

**TITLE**

**Paleocommunities of the Yorktown Formation (Pliocene) of  
Virginia**

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# Paleocommunities of the Yorktown Formation (Pliocene) of Virginia

by

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## (ABSTRACT)

The fossiliferous Yorktown Formation (Pliocene) of Virginia was used as a natural laboratory for testing predictions of ecological and evolutionary theories. Specifically, coordinated stasis and ecological locking models have testable elements that can be analyzed using data from the Yorktown Formation. The ecological locking model requires that species within an ecosystem have strong interactions in order to stabilize morphologies of multiple lineages over millions of years. Species interactions that are strong enough to do this should also be strong enough to be a major ordering force on the composition of paleocommunities.

Single and replicate samples were taken from 30 cm stratigraphic intervals within the Rushmere and Morgart's Beach Members at several localities. A total of 142 samples were collected from 5 localities, which yielded 29,000 specimens belonging to 140 species of bivalves, gastropods, and other taxonomic groups.

Principle components analysis, ANOVA, MANOVA, and other analyses were used to test the occurrence and recurrence of local paleocommunities, paleocommunities, and paleocommunity types. Three paleocommunity types which occurred under specific paleoenvironmental conditions were defined: rubbly bottom, transitional, and muddy bottom. Within a single locality samples from the same paleocommunity type yielded very similar faunal compositions, based on the relative abundance of the contained species. However, samples from the same paleocommunity type but different localities displayed low similarity values. This is consistent with local paleoenvironmental control of paleocommunity composition being more important than strong species interactions. The pattern predicted by the model of ecologic locking is absent from these Yorktown paleocommunities.

A guild analysis was performed on the data to test whether the same types of organisms recurred in a predictable fashion under similar paleoenvironmental conditions. While the guild structure of the rubbly bottom paleocommunity type did recur at several localities, the guild structure of the other paleocommunity types varied greatly from place to place.

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## TABLE OF CONTENTS

TITLE .....	i
ABSTRACT.....	ii
ACKNOWLEDGMENTS .....	iv
TABLE OF CONTENTS .....	v
TABLES .....	ix
FIGURES .....	xiii
CHAPTER ONE: INTRODUCTION .....	1
History and Overview.....	1
Definitions .....	2
Life and Fossil Assemblages .....	3
Local Communities and Local Paleocommunities.....	4
Communities and Paleocommunities .....	5
Community Types and Paleocommunity Types.....	6
Coordinated Stasis and Ecological Locking .....	6
Brief Outline of the Dissertation.....	15
Chapter 2: The Yorktown Formation.....	15
Chapter 3: Species Accumulation Analyses.....	15
Chapter 4: Diversity of Yorktown Samples.....	15
Chapter 5: Paleocommunity Analysis.....	15
Chapter 6: Guild Analysis .....	16
Chapter 7: Summary and Conclusions .....	16
CHAPTER 2: THE YORKTOWN FORMATION .....	19
Prehistory of the Yorktown Formation.....	19
Yorktown Biostratigraphy .....	21
Tectonic Setting of the Atlantic Coastal Plain.....	23
Paleoclimatology of the Pliocene.....	25
Relative Sea Level Record of Atlantic Coastal Plain Strata .....	26
Collection and Processing .....	31
CHAPTER 3: SPECIES ACCUMULATION.....	40
Sampling for Completeness .....	40
Analysis.....	41
Discussion .....	46
CHAPTER 4: DIVERSITY OF YORKTOWN FOSSIL ASSEMBLAGES.....	62
Diversity .....	62
Analysis.....	64

Discussion .....	69
CHAPTER 5: PALEOCOMMUNITY ANALYSIS OF THE YORKTOWN .....	89
Overview of Statistical Analyses.....	89
Species constancy.....	89
Principle Components Analysis.....	90
The Correlation Matrix .....	92
MANOVA .....	93
Analysis.....	94
PCA of Entire Data Set.....	94
Paleocommunity Classification and Analysis.....	96
Rubbly Bottom Paleocommunity Type (RBPT) .....	97
PCA .....	98
Correlation Analysis.....	99
Constancy Index .....	101
MANOVA .....	102
The Muddy Bottom Paleocommunity Type (MBPT).....	103
PCA .....	105
Correlation Analysis.....	106
Species Constancy.....	111
MANOVA .....	112
Transition Zone .....	113
PCA .....	114
Correlation Analysis.....	115
Species Constancy.....	118
MANOVA .....	119
Summary.....	120
Conclusion.....	121
CHAPTER 6: GUILD ANALYSIS OF THE YORKTOWN PALEOCOMMUNITY	
TYPES .....	136
Bivalve Guilds .....	138
Gastropod Guilds.....	141
Guild Structure at Different Localities.....	143
Burwell's Bay.....	143
Nottoway River.....	145
Day's Point .....	147
Kingsmill .....	148

Lieutenant's Run.....	150
Summary.....	152
Analysis of Guild Structure within Paleocommunity Types.....	152
RBPT.....	152
PCA .....	156
Correlation Analysis.....	157
Constancy Analysis.....	160
MANOVA .....	160
MBPT .....	161
PCA .....	163
Correlation Analysis.....	164
Species Constancy.....	168
MANOVA .....	169
Transition Zone .....	170
PCA .....	172
Correlation Analysis.....	173
Constancy Analysis.....	176
MANOVA .....	177
Conclusion.....	177
CHAPTER 7: SUMMARY AND CONCLUSIONS .....	191
REFERENCES .....	192
APPENDIX A: COLLECTION LOCALITIES .....	207
Burwell Bay (BWB).....	207
Day's Point (DYP).....	207
Kingsmill on the James (KGM).....	207
Lieutenant's Run (LTR).....	208
Nottoway River (NWR) .....	208
Species Occurrence and Abundances.....	210
Day's Point .....	210
Burwell's Bay.....	212
Lieutenant's Run.....	213
Nottoway River .....	214
Kingsmill .....	215
APPENDIX B: SYSTEMATICS .....	227
APPENDIX C: DIVERSITY MEASUREMENTS .....	272
APPENDIX D: SUPPLEMENTARY TABLES .....	284

VITA .....299

## TABLES

<b>Table 1.1.</b>	Correlation of three Coastal Plain.....	29
<b>Table 4.1</b>	Direction and significance of diversity changes .....	69
<b>Table 5.1</b>	Most abundant species in the RBPT .....	98
<b>Table 5.2</b>	Mean correlation values RBPT (NWR) .....	100
<b>Table 5.3</b>	Mean correlation values RBPT (LTR).....	101
<b>Table 5.4</b>	Mean correlation values RBPT (KGM) .....	101
<b>Table 5.5</b>	Constancy values ( $C_a$ ) for RBPT samples.....	102
<b>Table 5.6</b>	The 20 most abundant species of the RBPT.....	102
<b>Table 5.7</b>	Common species of the MBPT.....	104
<b>Table 5.8</b>	Mean correlation values MBPT (DYP).....	107
<b>Table 5.9</b>	Mean correlation values MBPT (BWB).....	107
<b>Table 5.10</b>	Mean correlation values MBPT (NWR).....	108
<b>Table 5.11</b>	Summary of correlation coefficient for MBPT .....	108
<b>Table 5.12</b>	Mean correlation values MBPT (DYP - <i>M. congesta</i> removed).....	109
<b>Table 5.13</b>	Mean correlation values MBPT (BWB - <i>M. congesta</i> removed).....	109
<b>Table 5.14</b>	Mean correlation values MBPT (NWR - <i>M. congesta</i> removed).....	110
<b>Table 5.15</b>	Summary of correlation coefficient for MBPT ( <i>M. congesta</i> removed)...	110
<b>Table 5.16</b>	Species constancy ( $C_a$ ) for MBPT samples. ....	111
<b>Table 5.17</b>	Comparison of constancy for MBPT samples.....	111
<b>Table 5.18</b>	The 18 most abundant species of the MBPT. ....	112
<b>Table 5.19</b>	Common species of the transition zone. ....	113
<b>Table 5.20</b>	Mean correlation values transition zone (DYP).....	116
<b>Table 5.21</b>	Mean correlation values transition zone (BWB).....	117
<b>Table 5.22</b>	Mean correlation values transition zone (NWR) .....	117
<b>Table 5.23</b>	Mean correlation values transition zone (KGM) .....	118
<b>Table 5.24</b>	Summary of correlation coefficient for the transition.....	118
<b>Table 5.25</b>	Species constancy ( $C_a$ ) for transitions samples .....	119
<b>Table 5.26</b>	Summary of constancy analysis ( $C_a$ ) for all paleoenvironments .....	119
<b>Table 5.27</b>	The 20 most abundant species of the transition zone .....	120
<b>Table 6.1</b>	Species richness of guilds. ....	142
<b>Table 6.2</b>	Percent of total species richness in each guild.....	143
<b>Table 6.3</b>	Percent abundance of guilds in paleocommunity types at BWB .....	144
<b>Table 6.4</b>	Percent abundance of guilds at BWB( <i>M. congesta</i> removed) .....	144
<b>Table 6.5</b>	Percent abundance of guilds in paleocommunity types at NWR .....	145

<b>Table 6.6</b>	Percent abundance of guilds at NWR ( <i>M. congesta</i> removed).....	146
<b>Table 6.7</b>	Percent abundance of guilds in paleocommunity types at DYP .....	147
<b>Table 6.8</b>	Percent abundance of guilds at DYP ( <i>M. congesta</i> removed) .....	147
<b>Table 6.9</b>	Percent abundance of guilds in paleocommunity types at KGM.....	149
<b>Table 6.10</b>	Percent abundance of guilds at KGM ( <i>M. congesta</i> removed).....	149
<b>Table 6.11</b>	Percent abundance of guilds in paleocommunity types at KGM.....	150
<b>Table 6.12</b>	Percent abundance of guilds at KGM ( <i>M. congesta</i> removed).....	151
<b>Table 6.13</b>	Number of species per guild in the RBPT .....	153
<b>Table 6.14</b>	Percent abundance of guilds of the RBPT .....	153
<b>Table 6.15</b>	Percent abundance of guilds of the RBPT ( <i>M. congesta</i> removed).....	154
<b>Table 6.16</b>	Mean correlation of RBPT (LTR), guild data .....	157
<b>Table 6.17</b>	Mean correlation of RBPT (LTR), guild data ( <i>M. congesta</i> removed)....	157
<b>Table 6.18</b>	Mean correlation of RBPT (KGM), guild data.....	158
<b>Table 6.19</b>	Mean correlation of RBPT (KGM), guild data ( <i>M. congesta</i> removed)...	158
<b>Table 6.20</b>	Mean correlation of RBPT (KGM), guild data.....	159
<b>Table 6.21</b>	Mean correlation of RBPT (KGM), guild data ( <i>M. congesta</i> removed)...	159
<b>Table 6.22</b>	Guild constancy values for RBPT samples ( <i>M. congesta</i> removed).....	160
<b>Table 6.23</b>	MANOVA results of guild data for the RBPT.....	160
<b>Table 6.24</b>	Number of species per guild in the MBPT.....	161
<b>Table 6.25</b>	Percent abundance of guilds of the MBPT.....	162
<b>Table 6.26</b>	Percent abundance of guilds of the MBPT ( <i>M. congesta</i> removed) .....	163
<b>Table 6.27</b>	Mean correlation of MBPT (DYP), guild data.....	166
<b>Table 6.28</b>	Mean correlation of MBPT (DYP), guild data ( <i>M. congesta</i> removed) ...	166
<b>Table 6.29</b>	Mean correlation of MBPT (BWB), guild data.....	166
<b>Table 6.30</b>	Mean correlation of MBPT (BWB), guild data ( <i>M. congesta</i> removed) ..	167
<b>Table 6.31</b>	Mean correlation of MBPT (NWR), guild data .....	167
<b>Table 6.32</b>	Mean correlation of MBPT (NWR), guild data ( <i>M. congesta</i> removed) ..	168
<b>Table 6.33</b>	Guild constancy ( $C_a$ ) for MBPT samples.....	168
<b>Table 6.34</b>	Guild constancy ( $C_a$ ) for MBPT samples ( <i>M. congesta</i> removed) .....	169
<b>Table 6.35</b>	Number of species per guild in the transition zone .....	170
<b>Table 6.36</b>	Percent abundance of guilds of the transition zone .....	171
<b>Table 6.37</b>	Percent abundance of guilds in transition zone ( <i>M. congesta</i> removed)...	172
<b>Table 6.38</b>	Mean correlation of transition zone (DYP), guild data .....	174
<b>Table 6.39</b>	Mean correlation of transition zone (BWB), guild data .....	175
<b>Table 6.40</b>	Mean correlation of transition zone (NWR), guild data .....	175
<b>Table 6.41</b>	Mean correlation of transition zone (KGM), guild data .....	176

**Table 6.42** Guild constancy ( $C_a$ ) for transition samples.....176

## FIGURES

<b>Figure 1.1</b>	Ranges of taxa in coordinated stasis.....	17
<b>Figure 1.2</b>	Stabilizing selection in ecological locking.....	18
<b>Figure 2.1</b>	Atlantic Coastal Plain embayments .....	35
<b>Figure 2.2</b>	Members of the Yorktown Formation.....	36
<b>Figure 2.3</b>	Map of Yorktown localities.....	37
<b>Figure 2.4</b>	Sampling procedure .....	38
<b>Figure 2.5</b>	Procedure for processing samples .....	39
<b>Figure 3.1</b>	Species accumulation curve for initial sampling effort .....	50
<b>Figure 3.2</b>	Occurrence frequency versus point of first appearance.....	51
<b>Figure 3.3</b>	Species accumulation for each sub-environment.....	52
<b>Figure 3.4</b>	Occurrence frequency of versus point of first appearance .....	53
<b>Figure 3.5</b>	Species accumulation curve for <i>Mulinia</i> dominated samples .....	54
<b>Figure 3.6</b>	Species accumulation curve for entire data set.....	55
<b>Figure 3.7</b>	Rate of new species accumulation .....	56
<b>Figure 3.8</b>	Occurrence frequency of versus point of first appearance (all data) ...	57
<b>Figure 3.9</b>	Species accumulation curve for CoBabe and Allmon (1994).....	58
<b>Figure 3.10</b>	Species accumulation curve for Crowell (1988) .....	59
<b>Figure 3.11</b>	Total abundance at first appearance (CoBabe and Allmon 1994) .....	60
<b>Figure 3.12</b>	Total abundance at first appearance (Crowell 1989).....	61
<b>Figure 4.1</b>	Species richness in individual and replicate samples .....	73
<b>Figure 4.2</b>	Species richness for each sub-environment in entire data set.....	74
<b>Figure 4.3</b>	Species versus specimens for individual samples.....	75
<b>Figure 4.4</b>	Species versus specimens for individual samples and replicates.....	76
<b>Figure 4.5</b>	Margalef diversity index versus other diversity measures .....	77
<b>Figure 4.6</b>	Pielou's J diversity index versus other diversity measures .....	78
<b>Figure 4.7</b>	Hill's evenness diversity index versus other diversity measures .....	79
<b>Figure 4.8</b>	Shannon H' diversity index versus other diversity measures .....	80
<b>Figure 4.9</b>	Simpson's dominance diversity index versus other measures.....	81
<b>Figure 4.10</b>	Berger-Parker diversity index versus other diversity measures .....	82
<b>Figure 4.11</b>	William's $\alpha$ diversity index versus other diversity measures.....	83
<b>Figure 4.12</b>	Diversity measures in sub-environments at Burwell's Bay.....	84
<b>Figure 4.13</b>	Diversity measures in sub-environments at Day's Point.....	85
<b>Figure 4.14</b>	Diversity measures in sub-environments at Nottoway River .....	86
<b>Figure 4.15</b>	Diversity measures in sub-environments at Kingsmill .....	87

<b>Figure 4.16</b>	Diversity measures in sub-environments at Lieutenant's Run.....	88
<b>Figure 5.1</b>	Geometric meaning of values in correlation matrix .....	122
<b>Figure 5.2</b>	Distribution of samples in PCA space.....	123
<b>Figure 5.3</b>	Correlation and covariance PCA organized by stratigraphic horizon ..	124
<b>Figure 5.4</b>	Cumulative variability of eigenvectors (PCA - correlation matrix).....	125
<b>Figure 5.5</b>	PCA of RBPT.....	126
<b>Figure 5.6</b>	Correlation values of the RBPT.....	127
<b>Figure 5.7</b>	Correlation values of the RBPT at different localities .....	128
<b>Figure 5.8</b>	PCA of MBPT .....	129
<b>Figure 5.9</b>	Correlation values of the MBPT .....	130
<b>Figure 5.10</b>	Correlation values of the MBPT at different localities.....	131
<b>Figure 5.11</b>	Correlation values of the MBPT ( <i>M. congesta</i> removed).....	132
<b>Figure 5.12</b>	PCA of transition zone .....	133
<b>Figure 5.13</b>	Correlation values of the transition zone .....	134
<b>Figure 5.14</b>	Correlation values of the transition zone at different localities.....	135
<b>Figure 6.1</b>	PCA of RBPT, guild data.....	179
<b>Figure 6.2</b>	Correlation values of the RBPT, guild data.....	180
<b>Figure 6.3</b>	Correlation values of the RBPT at different localities, guild data .....	181
<b>Figure 6.4</b>	Correlation of RBPT at different localities ( <i>M. congesta</i> removed)....	182
<b>Figure 6.5</b>	PCA of MBPT, guild data .....	183
<b>Figure 6.6</b>	PCA of MBPT, guild data ( <i>M. congesta</i> removed).....	184
<b>Figure 6.7</b>	Correlation values of the MBPT, guild data .....	185
<b>Figure 6.8</b>	Correlation values of the MBPT at different localities, guild data.....	186
<b>Figure 6.9</b>	Correlation of MBPT at different localities ( <i>M. congesta</i> removed) ...	187
<b>Figure 6.10</b>	PCA of transition zone, guild data.....	188
<b>Figure 6.11</b>	Correlation values of the transition zone, guild data.....	189
<b>Figure 6.12</b>	Correlation values of the transition at different localities, guild data...	190
<b>Figure A.1</b>	Map of Burwell Bay (BWB) locality .....	217
<b>Figure A.2</b>	BWB stratigraphic section .....	218
<b>Figure A.3</b>	Map of Day's Point (DYP) locality .....	219
<b>Figure A.4</b>	DYP stratigraphic section .....	220
<b>Figure A.5</b>	Map of Kingsmill (KGM) locality .....	221
<b>Figure A.6</b>	KGM stratigraphic section.....	222
<b>Figure A.7</b>	Map of Lieutenant's Run (LTR) locality .....	224
<b>Figure A.8</b>	LTR stratigraphic section .....	225
<b>Figure A.9</b>	Map of Lieutenant's Run (LTR) locality .....	226

**Figure A.10** LTR stratigraphic section ..... 227

## CHAPTER ONE: INTRODUCTION

### History and Overview

One of the most compelling questions addressed in the paleoecologic literature of the 1990s has been whether or not there is coordinated stasis punctuated by massive ecologic turnover in paleocommunities, and if so, can we recognize causal mechanisms for this phenomenon. While the question was discussed previously (e.g., Dockery 1986, but also in literature going back to the beginning of the 20th Century, see examples in Brett and Baird 1995), the phenomenon of coordinated stasis over relatively short time periods was brought into sharp focus, and given a name, because of the work of Brett and Baird (1992, 1995). They found that there appeared to be morphological and ecological stasis in 60-80% of the species over periods of 3-7 million years in Devonian deposits in the Appalachian Basin. The idea that this pattern might be characteristic of more than just that one basin has yielded a large number of interesting publications discussing the pattern, or lack thereof, and possible causal mechanisms for the pattern, if it exists (e.g., DiMichele 1994, Morris et al 1995, Alroy 1996, Brett et al. 1996, Bambach and Bennington 1996, Baumiller 1996, Bennington and Bambach 1996, Boucot 1996, DiMichele and Phillips 1996, Holland 1996, Holterhoff 1996, Ivany 1996, Lieberman and Dudgeon 1996, McKinney et al 1996, Miller 1996, Morris 1996, Prothero and Heaton 1996, Schopf 1996, Sheldon 1996, Westrop 1996, Aronson and Precht 1997, Miller 1997a, Miller 1997b, Morris 1995, Stanton and Dodd 1997).

The original kernel around which my project nucleated came out of discussions about how to test for both the patterns of coordinated stasis and causal mechanisms predicted by the various proposed models. Specifically, I wanted to test whether the strong species interactions predicted by the "ecological locking" model of Morris et al (1995) could be detected in temporally well constrained fossil assemblages. Any mechanism strong enough to cause evolutionary stabilizing selection in most species over millions of years should be expected to exert a rather strong ordering force on the composition and relative abundances of organisms in living assemblages, and thus should bequeath at least some signal to the fossil assemblages derived from those living assemblages.

"You should try the Atlantic Coastal Plain - just bring a shovel, and you can scoop up all of the material you could ever want." - Arnold I. Miller, 1993

A comment made in passing can sometimes yield unexpected results, and that particular comment started a thought process which culminated in the writing of this dissertation. Field trips with Buck Ward, Gerald Johnson, and Norm Gilinsky revealed that, indeed, many units of the Atlantic Coastal Plain can be sampled with a shovel, although a hoe pick is advisable for moving large amounts of sediment. Because much of the sediment is unconsolidated, almost any reasonable sampling scheme is feasible.

Many of the Atlantic Coastal Plain units are thin and bounded by obvious unconformities, allowing for good chronostratigraphic control on the samples taken from unconformity-bounded units. Coastal Plain strata are frequently full of the beautiful, easily liberated shells of bivalves, gastropods, and other organisms, making the coastal plain an ideal laboratory for analyzing questions that are best answered by analysis of large data sets, such as the those needed to test for ecologic locking.

The middle two members of the Yorktown Formation, the Rushmere and Morgart's Beach Members of Ward and Blackwelder (1980), form an unconformity-bounded shallow marine sequence that grades upwards from a rubbly sand to a silty sand to a silty mud. This sequence is bounded by unconformities, and was probably deposited in less than 500 k.y. (Ward, Bailey, and Carter 1991), and appears to contain the same basic cast of species throughout, although the relative abundances change rather drastically. At the very least, there are no obvious extinctions or evolution of species within the unconformity-bounded unit. The paleoenvironmental changes were rather gradual, but produced a rather marked set of faunal changes as bottom conditions shifted from rubbly to muddy bottom. By comparing the fossil assemblages found in each portion of the paleoenvironmental gradient, while also comparing the response of individual faunal elements through the paleoenvironmental change, it should be possible to tease apart paleoenvironmental versus organismally controlled faunal changes. Once the different factors have been teased apart, the presence or absence of the strong species interactions predicted by the ecologic locking model can be determined.

## **Definitions**

Before talking about a subject, let's define the terminology so that it does not obscure patterns seen in the observations. The term "community" in the ecologic sense alone has been used thousands of times, and seems to mean something at least slightly different to each worker that has used it (e.g., Erwin 1985; McIntosh 1985; Schluter and Ricklefs 1993; Jackson, Budd, and

Pandolfi 1996). To avoid the problem of form obscuring substance, the following definitions will be used in this study (for more discussions on the use of various terms, see Jarvinen et al 1986).

### **Life and Fossil Assemblages**

The term "assemblage" in this study will refer to any group of objects found in the same place at the same time. "Life assemblages" are therefore groups of organisms that are alive together in the same place at the same time, and "fossil assemblages" are groups of fossils found in the same strata at a locality. The terms are causally connected, but only in the loosest sense.

Fossil assemblages are derived from life assemblages, but not necessarily living assemblages that lived in the same place in which the fossils were deposited, since some material may have been transported. However, while transported assemblages are certainly part of the fossil record, based on the sedimentology of the Yorktown Formation (large shells in fine grained sediment), transportation was not a large factor, and so the majority of shells present in Yorktown were derived from organisms that lived locally.

Because of differential preservation potential, not all organisms in a life assemblage will contribute preservable remains to the fossil assemblage. This can be a problem if there are changes in what gets preserved over time, e.g., if the local conditions allowed for the preservation of aragonite only during some time intervals, and aragonitic remains dissolved at other times. Most of the Yorktown mollusks secreted tough calcite and aragonite shells, and both shell mineralogies are found in a wide variety of conditions (from pristine to rather chewed up) within single samples throughout the middle sequence. Therefore, while differential preservation potential does mean that not all organisms in the life assemblages are preserved in the fossil assemblages, the fossil assemblages should be taphonomically comparable to each other, i.e., those organisms with preservable hard parts should be preserved.

Finally, most fossil assemblages, with a very few specific examples, are not derived from a single life assemblage, but rather from a different life assemblages that occupied that area over the period of time, ranging from thousands to millions of years, it took to deposit the stratigraphic layer in which the fossil assemblage is found - a phenomenon termed "time-averaging" (Walker and Bambach 1971, Kidwell and Behrensmeier 1993). Thus, fossil assemblages contain the remains of some organisms, some of which may have come from individuals in the same life assemblage. However, in aggregate the fossil remains were derived from different life assemblages that inhabited that same area at different points in time.

In this study, "fossil assemblage" refers to the fossils found together in individual samples, or in some cases combined replicates from the same stratigraphic horizon.

### **Local Communities and Local Paleocommunities**

There are perhaps as many ideas about what constitutes an ecological community as there are ecologists (e.g., examples in McIntosh 1985). Almost all definitions contain the idea that a community is a group of organisms that lived together in a habitat, and interacted in some way. However, the term has been used to describe phenomena at such a variety of scales that what one ecologist means by "community" may have little to do with what another might consider a community. For reasons which I will elaborate upon a little later, I have decided to use the community definition used by Erwin (1985) for sublittoral marine communities:

"If a community is envisaged as a functional unit, it can be seen as a series of species populations inhabiting the different habitats available within the community and occupying the different niches in these habitats. [...] Thus functionally, the same community can exist when the same habitat and niches occur within it even if the actual species components are different." Erwin 1985, pg. 155

The local community is therefore the series of species populations (perhaps better termed "avatars" after Damuth 1985) inhabiting the niches present in a small geographic area.

Expanding on the definition of local community, the local paleocommunity is a fossil assemblage derived from the local communities that lived in that area in the ancient past (e.g., Bennington 1995, Bambach and Bennington 1996, Bennington and Bambach 1996), and the definition used in those publications will be used here:

"A local paleocommunity, then, is defined as the assemblage collectable from a single bed at one outcrop, assuming that sedimentological and taphonomic interpretations indicate that the fossil deposit does not contain specimens transported in the area from different habitats and mixed together." (Bennington 1995, pg. 6)

For the reasons outlined in the section on assemblages and expanded on in Bambach and Bennington (1996), the local communities and paleocommunities are not equivalent.

## Communities and Paleocommunities

As mentioned above, the ecologic definition of "community" varies greatly from worker to worker depending on spatial scale, temporal scale, taxonomic groups considered, as well as other considerations. However, all communities should have some properties in common:

"Communities can occur on a wide range of scales and can be nested - the tropical forest community encompasses the community living in the water-filled recessed of bromeliads, which in turn encompass the microfaunal communities of cellulose-digesting insects' guts. Once a community has been identified, we can describe the basic type of community present, determine the trophic structure (who eats whom), and determine the relative biomass of individual components. We can also count the number of species present and the abundance of each species and try to come up with an index of diversity." (Stiling 1999)

As suggested in Bennington (1995), the key to recognizing communities may be recognizing recurrence of ecologic structure in local communities. Two local communities with similar taxonomic membership, and the same basic proportion of faunal elements that occurred in a similar habitat would therefore belong to the same community.

Expanding on that definition, a paleocommunity contains all local paleocommunities containing similar taxa in similar abundances. The degree of similarity necessary to recognize a paleocommunity varies from worker to worker. For this study, the definition of sameness used in Bambach and Bennington (1996), Bennington (1995), and Bennington and Bambach (1996):

"A paleocommunity, then, is defined as the aggregate of local paleocommunities that are not statistically significantly different from one another." (Bambach and Bennington 1996, pg. 125)

will be used with some modification. Specifically, instead of limiting recognition of paleocommunities to demonstration of taxonomic identity, paleocommunities will also be recognized on the basis of similarity of ecologic guilds. The occurrence of individual species may be extremely variable, but the types of niches available to be filled by members of the various ecologic guilds should be consistent under similar environmental conditions. Thus, as with

Erwin's (1985) definition for marine communities, paleocommunities in this study were recognized based on the same types of niches being occupied, although not necessarily by the exact same organisms.

### **Community Types and Paleocommunity Types**

The least constrained level of the community/paleocommunity hierarchy is for local communities and paleocommunities that appear to be similar, but are statistically different (Bennington 1995, Bambach and Bennington 1996, Bennington and Bambach 1996). The paleocommunity type level is probably what is termed "paleocommunities" in many non-statistical studies of paleocommunity recurrence (e.g., Brett and Baird 1992).

### **Coordinated Stasis and Ecological Locking**

The recognition that organisms tend to have long periods of relative morphological stability, and that ecological structures tend to persist through long stretches of geologic time is not a discovery of this decade, or indeed of this century. However, the recognition of shorter periods of morphologic and ecologic stability as an important evolutionary and ecologic pattern is of relatively recent vintage. Twelve long intervals of geologic time (30-140 Ma) during which there was relative ecologic stability in the benthic marine realm were defined as Evolutionary Ecological Units (EEUs) by Boucot (1983). These periods of relative stability were each followed by a period of reshuffling, and the rapid establishment of new benthic paleocommunity types. These intervals of reorganization generally took between 3-8 Ma (Sheehan, 1996).

The phrase "coordinated stasis" was tacked on to a pattern that has been recognized in the rock record of New York since the turn of this century (e.g., examples in Brett and Baird 1995) - specifically that species in the Hamilton Group (Devonian) persist for long periods of time (Brett and Baird 1995). Brett et. al. (1996) defined coordinated stasis as, "an empirical pattern, common in the fossil record, wherein groups of coexisting species lineages display concurrent stability over extended intervals of geologic time separated by episodes of relatively abrupt change" (Brett et al. 1996, pg. 1). The term was originally proposed in Brett and Baird (1992), and was described as sub-divisions of Boucot's EEUs, specifically Boucot's EEU #6. The sub-EEUs of Hamilton Group studied by Brett and Baird had bi-modality (Fig. 1.1) in the persistence of faunal structure with the following characteristics (from Holland 1996, pg. 148):

**Periods of faunal stability:**

- less than 40% species extinction
- less than 40% species origination
- duration of stasis period is 2-8 m.y.
- faunal associations show little change in overall richness, dominance, diversity, guild structure, or species composition
- Few immigrants

**Periods of faunal reorganization**

- less than 40% species carryover and holdover
- duration of turnover period 100-500 k.y.
- abrupt extinction of long-ranging lineages
- accelerated species-level evolution
- increased immigration of exotic species
- new ecologic structure rapidly established
- associated with sequence boundaries (5 out of 14 events) or major transgressions (6 out of 14 events)

These characteristics were specific to Brett and Baird's strata in the Appalachian basin, but some general statements about pattern can be drawn from these characteristics, and the pattern of coordinated stasis has been identified in some other fossil assemblages, although not recognized in all others.

In a study that predated most of the more recent interest in patterns of paleocommunity recurrence, Dockery (1986) found a bimodal pattern of originations and extinctions among a large data set of mollusks from Paleogene strata on the Gulf Coastal Plain, which appeared to have the pattern of coordinated stasis. Using first and last appearance data, he recognized a steady, but low, rate of originations and extinctions within each major sedimentary sequence (intracycle, or background tempo) with greater turnover between sequences ("incongruity tempo"). The incongruity tempo dominated in regressional packages which also occasionally contained depositional hiatuses. He attributed the high level of extinctions between normal marine sequences to be the result of changes in the physical environment, specifically that during sea level regression on the Gulf Coastal Plain, large amounts of sediment were brought into the basin by large prograding delta systems, which would severely disturb some benthic marine paleocommunities. During transgressive events and sea level high stands, these fluvial sediments would be locked up in drowned river valleys and other depositional traps. Transgressive packages of sediment on the

Gulf Coastal Plain of this age contained a higher diversity fauna, while regressive packages of strata contained much lower faunal diversities.

DiMichele and Phillips (1996) found coordinated stasis in late Paleozoic tropical plant systems. Based on fossil plant material found primarily in coal balls, they were able to reconstruct a paleoenvironmental landscape gradient in which different clades of plants dominated the sub-environments for long periods of geologic time. When replacement within the paleocommunity type did occur, it was usually by a closely related species. In this case, cladistics and functional morphology were strongly correlated, so the replacement within the landscape by species within the same genus or family should not be surprising. The persistent association of the major groups of plants in the Pennsylvanian with specific paleoenvironments ended in the Permian, when a major vegetative change mediated by a major climatic change occurred.

Morris (1996) tested for coordinated stasis in the molluscan faunas of Neogene lake deposits of the Kivu-Nile Rift. Using multivariate methods, he demonstrated a correlation of morphologic and paleoecologic stasis. That period of stasis was terminated by coordinated change.

Alroy (1996) conducted an exhaustive survey of the ranges of North American mammals during the Cenozoic in order to examine whether or not coordinate stasis could be found in this group. He found that there seemed to be a constant rate of background extinction with pulses of origination. He interpreted this pattern as being the result of ecospace expansion due to the development of key adaptations overlying a strong incumbency effect, and that the pattern was not due to coordinated stasis.

Aronson and Precht (1997) examined the dramatic change in Caribbean reef assemblages at intermediate depths over the past 20 years, from an assemblage dominated by the staghorn coral *Acropora cervicornis* to one dominated by other elements. At Channel Cay, various species of "lettuce coral" (*Agaricia*) went from being a minor component of the reef assemblage to the dominant element in terms of area covered. The transition from *Acropora* to *Agaricia*, which is probably the result of disease decimating the *Acropora* standing crop, occurred in several steps, and was well documented by neontologists. Those same steps were recognizable in sedimentary samples collected from trenches dug into the reef.

This transition was not recognized in any other strata from cores of the reef, dating back some 3,800 years, indicating that the current *Acropora* to *Agaricia* transition is a unique occurrence in the recent history of that Caribbean reef system. Other than the decimation of *A. cervicornis* and

the opportunistic exploitation by the various *Agaricia* species, the other coral taxa did not show any great change in relative abundance: none disappeared, and none increased greatly in relative abundance. Whether that lack of response will continue remains to be seen, but over the short term the other species were apparently unaffected by this dramatic change in the dominant coral element on the reef. Therefore, in this case, the species within the assemblage responded independently, instead of the community responding in some sort of group fashion.

Stanton and Dodd (1997) compared paleocommunities of the Pliocene deposits in the San Joaquin embayment with modern communities of San Francisco Bay. They found that the origination and extinction patterns of the various taxa did not follow the pattern of coordinated stasis. In addition, they found that while the community structures in similar environments in the Pliocene and Recent deposits are similar, the species compositions differ. They suggested three possible explanations for the lack of pattern in their Cenozoic strata compared to Paleozoic strata:

**1. Data differences** - the pattern seen in the Paleozoic strata is the result of less paleoenvironmental detail and differences in taxonomic and taphonomic interpretations

**2. Evolutionary rate and pattern differences** - the rate and magnitude of sea level rise in California during the late Pliocene is greater, and the distribution of paleoenvironments more complex than the Paleozoic Appalachian strata, and thus rates of speciation differed

**3. Degree of community integration** - Cenozoic communities may be less integrated than their Paleozoic counterparts, perhaps due to the rapidity of environmental change

One of the most interesting parts of their analysis was their comparison of potential and actual species overlap between the two time slices. Among mollusks, 48% of the species recognized in the Pliocene zone they examined are present in the modern oceans, while 55% of the species in San Francisco Bay have ranges extending back at least to the Pliocene. However, only 7 species were found in both, accounting for 12% of the Pliocene fauna and 18% of the modern fauna. One of those species is only present in San Francisco Bay because it was reintroduced in the 19th Century. Even at the genus level, only 14 genera are present in both deposits - accounting for 38% of the Pliocene and 28% of the Recent faunas.

Holland (1996) suggested that the pattern of faunal occurrence expected in a typical cratonic package of cycles (in the sequence stratigraphic sense) would be similar to the pattern of coordinated stasis, and thus that some apparent examples of coordinated stasis may actually be stratigraphic artifacts, a possibility some have termed the "Holland Effect." The null model assumed a unimodal stochastic rate of origination and extinction, paleoenvironmental control on the distribution of most species, and a simple sequence stratigraphic architecture of stacked parasequences. The null model showed low turnover rates in the high-stand and low-stand systems tracts, with significantly higher turnover in the transgressive systems tract flooding surface and at the sequence boundary, in other words, where facies shifted rapidly relative to the amount of sedimentary record.

The Holland Effect should be most severe in cases where only single outcrops are examined, or only a small geographic area. Holland suggested being suspicious of turnover pulses associated with sequence boundaries or flooding surfaces, although turnover pulses not associated with these features are probably reliable. Data from multiple outcrops at various places along the paleoslope could be used to distinguish those taxonomic occurrences associated only with the appearance of their preferred facies at any particular locality from those that appeared simultaneously over a wide area of the basin.

Ivany (1996) outlined a number of causal mechanisms for explaining the apparent pattern of coordinated stasis. These mechanisms were broadly categorized into intrinsic mechanisms (basically biological factors such as ecology and evolution) and extrinsic mechanisms (physicochemical factors imposed by the environment). These factors can be broken down as such:

### **Extrinsic factors**

Ecologic and morphologic stasis maintained by relative stability of the physical environment to which incumbent taxa are well adapted, resulting in "faunal tracking" of paleoenvironments

Ecologic and morphologic change brought about by major environmental disturbance acting over short time periods

### **Intrinsic factors**

Ecologic and morphologic stasis maintained by incumbency or perhaps a more all-inclusive factor like ecologic locking excluding the invasion of the habitat by new species, and thus discouraging both speciation and immigration

Ecologic and morphologic change brought about by ecosystem collapse (either caused by primarily physical, or perhaps biological factors), during which new species can find a foothold in habitat, allowing a rapid shuffling of entire ecosystems

The two sets of factors are not mutually exclusive; environmental and biological factors can and do interact at any number of scales to produce the distribution of living organisms through both time and space. It is the determination of the relative strengths and frequencies of these factors that remains elusive.

The pattern of coordinated stasis observed in the fossil record exists independently of attempts to erect causal mechanisms to explain the pattern. Suggested causal mechanisms abound in the literature, but the mechanism that has attracted the most attention is the "ecologic locking" model of Morris et al. (1995). This model attempted to explain the observed pattern by invoking a high degree of ecologic integration imposing "stabilizing selection" on both species morphology and ecological persistence of community structures. If each species is optimized for its position in the ecological hierarchy, any aberrant morphology or behavior pattern would force the individual into competition with members of a species which are already optimized for the niche which that individual might be invading. Competitive exclusion would eliminate these non-optimized forms and behaviors, and the morphologic and ecologic pattern would therefore be maintained (Fig. 1.2), and each species "locked" into its place in the community.

Ivany (1996) distinguished ecologic locking from the more widely accepted principle of faunal incumbency. In incumbency, an organism that already occupies an ecologic niche should win out in competition with a possible niche invader, because it already occupies that position in the habitat (Fig. 1.2). Also, if a niche is already occupied, there should be limited opportunity for another species to invade that niche, since the resources are already being utilized. Thus, incumbency primarily involves competitive interactions, at least according to Ivany. Ecologic locking, on the other hand, involves a supposed hierarchical structuring of entire ecosystems, and presumably involves an enormous number of competitive, coevolutionary, predatory, symbiotic, and other ecologic interactions (Ivany, 1996, pg. 245). This strong structure of species interactions

is difficult to define, and its presence perhaps even harder to recognize. The concept appears to be based in the idea that communities constitute "superorganisms" maintained by a large multitude of strong species interactions. The "superorganisms" concept of communities has not achieved universal acceptance, and in fact has been heavily criticized in both the ecologic and paleoecologic literature (e.g., Underwood 1986).

Miller (1996) discussed ecologic models of coordinated stasis in terms of the development of regional, rather than local, ecologic stasis, and also separated controlling factors into intrinsic (which he terms "allogenic") and extrinsic ("autogenic") factors. While his extrinsic factors are very similar to Ivany's, he expanded on the list of intrinsic controls by incorporating modern neontologic ecology. He recognized four possible classes of intrinsic controls:

**"Classical" stability** - the evolution of persistence (stability), resilience (return of ecosystem to pre-disturbance structure), and resistance (ability of ecosystem to resist change in structure during disturbance)

**Metapopulation dynamics** - a metapopulation is the sum of all local populations of a species. Each local population is capable of exporting individuals to other localities, thus supporting an entire network of populations across a region. If the metapopulation is disturbed (i.e. via regional disturbance), the structure could collapse, but local disturbance are buffered by the presence of a potential crop of re-invaders

**Connectance stability** - a large web of interspecific interactions produce stability. This category includes ecologic locking (Morris et al., 1992, Schopf et al., 1992), the structural hubs and system breakpoints model (Miller, 1994), and the percolation theory of Plotnick and McKinney (1993).

**Ability to incorporate disturbance** - an ecosystem that can not abide small-scale disturbances (which abound in nature) will not persist for long periods of geologic time, while those that can accommodate disturbances have a chance of persisting

Once again, none of these factors are mutually exclusive, and all could potentially interact with environmental changes in various ways. Determining which, if any, of these intrinsic factors is

present within and ecosystem is highly problematic, particularly with the taphonomic and sampling problems endemic to paleontological study.

Miller (1994) and Miller (1996) displayed a disturbing trend toward treating biological systems as if they were mechanical systems. The very syntax of "structural hubs and system breakpoints" invokes a mechanistic vision that is at odds with the completely organic nature of the fossil record. This is perhaps analogous to using a clock to model the hours of the day and night. The clock may be completely accurate in determining the time of day or night, but the actual causal mechanisms for "day" and "night" have no relationship to the mechanisms contained within the clock. Even such a comparison as saying that both systems involve rotational movement is completely spurious. While Miller's structural hubs and system breakpoints analogy may successfully model ecosystems dynamics over geologic time, that does not mean that the causal mechanisms in the model have any relationship to what caused the patterns seen in the fossil record.

Holterhoff (1996) looked for coordinated stasis and ecologic locking in Upper Carboniferous crinoid fossil assemblages. Using multivariate analysis, he found that for individual cyclothems, there were well defined paleocommunity types associated with individual depth-controlled paleoenvironments, and that these biofacies were distinct from each other. Further analyses revealed that most of the local paleocommunities, defined by relative species abundance, grouped to form 5 distinct and recurring biofacies, each of which had a characteristic guild structure. The biofacies pattern is strongly correlated with the pattern of paleoenvironmental conditions important to crinoids. While paleocommunity types do recur in a consistent manner, the pattern of coordinated stasis does not appear to be explainable by the process of ecologic locking, but rather by the fact that paleocommunity types develop locally due to recruitment from a local species pool in response to local paleoenvironmental conditions, as expected from metapopulation dynamics theory.

Bennington and Bambach (1996) used statistical techniques to define and test for the recurrence of local paleocommunities, paleocommunities, and paleocommunity types in the marine units of the Pennsylvanian Breathitt Formation. They suggested a specific statistical definition of each level of the paleocommunity hierarchy, and tested for recurrence of paleocommunities through recurring similar paleoenvironmental conditions. Using ANOVA and MANOVA, they demonstrated that while similar fossil assemblages (paleocommunity types) do recur frequently in the various marine tongues of the Breathitt, they are not usually similar enough to be statistically indistinguishable, and thus that while there is paleocommunity type recurrence, there is no wide

spread pattern of paleocommunity recurrence . The recurrence was interpreted as the result of recruitment from a local species pool in response to paleoenvironmental conditions - a conclusion similar to that of Holterhoff (1996).

Lieberman and Dudgeon (1996) discussed the problems with invoking stabilizing selection to explain the observe pattern of long term morphologic stasis. An examination of two fossil brachiopod lineages within the Hamilton group revealed that while there was no directional change over all of Hamilton time, there were significant morphologic oscillations, and that the variation through time within a paleoenvironment was greater than the variation across paleoenvironments. Stable environmental conditions did not correlate with stable morphology. They concluded:

"Stabilizing selection has been invoked to explain stasis in a manner analogous to earlier extrapolations of concerted directional selection to explain purported trend-like phenomena across species. If stabilizing selection is to be a prominent mechanism mediating the long term stasis of species either communities must be at equilibrium and/or the physical environment must be invariant over long periods of time. However the majority of evidence from fossil and extant communities suggest that neither of these hold true. Rather communities are not at equilibrium, and selection pressures produced by the biotic and abiotic environment vary in strength and constancy. Thus some other mechanism must be acting to mediate stasis."  
(Lieberman and Dudgeon 1996, pg. 236).

The mechanism that they invoked works as long as species were broken into different demes occurring in different ecosystems, which experienced different selectional pressures. The net sum of morphologic variability over all paleoenvironments for the two Hamilton species summed to zero, so the apparent stability was the result of multiple, but non-directional, selective pressures. This mechanism could act in concert with internal mechanisms like developmental constraint.

The theory of ecologic locking has testable elements. The strong species interactions necessary to ecologically "lock" the various species in place should be strong enough to be a major ordering force both on what species are found together and at what abundances they occur. If these strong species interactions are present, fossil assemblages formed under similar paleoenvironmental conditions should have highly similar species compositions and abundances, assuming that taphonomic processes were relatively uniform (e.g., no large differences in transportation or destruction of the remains). The presence of these strong interactions necessary for ecologic locking to be considered a valid causal mechanism for coordinated stasis will be tested

for in the Yorktown strata sampled in this study by applying statistical methods suggested by Bennington and Bambach (1996), as well as others developed in this study.

