Examination of the abundance and geographic range of rare taxa: survivorship patterns of Miocene-Pliocene marine invertebrate fauna of the Virginia Coastal Plain

Austin L. Pryor
College of William and Mary

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Examination of the abundance and geographic range of rare taxa: survivorship patterns of Miocene-Pliocene marine invertebrate fauna of the Virginia Coastal Plain

A thesis submitted in partial fulfillment of the requirement for the degree of Bachelors of Science in Geology from The College of William & Mary

by

Austin L. Pryor

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(Honors, High Honors, Highest Honors)

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Williamsburg, VA
April 28, 2008
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Abstract

The concept of rarity is vital to the understanding of extinction selectivity. Ecological studies have demonstrated that rare taxa (e.g., those with small local abundance and limited geographic range) experience significantly elevated rates of extinction. Past paleontological work supports these conclusions with respect to geographic range and extinction selectivity. However, research to date, does not suggest that the same positive correlation applies when considering abundance-based selectivity in the fossil record. Analysis of the Miocene-Pliocene marine invertebrate fauna of the Virginia Coastal Plain indicates similar variable results with respect to abundance and geographic range during a period of background extinction. An overarching pattern of no selectivity across all taxa is illustrated through both a non-parametric victim-survivor comparison utilizing multiple abundance metrics and a comparison of β diversity partitioning to abundance-selectivity null models. Examination of solely the gastropod members of the community indicates extinction-selectivity for rare gastropods. The relationship between geographic range and selectivity is highlighted through a non-parametric victim-survivor comparison of geographic range data assembled from past work and quantified by the number of embayments in which particular taxa are found. The finding of rare-taxa selectivity among gastropods is strengthened by a comparison of abundance and geographic range, which indicates that victims tend to have low local abundance or limited geographic range. Therefore, there is an overall implication of both no selectivity and rare-taxa selectivity, suggesting spatial and taxonomic variance in ecological patterns of selectivity during background extinction.
Introduction

Empirical and theoretical ecological research indicates that rare taxa are most prone to extinction (Brook et al, 2006). Rarity is often defined in ecological literature in the context of abundance and geographic range. Paleontologists similarly use these notions of rarity to explore extinction selectivity, or which species went extinct and why in the fossil record. The majority of previous paleontological work focusing on geographic range and extinction concurs with ecological findings; endemic taxa go extinct at much greater rates than taxa with widespread geographic ranges (Jablonski, 2005). Furthermore, these patterns seem to hold true across all magnitudes of extinction (Payne and Finnegan, 2007). While the influence of geographic range on selectivity patterns has been thoroughly investigated, surprisingly few studies have explored the implications of abundance with respect to selectivity. A study of bivalves at the end-Cretaceous mass extinction suggests that abundance is not linked to survival (Lockwood, 2003). An investigation of Late Ordovician marine macroinvertebrate taxa implies that abundant taxa were targeted during a time of moderate extinction (Layou, 2007). These studies conflict with the ecological finding of selectivity against rare taxa.

Much of the previous paleontological work discussing rarity has focused on mass extinctions, with little attention paid to background extinction, or the continuous, low-level extinction that exists between episodes of mass extinction. Mass extinctions exhibit different characteristics than background extinction with respect to paleoecological communities, thus it is important to understand selectivity across both types of extinction. Additionally, most past work has focused on selectivity at the generic level or higher. An
examination of species level selectivity would contribute greatly to our understanding of the implications of rarity for survivorship at all taxonomic levels.

Miocene-Pliocene marine sedimentary units of the Virginia Coastal Plain provide an ideal setting for an investigation of the impacts of rarity on survivorship during a period of background extinction in the fossil record. The sedimentary record is relatively complete and well-exposed in this region, and features a well-preserved abundant fossil assemblage dominated by mollusks (Ward, 1992). Marine invertebrate assemblages provide the most robust fauna for exploring abundance in the fossil record (Kidwell, 2001).

This study seeks to address the following questions through an examination of Miocene-Pliocene invertebrate taxa of the Virginia Coastal Plain: 1) Is there a correlation between rarity (species-level abundance and geographic range) and survivorship during background extinction? 2) Is there a relationship between forms of rarity, specifically, abundance and geographic range?

Background

Definitions of rarity

Examinations of both modern ecological communities and paleocommunities frequently address the concept of rarity and apply different definitions. As a result, it is important to define what is meant when taxa are designated as rare. Definitions of rarity include: (i) geographic range – the area over which a taxon is distributed, (ii) habitat specificity – the number of different environments in which a taxon can live, and (iii) local population size – the abundance of a taxon in a given location (Rabinowitz et al,
1986). With multiple definitions of rarity, taxa are commonly labeled as rare by one or more of the definitions. It is thus important to understand what types of rarity a taxon exhibits, and how these rare taxa differ from one another.

Implications of rarity

Ecological studies commonly suggest that rare taxa are more likely to go extinct than those that are not. Both theoretical and empirical work generally indicate that species with reduced population size and geographic range face a considerably elevated risk of extinction (Brook et al, 2006). These findings concur with the intuitive idea that species that are widespread geographically, have large population sizes, or a combination of both, are harder to drive to extinction. Low abundance and limited geographic range substantially raise the risk of stochastic extinction (Gaston et al, 2000). Gaston and others (2000) further suggest the existence of a link between local abundance and geographic range and that this abundance-occupancy relationship is a widespread feature of ecological assemblages. Their research indicates that species with reduced abundance also show declines in the number of sites they occupy, or a reduced geographic range, while those with increasing abundance tend to have more widespread geographic ranges. This suggests that present-day environmental perturbations will most heavily impact rare, geographically restricted species, which will be unresponsive to adaptations honed by prolonged intervals of natural selection under background extinction (Jablonski, 1991).

While the impact of rarity in modern day ecological communities has been heavily studied and is well understood, much debate occurs over the implications of rarity when examining the fossil record. Paleontologists have attempted to understand
selectivity at extinction boundaries, with some examination of the different forms of rarity. Data from this research are further complicated because some researchers focus solely on periods of mass extinction while others focus on periods of background extinction. Mass extinctions stand out as a separate class of events from normal or background extinction and thus different processes could be impacting paleocommunities during these times (Raup and Sepkoski, 1982; Bambach et al, 2004; Jablonski, 2005). As a result, mass and background extinctions may have different patterns of selectivity with respect to rarity. Therefore it is important to distinguish mass extinction selectivity from the selectivity of background extinctions.

Limited paleontologic research has addressed the existence of extinction selectivity with regard to species level abundance. An examination of Late Maastrichtian bivalves from the North American Coastal Plain suggests the absence of a link between survivorship and abundance regardless of abundance metric or spatial scale across the end-Cretaceous mass extinction (Lockwood, 2003). Data from a moderate Late Ordovician regional extinction in the Appalachian Basin of eastern North America imply selectivity against abundant taxa (Layou, 2007). Thus, there is no clear indication that locally abundant taxa are more likely to survive extinction in the fossil record.

