Quantitative Studies of Late Neogene Coastal Environments Using Bivalve Subfossil and Fossil Assemblages

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Geosciences

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April 6th 2006, 2:00PM
Blacksburg, Virginia

Keywords: Actualistic Paleontology; Bivalvia; Taphonomy; Predation; Quantitative; Morphology

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ABSTRACT

Coastal environments are important in many ways: they provide food and energy for coastal communities, have a variety of unique biologic habitats, and influence global climate. These environments can change due to either anthropogenic or natural phenomena over a wide range of time scales. However, the often overlooked long-term (centennial to millennial) processes may be hidden behind short-term fluctuations observed today. The need for a reference baseline of coastal habitats provides a new opportunity for paleontology, which is ideally equipped to document the long-term trends and reconstruct historical and ancient environments and communities.

However due to taphonomic processes such as decay and diagenesis, there will always be some bias inherent to the fossil record. This bias has been often viewed as a negative aspect, undermining the utility of paleontological data for retrieving ecological and environmental records. Yet, fossils are still one of the best sources of direct data about the past faunas and their ecosystems. To overcome the biases introduced by the fossilization process, researchers have used observations and experiments in modern systems as models to compare fossil deposits, a method called actualistic paleontology. Over recent years, such actuopaleontological approaches have been used increasingly to exploit distinct signatures of fossil deposits in environmental reconstructions, quantify effects of anthropogenic processes on invertebrate faunas and regional ecosystems, and even augment archaeological studies

Three studied included in this dissertation exploit different aspects of paleontological techniques to study coastal systems, including both Recent and fossil settings. Two of the studies use modern environments to serve as models for investigating preservation potential and potential biases that affect subfossil and fossil assemblages forming in intertidal environments, from whether certain fauna will be preserved to the biases inherent in a shell deposit. The final study, conducted at a fine geologic resolution, focuses on the morphology of a fossil ancestor of an extant mactrid bivalve that is ecologically important in many present-day coastal habitats and well-studied by ecologists and malacologists. The study attempts to quantify morphological effects of environmental changes that occur over geological time scales.

Dedication

This work is dedicated to my parents, Dr. Richard and Suzanne Stempien; sister, Rebecca Stempien, esquire; and grandparents, Paul & Doris Mallon and Thomas & Anne Stempien. They may not have always understood what I was doing or why it eventually benefits them, but who stood by me anyway and proudly told anyone who listened that I am a geologist.

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ACKNOWLEDGMENTS

Completing a dissertation with three distinction projects instead of one large continuous project gave me the opportunity not only use a variety of techniques and approached to study different aspects of applied paleontology, but to also work with many talent people. Without the support, guidance and critiques of many people, these projects would not be able to be considered for publication.

Crab Preservation Potential - This study was initiated during the Summer 2002 Field Course in Marine Taphonomy taught by Dr. Michael LaBarbera (University of Chicago) and Dr. Michał Kowalewski (Virginia Tech) at Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington. I would like to thank Friday Harbor Laboratories for providing funding and facilities which allowed me to participate in the course and conduct this research. I am also grateful to: Dr. LaBarbera, Dr. Kowalewski, Thomas Rothfus, and Richard Krause Jr. for their invaluable input, assistance, discussions, comments, and criticism; Stephaney Puchalski for her field assistance and for being a continual source of encouragement; and Karla Parsons-Hubbard and Carrie Schweitzer for their constructive comments on the manuscript.

Effects of Avain Predation on Bivalve Subfossil Assemblages - I would like to thank in alphabetical order, John Huntley, Karen Koy, and Rich Krause for field and mental support. Thanks also to Lindsey Leighton and Mike Kowalewski for their valuable suggestions and meticulous reading that helped in the progression of this manuscript. The initial work for this project was supported by Friday Harbor Labs, University of Washington as part of the 2004 Predator-Prey Interaction field course and later analysis was supported by the Department of Geosciences, Virginia Tech and completed at the Center for Forensic Malacology, Appalachian Division, paper #2.

Effect of Temporal and Environmental Gradients on Bivalve Morphology - I would like to thank Susan Barbour-Wood, Rod Brame, Andy Bush, Gwen Daley, Alan Hoffmiester, John Huntley and Lauck Ward for provided valuable feedback and suggestions regarding this project. Data collection, research material and analysis were funded by the David R. Wones Fellowship, Virginia Museum of Natural History, and the Virginia Tech Graduate Student Assemble Dissertation Development Grant.

I would also like to thank the following funding agencies who provided various funds throughout my time at Virginia Tech that allowed me to complete research over the summer and to present my findings at various meetings: National Science Foundation, Petroleum Research Fund, Geological Society of America national and regional sections for travel grants, The Virginia Tech Graduate Student Assembly Travel Grants, Paleobiology Database, North American Paleontological Conference, and the Department of Geosciences at Virginia Tech.

Introduction

Coastal environments are important in many ways: they provide food and energy for coastal communities, have a variety of unique biologic habitats, and influence global climate. In the contiguous United States, 17% of the area is considered to be coastal however, over half of the population lives within a couple of hours' drive from the coast (USGS Coastal Program, 2004). The ecological importance of these highly productive habitats and the societal importance related to their extensive use by human society make for a unique interplay between natural and anthropogenic systems. The systems affect each other in diverse ways, including, for example, property damage from natural disasters or the destruction of ecosystems and water supplies due to pollution and overuse. Resulting changes can be economically important. For example, over the last three years, the Commonwealth of Virginia alone has spent $2 million on coastal habitat restoration of invertebrate fauna after habitat loss due to development and introduction of invasive species (Lergberg, 2005). To better understand causes and consequences of perturbations that affect coastal ecosystems, various processes that can change diverse aspects of coastal habitats need to be studied, both anthropogenic influences (e.g., pollution, overfishing, subsidence due to extensive aquifer pumping) and natural phenomena (e.g., sea-level change, sedimentation rates, shifts in natural populations, natural disasters). Coastal environments can change over a wide range of time scales, from within one season to years. However, the often overlooked long-term (centennial to millennial) processes may be hidden behind short-term fluctuations observed today. That is, a given change we observe today may spuriously correlate with recent anthropogenic or natural events that were not the only or even primary cause of that change. A baseline providing understanding of a long term dynamics of coastal environments, covering decades, centuries and millennia is thus critically needed. Only then will we be able to determine if the severity and "permanence" of changes observed today in the context of short-term perturbations are significantly exceeding the range of variation realized as a part of natural long-term cycles affecting coastal systems.

This need for a reference baseline provides a new opportunity for paleontology, which is ideally equipped to document the long-term trends and reconstruct historical and ancient environments and communities (Kowalewski, 2001; Olszewski, 2001). However due to taphonomic processes such as decay and diagenesis, there will always be some bias inherent to the fossil record. This bias, combined with the coarser temporal resolution of fossil deposits when compared to neontological studies (e.g., McKinney, 1991), has been often viewed as a negative aspect undermining the utility of paleontological data for retrieving ecological and environmental records. Even with the taphonomic bias, fossils are still one of the best sources of direct data about the past faunas and their ecosystems. The coarser resolution of the fossil record can be used to test differences in influence of temporal, geographical, and environmental factors while averaging the noise of yearly perturbation in factors such as nutrient supply that can result in a misinterpretation for the system as a whole.

To overcome the biases introduced by the fossilization process, researchers have used modern systems as models for ancient. This strategy, often termed “actuopalentology” or “actualistic paleontology”, relies on rigorous observations of, and experiments on, present day ecosystems, which aim to assess fossilization processes and resulting biases. The approach was first developed by the German school of ‘actuopaläontologie’ (Richter, 1929) and has recently become a cornerstone of taphonomic studies, and one of the most crucial research directions in paleontology (for review see Parsons and Brett, 1991; Flessa et al., 1993; Kidwell and Flessa, 1995). Over recent years, such taphonomic-actuopaleontological approaches have been used increasingly to exploit distinct signatures of fossil deposits in environmental reconstructions (e.g., Best and Kidwell, 2000; Zuschin and Stanton,2001; Zuschin et al., 2003), quantify effects of anthropogenic processes on invertebrate faunas and regional ecosystems (Kowalewski et al., 2000; Cintra-Buenrostro et al., 2005), and even to augment archaeological studies (e.g., McNiven, 1992)

The three papers included in this dissertation each exploit different aspects of paleontological techniques to study coastal systems, including both Recent and fossil settings. Two of the studies use modern environments to serve as models for investigating preservation potential and potential biases that affect subfossil and fossil assemblages forming in intertidal environments. The final study, conducted at a fine geologic resolution, focuses on the morphology of *Mulinia congesta*, a fossil ancestor of an extant mactrid bivalve that is ecologically important in many present-day coastal habitats and well-studied by ecologists and malacologists. The study attempts to quantify morphological effects of environmental changes that occur over geological time scales.

Preservation potential between different fauna: bivalves vs. brachyurans

The differences of preservational potential of different groups of marine invertebrate fauna may severely bias their relative representation in the fossil record (e.g., Behrensmeyer et al., 2005). Numerous studies have already addressed the probability of preservation for many types of fauna either by observational studies comparing live faunas to their subfossil assemblages (e.g., Kidwell and Bosence, 1991; Kidwell, 2001) or by deploying materials in decay experiments (e.g., Kidwell and Baumiller, 1990; Briggs et al., 1998). Most of these studies have focused on one type of fauna and rate and severity of its decay to determine the probability of its fossilization. The study, "Brachyuran Taphonomy in a Modern Tidal Flat Environment: Preservation Potential and Anatomical Bias" (Stempien, 2005), focused on relative abundances and taphonomic characteristics of non-crab and crab material observed at and directly below the sediment-water interface in a modern intertidal environment. Comparison of relative abundances and taphonomic characteristics between crab and non-crab material should provide relative estimates of the preservation potential of crabs compared to a taphonomic reference standard offered by co-occurring molluscan remains. It addition to comparing the preservation potential of crabs to a well-studied fauna, the degree to which brachyuran anatomical parts have different preservational potentials, (an anatomical taphonomic filter) is also quantified.

How can the bias in fossil record be used to study species interaction? Avian influence on bivalve middens.

There have been numerous studies and initiatives aimed at determining how shell deposits change in composition and relative abundances when passing through various taphonomic filters and how to correct for resulting biases when studying fossil shell-rich deposits. Depending on the factors of interest, these filters can possibly change the fossil deposits significantly, and the resulting biases can be perceived in either a positive or negative way when studying fossil deposits (McKinney, 1991; Kowalewski, 2001). For example, the alteration of shell material due to predation can be considered as “negative taphonomy” (i.e., undesirable bias induced by predatory activity) or “positive taphonomy” (i.e., changes in the deposits that can be used as an indirect record of species interaction). The latter approach has already become a dynamic part of paleontological and evolutionary research (for review see Vermeij, 1987; Kelley et al., 2003). Most of the predation studies using fossil remains have focused on intra-invertebrate predation, as these types of interaction can be relatively easily identified (chipped marks, repair scars, drill holes, etc.). The study, “Detecting Avian Predation on Bivalve Assemblages Using Indirect Methods” (Stempien, submitted 2006), combines paleontological approaches used in fossil predation studies with those applied to delineate taphofacies to determine if bird predation can be detected using shell deposits. If bird predation can be detected through indirect and non-invasive means, especially in intertidal habitats, it would be then possible to determine from fossil assemblages if avian predation affected ancient ecosystems. As important, such non-invasive approach could supplement, augment or even replace more invasive methods used in modern ecological surveys.

What can you do with the material that is there? Morphological variation in fossil bivalves

One of the critiques of applying actualistic studies to past ecosystems is that, for most of earth’s history, few fossil genera and species have direct representation in modern ecosystems for comparison. However, molluscan faunas from geologically young Pliocene-Pleistocene deposits are still very well represented in present day ecosystems. For example, 77% of living mollusk species from the Pacific coast of United States have fossil representation in the Pleistocene of California (Valentine, 1989). Comparing fossil samples of Plio-Pleistocene bivalve species to modern populations of the same or closely-related extant species can help to address causative mechanisms for morphological changes (or stasis) often observed in the fossil record but difficult to interpret. Modern *Mulinia* has been well-studied in terms of genotype, phenotype and reproductive history in the context of various environmental factors such as algal tide events, temperature, substrate, and so on. By quantifying the rate and degree of morphological change that can be observed in high resolution paleontological studies and comparing the results to known ecophenotypic effects of environmental influences known for the living species of *Mulinia,* a better understanding of evolutionary vs. environmental factors in controlling morphological trends observed in the fossil record can be achieved. Assessing morphological change/stasis at a temporal time range of less than a million years may also shed new light on a discrepancy between notable morphological responses displayed by present-day bivalves, such as observed in many neontological studies, and remarkably persistent intervals of long-term morphological stasis observed in many bivalve lineages in the fossil record.

Chapter 1: Brachyuran Taphonomy in a Modern Tidal Flat Environment: Preservation Potential and Anatomical Bias [1]

Abstract

The scarcity of fossil crab material compared to heavier calcified taxa implies either: (1) crab material is rarely preserved (taphonomic hypothesis); (2) crab remains are frequently overlooked/misidentified (taxonomic hypothesis); or (3) crabs were less abundant in ancient ecosystems (ecological hypothesis). To evaluate the taphonomic hypothesis, the preservational potential of the yellow shore crab, *Hemigrapsus oregonensis*, was evaluated in a modern tidal pool of False Bay, San Juan Islands, Washington, USA. Crab remains were compared to molluscan taxa which served as a taphonomic reference standard. The surface crab material (4.2 parts per m^2) displayed an anatomical bias: carapace and cheliped remains were more numerous than predicted while leg remains were underrepresented. Crab remains were often disarticulated, but other alterations (bioerosion, dissolution, or encrustation) were virtually absent. This contrasts with non-crab material (bivalves, gastropods, and barnacles), which was abundant in the tidal pool (41 parts per m^2), and dominated (94.7%) by highly taphonomic altered remains, suggesting long exposure at, or near, the surface. Ratios of non-crab to crab remains increased from 10:1 at the surface to 154:1 in the subsurface. Low taphonomic alteration of crab remains, low density of crab surface material, an increase in non-crab to crab ratio in the subsurface, and a severe anatomical bias imply nearly complete loss of crab remains prior burial. This suggests a low probability of preservation, especially when compared to co-occurring mollusks, providing quantitative support for the taphonomic hypothesis.

Keywords: taphonomy, arthropods, tidal environments, San Juan Islands, Recent

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[1] This chapter was published in PALAIOS http://www.sepm.org. Citation is Stempien, J. 2005. *Brachyuran Taphonomy in a Modern Tidal Flat Environment: Preservation Potential and Anatomical Bias.* PALAIOS vol. 20 no. 4, pp 400-411.

Introduction

Decapods are abundant in many modern ecosystems, with approximately 1200 genera and 10,000 species (Bowman and Abele, 1982). Yet, the known decapod fossil record is described as sparse and heavily biased (Bishop, 1986; Plotnick, 1986; Plotnick et al., 1990). For brachyurans (crabs), approximately 20% of modern genera have a known fossil record (Plotnick, 1986) and fossil crab remains are notoriously rare in facies representing coastal and nearshore environments (Schweitzer et al., 2003). The lack of a fossil record for a fauna that is abundant today has three possible explanations: (1) crab remains are removed from the system prior to preservation (taphonomic hypothesis); (2) crab remains preserved in the fossil record have been misidentified or overlooked (taxonomic hypothesis); or (3) crabs were less abundant in past ecosystems than in modern (ecological hypothesis). The taphonomic hypothesis appears to be the most viable given previous studies (e.g., Allison, 1986; Plotnick, 1986; Plotnick et al., 1990). To gain better understanding of the preservation potential, a rigorous quantitative assessment of the fossilization potential of crabs relative to taxa commonly present in the fossil record (e.g., mollusks) is needed

Previous crab taphonomic studies have focused on interpretation of fossil remains (Bishop, 1981, 1986; Speyer and Brett, 1985) and the qualitative description of the physical breakdown of molts and carcasses (Schäfer, 1972). The lack of arthropod fossil material has been attributed to the rapid decay of the cuticle (Martin, 1999), as it is composed mainly (> 90%) of chitin and proteins with only light calcitic biomineralization (Plotnick, 1990). In living organisms, chitin is highly resistant to chemical and physical degradation. Yet after death, chitin rapidly hydrolyzes and is susceptible to decay by fungi or bacteria within 2 to 4 weeks, especially in subaqueous conditions (Allison, 1986; Plotnick, 1986; Poulicek et al., 1988; Miller et al., 1993). Even in anoxic conditions with little to no physical disturbance, lightly skeletized arthropods decay quickly and are virtually destroyed within 25 weeks (Allison, 1988).

Conversely, other experimental studies have suggested that arthropod cuticle is capable of remaining intact at the sediment water interface from a couple of months to over a year (Seastedt and Tate, 1981; Allison, 1986; Plotnick, 1986; Plotnick et al., 1988; Poulicek et al., 1988). Lightly mineralized specimens subjected to bacterial degradation and physical agitation in laboratory experiments disarticulated rapidly, but fragmentation of the individual parts was not observed until week six of the experiment (Allison, 1986). Field studies involving specimens buried 5 – 10 cm below the sediment surface in fine mesh were recovered somewhat complete and intact up to two weeks later (Plotnick, 1986; Plotnick et al., 1988). Even in terrestrial settings (e.g., Veldkamp, 1955; Okafor, 1966; Seastedt and Tate, 1981), 15 to 30% of arthropod material can be recovered up to a year after burial. These results suggest that lightly-mineralized organisms may resists taphonomic effects long enough to be buried under some conditions.

Unlike crabs, heavier calcified organisms (e.g. mollusks) are well-represented in the fossil record of coastal and nearshore settings and have been the subject of numerous studies of preservation potential, environmental conditions, and rates of degradation (e.g., Schopf, 1978; Cummins et al., 1986). Estimated survival times for bivalve shells near the sediment water interface range from 78 days (Cummins et al., 1986) to several hundred years or more (e.g., Flessa et al., 1993; Kowalewski et al., 1998). Longer residence times are advantageous in increasing the probability for preservation, for example all nineteen bivalve genera on San Juan Island have a fossil record (Schopf, 1978).

The study focused on relative abundances and taphonomic characteristics of non-crab and crab material observed at, and directly below, the sediment-water interface in a modern intertidal environment. Comparison of relative abundances and taphonomic characteristics between crab and non-crab material should provide relative estimates of the preservation potential of crab compared to a taphonomic reference standard offered by co-occurring molluscan remains.