## **Brief Outline of the Dissertation**

### **Chapter 2: The Yorktown Formation**

Chapter 2 contains an overview of the previous work on the biostratigraphic, paleoenvironmental, and paleoclimatological aspects of the Yorktown Formation. Included are a brief summary of the colorful history of Yorktown stratigraphy, a short outline of the history of the Atlantic Coastal Margin of North America in the Cenozoic, and a discussion of the global and local causes of sea level change during the time in which the Yorktown was deposited. Also included are descriptions of the Yorktown as exposed at the localities collected in this study, and a description of the collection techniques used for this study.

### **Chapter 3: Species Accumulation Analyses**

Chapter 3 focuses on the special problem of determining whether or not a sampling scheme adequately samples the local paleocommunity for paleocommunity analysis. Without adequate sampling, any observed differences in species abundance and membership between the samples could simply be the result of sampling different parts of the same underlying distribution, and thus the differences could be completely spurious, and the issue of sampling is quantitatively addressed for both my data, and the published data sets from other Cenozoic coastal plain deposits.

### **Chapter 4: Diversity of Yorktown Samples**

As I analyzed my samples, I also became interested in the issue of diversity, and how to measure it in fossil assemblages. The performance of various diversity indices and what they said about diversity patterns in the Yorktown Formation are discussed in chapter 4. The difficulty in applying these indices to fossil assemblages is also addressed.

### **Chapter 5: Paleocommunity Analysis**

Chapter 5 contains statistical descriptions of local paleocommunities and paleocommunity types in the data set composed of the relative abundances of species using PCA, correlation

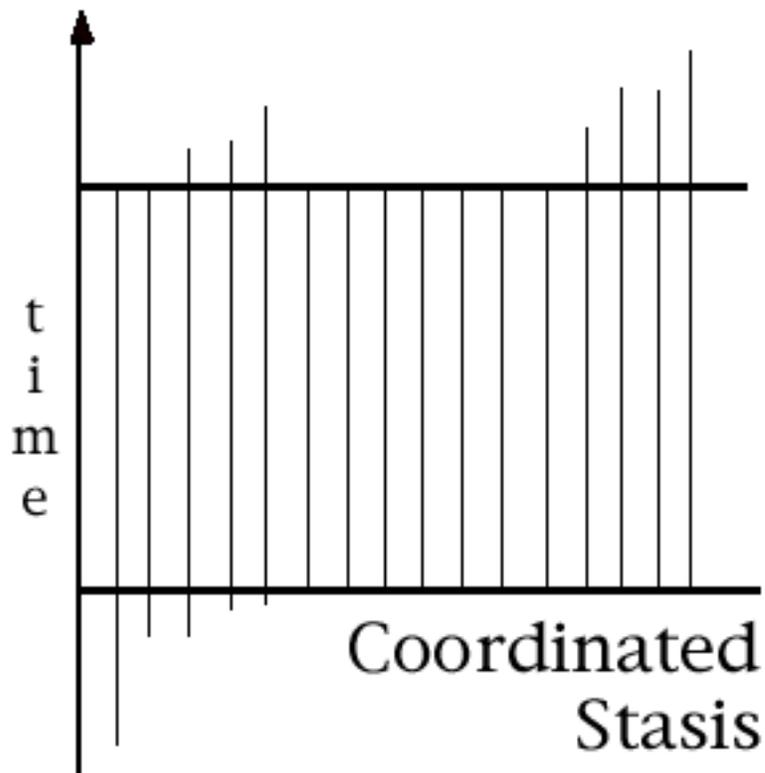
analysis, and species constancy analysis. Statistical testing for the recurrence pattern indicative of the presence paleocommunities is also performed using MANOVA.

### **Chapter 6: Guild Analysis**

Chapter 6 is similar to chapter 5, except the analyses are performed on a data set in which the species have been assigned to guilds. A large poster insert showing the guild structure of the local paleocommunities at each locality is included.

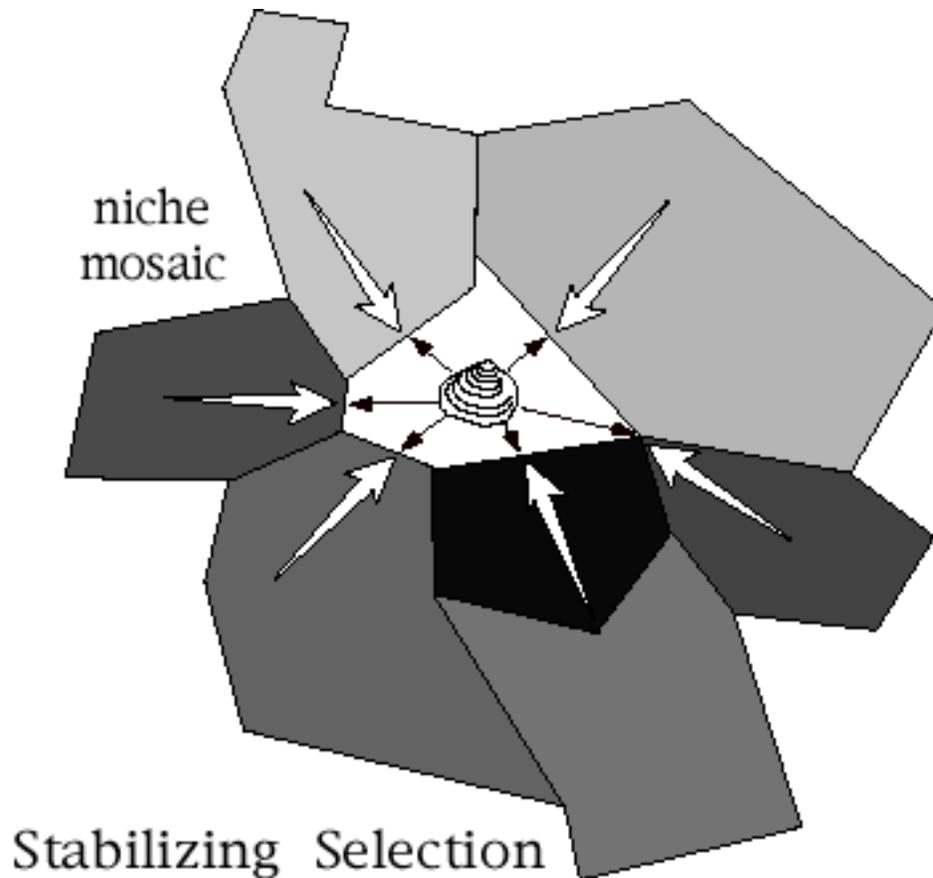
### **Chapter 7: Summary and Conclusions**

Chapter 7 is a brief summary and concluding remarks about the research in the dissertation.



**Figure 1.1.**  
**Ranges of taxa in coordinated stasis**

The pattern of coordinated stasis is of relatively long periods of morphologic stasis in many lineages separated by relatively short periods of reorganization. Most immigration, extinction and origination takes place during these periods of reorganization, so the ranges of taxa have the pattern seen above.



**Figure 1.2**  
**Stabilizing selection in ecological locking**

Schematic diagram of stabilizing selection. If each species is optimized for the niche it occupies, and all niches are occupied, any variation in morphology or behavior (black arrows in the center niche) will be competitively excluded by the species in the surrounding niche, thus imposing stabilizing selection on each species (white arrows).

## CHAPTER 2: THE YORKTOWN FORMATION

### Prehistory of the Yorktown Formation

Attempts at correlating the strata of the Yorktown Formation predates Clark and Miller's (1906) formal definition of the formation by up to one hundred years. One of the first, and most entertaining, attempts at correlating the strata of the Atlantic Coastal Plain with the rest of the world was Finch's (1823) account of his observations and interpretations of Tertiary Formations of North America. While his grasp of the concept of superposition, and its uses in correlation, is somewhat weak, his essay does contain the proclamation that the Coastal Plain strata of North America can be correlated with deposits in France, England, Germany, Spain, Italy, Hungary, Poland, Iceland, Egypt, and Hindoostan. He specifically correlated the group of strata containing the Yorktown Formation with the London Clay of England based in part on the presence of fossil shark's teeth from a deposit in Richmond, and the discovery of a "big fish" fossil outside of Williamsburg; both types of fossils were also found in the London Clay. This early attempt at biostratigraphic correlation leaves a bit to be desired, a fact that Finch clearly recognized in the following statement:

"Although to place the subject beyond dispute, it would be necessary personally to examine all the various fossils from each separate stratum, and the formations on the spot where they occur, yet still sufficient evidence may be collected to place the extent of the country in a different point of view, from that in which it seems to have been hitherto regarded." (Finch, 1823 pp. 32-33)

Lack of data did not stand in Finch's way. Finch's essay was an early attempt to correlate the strata of the North American Coastal Plain with the rest of the world. He left the development of a detailed correlation framework, as well as his extensive collection of Coastal Plain fossils, to later workers. Van Rensselaer (1825) and Vanuxem and Morton (1828) used fossil shell data to support Finch's correlation of Coastal Plain strata with the London Clay, and to further correlate the Coastal Plain strata with the Upper Marine of Europe.

A new method for age-correlating Tertiary strata based on the percentage of extant organisms found in fossil deposits was proposed by Lyell (1833). Based on the recognition that older strata contained a higher percentage of extinct species than younger strata, Lyell erected a biostratigraphic framework of nomenclature based on the following percentages:

<b>Pleistocene ("Newer" Pliocene)</b>	90-95% extant
<b>Pliocene</b>	at least 50% extant
<b>Miocene</b>	more than 50% extinct
<b>Eocene</b>	nearly all extinct

Lea (1833) immediately applied this formula to the fossil shells in his possession, and came up with a Pliocene age for the "Tertiary mass" described by Finch (1823). Ducatel and Alexander (1834) also determined a Pliocene, not Miocene age for the Tertiary strata. It is noteworthy that while a Pliocene age for some of this strata has been confirmed by modern analysis, that age can not be determined from a properly performed Lyellian analysis due to the relatively high percentage of extinct endemic species in these strata (e.g. Stanley 1986, but also earlier workers).

Rogers (1836) stated that at least some of the Tertiary strata should be assigned a Miocene age - a designation which was confirmed by many workers, including Charles Lyell (1845). As in much of the early work on Atlantic Coastal Plain strata, there appears to have been some confusion as to from where the fossils on which these dates were based came. Determining the regional stratigraphic relationships of the flat-lying layers of coastal plain strata is not a trivial exercise, even with the superb natural exposures offered by the various rivers of the region. The strata can be lithologically variable, even at the outcrop scale. Reevaluation of the collections of earlier workers, which were not always accompanied by accurate field notes, led to mistakes in the determination of the stratigraphic and geologic ranges of some important coastal plain fauna (Ward *pers. comm.*).

Even with the problems associated with the correlation of coastal plain strata, the attraction of such fossil-rich strata to biostratigraphers was irresistible. Dana (1876) suggested that the strata exposed at Yorktown, Virginia be used as the standard for his "Yorktown Period" of the Tertiary. This period:

"...correspond[s] to the Miocene, or Miocene and part of the Pliocene (so named for a locality in Virginia) to which a large part of the beds in view on the Atlantic Border belong." (Dana 1876, pg. 490)

The Yorktown Period would be used to designate the time in which those strata were being deposited, as determined from the presence of certain fossils. Dana assigned the name "Yorktown Period" to other formations of Miocene age from North America, including the freshwater White River Group of Colorado.

Not all early workers were impressed with the quality of the work done on the Yorktown strata. Meyer (1888) questioned the use of biostratigraphy in the correlation of Miocene strata, since fossils were not identified well enough to allow for accurate correlation. Heilprin (1883) had also questioned the quality of coastal plain correlation, citing that strata that have been considered to be deposited contemporaneously in fact show regional variation in the age determined from a Lyellian analysis. The fauna of Virginia and Maryland display 11% and 12% extant species respectively while correlated strata in North Carolina contained 26% extant species and South Carolina 35-38% extant species - a pattern of regional variation also recognized as early as Tuomey and Holmes (1857). Darton (1891) re-correlated the strata based on the differences in extant species. However, this type of analysis proved to be unsatisfying, leading to the recognition by Olsson (1914) that direct correlation using fossils of Miocene age was complicated by climatic differences between the northern and southern regions of the coastal plain.

In the first decade of this century, the state of Maryland authorized and allocated money for a publication series on the geology and systematic paleontology of the state of Maryland. Under the supervision of the State Geologist William Bullock Clark, the "Miocene" volume was released in 1904 (Clark 1904). Along with an excellent review of publications on coastal plain strata to that date (Shattuck 1904), the volume includes a very extensive faunal list, and a separate volume composed entirely of plates of fossils from the "Miocene of Maryland." Unfortunately, at least some of the fossils are not from the Miocene *or* Maryland, but are in fact from the Yorktown Formation of Virginia (Ward *pers. comm.*). To read the comments of some workers of the modern era (e.g. Campbell 1993), the publication and wide distribution of this series of volumes retarded the study of the Pliocene Yorktown strata. This misapplication of taxonomic nomenclature led to mis-identification of fossils due to what Campbell (1993) called the "closest Maryland "Miocene" illustration of species identification" adopted by workers faced with the bewildering array of Yorktown species. It is interesting to note that after the publication of the "Miocene" volume, the "possibly also Pliocene" age attributed to the Yorktownian "Period" by Dana (1876) disappeared from the literature. The Pliocene designation did not reappear until microfossil analysis was applied to the Yorktown Formation.

### **Yorktown Biostratigraphy**

While previous authors had referred to the strata exposed near Yorktown, Virginia, it is surprising that the formal designation of the Yorktown strata as the Yorktown Formation did not occur until Clark and Miller (1906) defined a type section for the formation on the "southwest side of York River, at Yorktown." Harris (1890) had defined the Yorktown Formation in an

unpublished manuscript, but had not designated a type-section. The history of formal correlation of the Yorktown Formation must begin with the formal definition of the formation, with pre-definition correlations being considered informal.

With the formal designation of the Yorktown as a formation, the serious work of correlating the formation with the rest of the Atlantic Coastal Plain could begin. Based on both biostratigraphic and lithological data, Vaughan (1924) in a summary paper of Tertiary strata correlations reports that the Yorktown Formation is considered to be a northern equivalent of the Duplin Formation of North Carolina, and identifies both as latest Miocene in age. Based on faunal similarity, the Duplin Formation was correlated as a northern time-equivalent to the Choctawhatchee Formation of Florida, and thus also correlative with the Yorktown Formation. All were designated as Miocene in age.

Lithologically defining the Yorktown Formation has proven to be very difficult, since the stratigraphic features can be highly variable, even at the outcrop scale. This combined with the abundance of large, attractive, fossils has led some workers to subdivide the Yorktown Formation on the basis of the molluscan fauna. Mansfield (1944) defined a successful zonation of the Yorktown based on the molluscan fauna. The lower zone, Zone 1, is defined as the *Placopecten clintonis* Zone, while the upper zone, Zone 2, was called the *Turritella alticostata* Zone. Zone 2 was further divided into an upper, middle, and lower zone, again based on faunal differences.

One of the first "modern" biostratigraphic analysis of the Yorktown Formation was Malkin's (1953) study of the ostracods of the Coastal Plain. This study incorporated both biostratigraphic and paleoecologic data to create a framework for the correlation of Atlantic Coastal Plain strata. She rejected the earlier zones of other workers and erects a more modern biostratigraphic framework based on microfossil "Opper zones" (microfaunal associations). Two microfossil zones (the *Hemicythere conradi* zone and the *Hemicythere schmidtae* zone) were recognized, although the usefulness of the zonation was somewhat limited since no correlation with the molluscan zones was provided. Faunal acme zones and epiboles were also recognized, as were teilzones, which were considered useful for local correlation of strata. The biostratigraphic analysis confirmed the correlation of the Yorktown with the Duplin Formation, as well as the Choctawhatchee Formation. However, the paleoecological comparison of the three formations indicated that the similarity between the northern (Duplin and Yorktown) and southern (Choctawhatchee) formations were due more to similarity in climate than similarity in age. The Yorktown Formation was still considered by Malkin to be Upper Miocene in age. The correlation of the Yorktown and Duplin Formations was most recently confirmed by Ward and Gilinsky

(1993), while the Choctawhatchee Formation is considered to belong to an earlier time (Blackwelder 1981b).

The erroneous Miocene age of the Yorktown Formation was finally discarded by Hazel (1971) and Akers (1972). Hazel assigned an early Pliocene age to the Yorktown Formation based on ostracods. Akers confirmed the Pliocene age, and correlated the Yorktown Formation with the Jackson Bluff Formation of Florida. This strata was assigned to either the N18 or N19 planktonic foraminifera zone. Blackwelder (1981a) placed the Yorktown Formation entirely within the N19 zone, a placement confirmed by Hazel (1983), although Snyder *et al*'s (1983) interpretation indicated that the upper Yorktown Formation may also include parts of the N20 zone.

Ward and Blackwelder's (1980) paper arguably contained the first serious attempt at defining lithostratigraphic units within the Yorktown Formation. Four members were defined: the lowermost Sunken Meadow Member (= Mansfield's Zone 1), the Rushmere, Morgart's Beach, and Moore House Members (= Mansfield's Zone 2). Ward and Blackwelder (1980) stated that the lowermost member in their new nomenclature contains planktonic forams from the Lower Pliocene N18 zone. The relative age assignment of the members have been refined in the years since 1980 based primarily on work done by Hazel on calcareous nannofossils and ostracods (Ward, *pers. comm.*). By the time of the publication of Ward and Gilinsky (1993), all the members of the Yorktown Formation except the lowermost had been moved into the lower Upper Pliocene (= Piacenzian (European) Stage). Campbell (1993) was critical of Ward and Blackwelder's classification, however, his suggested classification lacked the clarity necessary to make it useful in field identification of Yorktown strata.

### **Tectonic Setting of the Atlantic Coastal Plain**

The Atlantic Coastal Plain province of North America was formed when the North American and African continental plates of the supercontinent Pangaea rifted apart beginning in the Triassic Period. This event was the result of complex shearing forces between the plates which resulted in extensional forces concentrated along the plates' boundary, and the development of normal fault-bounded half-grabens, and general crustal thinning (Manspeizer 1985). Attenuation of the continental crust at the plate edge reduced the thickness, and thus the isostatic buoyancy, of the plate edge, which was further reduced by the accretion of dense oceanic crust to the continental crust of the North American plate (Manspeizer 1985). Loading of sediment onto this compromised plate edge, along with thermal contraction of the oceanic crust with age resulted in subsidence of the margin (Owens and Gohn 1985).

The history of the Atlantic Coastal Plain "passive" margin since the initial rifting event has been complex. When normal marine deposition on the coastal plain resumed during the Cretaceous Period, it was concentrated in a series of low lying basins, called embayments, separated by structural arches (Owens and Gohn 1985). These embayment and arches are long-term features which controlled sedimentation on the Atlantic Coastal Plain throughout the Mesozoic and Tertiary Periods (Fig. 2.1), however the origin of the features is somewhat problematic. Owens and Gohn (1985) explain the origin in terms of complex intraplate stresses of "uncertain origins." The crenelated geometry of the Atlantic Coastal Plain may be self-perpetuating, with basins continuing to sink due to sediment-loading, while the sediment-starved arches are subject to erosion, and thus not loaded as heavily (Cronin 1981).

Even along a passive margin, the contribution of tectonics to the relative sea level history must be taken into account. Cronin (1991) tracked the vertical neotectonic movement of the Coastal Plain over the last 3 million years, and found that while there is a subsidence rate of 2-4 cm/k.y near the depocenters of the basins, there is an overall uplift of the landward portions of the Coastal Plain of 1-3 cm/KY. This uplift rate is sufficient to explain the 60 m uplift recorded on the Orangeburg Scarp in the 3 Ma since the Pliocene. Cronin's mechanism involves upward structural flexure inland from the depositional troughs which received the greatest sediment load, coupled with some compressional stresses, possibly due to "aesthenospheric drag." Compressional forces are also evidenced by the en echelon, high-angle reverse faults and low-amplitude folds noted in seismic cross-sections by Mixon, Powars, and Daniels (1992). The reverse faults are oriented along a northeastern trend, indicating that the compressive force was oriented northwest-southeast. Although the fault displacements and fold amplitudes are small, they provide evidence that compressional forces have acted on the Atlantic Coastal Plain since the late Cretaceous. Unfortunately, Mixon, Powars, and Daniels (1992) did not offer any explanation for the source of these compressive forces.

While the overall tectonic displacement of the Atlantic Coastal Plain may be small, there is some evidence that the separate embayments may have moved independently of each other (Ward and Strickland 1985). Without good time control on the ages of sediments, this phenomenon can complicate the correlation of sea level events, since an embayment receiving a large sediment influx, and thus having a greater subsidence rate, will accumulate a much thicker sedimentary package than an embayment in which sediment influx was not as great. Differential downwarping also complicates the correlation of the Atlantic Coastal Plain strata to those of the Gulf Coast, which may have a less complex subsidence history (Ward and Strickland 1985). However, the

tectonic contribution to the relative sea level signal for the Atlantic Coastal Plain is small compared to other tectonic settings, and the overall control of relative sea level appears to be glacio-eustatic sea level changes (Cronin 1981).

### **Paleoclimatology of the Pliocene**

Climatic interpretations are inferred from a number of types of data. Paleoecological studies of organisms with well known environmental tolerances can be used with some expectation of accuracy. Pliocene ostracods, as well as some other microfossils, meet this criterion, and have been used in both marine and lacustrine studies of climatic variability (e.g. Cronin, 1981; Gladenkov *et al*, 1991; and Forester 1991). Pollen has been used to track the terrestrial record of climate change (Thompson 1991). Unfortunately, many of these same organisms have been used for biostratigraphic correlation, which introduces the possibility of circularity in the chronostratigraphic reconstruction of climatological events. Crowley (1991) used a reported retardation of the weathering rates of carbonate sediment as evidence for elevated CO<sub>2</sub> levels during the Pliocene, and thus elevated temperature, although even the author admitted that the evidence was somewhat speculative.

The best evidence for global climate change comes from the stable isotope record of  $\delta^{18}\text{O}$ , which in addition to being temperature dependent, tracks the production of glacial ice. During times of glacial build-up <sup>16</sup>O evaporates more easily than <sup>18</sup>O, and thus enters atmospheric weather systems more readily, is preferentially incorporated into snow, and then glacial ice. Thus the balance of the global water budget is enriched with the <sup>18</sup>O isotope. Hodell and Warnke (1991) used the stable isotope record in the carbonate tests of planktonic and benthic foraminifera from two DSDP cores in the sub-antarctic southern Atlantic ocean to determine the starting point of the southern polar glaciations during the Pliocene. Their analysis revealed that there were a number of distinctive cooling and/or glaciation events, with a general cooling trend in the mid-Pliocene (3.5-3.2 Ma) leading up to a  $\delta^{18}\text{O}$  maximum at 3.15 Ma, an analysis confirmed by Webb and Horwood (1991). The presence of ice-rafted sedimentary deposits lends evidence to the theory that the  $\delta^{18}\text{O}$  is recording the beginning of southern polar glaciation (Hodell and Warnke 1991).

During the same time period in the Northern Hemisphere there is a different trend in climate. Based on evidence from marine invertebrates from Eastern Kamchatka (Gladenkov *et al* 1991), siliceous microfossils in two northern Pacific DSDP cores (Morley and Dworetzky 1991); pollen (Thompson 1991) and lacustrine ostracods (Forester 1991) from the western United States; North Carolina ostracods (Cronin 1988, 1991); and pollen (Groot 1991) and mollusks (Ward *et al*

1991) from the Atlantic Coastal Plain, the climate of the northern hemisphere during the Pliocene was generally warmer and less seasonal than today.

While the climate record shows fluctuations consistent with the development of small scale northern hemisphere glaciers during the Pliocene Epoch, the development of large continental glaciers probably did not begin until after 3 Ma, during the latest Pliocene or early Pleistocene (Cronin 1988, Prentice and Matthews 1988, Hagemberg and Pisias, 1990, Krantz 1991, Gladenkov *et al* 1991, and Groot, 1991). Glacio-eustatic sea level fluctuations would be expected to be less pronounced before the beginning of the extensive northern glaciation than after. As expected, Haq *et al's* (1988) glacio-eustatic and coastal onlap curves show low amplitude sea level changes before 3 Ma relative to after 3 Ma.

### **Relative Sea Level Record of Atlantic Coastal Plain Strata**

The embayments of the Atlantic Coastal Plain are the landward extensions of larger depositional basins which extend out into the Atlantic Ocean. These embayments have remained topographically higher than the deeper oceanic basins throughout the post-Cretaceous history of the Atlantic Passive Margin, and have therefore only accumulated sediment during the highest part of sea level high stands (Ward and Strickland 1985). During low stands, the Coastal Plain was subject to erosion, as with the present emerged Coastal Plain. Thus each unconformity-bounded sedimentary package probably represents a single transgressive event. This record of sea level fluctuation may be regionally patchy due to tectonic and erosional forces, but major sea level transgressions, and the subsequent highstand sedimentation, should leave a signal in the stratigraphic record. Therefore, the strata of the various embayments of the Atlantic Coastal Plain should record roughly the same number of sea level fluctuations.

Analysis of high resolution seismic profiles of the Pliocene strata of the Apalachicola Embayment of the Gulf Coast of Florida revealed that sedimentary sequences could be recognized from these carbonate and clastic strata (Evans and Hine 1991, Locker and Doyle 1992). One, or possibly two unconformity-bounded depositional sequences were recognized in the Pliocene strata by Locker and Doyle (1992). The base of their AE4 sequence consisted of a strong reflection, indicative of a karstic erosional surface, and was correlated with the Upper Pliocene Jackson Bluff Formation, a formation that can be biostratigraphically correlated with the Yorktown Formation. However, their overlying AE5 sequence is of uncertain age, and probably was extensively reworked by Pleistocene sea level fluctuations.

Evans and Hine (1991) also invoked the development of karstic surfaces as important tools for recognizing the six unconformity-bounded units which they discovered in seismic and core hole data from Charlotte Harbor, Florida. Unfortunately, it is unclear how many of the units, if any, are Pliocene in age. It is possible that the depocenter of the basin was far enough to the south and east that this part of the Gulf Coast of Florida did not receive much sediment during the Pliocene high stands (Evans and Hine 1991). In general, the poor resolution of post-Miocene strata from Florida rendered direct comparison with the Atlantic Coastal strata difficult.

The Duplin Formation was deposited in the Albemarle and Charleston Embayments during the Pliocene Epoch. It has been firmly time-correlated with sections of the Yorktown Formation using ostracods, planktonic foraminifera, mollusks, and calcareous nannoplankton (Ward and Strickland 1985). One unconformity-bounded sequence has been recognized from the Duplin Formation of North and South Carolina; sea level was high enough during this transgression that sediment also accumulated on the Cape Fear Arch, between the two basins (Cronin 1988).

The Yorktown Formation is found in an outcrop belt on the Atlantic Coastal Plain which includes part of the Salisbury Embayment of southeastern Virginia and the Albemarle Embayment of North Carolina. Riggs *et al* (1982), in a study of the distribution of phosphorites in the Yorktown Formation of the Albemarle Embayment, recognized two distinct, unconformity-bounded units. The lower unit contained significant amounts of phosphate of either primary or detrital origin. The upper unit, which lies unconformably on the lower unit, is less phosphate-rich. Riggs *et al* (1982) invoke not two transgressive events to explain this phenomenon, but three. This appears to be a case of putting the sequence stratigraphic cart before the data interpretation horse. No explanation from the data analysis is given for needing three transgressive events to explain two high stand units; rather the authors appear to have tried to force the data to fit the conceptual model of Vail and Mitchum (1979), who showed three transgressive events during the period of time in which the Yorktown Formation was being deposited.

While deposition of Yorktown strata did occur in the Albemarle Embayment, that record is less complete than the record preserved in the Salisbury Embayment of Virginia. Ward and Blackwelder (1980) sub-divided the formation into four members: the basal Sunken Meadow; Rushmere; Morgart's Beach; and Moore House Beach Members (Fig. 2.2).

Ward and Strickland (1985) and Ward, Bailey, and Carter (1991) mapped the geographic distribution of all the members of the Yorktown Formation. The geographic distribution of the

Sunken Meadow Member extends from the Salisbury Embayment over the Norfolk Arch and into the northernmost sector of the Albemarle Embayment. Based in this geographic distribution, the sea level transgression that resulted in the deposition of the Sunken Meadow Member was a relatively large one. The Sunken Meadow Member is bounded by well defined unconformities. The contact between the Sunken Meadow and the overlying Rushmere Member is clearly an erosional surface, with concentrations of shark's teeth and pebbles along the boundary. There is also an obvious molluscan faunal change across this boundary. This unconformity also truncates sedimentary structures in the Sunken Meadow Member.

The contact between the Rushmere and Morgart's Beach Members is not defined by a sharp erosional break. In fact, at some places (e.g. Kingsmill, Virginia) there is intertonguing of the two members, indicating that this contact probably represents a facies boundary. The Rushmere Member is composed of fine to coarse silty sands with an abundant, diverse fauna including large mollusks, while the Morgart's Beach tends to be finer grained, with a less diverse fauna. The Rushmere Member was probably deposited in a high-energy, unprotected setting, while the Morgart's Beach Member was deposited in a more protected environment (Ward and Blackwelder 1980). Ward and Strickland (1985) invoked a structural failure, such as the reactivation of a Triassic fault, to explain the development of the barrier system responsible for the deposition of the two different facies types. Campbell (1993) suggested that multiple shoal fields developed during the transgressive stage of sea level rise could have formed a similar barrier, without needing to invoke tectonic forces. Deposits of these two units extend to the Fall Line in Virginia, as well as spilling over the Norfolk Arch into the Albemarle Embayment. Based on this wider geographic distribution, the transgressive event responsible for the deposition of these two units appears to be larger than the one responsible for deposition of the Sunken Meadow Member.

According to Ward and Blackwelder (1980), the uppermost member of the Yorktown Formation, the Moore House Member, overlies an erosional base. At Chuckatuck, Virginia this member consists of cross-bedded bioclastic sand shaped into dune forms. The presence of large marine mollusks indicates that these dunes are not aeolian in origin, but rather submarine sand waves formed in a high energy, and probably shallow water environment. This last member of the Yorktown Formation has the smallest geographic extent of all the Yorktown members; Ward, Bailey, and Carter (1991) show the Moore House Member being limited to the most seaward portion of the exposed Coastal Plain in the Salisbury Embayment. The rise in sea level responsible for the deposition of this member was probably much smaller than that responsible for the deposition of the underlying members.

Overall, the Yorktown Formation of the Salisbury Embayment reliably records three transgressive events (in temporal order: Ty1, Ty2, Ty3). The Yorktown Formation of the Albemarle Embayment records two transgressive events (Tya1, Tya2). The Duplin Formation probably records just one transgressive event (Td1). The Pliocene record of sea level change in Florida may record one, or possibly two transgressive events.

Not all of the Atlantic Coastal Plain embayments recorded the same level of detail. In this subset, the Yorktown Formation of the Salisbury Embayment showed the most complete record. The relative intensities of the transgressive events based on the geographic distributions of the members are: Ty2, Ty1, and Ty3 (from most to least intense). The Duplin Formation, which records only one transgressive event, was probably deposited during the most geographically extensive transgression, the Ty2. None of the other transgressive events impinged on the geographic area in which the Duplin Formation was deposited, or at least did not result in sediment accumulation. This is also the correlation picked by Ward and Strickland (1985) based on their mapping of the formations, and biostratigraphic considerations. Similarly, the two transgressive events recorded in the Yorktown Formation of the Albemarle Embayment should match up to the two larger transgressive events of the northern Yorktown Formation, the Ty1 and Ty2. The resultant correlation of the three units is shown in Table 1.1.

**Table 1.1.** Correlation of three Coastal Plain units based on the eustatic sea level signal. Ty1, Ty2, Ty3=transgressive events of the northern Yorktown Formation; Tya1, Tya2=transgressive events of the southern Yorktown Formation; Td1=the transgressive event of the Duplin Formation; *unconf.* = unconformity, no record of deposition.

Formation	Embayment	Transgressive Events		
Yorktown	Salisbury	Ty1	Ty2	Ty3
Yorktown	Albemarle	Tya1	Tya2	<i>unconf.</i>
Duplin	Albemarle/ Charleston	<i>unconf.</i>	Td1	<i>unconf.</i>

Independent evidence from biostratigraphic analyses lends support to this correlation of the units (Ward and Strickland 1985). Therefore, unless the correlation can be tied into the global eustatic sea level chronology, no new understanding of the temporal relationships of the Coastal Plain strata will be gained. Krantz (1991) suggested a testable model for correlating the Yorktown Formation with the global  $\delta^{18}\text{O}$  climate record. Krantz used the  $\delta^{18}\text{O}$  signal derived from benthic foraminifera from a DSDP well off of the Atlantic Coast to derive a sea level curve for the past 5.5 million years. This record shows 5 major transgressive/regressive events, 3 of which may be

correlatable with similar events in the Yorktown strata. By tying Krantz's  $\delta^{18}\text{O}$  curve in with the global 3rd Order glacio-eustatic curve and sequence chronostratigraphy of Haq *et al* (1988), Ward, Bailey, and Carter (1991) suggested the following chronostratigraphy for the initiation of the transgressive events.

- 2.3 Ma** Major regression caused by northern continental glaciation, possibly causing the emergence of the entire shelf.
- 2.8-2.4** A shelf sea occupied the southeastern portion of the Salisbury Embayment, resulting in the deposition of the Moore House Member.
- 3.0-2.8** Global cooling and southern polar ice build-up result in a brief regression, which exposed the Coastal Plain to erosion.
- 3.4-3.0** An extensive early Late Pliocene transgression, corresponding to a period of northern hemispheric warmth, and regional downwarping result in the deposition of the Rushmere and Morgart's Beach Members (=Ty2) and the Duplin Formation (=Td1). The  $\delta^{18}\text{O}$  record indicates that there were sea level oscillations of uncertain duration during this time.
- 3.7** A moderate drop in sea level to slightly below the present level exposes the Coastal Plain, which results in erosion of the Sunken Meadow Member, and the development of an unconformity.
- 4.0-3.8 Ma** A brief warming, and subsequent rise in sea level results in the deposition of the Sunken Meadow Member of the Yorktown Formation. (=Ty1).

The level of detail presented in this chronostratigraphic reconstruction was made possible by the development of a record of glacio-eustatic sea level fluctuations through time, and the correlation of 3rd Order fluctuations in that record. However, as attractive as the historical reconstruction is, it is important to remember that it is based on data that does not contain an intrinsic temporal component. Unlike fossil species, which exist only during a limited portion of the geologic record, sea level fluctuations differ only in intensity from one time to another. Even in a passive margin setting, local tectonics can cause a differential relative sea level signal from basin to basin. Different interpretations of the same data can lead to different chronostratigraphic reconstructions. Campbell (1993) took the same models as Ward, Bailey, and Carter (1991) and came up with a radically different chronostratigraphic reconstruction. While Ward and Gilinsky (1993) criticized Campbell's reconstruction, especially his odd internal correlations of the Yorktown strata, and the reconstruction may not have any basis in reality, it was still derived from

the same basic data set and assumptions as Ward, Bailey, and Carter's, and has been adopted other Coastal Plain workers (e.g., Petuch 1997).

## Collection and Processing

Samples were collected from outcrops in eastern Virginia (Fig. 2.3). All of the outcrops were natural cuts made by streams and rivers (see Appendix A for a complete list of localities). Many "classic" localities (such as those along the York River) could not be sampled because of natural and artificial destruction of the cliff faces. While natural slumping, and subsequent overgrowth of river cliffs is common, the process is accelerated by rip-rapping of riverbanks in a ill-advised attempt to stop natural erosive processes (Ward and Gilinsky 1993). Fortunately, many of the cliffs on rivers in less developed areas (e.g., along the banks of the James and Nottoway Rivers) have been left in a natural state, and thus are available for collecting. Landowners in these less developed regions proved to be friendly and cooperative when permission to collect was sought, and they even occasionally gave very good advice on excellent collecting localities.

Ideally, an initial survey of a potential collection site was done from a boat on the river. Large scale features, such as laterally extensive shell beds, burrowed horizons, indurated horizons, and large dissolution features are more easily seen from a distance than up close. The outcrop was then walked along its entire length, noting smaller scale features. Large non-molluscan fossils, such as large whale bones and bryozoan colonies, were noted so that they could be avoided in subsequent collection. The deep fossil burrows of *Panopea*, and other large, muscular clams, were also noted, so that they could also be avoided, if possible. Root systems of the modern flora were also noted, since plant root systems actively dissolve shelly material, and thus vegetative zones were avoided when possible. Large colonies of burrowing wasps, which were particularly prevalent in Morgart's Beach deposits, were also avoided when possible, as were bird nesting grounds.

Once the entire outcrop had been surveyed, an area to be sampled was chosen based on lack of groundwater alteration (e.g. dissolution and induration), good vertical exposure, and access. Each collection area was given a three letter designation (e.g. DYP for Day's Point, BWB for Burwell's Bay, etc.). The first section sampled in a collection area was designated by a "-1" suffix to the collection area name, the second a "-2" suffix, etc. (e.g. BWB-1 was the first section sampled from the Burwell's Bay collection area, BWB-2 was the second section, etc.).

For most localities, at least two vertical sections within the area were measured, described, and marked off at one foot (.33 m) intervals (Fig. 2.4). Collections were taken adjacent to these foot markers. A rectangular area approximately 1-2 feet (.33-.66 m) wide and 1-3 inches (2.7-7.5 cm) high was carved using a hoe-pick. A volume of sediment beneath this collecting interval was excavated, undercutting the collection interval to a depth of up to 1 foot (.33 m) into the outcrop. The edges of the collection interval were also excavated. The undercut collection interval was then struck from above, using the hoe end of the hoe-pick, dropping the sample into a waiting plastic bin. Ideally, at least 6 lbs (2.7 kg) of sediment were collected from each horizon, although since it was somewhat difficult to judge the dry weight of water-saturated sediment and so the actual collections varied in weight from 4.5 lbs (2.0 kg) to 15 lbs (6.8 kg). Each sample was transferred to a bag labeled with the collection area and sampling interval (e.g. BWB-1 +6.0 was a collection taken at the six foot interval marker of the first section measured at the Burwell's Bay collection site) for transport back to the laboratory. This procedure was repeated for each marked interval of each measured section.

After the initial sampling effort, three of the localities (LTR, DYP, and NWR) were resampled. Instead of single samples from each stratigraphic horizon, each horizon was sampled in triplicates. Thus each stratigraphic horizon yielded three replicate samples.

Once in the lab, the damp bags were opened and allowed to air dry for several days. The dried samples were weighed on a postal scale, and the weight of the sample written on the bag. Five pounds (2.3 kg) of sample was removed from the collection bags for processing. The rest of the collection was left unprocessed, but preserved for future examination. Collections that weighed less than 5.5 lbs (2.5 kg) had 0.5 lb (2.2 kg) samples removed and preserved to insure that some unprocessed remained after the sample was processed. The fact that less than 5 lbs (2.2 kg) of sample was available for processing in those cases was noted on all of the subsequent processing documentation.

The first step in the sample processing procedure (Fig. 2.5) was to wash each 5 pound sample through a #8 (1 mm) sieve. This sieve was placed in a tub of water, so that the finer portion which washed through the sieve was preserved for later examination. Gentle agitation was usually all that was required to remove most of the sediment from the shells, although in some cases, gentle scrubbing was also required. The largest shells (at least 1 cm in some dimension) were removed from the sieve and put aside. These larger shells proved to be rather fragile, and prone to disintegration if allowed to soak for too long. Smaller shells were not as easily damaged by either soaking or gentle agitation, and thus could be left in the sieve. After the sample had been washed

through the #8 sieve, the coarse fraction was wet-washed through a #5 (4 mm) sieve. The fine fraction of this sieving was allowed to dry, and then labeled and placed in small plastic bags. The coarse fraction was also allowed to dry, and then was processed for fossil material.

The molluscan remains in the coarse fraction were sorted into countable and uncountable shell fragments. Bivalve fragments were considered countable if they included enough of the hinge portion of the shell to allow positive identification of the bivalve species. Since one bivalve valve can contribute tens to hundreds of fragments to the fossil record, countable fragments must be defined so that each valve was only counted once. The hinge of most bivalves is relatively robust, easily recognized, and a unique, non-repeated element of each valve. Thus limiting countable fragments to those containing the hinge seems justified, and this procedure has been used by various workers for fragmentary bivalve material.

Many of these same workers count gastropod material only if the apex of the shell is included. However, unlike the bivalve hinge, the apex of most gastropod shells is the least robust part of the shell, and is sometimes even broken off during the life of the snail. Using only this most fragile portion of the shell to count gastropod material does not seem justified in most cases. All gastropod material was sorted and a type-specific scheme was used for counting different types of gastropods. During processing, recognizable snail fragments were put aside, and grouped by type. If more than one fragment of a particular gastropod was found, all of the fragments that could have come from one individual were grouped together, and number of individuals tabulated. It was rather unusual to find more than a few fragments of most gastropods, with the exception of the ones listed below, so it was relatively straightforward to determine how many of each type of snail were present.

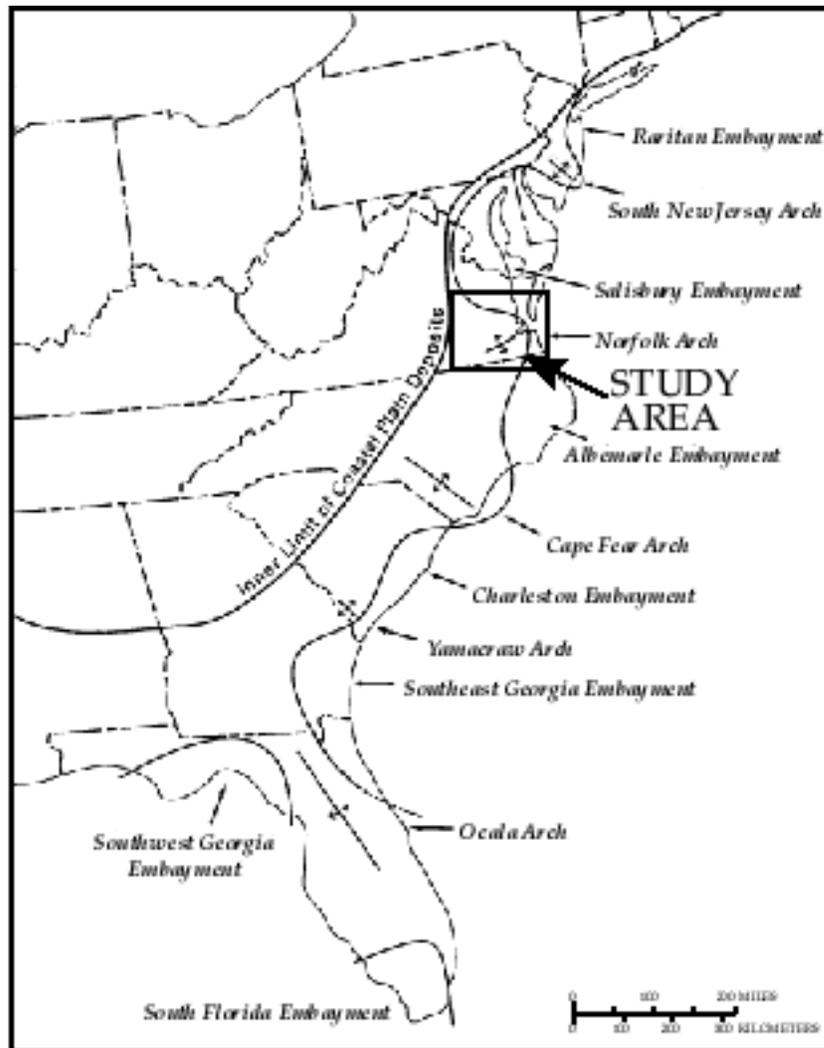
Unlike other gastropods, the apex of slipper snails (e.g., *Crepidula costata*) is the most robust part of the shell, and so for these snails, that was considered the countable, non-repeating element. The shells of *Turritella* break into 10s to 100s of nearly identical whorl fragments, which can not be readily sorted into non-repeating elements. Since there was no efficient way to get an accurate count of these snails, turritellids were counted as either present or absence without any attempt to quantify the number. The other high-spired gastropods were far less common than the turritellids, and thus it was relatively straightforward to determine count data for these taxa.

Scaphopod and polyplacophoran shells were also extracted during the sorting process, as were such non-molluscan remains as echinoid spines and plates, bone material, bryozoan material, decapod remains, and other unusual organic materials. Barnacles were present in all samples, and

thus were not specifically removed for counting. The uncountable portion of the sample was placed in a labeled plastic bag, and put aside.