Differences in survivorship between widespread and endemic genera have been recorded in mass extinction, second-order extinction, and background extinction. Initial studies of bivalve genera at the end-Cretaceous mass extinction suggested that widespread genera preferentially survive mass extinction (Jablonski, 1986; 1991). Further studies of the same taxa have strengthened the argument and suggest selectivity against those with limited geographic ranges (Jablonski and Raup, 1995). Research on the
molluscan fauna of the end-Permian mass extinction yielded similar patterns of selectivity with respect to geographic range (Erwin, 1996). While this relationship holds for most fauna during mass extinctions, researchers failed to detect geographic range selectivity of echinoid genera of the end-Cretaceous extinction (Smith and Jeffery, 1998; Smith and Jeffery, 2000). The relationship between selectivity and geographic range has also been documented for second-order and background extinction. An examination of early Jurassic bivalves indicates this correlation (Aberhan and Baumiller, 2003). Furthermore, more recent research evaluating fossil benthic marine invertebrates of the Cambrian through the Neogene using data from the Paleobiology Database shows a significant and positive relationship between survivorship and geographic range. This relationship is further strengthened by controlling for differences in species richness and abundance among genera (Payne and Finnegan, 2007).

While the previously mentioned studies address the possibility of a link between the many definitions of rarity and extinction, the majority of past work focuses on mass extinctions and selectivity at the generic level or higher. Understanding selectivity at a larger scale is important, but it would also be useful to understand selectivity at the species level (Gilinsky, 1994; McKinney, 1995). Species level selectivity is especially important because of current concerns about the fate of species as a result of human impact upon the Earth. As humans continue to develop the world and radically change natural habitats, restricting geographic ranges and reducing abundance, how will species react? Similarly, it would be useful to gain further insight about how selectivity operates during periods of background extinction and how it varies from the selectivity of mass extinctions.
Diversity Partitioning

Biodiversity is commonly examined at the $\alpha$, $\beta$, and $\gamma$ levels, which can be used to explain diversity at different spatial scales (Sepkoski, 1988; Powell and Kowalewski, 2002; Bush and Bambach, 2004). According to traditional partitioning, $\alpha$ diversity represents local diversity, $\beta$ diversity represents regional diversity, and $\gamma$ diversity represents global diversity (Sepkoski, 1988). Under this partitioning, diversity is multiplicatively calculated so that $\gamma$, total diversity, is the product of $\beta$ and mean $\alpha$ diversity ($\gamma = \alpha \beta$). $\beta$ diversity is commonly defined as a difference in community composition. One of the common calculations for $\beta$ diversity between two communities is the Jaccard similarity coefficient in which $\beta$ is equal to the quotient of the number of shared taxa and the total number of unique taxa in both communities ($\beta = S_{\text{shared}} / (S_1 + S_2 - S_{\text{shared}})$ where $S$ is equal to species richness in a give sample).

Additive diversity partitioning is a technique that allows for a slightly different approach to the three levels of diversity, more specifically redefining $\beta$ diversity as the difference between $\gamma$ and $\alpha$ ($\beta = \gamma - \alpha$) (Lande, 1996). Thus, $\gamma$ (total) diversity is equal to the sum of $\beta$ (among-sample) diversity and mean $\alpha$ (within-sample) diversities. The calculation for $\beta$ diversity is much simpler in that $\beta$ is equal to total diversity ($\gamma$) minus mean $\alpha$ diversity. With this new definition, diversity can be explored at even further levels if data are collected within a nested sampling hierarchy (Gering et al, 2003; Okuda et al, 2004). Partitioning of this kind allows for an examination of the amount of diversity added to total diversity by either increasing the number of samples or expanding sampling to a greater spatial scale (Layou, 2007; Patzkowsky and Holland, 2007). Based upon such a sampling hierarchy, it is possible to calculate several distinct levels of $\alpha$. 
diversity. $\alpha_1$ is representative of the lowest spatial scale of diversity, the richness, or number of species within a single sample. $\alpha_2$ then represents total richness at the next higher spatial scale. At the highest spatial scale, $\alpha$ diversity is equivalent to $\gamma$, the total richness of the study area.

As a result of the multiple levels of $\alpha$ diversity within this hierarchy, several levels of $\beta$ diversity can be calculated. For example, spatial hierarchy with four tiers would allow for the calculation of three tiers of $\beta$ diversity. The lowest level of $\beta$ diversity, $\beta_1$, is calculated by subtracting the mean richness of the lowest $\alpha$ spatial scale by the total richness of the next highest spatial location ($\beta_1 = \alpha_2 - \alpha_1$). Unlike $\alpha$ diversity, which can only increase or remain constant with an increase in spatial scale, $\beta$ diversity can also decrease in value. The partitioning among levels of $\beta$ diversity can then be compared to provide a rich understanding of spatial variability within paleocommunities. Comparison of partitioning patterns between two time periods, before and after an extinction event for example, can be examined to understand how paleocommunity structure is affected by extinction.

Null modeling of changes in $\beta$ diversity as a function of extinction provides a way to determine the selectivity of extinction with regard to taxon abundance (Layou, 2007). Extinctions targeting rare taxa exhibit increases in the proportional contribution of $\alpha_1$ to $\gamma$ and decreases in the proportional contribution of the highest level of $\beta$ (Figure 1). The opposite, decreases in the contribution of $\alpha_1$ and increases in the contribution of highest level of $\beta$, is indicative of selectivity against abundant taxa. No change in diversity partitioning signifies a non-selective extinction with respect to abundance.
Figure 1: Sample additive diversity partitioning extinction-selectivity patterns. Note the lack of change in ADP between pre- and post-extinction with no selectivity. Also note how decreased $\alpha_1$ and increased $\beta_3$ diversity indicate abundant selectivity, while increased $\alpha_1$ and decreased $\beta_3$ diversity reflects selectivity for rare-taxa.
Fidelity of fossil abundance

It is important to consider the extent to which fossil abundance reflects the original population size of the living community. Meta-analyses suggest that the marine invertebrate fossil record is much more complete and readily quantifiable than much of the paleontologic record (Maxwell and Benton, 1990; Jablonski, 1991). For example, live-dead taphonomic comparisons have revealed that species composition and metrics of relative abundance are faithfully recorded in the fossil record. (Kidwell and Bosence, 1991, Kidwell, 2001). This indicates that marine invertebrate assemblages with mineralized skeletons provide the most robust fauna for exploring paleoecological relationships regarding survivorship and abundance. Furthermore, the Yorktown and Eastover Formations in SE Virginia provided conditions for exceptional preservation of molluscan taxa (Ward, 1992). The sampling strategy utilized in this study is also of great importance in ensuring a precise representation of abundance. The collection of small replicate samples rather than few large samples provides the best estimate of species abundance in attempting to quantitatively describe paleocommunities (Bennington, 2003).