Study Area

The study was conducted in False Bay, a shallow intertidal embayment less than one kilometer wide, located on southwestern San Juan Island, Washington State, USA (Fig. 1.1A-C). The intertidal zone is characterized by slow currents (<0.05 m/s; Worchester, 1995), experiences semidiurnal tides that have a maximum range of -0.8 m to +2.6 m (NOAA, 1983), and contains concentric sandbars made of fine sand produced by waves shoaled from the Strait of Juan de Fuca (Miller, 1985). Close to shore are a series of shoreline-parallel tidal pools which vary in depth from 5 to 10 cm (during low tide) and a temperature range from 30 ºC to 10 ºC (Woodin, 1972). Large areas of the pools are covered with *Ulva* mats and barnacle encrusted boulders

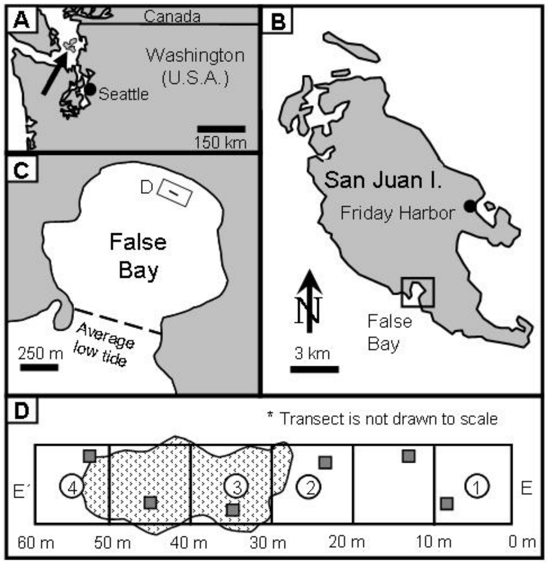

Figure 1.1: Schematic map of the study area. North direction applies to all insets. (A) Northwestern coast of Washington State, SJI stands for San Juan Island. (B) San Juan Island, Washington, USA. (C) False Bay, D indicates placement of the studied transect. (D) Diagram of the transect, not drawn to scale. Shaded boxes mark 1 m² grids where non-crab surface material was sampled for each 10 m section. Numbered circles indicate placement of 0-30 cm deep subsurface samples. Stippled area denotes seaweed coverage.

The dominant brachyuran species found within the tidal pools is *Hemigrapsus oregonensis* (Dana, 1851), commonly known as the Yellow Shore Crab (Family Grapsidae). The crab is identified by a square carapace with four anterior margin lobes, eyes on the front corners of the carapace, small size (a median width of 35.0 mm for males and 29.0 mm for females), and hair on the dull olive-yellow legs (Warner, 1977). This species is found in great abundance in high to low intertidal zones of bays and estuaries and is native to the west coast of North America, from Alaska to Baja California (Low, 1970). While *H. oregonensis* can be encountered in a variety of settings, it is found predominately beneath rocks, seaweed, or a very thin layer of sediment (Low, 1970). A similar species, *Hemigrapsus nudus* was observed frequently in the rocky periphery of the bay, though rarely observed within the interior. While these species sporadically cohabit, the two species are easily distinguished. *Hemigrapsus nudus* has a dark red coloring with spots on the carapace, whereas *H. oregonensis* has an olive-yellow coloring and fine hairs on the legs that can be observed on live and recently deceased specimens.

Methods

The sampling activities included two types of collecting efforts conducted during low tide in July and August of 2002: (1) surficial sampling along a 60-meter transect and (2) subsurface sampling within the transect. Placement of the transect was determined in a cursory survey by locating areas with abundant crab remains. Ten-meter intervals were marked using PVC pipes driven into the sediment to subdivide the sampling area into sections of equal area in order to quantify spatial patterns in the distribution of the skeletal material (Fig. 1.1D).

Surficial sampling

The first sampling occurred from July 30th to August 1st, 2002. All visible surface crab material located within a two-meter wide swath of the marked transect was collected and placed directly in bags of seawater. Carcasses and molts were identified from one another if the dorsal carapace could be easily lifted from the ventral section without tearing the specimen in two. For comparison, the more abundant non-crab material was sampled using a 1m^2 biological survey grid randomly within each ten meter section at 8, 12, 23, 36, 44, and 53 meters (Fig. 1.1D).

To scrutinize the possibility of an anatomical taphonomic filter, the crab remains collected at the surface were counted into their smallest possible units based on degree of calcification: leg, carapace, and claw (Table 1.4). Varying degrees of disarticulation, especially within the chelipeds, made finer divisions difficult to design. For remains that originated from the cheliped, each dactyl and propodus was counted separately. For example, an articulated chela or cheliped resulted in 2 claw parts (one dactyl and one propodus). The final tally of legs included individual legs found plus legs on articulated specimens. If no preservational bias due to surficial processes is present, the expected abundance would be similar to the proportions of one crab: one carapace (8%), four claw parts (30%), and eight legs (62%) (Fig.1.4A). These percent values were multiplied against the total amount of crab material collected in the analyzed section, and rounded to the nearest integer, to obtain expected counts for the sampled material (Table 1.4).

In order to estimate the rate new crab material is brought into the tidal pool, the transect was resampled on August 17, 2002. Using the same exhaustive sampling method as before, all crab material was collected from a part of the transect, from the 40 meter marker to the 60 meter marker due to time constraints. Since surficial mollusk material was not picked exhaustively during the first collecting effort, repeated sampling was not conducted for mollusks.

Subsurface sampling

Four subsurface samples were collected by use of a 5-gallon bucket with the bottom removed, marked internally at one cm intervals. The bucket was driven into the sediment and material was subdivided into two depth intervals, 0-15 cm and 15-30 cm. The material was wet-sieved back at Friday Harbor Labs using three sieve size fractions: 5 mm, 2.3 mm and 1 mm. All macroscopically visible biological material was separated into bivalve, gastropod, barnacle, and crab remains.

Both surficial and subsurface collections were counted and scored taphonomically for degree of surface alteration (e.g., dissolution, loss of color/sheen, etc.), bioerosion, and encrustation one the interior and exterior of the specimen. For all taphonomic variables, the following three-grade scale was used: (0) pristine; (1) less than 20% of the area affected; and (2) more than 20% of the area affected. In addition, information about the degree of disarticulation (e.g., loss of legs, claws) of the crab remains, articulation of bivalves, fragmentation, degree of edge modification, presence/absence of predation (e.g., drill holes), and/or repair scars was also recorded for taphonomic assessment.

Results

Surface collections

Abundance: A total of 504 crab remains were collected during the first sampling; 460 remains could be identified anatomically, the remaining 44 specimens (8.7%) were anatomically undeterminable. A total of 132 remains were collected during the resampling effort between the 40 and 60 meter marks (10.9%) were anatomically undeterminable. Specimens anatomically indeterminable were a result of an advanced state of decay. The average density of surficial crab material estimated from the first collection was 4.2 parts per m². Areas covered by seaweed, (30 to 60 meters), yielded the most abundant crab material with density ranging from 4.6 to 8.1 parts per m², (Fig. 1.2, Table 1.1). The average density of surficial crab material from the repeated sampling was 3.3 parts per m², (Table 1.1). The bulk of the surface non-crab specimens were the bivalves *Macoma, Clinocardium*, and *Protothaca*, along with one barnacle and two limpets. The average density of surface non-crab material was 41.3 parts per m², but ranged from 33 parts per m² in areas with little or no seaweed to 67 parts per m² in areas with seaweed (Fig. 1.2). Comparison of the average surface densities suggest a surface ratio of crab to non-crab remains of approximately 1:10.

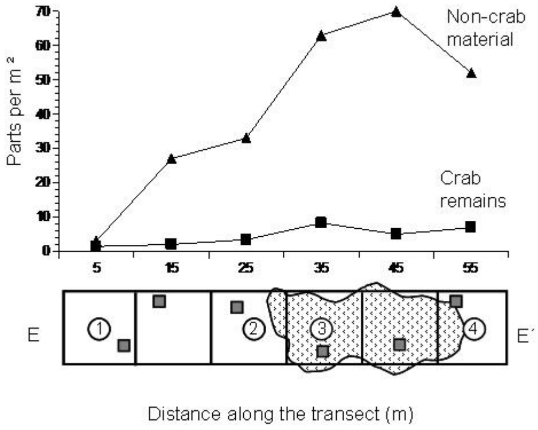

Figure 1.2: Density of surface material per m² for crab and non-crab material. Note the transect has been oriented so that 0 m mark is to the left. Stippled area indicates seaweed coverage.

Table 1.1 Raw abundance counts of surface crab material and calculated density per m².

	Partitions of the transect							Resampled intervals	
	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m	50-60 m	total	40-50m	50-60m
Entire body									
caracass	0	0	1	7	3	0	11	3	8
molt	1	2	6	12	8	9	38	5	7
Total	**1**	**2**	**7**	**19**	**11**	**9**	**49**	**8**	**15**
Carapace	**2**	**3**	**13**	**34**	**14**	**26**	**92**	**7**	**7**
Cheliped									
whole	2	3	6	18	18	14	61	10	12
chela	1	1	5	11	3	10	31	1	3
propodus	1	3	2	10	6	8	30	3	5
dactylus	0	3	1	7	5	4	20	5	3
Total	**4**	**10**	**14**	**46**	**32**	**36**	**142**	**19**	**23**
Legs	**8**	**12**	**21**	**53**	**29**	**54**	**177**	**18**	**22**
Indet. fragments	0	9	7	9	6	13	44	6	7
Total without indet. fragments	**15**	**27**	**55**	**152**	**86**	**125**	**460**	**52**	**67**
Total with indet. fragments	**15**	**36**	**62**	**161**	**92**	**138**	**504**	**58**	**74**
Material per m²	**0.8**	**1.8**	**3.1**	**8.1**	**4.6**	**6.9**	**4.2**	**2.9**	**3.7**

Appearance: Crab material collected at the surface exhibited little to no taphonomic alteration, with the exception of disarticulation and fragmentation (Table 1.2, Fig. 1.3). Complete crab carcasses/molts represented 10% of all remains. Of these, 3 carcasses and 5 molts were missing one or two legs, (16%) of the sample. Chipped edges occurred on all unidentified remains and frequently on individual carapace parts, (47 out of 92 specimens; 51%). Chelipeds showed varying degrees of articulation, from intact appendages (65%) to isolated prodopodi (21%) and dactyls (14%). The surface appearance of all crab remains appeared pristine with no signs of mechanical abrasion, dissolution, bioerosion, or encrustation (Table 1.2). Yet, carapace and leg material started to disintegrate in three to four days if left submerged in water, and fell apart when handled or agitated.

Surficial non-crab material displayed a high degree of taphonomic alteration and fragmentation (Table 1.3, Fig. 1.3). Less than 20% of the specimens were whole and 150 specimens had rounded edges (61.3%). This high rate of fragmentation and edge modification was observed regardless of placement and seaweed coverage. In addition, non-crab remains exhibited a high degree of surface alteration; 94.7% had some type of alteration and 85.7 % were chalky and eroded. High amounts of bioerosion, > 20% surface coverage, affected around half of the specimens: 50% of the interior and 58% of the exterior valves. Only 20% of specimens had no bioerosion present on either its interior or exterior surface. Unlike bioerosion, encrustation occurred on only 4 specimens distributed throughout and covered less than 20% of the total area on the specimen.

Table 1.2: Raw abundance counts and total percentage of taphonomic characteristics of surficial crab material.

	Placement of transect section							Percentage within characteristic
Taphonomic characteristics	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m	50-60 m	Total	
Articulation								
articulated	1	2	7	19	11	9	49	9.7%
disarticulated	14	34	55	142	81	129	455	90.3%
Fragmentation (individual pieces)								
whole	14	21	52	135	75	113	410	81.3%
fragments	1	15	10	26	17	25	94	18.7%
Edge Modification								
pristine	14	26	38	135	80	110	403	80.0%
chipped	1	10	24	26	12	28	101	20.0%
rounded	0	0	0	0	0	0	0	0.0%
Surface alteration								
none	15	36	62	161	92	138	504	100.0%
dull	0	0	0	0	0	0	0	0.0%
chalky & eroded	0	0	0	0	0	0	0	0.0%
Bioerosion								
none	15	36	62	161	92	138	504	100.0%
<20% area	0	0	0	0	0	0	0	0.0%
>20% area	0	0	0	0	0	0	0	0.0%
Encrustation								
none	15	36	62	161	92	138	504	100.0%
<20% area	0	0	0	0	0	0	0	0.0%
>20% area	0	0	0	0	0	0	0	0.0%
Predation	0	0	0	0	0	0	0	0.0%
Repair scars	0	0	0	0	0	0	0	0.0%
Total amount of crab material	15	36	62	161	92	138	504	

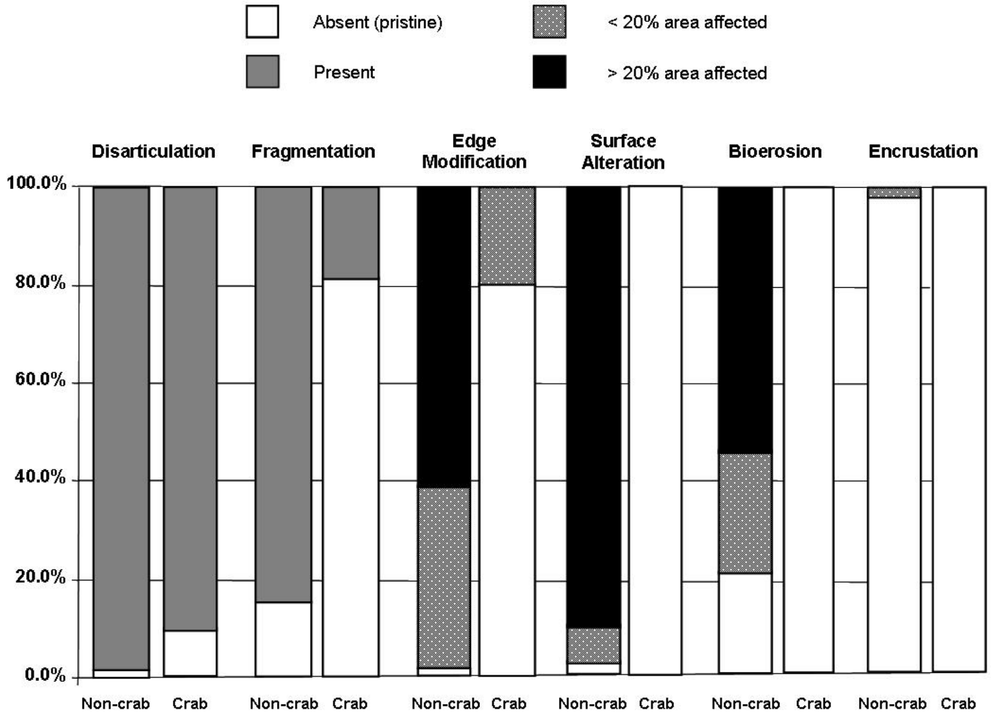

Figure 1.3: Comparison of taphonomic scores between surficial collection of non-crab and crab remains based on percentage. Taphonomic characteristics are disarticulation, fragmentation, edge modification, surface alteration, bioerosion, and encrustation. Percentage values plotted for the crab material are reported in Table 2. For non-crab material, percentages figures are average values for both interior and exterior observations reported in Table 1.3.

Table 1.3: Raw abundance counts and total percentage of taphonomic characteristics of surficial bivalve material collected in 1m² biological grids.

Taphonomic characteristics		Placement of survey grid							Percentage within characteristic
		8 m	12 m	23 m	36 m	44 m	53 m	Total	
	Articulation								
	articulated	0	0	1	2	1	0	4	1.60%
	disarticulated	3	27	32	61	66	52	241	98.40%
	Fragmentation								
	whole	0	11	2	6	12	7	38	15.50%
	fragments	3	16	31	57	55	45	207	84.50%
	Edge Modification								
	pristine	1	0	0	0	2	1	4	1.60%
	chipped	1	23	9	25	22	11	91	37.10%
	rounded	1	4	24	38	43	40	150	61.30%
Exterior	Surface alteration								
	none	0	0	0	0	4	2	6	2.40%
	dull	0	2	2	5	4	2	15	6.50%
	chalky & eroded	3	25	31	58	59	48	224	91.40%
	Bioerosion								
	none	2	6	9	15	7	11	50	20.40%
	<20% area	1	10	11	22	19	10	73	29.80%
	>20% area	0	11	13	26	41	31	122	49.80%
	Encrustation								
	none	3	27	32	62	61	52	237	96.70%
	<20% area	0	0	1	1	6	0	8	3.30%
	>20% area	0	0	0	0	0	0	0	0%
Interior	Surface alteration								
	none	1	0	0	2	4	0	7	2.80%
	dull	0	6	2	3	4	8	23	9.40%
	chalky & eroded	2	21	31	58	59	44	215	87.80%
	Bioerosion								
	none	2	12	10	12	6	10	52	21.20%
	<20% area	0	6	7	18	12	8	51	20.80%
	>20% area	1	9	16	33	49	34	142	58.00%
	Encrustation								
	none	3	27	33	62	66	52	243	99.20%
	<20% area	0	0	0	1	1	0	2	0.80%
	>20% area	0	0	0	0	0	0	0	0%
	Predation	0	0	0	0	0	0	0	0%
	Repair scars	0	2	0	0	1	0	3	1.20%
Total non-crab material in survey		3	27	33	63	67	52	245	

Anatomical Composition of Crab Remains: In all cases, the observed proportion of carapaces and claws is higher than expected and the observed proportion of legs is lower than expected, and became highly significant statistically when data are pooled among sections (Table 1.4, Fig. 1.4 B-E). In sections covered by seaweed, differences between the observed and expected anatomical abundances were statistically significant (Table 1.4), while in sections devoid of seaweed (0-30 meters) differences were not statistically significant (Table 1.4) despite the percentage of anatomical distribution between uncovered and seaweed covered section were similar, (Fig. 1.4D, E).

Table 1.4: Observed surface crab material and calculated expected abundances based on smallest anatomical unit: carapace, leg, claw. Expected counts were calculated by multiplying amount of material found per section by the percentages of parts observed in one crab specimen with no anatomical filter: one carapace (8%), four claws (30%), and eight legs (62%). Qp are the chi - square values. α = 0.05.

