some of the youngest faunules are functionally similar to much older faunules observed prior to closure of the CAS (Figure 2.3). Ratios of the two major groups of drilling gastropod predators are also highly variable. Assemblages dominated by naticid gastropods are characteristic of pre-closure molluscan communities, while younger assembalges have higher abundance of muricid gastropods. Nevertheless, naticid gastropods still dominated some assemblages as young as 2.05 Ma (Figure 3.1 C).

These results support previous findings that relict taxa (i.e. geographic heterochorony sensu Petuch 1982) persisted in the Caribbean for 2 Ma after closure of the isthmus (Smith and Jackson 2009). However, there is no evidence that these faunas were marginal, as Petuch (1982) hypothesized (Smith and Jackson 2009). Together with other work (Johnson et al 2007; Smith and Jackson 2009) my results suggest that instead of relicts persisting in marginal environments, geographical heterochrony is simply the result of a patchy environment. Patchiness appears to extend beyond the

Caribbean into the Western Atlantic. There are examples of temporal patchiness in the deep-sea foraminiferal record (Sexton and Norris 2008) and Pliocene molluscan communities from the Western Atlantic exhibit patchy distributions on a local scale (Allmon 1993).

All of these factors combined help to explain the taxonomic turnover in benthic groups as well as the time lag between documented environmental changes and turnover (Johnson et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009). The rise of Caribbean coral reefs was drawn out over two million years (Johnson et al. 2008), whereas the collapse in planktonic productivity ultimately responsible for increased reef development occurred much more rapidly (O'Dea et al. 2007). The changes in the relative abundance of bivalve functional groups I have documented , as well as changes in the intensity of biologic interactions, were important components of molluscan taxonomic turnover, especially in cases where turnover has an a clear ecological signature (Todd et al 2002; Smith and Jackson 2009). Changes in ecology and environment also played a major role in turnover in of corals and bryozoans (Johnson et al. 1995; Budd and Johnson 1999; O'Dea and Jackson 2009).

Finally, my research illustrates the strong non-linearity of the macroevolutionary response to environmental perturbations analagous to the trophic cascades, threshold effects, and alternate stable states demonstrated in studies of anthropogenic environmental degradation (Scheffer et al. 1993; Terborgh et al 2001; Scheffer 2009; Terborgh and Feeley 2010). A key to making useful predictions is in understanding the influence of both proximate and ultimate causes in a system, and rigorously analyzing the many potential pathways to change.

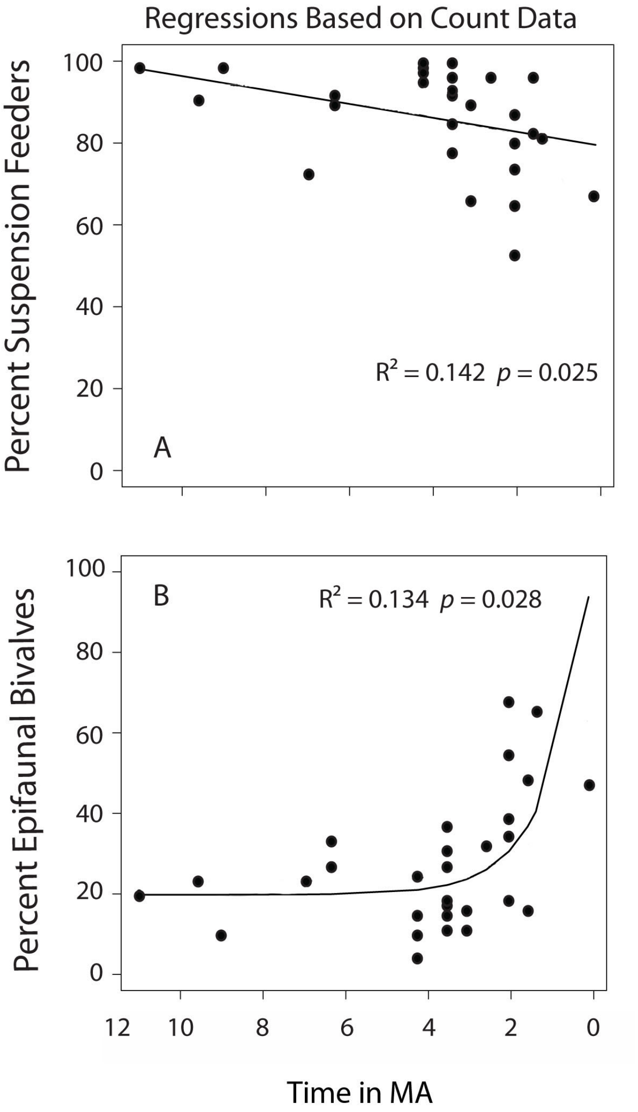

Figure 5.1: Relative abundance of major bivalve ecologies through time. A, A weighted least squares regression of the percentage of suspension feeding bivalves through time. B, A weighted least squares regression of the percentage of epifaunal bivalves through time.