Geologic Setting

The Atlantic Coastal Plain is composed of gently inclined, laterally-continuous, and well-preserved stratigraphic units. Along eastern North America, the Miocene to the Pliocene epochs were characterized by a series of regional marine transgressions interrupted briefly by short regressions. Deposition of thinly layered marine sediments took place primarily in a series of embayments or depocenters separated by areas of
higher topography or arches, spanning from New Jersey to the panhandle of Florida (Figure 2) (Ward, 1985). The location of these embayments and arches was likely structurally controlled by regional tectonism including block-faulting and oceanic transform faults (Ward and Powars, 1991). The Chesapeake Group of the Virginia Coastal Plain, consisting of marine to marginal-marine beds, represents a relatively complete stratigraphic record from the early Miocene through the late Pliocene. The units that compose this group exhibit excellent and widespread exposure of their beds and exceptional preservation (Ward, 1992). This study focuses on the Cobham Bay and Sunken Meadow Members of the Eastover and Yorktown Formations, respectively (Figure 3). Units were deposited within the Salisbury, and to some extent, the Albemarle embayments, which were protected, lagoonal environments of normal marine salinity that contained an open-shelf, diverse molluscan assemblage (Ward, 1992).

The Eastover Formation, one of the middle-to-upper units of the Chesapeake Group, is a 5-28 meter thick sequence of Upper Miocene sediments (Ward and Blackwelder, 1980). Eastover sediments were deposited in the Salisbury embayment, the boundaries of which extended from Virginia into adjacent areas of Maryland and North Carolina (Ward, 1985). Deposits occur as far south as the Nottoway and Meherrin Rivers in North Carolina where deposition overlapped limited portions of the Norfolk Arch, as far north as southeastern Maryland, and west to fall zone in the Petersburg and Richmond area, Virginia (Ward, 1985). There are no other lithogically similar units to the Eastover in neighboring embayments (Ward, 1985). The Eastover Formation consists of two members, the Claremont Manor and the Cobham Bay (Ward and Blackwelder, 1980).
Figure 2: Map of Atlantic Coastal Plain embayments. Note the study area location in the Salisbury Embayment (from Ward, 1992).
Figure 3: Stratigraphy of the Salisbury Embayment from the Upper Miocene through the Upper Pliocene. Black sections represent erosional unconformities indicating gaps in the sedimentary record. Note the overall relative completeness of the stratigraphic record (adapted from Ward, 1985).

<table>
<thead>
<tr>
<th>Series</th>
<th>Formation</th>
<th>Member</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pliocene</td>
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<td>Moore House</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Morgarts Beach</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rushmere</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sunken Meadow</td>
</tr>
<tr>
<td>Miocene</td>
<td>Yorktown</td>
<td>Cobham Bay</td>
</tr>
<tr>
<td></td>
<td>Eastover</td>
<td>Claremont</td>
</tr>
<tr>
<td></td>
<td>St. Mary’s</td>
<td>Windmill Point</td>
</tr>
</tbody>
</table>
The Cobham Bay Member is the upper bounding member of the Miocene Eastover Formation, and is composed of shelly, fine-grained, well-sorted, quartz-rich sand. The member’s type locality is along the James River at Cobham Bay, just south of Cobham Wharf in Surry County, Virginia (Ward and Blackwelder, 1980). This member contains an abundant and diverse molluscan fossil fauna, indicative of shallow subtropical conditions with a favorable substrate and abundant food supply. Unit thickness varies from 1.0 meter at Murfreesboro, North Carolina to 12 meters at Bayport, Virginia (Ward and Blackwelder 1980). The sedimentation preserved in the Cobham Bay Member is representative of a brief, LateMiocene marine transgression and is the only preserved stratigraphic record of that time period throughout the North American Coastal Plain (Ward, 1992). Isotopic (K/Ar) glauconite dating indicates that the lowest portions of the Cobham Bay Member were deposited 8.7 ± 0.4 Ma, while glauconite from upper beds of the member indicates a depositional date of 6.46 ± 0.15 Ma (Ward and Blackwelder, 1980). The Eastover Formation is distinguished by the dominance of the bivalve, *Isognomon*, the index fossil of this formation.

The Pliocene Yorktown Formation unconformably overlies the Eastover Formation, as an erosional unconformity representing an approximately 1.5 my gap in sedimentation separates the two formations. This gap in the sedimentary record represents a regression and corresponding lack of deposition (Ward, 1992). A basal lag consisting of coarse sand, pebbles, fish and whale bone, and shark and ray teeth can be noted at the contact between the two formations in many locations. The Yorktown Formation is more laterally extensive than the Eastover Formation, with deposition throughout North Carolina and Maryland, in addition to correlative units to the north into
New Jersey and to the south into South Carolina and Georgia (Ward, 1992). At its western most extent near Richmond, Virginia, the Yorktown Formation is only a few centimeters thick, but thickens to approximately 15 m near Yorktown, Virginia, before thinning to the east as a result of subsequent erosional and depositional events (Ward and Blackwelder, 1980). The Yorktown Formation has four members, the Sunken Meadow, Rushmere, Morgarts Beach, and Moore House. Maximum Pliocene transgression is represented in the Rushmere Member, and some sediments indicative of the beginning of regression are found in even younger members (Ward, 1980).

The Sunken Meadow Member is composed of quartz-rich, glauconitic and phosphatic coarse-to-medium grained, poorly-sorted, very shelly sand. Planktonic foraminifera correlations date the member to Zone N18, or approximately 5.0 Ma. Glauconite from the Rushmere Member has been isotopically dated to 4.4 ± 0.2 Ma (Ward and Blackwelder, 1980). The type locality for this member occurs along the bank of the James River in Surry County, Virginia just below Sunken Meadow Creek (Ward and Blackwelder, 1980). Unit thickness averages 3.0 meters. The Sunken Meadow reflect shallow shelf conditions, with a sandy substrate and mild-to-temperate temperatures, conditions under which a diverse and abundant molluscan fauna thrived (Ward, 1985). While the Cobham Bay and Sunken Meadow Members both represent similar shallow subtidal environments, the Yorktown Formation was deposited during times of comparatively cooler temperatures (Ward and Blackwelder, 1980). While the Sunken Meadow and Cobham Bay Members have similar lithologies, the contact between the two is distinguishable in many places by the basal lag. The index fossil for
this member, the scallop *Chesapeake jeffersonius*, allows for a clear demarcation of the lithologic units.

**Methods**

*Sampling Strategy*

Samples were collected based upon a sampling hierarchy, allowing for examination of diversity patterns at different spatial scales. Four levels of $\alpha$ diversity were considered: individual bulk samples ($\alpha_1$), cliff faces ($\alpha_2$), locations ($\alpha_3$), and total study area ($\alpha_4$ or $\gamma$). This hierarchy then allows for the examination of $\beta$ diversity at three levels for each stratigraphic member: among samples ($\beta_1$), between cliff faces ($\beta_2$), and between localities ($\beta_3$).