	Partitions of the transect													
	0-10 m		10-20 m		20-30 m		30-40 m		40-50 m		50-60 m		Total	
	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
Carapaces	2	3	4	5	12	20	33	53	19	25	21	35	91	141
Claws	9	11	17	22	45	53	122	151	72	97	77	96	342	430
Legs	19	16	34	28	93	77	254	205	148	117	159	126	707	569
Total material	30		55		150		409		239		257		1140	
Qp	0.65		1.33		4.15		12.96		6.58		9.41		35.73	
p-value	0.72		0.51		0.12		0.002		0.03		0.009		<0.0001	

	Resampled partitions						Partitions without seaweed		Partitions with seaweed	
	40-50 m		50-60 m		Total		0-30 m		30-60 m	
	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
Carapaces	12	15	21	22	33	37	18	28	73	113
Claws	45	62	79	98	123	160	71	86	271	344
Legs	92	72	162	142	255	214	146	121	561	448
Total material	149		262		411		235		905	
Qp	5.47		3.38		8.65		5.95		29.9	
p-value	0.06		0.18		0.01		0.05		<0.001	

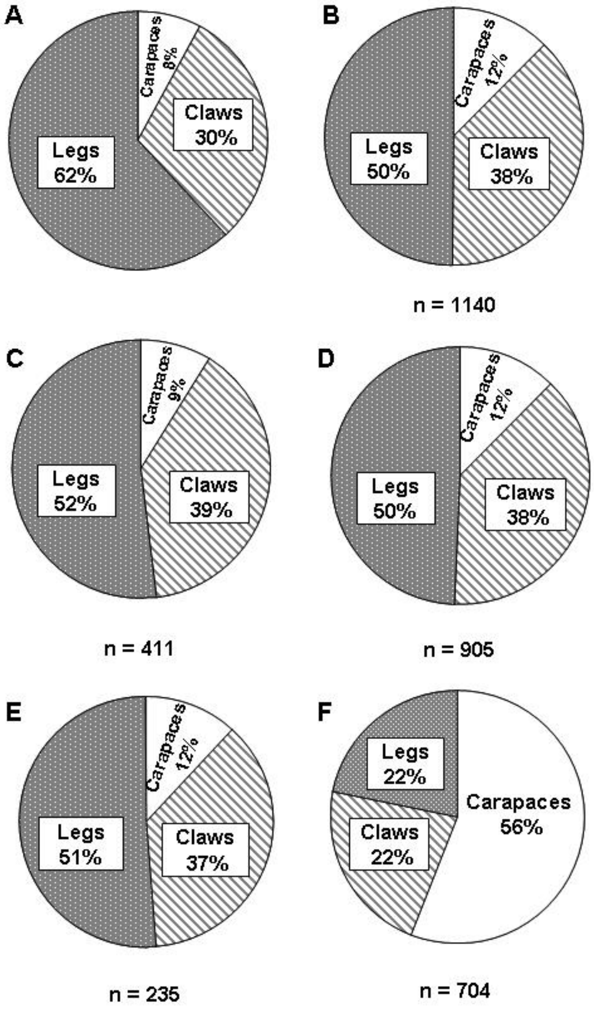

Figure 1.4: Percentage distribution of the abundance of carapaces (white portion), claws (diagonal striped portion) and legs (stippled portion). (A) Expected distribution of crab remains with no pre-burial anatomic filter: carapace (8%), claws (30%) and legs (62%). (B) Observed distribution of total surficial crab remains from first sample collection, n=1140. (C) Observed distribution from resampling collection (40-60 m section), n=411. (D) Observed distribution from seaweed covered section (30-60 m section), n=905. (E) Observed distribution from uncovered section, (0-30 m section), n=235. (F) Distribution observed from literature review of 24 fossil crab taxonomic papers.

Subsurface collection

The upper most layer of sediment (5 cm) consists of well sorted fine sands that overlie dark grey to black fine sand and mud, with a distinct sulphuric odor indicating oxygen-depleted sediments. Only three claw remains, two propodi and one dactyl, were retrieved from the sub-surface in the 0-15 cm depth interval at the 35 and 55 meter marks (Fig. 1.5D). Unlike the surficial crab remains, the subsurface claw remains had a chalky, pitted surface appearance and were highly eroded along the edges. No crab remains were recovered from the 15-30 cm depth interval. Bivalve, barnacle, and gastropod remains were found in both depth intervals (Fig. 1.5 D, E) and dominated by small, highly fragmented remains. The entire subsurface assemblage exhibits high degrees of surface alteration and fragmentation, only two bivalves were found whole within the subsurface samples (<1.0%), The majority of non-crab fragments had more than 20% of their area covered with bioerosion.

The density of subfossil material below the surface (0-30 cm depth range) is estimated at 30 parts per m^3 for crabs and 4620 parts per m^3 for non-crab material, suggesting a ratio of 1:154 crab remains to non-crab remain found in the subsurface. Overall, the amount of subsurface remains decreases with depth, with lower densities seen within the 15-30 cm interval (Fig. 1.5D, E). Subsurface samples collected from between 35 and 55 meters representing the area covered by seaweed, contained more material than the subsurface samples collected in areas without seaweed (Fig. 1.5C).

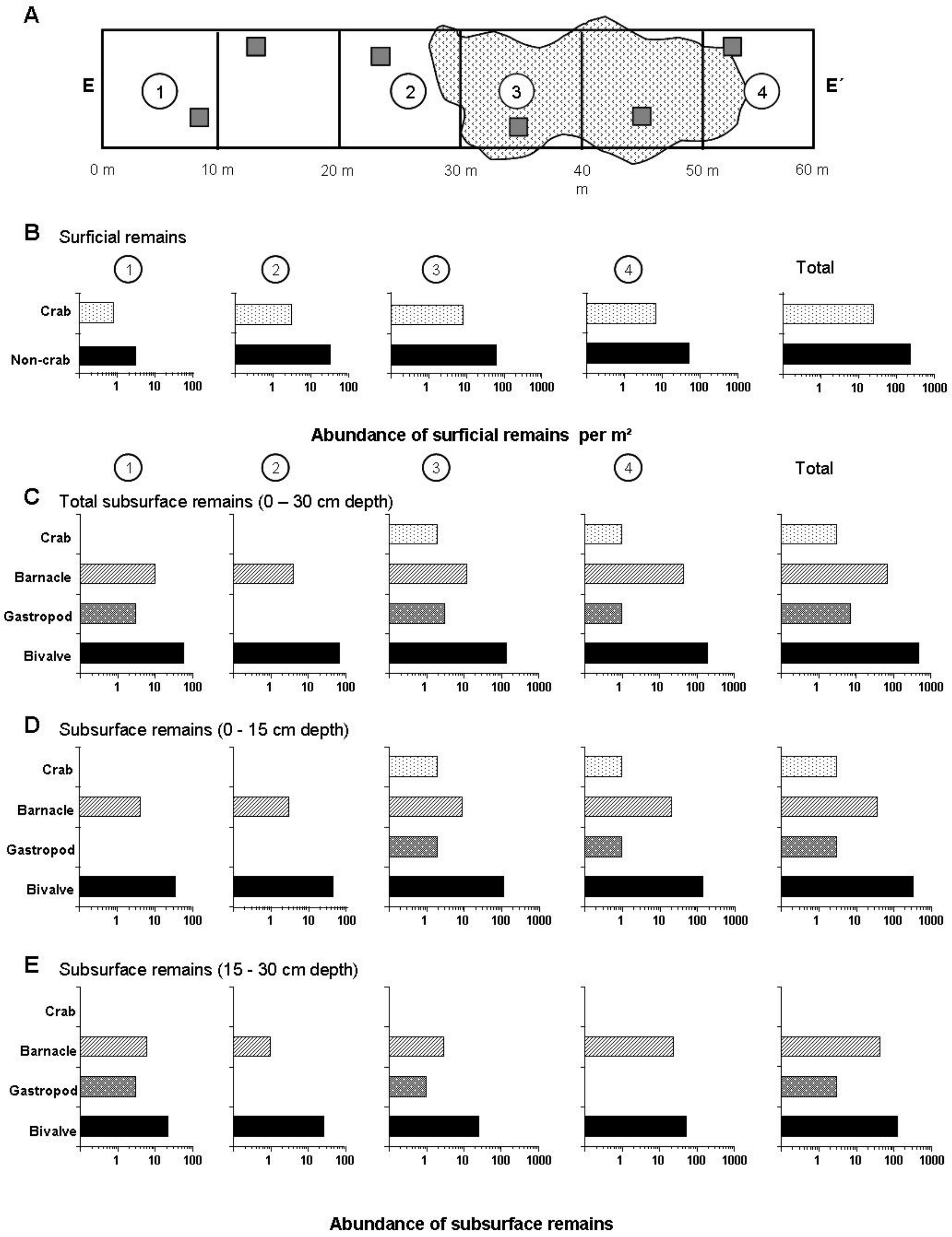

Figure 1.5: Logarithmic histograms reporting abundance of different taxa of subsurface material in reference to transect and surface material. (A) Schematic of the sampled transect. Note the transect has been oriented so that 0 m mark is to the left. Stippled area indicates seaweed coverage. Numbered circles indicate location of subsurface samples. (B) Abundance of surface remains. (C) Subsurface remains recovered from 0-30 cm depth interval. (D) Subsurface remains recovered from 0-15 cm depth. (E) Subsurface remains recovered from 15-30 cm depth interval.

Discussion

Fossilization potential of crabs

All results consistently indicate crab remains are destroyed quickly at the surface resulting in a low preservation potential. Little taphonomic alteration was seen on the surficial crab remains; no bioerosion or encrustation was visible and the color and sheen was comparable to living specimens (Table 1.2, Fig. 1.3). The rapid observed deterioration of carapace and leg remains stored in seawater at the lab suggests that crab material has a limited residence time at the sediment-water interface. A short residence time at the surface would limit chance for burial, an idea supported by a lack of subsurface crab material despite its abundance on the surface. Only heavier calcified parts of the crab skeleton, the propodus and dactyl, were found and it is unlikely that decay and other biological factors would completely remove these appendages from the subsurface.

A conservative estimate of the average survival time of crab remains in False Bay is, at most, several weeks. The density of crab remains from the second sampling, 3.3 parts per m², is comparable to the average abundance of 4.2 parts per m² observed during initial sampling. The second sampling in the seaweed covered sections had a greater percentage of legs and a lower percentage of carapaces than the initial sample (Fig, 1.4 C, D). Assuming a constant input during the field study, if crab remains possessed a residence time longer than a few weeks, a greater difference between the densities would be observed. The increased density seen from the first sampling can be explained by accumulation of more resistant anatomical parts (e.g., claws and carapaces), as legs are preferentially destroyed.

These estimates are consistent with short term experiments where soft tissue was broken down within weeks, including disarticulation of the exoskeleton (Allison, 1986; Plotnick, 1986; Plotnick et al., 1988). Results from previous field studies in False Bay, buried shrimp carcasses without cages, few partial fragments remained after three days while after nine days samples buried in cages contained only highly fragmented rostrum remains, Plotnick (1986). Tumbling experiments by Allison (1986) designed to simulate fast currents showed that turbulent energy conditions resulted in the disarticulation and fragmentation of lightly skeletized arthropod carcasses in five hours. Plotnick et al. (1988) placed mud crabs within fine mesh cages and buried them at depths of 5-10 cm in carbonate mud of Bermuda demonstrating breakdown of nearly all the soft tissue and disarticulation within two weeks of burial. All of these patterns and observations are striking when compared to non-crab material (Fig. 1.3), which exhibited high amounts of surface alteration, bioerosion and fragmentation, suggesting long residence times. The resistance of bivalve and gastropod shells to decay and their long post-mortem survival around the sediment-water interface have been well documented in previous studies (e.g., Cummins et al., 1986; Flessa et al., 1993; Flessa and Kowalewski, 1994; Kowalewski et al., 1998; Nielsen and Funder, 2003).

The importance of seaweed to crab preservation potential is two fold; to create a reservoir for material available for possible burial and preservation and may act as a buffer against physical factors and reduce amount of fragmentation and disarticulation. *Ulva* in False Bay is well suited to withstand tidal environments; it has a tough rhizoid holdfast that attaches to any hard substrate (e.g. rocks, shells, wood) and a sturdy sheet-like thallus. Plotnick et al. (1990) study in Laguna Madre, Texas, determined seaweed was considered as a trap for carcasses and molts, based on the high abundance of remains collected from seaweed-covered areas compared to uncovered areas. A similar correlation is seen within False Bay, Washington, with seaweed-covered areas possessing densities or crab material 2.5 times that of uncovered areas with twice as many surficial bivalve remains in covered areas then uncovered areas (Fig. 1.2, Table 1.1). In addition, the majority of whole bivalves, crab molts and carcasses, and intact chelipeds were recovered from seaweed-covered areas.

Anatomical fidelity

Schäfer (1972) stated three parts of a crab are occasionally found in the sediment: the carapace, claws, and legs. However, this study provides quantitative estimation for anatomical bias; suggesting that claws are over four times more likely to enter the fossil record than legs, whereas carapace parts are intermediate in terms of longevity. The resilience of the claws should be attributed to their heavier calcification. Carapace remains have an intermediate degree of calcification and their flat shape may allow for transportation without breakage. Legs, however, are not as heavily calcified and found in fewer numbers due to either transport or in situ removal.

Photographs and written descriptions of 44 fossil crab species from 24 randomly selected taxonomic papers were reviewed to determine the relative abundance the different crab anatomical parts were reported in the literature. The ratio of leg to claw remains reported was approximately 1:1, if there was no preferential loss of legs over claws, the expected ratio would be 4:1, suggesting a four-fold bias of claws preservation over legs, consistent with observations from the False Bay. The literature review revealed that the carapace are over-represented in the literature when compared to observations reported here, representing over 50% of reported anatomical remains, in contrast to only ~ 12% in field observations (Table 1.5, Fig. 1.4 B-F). The bias towards carapace representation in the literature reflects, most likely, preferential collecting and reporting of carapaces by systematists as crab taxonomy is primarily based on the carapace characters such as, number and placement of spines, nodes, and grooves (Haj and Feldmann, 2002).

Although brachyuran taxonomy is primarily based on carapace morphology, modern species are also distinguished by species size distribution and non-preservational characteristics such as color and non-calcified traits. The distinguishing characteristics for identification between the two *Hemigrapsus* species within False Bay are size, color, and the fine hairs present on the appendages of *H. oregonensis,* which could still be observed on recently dead specimens. The claw and leg remains found in the subsurface did not retain color or fine hairs making their species-level identification unclear. Since the description of crab species in neontological literature is based on carapace morphology, size distribution and non-preservational characteristics, diversity of brachyuran species within fossil deposits may be severely underestimated, (e.g., Feldmann, 2003; Schweitzer, 2003).

Table 1.5: Summary of a survey of 24 taxonomic papers for the relative abundance of carapaces, claws, and legs. Full citations are in references.

Reference					# of Anatomical Parts Reported			
Author	year	Geologic Age	# of species	Preservational quality	carapaces	legs	claws	Proposed depositional environment
Anderson & Feldmann	1995	Eocene	1	exceptional	9	4	4	shallow submarine delta
Berglund & Feldmann	1989	Eocene	1	poor	18	4	3	shallow water
Berglund & Goedert	1996	Miocene	1	good	3	.	2	.
Bishop	1983	Cretaceous	2	poor to exceptional	38	1	3	.
Collins & Morris	1973	Eocene	1	exceptional	33	15	13	.
Feldmann	1993	Cretaceous	6	poor to good	11	.	.	.
Feldmann	1994	Eocene	1	good	1	.	.	shallow nearshore
Feldmann	1998	Miocene	1	exceptional	6	24	10	offshore
Feldmann & Fordyce	1996	Miocene	1	poor	1	8	2	mid-outer shelf
Feldmann & Zinsmeister	1984	Eocene	2	exceptional	11	15	5	shallow sublittoral
Feldmann et al.	1993	Cretaceous		poor to exceptional	19	7	2	below storm wave base
Fraaije	2002	Cretaceous	2	good	25	.	2	.
Fraaye & van Bakel	1998	Cretaceous	3	good	4	.	.	.
Karasawa	1992	Miocene	1	good	1	.	1	intertidal
Karasawa	1998	Miocene	1	good	2	.	.	upper sublittoral zone
Kato & Koizumi	2001	Pliocene/ Pleistocene	1	good	3	11	3	lower sublittoral/upper bathyal
McLay et al.	1995	Miocene	2	good	2	.	.	shallow water shelf
Schweitzer et al.	1999	Cretaceous	4	good	126	2	.	nearshore
Schweitzer & Feldmann	2000	Eocene	6	good to exceptional	14	31	13	.
Schweitzer et al.	2003	Cretaceous	1	poor	1	3	1	mangrove-tidal flat
Squires	1980	Paleocene	1	not reported	11	.	9	shallow subtidal
Tucker et al.	1994	Miocene	1	good	11	7	.	inner to outer shelf
Vega et al	1997	Cretaceous	1	good	3	,	1	lagoonal
Vega et al	2001	Cretaceous	3	good to exceptional	41	24	80	lagoonal
					carapaces	legs	claws	
				Total	**394**	**156**	**154**	

Conclusions

(1) Most crab material is removed from the tidal pool area within weeks, as implied by: (1) high input rate into the tidal pool, yet little surficial accumulation; (2) little taphonomic alteration; and (3) an anatomical bias toward claw and carapace parts in surficial remains. This rapid rate of degradation implies a low possibility of burial and preservation, supported by lack of subsurface brachyuran material. In contrast, the sturdier molluscan and barnacle material exhibit high amounts of bioerosion and surface alteration, implying longer residence times at the sediment-water interface.

(2) The ratio of crab to non-crab material at the surface is 1:10 and increased in the subsurface to 1:154 implying molluscan and barnacle material is over ten times more likely to be buried than crab material.

(3) At the sediment-water interface, brachyuran anatomical parts have different preservational potentials, creating an anatomical taphonomic filter. Crab claws have the highest preservation potential and are four times more likely to be preserved than legs. Carapaces have an intermediate preservation potential.

(4) The preference for preservation of claws and low likelihood for preservation of such identifying characteristics as color and other non-mineralized traits may result in under estimating the number of brachyuran species in the fossil record.

The conclusions from this study are consistent with previous studies and observations within the paleontological literature. However, this study is based on a single species studied in a single locality, so generalizations resulting from this project need to be confirmed in future field investigations of other species in other settings. Further quantitative experiments and observations are needed to improve the understanding of the relative preservation potential of major groups of benthic invertebrates.

