HOW METABOLIC RATE AFFECTS SURVIVORSHIP: THE GRIM STORY OF BIVALVES ACROSS A PLIOCENE EXTINCTION

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This thesis is submitted in the style of Palaeogeography, Palaeoclimatology, Palaeoecology.

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Abstract

Previous work hypothesized that escalation, the adaptive response of organisms to changes in their enemies, affects survivorship across extinction events. Most studies of how escalation affects survivorship and extinction have been restricted to morphological antipredatory traits (e.g., spines, coarse ribs, and thick shells) and have yielded little support for the hypothesis that escalation negatively influences survivorship across extinction events. A closer look at physiological escalation was needed, especially because escape tactics are the primary way some species avoid being consumed by predators.

To observe the possible effect of behavioral escalation on community dynamics during a mass extinction, changes in relative abundance of groups of differing metabolic rates across an extinction event were studied. Collections representing the Moore House Member of the Yorktown Formation and the Chowan River Formation, which straddle an upper Pliocene extinction, were counted to determine relative abundances of bivalve taxa. Relative abundances of taxa before and after the event were compared to determine how well they fared across the event. Activity levels (high, moderate, and low), used as a proxy for metabolic rate, were assigned to the taxa in question based on primary literature. Metabolic rates of certain representative taxa reported in the literature were verified by oxygen isotopic analysis.

Stable isotopic analyses of representative shells from taxa of differing activity levels were performed serially from umbo to commissure to produce oxygen isotopic curves. From these curves, annual growth rates were determined, which allowed

confirmation of metabolic rate of taxa for which published activity level data were used as a proxy for metabolic rate.

Results suggest that high metabolism did not adversely affect survivorship. The relative abundance of high metabolism individuals increased from the Moore House to the Chowan River, while that of moderate and low metabolism individuals decreased. Tests performed to determine if remaining individuals of unknown metabolic rate would bias the results showed in most cases that the trends remained the same; where the trend was changed it was not reversed.

Keywords: Escalation; Metabolism; Oxygen Isotopic Analysis; Survivorship; Pliocene; Escape Tactics

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1. Introduction

1.1. Causes of Extinction

Marine molluscs were severely affected by a major multi-phased extinction during the Late Pliocene (Hansen et al., 1999; Stanley and Campbell, 1981; Stanley, 1986). The Upper Pliocene Yorktown and Chowan River Formations of Virginia and North Carolina (Fig. 1) straddle one of the events (Ward and Gilinsky, 1993) and show an 80% loss of species (Campbell, 1998). The exact cause of the Late Pliocene extinction is not fully known. Ideas range from onset of glaciation (Hansen et al., 1999; Stanley, 1986) to a nearby supernova (Benitez et al., 2002; Knie et al., 2004). Allmon (2001) suggested that closure of the Panama Seaway and the nutrient decline it caused was the major culprit of the extinction event; however, he focused primarily on tropical regions of the western Atlantic and acknowledged that global cooling patterns had a more significant effect north of Cape Hatteras.

The climate of the Late Pliocene was dominated by a glacial event beginning at approximately 3.6 Ma and ending at approximately 2.4 Ma (Mudelsee and Raymo, 2005). Knie et al. (2004) suggested that a nearby supernova may have affected Earth's climate and initiated glaciation at approximately 2.8 Ma. However, Mudelsee and Raymo (2005), studying oxygen isotopes in ice cores, found that the beginning of Northern Hemisphere glaciation was at approximately 3.6 Ma, long before any evidence of a nearby supernova appeared. Another popular idea is that the closure of the Panama Seaway was the major cause of Northern Hemisphere glaciation. Hypothetically, an increase in Atlantic thermohaline cycling intensified moisture build-up in high northern latitudes leading to the Northern Hemisphere glaciation (Bartoli et al., 2005). Lunt et al.

(2007) looked at the closing of the Isthmus of Panama as a possible culprit and concluded that, while it did have an effect, it was not the major trigger for glaciation. Other ideas as to the cause of glaciation include Milankovitch Cycles (Kukla and Gavin, 2004), eolian deposition in the North Pacific (Rea et al., 1998), and addition of freshwater from Siberian rivers to the Arctic Ocean (Driscoll and Haug, 1998).

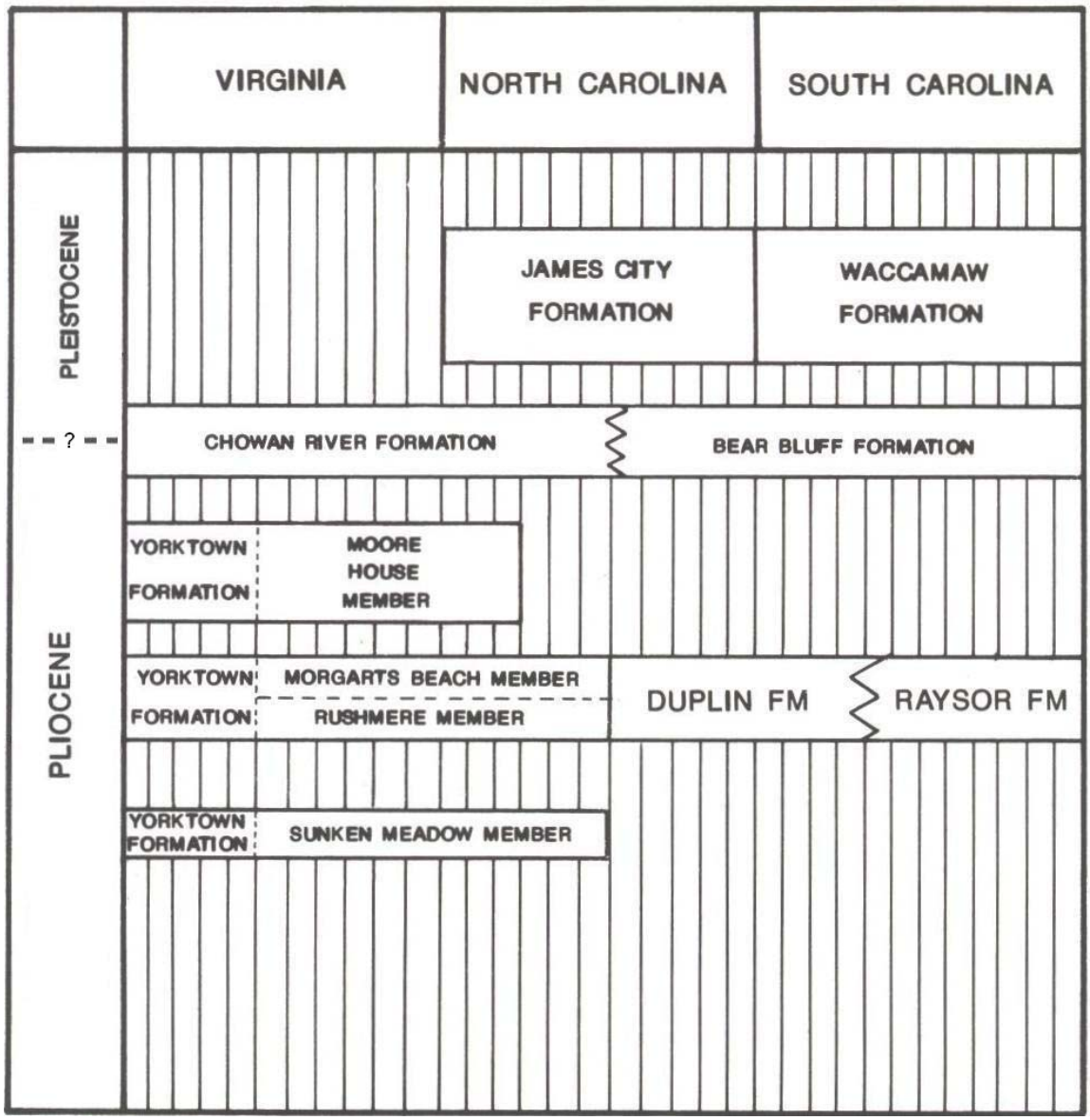


Figure 1: Spatial and temporal extent of lithologic formations in Virginia and the Carolinas from the Lower Pliocene to the Lower Pleistocene. The Yorktown and Chowan River Formations are found in Virginia and North Carolina; the Moore House Member of the Yorktown Formation is most prevalent in Virginia (from Ward et al., 1991). The exact age of the Chowan River Formation is debated; therefore the age of the boundary is uncertain (adapted from Ward and Gilinsky, 1993).

1.2. Effects of the Extinction on Paleocommunities

Regardless of what the ultimate cause of the disturbance was, the effect on marine paleocommunities was profound. Productivity loss in the Northern Pacific is seen as a loss and/or latitudinal shift of diatom flora (Shimada et al., 2009). Primary productivity loss affected higher trophic levels (Karlsson et al., 2007), which can be seen as a reduction or latitudinal shift in planktonic (Thunell and Belya, 1982) and benthic Foraminifera in the Atlantic (Jain and Collins, 2007). Bivalves, which are generally suspension-feeding primary consumers, would be affected early and harshly by a loss in primary productivity (Karlsson et al., 2007).

When a major disturbance drives a major extinction event, specialized and/or escalated (adapted to changes in enemies) species are usually preferentially decimated (McKinney, 1997). High metabolism is often an adaptation to predation, and can thus be considered an escalated trait (Dietl et al., 2002). Therefore, not only would an entire community be adversely affected by a loss in primary productivity, but species with higher metabolic rates, which require greater nutrient and energy intake than those with lower metabolism, should suffer greater declines in diversity and abundance.

1.3. Morphological versus Behavioral Escalation

Escalation in Cenozoic molluscan faunas has been widely researched (e.g. Dietl et al., 2002; Hansen et al., 2004; Hansen et al., 1999; Stanley, 1986; Vermeij 1977, 1983, 1987). Vermeij (1987) initiated studies regarding the effects of mass extinctions on morphologically escalated species. His hypothesis was that morphological escalation requires more raw materials to build the defensive structures and therefore an uninterrupted and abundant food supply. Hansen et al. (1999) expanded upon this idea

by studying the effects of mass extinctions on molluscan species and their recoveries across the Cretaceous/Paleocene, Eocene/Oligocene, middle Miocene, and Plio-Pleistocene extinctions. The result of that study was an overall lack of preferential decimation of escalated species. However, a drawback of studies to date is that they have not looked at behavioral escalation.

Vermeij (1983) noted that some bivalves rely on escape rather than armor for predator avoidance. Unfortunately, direct observation of behavioral traits is nearly impossible in the fossil record. To overcome this hurdle, Dietl et al. (2002) explored the use of oxygen isotope ratios in order to determine growth rates of bivalves. The basic concept is that the faster growing species would have a higher metabolism and be more capable of escape tactics such as rapid burrowing or swimming.

1.4. Oxygen Isotopes as a Proxy for Metabolic Rate

Oxygen isotopes can be used to determine growth rate, which provides a suitable proxy for metabolic rates among most bivalves (Dietl et al., 2002). There is a seasonal variation in $\delta^{18}O$ in marine environments; ^{18}O enrichment occurs during cooler periods and depletion occurs in warmer periods (Jones, 1998). Using this principle, Ivany et al. (2003) were able to measure the growth rate of the Atlantic surf clam *Spisula solidissima*, in mm/year (Fig. 2). They sampled along the shells from umbo to commissure, and generated sinusoidal curves from which annual growth rates could be measured based on isotope ratios plotted as $\delta^{18}O$ versus shell length. Lewis and Cerrato (1997), in a study of the soft shell clam *Mya arenaria*, determined that shell growth occurs independent of somatic growth in bivalves but remains linked to metabolic rate (i.e. faster shell growth equals higher metabolism). Thus species that exhibit higher metabolic rates also exhibit

higher shell growth rates (Dietl et al., 2002; Ivany et al., 2003). Therefore, sampling along a shell can yield estimates of annual growth and metabolic rates.

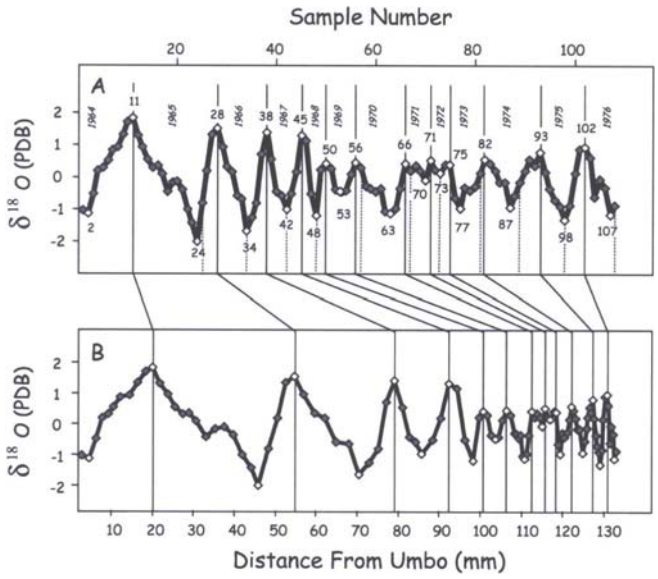


Figure 2: Annual growth rates of *Spisula solidissima* determined by oxygen isotopic ratios. The upper graph illustrates results by sample number, and the lower graph illustrates those results by distance along the shell. Peaks indicate cold conditions (i.e. winter) and troughs warm conditions (i.e. summer). A full wavelength measures an entire annual cycle, and the distance (mm/year) indicates growth rate (from Ivany et al., 2003).

After the concept of using oxygen isotopes to generate growth curves as proxies for metabolic rate was confirmed in modern organisms, the remaining task was to link those concepts to the paleontological record. Dietl et al. (2002) did that in a study of two bivalves from the middle Miocene Plum Point Marl Member of the Calvert Formation in Maryland. From observation of shell morphology, possible burrowing rates were inferred; *Macrocallista marylandica*, with a more flattened and elongate form, was predicted to be an active, rapid burrower while the more rounded *Glossus markoei* would more likely be a slower burrower. Specimens of each were sampled for oxygen isotopic analysis and the results plotted to create annual growth curves (Fig. 3). As expected, the more active *M. marylandica* showed greater spacing (mm/yr) of annual growth

increments than the less active *G. markoei*. This study demonstrated the viability of using oxygen isotope methods to infer metabolic rates in fossil bivalves.