*Field Methods*

Twenty-four bulk samples were collected from two locations along the southern bank of the James River, Surry County, Virginia: Cobham Wharf and Mount Pleasant (Figure 4). The two field sites are separated by approximately eight kilometers, with Cobham Wharf downstream of Mount Pleasant. At Cobham Wharf, bluffs along the river are about 8m high, whereas they are approximately twice as tall at Mount Pleasant. The Cobham Bay and Sunken Meadow Members are exposed at each site. At each location, two cliff faces along the river were chosen for sampling. At Mount Pleasant, the cliff faces were approximately 300m apart, while at Cobham Wharf the chosen cliff faces were separated by 200m. The contact between the two formations was determined using the index fossils for the units. At Mount Pleasant, the contact was high up on the
Figure 4: Shaded relief digital elevation model of study location (adapted from Bailey and Lamoreaux, 2007).
cliffs, approximately 10m from the base, whereas the contact was at approximately 3.5m above the cliff-base at Cobham Wharf (Figure 5). The Cobham Bay and Sunken Meadow Members had similar lithologies of well-sorted, sub-angular to sub-rounded, fine-grained, quartz sand. At both locations, the Cobham Bay Member contained approximately 5-10% heavy minerals and glauconite, while the Sunken Meadow had significantly less. The one difference in lithology between the two sites was the color of the sands, with the sands of Mount Pleasant having a grey hue while Cobham Wharf sands were brown to grey in color. Upon determining the contact, three bulk samples of the Sunken Meadow Member were collected from approximately 0.5 m above the contact and three samples of the Cobham Bay Member were collected from approximately 0.5 m below the contact at each cliff face. This one-meter buffer was used to prevent sampling where stratigraphic mixing could possibly have occurred. To collect each sample, a collection area of 0.2 m x 0.4 m was chiseled out, and then pried from the outcrop intact to ensure preservation of the fossil assemblage. Samples were later standardized by weight to mitigate sample size bias.

Sample Processing

In the lab, bulk samples were normalized by weight to minimize sample-size bias. Samples weighing more than ~7 kg were normalized to 7 kg and then processed, while those weighing less than 16 lb. were processed in whole (Table 1). No statistical correlation was noted between sample mass and the total abundance or species richness of a sample, thus sample size did not bias the data. Samples were then wet-sieved
Figure 5: Simplified stratigraphic columns of the two sampled localities. Note the indication of specific sampling sites.
<table>
<thead>
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<th>Locality</th>
<th>Unit</th>
<th>Mass (lb.)</th>
</tr>
</thead>
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<td>Mt. Pleasant</td>
<td>Cobham Bay</td>
<td>13.5</td>
</tr>
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<td>07CWYB3</td>
<td>Cobham Wharf</td>
<td>Sunken Meadow</td>
<td>21.0</td>
</tr>
</tbody>
</table>

Table 1: Record of sample masses. Samples that weighing more than 16 lb. were randomly normalized to 16.0 lb to prevent sampling bias.
through a 2mm (-1φ) screen and left to dry. During this process, obviously fragile pieces were removed to limit any preservational degradation during processing. Fossil material, including both vertebrate and invertebrate specimens, was picked from the sieved material and sorted. Specimens were identified to the species level using several Tertiary Coastal Plain monographs (Gardner, 1943; Gardner, 1948; Ward, 1992; Campbell, 1993). Individuals were counted and the abundance of each species was noted.

The following counting methods were utilized to provide the most accurate and consistent assessments of true abundances within a sample. For bivalves, the number of whole hinges was counted and for gastropods, the number of apertures was counted (Gilinsky and Bennington, 1994). For barnacles, the final count represents the number of whole individuals plus the number of plates with muscle scar divided by eight, the average number of elements produced by an individual barnacle. This counting method was used because the number of whole barnacles clearly did not represent their overall abundance within the entire bulk sample. *Dentalium* (scaphopod) pieces over 1cm in length were counted as individuals. In the case of samples with *Dentalium* fragments less than 1cm in length, one individual was noted to acknowledge its presence. Finally, for bryozoans and corals, each piece of approximately 0.5 cm³ signified an individual.

**Data Analysis**

The sampling hierarchy was utilized so that additive diversity partitioning (ADP) could be used to examine ecological changes relative to the Miocene-Pliocene boundary. Mean α and β diversity values were calculated for the Cobham Bay and Sunken Meadow Members. ADP was examined for survivor taxa only and later separately for bivalves.
and gastropods to examine whether patterns are consistent across the dominant taxa of the paleoecological community.

Five metrics were used to measure taxonomic abundance, specifically proportional abundance, average abundance, average abundance excluding zeros, occupancy, and coefficient of variation. Examination of abundance data from the Cobham Bay Member allows for an understanding of pre-extinction controls upon survivorship across the boundary. Proportional abundance represents the raw abundance of a species relative to the total raw abundance across all individuals within a sample. The proportional abundances of species were then averaged across the twelve samples for the respective member to calculate a mean proportional abundance for each species. Average abundances were calculated in two ways. The first average abundance metric, recognized herein as average abundance, was calculated by summing the raw abundances of a taxon across the samples and then dividing by twelve, the total number of samples for each member (Table 2). The second average abundance metric takes into account the fact that every species was not found in every sample. Therefore, the metric referred herein as average abundance excluding zeros was calculated as the quotient of the sum of raw abundances for a given taxon and the number of samples in which that particular species was found (Table 2). The occupancy metric is defined as the quotient of the number of samples in which a taxon was found and the total number of samples. This metric allows for an understanding of the geographic patchiness of a given taxon. Finally, the coefficient of variation is designated as the standard deviation of taxon abundance divided by the mean taxon abundance, thus providing information on the variability of taxon population size across the sample area.
<table>
<thead>
<tr>
<th>Species</th>
<th>Sample 1</th>
<th>Sample 2</th>
<th>Sample 3</th>
<th>Average Abundance</th>
<th>Average Abundance Excluding Zeros</th>
<th>Occupancy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
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<td>0</td>
<td>2</td>
<td>(3+0+2)/3 = 1.67</td>
<td>(3+2)/2 = 2.5</td>
<td>2/3 = 0.67</td>
</tr>
<tr>
<td>Species 2</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>(4+2+3)/3 = 3</td>
<td>(4+2+3)/3 = 3</td>
<td>3/3 = 1.00</td>
</tr>
</tbody>
</table>

Table 2: Sample calculations of abundance metrics.
Information on the geographic ranges of species was initially acquired from the U.S. Geological Survey card catalogue of Coastal Plain mollusks housed at the Virginia Museum of Natural History in Martinsville, Virginia. Cards were organized taxonomically to the species level. Each card within the catalogue represents an occurrence of a given taxon in a professional publication including journal papers and monographs. The publications summarized on these cards range in date from 1824 to the 1980s. Data on geographic location, stratigraphic formation, geologic time, and publication were collected. These data were supplemented with similar data from the Paleobiology Database (http://paleodb.org). The combined information allowed for an assessment of both the geologic duration and geographic range of each of the taxa.