Chapter 2: Detecting Avian Predation on Bivalve Assemblages Using Indirect Methods [2]

Abstract

Modern ecological studies suggest avian predation has significant ecological impacts on intertidal communities and can potentially alter the preservation of the subfossil record. To assess if bird predation can affect surficial mollusk deposits, life and death shell assemblages from lagoon, bar and gravel bar habitats known for bird predation on San Juan Island, WA were compared to a null model derived from the ecological literature: (1) minimal physical decay, (2) high shell fragmentation, (3) ubiquity of distinct fracture patterns, and (4) monospecific composition. In contrast to the highly degraded shells from the bay and lagoon, the gravel bar death assemblage displayed highly fragmented pristine shells, frequent presence (68%) of ligaments, a dominant (72%) of valve fracture pattern, and nearly monospecific composition. While overall fidelity between life and death assemblages was low, the similarities between the gravel bar death assemblage and life assemblages suggest the gravel bar approximates present day composition of the local mollusk fauna ecosystem better than either the bay or lagoon death assemblages. These results suggest bird predation can be identified indirectly using supratidal shell deposits, an attractive ecological tool for limited field observations, and the potential paleoecological perspectives of studying shell accumulations generated by molluscivorous birds.

Keywords: Avian; predation; bivalvia; fossil record

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[2] This chapter was submitted for review to Journal of Shellfish Research, March 1, 2006.

Introduction

Bird predation often has a tremendous effect upon invertebrate community structure despite relatively low avian abundance in intertidal systems (Clegg, 1972; Goss-Custard, 1980; Baird and Milne, 1981; Baird et al., 1985; Marsh, 1986; Richardson and Verbeek, 1986; Wotton, 1997). For example, a single oystercatcher can consume over 500 bivalves in a single day (Cummings, 1997), compared to invertebrates, such as a drilling gastropod, which can take hours to days to complete a kill (Boggs et al., 1984; Kabat, 1990). In some intertidal environments, birds can consume about 12% of the invertebrate community biomass in a single year (Moreira, 1997) and exhibit discriminatory prey selection such as removing specific size classes (Richardson and Verbeek, 1987, Cadée, 1989) or species in bulk depending on prey availability (e.g., Webster, 1941; Heppleston, 1971; Sutherland, 1982; Richardson and Verbeek, 1986; Cummings, 1997; Moreira, 1997; Rome and Ellis, 2004). Bias introduced by avian predation is not limited to modern ecosystems. Bird predation on invertebrates have been proposed to explain unusual fossil deposits as far back as the Oligocene (Lindberg and Kellogg, 1982; Iribarne et al., 1998). Despite the potential bias introduced into the fossil record by bird predation (Cadée 1989, 1994, 1995), the paleobiological and paleoecological literature has focused on inter-invertebrate predation especially for bivalve prey (for overview see Kelley et al., 2003). There is the potential that a significant component of ecological interaction in marine habitats is passed over in paleontological and biological studies if bird predation is disregarded

Direct observational and experimental studies on the impact of bird predation on modern intertidal communities can be problematic due to the high avian mobility and metabolism (Heppleston, 1971; Maron, 1982; Wotton, 1997). In this study, the plausibility of bird predation being recorded in the fossil record from a modern assemblage is evaluated by (1) quantifying breakage patterns and degree of overall alteration due to decay (taphonomic approach) to try to identify a unique predation trace and (2) comparison of live to death bivalve assemblages among environments to evaluate for prey selectivity. If bird predation can be detected through indirect and non-invasive means, especially in intertidal habitats, it should be possible to determine if bias has been introduced in the death assemblage, such as size or species predation bias, which can then be corrected accordingly for paleoecological and historical ecological studies. In addition, this study can test if avian predation can be detected in modern ecosystems using a non-invasive approach, which can be useful for ecological surveys.

Neontological studies can use direct observation to investigate predation and species interaction; paleontological studies have to focus on devising indirect methods to infer interaction. Within the paleontological literature, there are numerous studies dedicated to identifying and creating models to detect predation using a variety of trace fossils such as drill holes (e.g., Carriker and Yochelson, 1968; Kowalewski et al., 1998; Leighton 2001, 2002; Kowalewski, 2004), repair scars (e.g., Vermeij, 1987; Ebbestad and Peel, 1997, Alexander and Dietl, 2001), peeling (e.g., Bishop, 1975; Schindel et al., 1982), various bitemarks (e.g., Alexander, 1986), and even coprolites (e.g., Häntschel, 1968; Kloc, 1987). While in most cases it is difficult to identify the predator down to species in the fossil record, it is possible to narrow the list to a few suspects based on unique patterns left on the shell, e.g., circular punctures in Carboniferous goniatites associated with the shark *Symmorium* (Mapes and Hansen, 1984). Diet preferences of intertidal shorebirds have been well studied through direct observation, and reveal different prey-preferences, feeding, and prey-handling methods (e.g. Drinnan, 1958; Davidson, 1967; Feare 1970, 1971; Heppleston, 1971; Baker 1974; Goss-Custard 1977, 1980; Maron, 1982; Richardson and Verbeek 1986, 1987; Burger, 1988; Rome and Ellis, 2004).

Avain predation mark patterns on bivalve victims that result from different feeding methods recorded by modern observational studies may be distinctive enough to be identified in subfossil and fossil assemblages. Here a null model defining common characteristics of shell accumulations that result from bird predation is proposed and tested against data from shell assemblages from three distinct modern environments (lagoon, bay and terrestrial) in a locality known for bird predation on bivalves.

Study Area

The study was conducted at Argyle Bay and Argyle Lagoon, San Juan Island, Washington, USA (48°31’N, 123°00’ W; Fig. 2.1). Argyle Bay is a small partly protected marine embayment that is connected to the open ocean to the south. The bay’s northern end is connected to Argyle Lagoon by a 25 m long inlet that is up to several meter wide inlet at a high tide, known as Argyle

Creek. Argyle Lagoon is a triangle shaped area surrounded by raised sand bars. A sand and gravel bar separates Argyle Bay from Argyle Lagoon. The bar's sediments are distributed asymmetrically with the side adjacent to the bay dominated by cobbles and gravel and the side adjacent to the lagoon by sand. The entire area experiences to diurnal tides that are partially emptied during low tides, then flushed daily as the tide rises. As a result, the bay, creek, and lagoon share similar environmental characteristics, such as salinity and temperature (14-15°C) (Willings, Jr., 1957; Lazo, 2004).

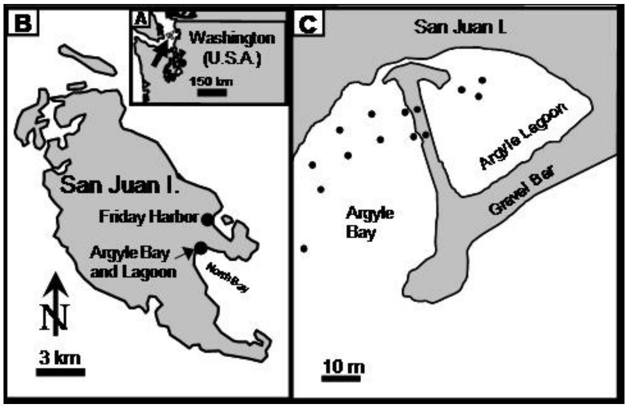

Figure 2.1: Location of the study site. North direction applies to all insets. (A) Northwest coast of Washington Stat, the arrow indicates San Juan Island. (B) San Juan Island, Washington, USA. (C) Argyle Bay and Lagoon. Dots indicate sampling localities.

Seven types of birds were observed in Argyle Bay over the course of the study: Oystercatchers (*Haematopus bachmani*,(Audubon)), gulls (*Larus glaucescens* (Naumann) and *L. occidentalis*,(Audubon)), crows (*Corvus caurinus*(Baird)), Great Blue Herons (*Ardea herodias* (Linnaeus), Greater Yellowlegs (*Tringa melanoleuca* (J.F. Gmelin)), Kingfishers (*Ceryle alcyon* (Linnaeus), and a variety of ducks. Of those seven, oystercatchers, gulls, and crows rely on bivalves as a substantial part of their diet (Heppleston, 1971; Maron, 1982; Richardson and Verbeek 1986, 1987; Rome and Ellis, 2004). The hunting and handling strategies used by these molluscivores can leave marks on prey shells; Gulls dropping bivalves resulting in high fragmentation (Barash et al., 1975; Fine and James 1976; Lewis and Sharpe 1987), crows can either hammer bivalves resulting in high fragmentation or breaks at certain area of the shell or size selectivity of prey for dropping, (Clegg, 1972, Richardson and Verbeek 1986), and predation of oystercatchers through hammering the shell result in fracture marks concentrated to one portion of the shell (Table 2.1).

Methods

Using the breakage patterns that are qualitatively described within the ecological literature, some general characteristics are proposed to identify a bivalve victim of birds that use dropping handling methods: (1) *Minimal bioerosion and physical decay* – previous studies have described the remains of avian prey to have a pristine shell interior, preserved ligament, and articulated valves (Hulscher, 1982; James and Verbeek, 1984; Cadée, 1989). These characteristics in modern environments imply a reduced residence time at the sediment water interface while fragmentation to the shell as a result of physical factors (e.g. energy) require longer surface residence times and often accompanied by a high degree of decay and degradation to the shell (e.g. loss of color, perisotrcum and ligament); (2) *High degree of fragmentation* - highly fragmented shell remains are interpreted often in the literature as the result of bird predation (e.g. Clegg 1972; Meldahl and Flessa 1990). For example, Cadée (1995) estimated that 75% of shells in the Dutch Wadden Sea sediment were fragmented as a result of bird predation; (3) *Common fracture patterns* - Common patterns that cut across growth lines or are concave into the shell have been described in multiple cases of observed bird predation (e.g. Hulscher, 1982; Lomovasky et al., 2005); and (4) *Evidence of prey selection* - concentration of shells that were victims of bird predation should be dominated by few species and have a limited size range compared to the general bivalve community (e.g. Richardson and Verbeek 1986, 1987; Rome and Ellis 2004). If bird predation cannot be detected in the Argyle Bay and Lagoon localities, the results should reveal (1) no pattern between degree of fragmentation and state of decay, (2) no prominent break patterns along the shell, (3) and random distribution of species.

TABLE 2.1 - A literature compilation of characteristic traces left on prey shells by molluscivorous birds.

Bird	Mollusk Prey	Grappling & Handling	Trace on Bivalve	Reference
Oystercatchers (*Haematopus*)				
Black Oyster-catcher (*H. bachmani*)	mussels (*Mytilus edulis and M. californianus*)	Rapid blow to the mussel then opening mussels through leverage.	Fracture marks on valve.	Webster, 1941
South Island Pied Oystercatcher (*H.ostalegus finschii*)	cockles (*Chione stutchburyi*)	Hammering through the umbo or thrusting into the commissure.	Holes within the umbo or fractures along the commissure	Baker, 1974
H. ostalegus	Limpets (Patella aspera and P. vulgata)	Thrust at margin with closed bill till limpet knocked off rock.	Chips and fracture concentrated on the anterior part of the shell.	Feare, 1971
H. ostalegus	Dogwhelks	Dogwhelk turned over and pecked at the operculum.	Chips and fracture concentrated on the anterior part of the shell.	Feare, 1971
Gulls (*Larus*)				
Herring Gulls (L. argentatus)	*Cerastoderma edule, Mytilus edulis*	Bivalves > 3cm in length are dropped; Bivalves < 3cm in length are ingested whole.	High fragmentation	Cadée, 1995
Crows (*Corvus*)				
Northwestern Crows (*C. caurinus*)	Littleneck clams (*Venerupis japonica*)	Repeated dropping	Prey-selectivity for clams with lengths 24.0-43.0 mm	Richardson & Verbeek, 1987
Carrion crow (*C. corone*)	*Mactra corallina, Spisula solida*, and *Lutraria lutraria*	Insertion of bill in gape and shake animal free. Occasional blows to thinner shells.	No noted marks; valve is smashed resulting in high fragmentation	Clegg, 1972
Carrion crow (*C. corone*)	mussels (*M. edulis*)	"Pick-axe" blows with bill to bivalve pressed against a rock.	Blows delivered to straight edge of shell	Clegg, 1972

Data Collection – Sampling localities were based on five days of exploratory observations of bird feeding habits during low tide which restricted the target area to the rim of the bay and the lagoon. The majority of initial captures occurred in the bay portion of the area, with numerous birds observed flying to the gravel bar or the lagoon to handle and consume prey. Fourteen samples were collected: seven in Argyle Bay, three in Argyle Lagoon, and four on the gravel bar (Fig 2.1). The bar is proposed to be the environment where evidence of bird predation will be easiest to identify based on the observations of crows dropping bivalves and the lack of living bivalve populations on the bar to mask results. The bay was used as a baseline for comparison of taphonomic and fidelity patterns since only prey selection was observed in this area, not handling or feeding, suggesting that degradation and fragmentation patterns in the bay death assemblage are primarily the result of physical and biological processes other than avian predation. The lagoonal environment may contain evidence of characteristics of avian predation, such as high fragmentation and common fracture pattern, as this was the local area where many birds would finish handling prey items. However, the input of bivalves by reproducing populations in the lagoon may have damped an avian predation signal by the input of bivalves in the death assemblage that were not fed upon.

All samples were collected within a 1m² biological grid placed randomly within the targeted sampling areas and all identifiable surficial bivalve material, shells and fragments, were collected. Subsurface samples were taken by penetrating the sediment to a depth of 15 cm and sieving the material through a 12 mm sieve, where bivalve material was exhaustively collected. The sampling depth does bias against deep burrowing species, such as *Mya.* However, many molluscivore birds prey on bivalve species that are either exposed at the surface or are shallow infaunal species. Therefore the depth of 15 cm is consistent with bird behavior for locating prey (e.g. Baker, 1974; Hulscher, 1981). Throughout the sampling process, species and abundances of live bivalves seen in the sampling grids were recorded. No samples were taken from the creek area as the creek bivalve population is highly disrupted throughout the year by clammers and biological research (Willings, Jr., 1957).

Data were collected using the semi-quantitative taphonomic scheme proposed by Davies et al. (1990). Information recorded for the specimens was: (1) taxonomic identification; (2) valve length and width; (3) valve preservation (left/right/both, presence/absence of ligament); (4)

Presence of fragmentation (left/right/both); (5) Location of fragmentation (Fig 2); (6) Degree of fragmentation (<25% / 25-50% / 50-75% / and >75%); (7) manner of fracture (subparallel to growth lines / straight line across growth lines/ concave fracture into the valve, Fig 2.2); (8) Edge modification (pristine/chipped/rounded; location on valve of chipping); (9) external and internal attributes: surface alteration (pristine/dull/chalky and eroded), bioerosion (absent/<20% area covered/>20% area covered), encrustation (absent/<20% area covered/>20% area covered). For characteristics that are judged in a rank order, such as original edge modification and external surface alteration, each rank category was given a number in ascending order that correlated with degree of change (Table 2.2).

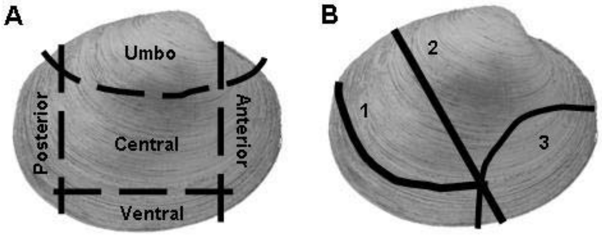

Figure 2.2: Valves of *Protothaca staminea* showing a section scheme used for taphonomic scoring of shell and types of line fracture used for quantifying fracture patterns. A. Designated sections of the bivalve used to quantify areas of fragmentation and chipping. Letters in parentheses are code letters used in the database. B. Fracture patterns observed among shell fragments: (1) fractures subparallel with the growth lines, (2) fracture straight across growth lines, (3) concave fracture into the shell.

Table 2.2 Explanation of semi-quantitative and rank scales for taphonomic characteristics, based from Davies et al., 1990.

Taphonomic Characteristic	Min.-Max. values	Explanation
Ligament present on recognizable hinge part	1/0 (present/absent)	
Degree of fragmentation	0-4	0 = no fragmentation, complete shell 1 = < 25 % of shell missing 2 = 25-50% of shell missing 3 = 50-75% of shell missing 4 = >75% of shell missing
Fracture pattern	0-3, (.)	0 = no fracture of the shell 1= fracture is parallel to growth lines 2 = fracture is straight across growth lines 3 = fracture in concave into the valve (.) = fracture pattern cannot be determined
Surface alteration	0-2	0 = pristine, still contains original color and luster 1 = surface is dull, both color and luster diminished 2 = chalky and eroded
Bioerosion coverage	0-2	0 = no bioerosion 1 = < 20% of valve area affected 2 = > 20% of valve area affected
Encrustation coverage	0-2	0 = no encrustation 1 = < 20% of valve area affected 2 = > 20% of valve area affected

Data analysis

To summarize the severity of surface alteration and the degree of bioerosion and encrustation to the interior and exterior of the shell, each shell was assigned a degradation score which indicated the overall decay of the shell and correlated to the amount of time the shell remained at the surface. A score of 0 indicated a specimen that is pristine on both the interior and exterior of the shell while the highest score possible was 12 indicating a severly altered specimen. A bivalve specimen that had a high degradation score due to surface alteration and degree of bioerosion and encrustation, was interpreted as having had a long residence time at the surface and was exposed to physical, chemical and biological agents. In addition, the presence of repair scars and drill holes was recorded to provide a baseline for the impact of non-avian predators. With the exception of some proposed blisters in razor clam shells (Lomoskvky et al., 2005), documentation of bivalves repairing their shell after a bird attack is rare, so all repair scars were assumed conservatively to be the result of failed non-avian attacks.

Based on qualitatively described prey-handling methods from the ecological literature, the null taphonomic hypothesis developed that is a bivalve victim of bird predation in Argyle Bay and Lagoon would exhibit either some or all of the following characteristics: (1) minimal bioerosion and physical decay, (2) a high degree of fragmentation, (3) a fracture pattern that is either straight across or concave into the valve, and (4) a concentration of a few abundant species. If bird predation could be detected on the gravel bar using this model, then the distribution of these characteristics should be significantly different in comparison with the bay area, where no bird was observed handling bivalve prey.

To investigate fracture patterns, the specimens were grouped into relatively thick-shelled bivalves; (*Clinocardium nuttallia* (Conrad*), Nuttallina californica* (Reeve)*, Protothaca staminea* (Conrad)*, Saxidomus gigantean* (Deshayes), and *Tapes japonica* (Deshayes); and relatively thin-shelled bivalves, *Macoma nasuta* (Conrad) and *Mya arenia* (Linnaeus)). This relative thickness distinction was to account for different prey-specific methods birds used to handle bivalve prey (Table 2.1) and durability of shells due partially controlled by thickness which can thus affect fragmentation (Zuschin and Stanton, Jr., 2001; Zuschin et al., 2003).