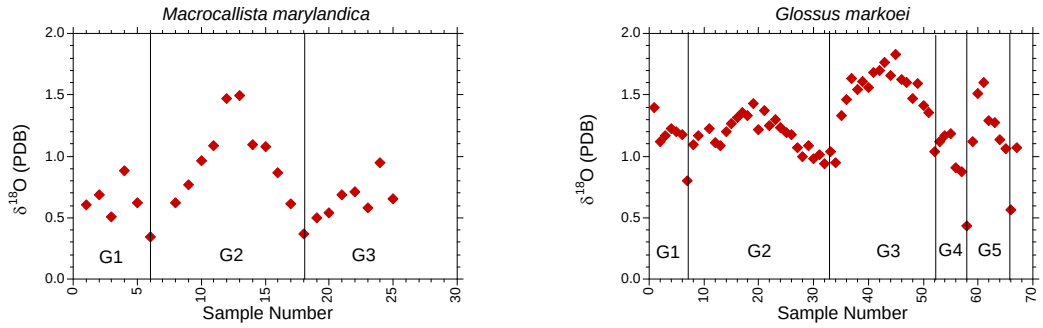


Figure 3: Seasonal growth curves of *Macrocallista marylandica* and *Glossus markoei* determined by ^{18}O ratios. Samples were taken 1 mm apart. Full annual growth cycles are indicated by vertical lines (from Dietl et al. 2002).

Kelley and Dietl, through a UNCW Center for Marine Science (CMS) pilot project funded in 2003, demonstrated the feasibility of this method for determining metabolic rates. Bivalves from the Moore House Member of the Pliocene Yorktown Formation were examined for chemical alteration. Unaltered shells were sampled regularly along the major growth axis for isotope analysis. The analysis demonstrated that the fossil material was sufficiently well preserved, and the isotopic signal sufficiently strong, to be used in determining growth rates.

1.5. Objectives of the Study

The objectives of this study are to: identify variation in metabolic rates of different bivalve species from the Moore House Member of the Yorktown Formation and the Chowan River Formation, chart relative abundance of said species across the Late Pliocene extinction event, and, using this information, determine if metabolic rates influenced abundance of species across the extinction event. It is hypothesized that species with higher metabolism, and thus higher nutrient demand, should be

preferentially decimated, during times of reduced primary productivity, relative to lower metabolism species.

2. Study area

2.1. Location

Outcrops of the Upper Pliocene Moore House Member of the Yorktown Formation occur along the York and James Rivers in Virginia (Ward and Gilinsky, 1993; Dowsett and Wiggs, 1992); exposures in quarries occur as far south as Aurora, North Carolina (Ward et al., 1991). The Upper Pliocene Chowan River Formation is exposed along the Chowan River in Bertie County, North Carolina, and in southeastern Virginia in the Hampton Roads area (Ward and Gilinsky, 1993; Jones, 1999).

2.2. Stratigraphy

The Moore House Member is the upper member of the Yorktown Formation (Fig. 1). The upper boundary is believed to be around 3.8 – 2.8 Ma (Krantz, 1990). The member is separated from the lower Rushmere and Morgarts Beach Members below and the overlying Chowan River Formation by unconformities (Ward and Gilinsky, 1993). Moore House lithology is highly calcareous, with shell hash, bioclastic sand, and in some locations clay and glauconite (Dowsett and Wiggs, 1992). The molluscan fauna of the Moore House Member is indicative of a warm temperate climate, with many species that disappear in the Late Pliocene extinction (Krantz, 1990; Ward and Gilinski, 1993) (Table 1).

The Chowan River Formation (Fig. 4) is bounded below by an unconformity with the Moore House Member and above by an unconformity with the James City Formation (Krantz, 1990; Ward et al., 1991). The Chowan River Formation is divided into the

lower Edenhouse and upper Colerain Beach Members (Ward et al., 1991). The Edenhouse Member is a shelly sand while the Colerain Beach Member is thinly bedded to thinly laminated estuarine or lagoonal clays containing interbedded shelly sands (Ward et al., 1991), which indicates that the Chowan River Formation was deposited under a regressive regime from middle-shelf to shallow-shelf and estuarine/lagoonal environments (Krantz, 1990; Ward et al., 1991). Numerous bivalve species occur within the formation, and one tends to see warm temperate species in the lower levels and subtropical species in the upper levels (Table 1), indicative of warming conditions up section (Krantz, 1990; Ward and Gilinsky, 1993).



Figure 4: The Edenhouse Member of the Chowan River Formation exposed along the banks of the Chowan River near Colerain, NC. Viewed from above. Scale bar = 10cm.

Table 1: Occurrence of mollusc species from the Upper Pliocene to Lower Pleistocene of North Carolina and Virginia by formation and age. Lines indicate extent of occurrence through these three formations. Asterisk indicates that species also occur below the Yorktown Formation (from Ward and Gilinsky, 1993). Individuals of *Anadara improcera* and *Ostrea raveneliana*, though listed on this table as occurring in both the Yorktown and Chowan River Formations, were found only in the Upper Yorktown Moore House Member when collections at the Virginia Museum of Natural History were examined for this study.

UPPER PLIOCENE		LOWER PLEISTOCENE	STRATIGRAPHIC UNITS / MOLLUSCAN SPECIES
Yorktown Formation	Chowan River Formation	James City Formation	
			Noetia incile (Say)
			Costaglycymeris subovata tuomeyi (Dall)
			Chesapecten madisonius (Say)
			"Pecten" decemnaria (Conrad)
			Chama congregata (Conrad)
			Pseudochama corticosa (Conrad)*
			Astarte undulata Say
			Marvacrassatella undulata (Say)
			Chesacardium acutilaqueatum (Conrad)
			Planicardium virginianum (Conrad)
			Leptomactra delumbis (Conrad)*
			Macoma virginiana Conrad
			Mercenaria tridacnoides (Lamarck)
			Pleiorytis centenaria (Conrad)
			Panopea reflexa Say
			Margaritaria abrupta (Conrad)
			Diadora redimicula (Say)
			Calliostoma michelli (Conrad)
			Turritella alticostata Conrad
			Crepidula spinosa Conrad
			Pterorytis umbrifer (Conrad)*
			Boreotrophon tetricus (Conrad)
			Scalaspira strumosa (Conrad)*
			Ecphora quadricostata (Say)
			Ptychosalpinx altilis (Conrad)
			Busycotypus incilis (Conrad)
			Fusinus exilis (Conrad)
			Oliva canaliculata (H. C. Lea)
			Conus marylandicus Green
			"Anadara" improcera (Conrad)
			Ostrea raveneliana Tuomey and Holmes
			Conradostrea sculpturata (Conrad)
			Parvilucina crenulata (Conrad)
			Timothynus subvexa (Conrad)
			Abra subreflexa (Conrad)
			Didianema carolinae Gardner
			Epitonium cornigera (H. C. Lea)
			Epitonium micropleura (H. C. Lea)
			Crepidula costata (Morton)
			Busycon maximus (Conrad)
			Lirosoma sulcosa (Conrad)
			Chrysallida granulata (H. C. Lea)
			Cadulus thallus (Conrad)

Table 1 continued

			Nuculana acuta ssp.
			Noetia carolinensis (Conrad)
			Costaglycymeri hummi (Ward and Blackwelder)
			Carolinapecten eboreus bertiensis (Mansfield)
			Sportella calpix Gardner
			Varicorbula chowanensis Bailey
			Verticordia chowanensis Gardner
			Urosalpinx trossula subsidus (Dall)
			Compsodrillia chowanensis Gardner
			Cryoturris serta Olsson and Harbison
			Dentalium carolinense Conrad
			Carolinapecten eboreus solanoides (Heilprin)
			Bellucina waccamawensis (Dall)
			Pleuromeris auroraensis Ward and Blackwelder
			Marvacrassatella kauffmani Ward and Blackwelder
			Crassinella johnsoni Ward and Blackwelder
			Semele bellastriata (Conrad)
			Chione (Chione) intapurpurea (Conrad)
			Pitar morrhuanus Linsley
			Macrocallista greeni Ward and Blackwelder
			Arene pergemma (Gardner)
			Rissoa geraea Dall
			Didianema duplinensis comes Olsson and Harbison
			Turritella beaufortensis Ward and Blackwelder
			Turritella perexilis Conrad
			Crucibulum lawrencei Ward and Blackwelder
			Eupleura caudata (Say)
			Aesopus gardnerae Ward and Blackwelder
			Busycotypus concinnum (Conrad)
			Nassarius albus (Say)
			Nassarius cornelliana (Olsson)
			Scaphella typus (Conrad)
			"Anadara" aequicostata (Conrad)
			Noetia limula (Conrad)
			Conradostrea sp.
			Mycella beaufortensis Ward and Blackwelder
			Sportella waccamawensis Gardner
			Macoma holmesii Dall
			Panopea floridana Heilprin
			Verticordia emmonsii (Conrad)
			Verticordia kelloggi Ward and Blackwelder
			Diadora auroraensis Ward and Blackwelder
			Diadora pamlicoensis Ward and Blackwelder
			Pterorytis conradi (Dall)
			Aesopus ithitoma (Dall)
			Busycon aruanum (Linné)
			Fasciolaria beaufortensis Ward and Blackwelder
			Pleuroploca cronlyensis Gardner
			Heilprinia caloosaensis kelloggi Ward and Blackwelder

3. Methods

3.1. Collections and counts

Sampling was attempted at known outcrops of the Moore House Member and the Chowan River Formation. Unfortunately, all known exposures of the Moore House member have been destroyed through construction or slope stabilization, so pre-existing collections from those exposures had to be used to complete the study. For consistency of methodology, existing collections from the Edenhouse Member of the Chowan River Formation sites along the Chowan River were also used.

Bulk samples from Zooks Pit and Rices Pit, representing the Moore House Member, as well as samples from Eden House, Black Rock, and Mt. Gould Landing, representing the Chowan River Formation, are stored at the Virginia Museum of Natural History (Fig. 5). Bivalves from these collections were identified at the family, genus, and species level, where possible. A compilation of counts of bivalves from the Moore House Member samples was created to obtain a total count of individuals from the Moore House Member; the same was done for Chowan River Formation samples (Appendix A).

Once total counts were obtained for each formation, the relative abundance of each taxon was determined before and after the extinction represented by the unconformity separating the Moore House Member from the Chowan River Formation. Relative abundance here is defined as the number of individuals of a given taxon divided by the total number of individual bivalves counted in the lithologic unit. Individuals are defined as the total number of valves that include the umbo, divided by two. Changes in relative abundance of each taxon across the extinction were tested for significance using Pearson's Chi-Squared test via Simple Interactive Statistical Analysis (SISA)

(http://quantitativeskills.com/sisa). Separate results were obtained for the family, genus, and species levels.

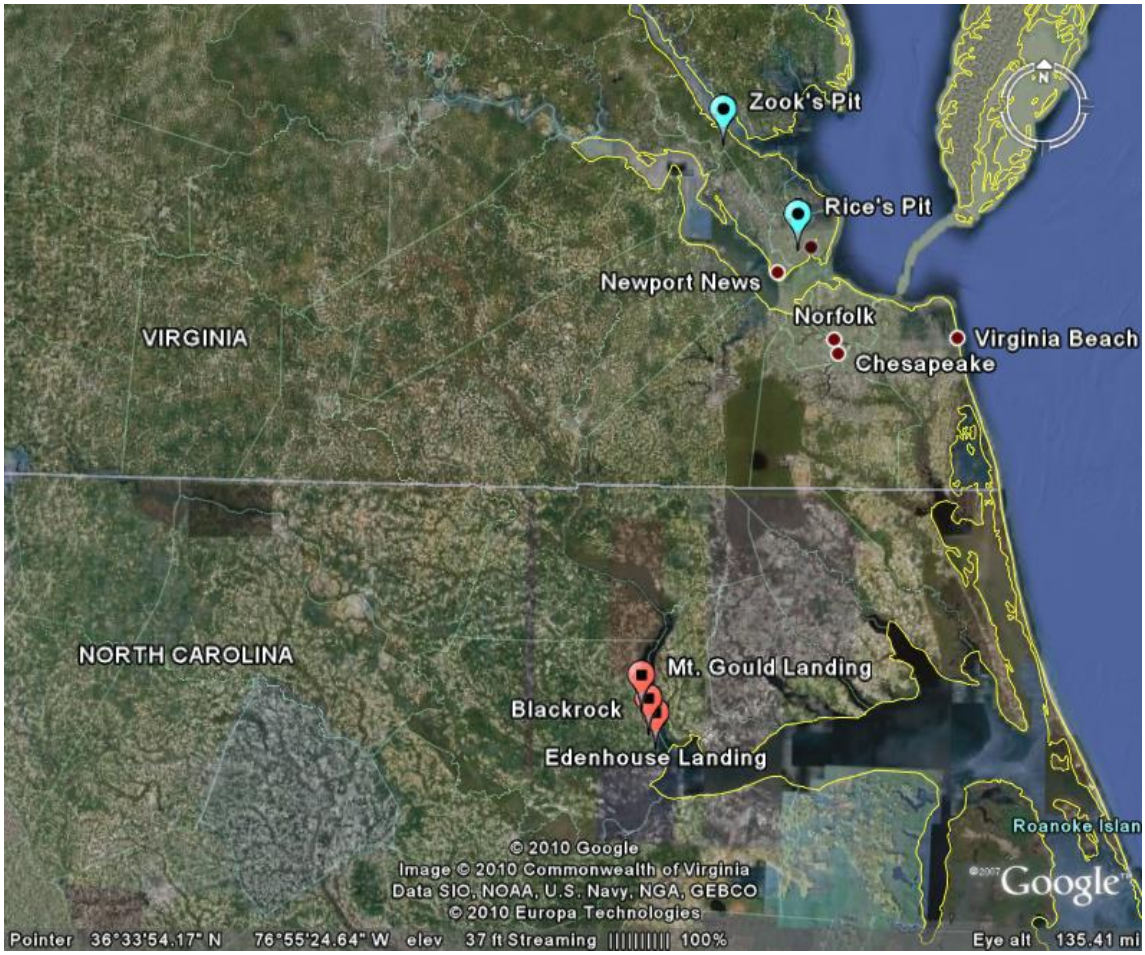


Figure 5: Exposures sampled in Virginia and North Carolina. The Moore House Member is exposed along the York and James Rivers in Virginia, while the Chowan River Formation is exposed at locations along the Chowan River in Bertie County, North Carolina. Moore House sites are labeled with circles in blue, and Chowan River sites are labeled with squares in red.