Geographic range of a species was calculated by counting the number of embayments in which the particular species occurs. The various embayments were defined according to those determined by Ward (1985). When location data were either unavailable or not specific enough to determine the particular embayment in which taxa were found, stratigraphic and geologic data were utilized to assign taxa to their respective embayments. This geographic range data spans the entire duration of a given taxon.

The geological duration of a species was determined first using the geologic timescale to the most specific level possible (USGS, 2007). Paleontological literature was utilized to assess the ages of various formations (Cronin et al, 1984; Ward, 1992). These age ranges were then converted to numerical durations ranging from 1 to 32 my. Age ranges were finally divided into categories of short (1-4 my), medium (5-14 my), and long (15+ my) durations. Durations were categorized, rather than examined as raw durations due to variable resolution in duration data.
Survivorship of a given species was defined several ways for this study, allowing for the examination of survivorship patterns at different spatial and temporal scales. Victims and survivors were assessed at the local level, through the twenty-four samples collected at Cobham Wharf and Mount Pleasant. Taxa that occurred in the Eastover samples but not in the Yorktown samples were defined as victims, those that occurred in both units were deemed survivors, and those that occur only in the Yorktown were identified as originators. Because of the limited spatial scale of the study area, status as victims, survivors, and originators was also determined using species duration data, allowing for the identification of those taxa that went extinct regionally, as opposed to locally, at the Miocene-Pliocene boundary.

Kolmogorov-Smirnov and Shapiro-Wilk statistical tests were used to analyze the normality of the data. Normal data were examined through the use of parametric statistics including two-sample t-tests assuming equal variances, and analysis of variance (ANOVA). Non-normal data were examined through the use of non-parametric statistics including Mann-Whitney U, Kruskal-Wallis, and Spearman Rank.

Results

A total of 98 different taxa were identified among the twenty-four bulk samples, with most identified to the species level. The number of individuals per sample ranged from 106 to 1872, with an average of 572 individuals per sample. Samples from the Sunken Meadow Member of the Yorktown Formation recorded almost three times as many individuals as the Cobham Bay Member of the Eastover Formation (867 individuals vs. 278 individuals). This difference can be attribute to the relative
dominance of two species in the Sunken Meadow, *Astarte exaltata* and *Cyclocardia granulata*. While there are a greater number of individuals in the Sunken Meadow Member samples, there is no statistical correlation between species richness and total abundance, or sample weight and total abundance. This suggests that the difference in number of individuals per sample is not a result of a sampling bias.

*Diversity partitioning*

Additive diversity partitioning (ADP) indicates an overall increase in total diversity (\(\gamma\)) from the Miocene to the Pliocene (Figure 6). A total of 60 species were noted in the samples of the Cobham Bay Member while 81 species were noted in the Sunken Meadow Member samples. This increase in total diversity from the Miocene to the Pliocene is a result of the local origination of 38 taxa while only 17 taxa went extinct locally. Mean \(\alpha_1\) and mean \(\beta_1\) are virtually equal across the boundary, while mean \(\beta_2\) and \(\beta_3\) values more than double (Table 3). These differences indicate that across the extinction boundary, there is a gain in species richness at the two highest hierarchical levels, between cliff-faces and between localities. Despite these differences, there is no statistically significant difference in pre- and post-extinction partitioning.

A total of 43 survivors, or holdover taxa, were present in samples of both the Cobham Bay and Sunken Meadow Members. ADP of the 24 samples based solely on these taxa yields a slightly different result than when considering all taxa. Mean \(\alpha_1\) and
Figure 6: Additive diversity partitioning for all taxa: (a) as contributions to total richness and (b) as percent contribution to gamma. Note the increase in total richness from the Eastover to the Yorktown. Similarly, note the increases in total contribution to diversity at the highest hierarchical levels ($\beta_2$ and $\beta_3$). The increase in diversity at those levels illustrates the addition of diversity between cliff-faces and between localities.
<table>
<thead>
<tr>
<th></th>
<th>Eastover</th>
<th></th>
<th>Yorktown</th>
<th>t-statistic</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean $\alpha_1$</td>
<td>24.58</td>
<td></td>
<td>27</td>
<td>-0.571</td>
<td>0.575</td>
</tr>
<tr>
<td>Mean $\beta_1$</td>
<td>18.17</td>
<td></td>
<td>17</td>
<td>0.341</td>
<td>0.737</td>
</tr>
<tr>
<td>Mean $\beta_2$</td>
<td>9.25</td>
<td></td>
<td>20</td>
<td>-0.924</td>
<td>0.423</td>
</tr>
<tr>
<td>Mean $\beta_3$</td>
<td>8</td>
<td></td>
<td>17</td>
<td>-0.750</td>
<td>0.590</td>
</tr>
<tr>
<td>Total Richness</td>
<td>60</td>
<td></td>
<td>81</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3: Mean additive diversity partitioning values of all taxa and results of two-sample t-tests assuming equal variances for comparison of individual hierarchical levels between formations.
mean $\beta_3$ values are consistent across the boundary while mean $\beta_1$ decreases and mean $\beta_2$ increases (Figure 7, Table 4). A two-sample t-test assuming equal variances indicates significant variation between $\beta_1$ values of the Cobham Bay and Sunken Meadow Members ($t_{12,12} = 2.237, p = 0.036$), while other partitioning values do not show similar statistically significant differences (Table 4).

Similar patterns emerge when considering only the surviving bivalve taxa. Mean $\alpha_1$ values are again consistent across the Miocene-Pliocene boundary, and mean $\beta_3$ values increase marginally. Meanwhile, mean $\beta_1$ decreases significantly from the Cobham Bay to Sunken Meadow Member and mean $\beta_2$ increases (Figure 8). Again, there is a statistically significant difference between the $\beta_1$ values of the pre- and post-extinction members ($t_{12,12} = 2.351, p = 0.028$). These variations imply an increase in habitat patchiness at a highly localized spatial scale.

When only considering surviving gastropod taxa, ADP results are slightly different from the above results. Mean $\alpha_1$ and mean $\beta_2$ increase across the boundary, $\beta_2$ increasing more so than mean $\alpha_1$ (Figure 9). Conversely, mean $\beta_1$ and mean $\beta_3$ decrease across the boundary. While apparent differences exist between all four levels of diversity, again the only level with statistically significant variation is $\beta_1$ ($t_{12,12} = 3.824$ and $p = 0.001$).
Figure 7: Additive diversity partitioning as percent contributions to total ($\gamma$) diversity when considering only survivor taxa. Note the lack of change in the percent contributions of $\alpha_1$ and $\beta_3$ to $\gamma$.