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Appendix

Faunule	***Abra*** Infaunal Deposit Feeder	***Acar*** Epifaunal Attached Suspension Feeder	***Acesta*** Epifaunal Attached Suspension Feeder	***Acila*** Infaunal Deposit Feeder	***Adrana*** Infaunal Deposit Feeder
Sand Dollar Hill	0	0	0	0	2
Isla Payardi	0	0	0	0	4
Mattress Factory	0	0	0	0	0
Rio Indio	0	0	0	166	0
Rio Tupisa	0	0	0	0	1
Rio Chico N17	0	0	0	0	2
Cayo Agua: Pt. Norte E	0	0	0	0	0
Cayo Agua: Pt. Piedra Roja W	3	0	0	0	0
Cayo Agua: Pt. Norte W	6	0	0	0	0
Isla Popa	0	0	0	0	0
Cayo Agua: Pt. Nispero S	0	0	0	0	0
Isla Solarte	12	15	0	0	0
Santa Rita	2	11	0	0	0
Rio Vizcaya	0	0	0	0	1
Cayo Agua: Pt Tiburon - Pt. Piedra	0	0	0	0	0
Cayo Agua: Pt. Nispero W	0	0	0	0	0
Quiteria	0	0	0	0	4
Quebrada Chocolate	0	0	0	0	0
Bomba	0	0	0	0	6
Fish Hole	0	11	0	0	0
Ground Creek Mud	0	3	0	0	9
Ground Creek Mangrove	0	3	0	0	3
Ground Creek Porites	0	30	0	0	28
Wild Cane Key	0	12	0	0	0
Wild Cane Reef	0	11	7	0	0
Upper Lomas	13	21	0	0	0
Empalme	0	20	0	0	0
Swan Cay	0	19	0	0	0
Lennond	0	10	13	0	0

Aequipecten	***Agripoma***	***Americardia***	***Amusium***	***Anadara***	***Angulus***	***Anodontia***
Epifaunal Attached Suspension Feeder	Infaunal Suspension Feeder	Infaunal Suspension Feeder	Epifaunal Free-living Suspension Feeder	Semi-Infaunal Suspension Feeder	Infaunal Deposit Feeder	Infaunal Chemosymbiotic Deposit Feeder
0	0	0	0	5	1	0
1	0	0	0	428	45	0
0	0	0	6	19	1	0
0	0	0	7	205	1	0
5	0	0	0	103	5	0
6	0	4	0	212	2	0
1	0	0	10	174	0	0
1	0	0	12	279	27	0
0	0	0	0	72	1	0
0	0	0	2	20	0	0
0	0	0	5	25	0	0
12	0	8	0	236	1	0
4	0	0	4	82	0	0
0	0	0	1	551	1	0
3	0	0	1	37	8	0
0	0	0	2	11	2	0
0	0	0	0	186	4	0
0	0	1	0	46	95	0
0	0	0	2	519	93	0
0	0	0	0	12	0	0
7	8	5	3	180	480	15
0	0	0	0	0	2	0
0	0	0	0	7	14	0
0	0	1	0	5	0	0
0	0	1	0	0	1	0
0	0	0	0	212	47	0
0	0	5	0	289	16	0
0	0	2	0	10	0	0
0	0	5	0	36	6	1