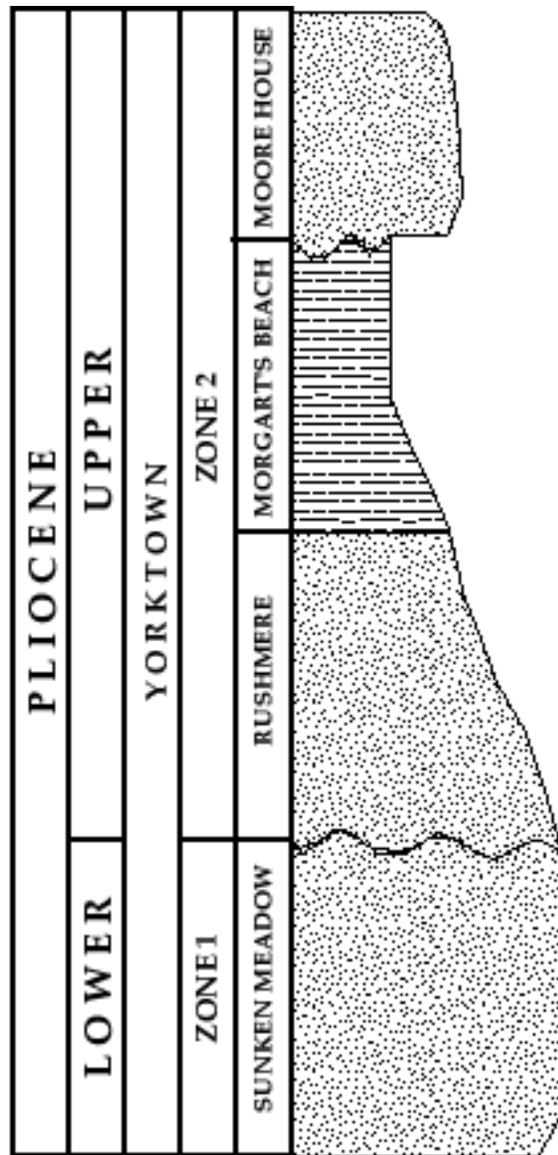
Most of the bivalve and gastropod shell fragments in the countable portion of the sample were identified to the species level using Gardner (1943), Gardner (1948), and Campbell (1993). For some genera (e.g. the fragile aragonite jewel-box shell *Pandora*), species identification was not practical because species-specific characteristics were not commonly preserved on countable fragments. These taxa were identified only to the genus level. The fragments were then counted, and the data tabulated. The presence of scaphopod, polyplacophoran, bryozoan, decapod, barnacle, echinoid, and bone material was also noted by recording a count of "1" in the appropriate box for each type of fossil. Scaphopod material was identified to the genus level, while the other types were simply noted.

A single living bivalve can contribute two different countable elements to the fossil record, its left and its right valves. In contrast, a living gastropod shell has only one valve, and thus only one countable element. Therefore, unless some kind of correction factor is used, the frequency of bivalve occurrence would be up to twice the frequency of gastropod occurrence in the data set, even if the same number of individuals contributed shells to the fossil assemblage (see also Bennington and Gilinsky 1994). To account for this difference in frequency when both bivalves and gastropods were compared in the same analysis, the number of bivalve valves were divided by two, and the fractions rounded up, in order to make them more comparable with the counts of snail individuals. This was not performed for the species accumulation analysis (chapter 3), but it was done for the other analyses.



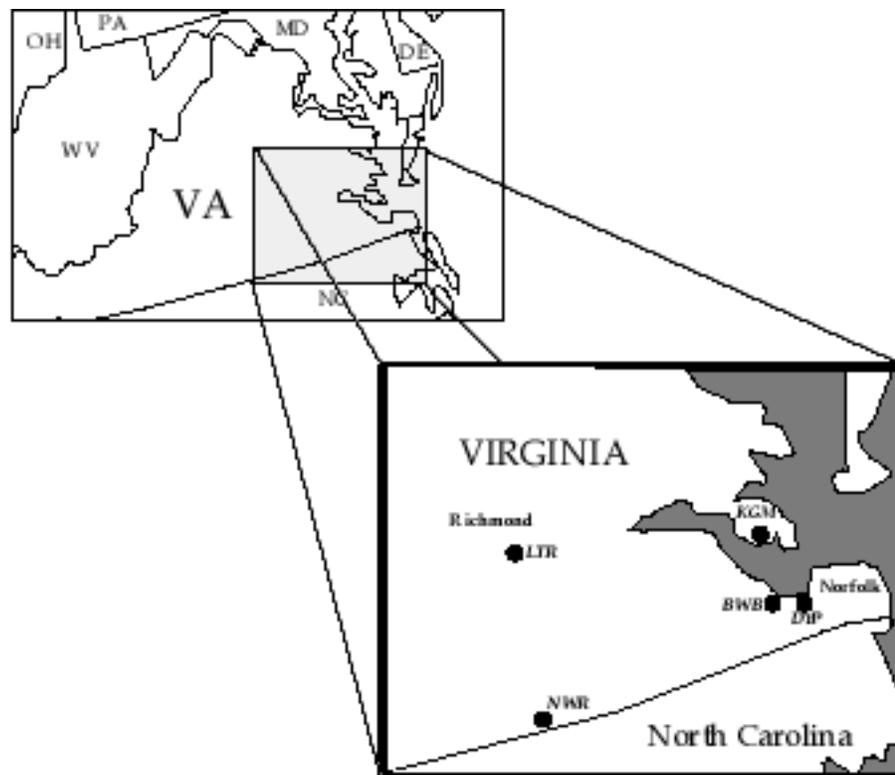
**Figure 2.1.**  
**The Atlantic Coastal Plain embayments**

Map of the major structural arches and embayments of the Atlantic Coastal Plain, with the study area of the present study. Modified from Ward and Strickland (1985).



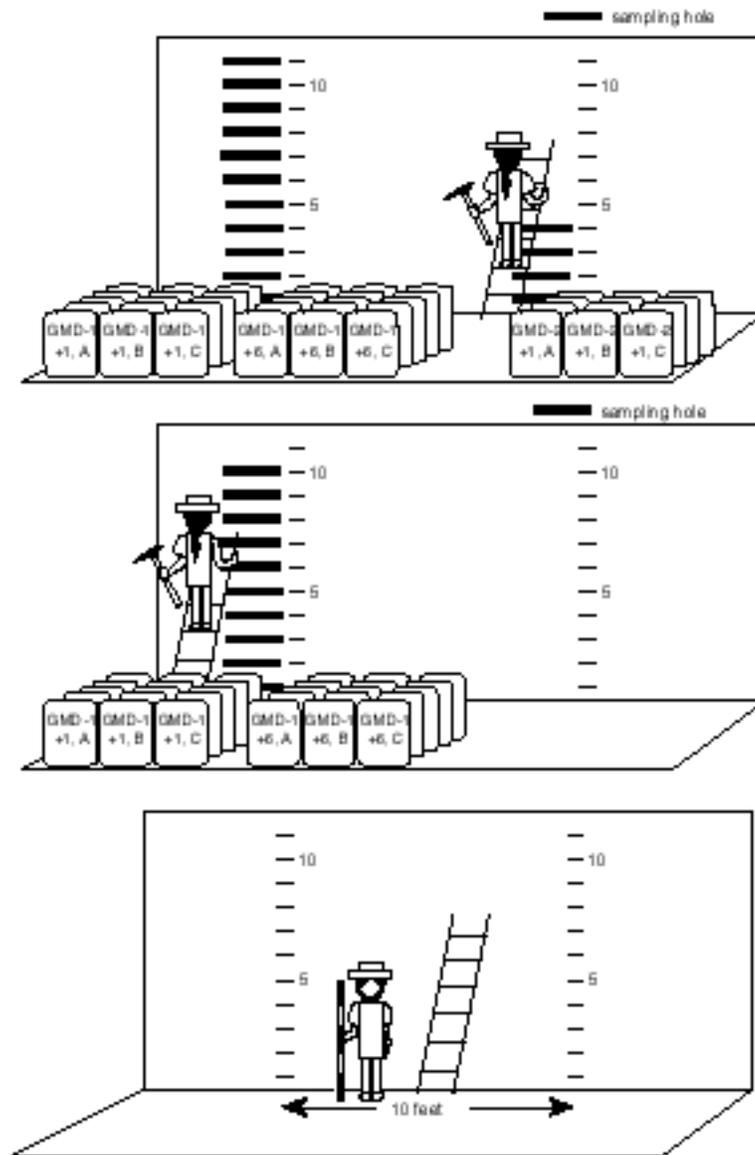
**Figure 2.2**  
**Members of the Yorktown Formation**

Members of the Yorktown Formation.



**Figure 2.3**  
**Map of Yorktown Localities**

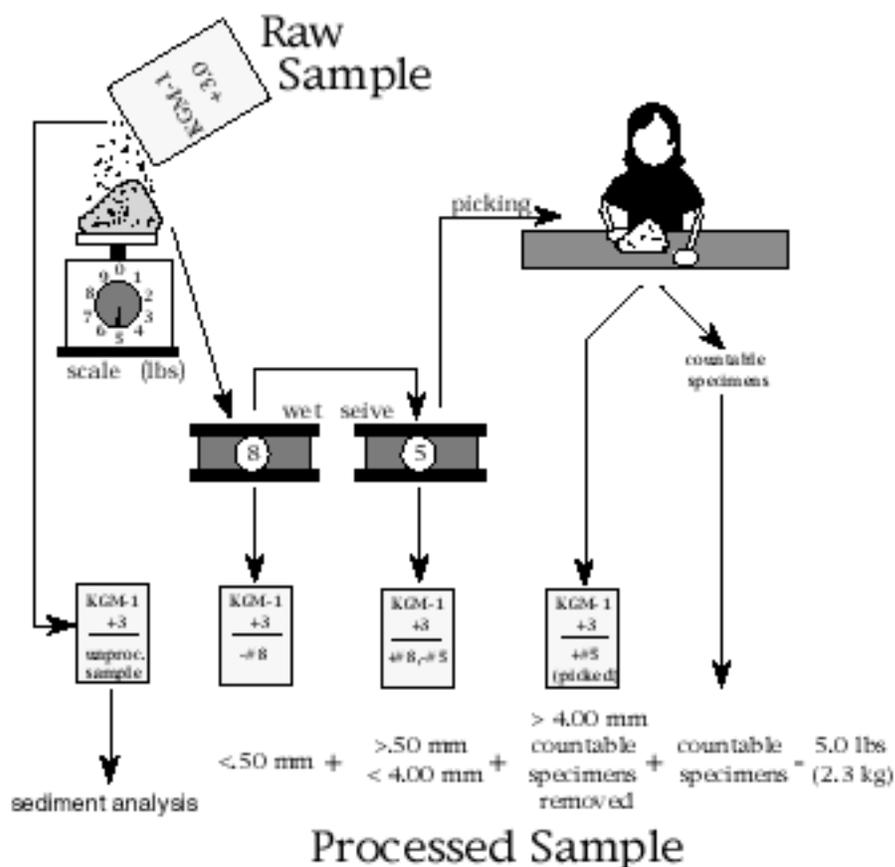
Map showing geographic position of sampling localities for this study.



**Figure 2.4**  
**Sampling procedure**

Diagram showing sampling procedure used in this study. Sections were marked off in one foot intervals, and bulk samples taken adjacent to each interval.

# Sample Processing Procedure



**Figure 2.5**  
**Procedure for processing samples**

Procedure for processing samples.

## CHAPTER 3: SPECIES ACCUMULATION

### Sampling for Completeness

The issue of sampling must be addressed before any meaningful interpretation of the results of the paleocommunity analyses can be made. Without adequate sampling, any observed differences in species abundance and membership between the samples could simply be the result of sampling different segments of the same underlying distribution, and thus the differences could be completely spurious..

It has been suggested (e.g., CoBabe and Allmon 1994), that highly diverse assemblages, such as the Yorktown Formation, can not be sampled adequately using bulk sampling techniques unless incredibly large samples are collected and processed. Other workers (e.g., Crowell 1988), came to the conclusion that small samples are sufficient for sampling these highly diverse assemblages.

Crowell (1988) analyzed samples from the Morgart's Beach Member at one of my sampling localities (Day's Point) to examine the biases and problems involved in sampling a highly diverse fauna such as that found in Yorktown assemblages. He set up a rectilinear grid along a single large outcrop, and collected 5 stratigraphic horizons in each of 5 stratigraphic sections for a total of 25 samples at that one outcrop. His data set contains 7,130 specimens belonging to 45 species of mollusks.

CoBabe and Allmon (1994) examined the distributions of mollusks in the Gosport Sand (Eocene) of Alabama to determine the effect of sampling on paleoecologic and taphonomic studies. Like the Yorktown Formation, the Gosport Sand contains a highly diverse Cenozoic molluscan fossil assemblage. They collected bulks samples from two localities, with each bulk sample coming from a single excavation at each locality. They report that this hole was approximately .5 x .5 m, and each sample consisted of 3 kg of sediment. At one site, they collected 4 bulk samples. At the other they collected 7 bulk samples, for a total of 11 samples. The CoBabe and Allmon data set contained 13,763 individual specimens belonging to 104 species of mollusks.

Since the purpose of this study is to analyze Yorktown molluscan paleocommunities, the sampling scheme must adequately sample the relative abundances of the various abundant and frequently recurring mollusks within each paleoenvironment. To determine if this was the case

with the sampling scheme employed, a species accumulation analysis was performed on both my data, and for comparison's sake, the data of Crowell (1988) and CoBabe and Allmon (1994).

## Analysis

A species accumulation analysis was performed on the first set of samples I collected during the initial survey of the collection area. This subset contains samples from Day's Point, Lieutenant's Run, Burwell Bay, and Kingsmill, but not from the Nottoway River. Also, since the data were collected as part of an initial survey, single samples were collected from each stratigraphic horizon, instead of the triplicate samples taken in the subsequent sampling effort. This initial data set contained 58 samples, from which nearly 14,000 specimens belonging to 110 species of bivalves and gastropods were recovered in the 4 mm and greater size class of the sediment.

Species accumulation curves were constructed by iteratively adding each of the 58 samples together, and then plotting the total number of species recovered versus the total number of specimens counted. The samples were sorted by diversity, and then two species accumulation curves were constructed (Fig. 3.1). For the first curve, the most diverse sample was added to the second most diverse sample, and then all other samples added in order of decreasing diversity, with the total diversity and running sum of the number of specimens tabulated at each step. For the other curve, the order was reversed. These two curves should approximate the best and worst case scenarios for rapid accumulation of diversity.

Half of all of species recognized are found in the first 2,000 specimens counted for both curves. The curves show an initial rapid increase in diversity, and then a leveling off at approximately 5,000 specimens counted. The rate of species accumulation decreases gradually over the next 9,000 specimens counted. The curves have a similar shape, although the rate of species accumulation is lower when lower diversity samples are added together first. However, in the lower curve, by the time 10,000 specimens have been counted, even adding the most diverse samples does not cause an increase in the rate of new species accumulation.

While the rate of new species accumulation is very low after 10,000 specimens have been counted, it is still possible that the new species encountered are very important for paleocommunity analysis. The total abundance of each species was plotted at the point along the running sum at which it was first encountered in both species accumulation analyses above (Fig. 3.2). Since the

linear scale obscured the pattern of occurrence for less abundant species, the abundance data were plotted on a log scale.

The three very common species (>1000 total specimens) were all recovered before 2,000 specimens had been counted, no matter which way the species accumulation was tabulated, and all but one very common species was recovered in the first sample of both analyses. The common species (100-1000 specimens) were all recovered before 4,000 specimens had been counted. All but one species were recovered before 2,000 specimens were counted. Even the uncommon species (10-100 specimens) were recovered before 8,000 specimens were counted. When only the top curve (filled circles) was considered, all uncommon species were recovered before 5,000 counted, and all but one species were recovered by the time 5,000 specimens were tabulated for both analyses. Once 5,000-8,000 specimens had been counted, only rare species (1-10 specimens) were recovered. The sampling scheme therefore was sufficient to recover all but the rarest species.

The initial data set was broken down to determine whether or not the sampling scheme had sufficiently sampled the diversity present in these subsets. The unconformity-bounded Rushmere-to-Morgart's Beach sequence contains at least three major paleoenvironments (see chapter 5):

1. The Rubbly Bottom Paleocommunity Type (RBPT), composed of sandy to rubbly lower portion of the Rushmere, which contains the *Chama congregata* as its dominant faunal element.
2. The transition zone, composed of silty sands forming a transition from the lower Rushmere to the Morgart's Beach. While there is no hyper-dominant faunal element in this transition, oysters of various species are frequently the most abundant faunal elements
3. The Muddy Bottom Paleocommunity Type (MBPT), composed of sandy silts and clays of the Morgart's Beach Member, which contains *Mulinia congesta* as its dominant faunal element.

For a discussion of how these paleoenvironments, and their contained paleocommunity types are classified, see chapter 5.

Species accumulation curves were generated for each of these three paleoenvironments (Fig. 3.3). For the *Mulinia* dominated paleoenvironment, the curve leveled out by the time 2,000 specimens had been tabulated, while the "oyster" dominated and *Chama* dominated curves level out

at approximately 1,000 specimens counted. When plotted on the same axes, all three curves have a similar shape, although the *Mulinia* group contained many more samples.

Because the total specimen count was so much lower in these subsets, instead of graphing the total abundance of each species at the point where it is first recovered in the species accumulation analysis, the number of occurrences (total number of samples in which that species occurs) were plotted (Fig. 3.4). For the *C. congregata* dominated, Lower Rushmere samples, once half the specimens (1,500) had been counted, no new species was found in more than two of the remaining 7 samples. For the *Mulinia* dominated Morgart's Beach samples, once 25% of the specimens had been tabulated (2,000 specimens), no new species occurred in more than 5 of the remaining 29 samples. In the transitional "oyster" dominated paleoenvironment, which frequently contained elements of both of the other paleoenvironments, no new species occurred in more than 2 of the remaining 8 samples once 850 specimens had been counted. The sampling scheme therefore seems to be sufficient for recovering all but the most infrequently occurring species within each paleoenvironment, and the common and very common species are found early and often.

Because it was the largest subset of the initial data set, the *Mulinia* dominated Morgart's Beach Member paleoenvironment was further subdivided for analysis. In the initial data set this paleoenvironment was collected at four localities, and species accumulation analysis was run for each of these locality subsets of this paleoenvironment (Fig. 3.5). While the number of samples and specimens is small, each of the localities shows the familiar initial rapid increase in diversity with the rate of new species accumulation leveling off after a relatively small number of specimens had been tabulated (400 for Burwell Bay, 600 for Day's Point, 400 for Kingsmill, 1000 for Lt.'s Run). An analysis of species abundances or occurrences at first appearance was not feasible for these small groupings of samples, although the very common species are all found in most samples, and therefore are recovered early.

The total diversity recovered from the *Mulinia* dominated assemblage at any one locality was lower than the total diversity recovered from all *Mulinia* dominated assemblages. When all samples are combined, the diversity curve levels out near a diversity of 90 species, while at the individual locality, that value varies from approximately 30 species (Burwell Bay), to 60 species (Kingsmill), to 70 species (Day's Point and Lt.'s Run). The very low abundance of specimens present in samples from taken from Burwell Bay (less than 1000 specimens from 5 samples) could account for that low value, but the Kingsmill and Day's Point localities have comparable numbers of specimens, even with their very different diversities. This issue will be addressed in more detail

in later chapters, but it is clear that this paleocommunity type as expressed at different localities differs in species diversity, and therefore also differ in species membership. Collecting bulk samples at a single locality is therefore an inefficient mechanism for collecting a large percentage of the diversity present in any deposit. If the purpose of the study is to maximize the diversity sampled, the formation or member should be sampled at as many different localities as possible.

Based on the initial, small data set, the sampling scheme was sufficient for complete sampling of the very common and common species at every level of resolution tested. Based on the species accumulation curves, I predicted that as long as I resampled the same stratigraphic horizons at the same localities, only rare species would be added to the total, a prediction that turned out to be correct when the same analysis was run on the entire data set. The addition of 15,000 new specimens, including several thousand from a new sampling locality (the Nottoway River), yielded 22 new species, all of which were present at very low abundances (each <10 specimens) and found in only a few samples.

A species accumulation analysis was performed on the entire data set (Fig 3.6). As before, there is a rapid initial increase in total diversity, which levels out after approximately 5,000 specimens have been counted. Diversity increases much more slowly after 15,000 specimens had been tabulated. This is consistent with the species accumulation analysis of the initial survey samples above.

The rate of new species accumulation drops off rather rapidly after 100 species have been recovered (approx. 10,000 specimens tabulated). The rate of species accumulation was calculated for the data points by taking a simple least square regression of the section of the curve in question. After 100 species had been recovered, the rate of new species accumulation was 1 new species per 1099 specimens. The rate after 110 species were recovered was 1 new species per 1408 specimens counted, and by the time 125 species had been recovered, 3125 additional specimens were required to recover a new species. However, as long as samples were added, new species continued to be found.

The rate of new species accumulation was determined by calculating the slope of the line for the data points in each of 30 segments of 1000 accumulated specimens using least square regression (Fig. 3.7A). After an initial very high rate of species accumulation in the first several thousand specimens counted, the rate drops to near zero, and in fact is zero for several segments past 15,000 specimens counted. The inverse of this slope was also determined for each segment (Fig. 3.7B). For segments with a slope of zero, the inverse of the slope was undetermined, and

thus there are fewer data points than in the first analysis, and overall, the derived rate of species accumulation is an overestimation of the true rate for these segments of the curve. Even so, the remaining data points show a linear rise in the number of specimens needed to recover a new species.

The total abundance of each species was plotted at the point along the running sum at which it was first encountered in the species accumulation analyses (Fig. 3.8). The data were plotted on both a linear (Fig. 3.8A) and semi-log scale (Fig. 3.8B), but the linear scale obscures the pattern of occurrence for less abundant species. All of the very common species (>1000 total specimens, 5 species) were found in the first few samples added in each analysis. All but three of the common species (100-1000 total specimens, 26 species) were recovered by the time 2,000 specimens have been counted, and all were found by the time 8,000 specimens had been counted. The uncommon species (10-100 specimens, 45 species) were all accounted for by the time 13,000 specimens have been tabulated, and after 13,000 specimens, only the rare species (1-10 specimens, 57 species) are found, thus once 13,000 specimens are accumulated, the new species encountered have very low abundances.

Even though species continued to be recovered as long as samples were added in all four studies, the relative abundances of the new species was very low. Over 735 pounds (334 kg) of sediment were processed to recover the 54 rare species I found, whereas all of the common and very common species were recovered by the time 100 pounds of sediment were processed. Species would be expected to be recovered as long as samples were taken, as the sampling recovers more and more rare species, and delves into new sub-environments. Taken to its absurd conclusion, all species present in the Yorktown Formation, or any other unit, could only be recovered if the entire formation was excavated and processed.

Species accumulation analyses were performed for two other Cenozoic molluscan data sets. An analysis of CoBabe and Allmon's (1994) compilation of mollusks from the Gosport Sand of Alabama (Fig. 3.9) has the same pattern of species accumulation seen in my data, and initial rapid increase in diversity, followed by a leveling off of the rate of species accumulation. Crowell's (1988) mollusks of the Morgart's Beach Member of the Yorktown Formation of Virginia (Fig. 3.10) show the same pattern. In CoBabe and Allmon's data, half of all species identified are found by the time 2,000 specimens have been counted, and the most diverse sample contains more than half of all species identified (67 of a total 104 species). Half of Crowell's species are found after counting 1,000 specimens, and once again, the most diverse sample contains more than half of the total number of species (25 out of a total 45 species).

These two data sets contained fewer specimens than my data set, but even with fewer specimens, the species accumulation curves flattened out before the last sample is added. The plot of the total abundances of each species at its point of first appearance in the species accumulation analyses for these data sets (Fig. 3.11 for CoBabe and Allmon's data, 3.12 for Crowell's data) shows the same pattern seen in my data - all common species were found within the first few thousand specimens tabulated, and once the flat portion of the curve was reached, all new species were uncommon or rare. No common or very common species were found once the rate of species accumulation had fallen off.

The total abundance of common and very common species is more than an order of magnitude greater than the abundance of the uncommon and rare species combined for all three data sets. For my study, the 27 common species account for 30.0% of the total abundance, with 5 very common species accounting for 64.3%, for a total of 94.3% of the total abundance of the localities sampled. The 47 uncommon species and 54 rare species account for 5.1% and 0.6% of the total abundance, for a grand total of 5.7% of the total abundance. CoBabe and Allmon's study had very similar results: the 32 common and 9 very common species account for a total of 95.2% of the total abundance, while the 22 rare and 41 uncommon species account for a measly 4.8% of the total abundance. Crowell's data yielded 12 common and 4 very common species which accounted for 98.0% of the total abundance, while the 16 rare and 15 uncommon species totaled a meager 2.0%. The uncommon species are therefore rather trivial in importance when total abundances are considered, and the rare species are incredibly trivial when viewed in terms of total abundances. The rare and uncommon species are too rare and uncommon to be treated quantitatively.

## Discussion

Crowell's (1988) study yielded 7,231 individual bivalve valves, gastropod shells, and scaphopod shells belonging to 48 species. Using ANOVA and MANOVA, he determined that the relative abundance of species within samples from a single stratigraphic horizon are not significantly different from each other, as long as the lateral extent of the stratigraphic horizon in question is not large. However, Crowell includes the strong warning that accurate census data can only be obtained if the sampling horizon has good time constraint. Like other workers, Crowell (1988) found that most species in his assemblages were rare, and that rare species are rare in all assemblages of the same stratigraphic horizon.

Of the 483 species known from the Gosport Sand, CoBabe and Allmon (1994) recovered 104 species (22%) in 13,946 specimens recovered from their 11 samples. Of the 400-500 species of mollusks known from the Rushmere and Morgart's Beach Members, only 125 have been recovered with my samples (25-30%), so CoBabe and Allmon's percentage is not as low as it would at first appear. Most species are rare. Of the 125 species of mollusks recovered in this study, 66 (53%) occur in 10 or fewer samples, and only 19 species (15%) occur in more than half of the samples.

Koch (1987) found that the distribution of species-occurrence frequencies in many fossil assemblages approximates a log series distribution, just as in many modern ecological distributions (e.g., Williams 1964). Based on that distribution, he determined that if a large paleontological data set was re-sampled from the same underlying distribution (e.g. if another set of samples were taken from the same localities in exactly the same fashion), then up to 25% of the species found in the first data set would be absent from the second. If the samples were not equal in size, the difference could be greater than 70%, as more rare species are found in the larger sample simply by chance. These discrepancies occur because most species are found infrequently, i.e. most species found in any assemblage are rare. In a study that based on presence/absence data, this effect can be extreme. However, when relative abundance, rather than simple occurrence, is examined, these rare species have much less effect on the analysis.

Based on the species accumulation analysis, additional sampling of the Gosport Sand at CoBabe and Allmon's two localities would yield new species at a very low rate. According to CoBabe and Allmon, application of the log series analysis proposed by Koch (1987) indicates that for another 11 samples of the same size, they could expect to recover between 7-27% of the species recovered in the original 11 samples. However, all of the missing species should be rare.

CoBabe and Allmon also reported that samples taken at a single locality do not have the same species diversities or relative abundances, and thus individual samples of this size appear to be inadequate for sampling the diversity of the Gosport Sand at any one locality. However, some species did occur in most samples with consistent relative abundances, while others with moderate frequencies had more variable abundances. Specifically, the 24 species that occur in 9 or more of the 11 samples show consistent patterns of occurrence. The 17 species found in 6-9 samples show consistent patterns when 7 or more samples are examined (i.e., 7 replicate samples of the same sample size per horizon). The remaining 62 species can not be sampled with any reasonable sampling scheme.

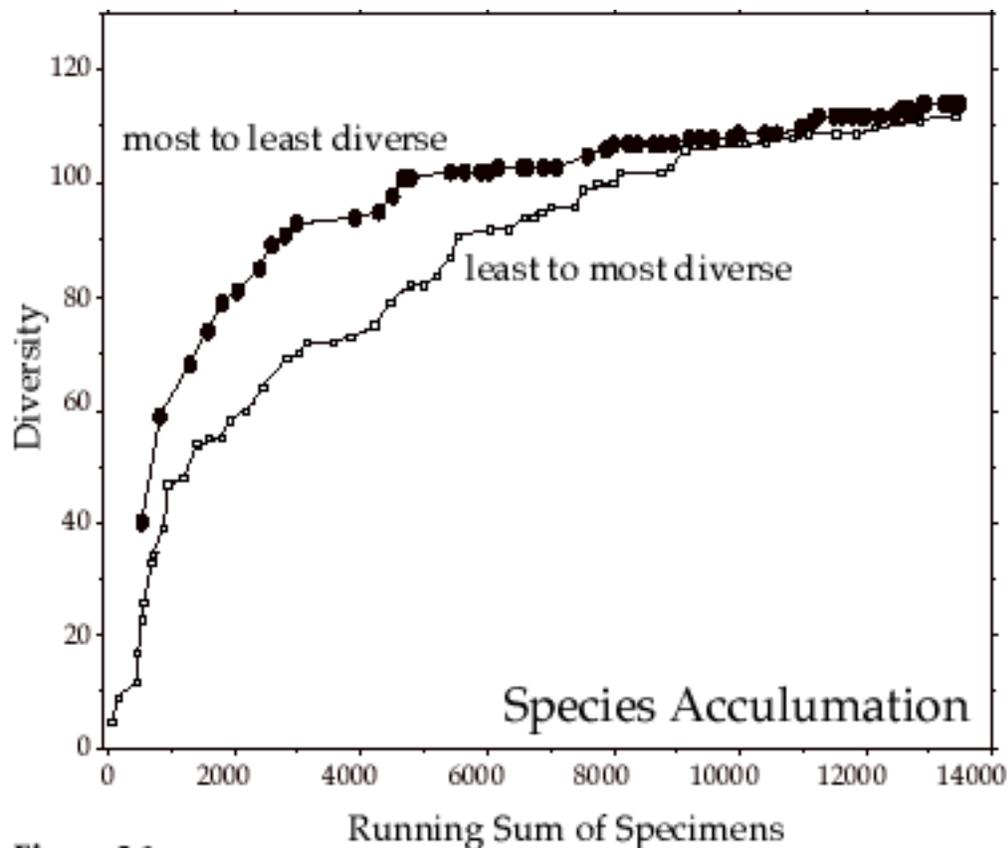
Both their reported results and the results of my re-analysis of their data indicates that the sampling scheme employed by CoBabe and Allmon was sufficient to sample the very common and common faunal elements of the Gosport Sand at the localities sampled. Only uncommon or rare species were found after a few thousand specimens had been tabulated. Thus, despite their statements to the contrary, they had probably adequately sampled the Gosport Sand for paleocommunity analysis. If they were concerned with the stratigraphic and paleoenvironmental ranges of all species, regardless of abundance, then their sampling scheme failed, but as long as the research question can be answered by using relative abundances of species (e.g., the paleocommunity analysis presented in this study), then their sampling scheme was sufficient.

Buzas and Gibson (1990) exploited a rare opportunity to examine the spatial distribution of forams when they collected samples from an excavation dug in the Calvert and Choptank Formations (Miocene) during construction of a nuclear power plant. They took a series of random samples from two stratigraphic horizons with areas of 400 m<sup>2</sup> and 50 m<sup>2</sup>, respectively. They found that the distribution of individual species in single beds was rather homogeneous, with only a few of the common species in each examined bed showing significant patchiness. When all species are examined together, the multispecies distribution in both beds is heterogeneous. However, removal of either the rare species or the few heterogeneous species results in a determination that the remaining species assemblage is homogenous. Buzas and Gibson also included these important observations about their data:

1. The most dominant 2-4 species at each stratigraphic level are always dominant in every sample taken from that level, although not always in the same rank order.
2. Moderately frequent species (3-10% of total abundance) are also consistent in their occurrence within each stratigraphic horizons.
3. Rare species (<3% of total abundance) are always found at low abundance where they are found at all.
4. Diversity present in each sample varies greatly. While samples containing more specimens tend to have higher diversities, even with equal sample sizes, diversity can vary by as much as 50% because of random additions of some rare species.

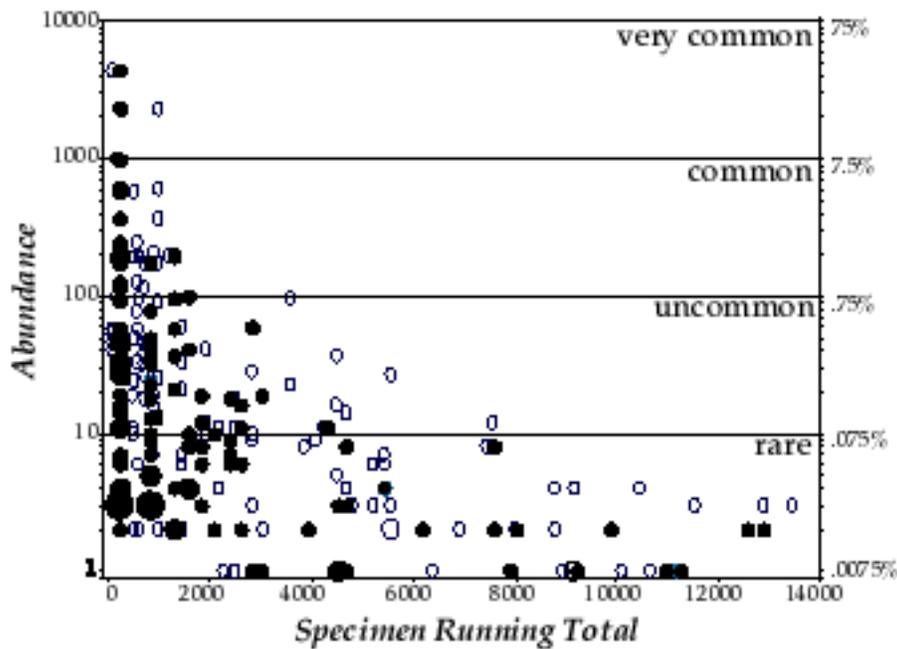
CoBabe and Allmon (1994) and Buzas and Gibson (1990) reported similar results, although they drew very different conclusions. Both studies found that the most common species occurred with consistent frequencies in all samples, moderately common species had somewhat more variable occurrence frequencies, and rare species had chance occurrences. It is unfortunate that CoBabe and Allmon did not compare their results to Buzas and Gibson's analysis.

The results of the analysis suggest that my sampling scheme has adequately sampled the common and very common species present in the Rushmere and Morgart's Beach Members of the Yorktown Formation at the collection localities for paleocommunity analysis. As with the other data sets analyzed, only the uncommon and rare species were not adequately sampled with my sampling scheme, and the rare species probably could never be sampled with any reasonable sampling scheme. However, since the paleocommunity analyses involve the relative abundance of the various species, rather than their simple presence or absence, the common and very common species will be much more heavily weighted in these analyses. Since these species are well sampled, sampling completeness should not be a major concern.



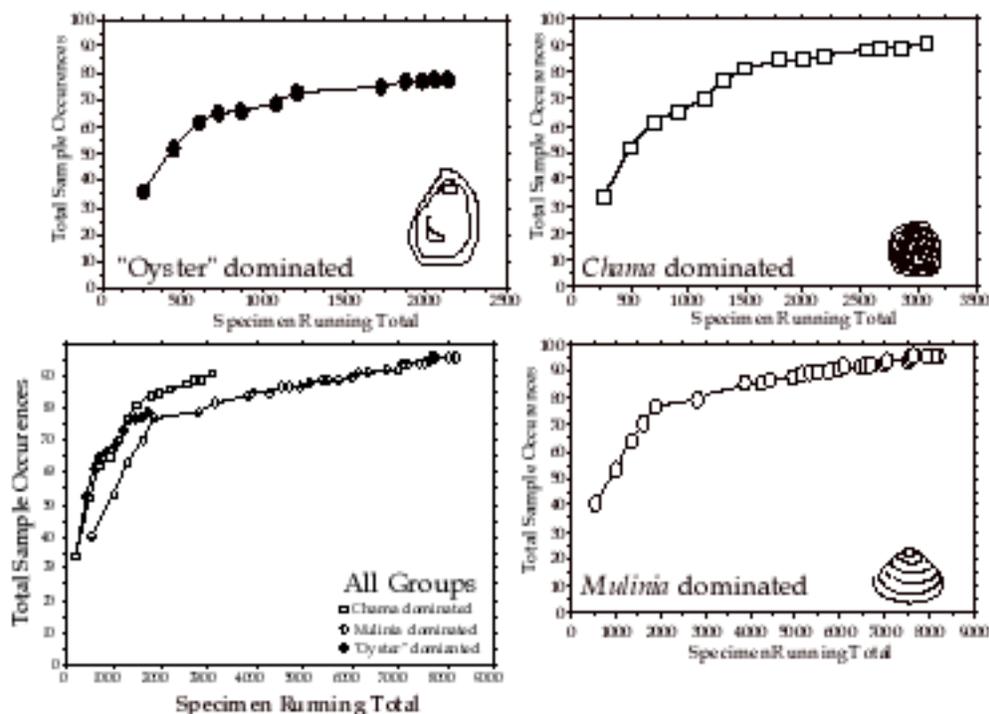
**Figure 3.1.**  
**Species accumulation curve for initial sampling effort**

The two curves were constructed by iteratively adding samples together, and accumulating both diversity (species present) and specimens counted. For the top curve, samples were added together in order of decreasing richness (species/sample). For the bottom curve, samples were added together in order of increasing species richness.



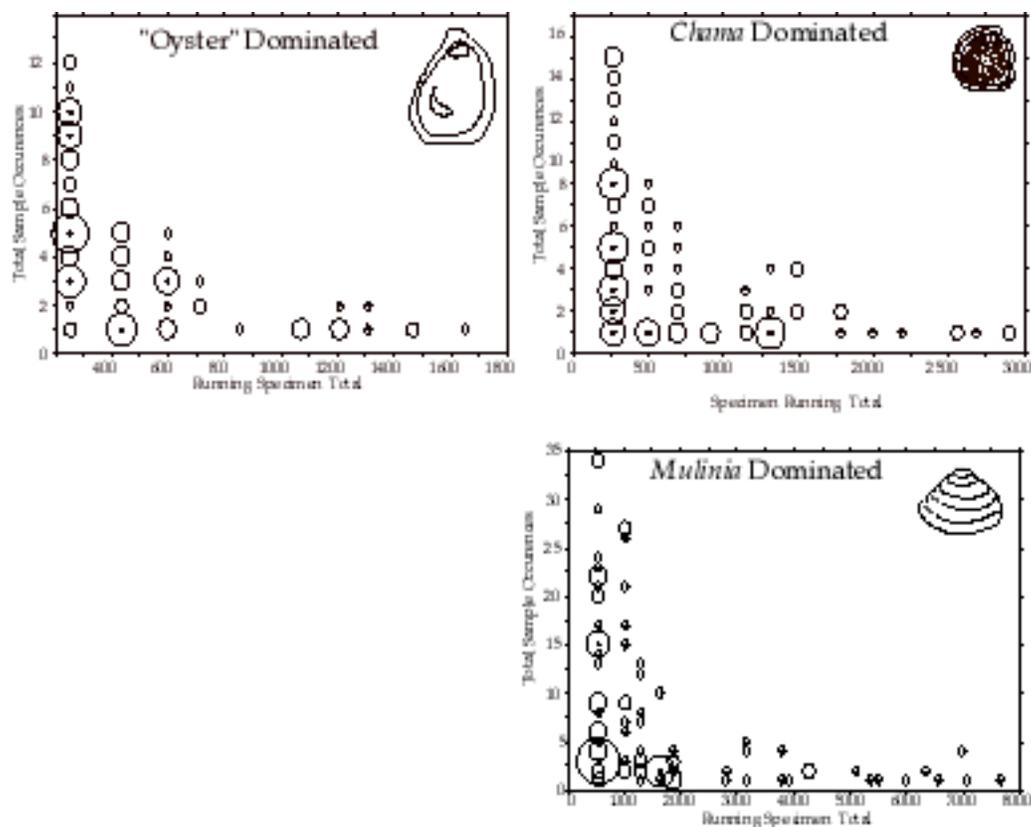
**Figure 3.2**  
**Occurrence frequency versus point of first appearance**

Plot of total number of specimens for each species plotted at the point in the species accumulation analysis at which it first appears. Larger points indicate that more than one species plots at those coordinates in space.



**Figure 3.3**  
**Species accumulation curve for each subenvironment**

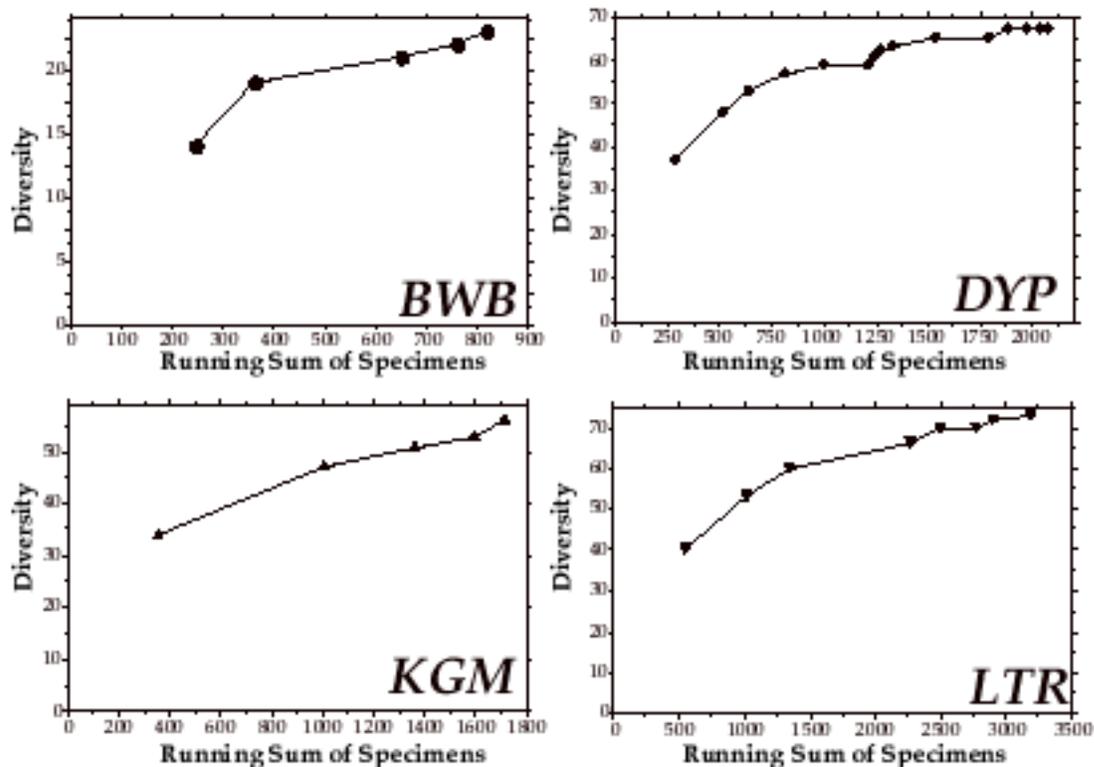
Each set of two curves was constructed by iteratively adding samples together, and accumulating both diversity (species present) and specimens counted. For the top curve, samples were added together in order of decreasing richness (species/sample). For the bottom curve, samples were added together in order of increasing species richness.



**Figure 3.4**  
**Occurrence frequency versus point of first appearance**

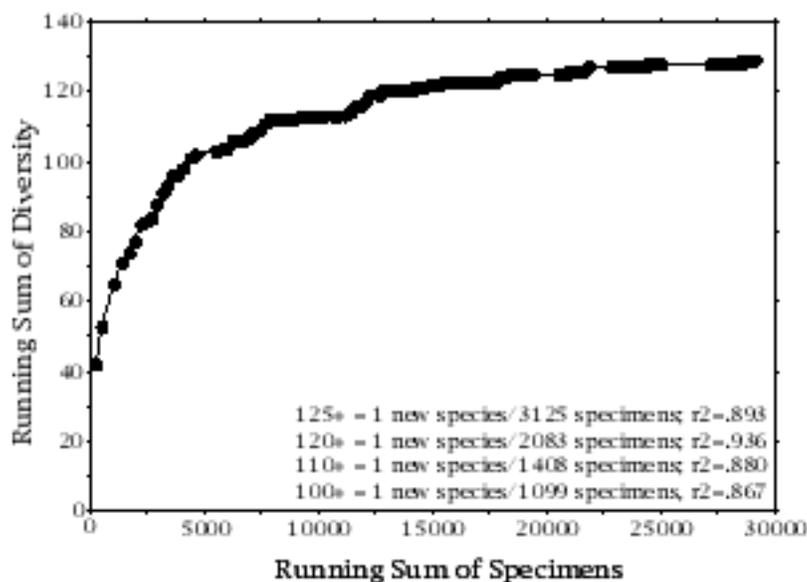
Plot of total number of samples in which a species occurs plotted at the point in the species accumulation analysis at which it first appears, for the three subenvironments. Larger points indicate that more than one species plots at those coordinates in space.

## *Mulinia* Dominated



**Figure 3.5**  
**Species accumulation curve for initial *Mulinia* dominated samples at each locality**

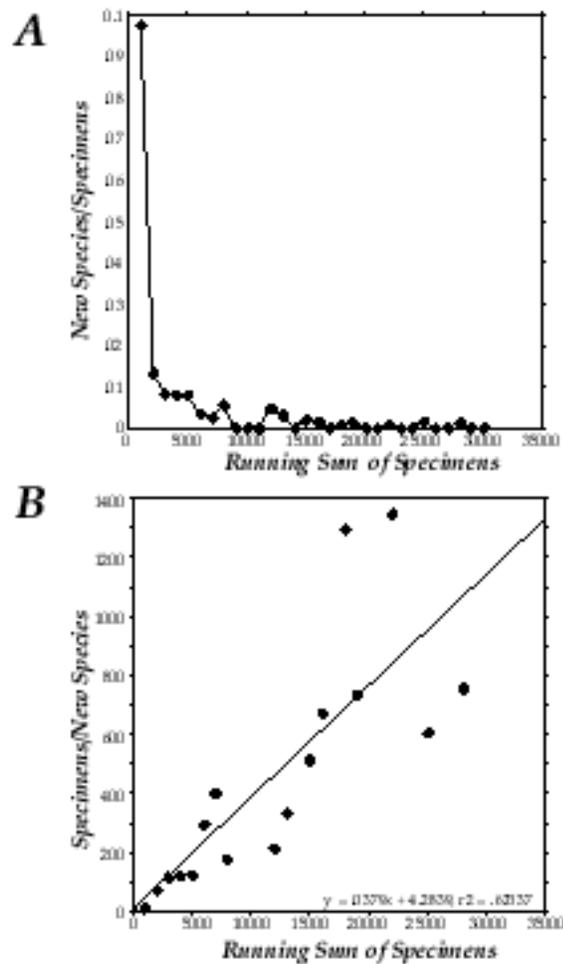
Each curve was constructed by iteratively adding samples together, and accumulating both diversity (species present) and specimens counted.