<table>
<thead>
<tr>
<th></th>
<th>Eastover</th>
<th>Yorktown</th>
<th>t-statistic</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean $\alpha_1$</td>
<td>18.5</td>
<td>18.5</td>
<td>0.000</td>
<td>1.000</td>
</tr>
<tr>
<td>Mean $\beta_1$</td>
<td>14</td>
<td>9.75</td>
<td>2.237</td>
<td>0.036</td>
</tr>
<tr>
<td>Mean $\beta_2$</td>
<td>6</td>
<td>9.75</td>
<td>-0.635</td>
<td>0.549</td>
</tr>
<tr>
<td>Mean $\beta_3$</td>
<td>4.5</td>
<td>5</td>
<td>-0.117</td>
<td>0.918</td>
</tr>
</tbody>
</table>

Table 4: Mean additive diversity partitioning values of survivor taxa and results of two-sample t-tests assuming equal variances for comparison of individual hierarchical levels between formations. Note the statistically significant difference between $\beta_1$ diversity values of the Eastover and Yorktown Formations.
Figure 8: Additive diversity partitioning of survivor bivalve taxa as percent contributions to total (γ) diversity. Note the similarity in the contributions of α₁ and β₃ between the Eastover and Yorktown Formations.

Figure 9: Additive diversity partitioning of survivor gastropod taxa as percent contributions to total (γ) diversity. Note the slight increase in contribution of α₁ and decrease in the contribution of β₃ across the extinction boundary (Eastover to Yorktown).
Abundance and survivorship

If rare selectivity exists during this time, it would be expected that survivors would have higher abundances than victims. Five metrics were used to examine abundance data and explore these relationships: 1) proportional abundance, 2) average abundance, 3) average abundance excluding zeros, 4) occupancy, and 5) coefficient of variation. When considering all 60 taxa found in Cobham Bay Member samples, data for all five abundance metrics are non-normally distributed (Appendix 1.1). Upon removing singletons, or taxa that occurred in only one of the twenty-four bulk samples, results of the coefficient of variation metric were normally distributed ($KS_{60} = 0.066$, $p = 0.200$, $SW_{60} = 0.989$, $p = 0.931$), while the results of the other four metrics remained non-normal in distribution. For data that were non-normally distributed, non-parametric statistics (Mann-Whitney U tests) were used to compare the abundance of survivors with the abundance of victims, while a two-sample t-tests assuming equal variances was used for normally distributed data.

Data for all taxa indicate that the proportional abundance of survivors ($s$) is slightly greater than, but virtually indistinguishable from, the proportional abundance of victims ($v$), with no statistically significant difference between the two groups ($v = 0.0162$, $s = 0.0168$; $Z_{17,43} = -1.772$, $p = 0.076$) (Figure 10a). With singletons removed, victims have a slightly higher proportional abundance than survivors, yet the relationship remains non-significant ($v = 0.249$, $s = 0.190$; $Z_{11,38} = -0.120$, $p = 0.905$).

Data from both abundance metrics yield similar trends (Figure 10b,c). When all data are considered, survivors have a slightly higher average abundance, yet the relationship is not statistically significant ($v = 4.41$ individuals, $s = 4.72$ individuals;
Examination of the data with singletons removed indicates a contrasting relationship with victims having a higher average abundance than survivors, though again this relationship is statistically non-significant ($\text{v} = 6.76$ individuals, $s = 5.31$ individuals; $Z_{11,38} = -0.060, p = 0.952$). The examination of all 60 taxa under the average abundance excluding zeros metric indicates that survivors have a greater average abundance ($\text{v} = 6.12$ individuals, $s = 7.91$ individuals), yet when singletons are removed victims have a greater average abundance excluding zeros ($\text{v} = 8.82$ individuals, $s = 8.63$ individuals). Neither of these relationships bears statistical significance (with singletons $Z_{17,43} = -1.361, p = 0.174$; without singletons $Z_{11,38} = -0.180, p = 0.857$).

An examination of occupancy data indicates that on average survivors were found in one more sample than victims, yet the relationship is not statistically significant ($\text{v} = 0.358, s = 0.430; Z_{17,43} = -1.361, p = 0.174$) (Figure 10d). Data with singletons removed show no differences in the average number of samples that survivors and victims occupy. Victims displayed a slightly higher coefficient of variation than survivors, though there is no statistical significance to the relationship ($\text{v} = 2.232, s = 1.851; Z_{17,43} = -1.662, p = 0.096$) (Figure 10e). With singletons removed, there is no difference between the average coefficient of variation of victims and survivors and thus no statistical significance either ($\text{v} = 1.672, s = 1.638; t_{11,38} = 0.179, p = 0.859$).

A victim-survivor comparison focusing on the abundance of gastropod taxa illustrates that victims had statistically significant lower abundances than survivors. Data for both proportional and average abundance metrics corresponded with this pattern (proportional abundance: $\text{v} = 0.028, s = 0.061, Z_{7,10} = -2.147, p = 0.032$; average abundance: $\text{v} = 0.357, s = 0.667, Z_{7,10} = -1.912, p = 0.055$).
Figure 10: Victim-survivor comparison utilizing (a) proportional abundance, (b) average abundance, (c) average abundance excluding zeros, (d) occupancy, and (e) coefficient of variation. Note the similarity in abundance of victims and survivors.
All five metrics used to calculate abundance yielded non-normally distributed data when considering the 47 taxa included for comparison with taxonomic duration (Appendix 1.2). With the removal of singletons, only the coefficient of variation data were normally distributed (\( KS_{47} = 0.075, p = 0.200, SW_{47} = 0.980, p = 0.703 \)). Kruskal-Wallis (KW) tests were used to understand the statistical significance of the relationships between pre- and post-extinction duration-abundances comparisons for non-normal data and an ANOVA tests were used for normally distributed data. Duration data were divided into three categories based on the length of duration: short (0-4my), medium (5-14my), and long (15+my). With these categorical duration definitions, there are 23 taxa with short durations, 18 taxa with medium length durations, and 6 taxa with long durations. With the exclusion of singletons, there are 18 taxa with short durations, 16 taxa with medium durations, and 6 taxa with long durations.

Proportional abundance data indicate that long-lived taxa are more abundant than shorter lived taxa (Figure 11a), however that relationship is not statistically significant (\( KW_{23,18,6} = 4.091, p = 0.129 \)). Similar relationships are documented when singletons are removed. Both metrics of average abundance data indicate an increase in duration with increases in abundance (Figure 11b,c). Based on the average abundance excluding zeros, the number of individuals within a species per sample is: 3.97 (short), 5.95 (medium), and 8.11 (long). While there is a noted increase in average abundance, the relationship is statistically non-significant (\( KW_{23,18,6} = 3.913, p = 0.141 \)).