Anomalocardia Infaunal Suspension Feeder	***Anomia*** Epifaunal Attached Suspension Feeder	***Arca*** Epifaunal Attached Suspension Feeder	***Arcinella*** Epifaunal Attached Suspension Feeder	***Arcopsis*** Epifaunal Attached Suspension Feeder	***Argopecten*** Epifaunal Attached Suspension Feeder	***Axinactis*** Semi-Infaunal Suspension Feeder
0	1	0	2	0	115	0
0	2	0	0	0	57	0
0	7	0	8	0	54	0
0	0	0	6	0	7	0
0	1	0	1	8	12	0
0	17	2	1	1	192	1
0	4	2	0	0	77	0
0	1	7	145	0	405	5
0	2	2	1	0	405	1
0	214	0	23	0	40	24
0	0	7	2	0	105	3
0	2	6	3	14	530	0
0	20	8	0	10	37	16
0	0	0	0	0	0	0
0	0	5	0	0	150	4
0	0	0	4	0	9	9
0	4	0	0	0	0	0
15	0	2	1	6	16	0
0	4	0	36	0	6	2
0	0	1	3	6	11	0
18	3	40	0	205	1138	0
18	0	8	0	4	2	0
0	0	53	7	36	5	0
0	0	2	0	4	2	0
0	0	6	0	34	1	0
0	0	62	1	229	353	0
0	10	12	6	38	9	0
0	0	6	4	99	27	0
4	7	65	0	126	0	0

Barbatia	***Bractechlamys***	***Bothrocorbula***	***Cardiomya***	***Carditamera***	***Cardites***	***Caribachlamys***
Epifaunal Attached Suspension Feeder	Epifaunal Attached Suspension Feeder	Infaunal Suspension Feeder	Infaunal Predatory Carnivore	Infaunal Suspension Feeder	Infaunal Suspension Feeder	Epifaunal Attached Suspension Feeder
0	0	0	0	0	0	0
0	0	9	0	0	1	0
0	0	0	0	0	12	0
0	0	0	0	0	0	0
0	0	0	0	2	11	0
0	0	1	0	2	16	0
0	0	0	0	0	5	0
2	0	0	2	0	243	0
1	0	0	0	0	33	0
0	0	0	0	0	8	0
4	0	0	0	0	0	0
32	0	0	4	3	182	0
6	0	0	0	0	38	0
0	0	0	0	0	9	0
2	0	0	0	0	0	0
0	0	0	0	0	15	0
0	0	0	0	0	9	0
5	0	0	49	0	0	0
0	0	0	0	0	199	0
2	0	0	0	4	36	0
96	0	0	47	4	0	20
38	0	0	1	0	0	1
107	2	0	1	0	0	19
11	0	0	2	0	1	0
16	0	0	0	0	0	1
362	0	0	12	0	2	0
43	0	0	1	0	47	0
14	0	0	0	0	41	6
76	0	0	0	0	0	2

Caryocorbula Infaunal Suspension Feeder	***Cavilinga*** Infaunal Chemosymbiotic Deposit Feeder	***Chama*** Epifaunal Attached Suspesion Feeder	***Chione*** Semi-Infaunal Suspension Feeder	***Chionista*** Infaunal Suspension Feeder	***Chionopsis*** Infaunal Suspension Feeder	***Circumphalus*** Infaunal Suspension Feeder
83	0	0	134	0	0	0
744	0	0	86	0	1	0
402	0	21	0	0	0	0
104	0	0	0	0	0	0
413	1	0	7	0	0	0
944	0	2	18	36	0	0
103	5	33	0	0	0	0
2446	16	67	15	0	0	0
296	0	48	1	0	0	0
1564	0	1	0	0	1	0
147	0	91	0	0	0	0
191	0	160	0	0	0	1
90	2	8	7	0	0	0
139	0	1	243	0	0	0
237	0	34	0	0	0	2
130	0	3	0	0	15	0
16	1	0	37	0	0	0
27	0	0	2960	0	0	0
79	6	0	33	0	1	0
20	0	19	0	0	2	1
137	8	29	10719	0	0	0
25	0	9	2	0	0	0
56	0	31	2	0	0	0
1	0	2	0	0	0	0
21	0	22	0	0	0	0
7447	0	170	991	0	0	0
1235	0	131	13	0	1	0
37	0	110	0	0	0	0
18	0	93	49	0	0	0