3.2. Determining metabolic rate

A review of the literature (Alexander et al., 1993; Checa and Jiminez-Jiminez, 2003; Rhoads and Pannella 1970; Stanley 1970) as well as online sources [Paleobiology Database (PBDB) (www.paleodb.org), Neogene Marine Biota of Tropical Biota (NMITA) (eusmilia.geology.uiowa.edu)] was used to determine the activity levels of most of the taxa in question, which were used as proxies for metabolic rate. Low activity

taxa (those that were non-mobile, sessile, sedentary, or slow burrowers) were considered to have low metabolic rates. High activity taxa (those that burrowed rapidly, swam, or jumped) were considered to have high metabolic rates. Those that were reported as moderate activity level (falling between the two extremes) were regarded as moderate metabolism. When a family was considered to be uniform in activity level, the included genera and species were labeled with that activity level. When a family varied in activity level, the activity levels of the included genera were determined and applied to the individual species.

To test the reliability of activity level data as a proxy for metabolic rate, oxygen isotopic analyses were conducted on shells representing species ranked as high and low metabolic rate based on activity level; these include *Noetia carolinensis*, *Glycymeris americana*, *Panopea americana* (a Miocene-age congener of *P. goldfussii* and P. *reflexa*), and *Marvacrassatella kauffmani* as low metabolism species, and *Carolinapecten eboreus* as a high metabolism species. Large shells were selected, sliced open along the growth axis, and sampled serially from umbo to commissure at intervals not exceeding 3mm along the outer shell layer using a Dremel rotary tool. Samples of sufficient size (at least 40μg, mostly 100-300 μg) were run on a Delta V Plus mass spectrometer (Thermo Electron Corporation) at the Center for Marine Science at the University of North Carolina Wilmington. Standards used for calibration were lithium carbonate (LSVEC) and limestone (NBS 19). Replication was achieved by 10 sequential gas samplings of each carbonate sample while on the mass spectrometer. The resulting isotopic ratios were plotted to display the annual growth curves. Shells that displayed longer seasonal growth increments (mm/yr) were considered to have higher metabolism, and those that

showed shorter seasonal growth increments were considered to have lower metabolism. Growth curves for *Carolinapecten eboreus* were derived by measuring the distance between winter growth cessation lines, identified visually, using calipers; carbonate samples of sufficient mass for the resolution of the mass spectrometer at our disposal could not be obtained from the thin shells without crossing into interior shell layers, which would have distorted the results (Chauvaud et al., 2005).

The shells used in the oxygen isotopic analyses, for which the original structural material was aragonite, were tested for diagenesis using two different methods. The first method used was staining with Feigl's solution, which stains aragonite black while leaving calcite white. The unsampled halves of the sliced valves were covered in the solution and allowed to sit overnight; afterwards they were compared to the unstained halves. The second method used was X-ray diffraction. Powdered samples from near the umbo of the unstained valves were run through the X-ray diffractometer (XRD) located in DeLoach Hall at UNCW. Resultant peaks were compared to known peaks of aragonite and calcite to determine composition.

3.3. Data Analyses

After metabolic rates had been determined for each taxonomic rank, they were divided into one of four metabolic rate categories: high metabolism, medium metabolism, low metabolism, or unknown metabolism. The total counts of each taxa and metabolic rate group were examined in three different ways: survivorship, relative abundance changes among taxa, and relative abundance changes between metabolic rate categories.

3.3.1. Survivorship

To determine survivorship, the number of taxa that occurred in the Moore House Member and Chowan River Formation versus those that occurred only in the Moore House Member was determined. Metabolic rates of each were compared at the family, genus, and species level. To avoid any confusion, taxa that first appeared in the Chowan River Formation were excluded, as they were irrelevant to a consideration of survival across the event. Since many taxa that did not occur in the Chowan River collections still occur today, those listed as "non-surviving" could be considered locally extirpated or an artifact of sampling error.

3.3.2. Comparison of Taxonomic Increases and Decreases

The taxa at the family, genus, and species level were compared to see how many increased significantly in relative abundance, how many decreased significantly, and how many did not change. At each taxonomic rank, the taxa of each metabolic rate category were compared to see what percentage of taxa were increasing, decreasing, or not changing. The results were graphed for easier visual comparisons between the metabolic rate categories. In this way, it could be determined which metabolic rate group, if any, had more families increasing in relative abundance, more decreasing in relative abundance, etc; the same was done at the genus and species level. Again, all first appearances in the Chowan River assemblages were omitted from the analysis.

3.3.3. Relative Abundance Changes between Metabolic Rate Categories

Issues arising from the comparison of increasing versus decreasing versus non-changing taxa (discussed in detail later in this paper) led to a different approach to analyzing the data. Among the issues was the omitting of taxa that first appear in the

Chowan River assemblages. Using the method described in this section, I was able to include all taxa counted, regardless of first appearance. Other problems with the above described data analysis included rare taxa being weighted equally with dominant ones, and sample size changes masked the larger picture (e.g. several species could individually show no significant change, but grouped together into their family, could artificially show a significant change). To overcome this problem, the overall relative abundance change of each metabolic rate category between assemblages was calculated (Appendix D).

The total individuals within each metabolic rate category were calculated as percent of the total assemblage for the Moore House and Chowan River assemblages, respectively. The resultant relative abundance change of each metabolic rate category across the extinction event was determined by comparing the relative abundance percent before the extinction (Moore House assemblages) to the percent after the extinction (Chowan River assemblages). Statistical significance was determined using the Pearson's chi square test program on SISA.

Many species of unknown metabolic rate remained, and the number of individuals of these species were incorporated into the calculations in several different ways: by assuming that all represented high metabolism, all moderate metabolism, all low metabolism, and as a split between different formations (all Moore House individuals as high metabolism with all Chowan River as either moderate or low, and all Chowan River individuals as high metabolism with all Moore House as either moderate or low). This way any possible errors in determining abundance caused by the omission of species of unknown metabolic rate could be identified.

4. Results

4.1. Oxygen Isotopic Analysis

Oxygen isotope results were plotted for the four species listed above (Fig. 6). Standard deviations for each data point are reported in appendix C. The growth curves show few, if any, discernible annual patterns. Possible reasons for this lack of usable data are discussed below, in section 5.1. Some that roughly approximated annual curves are illustrated in Figure 6. However, these divisions are speculative at best, and may not necessarily represent accurate annual curves.

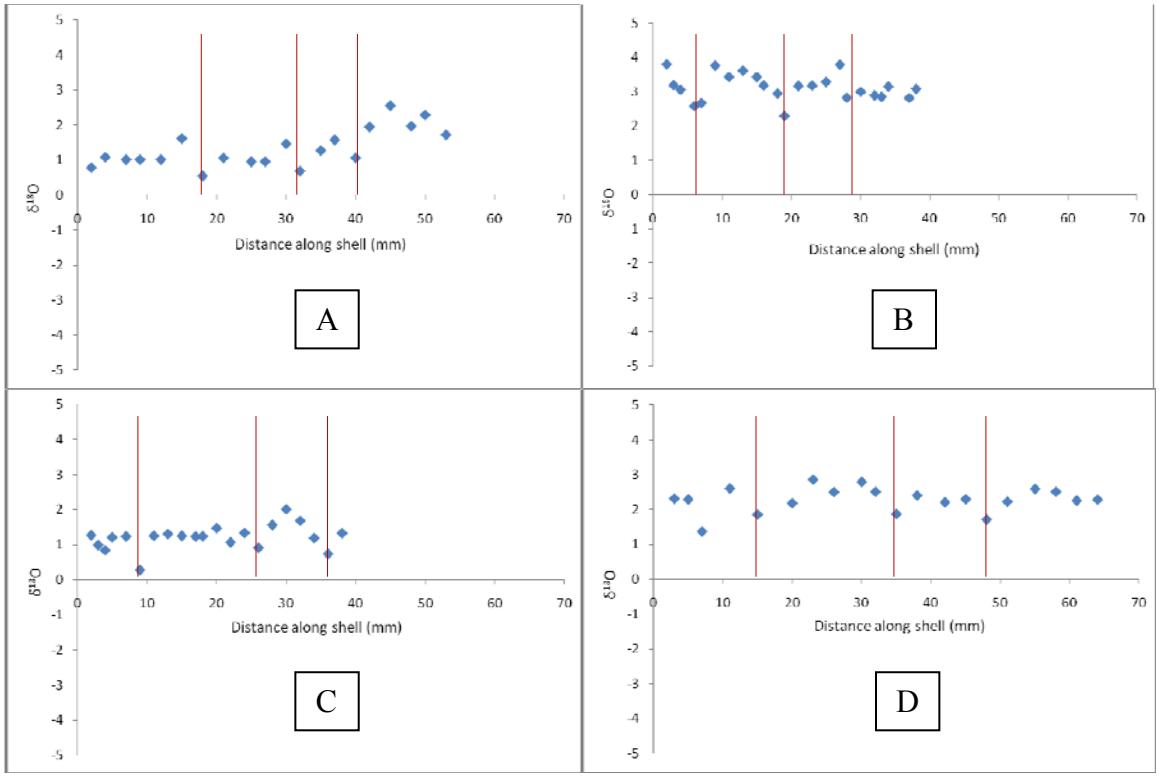


Figure 6: Growth curves of selected bivalves determined by oxygen isotope analyses. Vertical lines indicate approximate boundaries of annual cycles. (A) *Glycymeris americana*, (B) *Panopea americana*, (C) *Noetia carolinensis*, (B) *Marvacrassatella kauffmani.* For standard deviation values see Appendix C.

As mentioned above, the annual growth of *Carolinapecten eboreus* was determined by measuring the distances between growth lines visible on the outer shell.

The comparison of annual growth rate between *C. eboreus* and the roughly approximated growth rates from the other specimens is given in Table 2.

Feigl's solution tests were generally negative for diagenesis, but some patchiness was observed. However, the lightest shades of the stained halves of the shells were still darker than any parts of the unstained shells. X-ray diffraction of all splits from samples resulted in verification of their aragonite composition. However, concentrations of less than 5% cannot be identified; therefore all shells were at least 95% aragonite (Harris, pers. comm.). This result indicates that calcite, if present, was probably not at a high enough concentration to affect the oxygen isotope analyses.

Table 2: Comparison of annual growth rates of selected individuals from the Chowan River Formation. *derived from $\delta^{18}O$ curves

SPECIMEN		ANNUAL GROWTH (mm)			
Species	ID Tag	Year 1	Year 2	Year 3	Average
*Glycymeris americana**	CLGA-2	18	14	8	13.3333
*Panopea americana**	DCPA-1	6	13	13	10.6667
*Noetia carolinensis**	SLNC-1	9	13	14	12
*Marvacrassatella kauffmani**	CLEK-1	15	20	13	16
Carolinapecten eboreus	CLCE-1	14	15	9	12.6667

4.2. Data Analysis

4.2.1. Survivorship

Table 3 reports the total numbers, by taxonomic rank, of groups that occurred in both the Moore House Member and the Chowan River Formation collections versus those that were present only in the Moore House Member collections. Those that were present only in the Moore House were considered to have disappeared locally. Since many taxa that did not occur in the Chowan River collections still occur today, those listed as "non-surviving" should be considered locally extirpated or an artifact of sampling error.

In total, 28 families were considered in the family-level comparison (Fig. 7); 21 (75%) families survived the extinction and 7 (25%) did not. Of the 15 low metabolism

Table 3: Taxa that occurred in both the Moore House and Chowan River assemblages (surviving) versus those that appeared only in the Moore House assemblages (non-surviving).

FAMILY-LEVEL TOTALS				
CATEGORY	COUNT	% OF METABOLIC RATE	% OF SURVIVING/NON-SURVIVING	% OF TOTAL
Low Metabolism Surviving	11	73.33%	52.38%	39.29%
Low Metabolism Disappearing	4	26.67%	57.14%	14.29%
Medium Metabolism Surviving	1	50.00%	4.76%	3.57%
Medium Metabolism Disappearing	1	50.00%	14.29%	3.57%
High Metabolism Surviving	4	100.00%	19.05%	14.29%
High Metabolism Disappearing	0	0.00%	0.00%	0.00%
Unknown Metabolism Surviving	5	71.43%	23.81%	17.86%
Unknown Metabolism Disappearing	2	28.57%	28.57%	7.14%
Total Surviving	21	75.00%	100.00%	75.00%
Total Disappearing	7	25.00%	100.00%	25.00%
Total	28	100.00%	100.00%	100.00%
GENUS-LEVEL TOTALS				
CATEGORY	COUNT	% OF METABOLIC RATE	% OF SURVIVING/NON-SURVIVING	% OF TOTAL
Low Metabolism Surviving	26	65.00%	54.17%	32.91%
Low Metabolism Disappearing	14	35.00%	45.16%	17.72%
Medium Metabolism Surviving	3	42.86%	6.25%	3.80%
Medium Metabolism Disappearing	4	57.14%	12.90%	5.06%
High Metabolism Surviving	9	64.29%	18.75%	11.39%
High Metabolism Disappearing	5	35.71%	16.13%	6.33%
Unknown Metabolism Surviving	10	55.56%	20.83%	12.66%
Unknown Metabolism Disappearing	8	44.44%	25.81%	10.13%
Total Surviving	48	60.76%	100.00%	60.76%
Total Disappearing	31	39.24%	100.00%	39.24%
Total	79	100.00%	100.00%	100.00%
SPECIES-LEVEL TOTALS				
CATEGORY	COUNT	% OF METABOLIC RATE	% OF SURVIVING/NON-SURVIVING	% OF TOTAL
Low Metabolism Surviving	25	43.10%	52.08%	21.74%
Low Metabolism Disappearing	33	56.90%	49.25%	28.70%
Medium Metabolism Surviving	3	33.33%	6.25%	2.61%
Medium Metabolism Disappearing	6	66.67%	8.96%	5.22%
High Metabolism Surviving	10	43.48%	20.83%	8.70%
High Metabolism Disappearing	13	56.52%	19.40%	11.30%
Unknown Metabolism Surviving	10	40.00%	20.83%	8.70%
Unknown Metabolism Disappearing	15	60.00%	22.39%	13.04%
Total Surviving	48	41.74%	100.00%	41.74%
Total Disappearing	67	58.26%	100.00%	58.26%
Total	115	100.00%	100.00%	100.00%

families, 11 (73%) survived and four (27%) disappeared. Of the two medium metabolism families, one (50%) survived and one (50%) disappeared. Of the four high metabolism families, four (100%) survived and none (0%) disappeared. Of the seven unknown metabolism families, five (71%) survived and two (29%) disappeared.

In total, 79 genera were considered in the genus-level comparison (Fig. 8); 48 (61%) genera survived the extinction and 31 (39%) did not. Of the 40 low metabolism genera, 26 (65%) survived and 14 (35%) disappeared. Of the seven medium metabolism genera, three (43%) survived and four (57%) disappeared. Of the 14 high metabolism genera, nine (64%) survived and five (36%) disappeared. Of the 18 unknown metabolism genera, ten (56%) survived and eight (44%) disappeared.