**Figure 3.6**  
**Species accumulation curve for entire data set**

The two curves were constructed by iteratively adding samples together, and accumulating both diversity (species present) and specimens counted. For the top curve, samples were added together in order of decreasing richness (species/sample). For the bottom curve, samples were added together in order of increasing species richness.

### Rate of New Species Accumulation

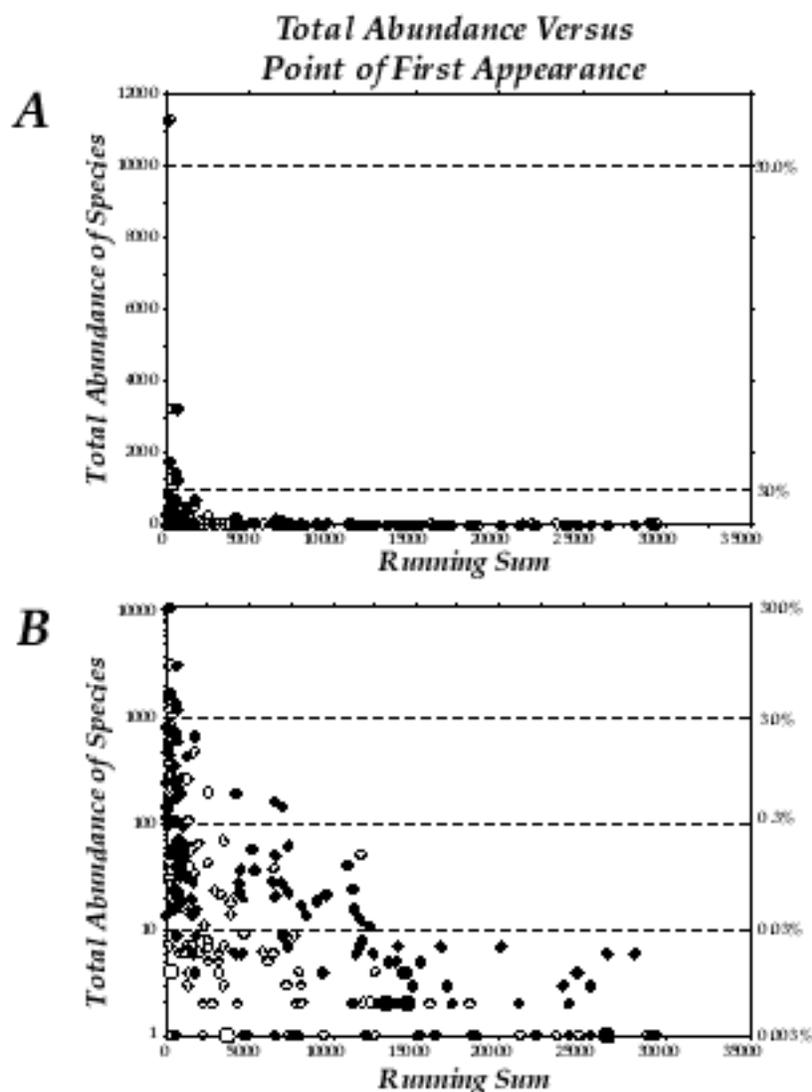


**Figure 3.7**

**Rate of new species accumulation versus running sum of specimens from species accumulation analysis**

A: Bivariate scatter plot of the slope tangential to curve for each 1,000 specimen segment along species accumulation curve. Regression line determined by least square regression analysis.

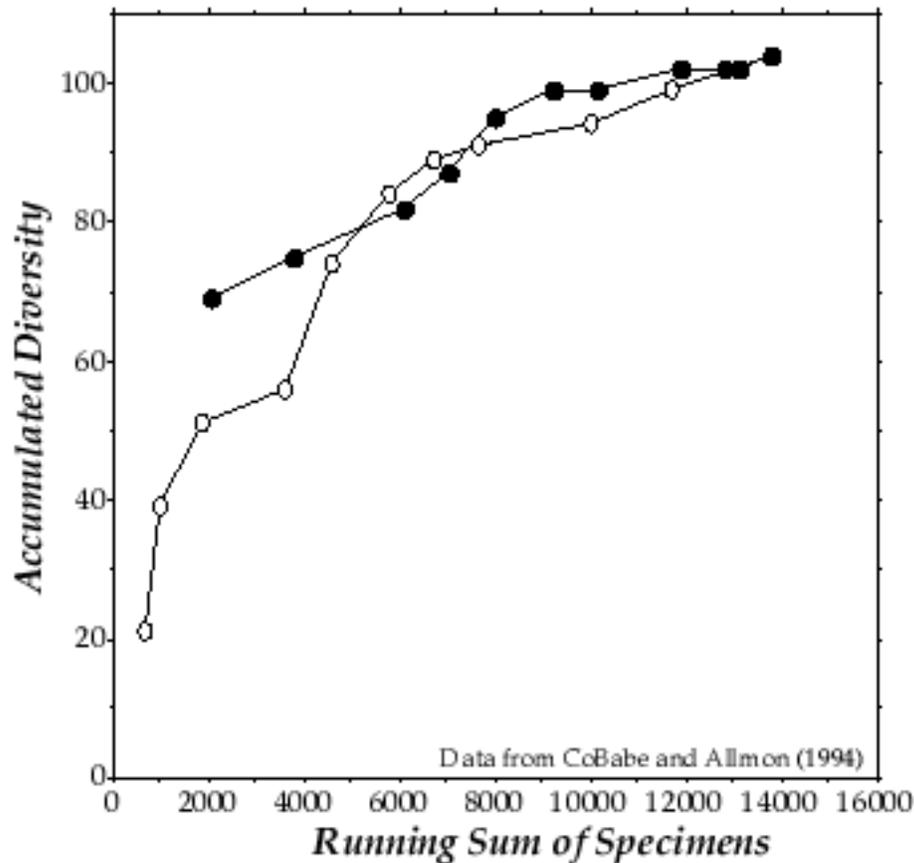
B: Bivariate scatter plot of the inverse of slope tangential to curve for each 1,000 specimen segment along species accumulation curve. Slope is undefined for segments with a slope of zero. Regression line determined by least square regression analysis.



**Figure 3.8**  
Occurrence frequency versus point of first appearance

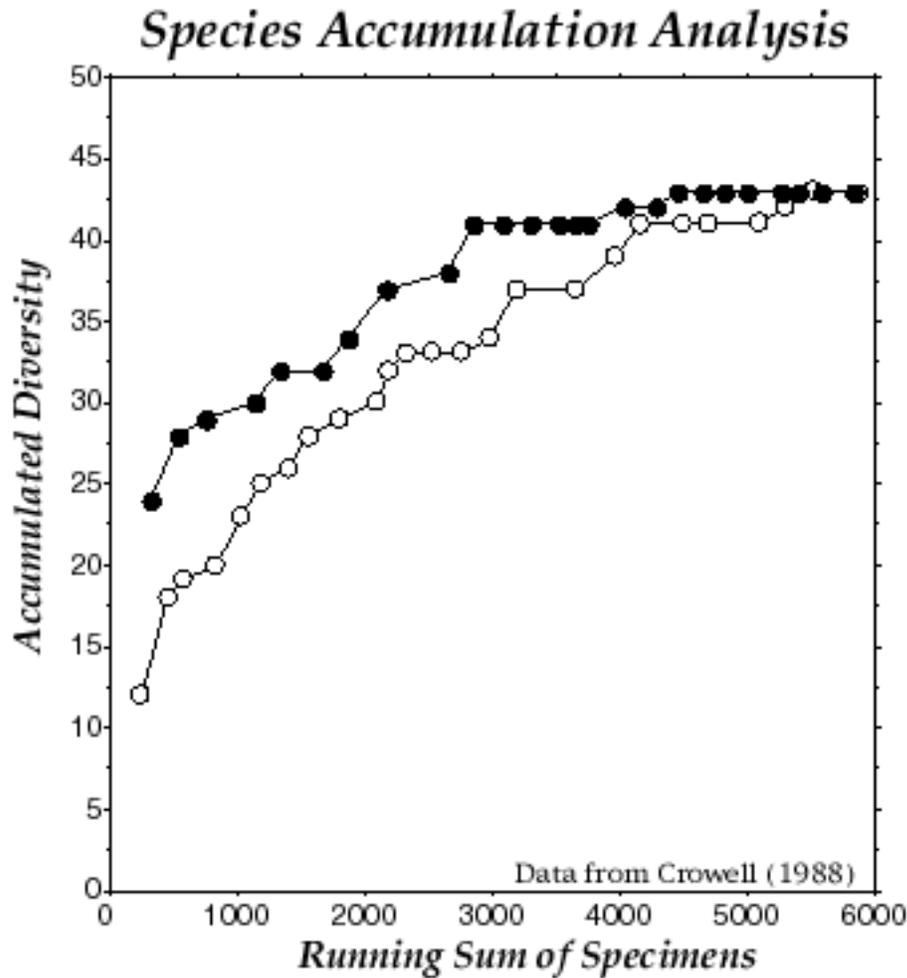
Plot of total number of specimens for each species plotted at the point in the species accumulation analysis at which it first appears. Larger points indicate that more than one species plots at those coordinates in space. (A) is plotted on a linear scale while (B) is plotted on a semi-log scale.

### Species Accumulation Analysis



**Figure 3.9**  
**Species accumulation curve for data from CoBabe and Allmon (1994)**

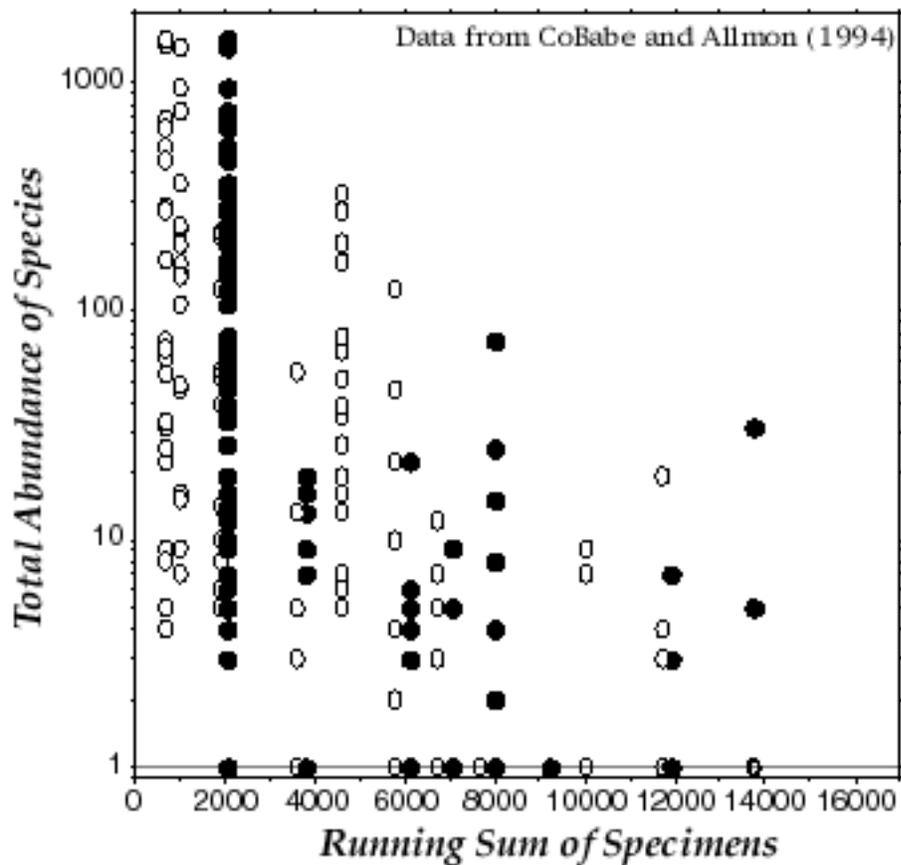
The two curves were constructed by iteratively adding samples together, and accumulating both diversity (species present) and specimens counted. For the top curve (closed circles), samples were added together in order of decreasing richness (species/sample). For the bottom curve (open circles), samples were added together in order of increasing species richness.



**Figure 3.10**  
**Species accumulation curve for data from Crowell (1988)**

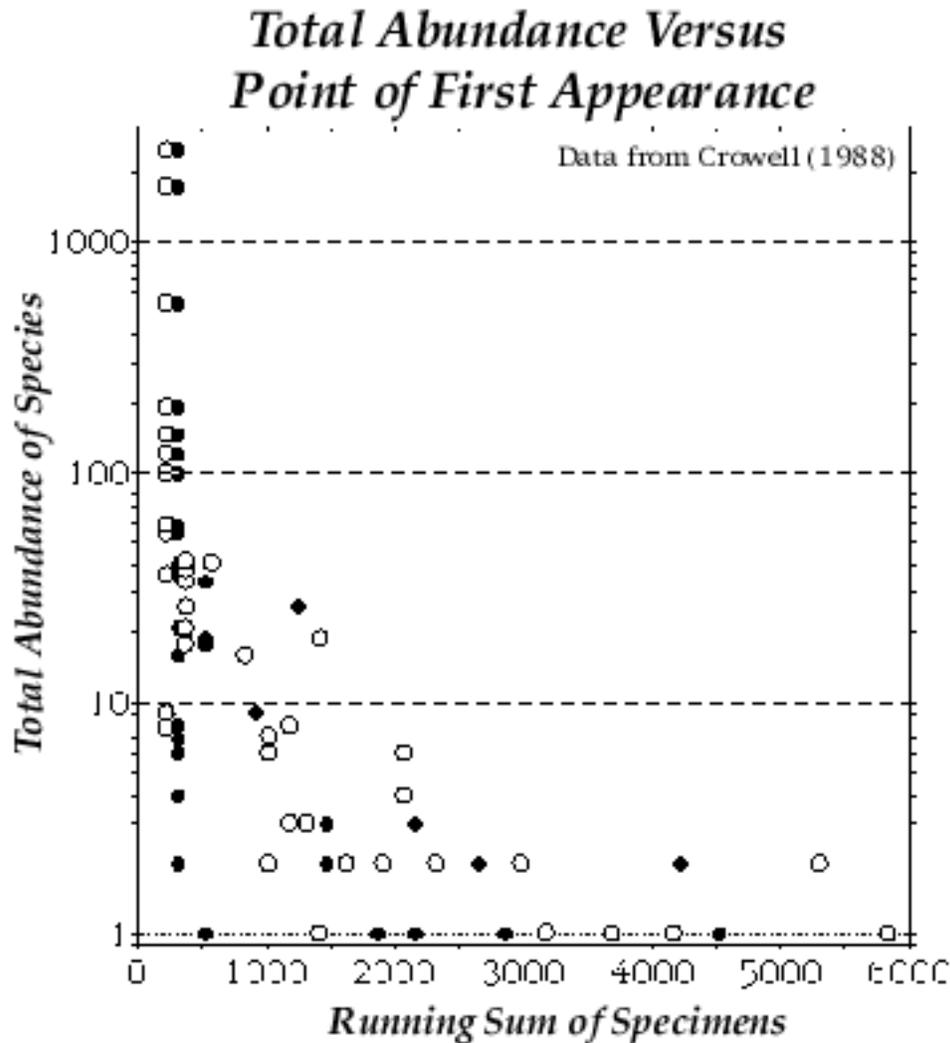
The two curves were constructed by iteratively adding samples together, and accumulating both diversity (species present) and specimens counted. For the top curve (filled circles), samples were added together in order of decreasing richness (species/sample). For the bottom curve (open circles), samples were added together in order of increasing species richness.

## *Total Abundance Versus Point of First Appearance*



**Figure 3.11**  
**Total abundance at point of first appearance**

Plot of total number of specimens for each species plotted at the point in the species accumulation analysis at which it first appears. Larger points indicate that more than one species plots at those coordinates in space. Filled circles are for species accumulation analysis with samples added from most to least diverse; empty circles are for species accumulation analysis with samples added from least to most diverse.



**Figure 3.12**  
**Total abundance at point of first appearance**

Plot of total number of specimens for each species plotted at the point in the species accumulation analysis at which it first appears, data from Crowell (1988). Larger points indicate that more than one species plots at those coordinates in space. Filled circles are for species accumulation analysis with samples added from most to least diverse; empty circles are for species accumulation analysis with samples added from least to most diverse.

## CHAPTER 4: DIVERSITY OF YORKTOWN FOSSIL ASSEMBLAGES

### Diversity

At first glance, measuring the diversity present in a paleocommunity seems a simple task: count up the number of species present in a sample then compare that value to those obtained from other samples. However, as Magurran (1988) aptly pointed out:

Diversity may appear to be a straight forward concept which can be quickly and painlessly measured. This is because most people have a ready intuitive grasp of what is meant by diversity and have little difficulty in accepting, say, that tropical rain forests are more diverse than temperate woodlands or that there is a high diversity of organisms in coral reefs. Yet diversity is rather like an optical illusion. The more it is looked at, the less clearly defined it appears to be and viewing it from different angles can lead to different perceptions of what is involved. (Magurran 1988, pg. 1)

Determining diversity is complicated by the inherent variability in the natural world, and exacerbated by the plethora of metrics that ecologists have used to describe diversity (Magurran 1988, Stiling 1999).

As noted in the chapter on species accumulation and in such studies as Buzas and Gibson (1990) the inclusion of rare species can increase the species richness value up to 50%. To avoid this problem, a measure of diversity should also include some sort of weighting of the more abundant species in order to more consistently measure the diversity present.

Diversity consists of several components, two of the most important of which are the number of different taxa and the relative abundance of each taxon. Any measurement that incorporates only one of these components must be used with caution and there are a very large number of ways to combine these elements to determine aspects of diversity. If the entire study area can be completely cataloged, then the number of species present is a true measure of the diversity. However, as complete sampling is impractical in most ecologic studies (Magurran 1988) and impossible in paleoecologic studies (due to non-preservation of some faunal elements), diversity measurements must take sampling problems into account.

In addition to the problems that paleoecologists have in common with ecologists (patchy distribution, small scale variability, etc.), paleoecologists must recognize and deal with the fact that the fossils found together in a fossil assemblage did not necessarily live together at the same time, and thus the diversity measurement could incorporate elements from several living assemblages (organisms that lived in the same place at the same time). Similarly the diversity of fossil assemblages can be affected by the rate of sediment accumulation. Samples from condensed sections potentially incorporate more sub environments, and thus might be expected to have higher diversities than samples from sections with a greater stratigraphic accumulation rate. Many of the ecologic models of diversity are associated with models of ecologic interaction such as the degree of niche partitioning, resource stability, or other controlling factors (e.g. examples in Magurran 1988, Pianka 1988, Ludwig and Reynolds 1988, Stiling 1999). The application of these models to the time-averaged assemblages found in the fossil record is problematic at best.

Magurran (1988) divided diversity measurements into three main categories:

1. **Species richness indices** measure the number of species per standard sampling unit. This category includes both rarefaction analyses, and such simple indices as Margalef's diversity index and Menhinick's index.
2. **Species abundance models** measure diversity in relationship to four main models of species abundance: log normal distribution, logarithmic series, geometric series, and MacArthur's broken stick model.
3. **Proportional abundance indices** incorporate the proportional abundance (usually expressed by some form of  $N_i/N$ , where  $N_i$  = abundance of species "i" and  $N$  = total abundance), and make no assumptions about the underlying distribution of abundances, and are therefor sometimes called "non-parametric" indices (e.g. Shannon index, Simpson dominance index).

No single diversity measurement is appropriate in every situation, and the guidelines for what measures are useful in biological situations are not always helpful for paleocommunity analysis. With all of this in mind, I have taken a "scorched earth" approach to measuring diversity by determining a variety of diversity indices for each sample, and then comparing the results. The main indices that I will use are:

### *Species Richness Indices*

**Margalef's Diversity Index**       $DMg = (S-1)/\ln(N)$

*Log Normal Species Abundance Models*

**William's  $\alpha$**                        $a = N(1-x)/x$

$$S/N = (-\ln(1-x))(1-x)/x$$

*Non-parametric indices*

**Shannon-Weiner Index**     $H' = -[\sum[(p_i)\ln(p_i)]]$

**Pielou's Evenness Index**     $J = H'/\ln(S)$

**Simpson's Dominance Index**     $D = \sum[(N_i(N_i-1)/N(N-1))]$

**Hill's Evenness Index**         $E = [(1/D-1)]/e^{H'-1}$

**Berger-Parker Dominance Index**         $d = N_{\max}/N$

(S = number of species present, N = total number of individuals,  $N_i$  = abundance of the "ith" species,  $p_i = N_i/N$ ,  $N_{\max}$  = abundance of the most abundant species)

For more information about the properties of these indices, see Appendix C.

For this study, I was interested in diversity for two reasons. Firstly, I wanted to determine what the overall diversity pattern was in order to see if it was comparable to other Cenozoic fossil assemblages. Secondly, I wanted to determine whether or not the observed paleoenvironmental trend in the Rushmere-Morgart's Beach transition affected the diversity present in a predictable way. The paleoenvironmental conditions changed from a rubbly to a muddy bottom, and presumably the local environmental conditions became less stable through time because of the inherent instability of the muddier bottom conditions. Theoretically, diversity should be higher under the more stable conditions, and lower under stressed conditions (Ludwig and Reynolds 1988, Stiling 1999) - a prediction that can be tested by comparing diversity present in each of the paleoenvironments.

### **Analysis**

The simplest measure of diversity is species richness, the number of species per unit sample. Figure 4.1A shows a histogram of the species richness of all samples. The distribution has

a mean of 24.8 species/sample and a median of 25.0 species/sample, and a slight left skew. For Figure 4.1B, each set of replicate samples was combined in order to triple the sample size. The new distribution is somewhat less regular, and not surprisingly, has a higher mean and median species richness.

For most localities, the samples can be subdivided into three large groupings based on the contained fossil assemblages (see chapter 5), the position in the stratigraphic sections, and the inferred paleoenvironments, namely:

1. The *Chama congregata* -dominated Lower Rushmere rubbly bottom paleocommunity type (RBPT)
2. A transitional zone, frequently dominated by some sort of oyster, in the upper Rushmere Member
3. The *Mulinia congesta*-dominated Morgart's Beach muddy bottom paleocommunity type (MBPT)

Histograms of the distribution of species richness present in each of these sub groupings are plotted in Figure 4.2. There appears to be higher species richness in the rubbly bottom paleocommunity type, than in either of the other groups, with the lowest richness present in the transition zone. An ANOVA shows that this variation is significant ( $p=0.001$ ). However, while significant, the difference is not necessarily meaningful, since it includes an uneven number of samples from a number of different localities. For instance, the RBPT was only collected at three of five localities, and there were not an even number of samples from each of those three. Also, the majority of transition and MBPT samples came from a large number of replicate samples from a single locality (Day's Point). Therefore, the apparent difference in mean is likely the result of Type I error, and little weight should be given to the apparent significance of the trend. To examine the variability in diversity through the different sub-environments, diversity should be examined separately at each locality.

For this study, a standard weight of sediment was used in processing samples. However, the abundance of identifiable fossil material varied greatly from sample to sample, from a maximum of 2,153 specimens in a sample from the Morgart's Beach Member at the Nottoway River, to a minimum of 2 specimens from a leached portion of the Upper Rushmere Member at Day's Point. Direct comparison of the species present in these two samples is clearly of little value. The median abundance for all sample was 175 specimens, so clearly the range of abundances found in my samples was great.

Figure 4.3A shows the relationship between sample abundance and the number of contained species. Samples with higher abundances have greater species richness. Four samples plotted well above the average for the rest of the samples. These four samples contained 500-2000 individual valves of *Mulinia congesta* and thus the number of specimens is distorted by the hyper-abundances of this one species. These four can therefore be treated as outliers. The rest of the samples display a correlation between sample size and species richness (Figure 4.3B). This is not surprising, since there is a greater chance of finding one or more of the rare species if more specimens are counted. To see what the effect of larger sample size would be, each set of true replicate samples was combined and plotted with the individual samples on Figure 4.4. Tripling the sample size increases the species richness, as expected, although the relationship between the single samples and the replicate samples appears to be non-linear, and the combined replicates yield a lower species richness than that predicted from extrapolation of the single sample distribution. This pattern fits in with what was seen in the species accumulation analysis; species accumulation is rapid for the first few hundred specimens counted, and then levels off as more specimens are tabulated.

Clearly, species richness, as measured by number of species per sample should not be used to determine whether there is variability in diversity in my Yorktown samples, and use of diversity indices incorporating both abundance and species richness is preferable. Seven diversity indices were calculated for each of the 145 samples in the data set. Initially, all samples were included regardless of sample size, since the first analysis will examine the behavior of each index relative to the others. The seven diversity indices incorporate proportional, logarithmic, and exponential calculations, yet each should yield higher values for samples with a higher proportion of species per number of specimens and lower values for samples with proportionally fewer species. Figures 4.5-4.11 are pairwise comparisons of the results of each index calculated.

Figure 4.5 shows the relationship of Margalef's diversity index against the other 6 diversity indices measured. Margalef's D contains a logarithmic function, and therefore it is not surprising that it shows a strongly linear relationship with the other logarithmic diversity index (William's  $\alpha$ ) and a non-linear relationship with the other diversity indices. The linearity between the two logarithmic functions implies that both are equally good measures of that aspect of diversity, and either will serve as a diversity measure. Because it has a firmer theoretical underpinning (Margurran 1988), William's  $\alpha$  was chosen for further analysis, and Margalef's D was not used in the ANOVA below.

Figure 4.6 shows the relationship of Pielou's J, an evenness measurement with the other 6 diversity indices. Pielou's J contains Shannon's H' in the formula, and thus it is not surprising that the two show a strong correlation. The one outlier is sample dyp5.8a, which contains 2 specimens representing 2 species. This completely inadequate sample is an outlier on several plots, and has an unusually high value of Pielou's J specifically because of the low diversity (the calculation involves dividing by the square root of the species abundances). With the exception of a small number of outliers, Pielou's J shows a linear relationship with Shannon's H', Simpson's D, and the Berger-Parker  $N_{max}/N$ , and therefore does not seem to be analyzing different aspects of diversity than these three indices. Therefore, it will not be included in the ANOVA below.

Figure 4.7 shows the relationship of Hill's Evenness measure with the other indices. Hill's Evenness is clearly extracting different aspects of diversity than the other diversity measurements. However, when the sample groupings are analyzed, those with high values of Hill's Evenness are those samples with the highest number of specimens, while those with low values tend to have the lowest number of specimens. Hill's Evenness therefore appears to be strongly influenced by sample size. If all samples had the same sample size, then the Hill's Evenness index might provide some information about some aspect of diversity, but it does not appear to be an appropriate analysis for my samples. It therefore will not appear in the ANOVA below.

Figure 4.8 shows the relationship of the very popular Shannon H' diversity measure. The relationship between Shannon's H' and Simpson's D appears to be linear, while there is a logarithmic pattern in the plot of Shannon's H' and William's  $\alpha$ , as one would expect from examining the equations, since both contain logarithmic terms. Shannon H' is popular in ecologic studies (e.g., examples in Stiling 1999), and it will be analyzed below.

Figure 4.9 shows the relationship of Simpson's dominance index with each of the other 6 indices. Like Shannon's H', it appears to be a well behaved diversity index, and as it is also popular in the ecologic literature, it also will be included in the ANOVA below.

Figure 4.10 shows the relationship between the Berger-Parker dominance index  $N_{max}/N$  and the other diversity indices. Considering the simplicity of the measure, and the disdain in which it is held by some ecologists (e.g., Stiling 1999), it is a remarkably well behaved index. It shows a strong linear relationship with Simpson's dominance index, and a somewhat weaker relationship with Shannon H'. Because what is actually being measured by this index is so much more easily understood than the other 4 diversity measurements ( $N_{max}/N$  is simply the proportional abundance of the most abundant species), this measurement was included in the ANOVA below.

Figure 4.11 shows the relationship of William's  $\alpha$  to the other diversity measurements. William's  $\alpha$  contains a logarithmic function, so compared to the other indices, this index will tend to spread out higher values more than the linear functions do. For higher diversity samples, William's  $\alpha$  will therefore show more differentiation than that found in the other indices - thus, the flattened curves seen in the plots of William's  $\alpha$  versus Shannon's H', Simpson's D, and Berger-Parker's Nmax/N. Since William's  $\alpha$  is measuring diversity differently from the linear indices, and since the underlying distribution of species abundance is log normal (see Appendix C), William's  $\alpha$  was included in the ANOVA below.

Of the seven diversity indices examined, four were chosen for further analysis: Shannon's H', Simpson's D, William's  $\alpha$ , and the Berger-Parker index. The change in diversity as determined by each of these indices was analyzed by performing an ANOVA on the index values of the contained sub-environments at each of the first localities. The tables with the ANOVA can be found in Appendix C. The figures for each analysis are frequency distributions of the four diversity measurements for each contained sub environment. For Simpson's D, Shannon's H', and William's  $\alpha$ , diversity increases toward higher values. Nmax/N measures the dominance of the single most abundant species in each sample, so diversity increases toward lower values.

At Burwell's Bay (BWB) and Day's Point (DYP) only the transition and MBPT were collected (Figure 4.12 and 4.13). The apparent decrease in diversity shown on all four indices from the transition zone to the MBPT at BWB is significant according to an ANOVA in each case ( $p=.001$ ). The slightly greater diversity in MBPT samples from Day's Point is significant for the Shannon H' index, but not for any of the others. Since only one index showed a significant change, the diversity is interpreted as remaining constant.

At the Nottoway River (NWR) and Kingsmill (KGM) all three sub-environments were present. ANOVA of the NWR sub-environment distributions shows that for the four indices calculated, diversity was significantly lower in the MBPT than in either of the other sub-environments, and essentially equal in the transition and RBPT environments (Fig. 4.14). At Kingsmill, there is no significant difference between in the mean diversity values of any of the sub-environments; diversity remained stable through the changing paleoenvironmental conditions (Fig. 4.15).

The conditions at Lieutenant's Run (LTR) were different from those present at the localities lower on the coastal plain, and subsequently, there was no transitional paleocommunity type

recognized. While some samples clearly fell into the RBPT, and at least one horizon had undoubted MBPT, many samples seemed to come from a different paleocommunity type, which for lack of a better name is termed "other." ANOVA of the distributions of these three sub-environments at LTR shows no significant difference in any of the diversity measurements (Fig. 4.16).

The results of the ANOVAs are summarized in Table 4.1. At LTR and KGM, there are no differences in diversity in the three sub environments present. At BWB and NWR, the MBPT has lower diversity, while at DYP, the MBPT has higher diversity. In other words, there is no consistent difference in diversity between the various sub-environments of the Yorktown Formation.

**Table 4.1** Direction and significance of diversity changes between paleoenvironments (e = no significant difference, - = significant negative difference, + = significant positive difference). All significance results determined by ANOVA of more than one diversity index.

	KGM	NWR	DYP	BWB		LTR
RBPT vs. MBPT	e	-			RBPT vs. MBPT	e
Transition vs. MBPT	e	-	+	-	Other vs. MBPT	e
RBPT vs. Transition	e	e			RBPT vs. Other	e

## Discussion

Based purely on species richness, the median diversities present in single Yorktown samples (25 species/sample) and combined replicates (40 species/sample) fall well within the range of species richness described in Bambach (1977) for near shore, level-bottom Cenozoic fossil assemblages. The median value for the combined replicates is right in the center of the range of observed values in Bambach (1977). The mean species richness values of samples from the three sub-environments of the Yorktown also fall in this range, even with the inclusion of extremely low abundance samples. So, the species richness observed is similar to other Cenozoic fossil assemblages from near shore environments, but not open marine level bottom environments (which have higher species richnesses) or restricted, highly stressed environments (which have lower species richnesses).

Using species per sample as a measure of species richness, diversity is not warranted when comparing the diversity present within the various sub-environments and different localities of the Yorktown, because this measure of species richness is highly sensitive to sample size. Buzas and Gibson (1990) found that in their samples, species richness could vary as much as

50%, and that the variation is controlled by the chance inclusion of rare species. The combination of replicates in this study, which tripled each sample size, increased the observed median species richness by a third. Therefore, other diversity measures were chosen to answer the second question: is the observed diversity higher under presumably more stable paleoenvironmental conditions of the RBPT than the unstable conditions of the MBPT?

The answer is no. If there is a trend, it was not expressed at every locality. At two localities, the diversity was lower in the MBPT, as predicted. At one locality, the MBPT contained a higher diversity. Of the remaining localities, one had no significant difference between any of the paleoenvironments while the other contained only a single MBPT sample, and thus nothing could be said about the statistical significance of the diversity measures for that paleoenvironment. It is worth noting that the single MBPT sample fell right in the center of the range observed for the other paleoenvironments present at that locality.

The reason that there is no diversity change observed is probably because the initial assumptions were faulty. If this were a biological system, and I had collected only organisms that lived at the same time, then the diversity test might have yielded the results expected. However, this is not an ecologic sampling, but rather a paleoecologic sampling. The contained fossil remains were derived from organisms not only did not necessarily live at the same time in their pre-mortem state, but also did not necessarily live together. A snapshot, or live census, of each paleoenvironment at any single point in time might yield the predicted results, but those results can not be expected from time-averaged fossil assemblages. When local paleoenvironmental conditions fluctuated, a variety of living assemblages could bequeath remains to the fossil assemblage. Since the rate of ecologic succession is higher than sedimentation rate, the fossil assemblage could incorporate representatives of all successional assemblages in a variable ecologic system, and therefore, the diversity present in a paleoecologic sample could include representatives from the entire suite of living assemblages present within any habitat.

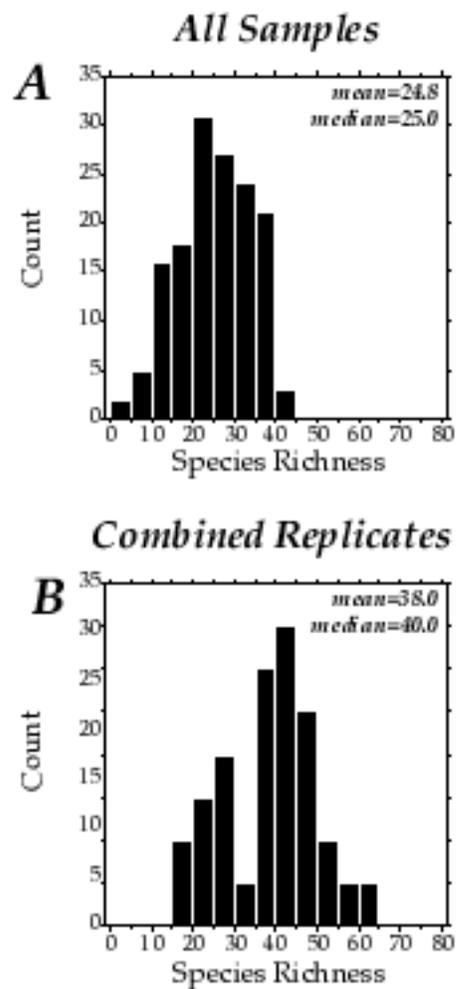
*Mulinia congesta*, the most abundant bivalve in the MBPT, was most likely an opportunist, like its modern counterpart *M. lateralis*, and therefore was only abundant when local conditions excluded most other organisms, at least for a period of ecologic time (perhaps as short as a season). Based on the high abundance of *M. congesta* found, those conditions must have occurred somewhat frequently, even assuming a very high preservation potential for *M. congesta* valves. Based on the autecology of *M. congesta* the more stressful conditions present in the MBPT allow for at least two distinct live assemblages of organisms, one assemblage composed primarily of *M. congesta*, and one or more assemblages formed when conditions were "normal." The

incorporation of these two types of assemblage, which did not occur at the same time in the same place can be thought of as a type of temporal patchiness. The rest of the species found in the MBPT might have all lived together, or at least nothing in their autecology excludes the possibility. However, some of the species found in the MBPT (e.g., *Ostrea sculpturata* and *Crepidula costata*) attach to hard surfaces in life. These species must have inhabited a patch of hard substrate within the muddy environment (e.g., isolated large shells), and thus the MBPT paleocommunity type also incorporates both spatial and temporal patchiness within a single deposit.

In addition to the problem of patchiness, bioturbation could also be mixing the remains of different living assemblages within the MBPT. Bioturbation is not easy to measure directly, but can be inferred from a number of different lines of evidence. While there are some small, discontinuous sandy beds, or perhaps simply small lenses of sand, in the MBPT, most of primary sedimentary structures have been obliterated. There are few primary sedimentary structures preserved in the Rushmere Member, also. In general, it should be easier to mix up mud than rubble or coarse sand, and all else being equal, the MBPT should be more easily blended than either the transition or RBPT. However, there is direct evidence that bioturbation may have been more severe in the MBPT. Many shells of the very large, muscular clam *Panopea reflexa* are found concentrated in the uppermost Rushmere and into the Morgart's Beach Member in life position. A burrow depth of one meter is not unreasonable for a geoduck of this size (Gordon 1996). While not common in my samples (almost certainly due to their large size), *P. reflexa* is frequently the most visible faunal element in an Upper Rushmere-Morgart's Beach outcrop. *P. reflexa* is also present in other Yorktown deposits, although it does not appear to have the same abundance in other sub-environments. These burrows alone could cause significant vertical mixing of fossil remains, and thus could contribute to the high diversity in MBPT fossil assemblages, not to mention moving the *P. reflexa* shells themselves up to a meter away from the shelly remains of their contemporaries that lived on the surface. In general, the MBPT contains a larger percentage of deeper burrowers than the RBPT (see chapter 6), and so perhaps bioturbation was more severe in the MBPT than in the RBPT.

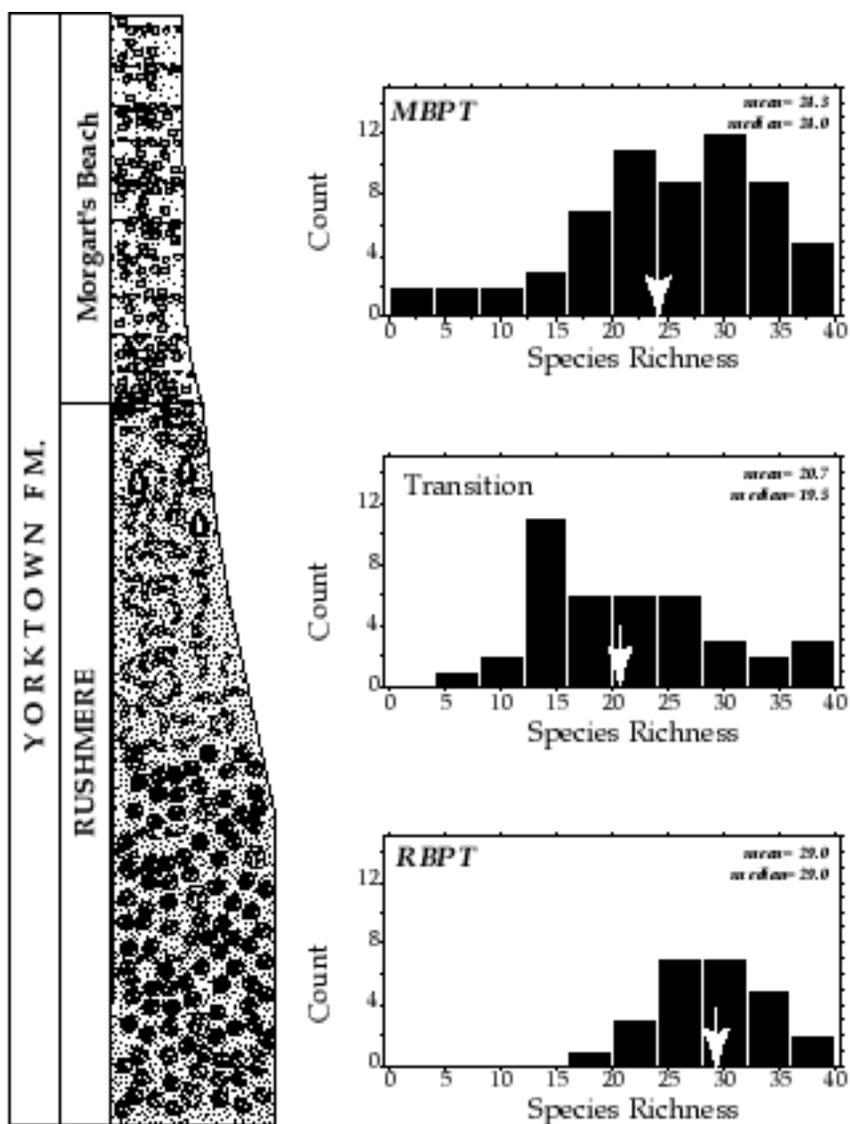
The apparently unusually high diversity value of MBPT assemblages could simply be the natural outcome of time-averaging, and ecological and environmental instability may perhaps be expected to result in high diversity fossil assemblages, even though the ecologic community present at any single point in time or space has lower diversity than that found under more stable conditions.

While diversity indices should measure aspects of diversity better than such simple measures of species richness as the number of species per sample, care must be taken when applying these metrics to fossil assemblages. Direct comparison to living assemblages is not recommended. Time averaging may tend to increase diversity by mixing representatives from different living assemblages within habitats. Since time averaging is not necessarily uniform across different environments, this effect must be accounted for when analyzing diversity.



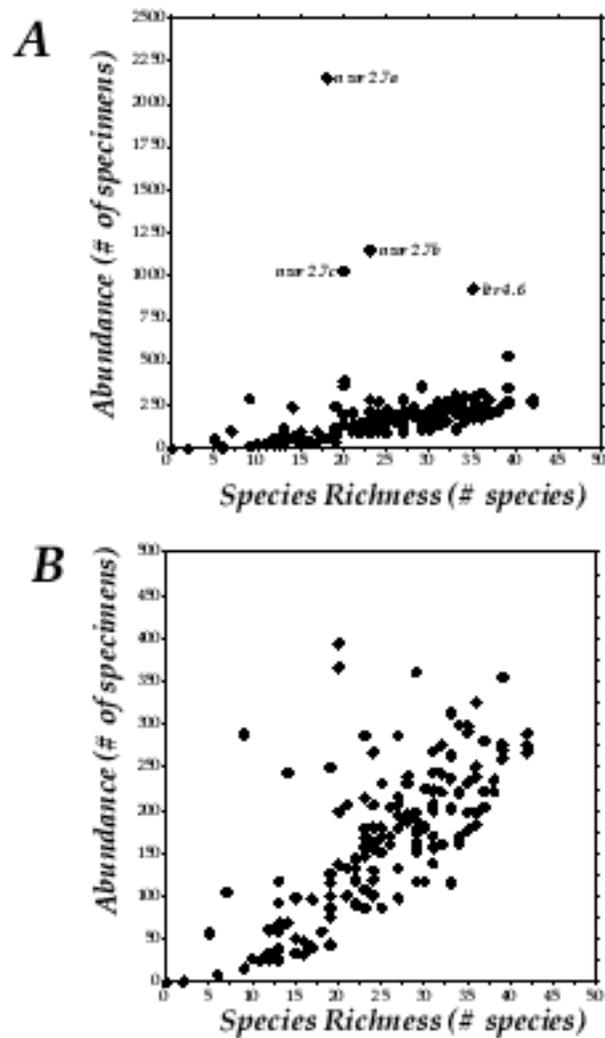
**Figure 4.1**  
**Species Richness for individual samples and combined replicates**

Histograms of species richness (species/sample) for single samples (A) and combined replicates (B).



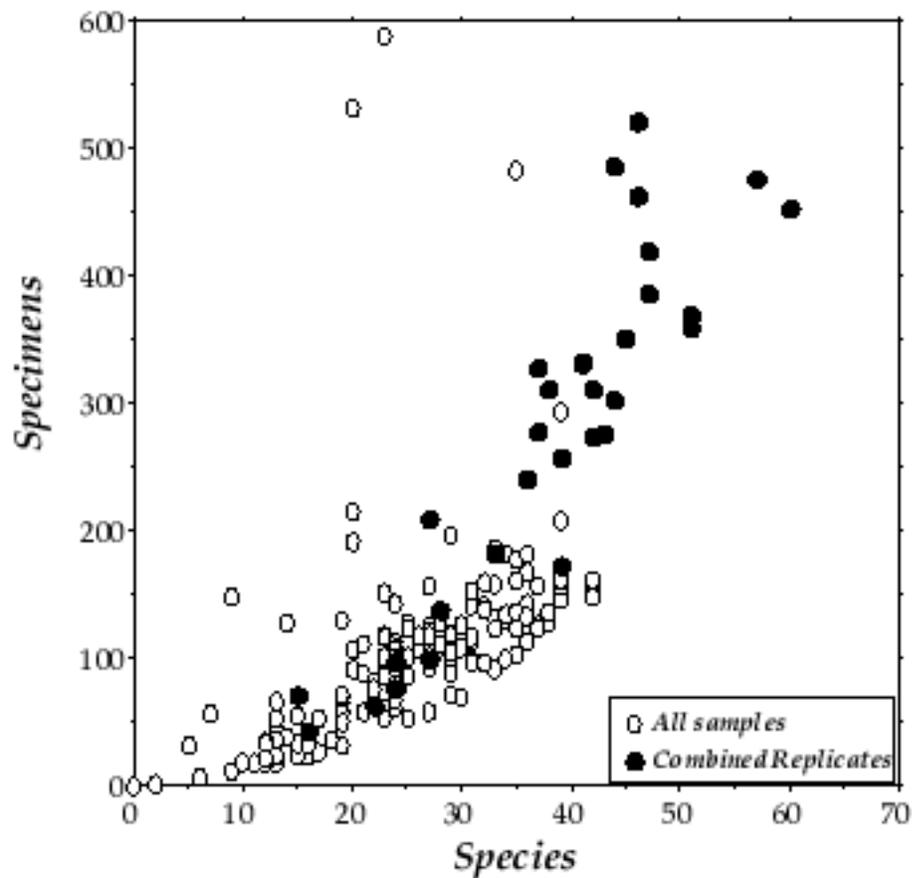
**Figure 4.2**  
**Species Richness for each subenvironment within the data set**

Histograms of species richness (species/sample) for single samples within each sub environment.