Codakia Infaunal Chemosymbiotic Deposit Feeder	***Costelloleda*** Infaunal Deposit Feeder	***Crassinella*** Semi-Infaunal Suspension Feeder	***Crassostrea*** Epifaunal Attached Suspension Feeder	***Crenella*** Epifaunal Attached Suspension Feeder	***Cryptopecten*** Epifaunal Attached Suspension Feeder	***Ctena*** Infaunal Chemosymbiotic Deposit Feeder
0	0	0	0	0	0	0
0	0	5	0	0	0	1
0	0	34	0	0	0	0
0	2	0	0	0	0	0
0	0	1	0	5	0	0
0	2	8	0	91	0	0
0	0	5	0	1	0	0
0	1	202	0	0	0	0
0	0	20	0	0	0	0
0	3	8	0	0	0	0
0	0	26	0	0	0	0
0	1	29	0	0	0	0
0	0	111	0	0	0	0
0	11	5	0	0	0	0
0	0	2	0	0	0	1
0	0	16	0	0	0	0
0	0	23	0	0	0	0
0	0	0	0	0	0	0
0	21	163	0	0	0	0
0	0	2	0	0	0	1
0	1	20	0	20	0	2
0	3	0	0	0	0	0
0	0	5	0	0	0	5
2	12	3	0	0	0	1
0	0	1	0	0	0	0
0	44	50	0	1	0	1
0	1	102	172	1	0	2
0	0	0	0	0	1	0
43	0	37	0	0	0	0

Ctenoides Epifaunal Attached Suspension Feeder	***Cumingia*** Infaunal Deposit Feeder	***Cyathodonta*** Infaunal Suspension Feeder	***Cyclinella*** Infaunal Suspension Feeder	***Cyclocardia*** Semi-Infaunal Suspension Feeder	***Cyclopecten*** Epifaunal Predatory Carnivore	***Cymatoica*** Infaunal Deposit Feeder
0	0	0	0	0	0	0
0	0	0	0	0	0	0
1	0	0	1	0	3	0
0	0	0	0	0	0	0
0	3	0	7	0	0	0
0	3	0	3	0	1	0
0	0	0	0	0	4	0
0	0	1	0	0	94	0
0	0	0	0	2	59	0
0	0	0	0	6	1	0
0	0	0	0	0	1	0
0	0	0	0	0	0	0
0	0	1	0	0	168	0
0	0	0	0	0	67	0
0	0	0	0	0	20	0
0	0	0	0	1	29	0
0	0	0	0	0	5	0
0	0	0	80	0	0	4
0	0	0	0	0	57	0
2	0	0	0	0	0	0
5	24	0	0	0	3	0
1	0	0	0	0	0	0
3	6	0	0	0	0	0
1	0	0	0	0	23	0
0	0	0	0	0	10	0
17	0	0	0	0	58	0
1	0	0	1	0	9	0
12	0	0	0	0	0	0
9	25	0	0	0	0	0

Dendostrea Epifaunal Attached Suspension Feeder	***Dimya*** Epifaunal Attached Suspension Feeder	***Diplodonta*** Infaunal Suspension Feeder	***Divilinga*** Infaunal Chemosymbiotic Deposit Feeder	***Donax*** Infaunal Suspension Feeder	***Dosinia*** Infaunal Suspension Feeder	***Elpidollina*** Infaunal Deposit Feeder
3	0	0	0	0	0	0
4	0	0	0	0	0	0
0	0	0	0	0	0	0
23	0	0	0	0	0	0
185	0	0	1	0	0	0
1032	0	0	0	0	13	0
30	0	0	0	0	1	0
14	0	2	8	0	0	0
5	0	0	0	0	0	0
73	0	0	0	0	0	0
1	0	0	0	0	0	0
6	1	0	0	0	0	0
19	7	0	0	0	0	0
13	0	0	1	0	4	0
1	1	0	1	0	0	0
18	0	0	1	0	0	0
0	0	0	0	0	1	0
233	0	0	0	0	48	34
3	0	0	0	0	8	0
5	2	0	0	0	0	0
2610	0	1	0	72	36	45
32	0	0	0	0	0	7
807	0	0	0	0	0	0
5	38	0	0	0	0	0
5	26	0	0	0	0	0
9	233	0	0	0	2	0
8	5	0	0	0	4	2
13	46	0	0	0	0	0
77	0	0	0	0	0	0