To assess the potential of prey-selectivity by birds biasing the remains by altering the distribution, fidelity between the life and death assemblages was assessed both within and across the three environmental settings. Two approaches were used; (1) an exploratory approach using multi-sample Kolmogorov-Smirnov analysis to compare an assemblage's species abundance distribution (e.g. live lagoonal assemblage) in relation to the pooled distribution of species abundance for the entire study site (Kowalewski and Demko 1997) and (2) Spearman rank correlation comparisons of patterns in the species'rank of species based on abundance within different assemblage to determine if they are significantly different (e.g.. comparing the lagoon life vs. death assemblage) (Kidwell, 2001).

Results

1207 dead bivalve specimens and 251 live specimens from seven bivalve species were collected from within the study area, Encrustation, repair scars and drill holes were rare in the entire death assemblage; 35 specimens had repair scars, 17 specimens had either internal or external encrustation, and 11 specimens with drill holes.

Taphonomic Patterns

The biggest difference in taphonomic patterns between environments occurs between the gravel bar and the other two environments (Table 2.3, Fig. 2.3). The median degradation score among specimens from the bay and lagoon is 4, indicating either (a) light surface alteration and minimum amounts of bioerosion or (b) high surface alteration with no bioerosion. The distribution of degradation scores observed between the bay and lagoon did not differ statistically from one another (Fig 2.3, Wilcoxon pairwise comparison, Z = 0.41, p = 0.67). In

Table 2.3: Summary of taphonomic characteristics by environment. Percentage values are for number of specimens within each environment.

	Total	Degred. score	Ligaments present on recognizable hinges*		Dominant Class of Frag.	Complete shells		Frag. < 75%		Most common break pattern	
	n	Median	n	%		n	%	n	%		
Lagoon	439	4	152	44.44%	0%	200	45.56%	110	25.06%	Straight across growth lines	26%
Bay	513	4	157	44.23%	<75%	150	29.24%	155	30.21%	Straight across growth lines	23%
Bar	255	0	83	68.03%	<75%	13	5.10%	139	54.51%	Straight across growth lines	72%

contrast, samples from the gravel bar region were primarily pristine valves with a median degradation score of 0, indicating no surface alteration or bioerosion (Fig. 3). The lack of degradation observed in shells from the gravel bar was significantly different from the amount observed in the other two environments (Wilcoxon pairwise comparisons: bar vs. bay, Z = 17.68, p< 0.0001; bar vs. lagoon, Z = -17.16, p < 0.0001). In both the bay and lagoon, 44% of specimens with a recognizable hinge still possessed a ligament; while 68% of the gravel bar specimens with recognizable hinges did. A log-likelihood test of the differences between percentages of ligaments present among the three environments was statistically significant (χ = 23.713, p < 0.0001). Since the bay and the lagoon had the same percentage of specimens with ligament, the significance should be attributed to the influence of the gravel bar area (Table 2.3).

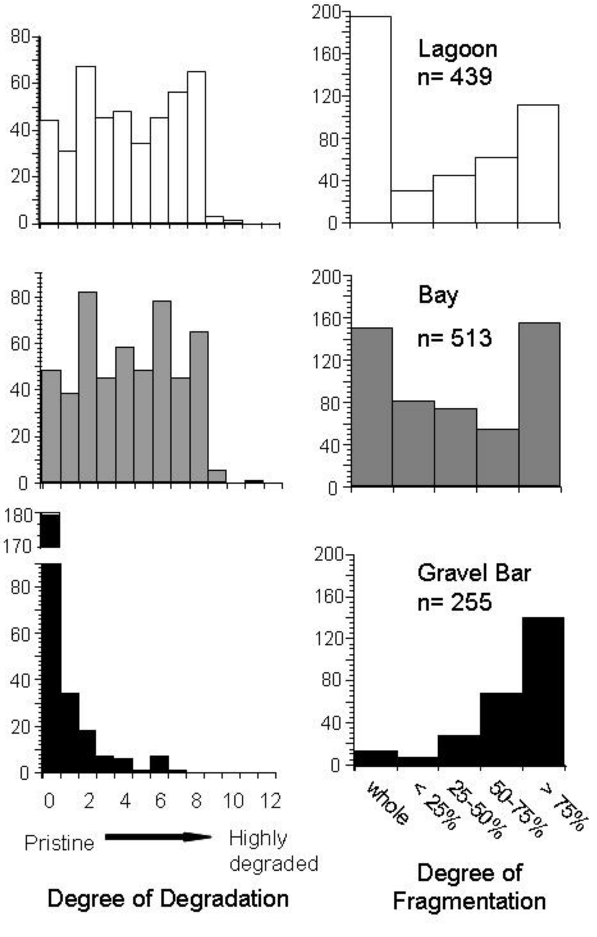

Figure 2.3: Distribution of degradation score and degree of fragmentation between the three collection environments: lagoon, bay, and gravel bar. Degradation score, the overall decay of the shell, is the sum of the summation of degrees of external and internal attributes, (ex. surface alteration, bioerosion, encrustations). Degree of fragmentation is based on area of shell missing.

Fragmentation patterns also varied significantly among the three environments as well (Kruskal Wallis, H = 140.2, p <0.0001; Fig 2.3), though pairwise comparisons reveal that each environment is significantly different from the other two. In the bay and gravel bar environments, specimens with greater than 75% fragmentation dominate. Despite that dominance, the degree of fragmentation differed between the two environments (Wilcoxon pairwise comparison Z=-11.20, $p < 0.0001$). This difference was most likely due to the higher percentage of complete shells in the bay; 150 specimens (29.2% of bay sample) compared to 13 complete shells from the bar (5.1 % of bar sample, Fig.2.4). In the lagoon environment, complete specimens dominated (44.2% of the lagoon sample, Fig 2.4). Based on class of fragmentation, the median bay and the lagoon median degradation scores fluctuated between 2 and 5. Yet, the median degradation scores for gravel bar specimens did not vary from pristine regardless of the class of fragmentation.

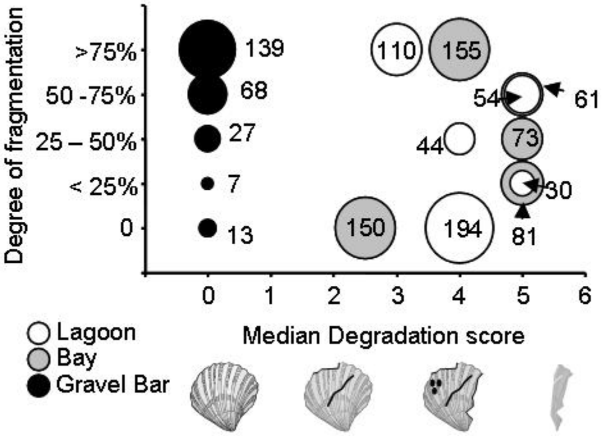

Figure 2.4: Bubble plot depicting the median taphonomic score for each degree of fragmentation for Argyle Bay, Argyle Lagoon, and gravel bar. Abundances of shells within each degree of fragmentation reported next to each bubble.

Breakage pattern was determinable for 637 specimens (52.7 %) of the entire death assemblage. The remaining specimens were not classified because they were either unbroken valves or so degraded and fragmented that a breakage pattern could not be reliably determined. Such specimens were more common in the bay than the other settings (Fig. 2.5). In the bay, 18% of the thin-shelled bivalves and 23% of the thick-shelled bivalves broke straight across growth lines. In the lagoon, 26% of the thick-shelled bivalves and 34% of the thin shelled bivalves broke straight across the growth lines (Fig. 2.5). On the gravel bar 72% of the specimens collected had a fracture that went straight across growth lines. Despite high fragmentation, the shells on the bar were pristine enough that growth lines could be determined on even very small fragments, unlike specimens in the bay or the lagoon which were so heavy degraded growth lines could not be distinguish. The frequency of different types of breakage patterns varied significantly among the three localities (log- likelihood test χ = 324.9 p<0.0001).

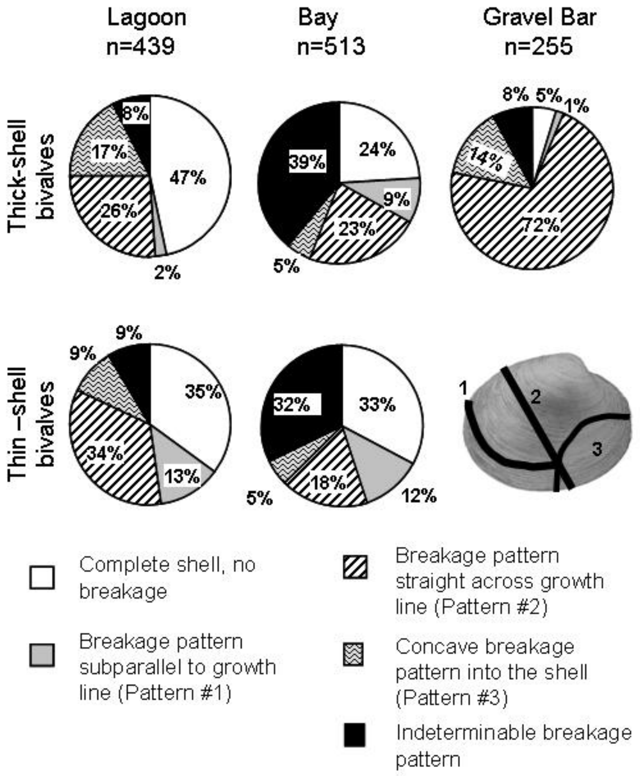

Figure 2.5: Fracture patterns observed on thick and thin shells from death assemblage, plotted separately for the bay, the lagoon and the gravel bar.

Fidelity Patterns

While species richness among the three environments were similar (Table 2.4), the abundance within most species differed notably between the assemblages within and across environments (Table 2.5) In Argyle Bay, the life and death assemblages were both dominated by *Macoma* (79% and 41 % respectively); while in the lagoon the life assemblage was dominated by *Protothaca* (95%) and the death assemblage dominated by *Tapes* (52%) even though live specimens of *Tapes* were rarely observed during data collection. In the gravel bar, 99% of the death assemblage consisted of bivalve species with thicker-shells, such as *Tapes* and *Protothaca* (Table 2.4). Rank correlation of species abundances between most assemblages across environments were weak ($r < 0.5$) and insignificant ($p > 0.05$). The correlation between death assemblages of the lagoon and gravel bar was higher, though still statistically insignificant ($r=0.53$, $p=0.21$). Within environments, only the bay had a strong, significant correlation between the life and death assemblages, ($r=0.81$, $p=0.02$). The correlation between the lagoon life and death assemblage was also high ($r=0.67$), but again not significant ($p = 0.09$).

When comparing the distribution of the individual assemblages to the pooled distribution, the life assemblages both have a positive deviation while the death assemblages have a negative deviation (Fig 2.6). The resulting deviations indicate that the death assemblages were more similar to each other then to their counterpart life assemblages, and vice versa for the life assemblages. This pattern is likely driven by the relative abundances of two bivalve species (*Clinocardium* and *Saxidomus)* found in high abundance in all three death assemblages ($n > 5$), but not having representation in the life assemblage in either the bay or the lagoon. A substantially higher abundance of *Tapes* in both bay and lagoon death assemblages compared to the life assemblages may have also contributed to the separation between life and death assemblages (Table 2.4). A life assemblage represents the current annual distribution of bivalve species for an ecosystem, while the death assemblage can averaged by thousands of years of production (Kowalewski et al. 1998). When looking at the assemblage distributions deviated from the average pooled distribution, the bar assemblage plotted closer to the life assemblages than either the bay or lagoon death assemblages (Fig 2.6). The deviation calculated for the bar assemblage suggests that, in comparison to either bay or lagoon death assemblage, the bar assemblage is less time-averaged with respect to the life assemblages.

Table 2.4: Total abundance of live and dead bivalves and their rank for each assemblage for Argyle Bay, Argyle Lagoon, and the gravel bar. Rank values are in parentheses.

		Argyle Bay				**Argyle Lagoon**				**Gravel Bar**	
		Live		Dead		Live		Dead		Dead	
	Bivalve species	n	rank	n	Rank	n	rank	n	rank	n	Rank
Thick-shelled	*Nuttalina californica*	0	(5)	5	(7)	1	(3)	11	(5)	*32*	(3)
	Clinocardium nuttalia	0	(5)	22	(6)	0	(4)	7	(6)	15	(4)
	Prototheca staminea	16	(3)	73	(3)	87	(1)	75	(3)	60	(2)
	Saxidomus gigantea	0	(5)	32	(5)	0	(4)	32	(4)	8	(5)
	Tapes japonica	18	(2)	65	(4)	1	(3)	196	(1)	137	(1)
Thin – shelled	*Macoma nasuta*	142	(1)	200	(1)	0	(4)	2	(7)	1	(7)
	Mya arenia	3	(4)	79	(2)	3	(2)	115	(2)	2	(6)
	Unidentifiable	0		37		0		1		0	
		Live		**Dead**		**Live**		**Dead**		**Dead**	
	Totals	**179**		**513**		**92**		**439**		**255**	

Table 2.5: Correlation between assemblages based on rank of bivalve species abundance using Spearman rank correlation. α = 0.05.

	Within environment		Correlation to Gravel Bar				Correlation between bay and lagoon		
	Live-dead		Live		Dead				
	r	p	r	p	r	p		r	P
Bay	0.81	0.02*	-0.03	0.93	-0.46	0.29	Live	0.19	0.67
Lagoon	0.67	0.09	0.45	0.31	0.53	0.21	Dead	0.10	0.81

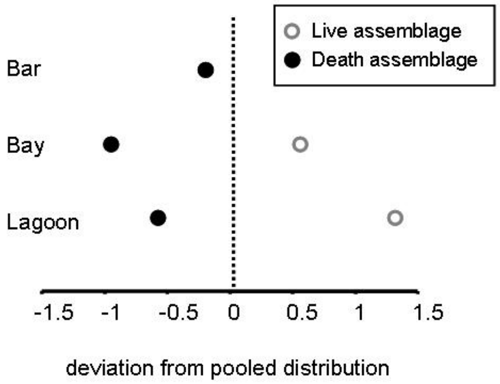

Figure 2.6: Graphical representation of multi-sample Kolmogorov-Smirnov analysis of the deviation of each sample (ex. live lagoonal assemblage) from the study area's pooled distribution of species abundance. Death assemblages are indicated by the black circles, life assemblages are indicated by the white.

Discussion

Out of all samples collected from the study site, the samples on the gravel bar best fit the model of avian predation, which suggests terrestrial or supratidal deposits are promising settings to detect bird predation. Since no live bivalve populations exist on the gravel bar, all samples collected from this region had to be deposited by either physical or biological transport. In addition, no reproducing bivalve populations have lived on the gravel bar since it was constructed in the 1930's when the a nearby cannery facility was built (Willings, Jr., 1957), so time averaging over thousands of years is not a issue. Normal high tides in the study site do not cover the gravel bar completely, as suggested by the heavy grass growth and terrestrial insects that live on the bar, and no recent high tide event or flooding has been document for the area in the past 10 years.

Over half of the bivalve shells from the gravel bar assemblage had greater than 75% fragmentation. As noted by previous studies, high abundance of fragmented shells in a deposit can be interpreted as either (1) high water turbulence or (2) high amounts of predation in low-energy environments (Trewin and Walsh, 1976; Cadée 1989, 1995; Zuschin et al., 2003). The low probability of supratidal deposition by wave or tides in the Argyle study area makes transport by a biological agent a much more likely explanation. This is further supported by the prevalence of pristine specimens and dominance of highly fragmented valves with a prevailing breakage pattern of straight fractures across growth lines (Table 2.3), similar to avian predation traces found in the literature (Table 2.1). In addition, the gravel bar remains are primarily one bivalve species, *Tapes japonica*, a result that is consistent with prey preference behavior observed in birds for one species (e.g., Heppleston, 1971; Sutherland, 1982; Richardson and Verbeek,1986; Cummings, 1997; Moreira, 1997; Rome and Ellis, 2004). If the gravel bar bivalve remains do become preserved the assemblage will reflect the birds' preference *Tapes*, a biased record of local bivalve faunas in terms of species richness and relative abundances.

The high correlation and statistical significance of fidelity between the bay life and death assemblages echoes previous live-death fidelity studies that claim death assemblage can be used to correctly reconstruct live assemblages, (e.g. Kidwell and Flessa 1995; Kidwell 2001, 2002; Kowalewski et al., 2003). The low fidelity between assemblages in the lagoon and between environments can be due to a variety of factors: (1) time averaging of variable annual population (e.g. more *Prototheca* one year than another); (2) preservational bias (some shells are destroyed more readily than others); or (3) predation-induced bias. The distribution of species between the live and death assemblages in the lagoon and gravel bar localities can be partially explained through predation. The high abundance of *Tapes* in the gravel bar, despite their paucity among the live specimens in both the lagoon and bay environments combined with taphonomic characteristics, are highly suggestive of bird predation.

If the predation model for the study is correct, then bird predation plays an important factor in molluscan ecology and the future fossil record of the area. The rare occurrences of repair scars and drill holes for the bivalve samples as a whole imply that inter-invertebrate predation was minimal in comparison to the number of bivalve remains on the gravel bar. Marine paleoecology studies would miss this biological interaction if just repair scars and drill holes were evaluated for predation. Modern studies based solely on observation may also underestimate the intensity of avian predation in the Argyle Bay ecology as only five instances of predation were witnessed directly over the observation period of the study, although the results of this study suggest a significantly greater predation rate.

A caveat of this model is that no one single characteristic is a sure indicator of avian predation, it is necessary to have multiple characteristics. This may pose a problem for paleontological studies due to taphonomic bias of the fossil record and time-averaging, since the initially pristine signature of shells is unlikely to be preserved. However, the lack of large monospecific shell deposits far above the shoreline provides indirect evidence for avian predation, e.g. >1000 *Prototheca* shells were found on hillsides near marine environments (James and Verbeek, 1984).

Conclusions

This study suggests that indirect detection of bird predation through use of assemblage fidelity and taphonomic studies is possible. The bivalve remains from the gravel bar were not exposed to wave or tidal forces, and exhibit characteristics similar to the model proposed from the literature: (1) high fragmentation rate, <75%, (2) fragmentation dominated by concave or parallel breakage patterns that are a common result of bird handling methods, (3) pristine interior and exterior surfaces of the shell, (4) abundant ligament remains, and (5) high abundance and concentration of species in deposits of low species diversity. This is promising for both ecological and paleontological studies in that indirect approaches can be used to analyze bird-mollusk interactions in ecological reconstructions and surveys.