In total, 115 species were considered in the species-level comparison (Fig. 9); 48 (42%) species survived the extinction and 67 (58%) did not. Of the 58 low metabolism species, 25 (43%) survived and 33 (57%) disappeared. Of the nine medium metabolism

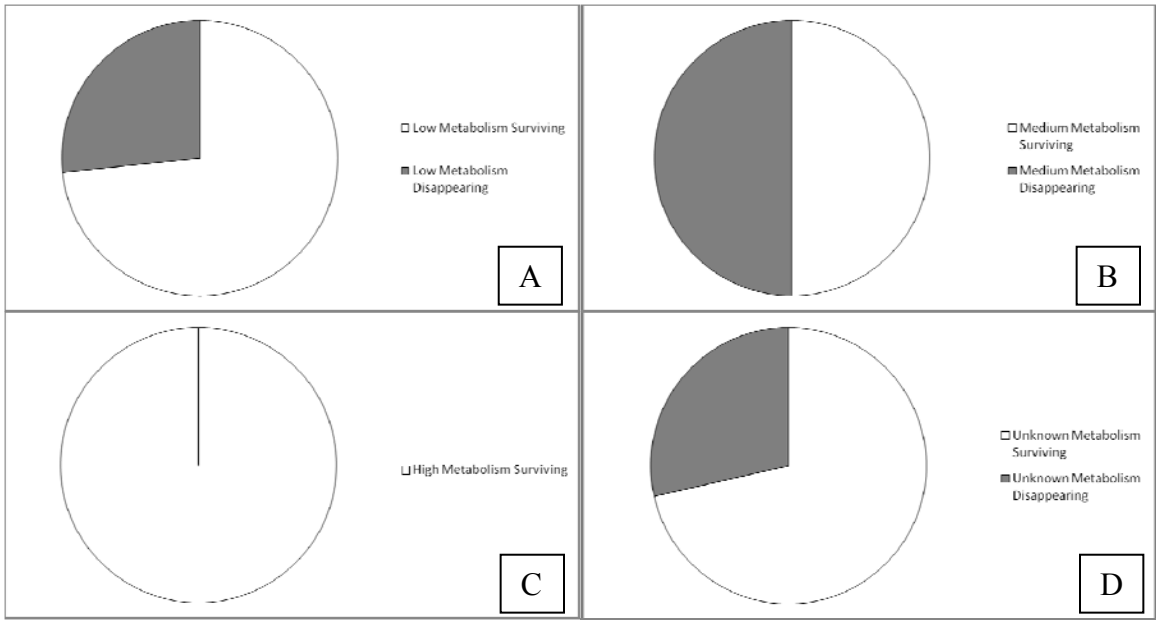


Figure 7: Families that occur in the Moore House Member and Chowan River Formation (surviving) versus those that only occur in the Moore House (non-surviving). Since the event is local in scale, non-survival in this sense could be considered as local extirpation. A) low metabolism, B) medium metabolism, C) high metabolism, D) unknown metabolism. Note that all high metabolism families are considered surviving.

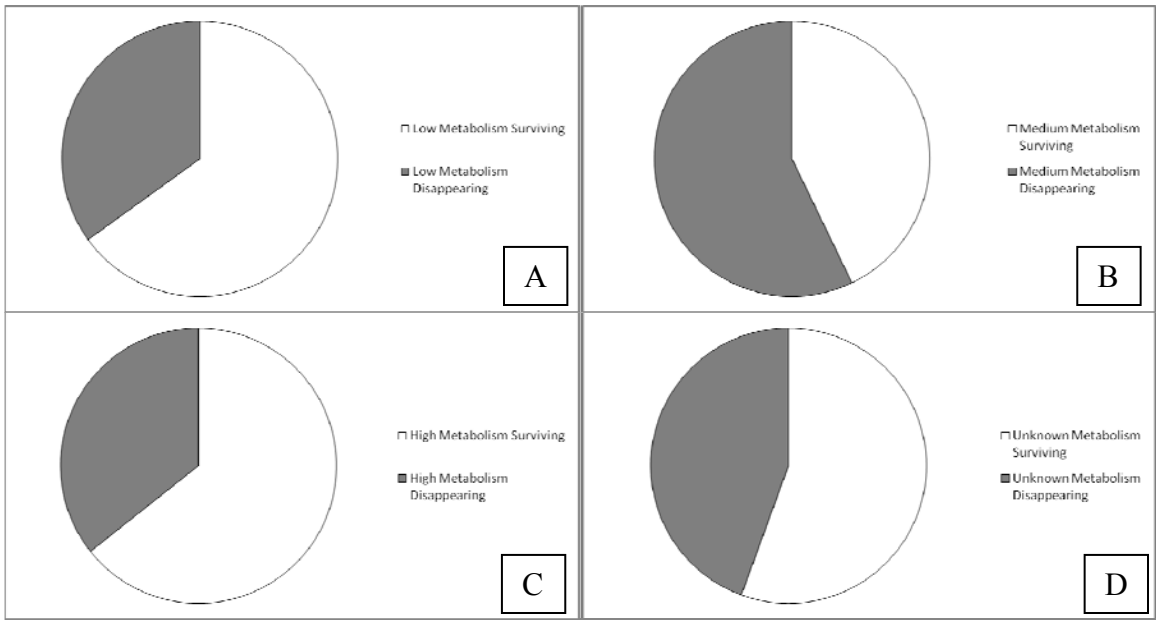


Figure 8: Genera that occur in the Moore House Member and Chowan River Formation (surviving) versus those that only occur in the Moore House (non-surviving). Since the event is local in scale, non-survival in this sense could be considered as local extirpation. A) low metabolism, B) medium metabolism, C) high metabolism, D) unknown metabolism.

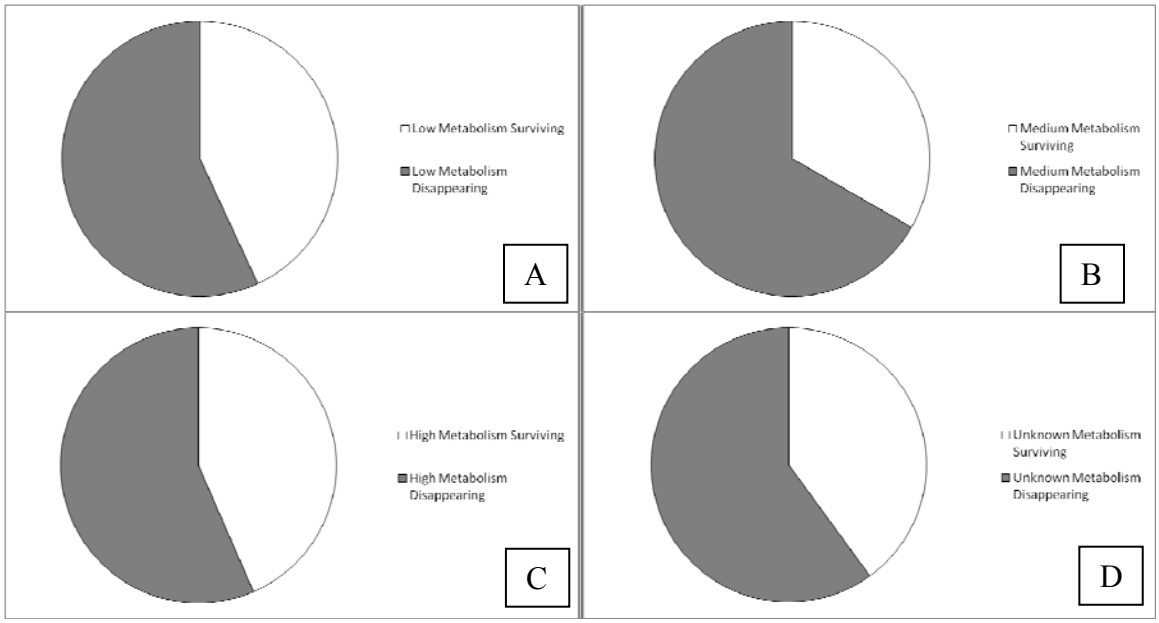


Figure 9: Species that occur in the Moore House Member and Chowan River Formation (surviving) versus those that only occur in the Moore House (non-surviving). Since the event is local in scale, non-survival in this sense could be considered as local extirpation. A) low metabolism, B) medium metabolism, C) high metabolism, D) unknown metabolism.

species, three (33%) survived and six (67%) disappeared. Of the 23 high metabolism species, ten (43%) survived and 13 (57%) disappeared. Of the 25 unknown metabolism genera, ten (40%) survived and 15 (60%) disappeared.

4.2.2. Comparison of Taxonomic Increases and Decreases

When changes are compared by taxonomic rank, there is little overall significant change (Table 4). Out of seven high activity families, three (43%) significantly increased in relative abundance, none (0%) decreased, and four (57%) did not change. Out of two moderate activity families, one (50%) significantly increased in relative abundance and one (50%) decreased. Out of 23 low activity families, eight (35%) significantly increased in relative abundance, seven (30%) decreased, and eight (35%) did not change. Out of eight families with unknown or variable activity, two (25%) significantly increased in relative abundance, one (12%) significantly decreased, and five (63%) did not change.

At the generic level the pattern stays roughly the same. Out of 15 high activity genera, seven (47%) significantly increased in relative abundance, two (13%) decreased, and six (40%) did not change. Out of six moderate activity genera, one (17%) significantly increased in relative abundance, four (66%) decreased, and one (17%) did not change. Out of 31 low activity genera, 12 (39%) significantly increased in relative abundance, nine (29%) decreased, and ten (32%) did not change. Out of 36 genera with unknown activity, three (8%) significantly increased in relative abundance, two (6%) decreased, and 31 (86%) did not change.

At the species level, patterns once again remain similar with only relatively minor variations (Fig. 10). Out of 27 high activity species, ten (37%) significantly increased in relative abundance, five (19%) decreased, and 12 (44%) did not change. Out of 12 moderate activity species, four (33%) significantly increased in relative abundance, three (25%) decreased, and five (42%) did not change. Out of 77 low activity species, 24 (31%) significantly increased in relative abundance, 16 (21%) decreased, and 37 (48%)

did not change. Out of 36 species with unknown metabolism, eight (22%) significantly increased in relative abundance, six (17%) decreased, and 22 (61%) did not change.

A potentially unusual case arises from the inclusion of lucinids in the samples. Lucinids are chemosymbiotic, and as such do not fit the general metabolic mold. As a family, their relative abundance increased significantly ($p<0.00005$) from the Moore

Table 4: Relative abundance change by taxonomic rank. Columns indicate how many taxa of each metabolic rate category show the indicated change (increase, decrease, no change) in relative abundance.

TOTAL COUNT				
	TOTAL	**INCREASE**	**DECREASE**	**NO CHANGE**
FAMILY LEVEL	**40**	**14**	**9**	**17**
High Activity	7	3	0	4
Moderate Activity	2	1	1	0
Low Activity	23	8	7	8
Unknown/Varies	8	2	1	5
GENUS LEVEL	**88**	**23**	**17**	**48**
High Activity	15	7	2	6
Moderate Activity	6	1	4	1
Low Activity	31	12	9	10
Unknown/Varies	36	3	2	31
SPECIES LEVEL	**152**	**46**	**30**	**76**
High Activity	27	10	5	12
Moderate Activity	12	4	3	5
Low Activity	77	24	16	37
Unknown	36	8	6	22

AS PERCENT OF COMPARATIVE ACTIVITY LEVEL				
	TOTAL	**INCREASE**	**DECREASE**	**NO CHANGE**
FAMILY LEVEL	**100.00%**	**35.00%**	**22.50%**	**42.50%**
High Activity	100.00%	42.86%	0.00%	57.14%
Moderate Activity	100.00%	50.00%	50.00%	0.00%
Low Activity	100.00%	34.78%	30.43%	34.78%
Unknown/Varies	100.00%	25.00%	12.50%	62.50%
GENUS LEVEL	**100.00%**	**26.14%**	**19.32%**	**54.55%**
High Activity	100.00%	46.67%	13.33%	40.00%
Moderate Activity	100.00%	16.67%	66.67%	16.67%
Low Activity	100.00%	38.71%	29.03%	32.26%
Unknown/Varies	100.00%	8.33%	5.56%	86.11%
SPECIES LEVEL	**100.00%**	**30.26%**	**19.74%**	**50.00%**
High Activity	100.00%	37.04%	18.52%	44.44%
Moderate Activity	100.00%	33.33%	25.00%	41.67%
Low Activity	100.00%	31.17%	20.78%	48.05%
Unknown	100.00%	22.22%	16.67%	61.11%

AS PERCENT OF DIRECTIONAL RELATIVE ABUNDANCE SHIFT				
	TOTAL	**INCREASE**	**DECREASE**	**NO CHANGE**
FAMILY LEVEL	**100.00%**	**100.00%**	**100.00%**	**100.00%**
High Activity	17.50%	21.43%	0.00%	23.53%
Moderate Activity	5.00%	7.14%	11.11%	0.00%
Low Activity	57.50%	57.14%	77.78%	47.06%
Unknown/Varies	20.00%	14.29%	11.11%	29.41%
GENUS LEVEL	**100.00%**	**100.00%**	**100.00%**	**100.00%**
High Activity	17.05%	30.43%	11.76%	12.50%
Moderate Activity	6.82%	4.35%	23.53%	2.08%
Low Activity	35.23%	52.17%	52.94%	20.83%
Unknown/Varies	40.91%	13.04%	11.76%	64.58%
SPECIES LEVEL	**100.00%**	**100.00%**	**100.00%**	**100.00%**
High Activity	17.76%	21.74%	16.67%	15.79%
Moderate Activity	7.89%	8.70%	10.00%	6.58%
Low Activity	50.66%	52.17%	53.33%	48.68%
Unknown	23.68%	17.39%	20.00%	28.95%

House to the Chowan River. The only species that occurred in both levels, *Parvilucina crenulata*, showed a lesser increase in relative abundance that was also significant (p=0.0028).