Eontia Semi-Infaunal Suspension Feeder	***Ervilia*** Infaunal Suspension Feeder	***Erycina*** Infaunal Suspension Feeder	***Eucrassatella*** Semi-Infaunal Suspension Feeder	***Eurytellina*** Infaunal Deposit Feeder	***Felaniella*** Infaunal Suspension Feeder	***Flabellipecten*** Epifaunal Free-living Suspension Feeder
0	26	0	0	0	0	0
0	123	0	26	31	1	0
0	1	0	0	0	0	0
0	0	0	0	0	0	0
0	3	0	0	1	0	0
0	209	0	11	6	3	0
0	0	0	3	0	0	0
0	230	0	1	0	0	0
0	0	0	0	0	0	0
0	0	0	1	0	0	0
0	0	0	0	0	0	0
0	0	0	18	7	0	5
3	0	0	5	0	0	0
0	0	0	0	75	1	0
0	0	0	2	0	0	0
0	1	0	2	0	0	0
0	0	0	0	11	0	0
0	0	0	0	7	21	0
0	0	0	3	0	0	0
0	0	0	0	1	0	0
0	4	0	0	358	65	0
0	0	0	0	0	0	0
0	0	0	0	0	3	0
0	0	0	0	21	0	0
0	0	0	0	1	0	0
2	0	1	0	15	0	0
0	0	0	0	1	4	28
0	0	0	0	1	0	0
0	1	0	0	0	2	3

Fragum Infaunal Suspension Feeder	***Gastrochaena*** Epifaunal Free-living Suspension Feeder	***Glyptoactis*** Infaunal Suspension Feeder	***Gouldia*** Infaunal Suspension Feeder	***Haliris*** Infaunal Predatory Carnivore	***Hiatella*** Infaunal Suspension Feeder	***Hyotissa*** Epifaunal Attached Suspension Feeder
0	0	0	0	0	0	1
0	0	0	4	0	0	1
0	0	0	43	0	0	1
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	7	49	0	0	1
0	0	0	22	0	0	3
0	0	0	293	0	0	23
0	0	0	22	0	0	0
0	0	0	307	0	0	0
0	0	0	26	0	0	8
0	0	4	130	0	0	20
0	0	7	16	0	0	2
0	0	0	29	0	0	0
0	0	0	80	0	0	20
0	0	0	26	0	0	0
0	0	0	1	0	0	0
0	0	0	8	0	0	0
0	0	0	14	0	0	0
0	0	0	11	0	0	2
0	0	0	135	0	1	0
0	0	0	4	0	0	0
0	0	0	7	0	0	0
0	0	0	35	0	0	3
0	0	0	29	1	0	0
0	0	0	433	0	0	80
0	0	0	187	0	0	7
0	0	0	3	0	0	81
1	6	0	68	0	0	0

Hysteroconcha	***Isognommon***	***Juliacorbula***	***Jupiteria***	***Laevicardium***	***Laevichlamys***	***Lamelliconcha***
Infaunal Suspension Feeder	Epifaunal Attached Suspension Feeder	Infaunal Suspension Feeder	Infaunal Deposit Feeder	Infaunal Suspension Feeder	Epifaunal Attached Suspension Feeder	Infaunal Suspension Feeder
0	0	0	0	56	0	8
0	0	0	0	0	0	18
0	0	0	0	3	0	2
0	0	0	0	0	0	0
0	0	1	0	0	0	7
0	0	0	0	2	0	3
0	0	0	0	0	0	0
0	1	0	0	12	0	5
0	0	0	0	1	0	11
0	0	0	0	2	0	0
0	0	0	0	2	0	0
0	2	0	0	2	0	0
0	0	0	0	0	0	3
0	0	0	0	10	0	15
0	3	0	0	3	0	0
0	0	0	0	1	0	0
0	0	0	0	0	0	5
0	0	0	0	33	0	0
0	0	0	0	1	0	28
0	0	0	0	0	0	0
0	51	0	0	70	0	188
0	0	0	0	0	0	0
0	1	0	0	8	0	0
0	0	0	1	3	1	0
0	0	0	0	1	0	0
0	0	0	20	0	0	7
1	1	0	1	0	0	1
0	4	0	1	0	0	0
0	14	0	0	0	0	1