Chapter 3: High Resolution Environmental and Temporal Geometric Morphological Trends in a Pliocene Mactrid, *Mulinia congesta*

Abstract

Biological and paleobiological studies of invertebrate marine organisms have documented, in numerous cases, a correlation between shell size/morphology and habitat setting, suggesting that morphological changes may often be induced by environmental changes, both over ecological and geological timescales. The goal of this study is to investigate the importance of changing environmental conditions over a geologically limited time interval of less than a million years. The right valves of 607 specimens of *Mulinia congesta* (Conrad), an opportunistic shallow infaunal siphonate suspension-feeding bivalve, were analyzed using geometric morphometric methods. The samples were collected vertically across a stratigraphic section of the Rushmere- Morgart's Beach members of the Yorktown Formation representing approximately 500 k.y. of deposition and a paleoenvironmental transition from a higher to a lower water energy setting, a transition also paralleled by a shift in dominant faunal fossil assemblages. The valves were digitally imaged and the Generalized Least Squares – Full Procrustes analysis was completed on x-y coordinates for fifteen landmarks. Tangent coordinates were used to derive principle components ordination to assess variations and trends in shell shape within and across different facies and faunal associations. In addition, size was estimated using shell length and centroid size.

Mulinia congesta collected along the environmental and temporal gradient across three successive paleocommunity types recognized within the Yorktown Formation in southeastern Virginia, do not exhibit trends in size or morphospace occupation that correspond to changing environmental conditions. Instead, the morphology of *M. congesta* shells is remarkably static, indicative of both ecophenotypic conservatism and remarkable morphological stasis over hundreds of thousands of years.

Introduction

Fossils have been used extensively to document and evaluate morphological trends in the context of patterns and processes operating over a wide range of taxonomic and spatio-temporal scales such as ontogentic changes (Savazzi, 2000; Tschudin, 2001) , morphological stasis (Kowalewski et al., 1997; Kim et al., 2001; Bush et al., 2002), diversity changes (Foote, 1995, 1999; Hautmann, 2004), environmental ecophenotypy (Bayer and McGhee, 1984; Hageman, 1995; Daley, 1999a; Drent et al., 2004), and extinction events (Lockwood, 2004; Saunders et al., 2004). Morphology is the end result of intrinsic and extrinsic influences, to list just a few examples, geographical separation of populations where genetic isolation and different environmental conditions can contribute simultaneously (Marko and Jackson, 2001), anagensis combined with ecophenotypy resulting in high phenotypic variability in a short time (Crampton and Gale, 2002) , and changes in life habit slightly modify conservative morphology (Thomas, 1978).

Understanding the amount of phenotypic variation that is possible in a group of organisms is a critical perquisite for delineating credible morphospecies as well as for carrying out realistic ecological and evolutionary inferences based on morphology. This is especially true in paleontology, where morphological data are a key component to species identification (e.g., Hageman, 1995). However, for many body plans and ecological modes, especially within marine invertebrates, a single factor can play an important or overriding role in the apparent morphological change or stasis of an organism (e.g., Vincent et al., 1994, Hageman, 1995; Daley, 1999a; Saunders et al., 2004) . Therefore, it is important to consider the relative importance of different environmental, temporal and geographical factors that can affect morphology of organisms and obscure the observed perception of species.

Morphological variability of marine invertebrates has been used as a primary source of data on the nature and rate of evolutionary and ecological processes. Shell morphology of both marine and freshwater invertebrates has been used in many situations as a proxy for environmental and ecological conditions such as sediment grain size (Stanley, 1940; Alexander, 1993; Daley, 1999), changes in faunal ecology (Anderson, 1994) , intensity of predation

(Leighton, 1999; Dietl and Kelley 2001), salinity (Gainey and Greenburg 1977), nutrient availability (Anderson, 2001;Drent et al. 2004), life habit (Stanley, 1970, 1975; Alexander, 1993) and other extrinsic and intrinsic processes.

In addition to the assessment of causative factors driving morphological changes, it is also beneficial to understand the time span over which observed morphological change in the fossil record. Studies have documented that shell shape can vary over a wide range of time scales, from abrupt shifts within a couple of generations (Brower, 1995) to gradual changes over tens of millions of years, (Daley, 1999a). Bivalve morphology can also be relatively stable over the time scale of hundreds to thousands of years (Bush et al., 2002) , and display minor changes over millions of years (Stanley and Yang, 1987). Alternatively, as shown by some other morphological studies, bivalves can exhibit rapid phenotypic changes over time spans of less than one million years (Crampton and Gale, 2002) .

The mactrid bivalve genus, *Mulinia,* is an ideal candidate for morphological studies due to its abundance in modern marine environments and its remarkable abundance in fossil deposts over the past three million years. The ecological and commercial importance of modern *Mulinia* in the western Atlantic and Gulf of Mexico has resulted in numerous studies focusing on genetics and reproduction (Calabrese, 1970; Garton et al, 1984; Churchill and Gaffney, 1990; Gaffney et al., 1990; Ludwig, 1990; Wada et al., 1990; Guo and Allen, 1994) , feeding behavior and mechanisms (Morrison et al., 1977; Montagna et al,, 1993; Navarro and Velasco 2003; Navarro et al., 2003); , and ecological and environmental influences (Kennedy et al., 1974 Fallaw, 1975; Jackim et al., 1977; Walker and Tenore, 1985; Williams et al.,1986; Ho et al., 1999; Velasco and Navarro 2003). *Mulinia* species have been shown to be an important contributor to food web, and decimation of populations have been documented to have a detrimental affect of local ecology (Rodriguez et al., 2001; Contra-Buenrostro et al., 2005) .

The purpose of this study is to test the importance of changing environmental conditions over a geologically limited time interval of less than one million years. By investigating the morphospace of the Pliocene mactrid *Mulinia congesta,* across different depositional environments and through time over a limited geographical area it will be determined if the morphological changes occurring over hundreds of thousands years, including differences induced by major environmental changes over longer time scales, notably exceed morphological variation observed within single fossil horizons. This type of study will address a series of important questions, especially for mactrid bivalves targeted in this analysis, including the relative importance of changing environmental conditions on bivalve morphology and the degree of variation within single morphospecies at a scale of geologically fine resolution.

Materials

Mulinia sp.

The genus *Mulinia* was erected by Gray (1836) to differentiate species of the family Mactridae that possess an internal ligament and non-gaping shell. Taxonomic uncertainties and diagnostic difficulties within the *Mulinia* lineage are well documented in the literature (Dall, 1898; Gardner and Aldrich, 1919; Keen, 1971). Throughout the late 1800's and early 1900's, new species of *Mulinia* were based on qualitative shell characters that were ambiguous to apply in practice and led to frequent misidentifications, especially as a high amount of variability was qualitatively observed in the genus (Gardner and Aldrich, 1919; Keen, 1971) . As a result, numerous species are likely to be synonyms, primarily separated by arbitrary boundaries such as state lines (e.g., *M. bryonensis, M. acuta* and *M. modesta* may all be synonyms of *M. coloradonesis*; Dall, 1898; Keen, 1971)

In addition to ambiguous species identification within the genus, the evolutionary history of *Mulinia* in North America is unclear. On the Atlantic Coastal Plain, *Mulinia* became stratigraphically prominent starting with *M. congesta* in the Pliocene, which suddenly appeared over a wide geographic range, from Prince Edward Island to South Florida (Brande, 1979). However, *M. congesta* was present in the Atlantic Coastal Plain for only a brief geologic time, restricted to the Yorktown Formation in Virginia and North Carolina and its temporal equivalents (Brande, 1979; Ward and Blackwelder, 1980). By the end of the Pliocene, *M. congesta* was replaced in many localities by *M. lateralis*, which is currently abundant over a geographically widespread area and can occupy a variety of environmental settings. The widespread distribution and high densities observed for fossil *M. congesta* are very similar to what is observed in the proposed descendant species, *M. lateralis*. Comparisons between the two species suggest that *M. congesta* could have been an ecologically important species for many

Pliocene benthic associations, just as *M. lateralis* is ecologically important in many benthic communities today. *Mulinia. congesta* certainly is on of the most abundant mollusks of the Yorktown Formation.

In modern environments, from Prince Edward Island in Canada to tropical waters of the Yucatan, Mexico, populations of *M. lateralis* (Atlantic) and *M. coloradoensis* (Pacific) often reach the extreme densities of hundreds to tens of thousands of individuals per square meter (Parker, 1975; Walker and Tenore, 1985; Williams et al., 1986; Van Dolah et al., 1991; Montagna et al., 1993; Kowalewski et al., 2000) . This is due to the r-selective traits of the genus; high fecundity (> 1000 larvae per 100 gallon sample can be observed in water temperatures between 19° to 21° C; Calabrese, 1970); high juvenile mortality (Levington and Bambach, 1970), and survival in salinities ranging from 5 ppt to 80 ppt (Parker, 1975). Calabrese (1970) documented populations of *M. lateralis* with abundant gametes produced by specimens as young as 60 days (~ 3 mm shell length), and probably more than one generation of *Mulinia* is produced within a year. The life habitat of *M. congesta* is described as being a shallow infaunal siphonate suspension feeder that can be found in a wide variety of substrates but prefers mud to muddy sand settings in estuarine habitats that are rich in organic detritus (Calabrese, 1970). Although classified as a suspension feeder, modern *M. lateralis* is capable of using the exhalent siphon to stir up the organic rich bottom so particles are suspended in water and then draw nutrients out of suspension, (Parker, 1975).

Study area

A paleogeographical, depositional, and paleoclimatic interpretation of the Yorktown Formation and its correlative units was proposed by Ward, Bailey and Carter (1991) using radiometric dating, planktonic foraminifera zones, and regional and global sea level curves. According to that study, global warming trends and regional subsidence occurred 3.4 to 3.0 million years ago and triggered a notable transgression that deposited the Rushmere and Morgart's Beach Members of the Yorktown Formation in the Salisbury and Albemarle embayments of southeastern Virginia and North Carolina. Initial studies of the Yorktown described several lithofacies from pebbly coarse-grained sand to shelly fine-grained sand clay units. Mansfield (1931, 1943) subdivided the formation into molluscan faunal zones; Zone 1, the *Pecten clintonius* zone, the lowermost section of the formation, and an upper Zone 2, or *Turritella alticostata* zone. Zone 2 was further divided into an upper, middle, and lower zone, based on faunal differences. Ward and Blackwelder (1980) redefined and divided the formation into four lithostratigraphic members (Sunken Meadow, Rushmere, Morgart's Beach, and Moorehouse) based on lithology, stratigraphy, and faunal relationships. The Sunken Meadow Member is equivalent to Mansfield's Zone 1 and the Rushmere, Morgart's Beach, and Moorehouse members are within Mansfield's Zone 2. Four unconformities have been described in relation to the Yorktown, two that bound the formation, one interpreted as a hiatus between Sunken Meadow and Rushmere members, and another between the Morgart's Beach and Moorehouse members (Ward and Blackwelder, 1980) . Three transgressive events have been proposed to explain the deposition pulses of the Sunken Meadow, Rushmere-Morgart's Beach, and Moorehouse members (Ward and Blackwelder, 1980; Ward and Strickland, 1985; Daley, 1999b).

The Rushmere member, a fine, well-sorted shelly sand that overlies the Sunken Meadow member and the older Eastover Formation or Piedmont rocks, was interpreted as being deposited during the maximum transgressive phase within the Yorktown, at a time when a shallow open sea with normal saline conditions covered a large area of the Virginia Coastal Plain. The unit contains a highly diverse mollusk fauna (> 250 species) (Ward and Blackwelder, 1980; Ward and Strickland 1985). The Morgart's Beach Member overlies the Rushmere and consists of a very fine sandy to silty clay interpreted as representing a low-energy setting (Ward and Strickland, 1985). There is no sharp erosional contact between the Rushmere and Morgart's Beach members, and in some localities the members are intertonguing suggesting a facies boundary (Ward and Blackwelder, 1980; Daley, 1999b). While faunal assemblages between the two members are similar, mollusks occurring in Morgart's Beach Member are less abundant and of smaller size (Ward and Blackwelder, 1980). Overall, the units within the Yorktown formation are very fossiliferous which suggests favorable environmental conditions for supporting abundant and diverse molluscan assemblages.

Paleocommunity association

The unconformity-bound Rushmere-Morgart's Beach units can be further subdivided into three paleocommunity types (*sensu* Bennington and Bambach, 1996) based on statistical analysis of the faunal composition of bulk samples (Daley, 1999b). The Rubbly Bottom Paleocommunity Type (RBPT) occurs within the lower Rushmere and is dominated faunally by *Chama congregata*, an epifaunal heterodont bivalve found today in shallow waters (<15 m water depth) where it cements to hard substrates (Rehder, 1995). While *Mulinia* is not dominant in the RBPT, it is abundant enough to be sampled. Other species found in abundance within the RBPT were *Cyclocardia granualata*, *Crepidula costata* and in some cases *Astarte undulata*, all sessile suspension feeders that today are found associated with sand to rubble substrates in shallow water settings (Rehder, 1995). The Muddy Bottom Paleocommunity Type (MBPT) was the result of "soupier" bottom conditions, with deposits dominated by sandy silts and clays and mud content typically exceeding 20% by weight (Daley, 1999b). The lower boundary of MBPT is associated with the contact between the Rushmere and Morgart's Beach members. *Mulinia congesta* is the dominant faunal type within MBPT, representing 32.5% to 91.9 % of the samples collected. Other very common taxa within the MBPT are *Yoldia laevis*, a shallow infaunal deposit feeder (Parker, 1975) and *Ostrea sculpturata*, a cemented epifaunal suspension-feeding oyster (Parker, 1975). The upper Rushmere represents a transition from the RBPT to the MBPT with fluctuating mud content from 5 to 20% by weight. This portion of the sequence is referred to as the Transition Zone (TZ), which is typified by a loss in abundance of *Chama congregata* and a concurrent increase in dominance of *Mulinia congesta*. The different and concordantly shifting sedimentological and faunal patterns across the three paleocommunity types justify using these units as proxies for environmental conditions.

Methods

The degree of influence that environmental factors such as energy can have on the bivalve shell morphology was assessed by quantifying and comparing the *Mulinia* morphospace through the change in paleocommunity associations observed in the Rushmere and Morgart's Beach sections. It was assumed that a bulk sample confined to a single stratigraphic level can be used as to estimate morphological characteristics (shape variance, mean shape, mean size, etc.)

of paleo-populations of *Mulinia*, despite the fact that such samples likely represent hundreds to thousands of years of time averaging (Kowalewski and Bambach, 2000; Kowalewski et al., 1998, 2000; Hunt, 2004). Previous studies on assessing the effects of time-averaging on morphospace of various invertebrate shells have showed that the amount of morphological variation observed in fossil and subfossil assemblages can be comparable to the full range of shape variability present in living populations, and can be potentially recognized despite taphonomic processes (Bush et al., 2002; Hunt, 2004; Krause, 2004).

If environmental factors, such as energy, can have a strong influence on bivalve shell morphology, then morphospace occupied by specimens sampled from different paleocommunity associations will be significantly different from one another. In addition, notable changes in shell shape and/or size should correspond to environmental shifts associated with lithofacies and faunal paleocommunity changes observed throughout the RBPT to MBPT succession. Conversely, if effects of changes in substrate and environmental energy effects on hard shell morphology are minimal, then no significant changes in shape or size between different paleocommunity associations should be observed.

Samples were collected by G.M. Daley from five natural outcrops along streams and rivers of southeastern Virginia (Fig. 3.1). Collections were made by bulk sampling along two vertical sections at 0.33 meter (1 ft) intervals at each outcrop locality. Each sample was excavated from the outcrop using a rectangular section 0.33-0.66m wide, 2.7-7.5 cm high, and 0.33 cm deep (Daley, 1999). Samples were air-dried for several days, and then 2.3 kg (5 lbs) of each sample was removed for processing. The rest of the collection was left unprocessed and preserved for future examination (the collection is housed at the Department of Geosciences, Virginia Polytechnic Institute and State University). The processed samples were washed through both 4 mm and 1 mm sieves using gentle agitation. The washing was done in a tub to ensure that fines were retained. Material larger than 1mm was allowed to dry and then picked for identifiable molluscan remains (for a more detailed description of methods see Daley, 1999b). The majority of countable specimens were identified to the species level using Gardner (1945, 1948) and Campbell (1993). Specimens in which species-specific characteristics were not preserved were identified only to the genus level.

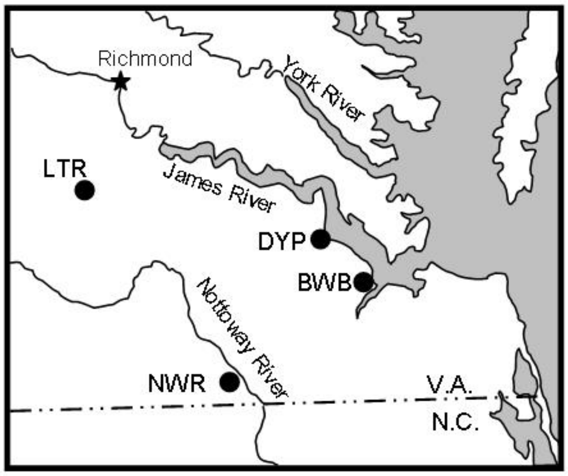

Figure 3.1 – Study site map showing location of collections localities, in southeastern, Virginia, U.S.A. Black dots indicate collection localities: (BWB) Burwell Bay, (DYP) Day's Point, (LTR) Lieutenant's Run, (NWR) Nottoway River), (KGM) Kingsmill. Star marks city of Richmond.

All *Mulinia* specimens found in samples were disarticulated. Since right and left valves may vary subtly and not represent exact mirror images of one another in some aspects (e.g., hinge); only right valves were used in this study. Samples were picked until either all *Mulinia* specimens were exhaustively separated or until a minimum of 100 photo quality whole right valves became available for analysis.

Landmark data acquisition

Each valve was given a unique identification number and the interior of the valve was photographed against a metric grayscale plate using a Nikon 990 Coolpix digital camera. Scion/NIH freeware (http://www.scioncorp.com) was used to calibrate each image using the metric grayscale and acquire Cartesian coordinates for each valve. Accompanying data about site, locality, location in the sampled section and paleocommunity type identified by Daley (1999b) were also recorded by the use of set numerical identifiers. Out of 607 *Mulinia* specimens, 154 specimens were classified into the RBPT, 195 specimens into the MBPT and 258 into the TZ.