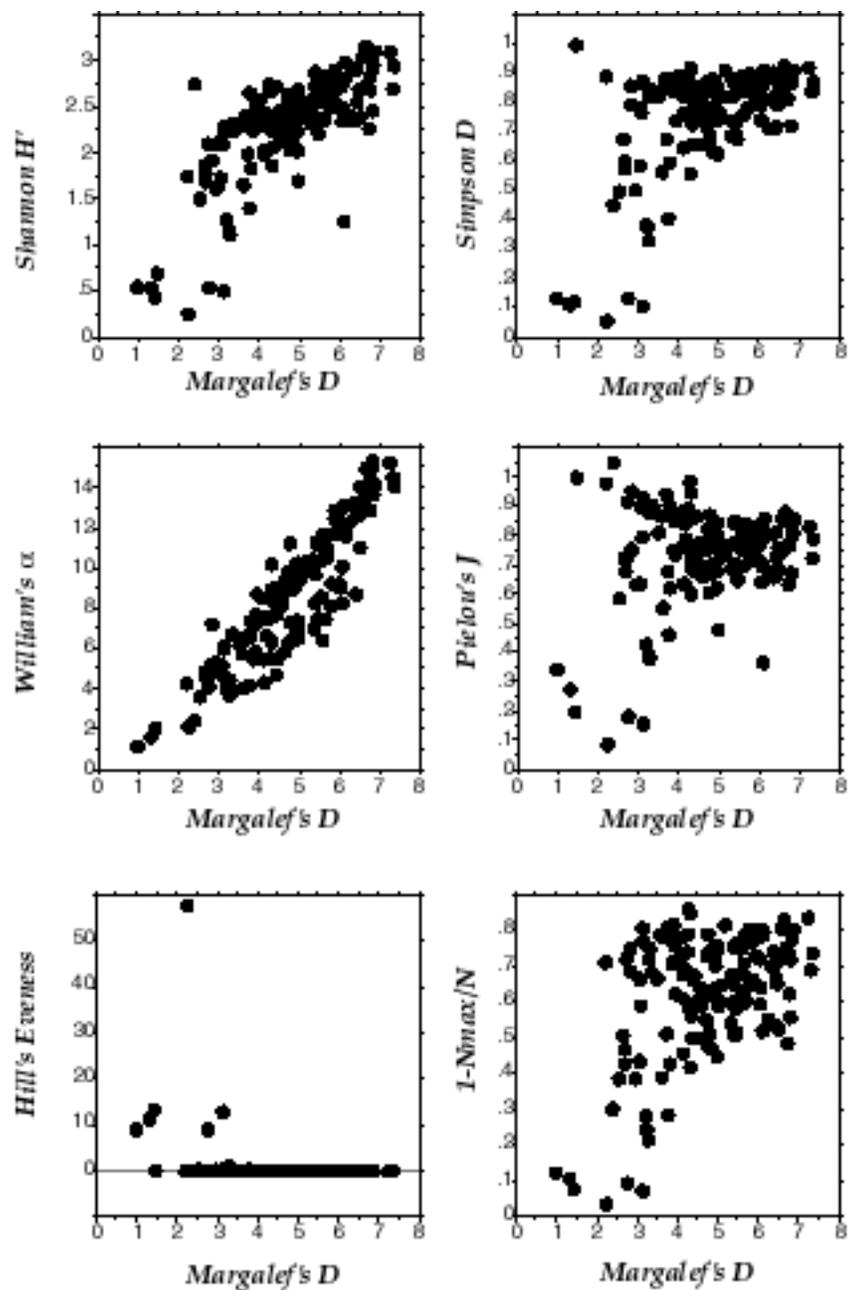
**Figure 4.3**  
**Species versus specimens for individual samples**

Bivariate scatter plot of species richness (species/sample) versus specimens for individual samples. Plot (A) includes all samples; plot (B) includes only samples containing 500 or fewer specimens.



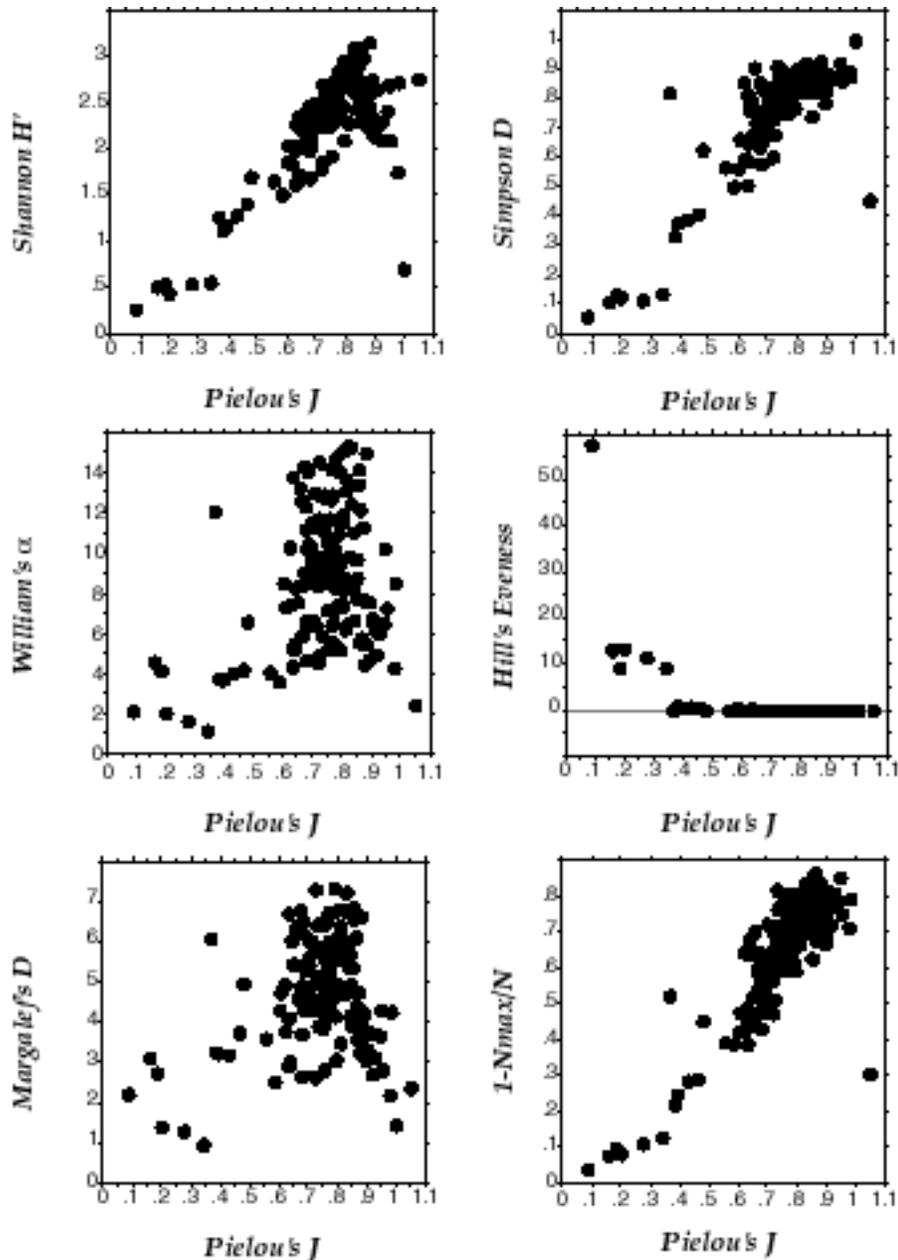
**Figure 4.4**  
**Species versus specimens for individual samples and combined replicates**

Bivariate scatter plot of species versus specimens for individual samples (open circles) and combined replicates (filled circles).



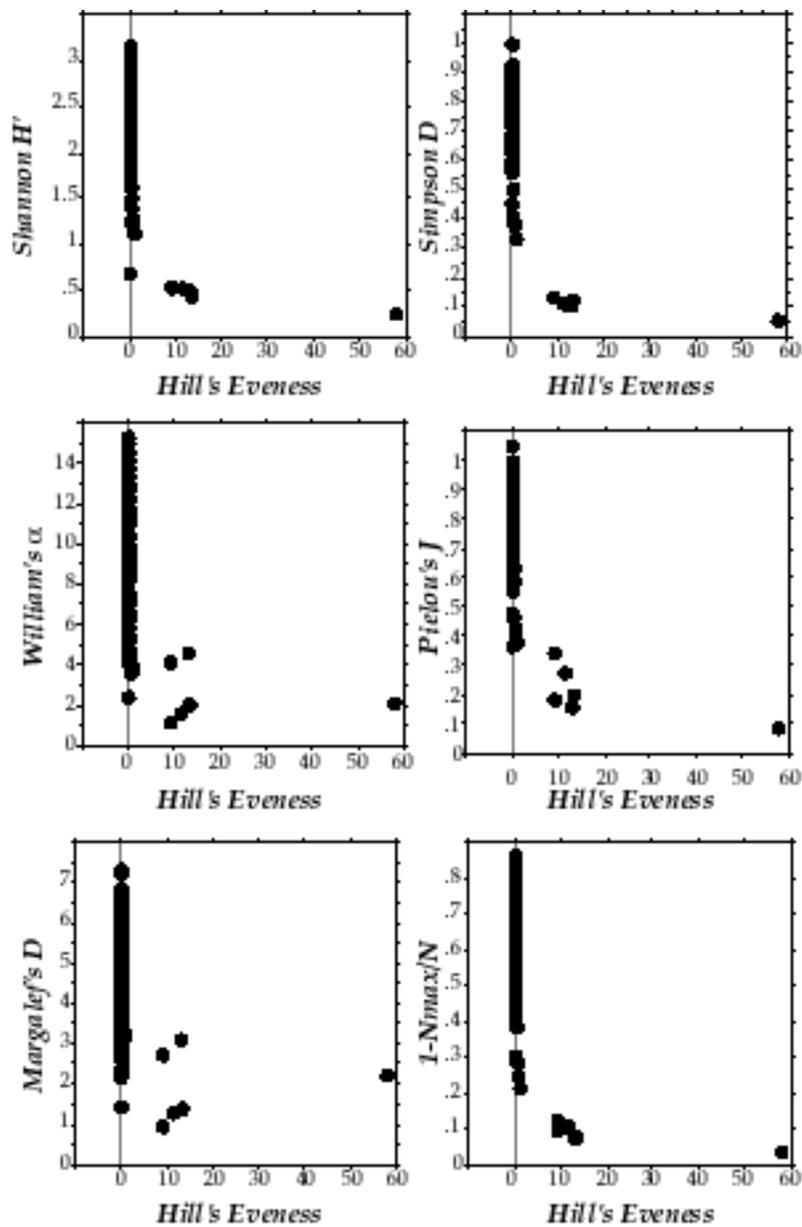
**Figure 4.5**  
**Margalef's diversity index versus other diversity measures**

Bivariate scatter plots of Margalef's diversity index versus the other 6 diversity measures.



**Figure 4.6**  
**Pielou's J diversity index versus other diversity measures**

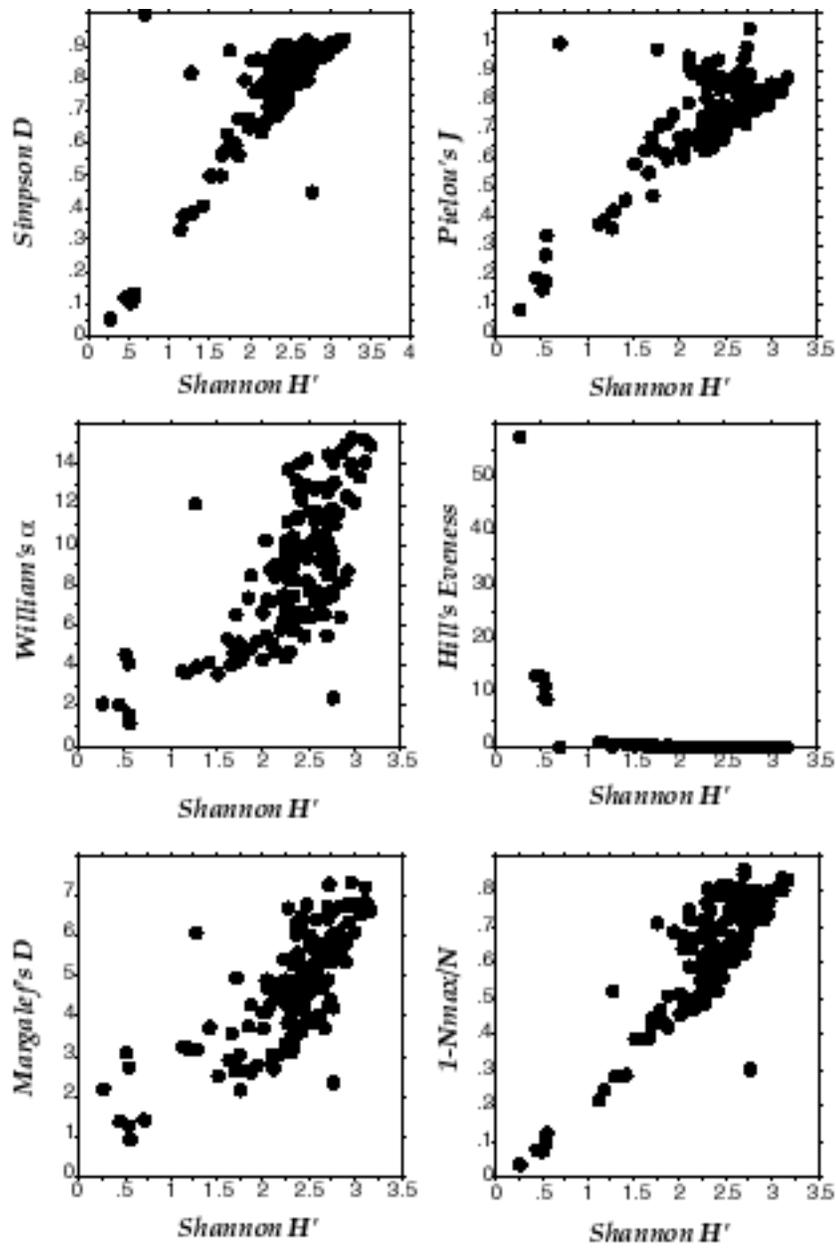
Bivariate scatter plots of Pielou's J diversity index versus the other 6 diversity measures.



**Figure 4.7**

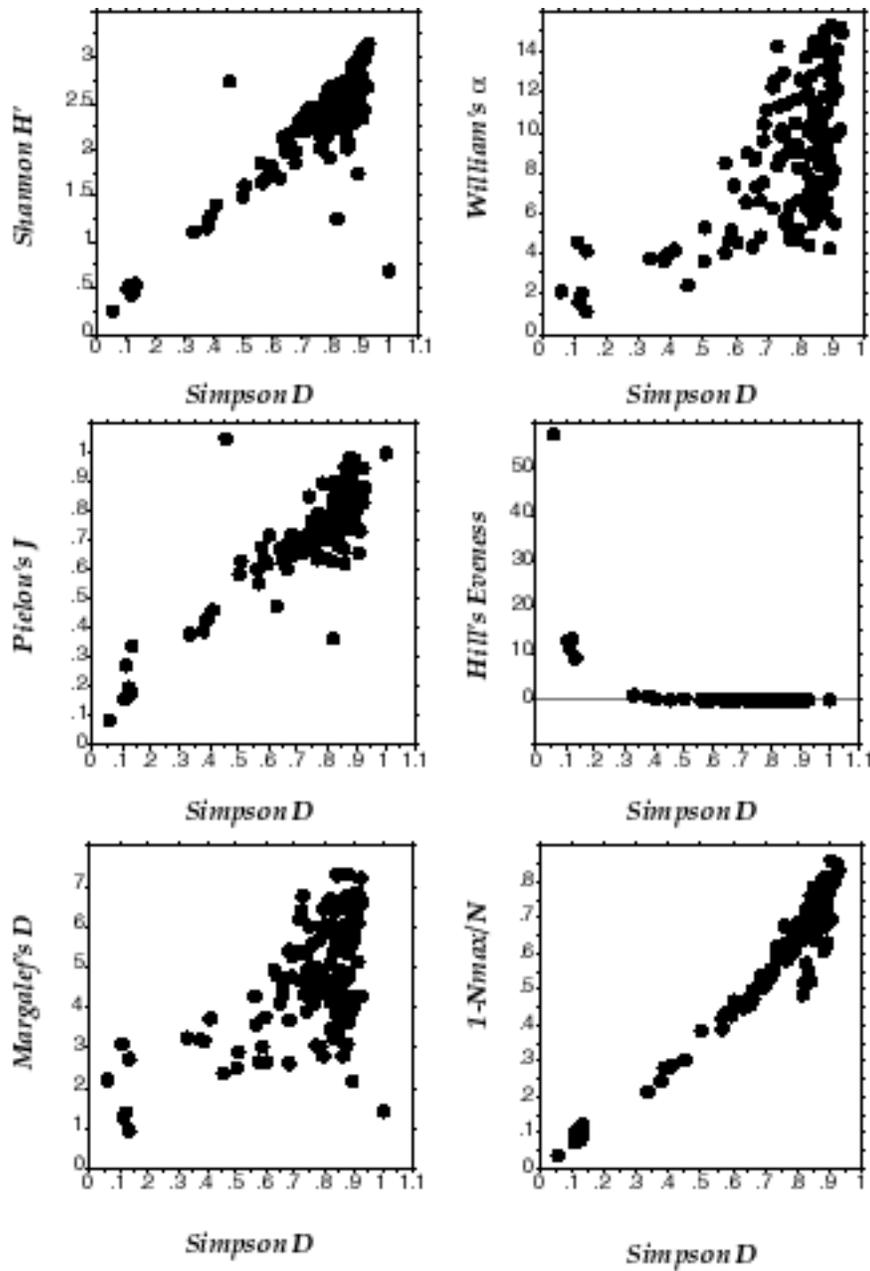
**Hill's evenness diversity index versus other diversity measures**

Bivariate scatter plots of Hill's evenness diversity index versus the other 6 diversity measures.



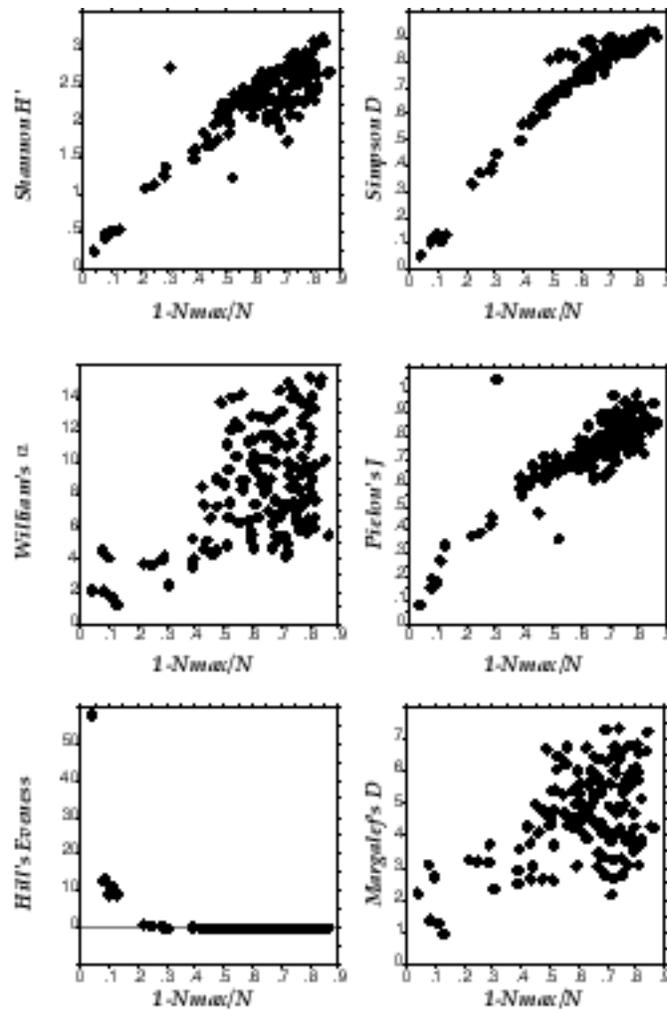
**Figure 4.8**  
**Shannon H' diversity index versus other diversity measures**

Bivariate scatter plots of Shannon H' diversity index versus the other 6 diversity measures.



**Figure 4.9**  
**Simpson's dominance diversity index versus other diversity measures**

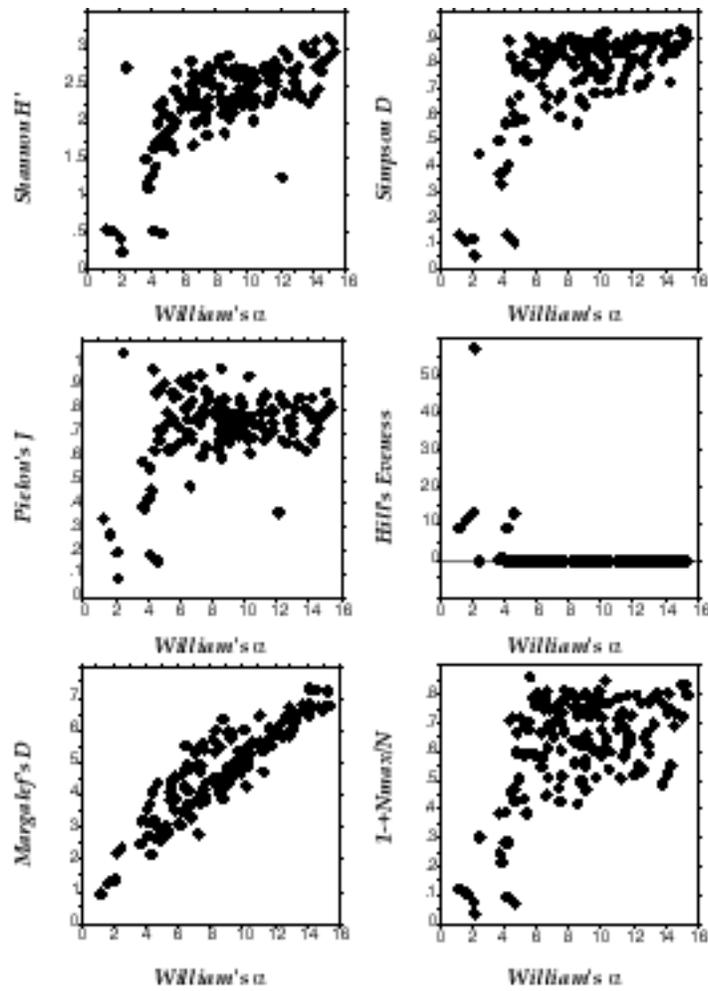
Bivariate scatter plots of Simpson's dominance diversity index versus the other 6 diversity measures.



**Figure 4.10**

**Berger-Parker diversity index ( $N_{max}/N$ ) versus other diversity measures**

Bivariate scatter plots of Berger-Parker diversity index ( $N_{max}/N$ ) versus the other 6 diversity measures. Since increasing values of this index indicate decreasing diversity the value was subtracted from 1 so that diversity increases in the same direction as the other plots.



**Figure 4.11**  
**William's  $\alpha$  diversity index versus other diversity measures**

Bivariate scatter plots of William's  $\alpha$  diversity index versus the other 6 diversity measures.

## BWB

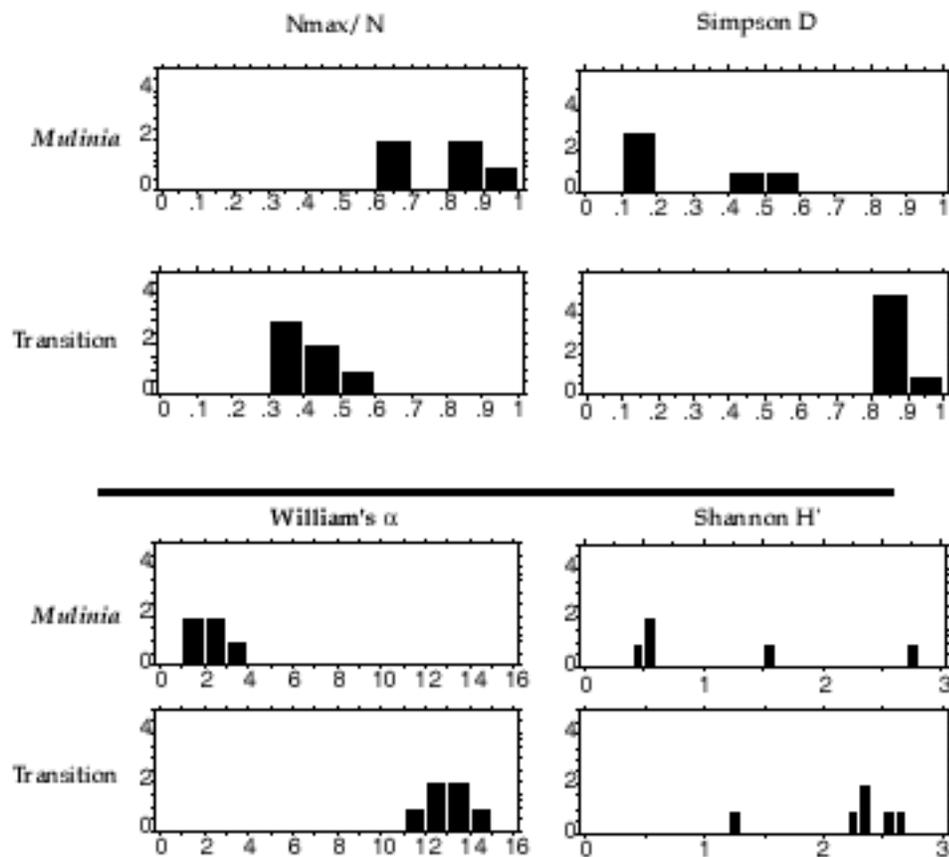
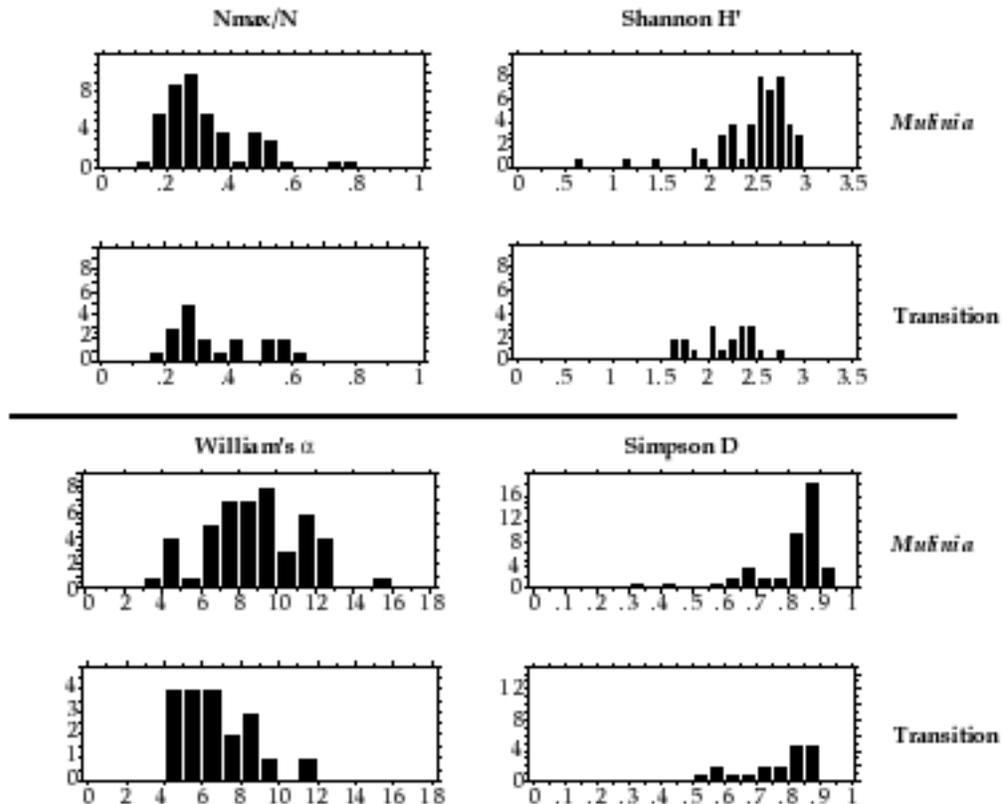


Figure 4.12

Distribution of each diversity measures in the *Mulinia* dominated and transitional assemblages at Burwell's Bay

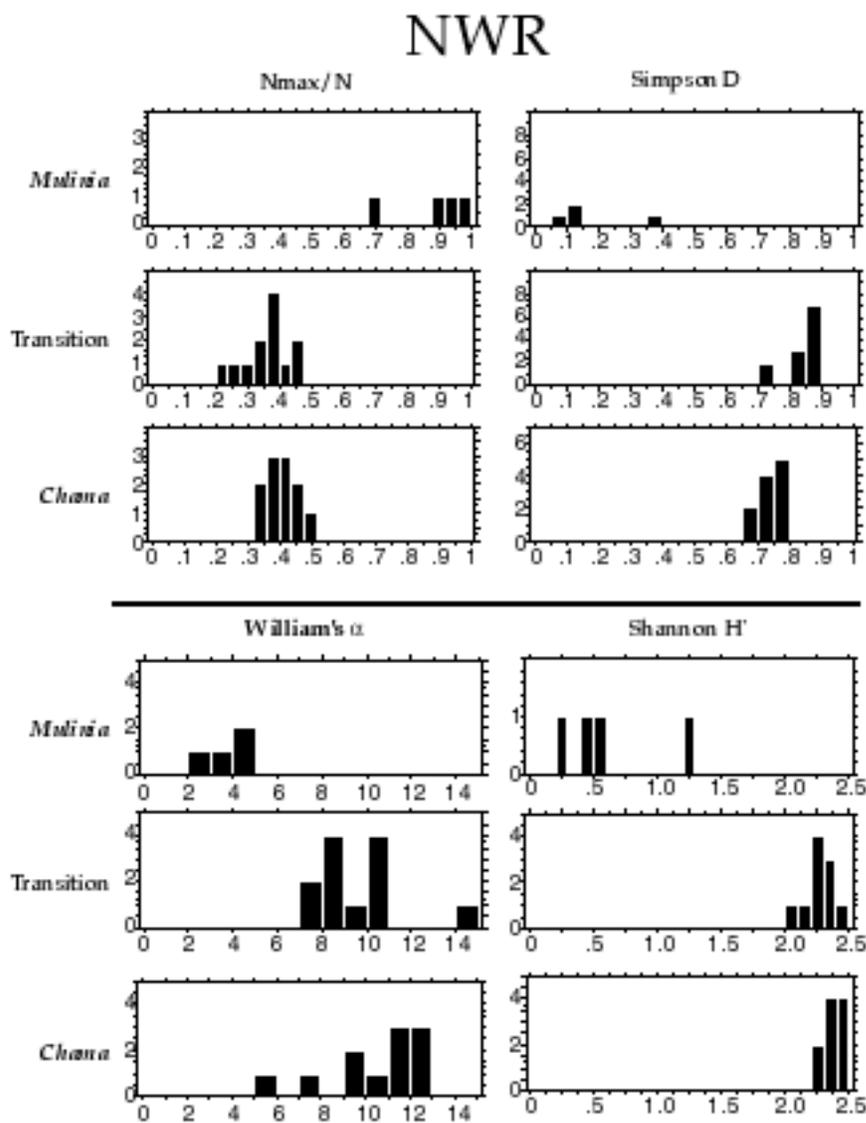
Histograms of diversity measures for individual samples within the sub environments collected at the Burwell's Bay locality.

## Day's Point



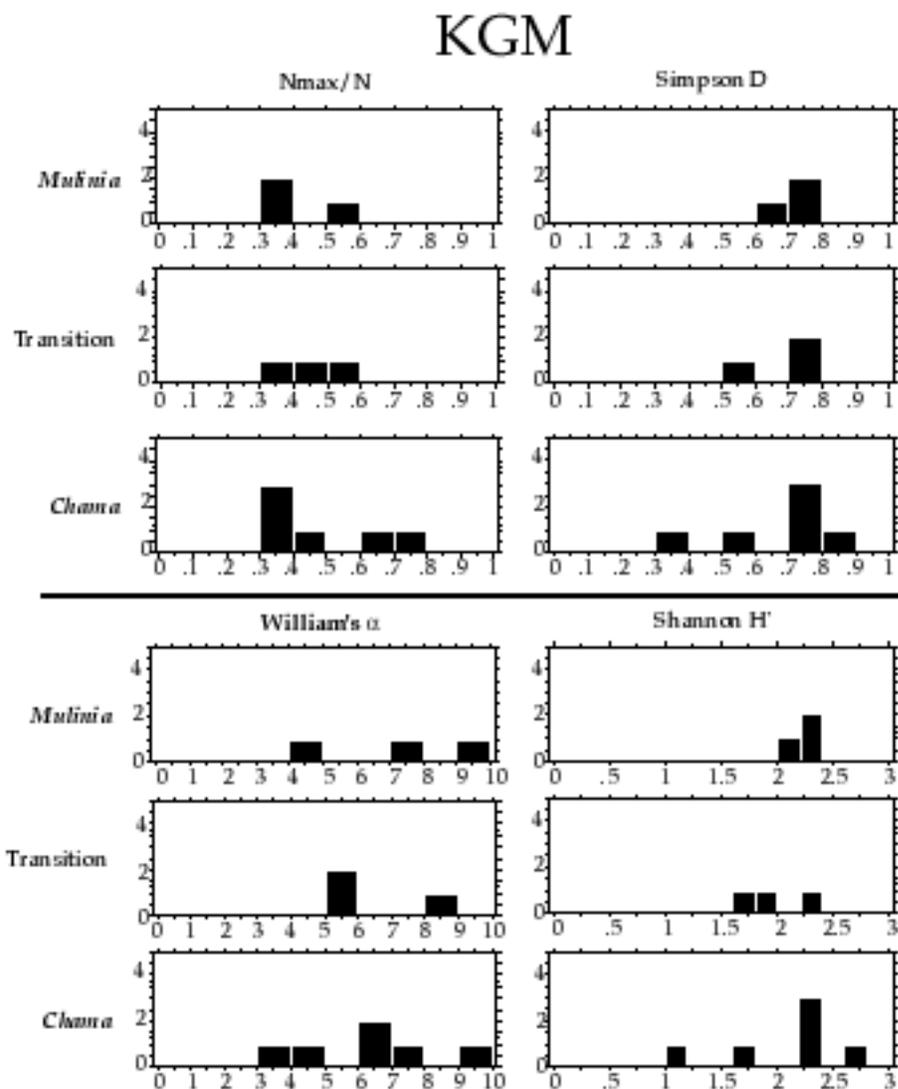
**Figure 4.13**  
**Distribution of each diversity measures in the *Mulinia* dominated and transitional assemblages at Day's Point**

Histograms of diversity measures for individual samples within the sub environments collected at the Day's Point locality.



**Figure 4.14**  
**Distribution of each diversity measures in the *Mulinia* dominated, *Chama* dominated, and transitional assemblages at the Nottoway River**

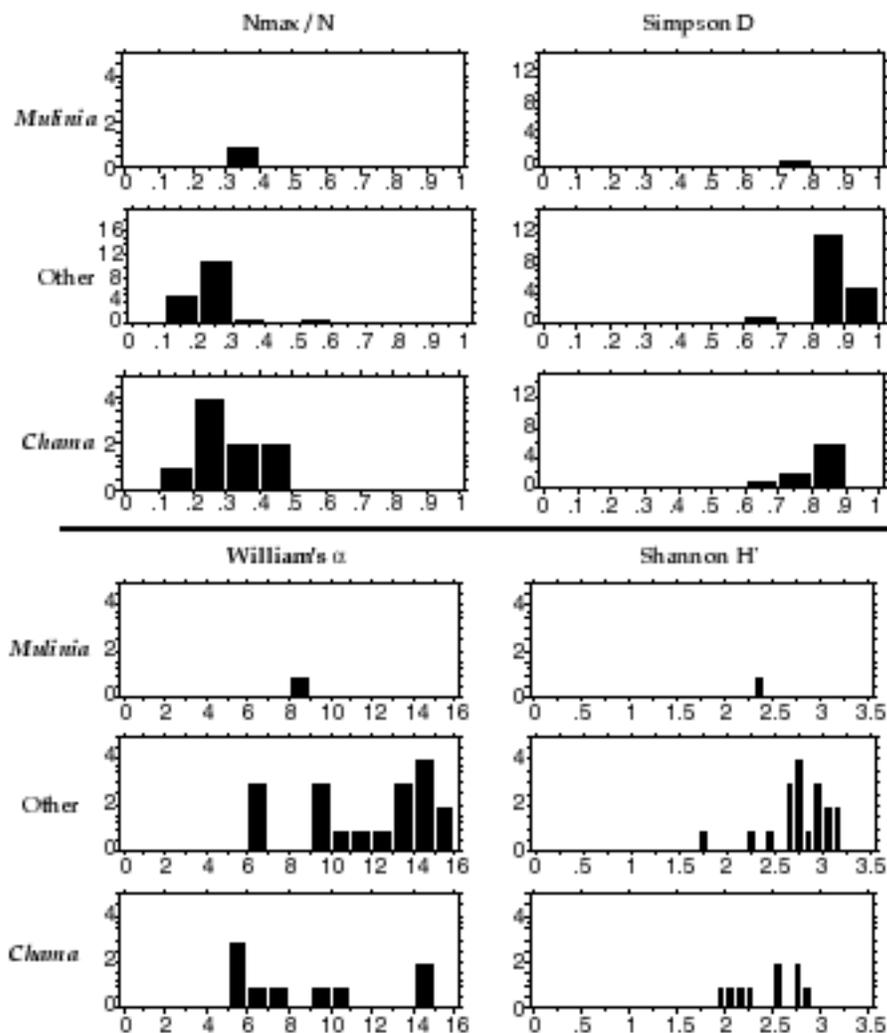
Histograms of diversity measures for individual samples within the sub environments collected at the Nottoway River locality.



**Figure 4.15**  
**Distribution of each diversity measures in the *Mulinia* dominated, *Chama* dominated, and transitional assemblages at Kingsmill**

Histograms of diversity measures for individual samples within the sub environments collected at the Kingsmill locality.

## LTR



**Figure 4.16**  
**Distribution of each diversity measures in the *Mulinia* dominated, *Chama* dominated, and other assemblages at Lieutenant's Run**

Histograms of diversity measures for individual samples within the sub environments collected at the Lieutenant's Run locality.

## CHAPTER 5: PALEOCOMMUNITY ANALYSIS OF THE YORKTOWN FORMATION

The process of ecological locking requires strong species interactions to be a major ordering force on the composition and structure of communities. These strong species interactions should impose a consistent ecological structure (membership and relative abundance) whenever the same species are put together under similar conditions. Therefore, when similar taxa are found together under similar environmental conditions, they should yield a recognizable paleocommunity (in the sense of Bennington and Bambach 1996) which recurs whenever similar paleoenvironmental conditions are recognized. The hypothesis that strong species interactions are a major ordering force of the Yorktown fauna is tested below.

### Overview of Statistical Analyses

*Three statisticians go duck hunting. After a morning of waiting, a lone duck flies overhead.*

*The first statistician shoots, a meter high.*

*The second statistician shoots, a meter too low.*

*The third statistician exclaims, "We got it!"*

Statistical methods used in this study can be divided into two main groups - methods designed to examine the data for contained patterns, and those meant to test hypotheses. PCA and species constancy analysis belong to the first group, while the correlation analyses and MANOVA belong to the second group. Rejection of the null hypothesis in the case of hypothesis testing was always at the  $p < 0.05$  level (5% chance or less that the two treatments are not different). Unless otherwise indicated, replicate samples are treated as individual samples in these analyses.

### Species constancy

Species constancy is used to gauge how uniform the distribution of species is in a set of samples (McIntosh 1985, Bennington 1995). Species constancy is a measure of the consistency of species membership within a set of samples, weighted by the relative abundance of species. For a data set composed of  $j$  species and  $i$  samples, it is calculated with the following equation:

$$Cc = (\sum(P_j \times k_j)/i)$$

$P_j$  is the percent abundance of species  $j$  in the pooled data set

$k_j$  = the number of samples in which species  $j$  occurs

$i$  = number of samples

If all samples contain the same species, the constancy index will be 1.0. However, the lower limit of  $C_c$  is dependent on the number of samples pooled (assuming that the samples have at least some species in common), and Bennington (1995) suggested the following correction:

$$C_a = (C_c - 1/i) / (1 - 1/i)$$

This correction allows  $C_a$  to vary from 0.0 to 1.0.

While the species constancy measure can not generally be used for statistical testing, it give a measure of the constancy ranking of various groups of samples.

### Principle Components Analysis

Principle Components Analysis (PCA) is a useful ordination tool for exploring the relationships of objects to one another based on measured variables, and is especially useful when there are both a large number of objects (e.g., paleoecologic samples), and a large number of measured variables (e.g., the species contained in those samples). The purpose of PCA is to take a large, unwieldy data set composed of probably correlated variables, and through the application of matrix algebra reduce the dimensions necessary to explain the data to a smaller number of uncorrelated axes. For instance, my data set consists of 145 samples containing 133 species. To graph those 145 samples in relationship to each other based on the relative abundance of the species would require a hyper-volume with 133 axes - one dimension for each species. However, not all of the species will vary independently of each other, and thus some of these axes will be correlated. PCA should allow that original 133 dimension hyper-volume to be reduced to a few dimensions - at least assuming that most of the variables are correlated. The data can then be replotted on these new axes, using new variables called principle components.

PCA *sensu strictu* should only be applied to data sets in which the variables are normally distributed, continuous, and uncorrelated - conditions rarely, if ever, met with ecological or paleoecological data. However, PCA can be successfully used for exploratory and descriptive purposes, even if there are rather serious departures from these assumptions, and as long as stringent statistical testing is not required, PCA can be profitably applied to ecologic data sets (Gauch 1995).

The PCA procedure first constructs a correlation or covariance matrix of the variables for the data set. PCA performed on the covariance matrix weighs each variable relative to its magnitude - so in my data, very abundant species would be given greater weight than rare species. PCA can also be performed on the correlation matrix, which is the suggested PCA for data matrices in which the variables are not "on equal footing" - e.g., their variances are not comparable (Johnson 1998). To make the footing more "equal" the raw data is converted to standardized data by converting the variables within each sample to Z-scores, which by definition have a mean of zero and a standard deviation of one. While the relative abundance of the variables (e.g., species) is preserved in correlation analysis, the absolute magnitude of each species is lost.

No matter which type of matrix is used, the next step is to extract eigenvalues and eigenvectors using matrix algebra. The eigenvectors extracted will be linear combinations of the vectors in the original matrix. The first eigenvector will have the largest value, and explain the most variability, and each subsequent eigenvector will account for less and less variability, until finally the eigenvalues will reach zero. For completely uncorrelated variables, the number of non-zero eigenvalues will equal the number of variables in the original data set. The more correlated the variables, the fewer eigenvectors are extracted before the eigenvalues of subsequent extracted eigenvectors equals zero. In other words, for completely uncorrelated data, the PCA will not decrease the number of dimensions needed to explain most of the variance, while the more correlated the data is, the fewer the number of dimensions needed to explain most of the contained variability.

Once the eigenvectors have been extracted, principle component scores can be determined for each sample, and the samples plotted in the reduced dimensions of the PCA space. Ideally, this space would be composed of 3 or fewer dimensions, although sometimes the next few dimensions hold interesting information, also. Depending on the structure of the data, as few as 2 dimensions may be sufficient for explaining a large percentage of the variability. Rules for determining how many PCA axes to plot vary from study to study, with "laboratory-type" data frequently accounting for 90-95% of the variability on 2-3 axes, while "people-type" data can require 5 or 6 principle components to explain 70-75% of the variability (Johnson 1998). For this study, I extracted eigenvalues until at least 90% of the variability was accounted for.

In addition to principle components scores, the original variables can be related to the new principle components by determining principle component loadings. Loadings are Pearson's correlations between the variable and the principle components (Stevens 1992), and can be thought

of geometrically as the cosine of the angle between the two normalized vectors in the new space. For ecologic data, a high positive loading for a variable (e.g., a species) on a principle component indicates that samples ordinate along that component axes based in large part on the relative abundance of that species. In other words, that species is important in determining the placement of samples on that axis. Very high negative values indicate that the lack of a species may also be important in ordinating samples along that axis, or at least that the species on either end of the axis are negatively correlated to each other in some samples, so that the presence of one in abundance usually means the lack of the other.

By examining the relationship of the samples in the PCA space, the structure of the data can be explored. Samples that plot near each other in PCA space are more similar to each other than samples that plot farther away from each other. Clusters of samples in PCA space therefore can be used to recognize which samples form natural groups. By looking at the loadings of the species on the PCA axes, the species responsible for the apparent similarity can also be recognized.