Leopecten Epifaunal Free-living Suspension Feeder	***Leptopecten*** Epifaunal Attached Suspension Feeder	***Lima*** Epifaunal Attached Suspension Feeder	***Limea*** Epifaunal Free-living Suspension Feeder	***Limopsis*** Epifaunal Attached Suspension Feeder	***Lindapecten*** Epifaunal Attached Suspension Feeder	***Lirophora*** Infaunal Suspension Feeder
0	0	0	0	0	0	0
3	346	0	0	0	0	23
4	0	0	0	0	0	0
1	0	0	0	0	0	6
0	0	0	0	0	0	20
9	28	0	0	0	0	541
7	0	0	0	0	0	6
31	19	0	0	0	0	1
4	1	0	0	0	0	2
3	4	0	0	0	0	147
6	1	0	0	0	0	0
114	0	1	1	10	0	7
18	1	0	17	0	0	22
0	0	0	0	0	0	0
12	11	0	0	0	0	3
1	1	0	0	0	0	20
1	0	0	0	0	0	0
0	0	0	0	0	0	4
2	29	0	3	0	0	6
4	0	5	0	1	3	0
0	0	3	0	0	0	0
0	0	0	0	0	0	1
0	0	0	0	0	0	1
9	0	0	0	1	0	1
8	0	1	0	6	0	0
175	0	0	0	188	0	7
12	96	0	0	21	0	21
51	1	1	8	258	0	0
6	0	1	0	1	0	0

Lucina Infaunal Chemosymbiotic Deposit Feeder	***Lucinoma*** Infaunal Chemosymbiotic Deposit Feeder	***Lunarca*** Semi-Infaunal Suspension Feeder	***Lyratellina*** Infaunal Deposit Feeder	***Macoma*** Infaunal Deposit Feeder	***Macrocallista*** Infaunal Suspension Feeder	***Mactrellona*** Infaunal Suspension Feeder
2	0	0	0	4	804	0
25	0	0	0	0	391	4
0	0	0	0	0	4	0
0	0	0	0	0	6	0
0	0	0	0	0	7	0
0	0	7	0	0	54	6
0	0	0	0	0	6	0
5	0	4	0	0	825	0
0	0	1	0	0	61	0
0	0	1	0	0	46	0
0	0	0	0	0	50	0
0	0	1	0	0	0	0
0	0	1	0	0	1	0
21	0	1	0	0	8	0
0	0	1	0	0	2	0
0	0	8	0	0	17	0
5	0	0	0	0	84	0
7	0	0	0	0	402	0
9	0	3	0	0	519	0
0	0	0	0	0	0	0
1900	0	1	0	0	968	11
10	0	0	0	0	6	0
10	0	0	0	0	5	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
129	0	3	0	0	85	0
8	0	4	0	0	54	0
0	0	0	0	0	0	0
3	3	0	1	0	0	0

Martesia Epifaunal Free-living Suspension Feeder	***Merisca*** Infaunal Deposit Feeder	***Microcardium*** Infaunal Suspension Feeder	***Moerella*** Infaunal Deposit Feeder	***Mulinia*** Infaunal Suspension Feeder	***Musculus*** Epifaunal Free-living Suspension Feeder	***Myrtea*** Infaunal Chemosymbiotic Deposit Feeder
0	0	0	0	0	0	0
0	2	0	0	8	0	0
0	1	0	3	0	0	0
0	0	0	0	0	0	2
1	1	0	0	18	0	0
0	4	0	0	0	0	1
0	0	0	0	0	0	1
0	0	1	276	0	0	1
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	7	0	0	0	0	172
0	0	4	0	0	0	25
0	0	0	0	0	0	0
0	0	0	6	0	0	1
0	0	0	0	0	0	1
0	0	0	0	0	0	0
0	436	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	1
0	32	0	0	0	0	0
0	0	0	0	0	0	0
0	75	0	0	0	0	0
0	0	0	0	0	0	14
0	0	0	0	0	0	19
0	0	0	0	0	0	964
0	2	2	0	0	3	0
0	0	0	0	0	0	41
0	3	0	0	0	0	0

Nodipecten Epifaunal Attached Suspension Feeder	***Noetia*** Semi-Infaunal Suspension Feeder	***Nucula*** Infaunal Deposit Feeder	***Nuculana*** Infaunal Deposit Feeder	***Ostreola*** Epifaunal Attached Suspension Feeder	***Pacipecten*** Epifaunal Attached Suspension Feeder	***Panchione*** Infaunal Suspension Feeder
0	10	0	0	0	31	0
0	2	5	0	0	0	13
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	20	0	0	8	0
0	10	1	0	0	15	0
0	0	0	0	0	0	7
0	0	5	0	1	0	10
0	0	0	0	0	0	6
0	0	1	0	12	0	4
0	0	0	0	0	0	1
0	0	4	0	1	0	0
0	0	19	0	0	0	0
0	45	0	0	3	9	80
0	0	0	0	0	0	0
0	0	6	0	0	1	17
0	1	0	0	0	6	0
0	0	1655	0	458	0	0
0	25	2	0	0	0	12
1	0	0	0	0	0	0
0	131	674	18	0	0	0
0	0	0	6	58	0	0
0	0	3	0	16	0	0
0	0	21	0	0	0	0
0	0	3	0	0	0	0
1	1	253	0	0	0	0
0	0	5	0	0	0	0
0	0	11	0	0	0	0
15	0	0	0	0	0	0