In the initial analysis, 17 landmarks and pseudolandmarks were used to describe the shape of the shell (Fig. 3.2; Table 3.1). For 7 valves, selected using a random number generator, the entire data collection process from capturing the image to extracting the Cartesian coordinates was repeated ten times to investigate the imprecision due to operator error. Two landmarks, both located in the hinge region, (landmarks 16 and 17), could not be acquired with high enough precision to be used in the final analysis (Fig 3.3); the amount of variation observed in the repeated measurements of those two landmarks for the same specimens did not differ significantly from variation in those landmarks observed between different specimens (F=10.85; p=0.06, ANOVA). This was most likely due to the small size of the valve and frequent taphonomic alteration to the hinge area. However, the loss of landmark data on the hinge plate may not be critical, since systematists working on the *Mulinia* species do not view hinge features as important diagnostic characteristics useful for differentiating species within that genus (Tuomey, 1857; Dall, 1898; Gardner and Aldrich, 1919; Keen, 1971). The 15 reliably measurable landmarks and pseudolandmarks (Table 3.1; Figs. 3.2, 3.3) were used in the final analysis presented below.

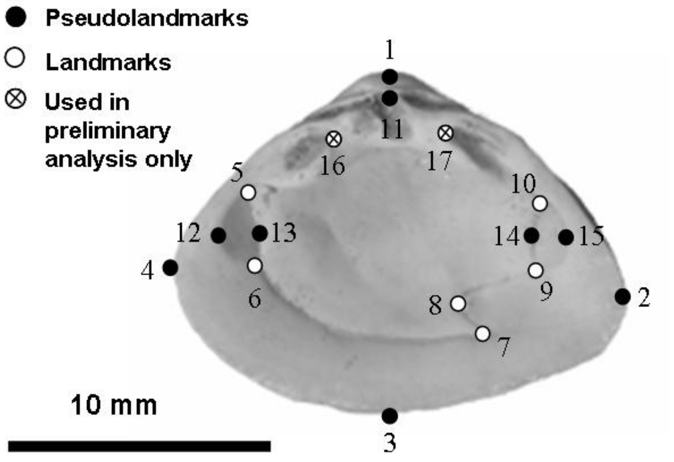

Figure 3.2 – Six landmarks (5-10) and 9 pseudolandmarks (1-4, 11-15) measured on *Mulinia congesta* to be used for analysis of geometric methods, explanation in table 3.1. Points 16, 17 on the hinge were initially included in preliminary analysis but were later excluded based on low precision, see figure 3.3.

Table 3.1. Description of landmark and pseudolandmarks chosen. Points 1-15 were proven to be reliable based on minimal operator error. Points 16 and 17 were removed due to high potential error.

	Abbreviation	Type	Description
1	dor	pseudolandmark (type II)	Dorsal most point of the valve
2	post	pseudolandmark (type II)	Posterior most point of the valve
3	ven	pseudolandmark (type II)	Ventral most point of the valve
4	ant	pseudolandmark (type II)	Anterior most point of the valve
5	p-ant-add	anatomical landmark (type I)	Peak of anterior adductor muscle scar
6	ant-add	anatomical landmark (type I)	Junction of the pallial line with anterior adductor muscle scar
7	out	anatomical landmark (type I)	Maximum curvature of the pallial line
8	sin	anatomical landmark (type I)	Maximum curvature of the pallial sinus
9	post-add	anatomical landmark (type I)	Junction of the pallial line with posterior adductor muscle scar
10	p-post-add	anatomical landmark (type I)	Peak of posterior adductor muscle scar
11	hinge	pseudolandmark (type II)	Maximum curvature in hinge line
12	o-ant-add	pseudolandmark (type II)	Maximum outward point of curvature in anterior muscle scar
13	i-ant-add	pseudolandmark (type II)	Minimum outward point of curvature in anterior muscle scar
14	i-post-add	pseudolandmark (type II)	Maximum outward point of curvature in posterior muscle scar
15	o-post-add	pseudolandmark (type II)	Minimum outward point of curvature in posterior muscle scar
16	hinge-add	anatomical landmark (type I)	
17	hinge-post	anatomical landmark (type I)	

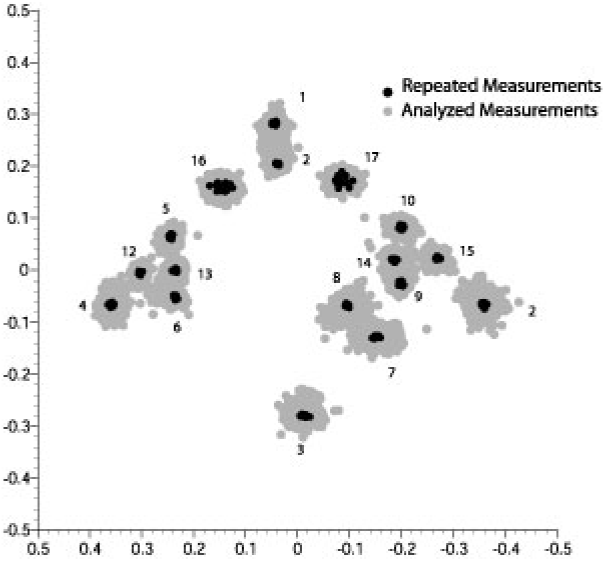

Figure 3.3 – Operator error. Full Procrustes fit of all specimens in gray points with ten replicates of seven specimens (black points). The spread of repeated measurements overlap heavily at each landmark with less spread than the full sample.

Analytical methods

There are a series of landmark based methods that may be chosen based on characteristics of the data set (for an overview of Procrustes analysis and landmark geometrics see Bookstein, 1990, 1996; Chapman, 1990; Rohlf 1990,1998,1999; Rohlf and Slice, 1990; Slice, 1996 Zeilditch et al., 2004). Preliminary analysis of the landmark coordinate was completed for both Resistant Fit and Least Squares Procrustes algorithms. Generalized Least Squares Full Procrustes Analysis (GLS- FPA) is preferred in situations where the variance of shape is spread evenly among the landmarks chosen (Chapman 1990). Resistant full-fit Procrustes Analysis (RF-FPA) uses median estimates for fitting parameters instead of least squares, which make this method less sensitive to extreme values compared to least-squares and is preferred in situations where change in shape is localized around one or a few landmarks (Rohlf, 1990; Slice, 1996). To compare the analysis of these two Procrustean methods, a GLS-FPA and RF-FPA were run on all landmark data using CoordGen6, part of the Integrated Morphometric Package (IMP ©, Sheets, 2004). In the case of this study, an ANOVA comparing the amount of variance at each point as a result of using Generalized Least Squares and Resistant fit was not significant at $\alpha= 0.05$, suggesting that the results from both methods are comparable.

As GLS-FPA has a better developed distributional theory than RF-FPA, the remaining analysis will be completed using Generalized Least Squares. Geometric morphometric analysis of the data was completed using a modified SAS/IML code designed to perform (GLS-FPA), from Bush et al. (2002). The program code creates a reference (mean) configuration from all 607 specimens and then landmarks from each specimen were translated, rotated and scaled to minimize using a least-squares algorithm (Figure 3.3).

Scaling was standardized using centroid size, defined as the square root of the summed squared distances from each landmark to the common centroid. While rescaling reduces the effect of size on variability, it does not remove allometric (size-related) shape changes that may affect landmark configurations, which could mask a possible environmental signal. By regressing the tangent coordinates of each landmark against centroid size and by using the resulting allometry – free residuals in subsequent analysis, differences in landmark positions due to age/size variation across the specimen can be assessed and minimized. While shape variability of a group compared to another can be roughly visually gauged by the amount of spread that is observed around the tangent coordinates of the landmarks on the Generalized Procrustes superimposition, the program also calculates the amount of morphological variability present in a given sample or set of samples. This is calculated as the square root of the mean square distance between specimen landmarks and the mean configuration. Variability of a sample was calculated using both the tangent coordinates and the allometry-free residuals, and then plotted based on stratigraphic location.

Mulinia morphology from the three paleocommunity associations was compared to one another using centroid size and shape both to assess the overall trends observed within the species throughout the sampled time interval as well as to test for morphometric correlatives of paleoenvironmental changes. While other measures of size such as length or width could be used, centroid size is the most common metric used in geometric morphometric studies (Dryden and Mardia, 1998). The mean and median centroid size of *Mulinia* was calculated for each sampling horizon and paleocommunity association. The statistical significance of differences in size was evaluated using non-parametric methods, including Kruskal Wallis and Wilcoxon two-sample tests, with the assumed α of 0.05. Confidence intervals for the median size and variance at each sampling horizon were calculated using a 1,000 iteration bootstrapping module.

To assess the patterns in morphospace based on paleocommunity associations, both exploratory and confirmatory multivariate statistical methods were employed. The general morphospace occupied by samples from each paleocommunity and its comparison to the other paleocommunities was explored using Principal Component Analysis (PCA). This was completed for both the set of initial tangent coordinates calculated from GLS-FPA and the allometric-free residuals.

While PCA explores the amount of variation present in the data without any a priori grouping assumptions, the use of canonical variate analysis (CVA) for a priori defined groups maximizes the differences with respect to within-group variation (Albrecht, 1980). We used paleocommunity association as the basis for the a priori groups. As with PCA, CVA was completed for the Procrustes tangent coordinates and the allometric-free residuals. As tangent coordinates are subject to four almost linear constraints that yield meaningless coefficients during the inversion of the covariance matrix (Bookstein, 1996), the smallest four eigenvalues from the tangent coordinates were removed according to the protocol to remove meaningless coefficients outlined by Bookstein (1996) and Rohlf (1999). In addition the significance of the morphological differences among the paleocommunity associations was based on a discriminant function using Mahalanobis distances.

While the statistical analysis of shape coordinates can depict the overall morphospace realized across all specimen groups, additional information may be gained by visualizing how landmarks are displaced relative to one another. To determine the possible direction of landmark movement in average specimen shape through time or across environments and paleocommunity association, a thin plates spline analysis using tpsSpline freeware (Rohlf, 2004) was completed using the mean configurations of each paleocommunity. Pairwise comparisons of splines were completed for RBPT - TZ, TZ –MBPT, and overall change from the RBPT to the MBPT.

Differences in results between analyses that were completed using tangent coordinates versus those based on allometric-free variables may indicate an allometric effect. This allometric effect could result in different morphologies that could be (1) the result of one paleocommunity population achieving a different size than the other or (2) a change in allometric growth patterns as a result of environmental changes. The potential allometric patterns were investigated by creating bivariate plots for each of the tangent coordinates derived from the Procrustes Analysis against the calculated centroid size. For each tangent coordinate, the Pearson’s correlation coefficient (r), was used to test for strength and significance of allometric correlations between the centroid size and a given landmark coordinate. The coefficient of determination (r^2) and adjusted coefficient (r_a^2) were used to estimate the percent of variance in the tangent coordinate that can be accounted for by centroid size. In addition, a second thin plate spline analysis was completed to visualize the transformation of shape from smallest specimens (i.e., those placed in the lowest quartile in terms of centroid size) to largest specimens (i.e., those placed in the highest quartile).

Results

Analysis of shape

For many landmark points, specimens from the RBPT appear to be more variable (i.e., specimens spread over a greater area for a given landmark) than for the two other paleocommunity types (Fig. 3.4). This elevated variability among the analyzed specimens, is particularly notable for landmarks associated with the pallial line and sinus, (landmark points 6, 7, and 8; Fig 3.4). When the total variability, estimated across all landmarks for each sampled layer, is plotted stratigraphically, there is a decrease in both the total and allometry-free variability from the RBPT to the TZ within the Rushmere member. In contrast, the amount of total and allometry-free variability remains relatively constant through the TZ and MBPT (fig 3.5). For the most part, the spreads of points around the landmarks for specimens in the MBPT and transition zone appear to be distributed in a circular fashion, which is expected if variation present around landmarks is random (e.g., Goodall, 1991; Dryden and Mardia, 1998; Klingenberg and Monteiro, 2005). Specimens associated with the RBPT are more elliptical in their distribution around landmarks associated with the posterior muscle scar and pallial line (Fig 3.4) suggesting a factor such as allometry, affecting the shape.

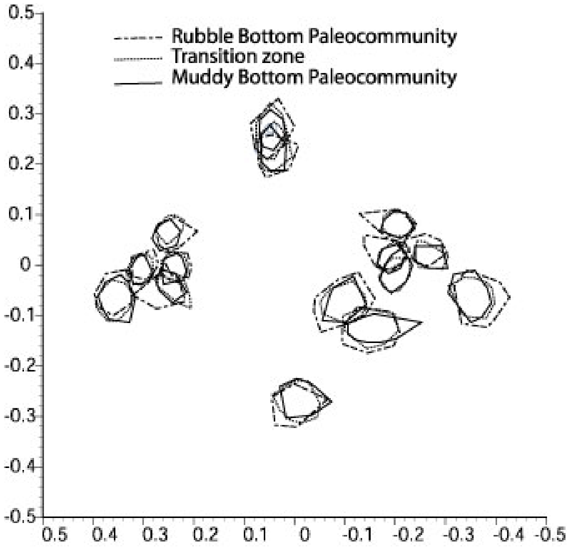

Figure 3.4 – Resulting space occupation of full Procrustes fit of all 607 specimens.

Principal component analyses based on tangent coordinates and allometry-free residuals both revealed a high degree of overlap between *Mulinia* morphospace from the three paleocommunity associations for PC1 vs. PC2 and PC2 vs. PC3 ordinations (Fig 3.6). Qualitatively, there is little difference between ordinations based on tangent coordinates versus those based on the allometry-free residuals; even the eigenvalues of the principal components are comparable. The first three principal components account for less than 50% of the observed variation in the data. For both tangent coordinates and allometry-free residuals, plotting the data using higher PCs does not reveal any notably different patterns when comparing the three paleocommunity types. The specimens from the RBPT occupy a greater amount of morphospace, compared to the other paleocommunity associations, but this is possibly due to a few outlier specimens (Fig 3.6).

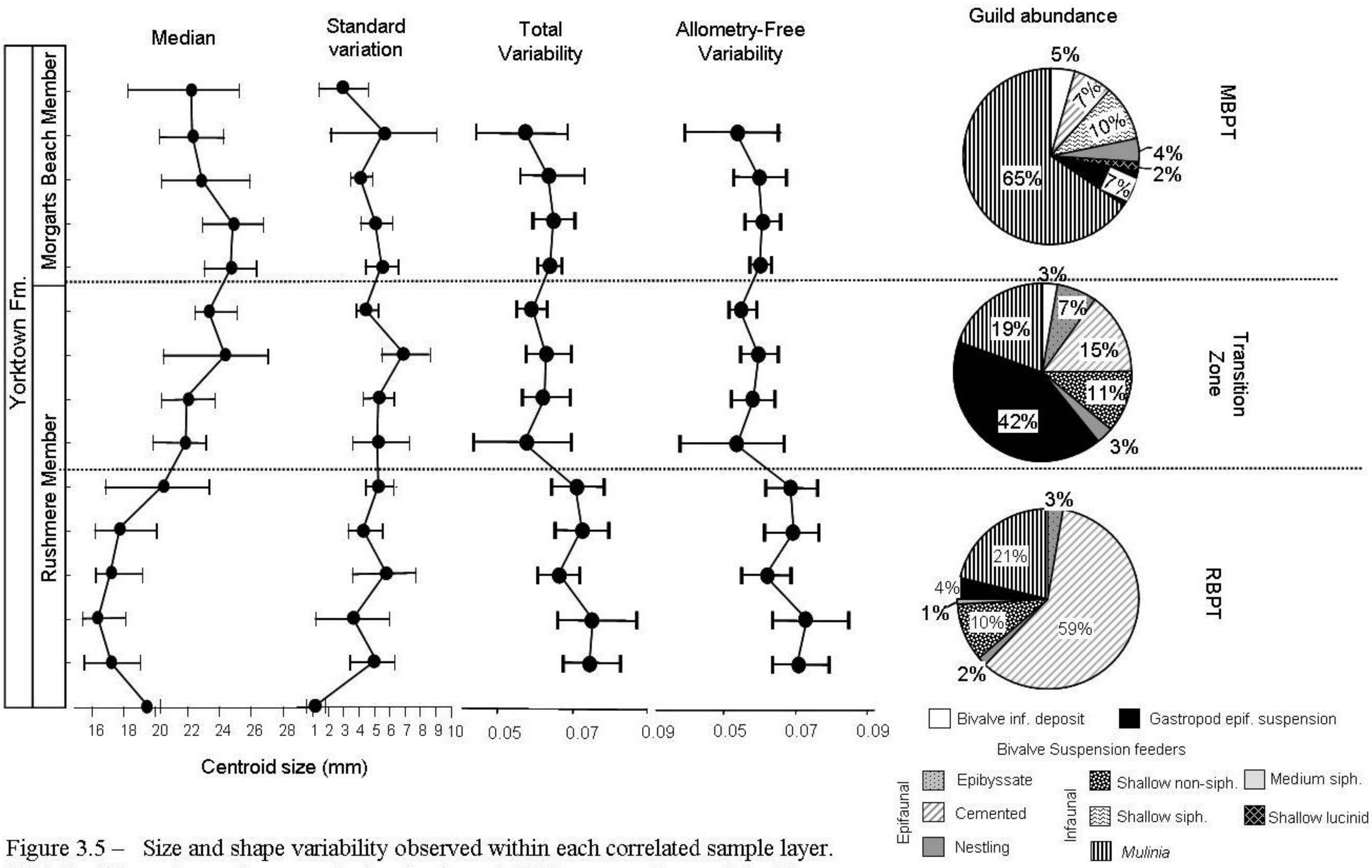

Figure 3.5 – Size and shape variability observed within each correlated sample layer. 95% Confidence intervals were calculated using a 1,000 bootstrapping module. The guild abundance indicated the percentage of specimens collected in each paleocommunity for the ten most abundant fauna.