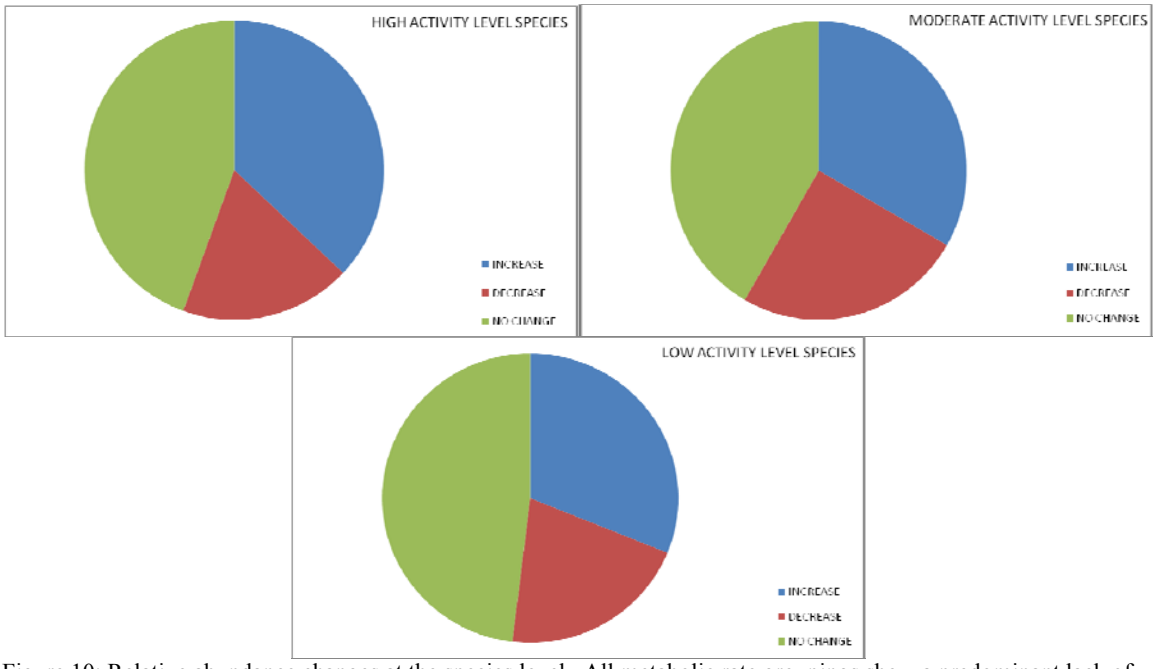


Figure 10: Relative abundance changes at the species level. All metabolic rate groupings show a predominant lack of change in relative abundance among their species, and more species of each increase in relative abundance rather than decrease.

4.2.3. Relative Abundance Changes between Metabolic Rate Categories

The percentage of high metabolism individuals significantly increased by 17.85% (Pearson's chi square, $p<0.00005$), the percentage of moderate metabolism individuals significantly decreased by 2.28% ($p=0.0040$), the percentage of low metabolism individuals significantly decreased by 15.07% ($p<0.00005$) (Fig. 11).

As discussed above, the possibility that the inclusion of the 36 species of unknown metabolic rate to the counts might have reversed the results was a potentially major issue that arose. To test the effect they might have had on the relative abundance counts they were incorporated into different metabolic rate counts as mentioned above (Table 5). A total of seven tests were run. Five showed the same pattern of significant increase of high metabolism individuals coupled with significant decrease of moderate and low metabolism individuals. Two tests showed a lack of significant change in high metabolism species; one also shows lack of significant change in low metabolism species, and the other shows significant increase in moderate metabolism species.

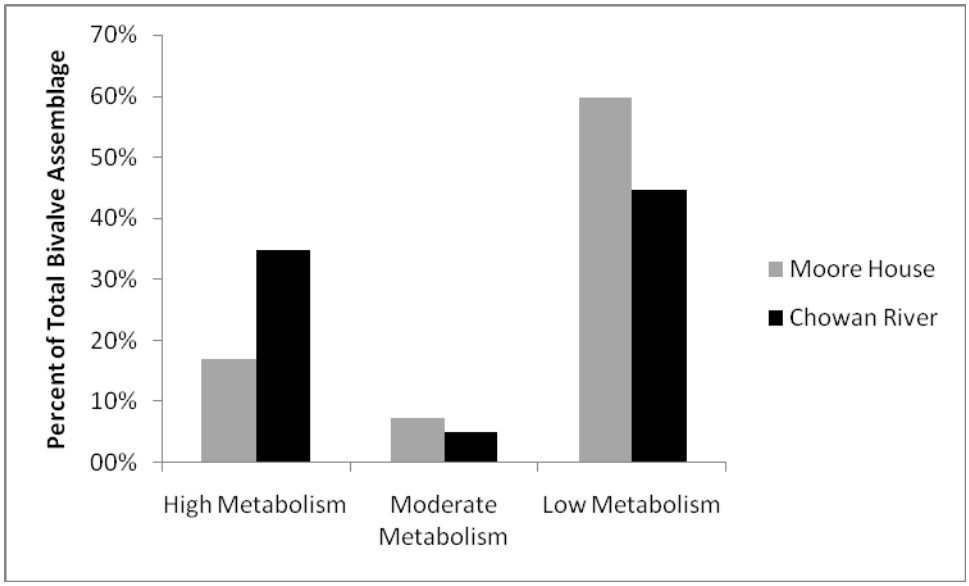


Figure 11: Percent composition of Moore House Member and Chowan River Formation bivalve assemblages based on metabolic rates. There is an increase in relative abundance of high metabolism individuals, coupled with a decrease in relative abundance of moderate and low metabolism individuals. All changes are significant ($p\leq0.0040$).

Table 5: Tests of possible errors of assemblage results caused by individuals of unknown metabolic rate

ALL SPECIES OF UNKNOWN METABOLIC RATE ASSIGNED TO HIGH METABOLISM CATEGORY						
	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	1220	653.5	261.5	69	2143	614.5
OUT OF	3588	1376	3588	1376	3588	1376
PERCENT	34.00%	47.49%	7.29%	5.01%	59.73%	44.66%
PERCENTAGE CHANGE	+13.49%		-2.28%		-15.07%	
PEARSON'S CHI SQUARE	77.033		8.273		91.458	
P=	0.0000		0.0040		0.0000	
RESULTS: Slightly lesser increase in high metabolism percentage, same overall pattern						

ALL SPECIES OF UNKNOWN METABOLIC RATE ASSIGNED TO MEDIUM METABOLISM CATEGORY						
	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	610	479.5	871.5	243	2143	614.5
OUT OF	3588	1376	3588	1376	3588	1376
PERCENT	17.00%	34.85%	24.29%	17.66%	59.73%	44.66%
PERCENTAGE CHANGE	+17.85%		-6.63%		-15.07%	
PEARSON'S CHI SQUARE	184.908		25.105		91.458	
P=	0.0000		0.0000		0.0000	
RESULTS: Greater decrease in medium metabolism percentage, same overall pattern						

ALL SPECIES OF UNKNOWN METABOLIC RATE ASSIGNED TO LOW METABOLISM CATEGORY						
	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	610	479.5	261.5	69	2753	788.5
OUT OF	3588	1376	3588	1376	3588	1376
PERCENT	17.00%	34.85%	7.29%	5.01%	76.73%	57.30%
PERCENTAGE CHANGE	+17.85%		-2.28%		-19.43%	
PEARSON'S CHI SQUARE	184.908		8.273		183.548	
P=	0.0000		0.0040		0.0000	
RESULTS: Greater decrease in low metabolism percentage, same overall pattern						

MOORE HOUSE UNKNOWNS AS HIGH METABOLISM, CHOWAN RIVER UNKNOWNS AS MEDIUM METABOLISM						
	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	1220	479.5	261.5	243	2143	614.5
OUT OF	3588	1376	3588	1376	3588	1376

PERCENT	34.00%	34.85%	7.29%	17.66%	59.73%	44.66%
PERCENTAGE CHANGE	+0.85%		+10.37%		-15.07%	
PEARSON'S CHI SQUARE	0.316		117.18		468.826	
P=	0.5743		0.0000		0.0000	
RESULTS: Lack of significant change in high metabolism individuals, significant increase in medium metabolism individuals, different overall patterns						

MOORE HOUSE UNKNOWNS AS HIGH METABOLISM, CHOWAN RIVER UNKNOWNS AS LOW METABOLISM

	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	1220	479.5	261.5	69	2143	788.5
OUT OF	3588	1376	3588	1376	3588	1376
PERCENT	34.00%	34.85%	7.29%	5.01%	59.73%	57.30%
PERCENTAGE CHANGE	+0.85%		-2.28%		-2.43%	
PEARSON'S CHI SQUARE	0.316		8.273		2.415	
P=	0.5743		0.0040		0.1206	
RESULTS: Lack of significant change in high metabolism individuals and low metabolism individuals, significant decrease in medium metabolism species, somewhat different overall pattern						

MOORE HOUSE UNKNOWNS AS MEDIUM METABOLISM, CHOWAN RIVER UNKNOWNS AS HIGH METABOLISM

	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	610	653.5	871.5	69	2143	614.5
OUT OF	3588	1376	3588	1376	3588	1376
PERCENT	17.00%	47.49%	24.29%	5.01%	59.73%	44.66%
PERCENTAGE CHANGE	+30.49%		-19.28%		-15.07%	
PEARSON'S CHI SQUARE	487.335		240.612		468.826	
P=	0.0000		0.0000		0.0000	
RESULTS: strengthens differences in relative abundance between high, medium, and low metabolism individuals, same overall pattern						

MOORE HOUSE UNKNOWNS AS LOW METABOLISM, CHOWAN RIVER UNKNOWNS AS HIGH METABOLISM

	HIGH METABOLISM		MEDIUM METABOLISM		LOW METABOLISM	
	Moore House	Chowan River	Moore House	Chowan River	Moore House	Chowan River
TOTAL	610	653.5	261.5	69	2753	614.5
OUT OF	3588	1376	3588	1376	3588	1376
PERCENT	17.00%	47.49%	7.29%	5.01%	76.73%	44.66%
PERCENTAGE CHANGE	+30.49%		-2.28%		-32.07%	
PEARSON'S CHI SQUARE	487.335		8.273		468.826	
P=	0.0000		0.0040		0.0000	
RESULTS: strengthens differences in relative abundance between high, medium, and low metabolism individuals, same overall pattern						

5. Discussion

5.1. Unusual Results of $\delta^{18}O$ Analysis

Growth curves based on the analyses run for this experiment (Fig. 5) are not as easy to interpret as desired when compared to other results (Figs. 1 and 2). Also, the faster average annual growth rate of the low activity *Glycymeris americana* and *Marvacrassatella kauffmani* versus the high activity *Carolinapecten eboreus* is suspect, as is the near-match in average growth rate between *Noetia carolinensis* and *C. eboreus*. From Figures 1 and 2, we see that the method is reliable and sound, so what went wrong here? There are a couple possibilities.

The first problem was the resolution of the mass spectrometer used. Dietl et al (2002) used 20-30 µg of carbonate material for each sample in their study. Results from the IRMS used in this study could not be obtained with less than approximately 40µg of carbonate sample, and for best results sample sizes of >90 µg were needed. Therefore, large amounts of sample were needed; most samples in this study were over 150 µg.

To obtain the larger sample sizes we needed, the samples had to spaced farther apart, which meant there weren't enough data points to establish trends. When Dietl et al. (2002) obtained samples from their shells, they were an even 1 mm apart and relatively thin (<1 mm wide) drilling. In this study, samples were taken as much as 5 mm apart, the drill bit available for use was wider than 1mm, and the drilling for the sample could be up to 2 mm wide. With that being the case, one sample from one of these shells could have encompassed what would have been several samples in other studies, which would have averaged out possibly important separate individual data points.

5.2. Differences between Data Analysis Methods

5.2.1. Survivorship

Survivorship comparisons failed to yield a clear link between metabolic rate and extinction survivability. At the species level, all metabolic rate groups showed more taxa being locally extirpated than surviving. At the family level, many metabolic rate groups had too few taxa to warrant any sort of conclusion. Even at the genus level, a clear-cut conclusion is difficult to obtain, as the only group to lose taxa preferentially was the medium metabolic rate group; they are more of an intermediary between the groups that should potentially better demonstrate whether or not the original hypothesis was correct.

5.2.2. Comparison of Taxonomic Increases and Decreases

Comparison of taxonomic increases and decreases also failed to yield a clear picture of changes in community structure among bivalves with regard to metabolic rate. Most metabolic rate categories at all taxonomic levels show the same pattern: over a third of included taxa do not change relative abundance significantly, followed by the number of those that increase, then those that decrease. As such, it is nearly impossible to tell if any metabolic rate was advantageous to survival.

5.2.3. *Relative Abundance Changes between Metabolic Rate Categories*

Combating the problems associated with the other analysis methods by looking at the relative abundance changes between metabolic rate categories seemed to work much better. Even if the changes in relative abundance by activity level had been statistically insignificant, high metabolism still wouldn't be shown to be detrimental. All changes proved to be significant, but in an unexpected way.

In contrast to the original hypothesis, low metabolism did not seem to confer any special immunity to the extinction event, at least not according to community composition. Comparing relative abundances of high versus moderate versus low metabolism individuals, the proportion of high metabolism individuals increased at the expense of the proportions of moderate and low metabolism ones.

Even when individuals of unknown metabolic rate were included in different rate groups, the results remain largely the same. Most (five of seven) tests show the same pattern of increase versus decrease, and even those that do not (two of seven) still do not show any decrease in high metabolism individuals. Therefore the unknowns do not skew the results to the point that they contradict them, and more often than not they do not have any real effect on the pattern.

These results, based on overall relative abundance of each metabolic rate grouping, suggest that, for at least these samples representing this event, high metabolism was not detrimental to survival. In fact, it may have actually been beneficial, since the high metabolism group increased in relative abundance in the assemblage following the extinction. Likewise, low metabolism may have been detrimental, as indicated by a decrease in relative abundance. These results don't necessarily indicate causality, and several possible reasons to the contrary are discussed below.

5.3. Misinterpreting paleoecology?

The major factors as to why high metabolism species didn't suffer during this supposed period of decreased primary productivity are biological/ ecological in nature. One possible reason is increased predation pressure during the extinction event itself (Dietl, pers. comm.) As the availability of prey items (i.e. lower trophic level taxa)

diminishes, competition increases among predators for dwindling food resources. When this happens, they increase the pressure on surviving prey taxa. If this is the case, then the benefit of increased escape capabilities, and therefore high metabolism, may outweigh the cost of increased nutrient demand.

Another paleoecological factor that could explain why species wouldn't suffer during this time of reduced primary productivity is that said reduction may not have been as severe as originally thought, or may have not happened at all. Preliminary work done by Research Experience for Undergraduates (REU) students on the formations in question suggests that the decline in primary producers was slight, if at all (Kelley et al., 2009). In that case species with higher metabolic rates wouldn't be limited by food availability and, if predation pressure were to increase, would have an even greater advantage over low metabolism species.