Pandora Infaunal Suspension Feeder	***Papyridae*** Infaunal Suspension Feeder	***Parvilucina*** Infaunal Chemosymbiotic Deposit Feeder	***Pectinid_A*** Epifaunal Free-living Suspension Feeder	***Periglypta*** Infaunal Suspension Feeder	***Petricola*** Epifaunal Free-living Suspension Feeder	***Phacoides*** Infaunal Chemosymbiotic Deposit Feeder
0	0	0	0	0	0	0
0	0	14	0	0	0	0
0	0	0	0	0	0	0
0	0	1	0	0	0	0
1	1	0	0	0	0	0
1	0	0	0	0	1	0
0	0	0	11	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	2	0	0	0	1	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	1	0	0	0	0	0
0	0	0	0	0	0	0
0	0	3	0	5	0	0
0	0	636	0	0	0	0
0	0	1	0	0	0	0
2	0	10	0	0	0	0
0	0	3	0	0	0	0
0	1	0	0	0	0	0
0	0	78	0	1	0	0
0	4	0	0	0	0	0
0	0	1	0	0	0	0
0	0	40	0	0	1	208

Pinctada Epifaunal Attached Suspension Feeder	***Pitar*** Infaunal Suspension Feeder	***Pleurolucina*** Infaunal Chemosymbiotic Deposit Feeder	***Plicatula*** Epifaunal Attached Suspension Feeder	***Propoleda*** Infaunal Deposit Feeder	***Pseudochama*** Epifaunal Attached Suspension Feeder	***Pteria*** Epifaunal Attached Suspension Feeder
0	0	0	0	0	0	0
0	10	0	0	0	0	5
0	0	0	11	0	0	1
0	3	0	0	0	0	0
0	46	0	0	0	0	1
0	19	0	2	0	0	13
0	10	0	11	1	0	0
0	24	0	26	0	0	16
0	8	0	150	0	0	1
0	0	2	9	0	0	1
0	0	0	81	0	0	0
0	45	0	53	0	0	5
0	2	0	12	0	0	2
0	4	1	0	0	0	0
0	15	0	6	0	1	3
0	1	0	99	0	0	0
0	1	0	0	0	0	0
0	230	0	0	0	3	22
0	4	0	7	0	0	5
0	2	0	9	3	2	0
0	310	0	0	0	1	1
0	8	0	0	0	0	0
2	40	0	1	0	0	1
0	4	0	1	23	0	0
0	1	0	0	0	0	1
0	70	0	19	0	0	3
0	111	0	209	0	6	78
0	5	0	5	0	1	0
6	17	0	42	0	3	10

Radiolucina Infaunal Chemosymbiotic Deposit Feeder	***Saccella*** Infaunal Deposit Feeder	***Scissula*** Infaunal Deposit Feeder	***Semele*** Infaunal Deposit Feeder	***Semelina*** Infaunal Deposit Feeder	***Sheldonella*** Infaunal Suspension Feeder	***Solecurtus*** Infaunal Suspension Feeder
1	10	0	0	0	0	0
0	96	0	3	2	0	0
0	1	0	1	0	0	1
0	26	0	0	0	0	0
0	17	0	16	3	0	0
2	357	0	20	2	0	0
1	25	0	0	0	1	1
4	21	0	0	0	8	0
0	42	0	0	0	1	0
13	126	0	0	0	2	0
0	10	0	0	0	0	0
0	9	0	0	0	0	1
18	22	0	7	0	0	0
0	50	0	0	0	0	0
0	3	0	0	0	2	0
5	24	0	1	0	2	0
0	5	0	0	0	10	0
0	59	0	0	0	0	1
6	24	0	0	0	0	0
0	3	0	0	0	0	0
30	591	0	0	0	0	0
0	120	0	0	0	0	0
8	387	0	0	0	0	0
0	26	0	0	0	0	0
0	0	0	0	0	0	0
3	898	0	0	0	0	0
2	28	0	0	0	35	1
0	63	0	0	0	0	0
13	21	2	1	0	0	0