### **The Correlation Matrix**

The correlation matrix is a  $n \times n$  matrix ( $n$  = samples) which is the minor product of the moment of the data matrix, in which each entry is the cosine of the angles between each sample vector in principle component space (Reyment and Joreskog 1996). Therefore, since the cosine is a unitless proportion of the lengths of the adjacent limb of a right triangle over the hypotenuse of that right triangle, the correlation matrix value is the measure of the trace, or projection, of one sample vector on another (Fig. 5.1). The more similar the two samples are, the more correlated their vectors in principle components space are, up to a maximum correlation of 1.0. The correlation matrix therefore consists of correlation values for each pair of samples within the data set. The correlation value of each sample with itself is 1.0, since the sample is identical to itself. Pairs of samples with no species in common would have values of 0.0 or less (in the case where some of the contained species are negatively correlated), while most pairs of samples would fall between 0.0 and 1.0.

The values in the correlation matrix can be used to approximate the amount of variability within groups within a data set. For instance, a data matrix consisting of one paleocommunity type sampled at several localities can be analyzed by comparing correlation values for pairs of samples collected from the same locality versus pairs in which the samples came from different localities. The distribution of correlation values within and between localities can then be examined using either ANOVA and non-parametric techniques to examine the distribution of correlation values in

each case. A correlation analysis run on all replicate samples yielded a mean correlation value of 0.908 and a median correlation value of 0.961, a highly skewed distribution, so non-parametric tests are clearly needed. High correlation values for both the within and the between locality groupings would imply a great deal of regional structure to the paleocommunities, while lower correlation values in the between locality pairings would imply that local conditions are a stronger controlling factor. Therefore, the correlation matrix can be used to test whether regional or local control is a stronger factor in determining the structure of paleocommunities.

### MANOVA

Multivariate Analysis of Variance (MANOVA) is used to test for differences in means of several variables (species) at once for two or more groups of samples. For a relatively understandable discussion of the procedure for performing MANOVAs see Johnson (1998).

Unlike ANOVA, there is no one best test for most situations, as the F-test is the best for ANOVA. Because of this, a number of tests are suggested for MANOVA, such as Roy's test, Lawley and Hotelling's test, Pillai's test, and Wilks' likelihood ratio test. The tests are all functions of the error, sums of squares, and cross-products matrices, and each behaves slightly differently. Most of the MANOVA performed were on pairs of groups (samples from 2 different groups compared to each other). For two groups, all the significance tests yield the same significance values, by definition, and thus only one probability value will be reported. All MANOVAs performed on three or more groups yielded probability values of less than 0.0001 for all tests, so only that probability was reported.

MANOVA testing requires that the underlying distribution have comparable variances, a condition that is almost never present in ecological or paleoecological data. Because of this, before MANOVA was applied, the data was transformed using the Freeman-Tukey variant of the arcsine transformation (Bishop et al 1975, Bennington and Bambach 1996):

$$a = 1/2(\arcsin(\sqrt{x/(n+1)}) + \arcsin(\sqrt{(x+1)/(n+1)}))$$

where x = abundance of species in sample; n = total abundance of specimens in sample

The transformation reduces the possibility of Type I error by stabilizing sample variances. It also makes the data proportional, and thus eliminates some of the errors introduced by having different sample sizes.

## Analysis

### PCA of Entire Data Set

PCA of the correlation matrix for the entire data set was performed first. For this analysis only replicates samples were combined to form single, large samples. The PCA extracted three major principle components, which together accounted for >95% of the variability. According to the component loadings, the first principle component axis ordinated samples based primarily on the proportional abundance of *Mulinia congesta*, while the second principle component axis distributed samples based on the proportional abundance of *Chama congregata*. Both *Ostrea sculpturata* and *Crepidula costata* had high loadings on the third principle components axis, but the key to the ordination on this axis is probably the very high negative loading of *Chama congregata*, which implied that the third axis distributed samples based both on lack of *Chama congregata* and the presence of the other two species.

The samples were plotted in the new principle components space (Fig. 5.2), and each sample was connected to the sample from the stratigraphic horizon above and below it with lines, except for the samples from Lieutenant's Run, which plot in their own part of the PCA space, and will therefore be discussed separately. The path that each of the other stratigraphic sections threads through factor space as one moves up section has the same directionality for each of the measured sections.

One of the advantages of PCA is that supplemental data can be rather easily mapped onto the PCA diagram by a posteriori projection onto the existing PCA diagram. All of the Lower Rushmere samples plot together at the high end of the second principle component axis, while all of the Morgart's Beach samples cluster together at the high end of the first principle component axis. The Upper Rushmere samples usually have high scores on the third principle components axis, which ordinated samples based on both a lack of *Chama congregata* and the relatively high abundance of oysters and slipper snails. Therefore, the distribution of samples along the three principle axes is related to their stratigraphic position in the Rushmere-Morgart's Beach Members.

There is a paleoenvironmental gradient from the Lower Rushmere through Morgart's Beach transition. According to a sediment analysis by Barbour (pers. comm.), Lower Rushmere strata is composed of a rubbly sand, generally with less than 5% mud. Mud increases as one moves up section, so that in the Upper Rushmere, mud accounts for 5-20% of the sediment by weight. The Morgart's Beach sediment generally contains >20% mud. This paleoenvironmental gradient was

recognized at all localities except for Lieutenant's Run, where the percentage of mud was always less than 10%. Therefore it is perhaps not surprising that the LTR samples plot in their own section of principle components space, since the mud transition in the Upper Rushmere at other localities is lacking at Lieutenant's Run.

A second PCA was performed on a somewhat distilled version of the data set in order to more clearly see the patterns in the PCA. The data set was condensed by consolidating all samples taken from single stratigraphic horizons into single samples by adding all of the samples from that horizon, including both true replicate samples and samples from the same stratigraphic horizon at a locality, but from different sections. Each stratigraphic horizon at each locality therefore yielded a single data point in PCA space. The Lieutenant's Run samples were not included in this condensed data set.

PCA was performed on both the correlation and covariance matrices for this condensed matrix (Fig. 5.3). The correlation matrix produced a very similar result to that above, which should not be surprising, since it is essentially the same data. The covariance PCA also produced a similar pattern, although somewhat distorted. The covariance PCA weighs variables based on their absolute magnitude, and thus samples which contain a high abundance of a species with a high loading plot further out on the principle components axes than samples with only a high abundance value for that species. However, for my data, this extra weight does not appear to add much to the understanding of the relationships between samples.

An accumulated variability analysis was also performed on these two PCAs. Each eigenvector explains a certain percentage of the contained variability within a data set. In PCA, the first eigenvector explains the greatest percentage of the variability, with each subsequent eigenvector explaining less and less of the variability. This decay in the amount of variability explained can be graphically illustrated by either a scree graph or by a graph of cumulative variability explained (Fig. 5.4). For the covariance analysis, the first eigenvector accounted for 92% of the variability, while the second accounted for 5%, and the third for nearly 3% of the variability. All remaining eigenvectors account for much less than 1% of the variability. In contrast, for the correlation PCA, the first eigenvector accounted for 51% of the variability, the second for 25% of the variability, and the third for 15% of the variability. The correlation PCA therefore seems to spread the data out better in three dimensions than the covariance PCA. The correlation PCA will be used for the rest of the PCAs in this analysis, since it seems to perform better when exploring and was not as heavily influenced by differing sample size.

Based on the correlation PCA, two major end-member fossil assemblage within the Rushmere to Morgart's Beach transition can be recognized - the *Chama congregata* dominated assemblage of the Lower Rushmere, and the *Mulinia congesta* dominated assemblage of the Morgart's Beach. Between these two end members there appear to be a variety of transitional assemblages that form during the paleoenvironmental shift from a rubbly to a muddy bottom. The transitional grouping is not nearly as tight as the Lower Rushmere and Morgart's Beach groupings, and if they have any distinguishing characteristic it is that they do not contain a high abundance of either *Mulinia congesta* or *Chama congregata*. Samples from this Upper Rushmere transitional group will be examined together, but based on the PCA, they should not be expected to be as similar to each other as the two end members.

### **Paleocommunity Classification and Analysis**

Fossil assemblages that can be shown to be similar, e.g. by their clustering in principle components space, can be called "paleocommunity types" using the terminology of Bennington and Bambach (1996). I named the *Chama congregata* dominated assemblage the Rubbly Bottom Paleocommunity Type (RBPT), and the *Mulinia congesta* dominated assemblage the Muddy Bottom Paleocommunity Type (MBPT). The samples that plot in the transitional zone do not form tight clusters in principle components space like the RBPT and MBPT, so they have not been given the "paleocommunity type" designation.

The sections from Lieutenant's Run do not follow the same path through factor space as the sections from the lower coastal plain. Lieutenant's Run is on the edge of the Yorktown outcrop belt, where Atlantic Coastal Plain sedimentary deposits onlap the crystalline rocks of the Piedmont. Because of its position, the LTR locality was both in shallower water than the other localities, and closer to the terrigenous source area. The clastic portion of the LTR sediments contains not only coarse sand, but also occasionally large pebbles and such terrigenous debris as tiny bits of amber. It should therefore not be surprising that the LTR samples plot differently from the samples from other localities. However, some of the LTR samples contain a similar assemblage to that found in the RBPT, and do plot near the RBPT samples in PCA space. Because of this similarity, those LTR samples were analyzed with the RBPT samples from the lower coastal plain. Two LTR samples (LTR 4.5 and LTR 4.6) contain a somewhat similar assemblage to that found in the MBPT at other localities, and these were included in the MBPT analysis. There is no paleoenvironmental transition in the Upper Rushmere at Lieutenant's Run, and therefore the samples that do not fit into the MBPT or RBPT will not be included in the "transitional" sample of the Upper Rushmere from other localities.

The samples in the defined subsets are similar enough to each other to plot near each other in a PCA space defined by the distribution of all samples, and they form natural sub groupings for further analysis. Just because samples are similar does not mean that they are identical. Each of the subgroups needed to be analyzed separately in order to determine whether or not the assemblages form coherent paleocommunities, instead of just being similar enough to group together as paleocommunity types.

Four analyses were done on each sub grouping. First, PCA were performed on each group of samples to determine the relationships among those samples. Second, the correlation matrix itself was analyzed to determine whether or not samples from different localities were highly correlated. Third, a constancy analysis was run for each group at each locality to determine whether the local paleocommunities were internally consistent. Finally, MANOVA was performed to test for significant differences among samples.

### **Rubblly Bottom Paleocommunity Type (RBPT)**

The rubbly appearance in the basal Rushmere is the result of the abundance of the round, thick shelled, weakly cemented bivalve *Chama congregata*. Where *C. congregata* is very abundant, it covers the sea floor creating a three dimensional substrate with plenty of crevices and hard attachment surfaces for other organisms. Similar substrate conditions are present in pebbly nearshore environments; in the case of the Yorktown RBPT, the pebble-sized clasts are replaced by *C. congregata*. The most important factor in making this rubbly substrate was therefore the overall abundance of the "gravel" grain size.

A total of 31 samples from three localities (Lieutenant's Run (LTR), Kingsmill (KGM), and the Nottoway River (NWR)) were classified as RBPT. All samples are from the lower Rushmere Member, and all cluster together at one end of the principle component space determined by analyzing the entire data set. The 31 samples contained 7,872 specimens which were assigned to 105 species. The most abundant species, *C. congregata* accounted for 2,847 (36%) of those specimens. Fifty-six species (53%) are represented by fewer than 10 specimens, and 12 species (11%) occur only once. The most abundant species and their life habits both overall and at each locality are listed in table 5.1.

**Table 5.1:** Most abundant species in the RBPT

<b>NWR</b>	<b>n=13</b>	<b>s=2629</b>		
<i>Chama congregata</i>	13(100%)	1253	cement. epifaun. susp. feed.	rubble, hard surfaces
<i>Cyclocardia granulata</i>	13(100%)	228	shallow infaun. susp. feed.	sand, gravel, rubble
<i>Crepidula costata</i>	13(100%)	176	epifaun. susp. feed.	attached to rubble
<i>Astarte undulata</i>	13(100%)	141	shallow infaun. susp. feed.	coarse substrate,
<i>Chesapecten madisonius</i>	13(100%)	105	epibyssate susp. feed.	sand or mud
<i>Semele sp. A</i>	13(100%)	62	shallow infaun. siph. susp. feed.	sand
<i>Pycnodonte sp.</i>	8(62%)	59	epibyssate susp. feed.	hard or soft substrate
<i>Ostrea sculpturata</i>	8(62%)	48	cement. epifaun. susp. feed.	hard or soft substrate
<i>Plicatula marginata</i>	11(85%)	47	cement. epifaun. susp. feed.	attached to rubble
<i>Marvcrassatella undulata</i>	12(92%)	43	medium infaun. susp. feed.	n/a
<b>LTR</b>	<b>n=12</b>	<b>s=3847</b>		
<i>Mulinia congesta</i>	12(100%)	1347	shallow infaun. siph. susp. feed.	large range of substrata
<i>Chama congregata</i>	12(100%)	827	cement. epifaun. susp. feed.	rubble, hard surfaces
<i>Plicatula marginata</i>	12(100%)	465	cement. epifaun. susp. feed.	attached to rubble
<i>Ostrea sculpturata</i>	12(100%)	247	cement. epifaun. susp. feed.	hard or soft substrate
<i>Cyclocardia granulata</i>	9(75%)	139	shallow infaun. susp. feed.	sand, gravel, rubble
<i>Chesapecten madisonius</i>	10(83%)	70	epibyssate susp. feed.	sand or mud
<i>Astarte concentrica</i>	7(58%)	68	shallow infaun. susp. feed.	coarse substrate,
<i>Mercenaria sp.</i>	12(100%)	67	medium infaun. susp. feed.	various substrata
<i>Noetia incile</i>	12(100%)	49	nest. epibyssate susp. feed.	nestling in crevices
<i>Crepidula costata</i>	11(92%)	45	epifaun. susp. feed.	attached to rubble
<b>KGM</b>	<b>n=6</b>	<b>s=1396</b>		
<i>Chama congregata</i>	6(100%)	767	cement. epifaun. susp. feed.	rubble, hard surfaces
<i>Ostrea sculpturata</i>	6(100%)	129	cement. epifaun. susp. feed.	hard or soft substrate
<i>Cyclocardia granulata</i>	6(100%)	81	shallow infaun. susp. feed.	sand, gravel, rubble
<i>Striarca centenaria</i>	6(100%)	52	nest. epibyssate susp. feed.	nestling in crevices on hard substrate
<i>Gemma magna</i>	5(83%)	48	shallow infaun. siph. susp. feed.	sand or mud flats
<i>Noetia incile</i>	5(83%)	39	nest. epibyssate susp. feed.	nestling in crevices
<i>Astarte undulata</i>	6(100%)	38	shallow infaun. susp. feed.	coarse substrate
<i>Crepidula costata</i>	5(83%)	19	epifaun. susp. feed.	attached to rubble
<i>Glycymeris americana</i>	5(83%)	16	shallow infaun. susp. feed.	n/a
<i>Ctena speciosa</i>	6(100%)	16	shallow infaun. luc. susp. feed.	n/a
<b>Total</b>	<b>n=31</b>	<b>s=7872</b>		
<i>Chama congregata</i>	31(100%)	2847	cement. epifaun. susp. feed.	rubble, hard surfaces
<i>Mulinia congesta</i>	14(45%)	1361	shallow infaun. siph. susp. feed.	various substrata
<i>Plicatula marginata</i>	27(87%)	524	cement. epifaun. susp. feed.	attached to rubble
<i>Cyclocardia granulata</i>	28(90%)	448	shallow infaun. susp. feed.	sand, gravel, rubble
<i>Ostrea sculpturata</i>	26(84%)	424	cement. epifaun. susp. feed.	hard or soft substrate
<i>Crepidula costata</i>	29(94%)	240	epifaunal susp. feed.	attached to rubble
<i>Astarte undulata</i>	28(91%)	211	shallow infaun. susp. feed.	coarse substrate
<i>Chesapecten madisonius</i>	26(84%)	187	epibyssate susp. feed.	sand or mud
<i>Noetia incile</i>	25(81%)	100	nest. epibyssate susp. feed.	nestling in crevices
<i>Marvcrassatella undulata</i>	23(74%)	79	shallow infaun. susp. feed.	n/a

### PCA

A PCA was performed on the correlation matrix of the RBPT samples (Fig. 5.5). The PCA extracted two major principle components. Principle component one had high loadings for *Chama congregata*, *Crepidula costata*, *Cyclocardia granulata*, and *Astarte undulata*, all of which were more

abundant in the KGM and NWR samples than the LTR samples. Principle component two had high loadings for *Mulinia congesta*, *Ostrea scupturata*, and *Plicatula marginata*, all of which had a higher relative abundance in the samples from Lieutenant's Run. Thus, there is a separation between LTR samples and the other samples on both axes.

The KGM and NWR samples plot together at high values of principle component one, and low values of principle component two. However, while they plot in the same general area, the NWR samples form a tight cluster separate from the KGM cluster. So, in addition to separating the LTR samples from the other samples, the PCA shows separation between the KGM and NWR samples. This implies that while all these samples plotted together in one part of the PCA for the entire data set, the RBPT differs from locality to locality.

### Correlation Analysis

A correlation matrix was determined for the RBPT samples. The correlation values were grouped by locality, and the distribution of pairwise correlation of samples within localities and between localities were determined. The data was graphed to show the distribution of correlation values for both (Fig. 5.6A).

Comparisons of samples within each locality display higher mean, minimum, and maximum correlation values than comparisons between localities. The Lieutenant's Run samples have much lower correlation values with the Kingsmill and Nottoway River samples than the correlation of the sample of those two localities with each other.

Even though the distribution of correlation values is not normal, and the distribution of this function probably does not conform to the assumptions necessary for standard analysis of variance (ANOVA), an ANOVA was performed on the distribution of correlation values both within and between sampling localities. This ANOVA indicates that the mean correlation values of the two groups were significantly different ( $p=0.0001$ ). A more appropriate non-parametric Mann-Whitney U test, also revealed significant difference in the mean values ( $p=0.0001$ ), as did all other non-parametric tests applied to the two groups of correlation values.

The correlation value is greatly effected by variables with high values, which in this case would be the most abundant species. Since all samples in the rubbly bottom paleocommunity type contain an abundance of *C. congregata*, removing that species from the analysis should lower all values in the correlations matrix, but high values will be more meaningful than high values prior to

removal. The analysis was run again on the RBPT with *C. congregata* removed from the data matrix (Fig 5.6B). Once again, ANOVA revealed that the mean correlation values of pairs of samples from the same locality was significantly higher than samples from different localities ( $p=0.0001$ ), a result verified by Mann-Whitney U tests ( $p=0.0001$ ) and all other non-parametric tests applied. There is a very large discrepancy between the within and between locality groupings. The removal of *C. congregata* eliminated much of the apparent similarity between localities.

The LTR samples yielded very low correlation values with samples from the other two localities. The most obvious faunal difference between LTR samples and those of other localities is that the small, opportunistic bivalve *Mulinia congesta* is very abundant in LTR samples, but not in samples from the RBPT at other localities. To determine the effect of this species, *M. congesta* was removed from the data set, and the analysis was rerun in order to determine its effect on the correlation matrix (Fig. 5.6C). As expected, the mean, minimum, and maximum correlations all increased somewhat with the exclusion of *M. congesta*, but the within-locality correlations were still higher than the between-locality correlations. ANOVA revealed that the mean correlation values of pairs of samples from the same locality were significantly higher than between samples from different localities ( $p=0.0001$ ), a result verified by Mann-Whitney U tests ( $p=0.0001$ ) and all other non-parametric tests applied. The differences in the expression of this paleocommunity at the three localities can not be accounted for by the removal of very abundant species.

The correlation data was also broken down by locality in order to examine the apparent differences more closely. The distributions of the NWR, LTR, and KGM correlation comparisons can be found in Fig. 7.

The Nottoway River locality yielded 13 RBPT samples. The results of comparisons of pairs of NWR samples versus pairs of NWR and non-NWR samples are summarized in Table 5.2.

**Table 5.2** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples.

	Mean	ANOVA	Mann-Whitney U
NWR vs NWR	.972	-	-
NWR vs KGM	.901	no ( $p=.066$ )	yes ( $p=.0001$ )
NWR vs LTR	.748	yes ( $p=.0001$ )	yes ( $p=.0001$ )

The Lieutenant's Run locality yielded 12 samples which were assigned to the RBPT. The results of comparisons of pairs of LTR samples versus pairs of LTR and non-LTR samples are summarized in Table 5.3.

**Table 5.3** Mean values and significance of difference between correlation coefficients of LTR pairs, and pairs of LTR and non-LTR samples.

	Mean	ANOVA	Mann-Whitney U
<b>LTR vs LTR</b>	.915	-	-
<b>LTR vs KGM</b>	.800	yes (p=.0001)	yes (p=.0001)
<b>LTR vs NWR</b>	.748	yes (p=.0001)	yes (p=.0001)

The Kingsmill locality yielded 6 samples which were assigned to the RBPT. The results of comparisons of pairs of KGM samples versus pairs of KGM and non-KGM samples are summaries in Table 5.4.

**Table 5.4** Mean values and significance of difference between correlation coefficients of KGM pairs, and pairs of KGM and non-KGM samples.

	Mean	ANOVA	Mann-Whitney U
<b>KGM vs KGM</b>	.960	-	-
<b>KGM vs LTR</b>	.800	yes (p=.0001)	yes (p=.0001)
<b>KGM vs NWR</b>	.901	no (p=.0900)	yes (p=.0330)

As expected from their relative position in the PCA of the RBPT, the NWR and KGM samples are very similar to each other according to the analysis of the correlation matrix. In every case, comparison of LTR to non-LTR samples yielded significant differences, so the LTR samples are rather dissimilar from the samples from the other two localities, also as expected from the PCA.

The within locality comparisons are consistently high for all localities. Even without the most abundant species, *C. congregata*, the within locality comparisons have high similarity. The between locality comparisons are consistently lower than the within locality comparisons, and removal of *C. congregata* eliminated much of the apparent similarity.

### Constancy Index

A constancy analysis was performed by pooling all samples from a single locality, and determining the constancy, and then repeating that analysis on all sample of the RBPT (Table 5.5).

All of the localities have high internal consistency (.862 to .872). When all localities are combined, the constancy value drops to .755.

**Table 5.5** Constancy values ( $C_a$ ) for RBPT samples.

	samples	$C_a$
<b>NWR</b>	12	.863
<b>LTR</b>	9	.872
<b>KGM</b>	6	.862
<b>all</b>	27	.755

Unfortunately, the constancy values themselves do not have statistical significance. However, the conclusion that the samples from each locality are more similar to each other than to samples from other localities is consistent with the results of the PCA and correlation matrix analyses, even though the method of determination was much different.

## MANOVA

MANOVAs were performed on the 20 most abundant species in the RBPT (Table 5.6) for the three localities at which the RBPT was recognized.

**Table 5.6** The 20 most abundant species of the RBPT.

Taxon	Specimens
<i>Chama congregata</i>	1288
<i>Mulinia congesta</i>	299
<i>Crepidula costata</i>	201
<i>Cyclocardia granulata</i>	180
<i>Ostrea sculpiurata</i>	177
<i>Plicatula marginata</i>	150
<i>Astarte undulata</i>	111
<i>Chesapecten madisonius</i>	94
<i>Noetia incile</i>	44
<i>Semele</i> sp. A	42
<i>Marvcrassatella undulata</i>	39
<i>Lunatia heros</i>	35
<i>Crepidula plana</i>	34
<i>Corbula inaequalis</i>	33
<i>Pycnodonte</i> sp.	32
<i>Corbula retusa</i>	29
<i>Glycymeris americana</i>	28
<i>Gemma magna</i>	28
<i>Mercenaria campechiensis</i>	27
<i>Striarca centenaria</i>	27

A MANOVA of all RBPT samples grouped by locality revealed that there are differences in the three groups that are significant at the  $p < 0.0001$  level. MANOVAs were also performed on each pair of localities (KGM and LTR, KGM and NWR, and LTR and NWR), which also all yielded difference significant at the  $p < 0.0001$  level. Samples from different localities are dissimilar enough that the null hypothesis that they are the same can be rejected at the 95% confidence level. As expected from the PCA, correlation analysis, and constancy analysis, samples from the RBPT at different localities are statistically dissimilar.

### **The Muddy Bottom Paleocommunity Type (MBPT)**

Samples of the MBPT sediments generally contain >20% mud by weight (Barbour, pers. comm.). At the time of deposition the bottom conditions were probably very soupy, especially compared to the RBPT. At outcrop, the change from the top of the transition zone to the base of the MBPT appears to be a sharp boundary, and in fact this marks the boundary between the Rushmere and Morgart's Beach Members of the Yorktown Formation. On closer examination, the boundary is not very lithologically sharp (Barbour, pers. comm.), but rather gradational. There is an apparently abrupt change in the fauna at this boundary, but this too is a bit of a mirage. The real change at this boundary is in the size of shelly remains. Many of the species that are abundant in the transition are also present in the MBPT, but they do not appear to have grown as large under MBPT conditions as they did under previous conditions. There appears to be some sort of threshold reached that causes this abrupt-looking change in the fauna even though the paleoenvironmental conditions change gradually.

A total of 54 samples of the MBPT were collected from the 5 collection localities. The majority of these samples (46) came from Day's Point, where intensive replicate sampling was performed. The other localities each yielded 5 or fewer MBPT samples (BWB: 5; NWR: 4; KGM: 2; LTR: 2).

All MBPT samples contain *Mulinia congesta* at relatively high abundances. The average relative abundance of *M. congesta* varies greatly from locality to locality from a high of 91.9% of the total abundance NWR samples to a low of 32.5% in DYP samples. The total abundance also varied greatly. At DYP, 46 samples yielded 1,575 specimens of *M. congesta*, while at NWR, 2,226 specimens were liberated from only 4 samples. Other common taxa in the MBPT are listed in Table 5.7.

**Table 5.7** Common species of the MBPT.

<b>TOTAL</b>	<b>Life Habit</b>	<b>N=8,707</b>	<b>S=54</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	4671(53.1%)	54(100.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	472(5.4%)	44(81.5%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	376(4.3%)	52(98.1%)
<i>Yoldia laevis</i>	01.shallow infaunal deposit feeder	321(3.6%)	51(94.4%)
<i>Dosinia acetabulum</i>	08.medium infaunal siph susp feeder	289(3.3%)	47(87.0%)
<i>Corbula inaequalis</i>	07.shallow infaunal siph susp feeder	282(3.2%)	45(83.3%)
<i>Corbula cuneata</i>	07.shallow infaunal siph susp feeder	272(3.2%)	43(80.0%)
<i>Corbula retusa</i>	07.shallow infaunal siph susp feeder	172(2.0%)	44(81.5%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	142(1.6%)	11(20.4%)
<i>P. multilineatus</i>	10.shallow infaunal lucinid susp feed	128(1.5%)	46(85.2%)
<b>DYP</b>	<b>Life Habit</b>	<b>N=4,842</b>	<b>S=43</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	1575(32.5%)	43(100.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	385(8.0%)	36(83.7%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	289(6.0%)	43(100.0%)
<i>Dosinia acetabulum</i>	08.medium infaunal siph susp feeder	283 (5.8%)	42(97.7%)
<i>Yoldia laevis</i>	01.shallow infaunal deposit feeder	275(5.7%)	42(97.7%)
<i>Corbula inaequalis</i>	07.shallow infaunal siph susp feeder	262(5.4%)	42(97.7%)
<i>Corbula cuneata</i>	07.shallow infaunal siph susp feeder	255(5.3%)	40(93.0%)
<i>Corbula retusa</i>	07.shallow infaunal siph susp feeder	156(3.2%)	42(97.7%)
<i>P. multilineatus</i>	10.shallow infaunal lucinid susp feed	113(2.3%)	41(95.3%)
<i>Abra subreflexa</i>	02.shallow infaunal tellinid dep feeder	103(2.1%)	33(76.7%)
<b>NWR</b>	<b>Life Habit</b>	<b>N=2,421</b>	<b>S=4</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	2226(91.9%)	4(100.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	49(2.0%)	4(100.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	22(0.9%)	4(100.0%)
<i>Yoldia laevis</i>	01.shallow infaunal deposit feeder	21(0.9%)	4(100.0%)
<i>Cyclocardia granulata</i>	06.shallow infaunal suspension feeder	16(0.7%)	4(100.0%)
<i>Astarte undulata</i>	06.shallow infaunal suspension feeder	16(0.7%)	4(100.0%)
<i>P. multilineatus</i>	10.shallow infaunal lucinid susp feed	8(0.3%)	3(75.0%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	7(0.3%)	3(75.0%)
<i>Turritella sp.</i>	12.attached epifaunal suspension feeder	4(0.2%)	4(100.0%)
<b>LTR</b>	<b>Life Habit</b>	<b>N=778</b>	<b>S=2</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	371(47.7%)	2(100.0%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	113(14.5%)	2(100.0%)
<i>Plicatula marginata</i>	04.cemented epifaunal suspension feeder	92(11.8%)	2(100.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	27(3.5%)	2(100.0%)
<i>Astarte concentrica</i>	06.shallow infaunal suspension feeder	22(2.8%)	2(100.0%)
<i>Cyclocardia granulata</i>	06.shallow infaunal suspension feeder	21(2.7%)	2(100.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	14(1.8%)	2(100.0%)
<i>Noetia incile</i>	05.nestling suspension feeder	11(1.4%)	2(100.0%)
<i>M. campechiensis</i>	08.medium infaunal siph susp feeder	10(1.3%)	2(100.0%)
<i>Corbula inaequalis</i>	07.shallow infaunal siph susp feeder	8(1.0%)	2(100.0%)
<b>KGM</b>	<b>Life Habit</b>	<b>N=324</b>	<b>S=2</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	154(47.5%)	2(100.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	34(10.5%)	2(100.0%)
<i>M. campechiensis</i>	08.medium infaunal siph susp feeder	19(5.9%)	2(100.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	18(5.6%)	2(100.0%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	16(4.9%)	2(100.0%)
<i>Corbula inaequalis</i>	07.shallow infaunal siph susp feeder	11(3.4%)	2(100.0%)
<i>Corbula cuneata</i>	07.shallow infaunal siph susp feeder	9(2.8%)	2(100.0%)
<i>Corbula retusa</i>	07.shallow infaunal siph susp feeder	8(2.5%)	2(100.0%)

<i>Plicatula marginata</i>	04.cemented epifaunal suspension feeder	5(1.5%)	2(100.0%)
<i>Noetia incile</i>	05.nestling suspension feeder	5(1.5%)	2(100.0%)
<b>BWB</b>	<b>Life Habit</b>	<b>N=324</b>	<b>S=5</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	345(79.9%)	5(100.0%)
<i>Yoldia laevis</i>	01.shallow infaunal deposit feeder	23(5.3%)	4(80.0%)
<i>Lucinisca cribrarius</i>	10.shallow infaunal lucinid susp feed	15(3.5%)	4(80.0%)
<i>Lunatia heros</i>	16.vagrant epifaunal v semi-infaunal	6(1.4%)	2(40.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	6(1.4%)	2(40.0%)
<i>Turritella sp.</i>	12.attached epifaunal suspension feeder	5(1.2%)	5(100.0%)
barnacles	-	5(1.2%)	5(100.0%)
<i>Pitar sayana</i>	07.shallow infaunal siph susp feeder	5(1.2%)	2(40.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	4(0.9%)	3(60.0%)
<i>Corbula retusa</i>	07.shallow infaunal siph susp feeder	3(0.7%)	1(20.0%)

In terms of occurrence, the deposit feeder *Yoldia laevis* (94.4%) and oyster *Ostrea sculpturata* (98.1%) have the highest frequency next to *M. congesta* (100.0%). The other abundant species range in occurrence frequency from 20.4% (*Chama congregata*) to 87.0% (*Dosinia acetabulum*).

### PCA

PCA of the MBPT samples yielded 3 major principle components which together accounted for 95% of the total variability (Fig. 5.8). The first principle component ordinated samples based primarily on the relative abundance of *Mulinia congesta*, although *Crepidula costata*, *Yoldia laevis*, *Ostrea sculpturata*, and *Dosinia acetabulum* also have relatively high loadings on this axis.

The second principle component has high loadings of all those species except for *M. congesta*, which had a high negative loading. Therefore, this axis seems to be ordinating data based on low relative abundances of *M. congesta*. The lowest relative abundances are found at Day's Point, and many of the DYP samples plot high on this axis.

The third principle components has high loading values for *Yoldia laevis*, *Abra subreflexa*, *Dosinia acetabulum*, *Pitar sayana*, and *Parvilucina multilineatus*. This principle component spreads out the DYP samples quite a bit, since those species are rather variable at Day' Point, but samples from the other localities all plot near zero on this axis.

The plot of principle component one versus two shows an arcuate distribution of data points. This may indicate non-linearity in the data that can not be resolved using PCA. In general, the NWR, KGM, LTR, and BWB samples all plotted at low values on all three axes, while the larger DYP group was more dispersed in the PCA space.

The tight clusters seen in the RBPT samples are not seen in the PCA of the MBPT. However, other than Day's Point, the localities plot together reasonably well.

### Correlation Analysis

A correlation matrix was determined for the samples of the MBPT. Correlation values were grouped based on the localities the two samples in each correlation, and the distribution of these localities determined. The distributions of pairs from the same locality and pairs in which the two members are from different localities is plotted in figure 9A.

While the distributions appear to be very similar, especially compared to the same plot of RBPT samples, according to an ANOVA, there is still a significant difference ( $p=.0282$ ). However, the distribution is rather clearly non-normal, so non-parametric testing was also performed. A Mann Whitney U found no significant difference ( $p=.194$ ). Other non-parametric tests were equally ambiguous, so there is no strong evidence that the distributions were not drawn from the same underlying distribution, and thus the null hypothesis that the two distributions are the same can not be rejected.

As with the RBPT samples, MBPT samples contain a hyper-abundance of one species. The RBPT samples all contained *Chama congregata*, while the MBPT samples all contain abundant *Mulinia congesta*. Correlation can be greatly effected by the over abundance of a single species. To test the similarity of the non-*Mulinia* portion of the samples, *M. congesta* was removed from the data matrix, and the correlation analysis re-run. Those distributions are plotted on Figure 9B.

Removing *M. congesta* decreases the correlation values of both the pairs from the same locality and pairs with samples from different localities. However, the change in the between locality pairings (.491) is much greater than the change in the within locality pairings (.176), indicating that the non-*Mulinia* component of samples from the same locality are more similar to each other than they are to samples from other localities.

ANOVA indicates that the means of the distributions of the non-*Mulinia* component are significantly different ( $p=.0001$ ). While the distributions appear almost normal, non-parametric tests were also applied. A Mann-Whitney U test indicated a significant difference in the means ( $p=.0001$ ), as did every other non-parametric test applied. As with *C. congregata* of the RBPT, once *M. congesta* is removed, the apparently high similarity between different localities disappears.

The correlation analysis was also performed for each locality individually versus the other localities. Only two sample each were collected from Kingsmill and Lieutenant's Run. Therefore, each locality yielded only a single correlation value for comparisons within locality - e.g., the comparison of one KGM sample to the other KGM sample. With only a single data point, no examination of distribution can be performed, so the KGM and LTR samples have not been analyzed separately. They will, however be included in the analysis of the localities with more samples. The distributions of correlation values for the DYP, BWB, and NWR were plotted in Fig. 5.10.

Day's Point had the lion's share of MBPT samples, and thus the largest number of correlation coefficient comparisons. The results of comparisons of pairs of DYP samples versus pairs of DYP and non-DYP samples are summaries in Table 5.8.

**Table 5.8** Mean values and significance of difference between correlation coefficients of DYP pairs, and pairs of DYP and non-DYP samples.

	Mean	ANOVA	Mann-Whitney U
<b>DYP vs DYP</b>	.833	-	-
<b>DYP vs. NWR</b>	.819	no (p=.190)	no (p=.702)
<b>DYP vs. BWB</b>	.819	no (p=.168)	no (p=.497)
<b>DYP vs. LTR</b>	.735	yes (p=.0001)	yes (p=.0001)
<b>DYP vs KGM</b>	.834	no (p=.952)	no (p=.938)

Other than LTR samples, DYP samples have rather high mean correlation values with the samples from other localities.

The Burwell's Bay locality yielded a smaller number of samples than Day's Point, but there are still enough pairwise comparisons to analyze. The results of comparisons of pairs of BWB samples versus pairs of BWB and non-BWB samples are summaries in Table 5.9.

**Table 5.9** Mean values and significance of difference between correlation coefficients of BWB pairs, and pairs of BWB and non-BWB samples.

	Mean	ANOVA	Mann-Whitney U
<b>BWB vs BWB</b>	.985	-	-
<b>BWB vs. DYP</b>	.819	yes (p=.0004)	yes (p=.0001)
<b>BWB vs. NWR</b>	.989	no (p=.438)	no (p=.454)
<b>BWB vs. KGM</b>	.930	yes (p=.0003)	yes (p=.0003)
<b>BWB vs LTR</b>	.881	yes (p=.0001)	yes (p=.0002)

With the exception of the comparison to NWR samples, BWB samples are more similar to each other than to samples from other localities according to the correlation coefficient comparison.

The Nottoway River locality yielded only 4 MBPT samples, but that is still sufficient for this analysis. The results of comparisons of pairs of NWR samples versus pairs of NWR and non-NWR samples are summaries in Table 5.10.

**Table 5.10** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples.

	Mean	ANOVA	Mann-Whitney U
NWR vs NWR	.996	-	-
NWR vs. DYP	.833	yes (p=.004)	yes (p=.0001)
NWR vs. BWB	.891	no (p=.141)	no (p=.05)
NWR vs. KGM	.944	yes (p=.010)	yes (p=.003)
NWR vs LTR	.893	yes (p=.005)	yes (p=.002)

With the exception of the comparison between NWR vs BWB correlation values, the correlation values of NWR versus NWR samples are significantly greater than the comparisons with other localities.

The results of the within and between locality correlation analysis are summarized in Table 5.11.

**Table 5.11** Summary of correlation coefficient for MBPT. Significant negative differences between the within locality mean correlation value and the between locality mean correlation values are indicated with a "yes."

	DYP	BWB	NWR
vs. DYP	-	yes	yes
vs. BWB	no	-	no
vs. NWR	no	no	-
vs. LTR	yes	yes	yes
vs. KGM	no	yes	yes

There are 7 significant differences in the summary table, and 5 results of no significant differences. As with the pooled data, the results when broken down by localities is somewhat ambiguous.

As before, the high abundance of *M. congesta* in the MBPT samples may be masking large differences in the non-*Mulinia* component of the MBPT samples. *M. congesta* was removed from

the data set, and the analysis of within and between locality correlation coefficients re-run. The distributions of correlation values for the DYP, BWB, and NWR were plotted in Fig. 5.11.

Since the largest number MBPT samples were collected from Day's Point, this group contains the largest number of correlation coefficient comparisons. The results of comparisons of pairs of DYP samples versus pairs of DYP and non-DYP samples are summaries in Table 5.12.

**Table 5.12** Mean values and significance of difference between correlation coefficients of DYP pairs, and pairs of DYP and non-DYP samples, with *M. congesta* removed.

	Mean	ANOVA	Mann-Whitney U
<b>DYP vs DYP</b>	.661	-	-
<b>DYP vs. NWR</b>	.468	yes (p=.0001)	yes (p=.0001)
<b>DYP vs. BWB</b>	.287	yes (p=.0001)	yes (p=.0001)
<b>DYP vs. LTR</b>	.096	yes (p=.0001)	yes (p=.0001)
<b>DYP vs KGM</b>	.463	yes (p=.0001)	yes (p=.0001)

Without *M. congesta* in the data set, DYP samples are clearly dissimilar from non-DYP samples.

The Burwell's Bay locality yielded a smaller number of samples than Day's Point, but there are still enough pairwise comparisons to analyze. The results of comparisons of pairs of BWB samples versus pairs of BWB and non-BWB samples are summaries in Table 5.13.

**Table 5.13** Mean values and significance of difference between correlation coefficients of BWB pairs, and pairs of BWB and non-BWB samples, with *M. congesta* removed

	Mean	ANOVA	Mann-Whitney U
<b>BWB vs BWB</b>	.420	-	-
<b>BWB vs. DYP</b>	.287	yes (p=.031)	no (p=.061)
<b>BWB vs. NWR</b>	.298	no (p=.169)	no (p=.218)
<b>BWB vs. KGM</b>	.126	yes (p=.0001)	yes (p=.0002)
<b>BWB vs LTR</b>	.003	yes (p=.004)	yes (p=.012)

With the exception of the comparison to NWR samples, BWB samples tend to be more similar to each other than to samples from other localities according to the correlation coefficient comparison. However, the correlation values are very low for both between locality and with BWB sample pairs (.420), so the similarity between the distributions may be as much the result of very low correlation values in the BWB vs BWB comparisons as any high correlation between the localities.

The Nottoway River locality yielded only 4 MBPT samples, but that is still sufficient for this analysis. The results of comparisons of pairs of NWR samples versus pairs of NWR and non-NWR samples are summaries in Table 5.14.

**Table 5.14** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples with *M. congesta* removed.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.774	-	-
<b>NWR vs. DYP</b>	.468	yes (p=.0002)	yes (p=.0004)
<b>NWR vs. BWB</b>	.298	yes (p=.0001)	yes (p=.0004)
<b>NWR vs. KGM</b>	.164	yes (p=.0045)	yes (p=.0006)
<b>NWR vs LTR</b>	.477	yes (p=.0001)	yes (p=.002)

Without *M. congesta* in the correlation analysis, there is little similarity between NWR samples, and samples from other localities.

The results of the within and between locality correlation analysis with *M. congesta* removed are summarized in Table 5.15.

**Table 5.15** Summary of correlation coefficient for MBPT, with *M. congesta* removed.

Significant negative differences between the within locality mean correlation value and the between locality mean correlation values are indicated with a "yes."

	DYP	BWB	NWR
<b>vs. DYP</b>	-	yes	yes
<b>vs. BWB</b>	yes	-	yes
<b>vs. NWR</b>	yes	no	-
<b>vs. LTR</b>	yes	yes	yes
<b>vs. KGM</b>	yes	yes	yes

There is only one situation in which the analysis did not yield a significant difference between the within and between locality distributions of correlation values. In that single case, the correlation values of the correlation values of BWB vs BWB samples were extremely low to begin with (mean = .420), and thus the equally low mean similarity value of BWB vs NWR samples (.298) was not found to be significantly different. Unlike the analysis of the entire data set, the analysis of the non-*Mulinia* component of the data set is unambiguous - there samples from a single locality are more similar to each other than samples from other localities.

The correlation values are consistently high for within locality comparisons, and the between locality comparisons are consistently lower than the within locality comparisons. Removal

of the very abundant species *M. congesta* eliminated most of the apparent similarity between localities, but the within locality numbers remained relatively high.

### Species Constancy

A constancy analysis was performed for each locality in the MBPT, and for all pooled samples in the MBPT (Table 5.16).

**Table 5.16** Species constancy ( $C_a$ ) for MBPT samples.

	samples	$C_a$
<b>DYP</b>	43	.866
<b>NWR</b>	4	.985
<b>BWB</b>	5	.905
<b>LTR</b>	2	.936
<b>KGM</b>	2	.948
<b>all</b>	56	.847

As with the RBPT constancy analysis, constancy was higher for groups taken from single localities than from all localities pooled. Because of the great number of samples from Day's Point, the  $C_a$  value for the pooled data set must have been strongly influenced by the structure present in the DYP samples. When each locality in the analysis was given equal weight (by pooling all samples from each locality, and then pooling all localities together and dividing by the number of localities), the constancy of the pooled data set only dropped to .831.

The very high abundance of *M. congesta* in most MBPT samples, coupled with the high occurrence of the small opportunist in all MBPT samples could inflate the constancy value for the MBPT samples. A second constancy analysis was run with *M. congesta* removed from the data set (Table 5.17).

**Table 5.17** Species constancy ( $C_a$ ) for MBPT samples, and species constancy with *M. congesta* removed ( $C_a'$ ).

	samples	$C_a$	$C_a'$	$\Delta C_a$
<b>DYP</b>	43	.866	.802	-.064
<b>NWR</b>	4	.985	.821	-.164
<b>BWB</b>	5	.905	.526	-.379
<b>LTR</b>	2	.936	.888	-.048
<b>KGM</b>	2	.948	.900	-.048
<b>all</b>	56	.847	.673	-.174

As expected, in every case, the constancy value dropped, although in some cases much less than others. Removing *M. congesta* from caused the most severe drop in the constancy of BWB samples, perhaps indicating that those samples do not contain as consistent a species pool as the original high constancy value might indicate. The samples from Burwell's Bay had much lower correlation values than the other localities in the correlation matrix analysis of the non-*Mulinia* component. While all the values dropped, all the locality constancy measures but BWB are still higher than the pooled data set of all MBPT samples.

Other than the BWB samples, the constancy analysis confirms the results of the PCA analysis and the correlation matrix analysis - there is higher species constancy within localities than among all pooled localities.

### MANOVA

MANOVAs were performed on the 18 most abundant species in the MBPT (Table 5.18) for the five localities at which the MBPT was recognized (LTR, KGM, NWR, BWB, and DYP).