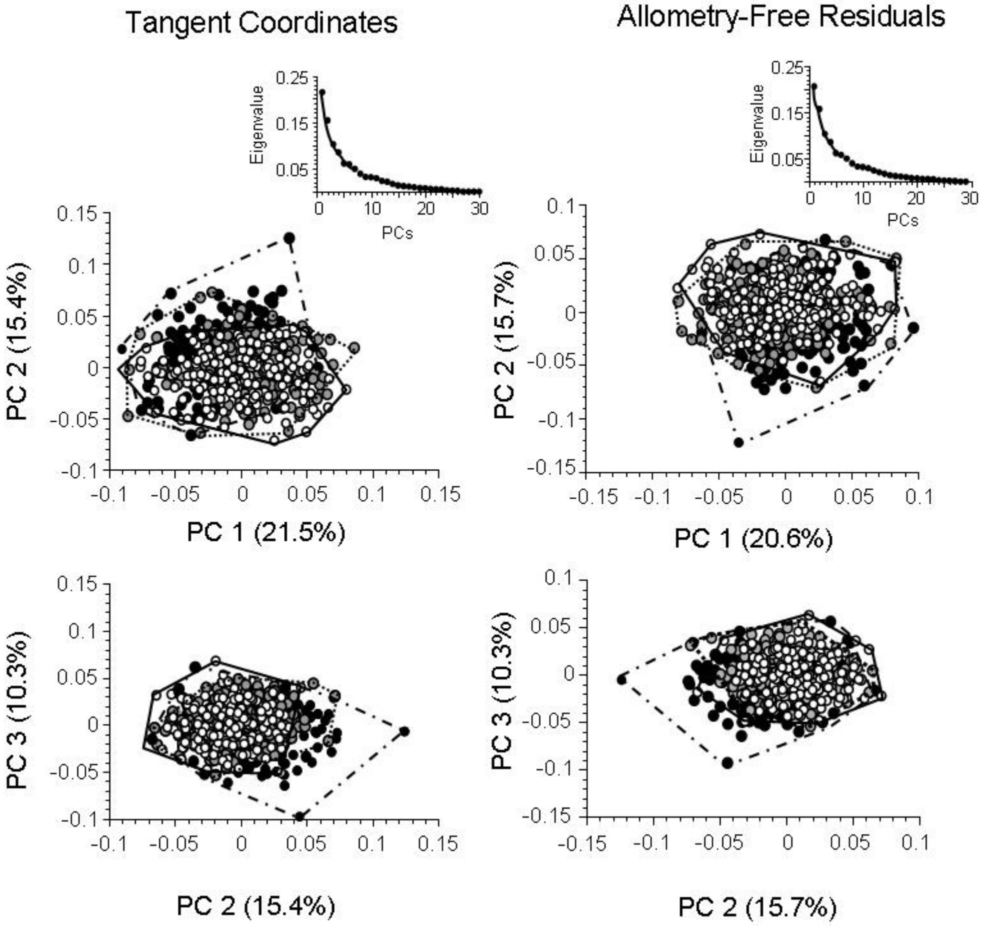

Figure 3.6 – PC ordination of all 607 specimens using tangent coordinates and allometry-free residuals. Nearly perfect overlap of morphospace between all three paleocommunity types. All 607 specimens were analyzed simultaneously, then plotted separately based on paleocommunity type classification Black dotes are RBPT, gray are the transition zone and white indicate MBPT.

Even when the data are plotted using a canonical variate ordination designed to maximize the differences between the groups, there still is a high degree of overlap between groups (Fig. 3.7). As in the case of PC ordinations, the scatter plots and eigenvalues do not differ notably whether tangent coordinates or allometry-free residuals are used. The most discernable difference observed along CV1 is the partial separation of the specimens from the RBPT from the other two paleocommunity types. As for the other two paleocommunity types, while the specimens from the MBPT and the transition zone do not overlap as completely in CV ordinations as they do in PC ordinations, there still is a heavy amount of overlap between the two groups.

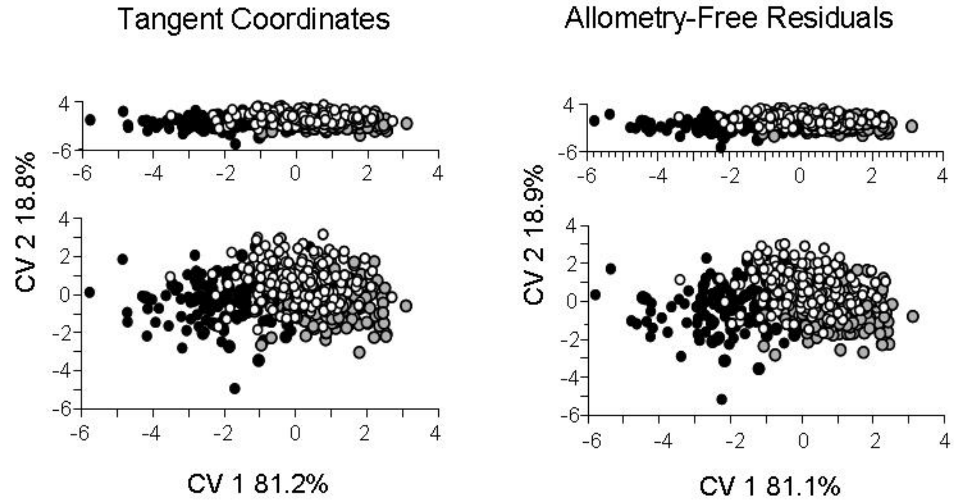

Figure 3.7 – Scatter plot of canonical ordination of tangent coordinates in the left column and allometry –free residuals in the right column. Blacks dots represent RBPT samples, grey dots the transition zone and white dots the MBPT. (A) Plots with axes to scale of one another (B) Plots were the y-axis as been extended x4 to better show the

Discriminant analyses suggest a high rate of misclassification of specimens into incorrect paleocommunity types: error rates for both the tangent coordinates and allometry-free residuals are around 33%, which is the error rate expected if a single statistical population were randomly split into three groups (Table 3.2). This “maximally insignificant” error rate of misclassification, not only supports the visual conclusion from the ordination scatterplots that *Mulinia* specimens from different paleocommunities overlap greatly in morphospace, but in fact strongly suggests that these specimens may have come from the same morphospace. Interestingly, however, there is a gradient in the amount of misclassification for specimens that have an *a priori* MBPT assignment: 28% specimens were *a posteriori* classified into the transition zone, but only 11% were misclassified into the RBPT. Contrary to that, the misclassification rates for the TZ and RBPT do not exhibit any obvious gradients in misclassification (Table 3.2). For the TZ, only 2.3% of the sample was misclassified into the RBPT compared to 23.6% of the sample that was classified into the MBPT. For the RBPT, the majority of specimens was misclassified into the MBPT (21.4%), and not the TZ (12.3%).

Table 3.2. Cross-validation of specimens. A priori classification was based on paleocommunity association, a posteriori are based on Malahanobis distances of individuals from the means of the a priori group. Total error refers to the rate that specimens from the entire data set were incorrectly classified.

Posteriori Classification

			Tangent coordinates				Allometry-free residuals			
			RBPT	TZ	MBPT	Total	RBPT	TZ	MBPT	Total
A priori classification	MBPT	n	22	56	117	195	20	63	112	195
			11.30%	28.70%	60.00%		10.20%	32.14%	57.65%	
	Transition zone	n	6	191	61	258	9	187	62	258
			2.30%	74.03%	23.64%		3.50%	72.76	23.74	
	RBPT	n	102	19	33	154	102	17	35	154
			66.20%	12.34%	21.43%		66.23	11.04	22.73	
	Total		130	266	211	607	131	267	209	607
			21.42	43.82	34.76		21.58	43.99	34.43	
			Error Count Estimates				Error Count Estimates			
	Rate		0.3377	0.2597	0.4	Total Error	0.3377	0.2724	0.4235	Total error
	Priors		0.3333	0.3333	0.3333	0.3325	0.3333	0.3333	0.3333	0.3445

A thin plate spline (TPS) analysis of the mean shape configurations from the RBPT to the Transition Zone, supports the above-discussed Procrustes-based analyses. Specifically, TPS also suggests that the greatest amount of change occurs between the RBPT and the Transition Zone (Fig 3.8), primarily driven by a ventral displacement of the posterior adductor muscle landmarks and a dorsal shift of the anterior muscle landmarks. The net change observed from RBPT to MBPT appears to be slight movement of the posterior muscle scar.

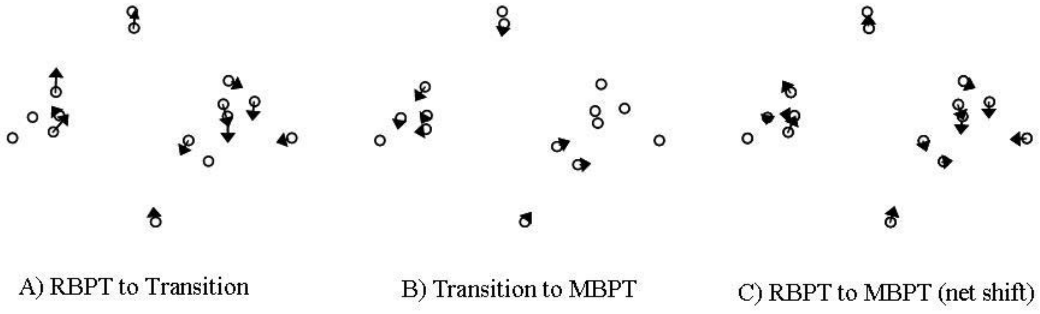

Figure 3.8– Thin plate spline visualization of the mean configurations of *Mulinia*, with the older paleocommunity serving as the reference shape using the tangent coordinates. The arrows indicate direction and magnitude (x4) of the landmark movements.

Analysis of size

When the data are pooled based on paleocommunity type, the mean centroid size is smallest for the RBPT (18.1mm), intermediate for the MBPT (22.4mm) and largest for the TZ (24.2mm) (Fig. 3.5). Median centroid size values, which is close to the mean centroid size values within each group (RBPT, 17.4 mm; TZ 23.9 mm; and MBPT, 22.27mm), varies significantly in central tendency among the three paleocommunity types ($p < 0.001$, $\chi^2 = 105.3$. Kruskal Wallis test). Pairwise comparisons between the paleocommunity types also were all significant ($p< 0.05$ in all three cases; Table 3.3). When looking at the centroid size pattern upward throughout the compiled stratigraphic section the median centroid size increases from the RBPT to the transition zone and then remains relatively stable through the MBPT (Fig 3.5). The amount of variance in centroid size fluctuates through the section as well, although fluctuations in variance appear much less pronounced than those in central tendency, as estimated by the median centroid size.

Table 3.3 - Centroid size (mm) for samples results from pairwise comparisons

	Centroid size (mm)			Wilcoxon two-sample test		
	Mean	Median	std		Z	p
MBPT	22.4	22.3	4.1	RBPT vs. MBPT	-7.84	<0.0001
TZ	24.2	23.9	5.4	MBPT vs. TZ	-3.83	0.0003
RBPT	18.1	17.4	4.8	RBPT vs. TZ	-10.24	<0.0001

Analysis of allometry

Allometric analyses, whether carried out on pooled data or separately by paleocommunity type, did not reveal any strong allometric pattern. As illustrated on bivariate plots of the tangent coordinates versus centroid size, no visible relationships between the two variables can be observed for a great majority of landmarks (Fig 3.6). Indeed, most of the tangent coordinates have Pearson's correlation values ranging from $0.01 < |r| < 0.4$. Only the y-coordinates for the maximum width of the posterior adductor muscle (points 14 and 15) possessed r values greater than 0.5 (for specimens from the Transition Zone and MBPT only). All possible Pearson's correlation coefficients for the specimens from the RBPT were less then 0.5. Weak allometry affects most variables: 23 out of 30 tangent coordinates were significantly correlated with Centroid Size ($p<0.001$).

The adjusted coefficients of determination (r_a^2) were very low, with twenty four of the coordinates having $r_a^2 < 0.1$ for the data group as a whole, implying less than 10% of the variation can be accounted for by centroid size for most of the coordinates. When the data were analyzed by paleocommunity type, landmarks coordinates used to indicate the width of the posterior adductor muscle had r_a^2 values between 0.1 and 0.3 in all three paleocommunity types, implying that at most, 30% of variation in the landmark could be attributed to centroid size.

Discussion

The results indicate that the samples of *Mulinia congesta,* collected along the temporal-environmental gradient encompassing three Paleocommunity Types recognized within the Yorktown Formation of the southeastern Virginia, do not display any notable morphometric trends that could be correlated with environmental changes though time. Moreover, the *M. congesta* morphospace remains remarkably stable over a temporal gradient of approximately 500 k.y., except that the average shell size varies significantly across the three Paleocommunity Types. Allometric patterns and the span of morphospace occupied by *M. congesta* specimens do not differ significantly across the three Paleocommunity Types.

Significant shape changes may not have been detected for many reasons: (1) environmental conditions do not induce a shape change, (2) Environmental factors can affect *Mulinia* shell morphology, however, the rate of shape change cannot be detected in the rock record at a temporal scale of less than a 1 million years, or (3) *Mulinia* does respond morphologically to environmental changes regardless of how these changes are restricted to soft anatomical parts not otherwise recorded in the analyzed shell landmarks or (4) environmental conditions that control Mulinia ecophenotypy change at such a fine resolution that all samples contain mixed assemblages of ecophenotypes .

Fallaw (1975) study on *Mulinia lateralis,* a proposed descendant species of *M. congesta,* from Pleistocene deposits of the Atlantic Coastal Plain, suggest a positive correlation between shell length and energy level, where the minimum and maximum shell length within a given population increased with the percentage of sand content, a proxy for environmental energy conditions (Fallaw, 1975). This observation is opposite to the pattern demonstrated in this study, where specimens from the Muddy Bottom Paleocommunity Type and the Transition Zone, derived from sediments with a relatively smaller sand content, had a greater range and significantly larger mean shell size than the specimens derived from the Rubble Bottom Paleocommunity.

Many factors may affect bivalve size. Experimental studies of *Mulinia* have revealed that growth rates can be affected by temperature (Calabrese, 1970) and genetics (Gaffney et al, 1990). In addition, bivalve size can be influenced by (1) predation, where large size is an antipredatory trait (Boulding, 1984); (2) changing climate conditions, where bivalve growth rate and size are correlated with temperature (Vermeij, 1978; Harrington, 1987; Anderson, 2001) ; (3) nutrient availability and primary productivity (e.g., Vermeij, 1978; Allmon et al., 1993, 1996; Roopnarine, 1996); and (4) population density levels.

The apparent size increase from the RBPT through to the TZ and MBPT parallels an increase in the relative abundance of siphonate infaunal suspension feeders (Fig 3.5). While known to attain great densities, modern *Mulinia* populations never become exceedingly abundant if numerous invertebrate and vertebrate predators of mollusks are present locally. The reduced competition from the epifauna in the TZ and MBPT may have allowed for an increase in the relative abundance of shallow and medium infaunal suspension feeders, much as *Mulinia*. It is noteworthy that modern epifaunal bivalves tend to exhibit high efficiency at obtaining food from low nutrient environments compared to infaunal bivalves (i.e., their removal would notably increase accessible resources for other suspension feeders). While an increased availability of food could explain the size trend observed through the section, future studies evaluating individual specimens in terms of ontogenetic age (i.e., via stable isotope sclerochronology) placed in a more precise paleo-environmental context (e.g., via geochemical estimates of temperature and salinity) are needed to identify the primary causative factors controlling size changes in *Mulinia* shells.

Opportunistic bivalves such as *Mulinia,* characterized by rapid shell growth, have a potential to generate high amounts of morphometric variation due to allometry. However, the greatest amount of shape variation observed in the studied samples is within the RBPT, where *Mulinia* specimens encompassed the smallest size range among all available collections. Thus, the relatively higher amounts of shape variability cannot be attributed to allometric influences (i.e., greater size ranges that should result in stronger allometric effects were observed within the TZ and MBPT, yet both those groups of samples display lower amounts of shape variability). The greater shape variability seen within the RBPT sample may be a by-product of a more variable pioneer population of *Mulinia* first colonizing the Atlantic Coastal Plain during the studied transgressive-regressive cycle. In modern environments, *Mulinia* is extremely transient in terms of habitat occupation and its population dynamics are highly unpredictable; that is, *Mulinia* colonization events can be temporally and spatially sporadic (Sanders, 1956), and initial populations can achieve high densities only to disappear quickly, within a couple of years (Parker, 1956; Levinton, 1984).

There were large overlap and high rates of misidentification between non-adjacent paleocommunity types when specimens are reclassified using a more reliable jackknife cross-validation, thus suggesting that observed changes in morphospace do not follow a gradient that would correspond with the changing energy levels. The lack of a morphometric gradient may mean that shell morphology is not affected by substrate type/depositional environment. However, canonical variate analysis can only verify that there is non-significant difference between *a priori* defined groups; it cannot offer any biological reasons as to why a difference is not observed (Albrecht, 1980; Bookstein, 1991). This is because, due to rescaling induced by CVA, distances observed in CVA ordination cannot be directly related back to the original morphospace (Zelditch et al, 2004, Kligenberg and Monterio 2005)

Finally, the remarkable congruence between analyses based on tangent coordinates and the allometry-size free residuals strongly suggests that allometry does not play an important role in controlling the reported morphometric patterns.

Conclusions

1. The shell morphology of *Mulinia congesta* was remarkable stable over a temporal gradient of approximately 500,000 years despite a shift in paleoenvironmental conditions from high energy to low energy environments

2. A significant change in size of *Mulinia congesta* was observed between the different paleocommunity types. However, it does not follow the energy gradient preserved in the rock record.

3. It appears that there is a separation between rates of change in size versus shape of the *Mulinia congesta* shell. Size appears to be more volatile then shape, suggesting size is preferable as a paleoenvironmental indicator, while shape may be preferred to investigate slower trends such as those induced by changes in community structure over evolutionary time scales.

4. The lack of shape and size gradients that can be correlated with environmental gradients has several implications. It is possible that ecophenotypy cannot be detected within the fossil record at small temporal scales. The other possibility is that opportunistic species have great morphological stability that is not affected by changes of environmental conditions.

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Vita

Jennifer A. Stempien was born in Syracuse, NY in August 1978. After graduating with honors from Cicero- North Syracuse High School with and emphasis on science and French, Jennifer attended the State University of New York at SUNY Binghamton with the intent of getting a degree in Biology with a minor in Geology. However with her first year of undergraduate studies she switched to a Geology major with emphasis in structural geology. In addition to her studied, Jennifer was very active as the treasurer of the undergraduate geology club and officer on the SUNY Binghamton Fencing club. For her excellence in both academic work and service to the department, Jennifer was awarded the Glenn G. Bartle award in 2000. Continuing her education at Virginia Tech Jennifer became involved with the maintenance of the Museum of Geosciences mineral collections and outreach activities, such as tours and creation of educational kits under the guidance of Susan Eriksson and Llyn Sharp. Her endeavors with the museum earned her the Department of Geosciences Service award in 2004 and College of Science Outstanding Graduate Student of the Year in 2006.