Spathochlamys	***Spengleria***	***Sphenia***	***Spondylus***	***Strigilla***	***Tagelus***	***Tellidora***
Epifaunal Attached Suspension Feeder	Epifaunal Free-living Suspension Feeder	Infaunal Suspension Feeder	Epifaunal Attached Suspension Feeder	Infaunal Deposit Feeder	Infaunal Suspension Feeder	Infaunal Deposit Feeder
0	0	0	0	0	0	5
3	0	0	0	0	1	2
1	0	0	2	0	0	0
0	0	0	0	0	0	0
0	0	0	0	10	6	0
0	0	0	0	21	35	5
1	0	0	0	0	0	0
1	0	0	0	20	0	0
0	0	0	1	0	0	0
5	0	0	1	0	0	0
0	0	0	0	0	0	0
115	0	0	2	0	0	0
4	0	0	1	0	0	0
0	0	0	0	20	3	2
3	0	0	2	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	7	0
1	0	0	0	0	15	0
2	0	0	0	14	1	0
9	0	0	3	0	0	0
0	0	6	0	0	1145	8
0	0	0	0	0	0	0
2	2	0	0	0	4	0
6	0	0	1	0	0	0
28	0	0	1	0	0	0
286	0	0	23	0	22	0
38	0	0	8	0	0	0
72	0	0	15	0	0	0
4	0	0	0	0	1	0

Tellidorella	***Tellina***	***Tellinella***	***Temblornia***	***Tivela***	***Trachycardium***	***Transennella***
Semi-Infaunal Suspension Feeder	Infaunal Deposit Feeder	Infaunal Deposit Feeder	Infaunal Suspension Feeder	Infaunal Suspension Feeder	Infaunal Suspension Feeder	Infaunal Suspension Feeder
0	0	0	4	0	48	0
0	50	0	19	0	69	0
0	4	0	0	0	2	0
0	0	0	0	0	3	0
0	12	0	0	0	16	0
0	58	0	5	3	19	1
0	1	0	0	0	10	0
0	0	0	0	0	7	0
1	9	0	0	0	14	0
0	1	0	0	0	0	0
0	4	0	0	0	2	0
0	0	0	0	0	3	1
0	5	0	0	2	1	0
0	0	0	0	0	3	0
1	0	0	0	0	1	0
0	17	0	0	0	1	0
0	0	0	0	0	0	0
0	50	0	0	0	6	0
0	0	0	0	0	0	0
1	0	0	0	0	0	0
0	20	0	0	0	7	0
0	0	0	0	0	0	0
0	15	0	0	0	0	0
2	0	0	0	0	0	0
0	1	0	0	0	0	0
2	37	0	0	0	0	0
0	5	0	0	18	83	0
1	10	0	0	0	0	0
0	31	1	0	0	6	0

Trigoniocardia Epifaunal Free-living Suspension Feeder	***Trigonulina*** Infaunal Predatory Carnivore	***Tucetona*** Semi-Infaunal Suspension Feeder	***Varicorbula*** Infaunal Suspension Feeder	***Varinucula*** Infaunal Deposit Feeder	***Ventricolaria*** Infaunal Suspension Feeder	***Yoldia*** Infaunal Deposit Feeder
156	0	0	0	0	0	0
291	1	3	24	0	0	0
12	3	405	304	0	0	0
0	0	0	27	0	0	1
51	0	6	0	0	0	0
126	0	122	213	0	0	0
16	3	229	654	0	0	0
124	20	1094	3455	0	9	0
78	0	533	1222	0	8	0
108	0	209	8025	0	0	0
3	1	186	1097	0	9	0
1	3	697	100	0	15	0
5	2	261	43	0	1	0
155	1	40	16	0	0	0
8	1	330	14	0	7	0
10	0	105	350	0	1	0
33	0	6	10	0	0	0
0	0	0	0	0	0	0
205	3	50	95	0	0	0
3	0	88	14	0	7	0
96	0	0	497	0	0	0
8	0	1	43	0	0	0
14	0	2	262	0	0	0
0	3	7	25	0	0	17
1	0	4	3	0	0	0
5	29	8	256	4	10	90
59	0	28	214	0	3	0
0	0	57	35	124	3	0
0	0	0	0	0	0	0