**Table 5.18** The 18 most abundant species of the MBPT.

<b>Taxon</b>	<b>Specimens</b>
<i>Mulinia congesta</i>	4671
<i>Crepidula costata</i>	472
<i>Ostrea sculpiurata</i>	376
<i>Yoldia laevis</i>	321
<i>Dosinia acetabulum</i>	289
<i>Corbula inaequalis</i>	282
<i>Corbula cuneata</i>	272
<i>Corbula retusa</i>	172
<i>Chama congregata</i>	142
<i>Parvilucina multilineatus</i>	128
<i>Chesapecten madisonius</i>	115
<i>Abra subreflexa</i>	105
<i>Plicatula marginata</i>	101
<i>Lucinisca cribrarius</i>	99
<i>Macoma virginiana</i>	77
<i>Semele</i> sp. A	69
<i>Carolinapecten eboreus</i>	59
<i>Marvcrassatella undulata</i>	57

A MANOVA of all MBPT samples grouped by locality revealed that there are differences between the localities that are significant at the  $p < 0.0001$  level. MANOVAs were also performed on each pair of localities for which there were more than 2 samples (BWB and DYP, BWB and NWR, DYP and NWR), which also all yielded difference significant at the  $p < .0001$  level. Samples from

different localities are dissimilar enough that the null hypothesis that they are the same can be rejected at the 95% confidence level. As expected from the PCA, correlation analysis, and constancy analysis, samples from the MBPT at different localities are statistically dissimilar.

### Transition Zone

The sediment of the transition zone of the between the basal Rushmere RBPT and the Morgart's Beach MBPT generally contains between 5-20% mud by weight. The base of the transition zone is characterized faunally by the loss of *Chama congregata* while *Mulinia congesta* commonly is found in abundance near the top of the transition zone. Paleoenvironmental conditions within the transition zone were clearly not stable over the entire period during which it was deposited, and thus there is no single paleocommunity type for this zone. However, since every locality except Lieutenant's Run experienced the same basic paleoenvironmental change between the RBPT and MBPT, by examining the fossil assemblages present at each locality, we can determine whether or not there is a coordinated faunal response to this paleoenvironmental change at each locality.

A total of 30 samples of the transition zone were collected from the 4 collection localities. Unlike the MBPT, similar number of samples were taken from the the transition zone at most of these localities: BWB: 6 samples; DYP: 11 samples; NWR: 10 samples; KGM: 3 samples. The most common taxa in the samples is listed in Table 5.19.

**Table 5.19** Common species of the transition zone.

<b>TOTAL</b>	<b>Life Habit</b>	<b>N=2,345</b>	<b>S=30</b>
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	687(29.3%)	21(70.0%)
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	323(13.8%)	21(70.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	137(5.8%)	15(50.0%)
<i>Cyclocardia granulata</i>	06.shallow infaunal suspension feeder	122(5.2%)	20(66.7%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	112(4.8%)	17(56.7%)
<i>Pycnodonte</i> sp.	03.epibyssate suspension feeder	72(3.1%)	21(70.0%)
<i>Astarte undulata</i>	06.shallow infaunal suspension feeder	62(2.6%)	15(50.0%)
<i>Chesapecten madisonius</i>	03.epibyssate suspension feeder	50(2.1%)	15(50.0%)
<i>Dosinia acetabulum</i>	08.medium infaunal siph susp feeder	48(2.0%)	21(70.0%)
<i>Yoldia laevis</i>	01.shallow infaunal deposit feeder	44(1.9%)	20(66.7%)
<b>DYP</b>	<b>Life Habit</b>	<b>N=397</b>	<b>S=11</b>
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	186(46.9%)	11(100.0%)
<i>Yoldia laevis</i>	01.shallow infaunal deposit feeder	36(9.1%)	11(100.0%)
<i>Dosinia acetabulum</i>	08.medium infaunal siph susp feeder	22(5.5%)	10(90.9%)
<i>Parvilucina multilineatus</i>	10.shallow infaunal lucinid susp feed	14(3.5%)	8(72.7%)
<i>Ensis directus</i>	09.deep infaunal siph susp feeder	12(3.0%)	8(72.7%)
barnacles	attached epifaunal suspension feeder	11(2.8%)	11(100.0%)
<i>Dentalium</i> sp.	shallow infaunal scav pred	10(2.5%)	10(90.9%)

<i>Corbula cuneata</i>	07.shallow infaunal siph susp feeder	8(2.0%)	6(54.5%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	8(2.0%)	5(45.5%)
<i>Corbula retusa</i>	07.shallow infaunal siph susp feeder	8(2.0%)	6(54.5%)
<i>Pandora sp. A</i>	07.shallow infaunal siph susp feeder	8(2.0%)	7(9.1%)
<b>NWR</b>	<b>Life Habit</b>	<b>N=976</b>	<b>S=10</b>
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	333(34.1%)	10(100.0%)
<i>Cyclocardia granulata</i>	06.shallow infaunal suspension feeder	116(11.9%)	10(100.0%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	87(8.9%)	10(100.0%)
<i>Pycnodonte sp.</i>	03.epibyssate suspension feeder	70(7.2%)	9(90.0%)
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	63(6.5%)	3(30.0%)
<i>Astarte undulata</i>	06.shallow infaunal suspension feeder	53(5.4%)	10(100.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	28(2.9%)	6(60.0%)
<i>Lunatia heros</i>	16.vagrant epifaunal v semi-infaunal	17(1.7%)	5(50.0%)
<i>Chesapecten madisonius</i>	03.epibyssate suspension feeder	14(1.4%)	8(80.0%)
<i>Marvcrassatella undulata</i>	08.medium infaunal siph susp feeder	11(1.1%)	8(80.0%)
<b>KGM</b>	<b>Life Habit</b>	<b>N=168</b>	<b>S=3</b>
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	56(33.3%)	3(100.0%)
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	32(19.0%)	3(100.0%)
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	16(9.5%)	2(66.7%)
<i>Mercenaria campechiensis</i>	08.medium infaunal siph susp feeder	11(6.5%)	3(100.0%)
<i>Chesapecten madisonius</i>	03.epibyssate suspension feeder	9(5.4%)	3(100.0%)
<i>Corbula cuneata</i>	07.shallow infaunal siph susp feeder	4(2.4%)	3(100.0%)
<i>Noetia incile</i>	05.nestling suspension feeder	4(2.4%)	2(66.7%)
acrotretids	attached epifaunal suspension feeder	3(1.8%)	3(100.0%)
<i>Diplodonta leana</i>	06.shallow infaunal suspension feeder	3(1.8%)	3(100.0%)
barnacles	attached epifaunal suspension feeder	3(1.8%)	1(33.3%)
bryozoans	attached epifaunal suspension feeder	3(1.8%)	3(100.0%)
<i>s. Dentalium sp.</i>	shallow infaunal scav pred	3(1.8%)	1(33.3%)
<i>Plicatula marginata</i>	04.cemented epifaunal suspension feeder	3(1.8%)	3(100.0%)
<b>BWB</b>	<b>Life Habit</b>	<b>N=804</b>	<b>S=6</b>
<i>Crepidula costata</i>	12.attached epifaunal suspension feeder	333(41.4%)	6(100.0%)
<i>Ostrea sculpturata</i>	04.cemented epifaunal suspension feeder	45(5.6%)	6(100.0%)
<i>Mulinia congesta</i>	07.shallow infaunal siph susp feeder	42(5.2%)	4(66.7%)
<i>Chama congregata</i>	04.cemented epifaunal suspension feeder	24(3.0%)	6(100.0%)
<i>Noetia incile</i>	05.nestling suspension feeder	23(2.9%)	6(100.0%)
<i>Chesapecten madisonius</i>	03.epibyssate suspension feeder	22(2.7%)	6(100.0%)
<i>Mercenaria campechiensis</i>	08.medium infaunal siph susp feeder	22(2.7%)	6(100.0%)
<i>Corbula inaequalis</i>	07.shallow infaunal siph susp feeder	21(2.6%)	6(100.0%)
<i>Lucinisca cribrarius</i>	10.shallow infaunal lucinid susp feed	20(2.5%)	5(83.3%)
<i>Dosinia acetabulum</i>	08.medium infaunal siph susp feeder	20(2.5%)	3(50.0%)

All transition samples contain *Mulinia congesta*, although its rank varies from locality to locality, and it does not have the dominance it does in the MBPT samples. *Ostrea sculpturata* is also common at all localities. The occurrence values are all low for the most abundant species, which is an indication that the similarity between samples is probably low.

### PCA

PCA of the transition zone samples yielded 4 major principle components which together accounted for 94.1% of total variability (Fig. 5.12).

The first principle component ordinated samples based primarily on the relative abundance of *Crepidula costata*, *Chama congregata*, *Cyclocardia granulata* and *Astarte undulata*. These four species are all in the top ten for the RBPT at the Nottoway River and Kingsmill localities, and thus this first principle component axes separated those samples that are similar to RBPT samples from those that are dissimilar. The BWB samples all plot high on this axis, while the DYP samples have low values on the axis.

The second principle component has high loadings *Mulinia congesta*, *Yoldia laevis*, *Dosinia acetabulatum*, and *Parvilucina multilineatus*. These four species are all important MBPT species in the BWB, DYP, KGM, and NWR samples. Thus, the second principle component axis separated samples similar to MBPT samples from those that are not. DYP samples all plot high on this axis, and BWB samples all plotted low on this axis. The other two localities had samples spread out along this axis.

The third principle component has high loading values for *Ostrea sculpturata*, *Chesapecten madisonius*, *Mercenaria campechiensis*, and *Crepidula costata*. This axis separates KGM samples from the other localities.

The fourth principle component had high loading values for *Yoldia laevis*, *Dosinia acetabulatum*, *Corbula retusa*, and *Carolinapecten eboreus*. This is similar to the second principle component, with the absence of *Mulinia congesta*. DYP samples are spread all along this axis, while samples from all other localities have plot low on this axis.

The best clustering is found on the plot of principle component 1 and 3. The DYP samples form a tight cluster around the origin. All of the BWB samples plot low on principle components axis 3, and high on the first principle components axis, as do most of the NWR samples. The KGM samples do not form a tight cluster like the other localities, but in this plot, they do occupy a different portion of PCA space than that occupied by samples from other localities.

### **Correlation Analysis**

A correlation matrix was determined for the samples of the transition zone. The correlation values were grouped based on the localities the two samples in each correlation, and the

distribution of these groups determined. The distributions of pairs from the same locality and pairs in which the two members are from different localities is plotted in figure 5.13.

As expected of samples from such a heterogenous grouping, the mean correlation value for within and between locality groupings are both somewhat lower than for the presumably more homogenous MBPT and RBPT. According to an ANOVA, there is a significant difference ( $p=.0001$ ) between the within and between locality groupings for the transition zone. As before, the distributions are rather clearly non-normal, so non-parametric testing was also performed. Both Wilcoxon signed rank and Mann-Whitney U analyses indicate that the difference is significant ( $p=.0001$ ).

The correlation analysis was also performed for each locality individually versus the other localities. The conditions prevalent in the transition zone on the lower coastal plain were apparently not present at the Lieutenant's Run locality, and so there was no LTR transition zone samples collected. The transition zone was sampled at the other four localities. Only 3 of the KGM samples belong to this group, which is probably too small a number to consider separately, since those 3 samples only yield 3 KGM versus KGM comparisons. However, the analysis was performed, even though the results are most likely suspect. The distributions of correlation values for the DYP, BWB, KGM, and NWR were plotted in figure 5.14.

The 11 samples from Day's Point yielded a mean correlation value of .796 when compared to each other. The results for the comparisons between this mean, and the mean correlation values of DYP and non-DYP samples are summarized in Table 5.20.

**Table 5.20** Mean values and significance of difference between correlation coefficients of DYP pairs, and pairs of DYP and non-DYP samples.

	Mean	ANOVA	Mann-Whitney U
<b>DYP vs DYP</b>	.796	-	-
<b>DYP vs BWB</b>	.175	yes ( $p=.0001$ )	yes ( $p=.0001$ )
<b>DYP vs KGM</b>	.350	yes ( $p=.0001$ )	yes ( $p=.0001$ )
<b>DYP vs NWR</b>	.097	yes ( $p=.0001$ )	yes ( $p=.0001$ )

The samples from Day's Point are much more similar to each other than they are to the samples from the other localities.

The 6 samples from Burwell's Bay yielded a rather high mean correlation value of .936 when compared to each other. The results for comparisons between this mean, and the mean correlation values of BWB and non-BWB samples are summarized in Table 5.21.

**Table 5.21** Mean values and significance of difference between correlation coefficients of BWB pairs, and pairs of BWB and non-BWB samples.

	Mean	ANOVA	Mann-Whitney U
<b>BWB vs BWB</b>	.935	-	-
<b>BWB vs DYP</b>	.175	yes (p=.0001)	yes (p=.0001)
<b>BWB vs KGM</b>	.375	yes (p=.0001)	yes (p=.0001)
<b>BWB vs NWR</b>	.797	yes (p=.0001)	yes (p=.0001)

Once again, the BWB samples are much more similar to each other than they are to samples from other localities. The high correlation value for BWB vs NWR is consistent with how they plotted in PCA space.

The 10 samples from the Nottoway River yielded a mean correlation value of .936 when compared to each other. The results for comparisons between this mean, and the mean correlation values of NWR and non-NWR samples are summarized in Table 5.22.

**Table 5.22** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.817		
<b>NWR vs BWB</b>	.797	no (p=.536)	yes (p=.007)
<b>NWR vs DYP</b>	.175	yes (p=.0001)	yes (p=.0001)
<b>NWR vs KGM</b>	.291	yes (p=.0001)	yes (p=.0001)

The NWR and BWB samples appear to be rather similar to each other, which is consistent with the results of the PCA. The Nottoway River samples are not very similar to the samples from Day's Point and Kingsmill.

The 3 samples from the Kingsmill yielded a mean correlation value of .566 when compared to each other. With only 3 samples, this mean is not a very robust number. The results for comparisons between this mean, and the mean correlation values of NWR and non-NWR samples are summarized in Table 5.23.

**Table 5.23** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of KGM and non-KGM samples.

	Mean	ANOVA	Mann-Whitney U
<b>KGM vs KGM</b>	.566		
<b>KGM vs BWB</b>	.375	no (p=.289)	no (p=.366)
<b>KGM vs DYP</b>	.350	no (p=.210)	no (p=.188)
<b>KGM vs NWR</b>	.291	no (p=.121)	no (p=.150)

While there is no difference between the mean value of KGM versus KGM and non-KGM samples correlations, it is more due to the rather low mean correlation value of KGM versus KGM, rather than high correlation values of the samples from other localities. Once again, the correlation are low enough to say that there is not much similarity between KGM and non-KGM samples.

Many of the KGM histograms show a bi-modality in the distribution of correlation values, which may be the result of the small number of samples. The bi-modality may be present in other distributions, although what the cause of such a pattern would be is somewhat mysterious.

The results of the correlation analysis are summarized in Table 5.24.

**Table 5.24** Summary of correlation coefficient for the transition. Significant negative differences between the within locality mean correlation value and the between locality mean correlation values are indicated with a "yes."

	DYP	BWB	KGM	NWR
<b>vs DYP</b>	-	yes	no	yes
<b>vs BWB</b>	yes	-	no	no
<b>vs KGM</b>	yes	yes	-	yes
<b>vs. NWR</b>	yes	yes	no	-

The DYP and BWB samples are very dissimilar from each other. The DYP and NWR samples are also rather dissimilar. There is some evidence of similarity between NWR and BWB samples. The results for KGM are ambiguous because of the small number of KGM samples.

With the exception of KGM, the correlation values are consistently high for within locality comparisons, while the between locality correlation values are very low. The transition zone as expressed at different localities does not have a consistent structure, although at any one locality, it is consistent.

### Species Constancy

A constancy analysis was performed for each locality in the transition, and for all pooled samples in the transition (Table 25).

**Table 5.25** Species constancy ( $C_a$ ) for transitions samples.

	samples	$C_a$
<b>DYP</b>	11	.756
<b>NWR</b>	10	.800
<b>BWB</b>	6	.819
<b>KGM</b>	3	.822
<b>all</b>	30	.445

As with the RBPT and MBPT constancy analysis, constancy was higher for groups taken from single localities than from all localities pooled. The larger difference between the pooled and individual samples indicates a greater difference between the localities in the transitions zone versus the RBPT or MBPT. This result is entirely consistent with the PCA and correlation coefficient analysis for the transition zone.

The highest constancy values are found in the MBPT (Table 5.26). However, these constancy values are potentially inflated by the hyper-abundance of *M. congesta*, and once that taxon is removed, the resultant constancy values are closer to those of the transition and RBPT. The RBPT has the highest between localities constancy number, perhaps indicating that it has a more consistent faunal structure than the other two groups.

**Table 5.26** Summary of constancy analysis ( $C_a$ ) for the MBPT, transition zone, and RBPT. The number before the slash in the MBPT column includes all taxa, while the number after the slash is for the non-*Mulinia* component of the MBPT samples.

	MBPT	transition	RBPT
<b>BWB</b>	.905/.526	.819	-
<b>DYP</b>	.866/.802	.756	-
<b>KGM</b>	.948/.900	.822	.862
<b>LTR</b>	.936/.888	-	.872
<b>NWR</b>	.985/.821	.800	.863
<b>All</b>	.847/.673	.445	.755

## MANOVA

MANOVAs were performed on the 20 most abundant species in the transition zone (Table 5.27) for the four localities at which the transition zone was recognized (KGM, NWR, BWB, and DYP).

**Table 5.27** The 20 most abundant species of the transition zone.

<b>Taxon</b>	<b>Specimens</b>
<i>Crepidula costata</i>	720
<i>Mulinia congesta</i>	596
<i>Cyclocardia granulata</i>	383
<i>Ostrea sculpturata</i>	287
<i>Chama congregata</i>	156
<i>Dosinia acetabulum</i>	107
<i>Astarte undulata</i>	92
<i>Yoldia laevis</i>	88
<i>Chesapecten madisonius</i>	88
<i>Corbula inaequalis</i>	74
<i>Plicatula marginata</i>	73
<i>Pycnodonte sp.</i>	72
<i>Marvcrassatella undulata</i>	67
<i>Parvilucina multilineatus</i>	63
<i>Corbula retusa</i>	63
<i>Mercenaria campechiensis</i>	55
<i>Glycymeris americana</i>	55
<i>Ensis directus</i>	45
<i>Luciniscia cribrarius</i>	43
<i>Astarte concentrica</i>	41

A MANOVA of all transition zone samples grouped by locality revealed that there are differences in the three groups that are significant at the  $p < 0.0001$  level. MANOVAs were also performed on each pair of localities for which there were more than 2 samples (BWB and DYP, BWB and NWR, BWB and KGM, DYP and KGM, DYP and NWR, NWR and KGM), which also all yielded difference significant at the  $p < 0.0001$  level. Samples from different localities are dissimilar enough that the null hypothesis that they are the same can be rejected at the 95% confidence level. As expected from the PCA, correlation analysis, and constancy analysis, samples from the transition zone at different localities are statistically dissimilar.

## Summary

The PCA of the entire data set indicated that there were two well defined end-member paleocommunity types with a transition between them. For each of these three paleocommunity types, the similarity of samples taken from within a locality was greater than similarity between samples from different localities. In the PCA, this similarity showed by the clustering of samples by locality in the same part of PCA space. For the correlation analyses, the similarity was

demonstrated by the high correlation values for within versus between locality comparisons. In the constancy analyses, the constancy values were highest for single localities than for all samples pooled together.

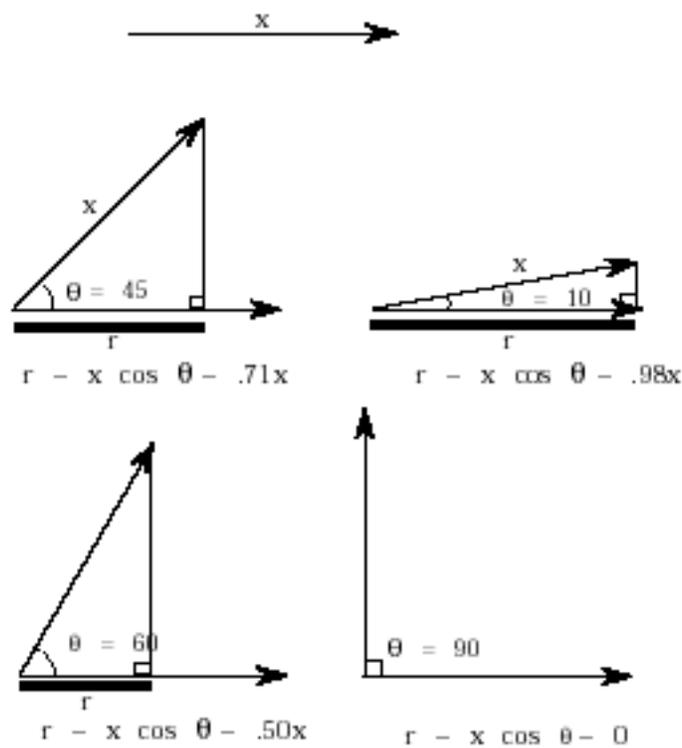
The similarity values for the RBPT are usually higher for between locality comparisons than the MBPT or transition samples. The transition zone shows very little similarity between localities, although it has a consistent structure within a single locality. When all taxa are considered, the MBPT samples from different localities appear to be very similar. If *M. congesta* is removed from the analysis, the apparent similarity drops. However, the MBPT still has higher between locality similarity than the transition zone.

All of the MANOVAs indicated that the samples of the same paleocommunity type but different localities are statistically distinguishable at the 95% confidence level. In other words, the three natural groups in this study did not constitute paleocommunities in the sense of Bennington and Bambach (1996), at least not when only the species are considered.

## Conclusion

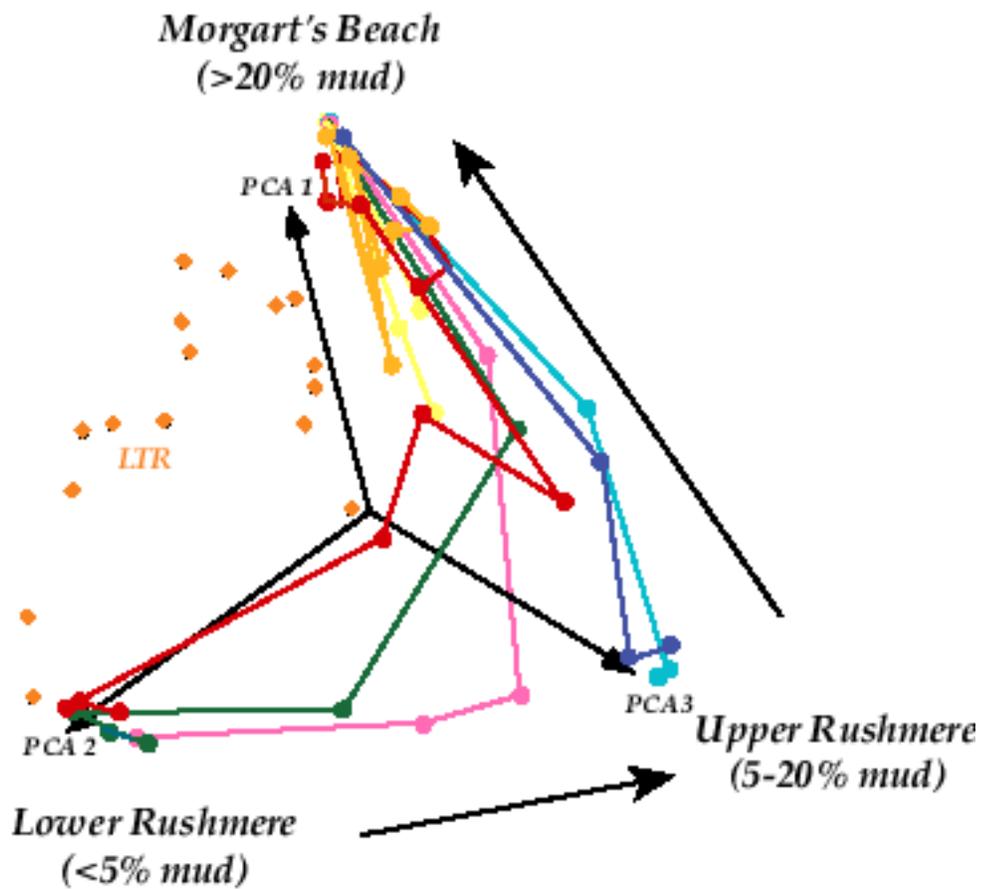
The strongest correlations among Yorktown fossil assemblages were between samples from the same basic paleocommunity type collected at the same locality. Samples from the same paleocommunity type collected at different localities were dissimilar enough that the null hypothesis that they were the same could be discarded. Therefore, the strongest ordering force in Yorktown fossil assemblages is clearly local - i.e., local paleoenvironmental conditions.

The strong species interactions required for ecological locking to work are not recognizable in Yorktown faunas. Rather, the structure of the paleocommunities appears to be controlled by local paleoenvironmental conditions, as with Bambach and Bennington (1996), Bennington and Bambach (1996), Holterhoff (1996), and Stanton and Dodd (1997). Ecological locking can most likely be discarded as a major factor in maintaining the morphologic stasis seen in Yorktown lineages.



**Figure 5.1**  
**Geometric meaning of values in correlation matrix**

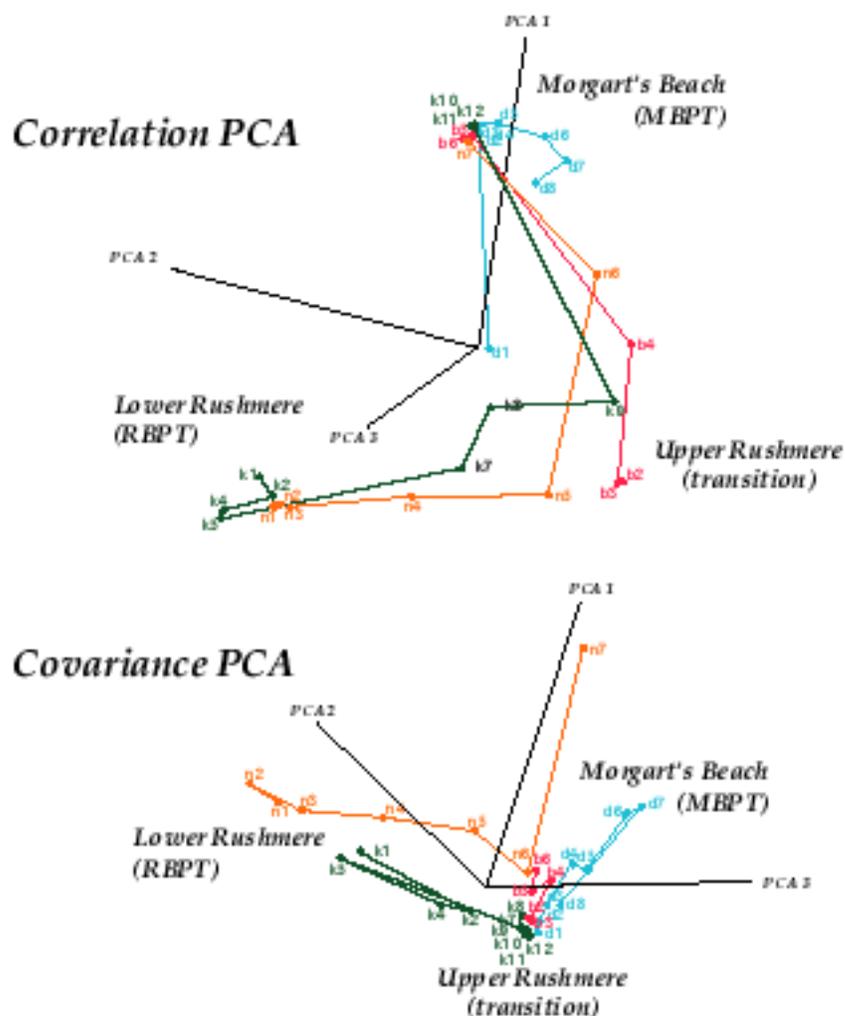
Each value in the correlation matrix is the cosine of the angle between two sample vectors in PCA. The higher the correlation value, the closer the samples plot to each other in PCA space, and the smaller the angle between the two vectors.



**Figure 5.2**  
**Distribution of samples in PCA space**

Three dimensional spatial plot of all samples in the space defined by the PCA. Each color represents a single measured section and lines connect samples from adjacent stratigraphic horizons within a single section. LTR samples (diamonds) have not been connected with lines.

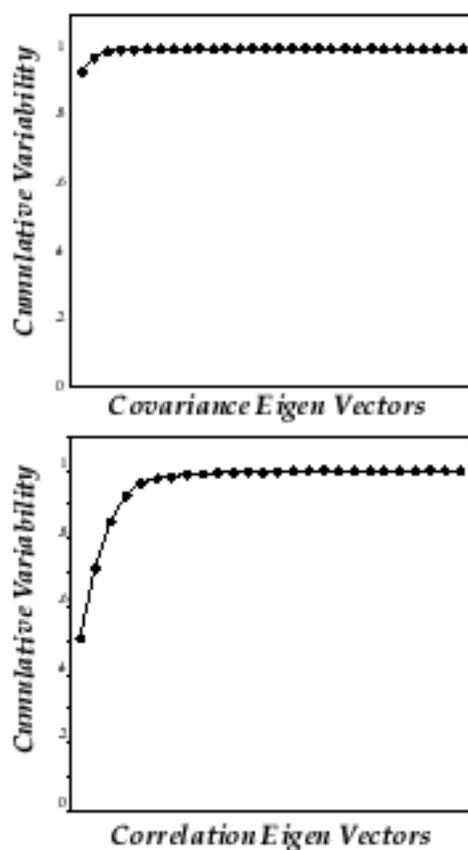
## PCA of Stratigraphic Levels using Species Data



**Figure 5.3**  
**Correlation and Covariance PCA for non-LTR samples organized by stratigraphic horizon**

Three dimensional spatial plots of PCA on both the covariance and correlation matrices. Each color represents a single locality and lines connect the combined samples from each horizon to the adjacent stratigraphic horizons within a single locality.

## *Eigen Values for PCA of Stratigraphic Levels using Species Data*

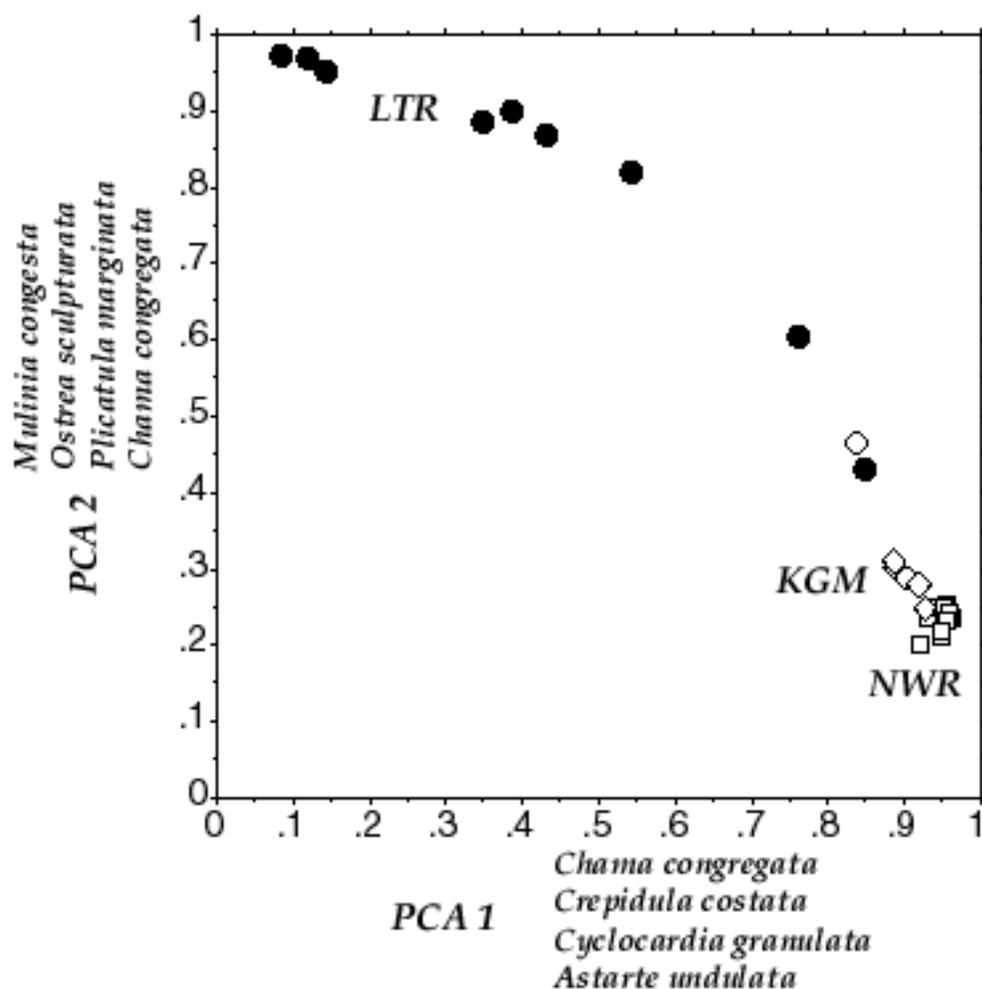


**Figure 5.4**

**Cumulative variability account for by successive eigenvectors in the PCA on the correlation matrix**

Bivariate scatter plot of cumulative variability versus the number of extracted eigenvectors.

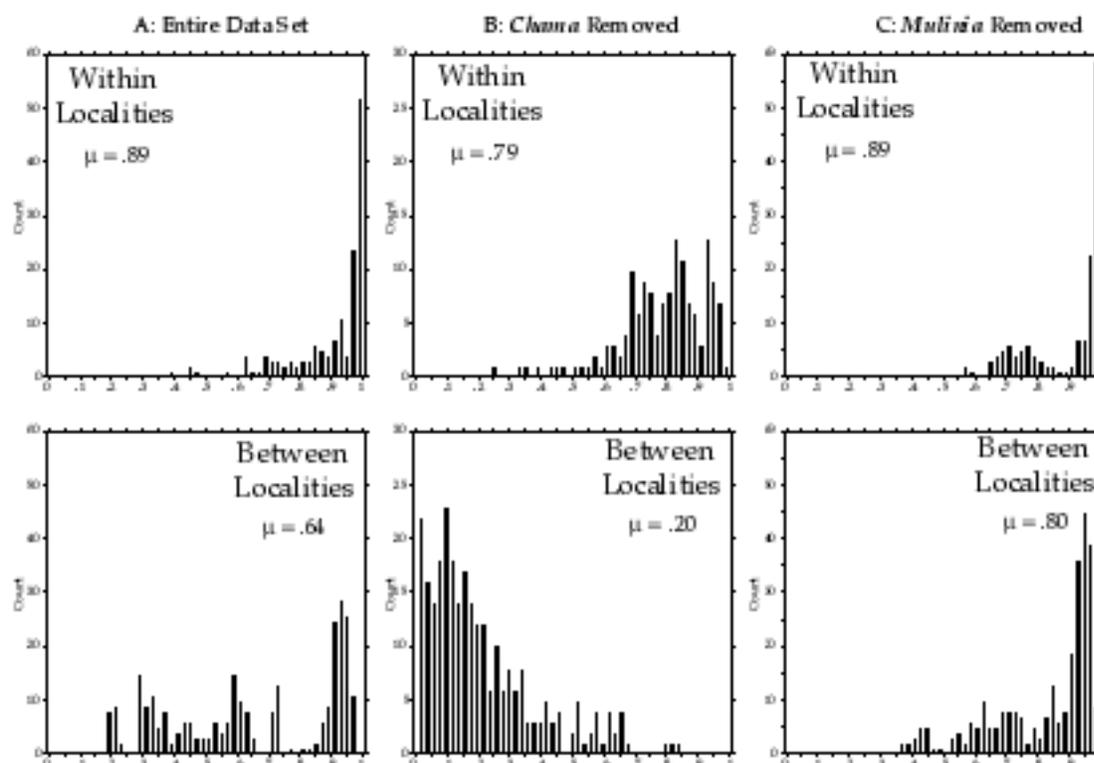
## PCA - RBPT



**Figure 5.5**  
PCA of RBPT

Bivariate scatter plot of principle component one and two of the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities. The species listed on each axis have the heaviest loading for that axis.

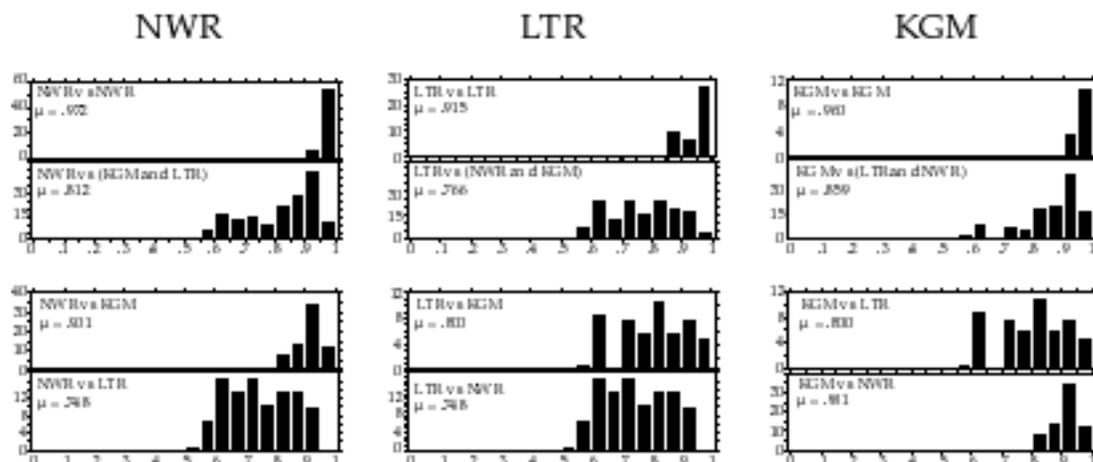
## Correlation Coefficients - RBPT



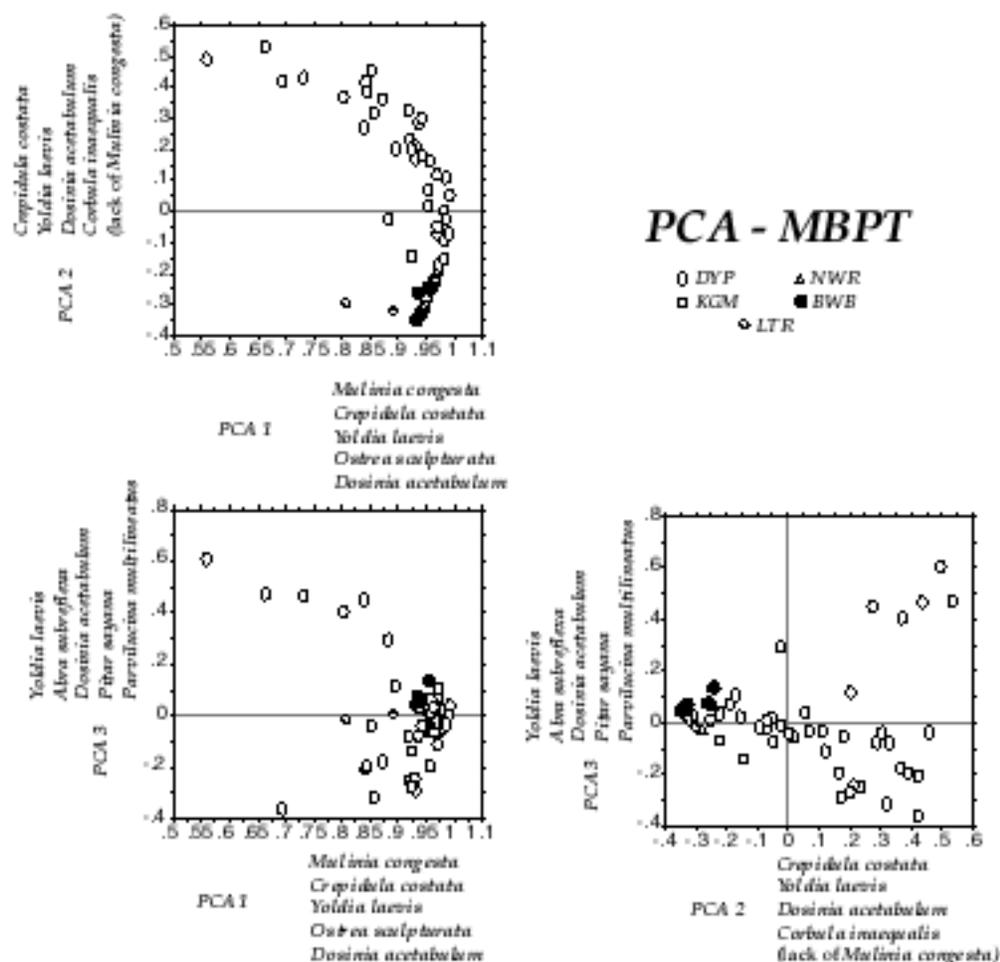
**Figure 5.6**  
**Correlation values of the RBPT**

Histogram of correlation matchups for pairs of sample from the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The bottom graph in each set contains all pairs of samples from different localities (e.g., KGM vs LTR). (A) All taxa included. (B) *Chama congregata* removed from analysis. (C) *Mulinia congesta* removed from analysis.

## Correlation Coefficients - RBPT

**Figure 5.7****Correlation values of the RBPT at different localities**

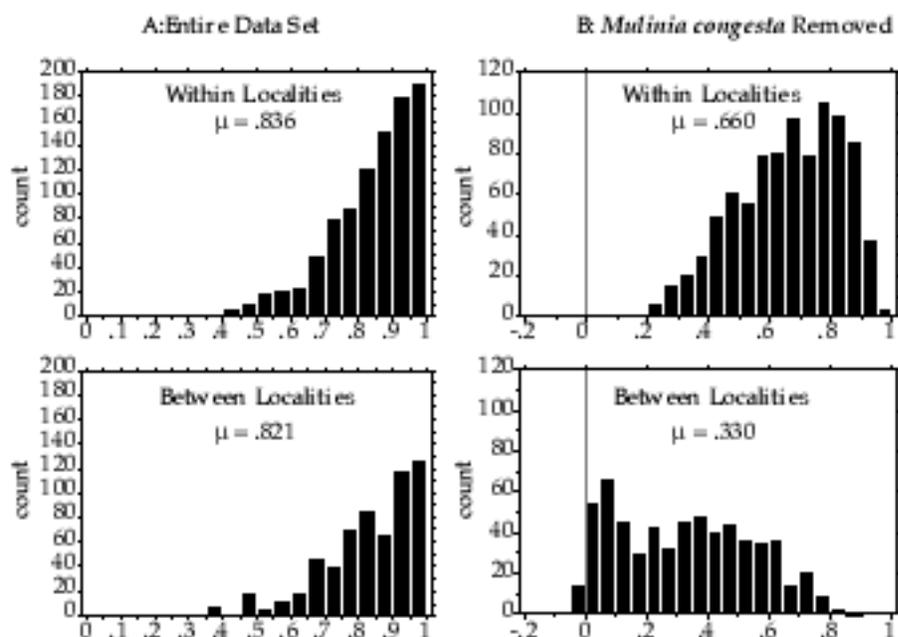
Histogram of correlation matchups for pairs of sample from the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The second graph in each set contains all pairs of samples from different localities (e.g., KGM vs LTR). The third and fourth graphs are comparisons with the other two localities individually.



**Figure 5.8**  
**PCA of MBPT**

Bivariate scatter plots of principle component one, two, and three of the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities. The species listed on each axis have the heaviest loading for that axis.

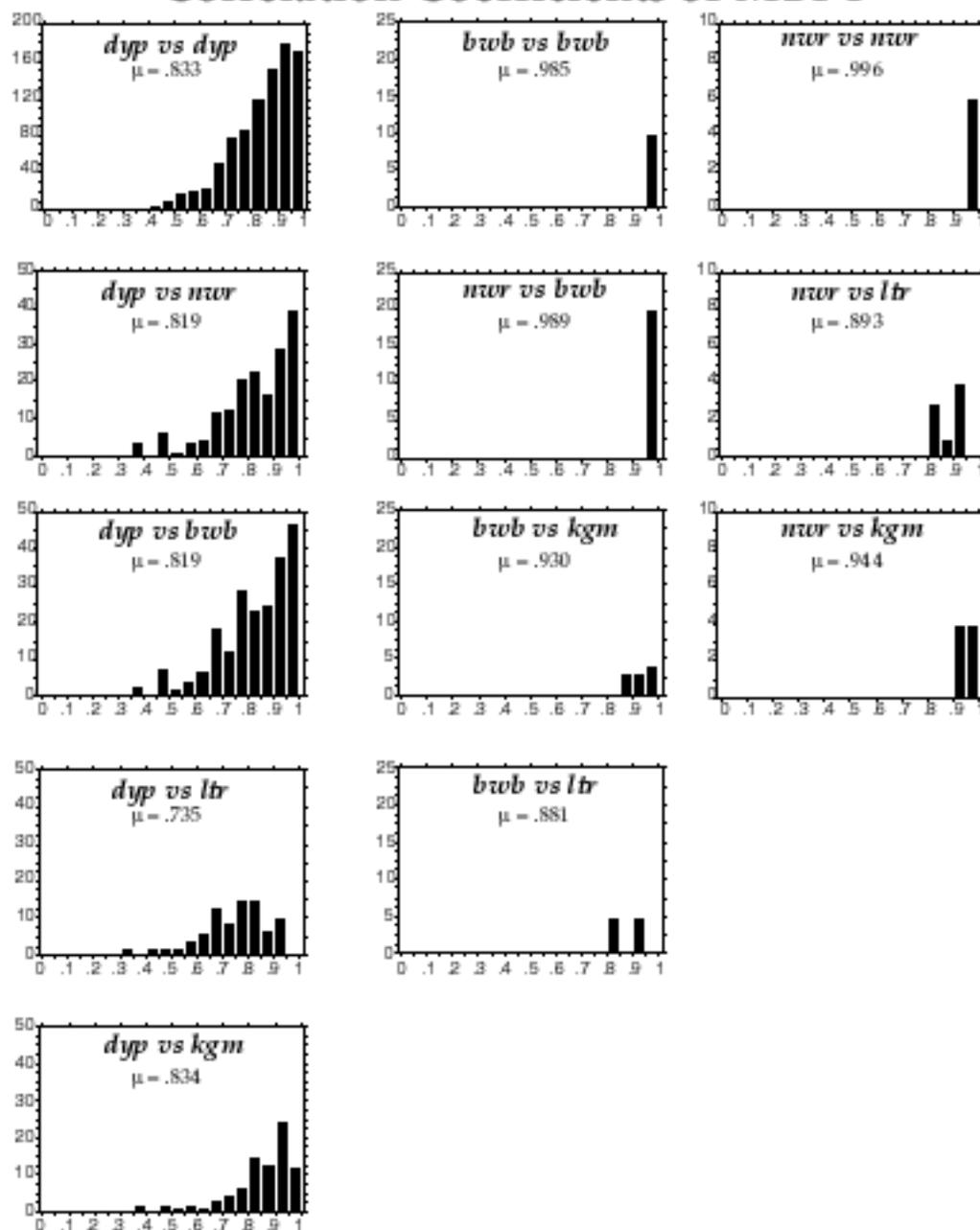
## Correlation Coefficients - MBPT



**Figure 5.9**  
**Correlation values of the MBPT**

Histogram of correlation matchups for pairs of sample from the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., BWB vs BWB). The bottom graph in each set contains all pairs of samples from different localities (e.g., KGM vs LTR). (A) All taxa included; (B) *Mulinia congesta* removed from analysis.