Occupancy data also suggests an increase in occupancy with increase in duration (short = 0.36, medium = 0.44, long = 0.67), yet the differences between all three are not
statistically significant ($KW_{23,18,6} = 5.917, p = 0.052$) (Figure 11d). However, a Mann-Whitney U test indicates that the percentage occupancy of short duration taxa is significantly smaller than the percentage occupancy of long duration taxa ($Z_{23,6} = -2.501, p = 0.012$). Similar, but dampened and less statistically significant results are noted when singletons are removed. Another link between duration and abundance is noted in the coefficient of variation data (Figure 11e). Longer duration taxa have a smaller mean coefficient of variation than do short and medium duration taxa and the relationship is statistically significant ($KW_{23,18,6} = 6.745, p = 0.034$; short-medium: $Z_{23,18} = -0.224, p = 0.823$; medium-long: $Z_{18,6} = -2.269, p = 0.023$; short-long: $Z_{23,6} = -2.537, p = 0.011$). When singletons are removed, this relationship among duration and coefficient of variation remains, but is less obvious and statistically non-significant.
Figure 11: Abundance-duration comparisons utilizing (a) proportional abundance, (b) average abundance, (c) average abundance excluding zeros, (d) occupancy, and (e) coefficient of variation. Note the relationship between short and long duration taxa with respect to occupancy (d) and the relationship between taxa of all durations and coefficient of variation (e).
Geographic Range and survivorship

Geographic range data are non-normally distributed (KS47 = 0.241, p = 0.000, SW47 = 0.842, p = 0.000), a result the use of non-parametric statistics, Mann-Whitney for geographic range-survivorship comparisons and Kruskal-Wallis for geographic range-survivorship comparison, is necessary. Survivors on average occupied one more embayment than victims (v = 2.38 embayments, s = 3.32 embayments) (Figure 12). This relationship however lacks statistical significance (Z16,31 = -1.298, p = 0.194).

Examination of geographic range and duration data indicates that taxa with longer durations also have larger geographic ranges (greater number of embayments): short duration = 2.08 embayments, medium durations = 3.73 embayments, and long durations = 6.28 embayments (Figure 13). These differences in the geographic range are statistically significant (KW37,26,7 = 23.434, p < 0.001). Furthermore, the differences between any two of the three durations are significant as indicated by further Mann-Whitney tests (short-medium: Z37,26 = -3.650, p < 0.001; medium-long: Z26,7 = -2.663, p = 0.007; short-long: Z37,7 = -3.927, p < 0.001).
Figure 12: Victim-survivor comparison of geographic range. Note how survivors were on average found in more embayments than victims.

Figure 13: Comparison of geographic range and duration. Note the correlation of an increase in taxon duration with an increase in geographic range.
**Abundance and Geographic Range**

Abundance and geographic range data for 47 taxa were jointly evaluated to understand the relationship between these two forms of rarity. Data for geographic range and the five metrics of abundance were all non-normally distributed (Appendix 1.3). With singletons removed, all data remain non-normally distributed with the exception of coefficient of variation ($\text{KS}_{47} = 0.075, p = 0.200, \text{SW}_{47} = 0.980, p = 0.703$). The statistical significance of any correlation between abundance and geographic range is explored through Spearman Rank Indices because of the non-normal distribution of the data. When mean proportional abundance is graphed against geographic range, there is a concentration of taxa in the lower-left quadrant with both low proportional abundance and few total embayments (Figure 14a). Additionally, there is a sparse distribution of taxa in the upper-left and lower-right quadrants, but no data are plotted in the upper-right quadrant. This indicates that there are no taxa that have both a sizeable local abundance and a wide geographic range. Converting the x-axis (proportional abundance) to a logarithmic scale reveals no underlying patterns in the lower-left hand corner of the plot (Figure 14b). These graphs depict an interesting pattern upon plotting victims and survivors; many of the victims are on the bottom or left edge of the graph suggesting that the victims of this extinction were rare taxa. However, there is no statistically significant relationship between these data ($R_{47} = 0.090, p = 0.547$). Furthermore, this relationship between abundance and geographic range holds constant for all abundance metrics with and without singletons.
Figure 14: Graphical distribution of abundance and geographic range data, (a) on a linear-linear graph, and (b) on a log-linear graph. Note the lack of widespread, abundant taxa. Also note the distribution of victims along the axes of the graph, indicating rarity of one of the two forms or both.
Discussion

Abundance selectivity

Three sets of analyses were conducted to evaluate the impact of abundance upon selectivity: 1) additive diversity partitioning, 2) a victim-survivor comparison of abundance data, and 3) an evaluation of an abundance-duration relationship. Patterns within these analyses are varied, with indications of both non-selective and rare-selective background extinction.

The examination of the diversity partitioning of survivors, or holdover taxa only, allows for an analysis of the effects of extinction separate from the impacts of origination. Analysis of ADP for survivor taxa yields a noted increase in $\beta_1$ from the Eastover to the Yorktown and a corresponding decrease in $\beta_2$. The absence of change in partitioning at the lowest (mean $\alpha_1$) and highest (mean $\beta_3$) hierarchical levels corresponds with null models of ADP across extinction boundaries indicating that there was no selectivity with respect to abundance during this period of background extinction (Layou, 2007) (Figure 1, 7). Similar ADP patterns exist for survivor bivalve taxa among samples (Figure 1, 8). The concurrence of patterns suggests that the diversity partitioning of all taxa in the study area is driven by the bivalve taxa that dominate the paleocommunity.

An assessment of the ADP of gastropod taxa resulted in an increase in diversity at the lowest (mean $\alpha_1$) and a decrease in diversity at the highest level (mean $\beta_3$). According to the null model of Layou (2007), these patterns suggest that rare gastropod taxa may have been targeted during this period of background extinction (Figure 1, 9). Gastropod taxa were limited in the study, both in taxonomic richness (few taxa noted per sample) and in abundance (few individuals per taxa), thus most of the gastropods are
classified as rare taxa. This result could be a result of the small sample size of gastropods.

A victim-survivor comparison utilizing five metrics of abundance data indicates no selectivity based on abundance. Survivors on average have slightly greater proportional and average abundances than victims, but these relationships lack statistical significance. Similarly, survivors have greater sample occupancy and lower coefficients of variation than victims, yet these differences are statistically non-significant. These results could indicate selectivity against rare taxa during this extinction; nevertheless, the differences between survivors and victims are minute and statistically non-significant. This suggests that there is no selectivity with regard to abundance during this period of background extinction.

A similar victim-survivor comparison focusing solely on gastropod taxa provides additional evidence for the preferential selection of rare-gastropod taxa. Statistically significant differences in proportional and average abundance between victims and survivors indicates that gastropod taxa with low local abundances went extinct at much greater rates than highly abundant gastropod taxa. Sample sizes for these analyses were small, thus calling into question the significance of this relationship. Needless to say, this result coincides with the ADP results suggesting that rare gastropod taxa were targeted during this extinction.