5.4. Environmental issues?

Other factors that could be at play here are environmental. Previous work has suggested there is a slight climate difference between the two formations, with the Chowan River Formation being both warm temperate and subtropical, and the Moore House being strictly warm temperate (see section 2.2). The samples considered in this study were also separated latitudinally, with the possibly warmer depositional regime Chowan River localities south of the possibly cooler depositional regime Moore House localities (Fig. 4). This difference in latitude, coupled with the slight climatic warming between the times of deposition, could lead to climatic differences that could account for some variability in the assemblages independent of biotic factors.

There is also the possibility that water depth at the time of deposition of each formation was different, as the transgression that occurred during the deposition of the Yorktown Formation reached further inland than that of the Chowan River Formation (Ward et al., 1991). Since bivalve species often prefer specific water depths, this factor could also account for differences between assemblages.

6. Further Work

6.1. Re-evaluating the Moore House/Chowan River Event

The factors that can most be controlled through sampling are abiotic in nature. To correct for distance, samples from the Hampton Roads area (e.g., Moore House and Chowan River in Chuckatuck Pit and Chowan River in Gomez Pit) could be analyzed the same way the samples used in this study were. New sites may have to be discovered, as those used by previous workers (as discussed above) have been destroyed.

The above approach may not resolve potential differences in water depth, so another approach may be necessary. Collecting from sites that are at similar latitude should keep climate variables roughly similar, but to correct for water depth they would need to be separated longitudinally. Because the Moore House represents greater transgression onto the shelf, an ideal site would be due west of a suitable Chowan River site, which may require new sites to be identified.

6.2. Usefulness of Different Events

When this study was originally conceived, it was proposed to use the Eocene-Oligocene extinction event. A survey of unpublished data from localities in Mississippi showed that very few species that carried over across the event, which was thought would hamper the study. The Pliocene Moore House-Chowan River event was selected because

there was less of a drastic taxonomic shift, especially at the family and genus level. Unfortunately the possible ineffectiveness of using the Moore House-Chowan River event was not discovered until the end of the study. It was not until then that the relative abundance of metabolic rate groups, and not the change in relative abundance among taxa, was decided to be the most logical method of assessing whether or not high metabolism affected survival across an extinction event. Therefore, a new study will be needed to more rigorously test the original hypothesis to determine its validity.

Perhaps the best way to test ideas about behavioral escalation and how it affects survivorship is to look at other extinction events. The Plio-Pleistocene extinction was multi-phased, and the phase considered here was small and regional in extent. A larger extinction event would be more ideal for several reasons.

One reason a larger event would be more ideal is that such events are generally better studied. Information on what caused the event would be more readily available, as would information on impacts at various trophic levels. This way, the pitfall of studying a cause-and-effect situation where the cause turns out to be minimal at best (in this case a reduction in primary productivity that may not have happened as severely as thought, if at all), can be avoided.

A necessary condition would be short duration of the extinction episode. If the causes of an extinction event occur over long periods of time the organisms may be able to adapt to the adverse conditions, and the effects of that initial stress may be masked. If the event is relatively sudden and quick, and results in a loss of primary productivity, the effects of that productivity loss will be more readily apparent.

Any extinction used should not have too catastrophic a cause. If environmental factors are at work that supersede biotic factors, those biotic factors will be impossible to study. For instance, several studies link the end-Permian extinction, at least partly, to tectonically driven changes in atmospheric and oceanic chemistry (see Saunders and Reichow, 2009, for a more thorough list of possible causes). These changes would have led to ocean anoxia, increased ocean pH due to high CO_2 levels, and filled the air with poisonous gases such as sulfur dioxide (Saunders and Reichow, 2009). These events would have made life difficult for both high and low metabolism species solely because of chemical effects, so food availability may have been the least of their concerns. To really see if behavioral escalation has an effect on survivorship we need to first study it where it could potentially be a primary factor.

Many of the extinctions that occurred during the Cenozoic are prime candidates for a new study based on the concepts of this one. The larger ones should be large enough in scale to show major community-level changes but not so large as to create drastically different recovery faunas, thus minimizing possible variables affecting changes in community composition. Most environmental changes in the Cenozoic have been climate-related (Hansen et al., 1999), which works well for studying ecological change driven by productivity. There is also a wealth of studies on these events, so that a thorough understanding of the events and how they occurred is possible. Perhaps most importantly, there is a wealth of fossil material in collections and *in situ* along the Atlantic and Gulf Coastal Plains. Therefore, all events are straddled by lithologic formations and bulk samples can be collected from sites at which cross-comparisons can be easily controlled for factors such as water depth, climate, *et cetera*. A potential

drawback of a larger event is lack of taxonomic uniformity. It follows that if more species disappear, then so do more genera, families, *et cetera* on up the taxonomic scale, until direct comparison of assemblages is hindered. However, it became apparent that the main focus should be on numbers of individuals based on metabolic rate and life mode, not taxonomic affinity. Therefore, taxonomic uniformity should not be an issue so long as the metabolic rates of the species in the assemblage before the event and the assemblage after the event can be determined.

6.3. Higher Resolution Isotopic Analysis

It is clear from other studies that $\delta^{18}O$ analysis is a reliable tool for determining growth rates (Dietl et al., 2002, Ivany et al. 2003), and that growth rates are indicative of metabolic rate (Lewis and Cerrato, 1997). It is also clear that the isotopic results from this study are unsatisfactory. In any future treatment of the hypothesis explored herein, oxygen isotopes will remain an essential tool, but will have to be obtained in a more thorough and complete fashion.

First of all, samples will have to be gathered in such a way that collection from the same shell layer is ensured. Mixing of shell layers in one sample will render the data useless, since comparison between different layers in this study led to unusable results.

Secondly, samples will have to be small, as this will avoid averaging data and allow for samples to be taken at closer spacing in bivalves.

Third, samples will have to be taken more closely together, and at even intervals of 1 mm or less. This way better resolution will be achieved along the growth axis, making the growth curve much easier to read. Also, the flatness of the curves in this study may be avoided in future studies. The best way to achieve this (and small sample

size) would be to use equipment such as the microsampler under the direction of Donna Surge at University of North Carolina Chapel Hill.

Fourth, a mass spectrometer capable of better resolution with smaller samples will have to be used. That is the only way we could measure the small, closely spaced samples that are essential to more successfully generating growth curves.

If all these criteria are met, the fifth important thing to do would be to take many more samples for many more species involved in the study. The ideal would be to generate $\delta^{18}O$-based annual growth curves for all species in each assemblage. If that is not feasible, then enough should be done to make the high-versus-low metabolism comparisons statistically significant. Funding, time, and equipment constraints limited the ability to make these corrections but, now that they are known, should be among the first priorities in any new, related study.

7. Conclusions

- High metabolism species were not adversely affected by the mass extinction.
- Low metabolism species seem to have been adversely affected by the events of the mass extinction.
- More, better-collected carbonate samples from more bivalve species run on a higher resolution mass spectrometer for oxygen isotopic analysis will better resolve differences in metabolic rate.
- Studies of other, more well-known mass extinctions should shed more light on the effects of behavioral escalation on survivorship.

References

Alexander, R.R., Stanton, R.J., Dodd, J.R., 1993. Influence of sediment grain-size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected Neogene clams. Palaios 8, 289-303.

Allmon, W.D., 2001. Nutrients, temperature, and evolution: a model for the late Cenozoic marine record of the western Atlantic. Palaeogeogr. Palaeoclimatol. Palaeoecol. 166, 9-26.

Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schonberg, D., Lea, D.W., 2005. Final closure of Panama and the onset of northern hemisphere glaciation. Earth Planet. Sci. Lett. 237, 33-44.

Benitez, N., Maiz-Apellaniz, J., Canelles, M., 2002. Evidence for nearby supernova explosions. Phys. Rev. Lett. 88, 1-4.

Campbell, M.R., 1998. Plio-Pleistocene Bivalvia of the western Atlantic Ocean: Temporal and taxonomic resolution and the anatomy of extinction. MS thesis, University of North Carolina, Chapel Hill, NC.

Chauvaud, L., Lorrain, N., Dunbar, R.B., Paulet, Y-M., Thouzeau, G., Jean, F., Guarini, J-M., Mucciaroni, D., 2005. Shell of the Great Scallop *Pecten maximus* as a high frequency archive of paleoenvironmental change. Geochem. Geophy. Geosy. 6 (8), 1-15.

Checa, A.G., Jiminez-Jiminez, A.P., 2003. Evolutionary morphology of oblique ribs of bivalves. Palaeontology 46(4), 709-724.

Dietl, G.P., Kelley, P.H., Barrick, R., Showers, W., 2002. Escalation and extinction selectivity: Morphology versus isotopic reconstruction of bivalve metabolism. Evolution 56 (2), 284-291.

Dowsett, H.J., Wiggs, L.B., 1992. Planktonic foraminiferal assemblages of the Yorktown Formation, Virginia. Micropaleontology 38 (1), 75-86.

Driscoll, N.W., Haug, G.H., 1998. A short circuit in thermohaline circulation: a cause for Northern Hemisphere Glaciation? Science 282 (5388), 436-438.

Hansen, T.A., Kelley, P.H., Haasl, D.M., 2004. Paleoecological patterns in molluscan extinctions and recoveries: comparison of the Cretaceous-Paleogene and Eocene-Oligocene extinctions in North America. Palaeogeogr. Palaeocl. 214 (3), 233-242.

Hansen, T.A., Kelley, P.H., Melland, V.D., Graham, S.E., 1999. Effect of climate-related mass extinctions on escalation in molluscs. Geology 27 (12), 1139-1142

Ivany, L.C., Wilkinson, B.H., Jones, D.S., 2003. Using stable isotopic data to resolve rate and duration of growth throughout ontogeny: An example from the surf clam, *Spisula solidissima*. Palaios 18 (2), 126-137.

Jain, S., Collins, L.S., 2007. Trends in Caribbean paleoproductivity related to the Neogene closure of the Central American Seaway. Mar. Micropaleontol. 63 (1-2), 57-74.

Jones, D.S., 1998. Isotopic determination of growth and longevity in fossil and modern invertebrates. In: Norris, R.D., Corfield, R.M. (Eds.), Isotope Paleobiology and Paleoecology. Paleontological Society Papers 4, Carnegie Museum of Natural History, Pittsburgh, PA, pp. 37-67.

Jones, M.A., 1999. Cost-benefit analysis of naticid gastropod predation across the Plio-Pleistocene boundary from North Carolina and Virginia. MS thesis, University of North Carolina Wilmington, Wilmington, NC.

Karlsson, P., Jonsson, T., Jonsson, A., 2007. Food web structure and interaction strength pave the way for vulnerability to extinction. J. Theor. Biol. 249 (1), 77-92.

Kelley, P.H., Dietl, G.P., Visaggi, C.C., Christie, M., Durham, S., Graybill, E., Monarrez, P., Parnell, B., 2009. Effects of a late Pliocene extinction in North Carolina on mollusk diversity and ecology: preliminary results. Geol. Soc. America Abstr. Prog. 41(1), 39.

Knie, K., Korschinek, G., Faestermann, T., Dorfi, E.A., Rudel, G., Wallner, A., 2004. ^{60}Fe anomaly in a deep-sea manganese crust and implications for a nearby supernova source. Phys. Rev. Lett. 93 (17), 1-4.

Krantz, D.E., 1990. Mollusk-isotope records of Plio-Pleistocene marine paleoclimate, U.S. Middle Atlantic Coastal Plain. Palaios 5(4), 317-335.

Kukla, G., Gavin, J., 2004. Milankovitch climate reinforcements. Global Planet Change 40 (1-2), 27-48.

Lewis, D.E., Cerrato, R.M., 1997. Growth uncoupling and the relationship between shell growth and metabolism in the soft shell clam *Mya arenaria*. Mar. Ecol.-Prog. Ser. 158, 177-189.

Lunt, D.J., Valdes, P.J., Haywood, A., Rutt, I.C., 2007. Closure of the Panama Seaway during the Pliocene; implications for climate and Northern Hemisphere glaciation. Clim. Dynam. 30 (1), 1-18.

McKinney, M.L., 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annu. Rev. Ecol. Syst. 28, 495-516.

Mudelsee, M., Raymo, M.E., 2005. Slow dynamics of the Northern Hemisphere glaciation. Paleoceanography 20 (4), 1-14.

Rea, D.K., Snoeckx, H., Joseph, L.H., 1998. Late Cenozoic eolian deposition in the North Pacific: Asian drying, Tibetan Uplift, and cooling of the Northern Hemisphere. Paleoceanography 13 (3), 215-224.

Rhoads, D.C., Pannella, G., 1970. Use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3 (2), 143-161.

Saunders, A., Reichow, M., 2009. The Siberian Traps and the End-Permian mass extinction: a critical review. Chinese Sci. Bull. 54 (1), 20-37.

Shimada, C., Sato, T., Yamasaki, M., Hasegawa, S., Tanaka, Y., 2009. Drastic change in the late Pliocene subarctic Pacific diatom community associated with the onset of the Northern Hemisphere Glaciation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 279 (3), 207-215.

Stanley, S.M., 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). The Geological Society of America, Inc., Boulder, CO.

Stanley, S.M., 1986. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of western Atlantic bivalve fauna. Palaios 1 (1), 17-36.

Stanley, S.M., Campbell, L.D., 1981. Neogene mass extinction of western Atlantic Molluscs. Nature 293 (5832), 457-459.

Thunell, R., Belya, P., 1982. Neogene planktonic foraminiferal biogeography of the Atlantic Ocean. Micropaleontology 28 (4), 381-398.

Ward, L.W., Bailey, R.H., Carter, J.G., 1991. Pliocene and Pleistocene stratigraphy, depositional history, and molluscan paleobiogeography of the Coastal Plain. In: Horton, J.W., Zullo, V.A. (Eds.), The Geology of the Carolinas. University of Tennessee Press, Knoxville, TN, pp. 274-289.

Ward, L.W., Gilinsky, N.L., 1993. Biostratigraphic assemblages of the Chowan River Formation (upper Pliocene) and adjoining units, the Moore House Member of the Yorktown Formation (upper Pliocene) and the James City Formation (lower Pliocene). Virginia Museum of Natural History Memoir 3 (A), 1-33.

Vermeij, G.J., 1977. The Mesozoic marine revolution: Evidence from snails, predators, and grazers. Paleobiology 3(3), 245-258.

Vermeij, G.J., 1983. Traces and trends in predation, with special reference to bivalved animals. Palaeontology 26 (3), 455-465.

Vermeij, G.J., 1987. Evolution and escalation: An ecological history of life. Princeton University Press, Princeton, NJ.