When considering abundance and duration data, proportional and average abundance metrics suggest that taxa of longer durations have higher abundances. This relationship however lacks statistical significance, thus suggesting a lack of selectivity with respect to abundance. Occupancy data indicates that occupancy of short duration
taxa is statistically lower than the occupancy of long duration taxa in that longer-lived taxa occupy more samples than those of shorter durations. This relationship between long and short duration taxa potentially indicates selectivity against taxa that occupy few samples within the overall sampling hierarchy. Furthermore, this suggests that species distributed with limited patchiness are more likely to survive than those with high degrees of patchiness. This further indicates that taxa with the most variable abundances are prone to extinction. Another significant relationship can be noted between duration and coefficient of variation. These data suggest that longer duration taxa have less variation in abundance among samples than those of shorter duration, thus indicating selectivity against taxa that have highly variable abundances among samples. The overall results of an abundance-duration comparison indicate the possibility of rare-selectivity with respect to abundance data.

The findings of these analyses are to some degree comparable with the conclusions of Lockwood (2003) suggesting a lack of abundance-selectivity. This is supported by the results of the ADP of survivors and a victim-survivor comparison of taxon abundance. However, results of the additive diversity partitioning of gastropod taxa and an abundance-duration comparison indicate rare taxa selectivity, a contrasting result to the findings of previous research. The different patterns of selectivity evidenced between gastropod and bivalve taxa through ADP and victim-survivor abundance comparisons indicate that selectivity can vary across different taxonomic classes. This indicates that different members of the ecological community may have reacted differently to the pressures associated with Miocene-Pliocene background extinction. One marked difference between gastropods and bivalves is shell mineralogy, as all
gastropods are aragonitic while bivalves are both aragonitic and calcitic. As a result it is possible that the Sunken Meadow Member did not preserve aragonitic components nearly as well as it did calcitic remains.

**Geographic range selectivity**

Two analyses intended to determine the impact of geographic range upon extinction selectivity provide inconsistent results. A victim-survivor comparison of geographic range indicates that there is no selectivity with respect to species level geographic range. While survivors on average occupied one more embayment than victims, the difference is small and statistically non-significant. A further analysis comparing geographic range and duration data illustrates slightly different results. Taxa of longer durations on average have larger geographic ranges. Results further indicate that there are statistically significant differences between the geographic ranges of short, medium, and long duration taxa. This relationship suggests that there is a link between survivorship and geographic range, in that taxa with larger geographic ranges can more easily survive periods of background extinction and that there is selectivity against taxa that are endemic. The second set of findings corresponds with previous studies such as Payne and Finnegan (2007) indicating a significant and positive relationship between survivorship and geographic range.

These two data sets offer conflicting results, thus the implications of geographic range on survivorship in this study are unclear. These patterns may be a result of survivorship determinations. The victim-survivor comparison of geographic range defines victims as taxa that went locally extinct at the Miocene-Pliocene boundary. It is
possible that collected samples do not accurately represent survivorship, and that victim-
survivor data are artifacts of incomplete sampling. Duration data are used as a proxy of
survivorship in the second comparison. This duration data expands the definition of
survivorship to that of a more regional scale. The use of these data allows for an
assessment of the true extinction of a species, not just the localized extinction limited to
the Cobham Bay and Mount Pleasant area. Thus, the two definitions of survivorship in
these analyses represent different spatial scales of extinction.

Relationship between forms of rarity

The graphical distribution of proportional abundance and geographic range data
indicates that all taxa in this study can be defined as rare by one of the two definitions of
rarity or both (Figure 13). No taxa are both abundant and widely geographically
distributed. In part, this distribution of taxa directly conflicts with the findings of
Rabinowitz and others (1986), which identify the majority of taxa as widely
geographically distributed with large abundances. As depicted on Figure 13, the majority
of the victims had a low abundance, limited geographic range, or both. The apparent
distribution of taxa indicates that rare taxa are most susceptible to extinction. Meanwhile,
many of the survivors had medium-to-high geographic ranges and medium-to-high
abundances.

The results of this abundance-geographic range comparison also conflict with the
direct correlation between local abundance and geographic range. Results of a Spearman
Rank Index implies no direct statistical correlation between the two definitions of rarity.
Furthermore, there are no graphical patterns indicative of such a relationship. Overall, these findings suggest that there are three types of taxa found in this study area: a) endemic with large local populations, b) widespread with small local populations, and c) endemic with small local populations.

**Conclusions**

Several overarching patterns regarding extinction selectivity emerge through his study. The comparison of species-level abundance and taxon geographic range illustrates an interesting dispersal of rarity across the taxa of this study. This distribution of taxa indicates a lack of widespread, locally abundant taxa and a profusion of endemic taxa with small local populations. Furthermore, the victims of the Miocene-Pliocene background extinction tended to be some of the rarest with some of the lowest abundances and most limited geographic ranges, indicating selectivity against rare taxa.

The comparison of ADP results and abundance-based victim-survivor comparisons suggest non-selective extinction of all taxa, but a rare-selective extinction of gastropods. These results indicate that: 1) bivalve taxa were dominant members of the ecosystem and controlled much of the overall extinction patterns, and 2) members of the ecological community react differently to extinction pressures, thus resulting in differences in selectivity across taxonomic classes.

Results using duration as a proxy for survivorship status consistently suggested slightly different results than when victims and survivors were defined by the collected samples. This is potentially indicative of a variation in spatial and temporal scales between the two survivorship metrics. Further analysis could be done to understand the
implications of each of these definitions on survivorship. Comparisons with duration yielded several statistically significant relationships indicating that the Miocene-Pliocene extinction was selective for both taxa of limited geographic range and limited abundance. These results are echoed by the notion that the rarest of taxa went extinct as determined by the comparison of abundance and geographic range. Rare-selectivity is evident for the molluscan fauna of Miocene-Pliocene Coastal Plain units as indicated by patterns, both significant and non-significant, of victim-survivor comparison and and additive diversity partitioning.
Acknowledgements

I would like to thank Dr. Lauck Ward of the Virginia Museum of Natural History for making available the USGS card catalogue of Coastal Plain mollusks and for the knowledge that he contributed to this research. Thanks also to Susan Barbour Wood for her assistance with specimen identifications. I would also like to thank the landowners at Cobham Wharf and Mount Pleasant for allowing access to field sites.

A huge thanks goes out to the Paleobiology Seminar class (Andrew Zaffos, Max Christie, Jason Lunze, and Ryan Bonnette) and AJ Saltz and Sean Moran for their assistance with sample processing.

Thank you to all of the amazing friends and colleagues inside and out of the Geology Department. You all have been wonderful people to get to know and interact with on a daily basis.

And last but not least, thank you to the Geology Department faculty, as you all have created a fantastic learning environment over the past four years, but especially to Karen Layou and Rowan Lockwood, my advisors, who provided continual feedback and support throughout this entire project.
References Cited


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Ward, L., 1992, Molluscan biostratigraphy of the Miocene, Middle Atlantic Coastal Plain of North America.

Appendices
### Appendix 1: Results of Normality Tests

#### Appendix 1.1 – Abundance and Survivorship

**Tests of Normality**

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#### Appendix 1.2 – Abundance and Duration

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#### Appendix 1.3 – Abundance and Geographic Range

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