Appendices

Appendix A: Moore House Member count of individual bivalves

Family	Genus	Species	Species Count	Genus Count	Family Count
?	*Cooperella*	*carpenteri*	7	7	7
?	*Eonita*	*trigintinaria*	60	60	60
Anomiidae	*Anomia*	*simplex*	9.5	9.5	9.5
Arcidae	*Anadara*	*improcera*	22.5	22.5	35.5
	Barbatia	*propatula*	4.5	4.5	
	Rasia	*lienosa*	8.5	8.5	
Astartidae	*Astarte*	*concentrica*	24.5	47.5	47.5
		sp	0.5		
		undulata	9		
		vicina/undulata	13.5		
Cardiidae	*Cardium*	*sublineatum*	0.5	0.5	18.5
	Chesacardium	*acutilaqueatum*	14.5	14.5	
	Papyridea	*soleniformis*	2	2	
	Planicardium	*virginianum*	1.5	1.5	
Carditidae	*Carditamera*	*arata*	133.5	133.5	310
	Cyclocardia	*granulata*	115	115	
	Pleuromeris	*decemcostata*	29	44	
		sp	12.5		
		tridentata	2.5		
	Pteromeris	*perplana*	17.5	17.5	
Chamidae	*Chama*	*congregata*	296	296	418
	Pseudochama	*corticosa*	122	122	
Condylocardiidae	*Erycinella*	*ovalis*	16.5	16.5	16.5
Corbulidae	*Caryocorbula*	*cuneata*	43.5	91	91
		inaequalis	43		
		sp	4.5		
Crassatellidae	*Crassatella*	*marylandica*	15	96.5	322
		sp	81.5		
	Crassinella	*lunulata*	199	199	
	Marvacrassatella	*undulata*	26.5	26.5	
Erycinidae	*Erycina*	*carolinensis*	1.5	1.5	1.5
Gastrochaenidae	*Gastrochaena*	*ligua*	2.5	27	27
		sp	24.5		
Glossidae	*Glossus*	*fraterna*	2	2	2

Glycymerididae	*Costaglycymeris*	*subovata*	38	38	99
	Glycymeris	*americana*	22.5	61	
		aratus	38.5		
Hiatellidae	*Hiatella*	*arctica*	39.5	39.5	51
	Panopea	*goldfussii*	2.5	11.5	
		reflexa	9		
Kelliidae	*Aligena*	*rhomboidea*	0.5	0.5	13.5
	Bornia	*bladensis*	3	13	
		triangula	10		
Limidae	*Limea*	sp	1	1.5	1.5
		sp	0.5		
Lucinidae	*Ctena*	*speciosa*	6.5	6.5	129
	Lucinisca	*cribrarius*	1.5	1.5	
	Parvilucina	*crenulata*	121	121	
Mactridae	*Leptomactra*	*delumbis*	3.5	3.5	106
		harrisi	0		
		sp	0		
	Mactra	*confraga*	0.5	0.5	
	Mulinia	*congesta*	88	88	
	Spisula	*modicella*	7.5	14	
		solidissima	6.5		
Montacutidae	*Mysella*	*bladensis*	0.5	1.5	1.5
		sp	1		
Myidae	*Paramya*	*subovata*	5.5	5.5	9
	Sphenia	*dubia*	3.5	3.5	
Mytilidae	*Lithophaga*	*yorkensis*	1.5	1.5	12
	Modiolus	*modiolus*	2	6.5	
		sp	4.5		
	Musculus	sp	1	3	
		sp	1		
		sp	1		
	Mytilus	*lateralis*	1	1	
Noetiidae	*Noetia*	*incile*	123	123	123.5
	Striarca	*centenaria*	0.5	0.5	
Nuculanidae	*Nuculana*	sp	0.5	28.5	28.5
		acuta	28		
Nuculidae	*Nucula*	*proxima*	57.5	65	65
		taphria	7.5		

Ostreidae	*Conradostrea*	*sculpturata*	175	175	181.5
	Ostrea	*raveneliana*	5.5	5.5	
	X	*unk. oyster*	1	1	
Pandoridae	*Pandora*	*arenosa*	1.5	4.5	4.5
		prodromos	3		
Pectinidae	"Pecten"	*decemnaria*	0.5	0.5	108.5
	Carolinapecten	*eboreus*	5	5	
	Chesapecten	*madisonius*	98.5	103	
		sp	4.5		
Periplomatidae	*Cochlodesma*	sp	1	1	1
Pharidae	*Ensis*	*directus*	56	61.5	61.5
		ensiformis	3		
		schmidti	2.5		
Pholadomyacidae	*Margaritaria*	*abrupta*	3	3	3
Plicatulidae	*Plicatula*	*marginata*	462	462	462
Semelidae	*Abra*	*subreflexa*	12	12	94.5
	Cumingia	*tellinoides*	9.5	9.5	
	Semele	*nuculoides*	1	73	
		subovata	72		
Sportellidae	*Anisodonta*	*carolina*	1	1	37.5
	Sportella	sp	1.5	36.5	
		yorkensis	35		
Tellinidae	*Macoma*	*virginiana*	21.5	21.5	225.5
	Tellina	*aequistriata*	54	204	
		dupliniana	0.5		
		sp	102		
		sp	22.5		
		sp	25		
Thraciidae	*Thracia*	*conradi*	1	1.5	1.5
		transversa	0.5		
Ungulinidae	*Diplodonta*	*acclinis*	10.5	26.5	26.5
		leana	5.5		
		sp	0		
		sp	6.5		
		sp (*subvexa*?)	4		
Veneridae	*Chione*	*cortinaria*	0.5	1	335.5
		grus	0.5		

	Dosinia	*acetabulum*	8.5	8.5	
	Gemma	*magna*	5	5	
	Gouldia	*metastriata*	144.5	144.5	
	Lirophora	*athleta*	2	2	
	Macrocallista	sp	0.5	0.5	
	Mercenaria	*corrugata* *tridacnoides*	2.5 80.5	83	
	Pitar	*sayana*	86.5	86.5	
	Pleiorytis	*centenaria*	4.5	4.5	
Verticordiidae	*Verticordia*	*rogersi*	0.5	0.5	0.5
X	X	unk. bivalve 1	1	1	1
Yoldiidae	*Yoldia*	*laevis*	38	38	38

Appendix B: Chowan River Formation count of individual bivalves

Family	Genus	Species	Species Count	Genus Count	Family Count
?	*Cyrtapleura*	sp *arcuata*	0.5 0.5	1	1
Anomiidae	*Anomia*	*simplex*	1.5	1.5	1.5
Arcidae	"Anadara"	sp sp sp	2 1 24.5	27.5	27.5
Astartidae	*Astarte*	*berryi* *concentrica* sp sp	8 44 6 0.5	58.5	58.5
Carditidae	*Carditamera*	*arata*	2	2	118.5
	Cyclocardia	*granulata*	91.5	91.5	
	Pleuromeris	*auroraensis* *decemcostata* *tridentata*	1.5 8 9	18.5	
	Pteromeris	*auroraensis* *perplana*	5 1.5	6.5	
Chamidae	*Chama*	*striata*	0.5	0.5	0.5
Condylocardiidae	*Erycinella*	*ovalis*	13.5	13.5	13.5
Corbulidae	*Caryocorbula*	*conradi* *contracta* sp sp	67.5 1 4.5 4	77	77.5
	Varicorbula	*chowanensis*	0.5	0.5	
Crassatellidae	*Crassinella*	*dupliniana* *lunulata* sp	0.5 62.5 1	64	94.5
	Marvacrassatella	*kauffmani* sp	25.5 5	30.5	
Donacidae	*Donax*	*fossor*	9	9	9
Erycinidae	*Erycina*	*carolinensis*	1	1	1
Glycymerididae	*Glycymeris*	*arata*	0.5	0.5	57
	Costaglycymeris	*subovata*	23	23	
	Glycymeris	*americana*	33.5	33.5	
Hiatellidae	*Hiatella*	*arctica*	1	1	1

Kelliidae	*Aligena*	*laevis*	1	12	19
		sp	0.5		
		striata	10.5		
	Bornia	*triangula*	7	7	
Lucinidae	*Divaricella*	*quadrasuliata*	1.5	1.5	98.5
	Cavilinga	*trisulcatus*	13	13	
	Parvilucina	*crenulata*	71.5	82.5	
		multilineata	11		
	Stewartia	*anodonta*	1.5	1.5	
Mactridae	*Spisula*	*solidissima*	54	54	75
	Mulinia	*congesta*	14	21	
		sp	6.5		
		sp	0.5		
Montacutidae	*Mysella*	sp	1.5	2	2
		velaini	0.5		
Myidae	*Paramya*	*subovata*	1	1	10.5
	Sphenia	*dubia*	9.5	9.5	
Mytilidae	*Crenella*	*decussata*	0.5	0.5	6
	Modiolus	*modiolus*	5	5	
	Mytilus	sp	0.5	0.5	
Noetiidae	*Noetia*	*carolinensis*	15.5	15.5	15.5
Nuculanidae	*Nuculana*	*acuta*	81	166.5	166.5
		sp	1.5		
		sp	84		
Nuculidae	*Nucula*	*proxima*	27	39.5	39.5
		taphria	12.5		
Ostreidae	*Conradostrea*	*sculpturata*	24.5	24.5	24.5
Pandoridae	*Pandora*	*prodomos*	53	53	53
Pectinidae	*Carolinapecten*	*eboreus*	80.5	80.5	81
	"Leptopecten"	*irremotis*	0.5	0.5	
Pharidae	*Ensis*	*directus*	28	28	28
Plicatulidae	*Plicatula*	*marginata*	27	27	27
Semelidae	*Abra*	*aequalis*	38.5	71	74.5
		subreflexa	32.5		
	Cumingia	*tellinoides*	3.5	3.5	
Sportellidae	*Anisodonta*	*carolina*	2	2	20.5
	Ensitellops	*elongata*	5.5	5.5	
	Sportella	*calpix*	13	13	

Tellinidae	*Strigilla*	*pisiformis*	0.5	0.5	72.5
	Tellina	*agilis*	66.5	72	
		sp	5.5		
Ungulinidae	*Diplodonta*	*acclinis*	7	7.5	7.5
		sp	0.5		
Veneridae	*Chione*	*grus*	1	2.5	81.5
		intapurpurea	1.5		
	Gemma	*magna*	24.5	24.5	
	Gouldia	*metastriata*	12.5	12.5	
	Macrocallista	sp	2.5	2.5	
	Mercenaria	*carolinensis*	5.5	8.5	
		sp	3		
	Pitar	*morrhuanus*	22.5	23.5	
		sp	1		
	Transennella	*stimpsoni*	7.5	7.5	
Verticordiidae	*Verticordia*	*chowanensis*	2.5	2.5	2.5
X	X	unknown	0.5	0.5	0.5
Yoldiidae	*Yoldia*	*laevis*	9.5	9.5	9.5

Appendix C: Reults of oxygen isotopic analyses of selected individuals

SHELL: CLGA-2			
SPECIES: *Glycymeris americana*			
Sample #	Distance (mm)	Average $\delta^{18}O$	Std. Deviation
1	2	0.786652343	0.040642579
2	4	1.08412	0.038751842
3	7	1.015790514	0.067786467
4	9	1.016926971	0.068608453
5	12	1.017779314	0.025447797
6	15	1.617260457	0.551122
7	18	0.551122	0.066578845
8	21	1.0632376	0.093843125
9	25	0.957689143	0.053363339
10	27	0.95982	0.027038417
11	30	1.465259314	0.027061047
12	32	0.689201143	0.0450103
13	35	1.2760392	0.041264605
14	37	1.579047086	0.043902936
15	40	1.065794629	0.081631412
16	42	1.949801143	0.058591128
17	45	2.553893486	0.070086531
18	48	1.9714176	0.056253683
19	50	2.289676114	0.04675441
20	53	1.723558629	0.077623566
SHELL: DCPA-1			
SPECIES: *Panopea americana*			
Sample #	Distance (mm)	Average $\delta^{18}O$	Std. Deviation
1	2	3.805895314	0.090384081
2	3	3.190702629	0.118681892
3	4	3.058813029	0.051506564
4	6	2.571274286	0.090386009
5	7	2.670301029	0.195666862
6	9	3.767628343	0.042156403
7	11	3.4365168	0.079159558
8	13	3.617773714	0.026750397
9	15	3.434618057	0.088883022
10	16	3.184860343	0.061399152
11	18	2.9406528	0.138050504
12			
13	19	2.283833829	0.15077524
14	21	3.169816457	0.069486676
15	23	3.180186514	0.071010113
16	25	3.289875429	0.081014813
17	27	3.795087086	0.032361904
18	28	2.819133257	0.041703513
19	30	2.998053257	0.04787274
20	32	2.888802514	0.091172849
21	33	2.848344686	0.022828876
22	34	3.149806629	0.059930018

23	37	2.812998857	0.050782957
24	38	3.082182171	0.038544422
SHELL: SLNC-1			
SPECIES: *Noetia carolinensis*			
Sample #	Distance (mm)	Average $\delta^{18}O$	Std. Deviation
1	2	1.271219657	0.055988042
2	3	0.990936	0.135505611
3	4	0.840789257	0.057088105
4	5	1.210605943	0.063880036
5	7	1.237772571	0.046955725
6	9	0.278031086	0.059351221
7	11	1.254861257	0.06359029
8	13	1.305981257	0.07090875
9	15	1.252086171	0.061309505
10	17	1.234413257	0.046349158
11	18	1.241277943	0.072627419
12	20	1.47366864	0.083182772
13	22	1.06742888	0.057139511
14	24	1.3371012	0.049956416
15	26	0.9124284	0.05461142
16	28	1.56288048	0.031556891
17	30	2.01189304	0.054521031
18	32	1.6843756	0.03715028
19	34	1.1894332	0.060938285
20	36	0.73716176	0.035331289
21	38	1.32987056	0.031216909
SHELL: CLEK-1			
SPECIES: *Marvacrassatella kauffmani*			
Sample #	Distance (mm)	Average $\delta^{18}O$	Std. Deviation
1	3	2.30855296	0.064380997
2	5	2.28808312	0.036203925
3	7	1.36296856	0.051056622
4	11	2.60592576	0.045382516
5	15	1.85353184	0.042014949
6	20	2.18054008	0.032486268
7	23	2.86337728	0.05578585
8	26	2.50133608	0.04751818
9	30	2.79606104	0.028508935
10	32	2.5113164	0.051281381
11	35	1.86911336	0.035850155
12	38	2.40326416	0.057649796
13	42	2.20712032	0.075818647
14	45	2.29531376	0.044149464
15	48	1.70840984	0.104866578
16	51	2.22534968	0.041965138
17	55	2.5907516	0.03324781
18	58	2.51202928	0.054852603
19	61	2.2562072	0.025033221
20	64	2.28187088	0.039154504

Appendix D: Numbers of high, moderate, and low metabolism individuals in each stratigraphic level.

HIGH METABOLISM		
Species	Moore House	Chowan River
Abra aequalis	38.5	0
Abra subreflexa	12	32.5
Carolinapecten eboreus	5	80.5
Donax fossor	0	9
Ensis directus	56	28
Gemma magna	5	24.5
"Leptopecten" irremotis	0	0.5
Macrocallista sp	0.5	2.5
Nuculana acuta	28	81
Nuculana sp	0.5	85.5
Spisula solidissima	6.5	54
Tellina agilis	0	66.5
Chesacardium acutilaqueatum	14.5	0
Dosinia acetabulum	8.5	0
Ensis ensiformis	3	0
Ensis schmidti	2.5	0
Leptomactra delumbis	3.5	0
"Pecten" decemnaria	0.5	0
Semele nuculoides	1	0
Semele subovata	72	0
Spisula modicella	7.5	0
Tellina aequistriata	54	0
Tellina dupliniana	0.5	0
Tellina sp	149.5	5.5
Yoldia laevis	38	9.5
Chesapecten madisonius	98.5	0
Chesapecten sp	4.5	0
TOTAL	610	479.5
OUT OF	3588	1376
PERCENT	17.00%	34.85%
PERCENTAGE CHANGE	+ 17.85%	
PEARSON'S CHI SQUARE	184.908	
P<	0.00005	

MEDIUM METABOLISM		
Species	Moore House	Chowan River
Mercenaria carolinensis	0	5.5
Mercenaria sp	0	3
Mulinia sp	0	7
Nucula proxima	57.5	27
Nucula taphria	7.5	12.5
Macoma virginiana	21.5	0
Mactra confraga	0.5	0
Mercenaria corrugata	2.5	0
Mercenaria tridacnoides	80.5	0
Mulinia congesta	88	14
Papyridea soleniformis	2	0
Planicardium virginianum	1.5	0
TOTAL	261.5	69
OUT OF	3588	1376
PERCENT	7.29%	5.01%
PERCENTAGE CHANGE	-2.28%	
PEARSON'S CHI SQUARE	8.273	
P=	0.0040	

LOW METABOLISM		
Species	Moore House	Chowan River
"Anadara" sp	0	2
"Anadara" sp	0	1
"Anadara" sp	0	24.5
Astarte berryi	0	8
Astarte concentrica	24.5	44
Astarte sp	0.5	6.5
Caryocorbula conradi	0	67.5
Caryocorbula contracta	0	1
Caryocorbula sp	4.5	8.5
Cavilinga trisulcata	0	13
Chama striata	0	0.5
Chione grus	0.5	1
Chione intapurpurea	0	1.5
Costaglycymeris subovata	38	23
Crenella decussata	0	0.5
Cyclocardia granulata	115	91.5

Cyrtapleura arcuata	0	0.5
Cyrtapleura sp	0	0.5
Diplodonta acclinis	10.5	7
Divaricella quadrisuliata	0	1.5
Erycinella ovalis	16.5	13.5
Glycymeris americana	22.5	33.5
Glycymeris arata	38.5	0.5
Marvacrassatella kauffmani	0	25.5
Marvacrassatella sp	0	5
Modiolus modiolus	2	5
Mytilus sp	0	0.5
Noetia carolinensis	0	15.5
Pandora prodromos	3	53
Parvilucina crenulata	121	71.5
Parvilucina multilineata	0	11
Sphenia dubia	3.5	9.5
Stewartia anodona	0	1.5
Verticordia chowanensis	0	2.5
Varicorbula chowanensis	0	0.5
Anadara improcera	22.5	0
Astarte undulata	9	0
Astarte vicina/undulata	13.5	0
Caryocorbula cuneata	43.5	0
Caryocorbula inaequalis	43	0
Chama congregata	296	0
Chione cortinaria	0.5	0
Cochlodesma sp	1	0
Conradostrea sculpturata	175	24.5
Crassatella marylandica	15	0
Crassatella sp	81.5	0
Cumingia tellinoides	9.5	3.5
Diplodonta leana	5.5	0
Diplodonta sp	10.5	0.5
Gastrochaena ligua	2.5	0
Gastrochaena sp	24.5	0
Glossus fraterna	2	0
Hiatella arctica	39.5	1
Margartaria abrupta	3	0
Marvacrassatella undulata	26.5	0
Noetia incile	123	0
Ostrea raveneliana	5.5	0

Pandora arenosa	1.5	0
Panopea goldfussii	2.5	0
Panopea reflexa	9	0
Plicatula marginata	462	27
Striarca centenaria	0.5	0
Verticordia rogersi	0.5	0
Anomia simplex	9.5	1.5
Barbatia propatula	4.5	0
Carditamera arata	133.5	2
Limea sp	1.5	0
Lithophaga yorkensis	1.5	0
Lucinisca cribrarius	1.5	0
Modiolus sp	4.5	0
Musculus sp	3	0
Mytilus lateralis	1	0
Paramya subovata	5.5	1
Pseudochama corticosa	122	0
Pteromeris perplana	17.5	1.5
Rasia lienosa	8.5	0
TOTAL	2143	614.5
OUT OF	3588	1376
PERCENT	59.73%	44.66%
PERCENTAGE CHANGE	-15.07%	
PEARSON'S CHI SQUARE	91.458	
P<	0.00005	

UNKNOWN METABOLISM		
Species	Moore House	Chowan River
Aligena laevis	0	1
Aligena sp	0	0.5
Aligena striata	0	10.5
Anisodonta carolina	1	2
Bornia triangula	10	7
Crassinella dupliniana	0	0.5
Crassinella sp	0	1
Ensitellops elongata	0	5.5
Erycina carolinensis	1.5	1
Mysella sp	1	1.5
Mysella velaini	0	0.5
Pitar morrhuanus	0	22.5

Pitar sp	0	1
Pleuromeris auroraensis	0	6.5
Pleuromeris tridentata	2.5	9
Sportella calpix	0	13
Strigilla pisiformis	0	0.5
Transennella stimpsoni	0	7.5
Aligena rhomboidea	0.5	0
Bornia bladensis	3	0
Cardium sublineatum	0.5	0
Cooperella carpenteri	7	0
Crassinella lunulata	199	62.5
Ctena speciosa	6.5	0
Eonita trigintinaria	60	0
Gouldia metastriata	144.5	12.5
Lirophora athleta	2	0
Mysella bladensis	0.5	0
Pitar sayana	86.5	0
Pleiorytis centenaria	4.5	0
Pleuromeris decemcostata	29	8
Pleuromeris sp	12.5	0
Sportella sp	1.5	0
Sportella yorkensis	35	0
Thracia conradi	1	0
Thracia transversa	0.5	0
TOTAL	610	174
OUT OF	3588	1376
PERCENT	17.00%	12.65%
PERCENTAGE CHANGE	-4.35%	
PEARSON'S CHI SQUARE	14.189	
P=	0.0001	

Appendix E: Families that occur in the Moore House Member and Chowan River Formation (surviving) versus those that only occur in the Moore House (non-surviving). Since the event is local in scale, non-survival in this sense could be considered as local extirpation or an artifact of sampling error.

SURVIVORS		**NON-SURVIVORS**	
FAMILY	METABOLIC RATE	FAMILY	METABOLIC RATE
Mactridae	High	Gastrochaenidae	Low
Nuculanidae	High	Glossidae	Low
Pectinidae	High	Limidae	Low
Pharidae	High	Pholadomyacidae	Low
Arcidae	Low	Cardiidae	Medium
Astartidae	Low	Periplomatidae	Unknown
Condylocardiidae	Low	Thraciidae	Unknown
Corbulidae	Low		
Glycymerididae	Low		
Lucinidae	Low		
Myidae	Low		
Mytilidae	Low		
Pandoridae	Low		
Ungulinidae	Low		
Verticordiidae	Low		
Nuculidae	Medium		
Erycinidae	Unknown		
Kelliidae	Unknown		
Montacutidae	Unknown		
Semelidae	Unknown		
Sportellidae	Unknown		

Appendix F: Genera that occur in the Moore House Member and Chowan River Formation (surviving) versus those that only occur in the Moore House (non-surviving). Since the event is local in scale, non-survival in this sense could be considered as local extirpation or an artifact of sampling error.

SURVIVORS		**NON-SURVIVORS**	
GENUS	METABOLIC RATE	GENUS	METABOLIC RATE
Abra	High	*Chesacardium*	High
Carolinapecten	High	*Chesapecten*	High
Ensis	High	*Dosinia*	High
Gemma	High	*Leptomactra*	High
Macrocallista	High	*Semele*	High
Nuculana	High	*Anadara*	Low
Spisula	High	*Barbatia*	Low
Tellina	High	*Crassatella*	Low
Yoldia	High	*Gastrochaena*	Low
Anomia	Low	*Glossus*	Low
Astarte	Low	*Limea*	Low
Carditamera	Low	*Lithophaga*	Low
Caryocorbula	Low	*Lucinisca*	Low
Chama	Low	*Margaritaria*	Low
Chione	Low	*Musculus*	Low
Conradostrea	Low	*Ostrea*	Low
Costaglycymeris	Low	*Panopea*	Low
Cumingia	Low	*Pseudochama*	Low
Cyclocardia	Low	*Rasia*	Low
Diplodonta	Low	*Macoma*	Medium
Erycinella	Low	*Mactra*	Medium
Glycymeris	Low	*Papyridea*	Medium
Hiatella	Low	*Planicardium*	Medium
Marvacrassatella	Low	*Cardium*	Unknown
Modiolus	Low	*Cochlodesma*	Unknown
Mytilus	Low	*Cooperella*	Unknown
Noetia	Low	*Ctena*	Unknown
Pandora	Low	*Eonita*	Unknown
Paramya	Low	*Lirophora*	Unknown
Parvilucina	Low	*Pleiorytis*	Unknown
Plicatula	Low	*Thracia*	Unknown
Pteromeris	Low		
Sphenia	Low		
Striarca	Low		
Verticordia	Low		
Mercenaria	Medium		

Mulinia	Medium
Nucula	Medium
Aligena	Unknown
Anisodonta	Unknown
Bornia	Unknown
Crassinella	Unknown
Erycina	Unknown
Gouldia	Unknown
Mysella	Unknown
Pitar	Unknown
Pleuromeris	Unknown
Sportella	Unknown

Appendix G: Species that occur in the Moore House Member and Chowan River Formation (surviving) versus those that only occur in the Moore House (non-surviving). Since the event is local in scale, non-survival in this sense could be considered as local extirpation or an artifact of sampling error.

SURVIVORS		**NON-SURVIVORS**	
SPECIES	METABOLIC RATE	SPECIES	METABOLIC RATE
Gemma magna	High	*Chesacardium acutilaqueatum*	High
Macrocallista sp	High	*Dosinia acetabulum*	High
Nuculana acuta	High	*Leptomactra delumbis*	High
Nuculana sp	High	*Semele nuculoides*	High
Spisula solidissima	High	*Semele subovata*	High
Tellina sp	High	*Spisula modicella*	High
Abra subreflexa	High	*Tellina aequistriata*	High
Carolinapecten eboreus	High	*Tellina dupliniana*	High
Ensis directus	High	*Chesapecten madisonius*	High
Yoldia laevis	High	*Chesapecten* sp	High
Chione grus	Low	*Ensis ensiformis*	High
Astarte concentrica	Low	*Ensis schmidti*	High
Astarte sp	Low	"Pecten" decemnaria	High
Caryocorbula sp	Low	*Anadara improcera*	Low
Costaglycymeris subovata	Low	*Astarte undulata*	Low
Crenella decussata	Low	*Astarte vicina/undulata*	Low
Cyclocardia granulata	Low	*Chione cortinaria*	Low
Cyrtapleura sp	Low	*Gastrochaena ligua*	Low
Diplodonta acclinis	Low	*Gastrochaena* sp	Low
Erycinella ovalis	Low	*Glossus fraterna*	Low
Glycymeris americana	Low	*Margartaria abrupta*	Low
Glycymeris arata	Low	*Noetia incile*	Low
Modiolus modiolus	Low	*Rasia lienosa*	Low
Pandora prodromos	Low	*Striarca centenaria*	Low
Parvilucina crenulata	Low	*Barbatia propatula*	Low
Sphenia dubia	Low	*Caryocorbula cuneata*	Low
Anomia simplex	Low	*Caryocorbula inaequalis*	Low
Carditamera arata	Low	*Chama congregata*	Low
Conradostrea sculpturata	Low	*Cochlodesma* sp	Low
Cumingia tellinoides	Low	*Crassatella marylandica*	Low
Diplodonta sp	Low	Crassatella sp	Low
Hiatella arctica	Low	*Diplodonta leana*	Low
Paramya subovata	Low	*Limea* sp	Low
Plicatula marginata	Low	*Lithophaga yorkensis*	Low
Pteromeris perplana	Low	*Lucinisca cribrarius*	Low
Nucula proxima	Medium	*Marvacrassatella undulata*	Low
Nucula taphria	Medium	*Modiolus* sp	Low
Mulinia congesta	Medium	*Musculus* sp	Low
Anisodonta carolina	Unknown	*Mytilus lateralis*	Low
Bornia triangula	Unknown	*Ostrea raveneliana*	Low
Crassinella sp	Unknown	*Pandora arenosa*	Low
Erycina carolinensis	Unknown	*Panopea goldfussii*	Low
Mysella sp	Unknown	*Panopea reflexa*	Low
Pitar sp	Unknown	*Pseudochama corticosa*	Low
Pleuromeris tridentata	Unknown	*Verticordia rogersi*	Low

Crassinella lunulata	Unknown
Gouldia metastriatum	Unknown
Pleuromeris decemcostata	Unknown

Macoma virginiana	Medium
Mactra confraga	Medium
Mercenaria corrugata	Medium
Mercenaria tridacnoides	Medium
Papyridea soleniformis	Medium
Planicardium virginianum	Medium
Aligena rhomboidea	Unknown
Bornia bladensis	Unknown
Cardium sublineatum	Unknown
Cooperella carpenteri	Unknown
Ctena speciosa	Unknown
Eonita trigintinaria	Unknown
Lirophora athleta	Unknown
Mysella bladensis	Unknown
Pitar sayana	Unknown
Pleiorytis centenaria	Unknown
Pleuromeris sp	Unknown
Sportella sp	Unknown
Sportella yorkensis	Unknown
Thracia conradi	Unknown
Thracia transversa	Unknown