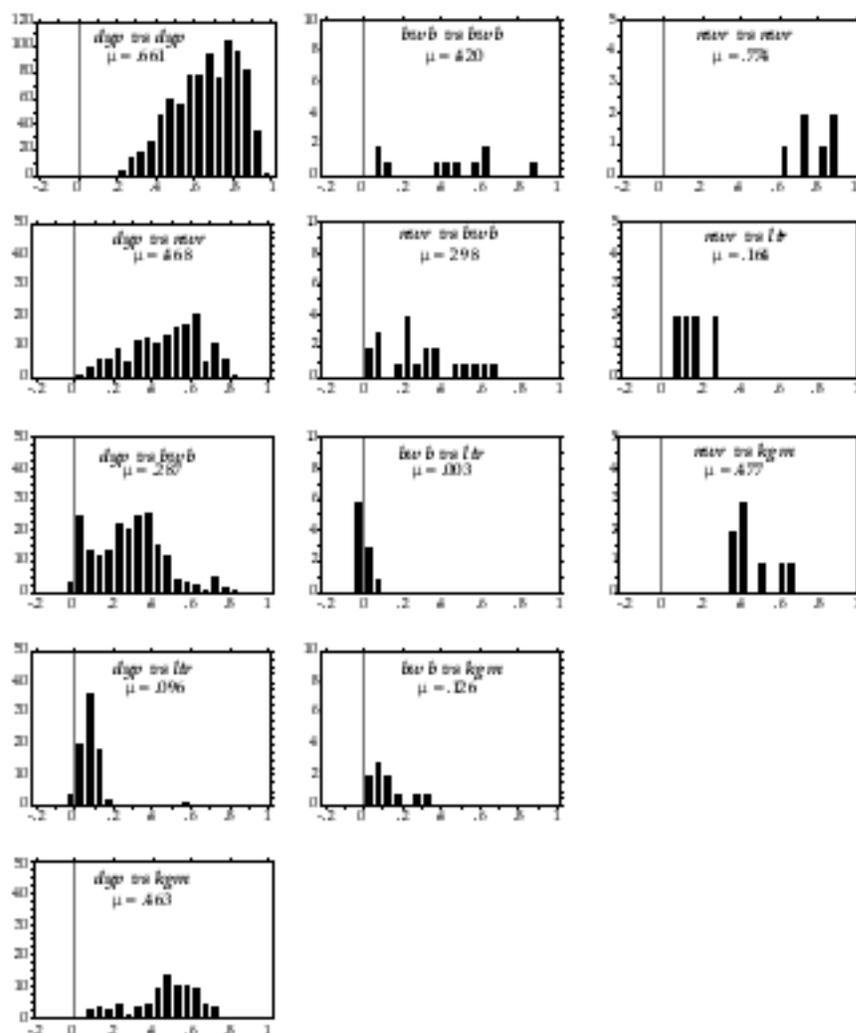
## Correlation Coefficients of MBPT



**Figure 5.10**  
Correlation values of the MBPT at different localities

Histograms of correlation matchups for pairs of sample from the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The other graphs in each set contain pairs of samples from different localities (e.g. BWB vs KGM).

### Correlation Coefficients of MBPT (*Mulinia congesta* removed)



**Figure 5.11**

**Correlation values of the MBPT at different localities with *Mulinia congesta* removed from the analysis**

Histograms of correlation matchups for pairs of sample from the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The other graphs in each set contain pairs of samples from different localities (e.g. BWB vs KGM).

## PCA - Transition Zone

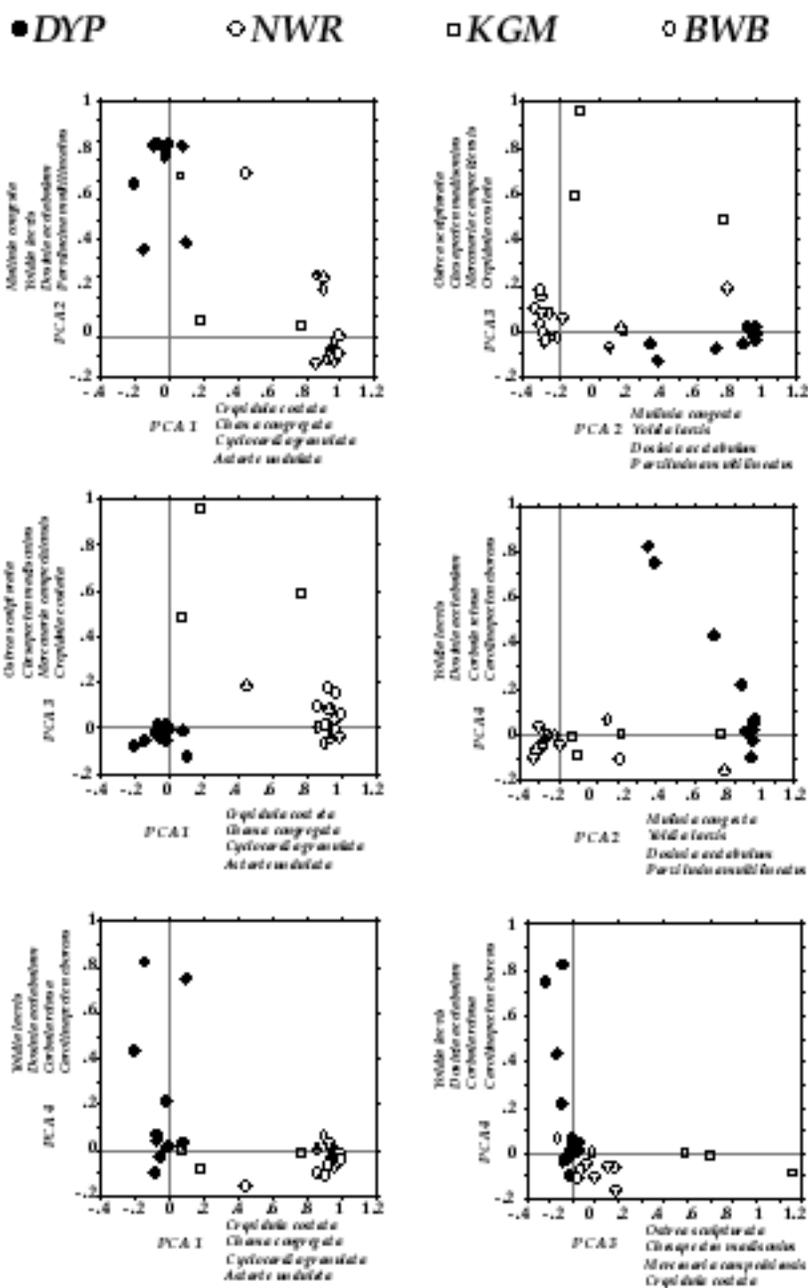
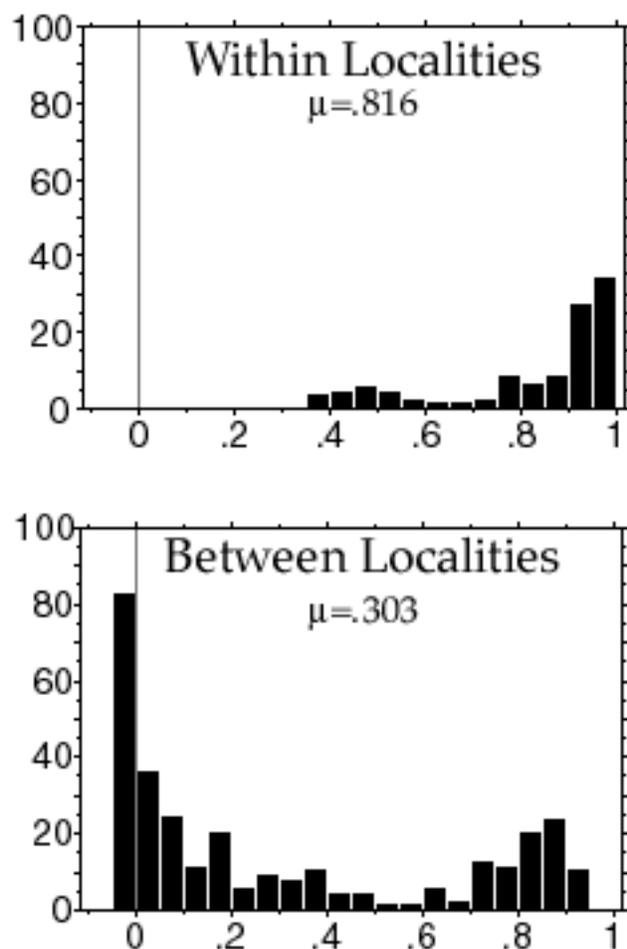


Figure 5.12  
PCA of Transition Zone

Bivariate scatter plots of principle components one, two, three, and four of the transition zone samples from the Burwell's Bay, Day's Point, Nottoway River, and Kingsmill localities. The species listed on each axis have the heaviest loadings for that axis.

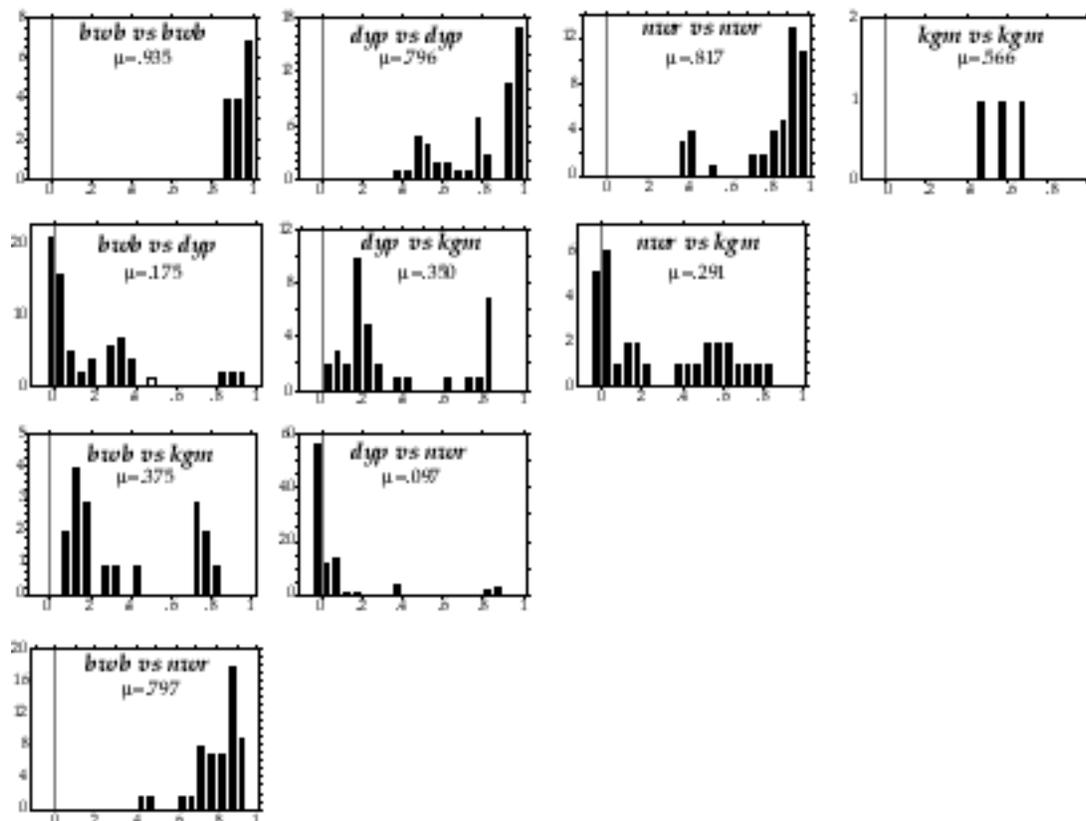
## Correlation Coefficients - Transition Zone



**Figure 5.13**  
**Correlation values of the transition zone**

Histogram of correlation matchups for pairs of sample from the transition zone samples from the Burwell's Bay, Day's Point, Nottoway River, and Kingsmill localities. The top graph is the distribution of all pairs of samples from the same locality (e.g., BWB vs BWB). The bottom graph contains all pairs of samples from different localities (e.g., KGM vs NWR).

## Correlation Coefficients - Transition



**Figure 5.14**  
Correlation values of the transition zone at different localities

Histograms of correlation matchups for pairs of sample from the transition zone samples from the Burwell's Bay, Day's Point, Nottoway River, and Kingsmill localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The other graphs in each set contain pairs of samples from different localities (e.g. BWB vs KGM).

## CHAPTER 6: GUILD ANALYSIS OF THE YORKTOWN PALEOCOMMUNITY TYPES

PCA, correlation analysis, constancy analysis, and MANOVA of my taxonomic data revealed that there were both local paleocommunities and paleocommunity types in my Yorktown samples, but no paleocommunities in the sense of Bennington and Bambach (1996). However, the distribution of individual species can be controlled by a plethora of paleoenvironmental factors (e.g., salinity, water depth, light penetration, turbidity, sediment conditions, etc.) and/or ecologic factors (e.g., predation, vegetation, bioturbation, food supply, etc.). The conditions are also frequently dependent (e.g., light penetration and sediment conditions can effect vegetation, which in turn can effect sediment conditions and bioturbation, etc.). Unfortunately, many of these factors are difficult to measure directly with geological data, and are approached using evidence from the distributions of individual species. Since the distribution of species is what is being examined in this study, using species distributions to interpret paleoenvironment introduces a circularity.

The distributions of closely related species indicate that the species level may contain too much variability to clearly define paleocommunities. For example, *Astarte undulata* and *Astarte concentrica* are both found in greatest abundance in the RBPT. However, *A. concentrica* is common at the Lieutenant's Run locality, and rare at the other localities, while *A. undulata* is common at all three localities sampled for the RBPT. Whatever conditions allowed for the abundance of *A. concentric* in LTR samples was apparently not present at the other localities, but what those exact conditions were can not really be determined with absolute certainty. The lack of *A. concetrica* at the other localities could also be the result of chance. Both *A. undulata* and *A. concentrica* undoubtedly occupied similar niches in the RBPT, and so classifying these two species into a single group based on their life history seems justified. Using this same logic, all species present in my data set could be classified into what might be termed "functional ecologic units" or guilds.

Ecologic guilds were first defined for living assemblages of birds by Root (1967). He defined a guild as:

"A group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements ... [That is] the most

evocative and succinct term for groups of species having similar exploitation patterns." (Root 1967, pg. 335)

The concept was originally defined to distinguish birds that fed on foliage dwelling insects from those which captured flying insects out of the air, and those that ate seeds. Ecologic guilds can probably best be viewed as all taxa capable of exploiting the same ecologic niche in the same way (Kormondy 1996).

Grouping species into guilds has both advantages and disadvantages when analyzing living assemblages. Stiling (1999) lists the following pros and cons for guild analysis:

**Advantages of guild analysis:**

1. Attention is focused on all species which compete for the same resources, regardless of their taxonomic relationships.
2. The guild level of organization may define the "basic building blocks" of ecological communities.
3. Guilds help focus attention on the arenas of greatest competition.

**Problems with guild analysis**

1. Complete guild analysis is only possible if all faunal components are included.
2. Defining the degree of overlap in diet can be problematic, especially for organisms which are not particular about what they eat.

Both the advantages and problems with guild analysis are affected by the scale at which guilds are defined. Pianka (1988, pg. 265) suggested a "periodic table of niches" to define all possible guilds within a habitat. While some attempt had been made to differentiate the various sub groupings, one of his carnivore guilds contained flycatchers and insectivorous bats. While both eat flying insects, one eats insects that are active at nights, while the other hunts by day, so clearly they are not exploiting the exact same prey, and Pianka suggested that perhaps time of activity would enhance the analysis. They also do not catch insects in the same way, nor have the same modes of reproduction or other aspects of life habit, and eliminating the non-feeding aspects of life history leaves something to be desired.

Combining morphologically distinct organisms based only on ecospace utilization (habitat) and food source is somewhat problematic. One way to get around the problem is to extend the guild analysis as suggested by Bambach (1983). In addition to the habitat and food source axes

present in all guild analyses, an additional dimension was added to accommodate gross morphologic differences, or bauplan. Since more closely related organisms tend to have much more similar morphologies and life histories than less closely related organisms, this axis can be thought of as a taxonomic axis. Bambach (1983) suggested that the class level was an appropriate taxonomic level along which to split guilds - so for Pianka's example above, flycatchers would occupy an insectivorous guild in Class Aves, while the bats would be assigned their own guild in Class Mammalia.

For my study, bivalve and gastropod species were assigned to one of 17 guilds. In addition to bivalves and gastropods, my data set contained scaphopod, polyplacophoran, lingulid brachiopod, acrotretid brachiopod, scleractinian coral, bryozoan, barnacle, decapod, and vertebrate remains. However, while the presence of these groups was noted, no count data was collected. Also, most of the remains of these groups with the exception of bryozoans and barnacles were uncommon, fragmented, and difficult to identify to the species level. In contrast, most of the bivalves and gastropods were identified to the species level, and very good count data was collected for these taxa. Several bivalves and gastropods defied identification due to a paucity of material, and this small group of exceedingly rare bivalves and gastropods was also eliminated from the guild analysis.

Species were assigned to guilds using several lines of evidence. The shell of bivalves contains a wealth of information about the life habit of the original occupant. Using guidelines originally set out in Stanley (1970), the probable food source (suspended organic material or detrital organic matter) and space utilization (e.g., epibyssally attached, shallow infaunal burrower, cementing) were determined. The life habit of other species within the same taxonomic family was then examined to see if they had similar life habits to that determined by the analysis of the shell morphology. Finally, each species was assigned a modern analog, and the life habit of that modern species compared to the life habit derived from morphology and comparison to other members of the family for the ancient species. Some of the species in the Yorktown fauna are still living, and when this was the case, the modern version of the species was assigned to its ancient counterpart. Many the genera of the Yorktown fauna are extant, and extinct species were assigned a modern analog species with a similar morphology in the same genus whenever possible. Some of the genera in the Yorktown fauna are extinct (e.g. *Chesapecten*, *Ecphora*). In this case, the modern analog was assigned from a genus with a similar morphology in the same family. The procedure for the gastropods was similar, although the shell of gastropods does not contain the same wealth of life habit information as the bivalve shell, so the first step was not always very useful in determining the guild.

## Bivalve Guilds

### **Guild 01. Shallow Infaunal Paleotaxodont Deposit Feeder (2 species)**

This guild contains two genera of nuculoid bivalves, *Nucula* and *Yoldia*. These "nut clams" burrowed shallowly in mud, and were deposit feeders. The mode of burrowing differs among the yoldiids (which are siphonate) and nuculids (which lack siphons), so perhaps this guild could be split along those lines. Common Yorktown examples: *Yoldia laevis*, *Nucula proxima*.

### **Guild 02. Shallow Infaunal Tellinid Deposit Feeder (4 species)**

This group includes all tellinids. While both paleotaxodonts and tellinids deposit feed, the feeding mechanism was different. Tellinids also burrow, but instead of moving through the sediment and licking up organic matter, they extruded their inhalant siphon onto the surface, and "vacuumed up" organic matter. Common Yorktown examples: *Abra reflexa*, *Macoma virginiana*, *Semele sp. A*.

### **Guild 03. Epibyssate Suspension Feeder (8 species)**

This guild includes most epifaunal bivalves that attached as adults by means of a byssus and suspension fed. Most members of this groups fell into one of two categories: pectens and mussels, but there were also such bivalves as jingle shells in this group. Common Yorktown examples: *Chesapecten madisonius*, *Carolinapecten eboreus*, *Anomia simplex*.

### **Guild 04. Cemented Epifaunal Suspension Feeder (5 species)**

This guild includes all epifaunal bivalves that cemented one valve down to an attachment surface and suspension fed, primarily oysters and jewel box clams. Common Yorktown examples: *Chama congregata*, *Pseudochama corticosa*, *Ostrea sculpturata*, *Plicatula marginata*.

### **Guild 05. Nestling Suspension Feeder (5 species)**

The nestling group includes many epibyssate forms, and was distinguished from the epibyssate guild by a tendency to nestle in crevices, instead of simply attaching to surfaces. The distinction was not immediately obvious from morphology, and was determined primarily by

comparison to modern analogs. Common Yorktown examples: *Saxicava* sp., *Carditermera arata*, *Noetia incile*, *Striarca centenaria*.

**Guild 06. Shallow Infaunal Non-Siphonate Suspension Feeder (12 species)**

This guild includes all active burrowing suspension-feeding bivalves which lacked siphons. The non-siphonate bivalves were all shallow burrowers. Common Yorktown examples: *Astarte undulata*, *Cyclocardia granulata*, *Crassinella lunulata*.

**Guild 07. Shallow Infaunal Siphonate Suspension Feeder (18 species)**

This very large guild contains all shallow burrowing bivalves in which posteriorly located siphons were formed from the extension and fusion of the mantle. Common Yorktown examples: *Corbula cuneata*, *Hemimacra duplinensis*.

**Guild 08. Medium Infaunal Siphonate Suspension Feeder (4 species)**

These siphonate suspension feeding bivalves burrowed somewhat more deeply than the shallow burrowers, and had longer siphons. Common Yorktown examples: *Macrocallista reposta*, *Dosinia acetabulum*

**Guild 09. Deep Infaunal Siphonate Suspension Feeder (3 species)**

These siphonate suspension feeding bivalves had very long siphons, and sometimes gapes in the shell, indicating that they were deeper burrowers than the shallow or medium burrowers. Common Yorktown example: *Panopea reflexa*.

**Guild 10. Shallow Infaunal Lucinid Suspension Feeder (3 species)**

The lucinids differed from the other siphonate forms in that only one siphon was formed from mantle fusion. The other siphon was a mucus tube formed from the action of the foot, and because of this morphological, and thus functional difference, lucinids were grouped into their own guilds. Common Yorktown examples: *Lucinisca cribrarius*, *Parvilucina multilineatus*, *Ctena speciosa*.

**Guild 11. Medium Infaunal Lucinid Suspension Feeder (2 species)**

The lucinids in this guild were larger, and presumably deeper burrowers than the other lucinid guild. Common Yorktown examples: *Stewartia anodonta*.

## **Gastropod Guilds**

### **Guild 12. Epifaunal Suspension Feeder (9 species)**

This group included all epifaunal suspension feeding gastropods plus very shallow burrowing suspension feeding gastropods (e.g., turritellids). It includes both attached and free lying forms. While turritellids were quite common in some samples, no count data was taken for them; were counted as present or absent. Thus, any sample with a high abundance value for this guild does not necessarily have a high abundance of turritellids, but rather most likely has a high abundance of crepidulids. Common Yorktown examples: *Crepidula costata*, *Serpulorbis graniformis*, *Turritella* sp.

### **Guild 13. Vagrant Epifaunal Grazer (4 species)**

This guild includes all gastropods that graze on vegetation. All species in this guild are archaeogastropods. Common Yorktown examples: *Diodora catelliformis*, *Calliostoma mitchelli*.

### **Guild 14. Vagrant Epifaunal Scavenger/Predator (20 species)**

This group of mesogastropods and neogastropods contained a very large number of species, and could be split into a number of different guilds. However, the aggregate frequency of members of this guild was rarely more than 2% of the total abundance in any collection, and individual species had very low frequencies of occurrence. Common Yorktown examples: *Terebra carolinensis*, *Cancellaria rotunda*.

### **Guild 15. Vagrant Epifaunal Boring Predator (7 species)**

This group included all muricids, which bored predatory holes in their bivalve prey. Common Yorktown examples: *Eupleura caudata*, *Ecphora quadricostata*, *Ptychosalpinx multirugata*.

### **Guild 16. Vagrant Epifaunal / Semi-infaunal Boring Predator (2 species)**

This group included all moon snails, which bored holes in bivalve prey excavated from the sediment. Therefore, unlike the muricids, they were semi-infaunal, and were given their own guild. Common Yorktown examples: *Lunatia heros*, *Polinices duplicata*.

### **Guild 17. *Mulinia congesta***

*Mulinia congesta* was an opportunistic shallow infaunal siphonate suspension feeder. It was found in hyper-abundance in the MBPT, but was present in nearly all fossil assemblages of the Rushmere and Morgart's Beach Members. While it could be listed with other shallow infaunal siphonate suspension feeder, it was given its own guild because of the life history differences between *M. congesta* and the other, non-opportunistic small clams.

All guilds except for guild 17 (which contains one species) were represented by at least two species within the samples of the RBPT, transition zone, and MBPT (Table 6.1). Guilds 06, 07, and 14 contain 10 or more species in every subset except guild 07 of the RBPT.

**Table 6.1** Species richness of guilds.

<b>Guild</b>	<b>RBPT</b>	<b>trans.</b>	<b>MBPT</b>	<b>total</b>
01: shallow infaunal deposit feeding bivalves	2	2	2	2
02: shallow infaunal tellinid deposit feeding bivalves	3	3	4	4
03: epibyssate suspension feeding bivalves	6	7	6	8
04: cementing epifaunal suspension feeding bivalves	5	5	5	5
05: nestling epifaunal suspension feeding bivalves	5	3	4	5
06: shallow infaunal non siphonate suspension feeding bivalves	9	11	11	12
07: shallow infaunal siphonate suspension feeding bivalves	12	16	11	18
08: medium infaunal siphonate suspension feeding bivalves	4	4	3	4
09: deep infaunal siphonate suspension feeding bivalves	2	3	2	3
10: shallow infaunal suspension feeding lucinids	3	3	3	3
11: medium infaunal suspension feeding lucinids	2	2	2	2
12: epifaunal suspension feeding gastropods	7	7	8	9
13: vagrant epifaunal grazing gastropods	4	3	4	4
14: vagrant epifaunal gastropod scavenger/predators	15	12	12	20
15: vagrant epifaunal boring predatory gastropod	7	7	7	7
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	2	2	2	2
17: <i>M. congesta</i> (opportunist)	1	1	1	1
All others	7	16	11	18

The percentage of the total species richness found in each sub-environmental of my data set is shown in Table 6.2. At least 60% of the species within each guild are at least present in each sub-group, and all possible species are present in 28 out of a possible 51 cells (54.9%).

**Table 6.2** Percent of total species richness for each guild present within each subset.

<b>Guild</b>	<b>RBPT</b>	<b>trans.</b>	<b>MBPT</b>	<b>total</b>
01: shallow infaunal deposit feeding bivalves	100.0%	100.0%	100.0%	2
02: shallow infaunal tellinid deposit feeding bivalves	75.0%	75.0%	100.0%	4
03: epibyssate suspension feeding bivalves	75.0%	87.5%	75.0%	8
04: cementing epifaunal suspension feeding bivalves	100.0%	100.0%	100.0%	5
05: nestling epifaunal suspension feeding bivalves	100.0%	60.0%	80.0%	5
06: shallow infaunal non siphonate suspension feeding bivalves	75.0%	91.7%	91.7%	12
07: shallow infaunal siphonate suspension feeding bivalves	66.7%	88.9%	61.1%	18
08: medium infaunal siphonate suspension feeding bivalves	100.0%	100.0%	75.0%	4
09: deep infaunal siphonate suspension feeding bivalves	66.7%	100.0%	66.7%	3
10: shallow infaunal suspension feeding lucinids	100.0%	100.0%	100.0%	3
11: medium infaunal suspension feeding lucinids	100.0%	100.0%	100.0%	2
12: epifaunal suspension feeding gastropods	77.8%	77.8%	88.9%	9
13: vagrant epifaunal grazing gastropods	100.0%	75.0%	100.0%	4
14: vagrant epifaunal gastropod scavenger/predators	75.0%	60.0%	60.0%	20
15: vagrant epifaunal boring predatory gastropod	100.0%	100.0%	100.0%	8
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	100.0%	100.0%	100.0%	2
17: <i>M. congesta</i> (opportunist)	100.0%	100.0%	100.0%	1

## Guild Structure at Different Localities

Each locality in my collection area was sampled for at least two of three paleoenvironments: RBPT, transitional zone, and/or MBPT. At most localities, there was a paleoenvironmental change from rubbly bottom to muddy bottom conditions, with a resultant change in the faunal composition. The guild structure of each locality was examined below to determine whether there were any consistent trends in the change in guild structure as the paleoenvironmental conditions changed. For a graphical representation of the guild structure at each locality, please see the pull out poster.

### Burwell's Bay

The percent abundances of the different guilds at Burwell's Bay were determined both with all guilds included (Table 6.3) and with *M. congesta* removed (Table 6.4). The relative abundance of shallow infaunal deposit feeding bivalves (guild 01) clearly increased from the transition to the MBPT, along with *M. congesta*. The relative abundance of epifaunal suspension feeding gastropods (guild 12) appeared to decrease. However, since this observation might have been skewed by the hyper-abundance of *M. congesta*, the comparison should only be made for the percentages with *M. congesta* removed from the calculations.

**Table 6.3** Percent abundance of guilds in different paleocommunity types at BWB.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	n/a	0.8%	5.7%
02: shallow infaunal tellinid deposit feeding bivalves	n/a	1.3%	-
03: epibyssate suspension feeding bivalves	n/a	3.9%	0.7%
04: cementing epifaunal suspension feeding bivalves	n/a	9.6%	0.9%
05: nestling epifaunal suspension feeding bivalves	n/a	3.1%	0.2%
06: shallow infaunal non-siphonate suspension feeding bivalves	n/a	2.6%	-
07: shallow infaunal siphonate suspension feeding bivalves	n/a	5.6%	2.1%
08: medium infaunal siphonate suspension feeding bivalves	n/a	7.1%	0.5%
09: deep infaunal siphonate suspension feeding bivalves	n/a	1.3%	-
10: shallow infaunal suspension feeding lucinids	n/a	3.0%	3.5%
11: medium infaunal suspension feeding lucinids	n/a	-	-
12: epifaunal suspension feeding gastropods	n/a	44.9%	2.8%
13: vagrant epifaunal grazing gastropods	n/a	1.9%	0.2%
14: vagrant epifaunal gastropod scavenger/predators	n/a	4.5%	0.2%
15: vagrant epifaunal boring predatory gastropod	n/a	3.1%	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	n/a	1.7%	1.4%
17: <i>M. congesta</i> (opportunist)	n/a	5.5%	81.6%

*M. congesta* was removed from the data set, and the percentages recalculated (Table 6.4). The increase in the relative abundance of guild 01 was accentuated in this analysis. In addition, there were clearly relative increases in both shallow infaunal siphonate suspension feeding bivalves (guild 07) and shallow infaunal suspension feeding lucinids (guild 10). The decrease in the relative abundance of guild 12 suggested above was confirmed by this analysis. In addition there were decreases in both medium infaunal and deep infaunal siphonate suspension feeding bivalves (guilds 08 and 09), and a complete loss of non-siphonate suspension feeding bivalves (guild 06).

**Table 6.4** Percent abundance of guilds in different paleocommunity types at BWB, *M. congesta* removed from calculation.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves		0.8%	30.8%
02: shallow infaunal tellinid deposit feeding bivalves		1.4%	-
03: epibyssate suspension feeding bivalves		4.1%	3.8%
04: cementing epifaunal suspension feeding bivalves		10.2%	5.1%
05: nestling epifaunal suspension feeding bivalves		3.3%	1.3%
06: shallow infaunal non-siphonate suspension feeding bivalves		2.7%	-
07: shallow infaunal siphonate suspension feeding bivalves		5.9%	11.5%
08: medium infaunal siphonate suspension feeding bivalves		7.6%	2.6%
09: deep infaunal siphonate suspension feeding bivalves		1.4%	-
10: shallow infaunal suspension feeding lucinids		3.2%	19.2%
11: medium infaunal suspension feeding lucinids		-	-
12: epifaunal suspension feeding gastropods		47.5%	15.4%
13: vagrant epifaunal grazing gastropods		2.1%	1.3%
14: vagrant epifaunal gastropod scavenger/predators		4.8%	1.3%
15: vagrant epifaunal boring predatory gastropod		3.3%	-

16: vagrant epifaunal/semi-infaunal boring predatory gastropod	1.8%	7.7%
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The pattern of increasing relative abundance of guild 01 and guild 07 with decreasing relative abundance of both guild 06 and guild 12 should be expected from a paleoenvironmental shift from a less muddy to a more muddy setting. As the bottom conditions became muddier, there should have been more detrital organic matter for the deposit feeders to eat. The siphonate suspension feeding bivalves should have been able to handle the muddier conditions better than the non-siphonate forms, due to mantle fusion. The epifaunal suspension feeding gastropods, which lived attached primarily to shell rubble, would in theory be limited in abundance by the paucity of attachment surfaces as muddiness increased. The increase in relative abundance of the shallow burrowing lucinids is somewhat problematic to interpret, but they are probably exploiting the same conditions that allowed for the increase in relative abundance of guild 07. It is possible that the lucinids are associated with increased bottom vegetation, but there is no direct evidence for this. This could be explored more fully by a more detailed examination of the life habits of the modern analogs of the lucinid species.

### Nottoway River

The percent abundances of the different guilds at Day's Point were determined both with all guilds included (Table 6.5) and with *M. congesta* removed (Table 6.6). Cementing epifaunal bivalves (guild 04) appeared to decrease in relative abundance through the RBPT-MBPT transition, while *M. congesta* increased through that same interval. Epifaunal suspension feeding gastropods (guild 12) reached their maximum abundance in the transition zone.

**Table 6.5** Percent abundance of guilds in different paleocommunity types at NWR.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	0.3%	0.4%	0.9%
02: shallow infaunal tellinid deposit feeding bivalves	3.4%	1.0%	-
03: epibyssate suspension feeding bivalves	6.7%	9.5%	0.3%
04: cementing epifaunal suspension feeding bivalves	45.6%	13.2%	1.2%
05: nestling epifaunal suspension feeding bivalves	0.8%	0.3%	-
06: shallow infaunal non-siphonate suspension feeding bivalves	12.9%	19.4%	1.6%
07: shallow infaunal siphonate suspension feeding bivalves	3.0%	2.8%	0.2%
08: medium infaunal siphonate suspension feeding bivalves	2.2%	2.1%	0.3%
09: deep infaunal siphonate suspension feeding bivalves	1.0%	1.5%	0.1%
10: shallow infaunal suspension feeding lucinids	-	0.3%	0.3%
11: medium infaunal suspension feeding lucinids	0.1%	-	-
12: epifaunal suspension feeding gastropods	16.4%	38.0%	2.2%
13: vagrant epifaunal grazing gastropods	2.2%	0.5%	-
14: vagrant epifaunal gastropod scavenger/predators	1.9%	1.1%	-
15: vagrant epifaunal boring predatory gastropod	1.6%	1.3%	0.2%

16: vagrant epifaunal/semi-infaunal boring predatory gastropod	2.1%	1.8%	0.1%
17: <i>M. congesta</i> (opportunist)	-	6.7%	92.5%

Since the hyper-abundance of *M. congesta* in the MBPT samples obscured the guild structure of the MBPT, the percentages were recalculated with *M. congesta* removed from the data set (Table 6.6). Without *M. congesta*, the percent abundance of infaunal deposit feeding bivalves clearly increased from the RBPT to the MBPT. The apparent decrease in cementing epifaunal suspension feeding bivalve guild (guild 04) appears to actually be a decrease from the RBPT to the transition, with the same relative abundance in the MBPT as in the transition. The suspension feeding gastropod guild (guild 12) still has a relative maximum in the transition zone, as do epibyssate bivalves (guild 03).

**Table 6.6** Percent abundance of guilds in different paleocommunity types at NWR, *M. congesta* removed from calculation.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	0.1%	0.5%	11.7%
02: shallow infaunal tellinid deposit feeding bivalves	3.4%	1.0%	-
03: epibyssate suspension feeding bivalves	6.8%	10.2%	3.9%
04: cementing epifaunal suspension feeding bivalves	46.3%	14.1%	16.1%
05: nestling epifaunal suspension feeding bivalves	0.6%	0.3%	-
06: shallow infaunal non-siphonate suspension feeding bivalves	13.1%	20.8%	21.1%
07: shallow infaunal siphonate suspension feeding bivalves	3.1%	3.0%	2.8%
08: medium infaunal siphonate suspension feeding bivalves	2.2%	2.3%	4.4%
09: deep infaunal siphonate suspension feeding bivalves	0.9%	1.6%	1.7%
10: shallow infaunal suspension feeding lucinids	-	0.3%	4.4%
11: medium infaunal suspension feeding lucinids	-	-	-
12: epifaunal suspension feeding gastropods	16.7%	40.8%	29.4%
13: vagrant epifaunal grazing gastropods	2.0%	0.6%	0.6%
14: vagrant epifaunal gastropod scavenger/predators	1.8%	1.1%	-
15: vagrant epifaunal boring predatory gastropod	1.5%	1.4%	2.2%
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	1.6%	2.0%	1.7%

The decrease in the cementing suspension feeding bivalve guild (guild 04) plus the increase in deposit feeding bivalve guild (guild 01) should be expected in this system, in which the muddiness of the bottom conditions increased from <5% (RBPT), to 5%-20% (transitions), to greater than 20% (MBPT). However, the increase in the relative abundance of the non-siphonate suspension feeding bivalves (guild 06) and the lack of response in siphonate suspension feeding bivalves (guild 07) were not expected responses to this paleoenvironmental gradient. However, if mantle fusion makes sanitary processes harder to perform under soupy conditions, this pattern may in fact be logical (Bambach, pers. comm.). Once again, more detailed analysis of the specific life habits of modern analogs might shed light on this problem.

### Day's Point

The percent abundances of the different guilds at Day's Point were determined both with all guilds included (Table 6.7) and with *M. congesta* removed (Table 6.8). From the transition zone to the MBPT, there was a decrease in the relative abundance of deposit feeding bivalves (guild 01), and slight increases in the relative abundance of shallow infaunal siphonate suspension feeding bivalves (guild 07) and epifaunal suspension feeding gastropods (guild 12). Beyond those difference, the samples of the transition zone and the MBPT appeared rather similar with *M. congesta* included in the analysis.

**Table 6.7** Percent abundance of guilds in different paleocommunity types at DYP.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	n/a	14.8%	6.3%
02: shallow infaunal tellinid deposit feeding bivalves	n/a	4.4%	5.2%
03: epibyssate suspension feeding bivalves	n/a	2.5%	3.6%
04: cementing epifaunal suspension feeding bivalves	n/a	2.5%	6.5%
05: nestling epifaunal suspension feeding bivalves	n/a	-	0.4%
06: shallow infaunal non-siphonate suspension feeding bivalves	n/a	0.6%	1.1%
07: shallow infaunal siphonate suspension feeding bivalves	n/a	10.1%	16.2%
08: medium infaunal siphonate suspension feeding bivalves	n/a	8.4%	7.2%
09: deep infaunal siphonate suspension feeding bivalves	n/a	4.2%	1.1%
10: shallow infaunal suspension feeding lucinids	n/a	4.4%	4.3%
11: medium infaunal suspension feeding lucinids	n/a	-	-
12: epifaunal suspension feeding gastropods	n/a	3.6%	10.8%
13: vagrant epifaunal grazing gastropods	n/a	0.8%	0.4%
14: vagrant epifaunal gastropod scavenger/predators	n/a	1.3%	1.7%
15: vagrant epifaunal boring predatory gastropod	n/a	0.8%	1.1%
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	n/a	0.8%	0.3%
17: <i>M. congesta</i> (opportunist)	n/a	41.1%	33.9%

Removing *M. congesta* accentuates the differences between these two groups at Day's Point (Table 6.8). The decrease in the relative abundance of deposit feeding bivalves guild (guild 01) and increase in relative abundances of infaunal siphonate suspension feeding bivalves (guild 07) and suspension feeding gastropods (guild 12) are more clearly seen with *M. congesta* removed. In addition, a decrease in the relative abundance of both medium infaunal suspension feeding bivalves (guild 08), and an increase in the relative abundance of cementing epifaunal suspension feeding bivalves (guild 04) is more clearly seen. All other guilds have similar abundances in both groups.

**Table 6.8** Percent abundance of guilds in different paleocommunity types at DYP, *M. congesta* removed from calculation.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	n/a	25.2%	8.2%

02: shallow infaunal tellinid deposit feeding bivalves	n/a	7.4%	7.3%
03: epibyssate suspension feeding bivalves	n/a	4.2%	5.5%
04: cementing epifaunal suspension feeding bivalves	n/a	4.2%	10.3%
05: nestling epifaunal suspension feeding bivalves	n/a	-	0.6%
06: shallow infaunal non-siphonate suspension feeding bivalves	n/a	1.0%	1.8%
07: shallow infaunal siphonate suspension feeding bivalves	n/a	17.1%	25.1%
08: medium infaunal siphonate suspension feeding bivalves	n/a	14.2%	10.7%
09: deep infaunal siphonate suspension feeding bivalves	n/a	7.1%	1.6%
10: shallow infaunal suspension feeding lucinids	n/a	7.4%	6.0%
11: medium infaunal suspension feeding lucinids	n/a	-	-
12: epifaunal suspension feeding gastropods	n/a	6.1%	17.3%
13: vagrant epifaunal grazing gastropods	n/a	1.3%	0.6%
14: vagrant epifaunal gastropod scavenger/predators	n/a	2.3%	2.7%
15: vagrant epifaunal boring predatory gastropod	n/a	1.3%	1.8%
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	n/a	1.3%	0.5%

The decrease in relative abundance of deposit feeders that are active burrowers (guild 01), plus the decreases in both medium and deep infaunal burrowers may indicate that for some reason the sediment became more difficult to move through, perhaps due to an increase in the percent of clay in the sediment.. The shallow burrowing bivalves might not be as greatly effected by this. The relative increase of the epifaunal suspension feeding bivalves and gastropods is somewhat more difficult to interpret, although their increase argues for an increase in the availability of hard attachment surfaces.

### Kingsmill

The percent abundances of the different guilds at Kingsmill were determined both with all guilds included (Table 6.9) and with *M. congesta* removed (Table 6.10). Both shallow siphonate suspension feeding bivalves (guild 07) and *M. congesta* increase in relative abundance from RBPT through MBPT samples. However, the apparent decreases in the other guilds might have been artifacts of the high abundance of *M. congesta* in the transition zone, and the hyper-abundance of *M. congesta* in the MBPT. Before these apparent decreases can be analyzed, *M. congesta* must be removed from the data set, the percentage recalculated.

**Table 6.9** Percent abundance of guilds in different paleocommunity types at KGM.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	1.5%	0.6%	0.3%
02: shallow infaunal tellinid deposit feeding bivalves	0.7%	0.6%	1.6%
03: epibyssate suspension feeding bivalves	1.7%	7.1%	1.3%
04: cementing epifaunal suspension feeding bivalves	62.3%	39.7%	18.1%
05: nestling epifaunal suspension feeding bivalves	7.5%	2.6%	2.5%
06: shallow infaunal non-siphonate suspension feeding bivalves	11.3%	1.9%	1.0%
07: shallow infaunal siphonate suspension feeding bivalves	5.5%	5.1%	10.2%
08: medium infaunal siphonate suspension feeding bivalves	0.8%	7.7%	6.3%
09: deep infaunal siphonate suspension feeding bivalves	1.1%	-	1.3%
10: shallow infaunal suspension feeding lucinids	1.5%	0.6%	1.3%
11: medium infaunal suspension feeding lucinids	-	-	-
12: epifaunal suspension feeding gastropods	4.0%	12.2%	7.0%
13: vagrant epifaunal grazing gastropods	0.4%	1.3%	0.3%
14: vagrant epifaunal gastropod scavenger/predators	0.5%	-	-
15: vagrant epifaunal boring predatory gastropod	0.1%	-	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	-	-	-
17: <i>M. congesta</i> (opportunist)	1.1%	20.5%	48.9%

*M. congesta* was removed from the data set, and the percentages recalculated (Table 6.10). There were decreases in relative abundance of guild 04 and 06, and increases in the relative abundances of guilds 07 and 08. Guild 12 and guild 03 reached their maximum relative abundances in samples from the transition zone.

**Table 6.10** Percent abundance of guilds in different paleocommunity types at KGM, *M. congesta* removed from calculation.

Guild	RBPT	transition	MBPT
01: shallow infaunal deposit feeding bivalves	1.5%	0.8%	0.6%
02: shallow infaunal tellinid deposit feeding bivalves	0.3%	0.8%	3.1%
03: epibyssate suspension feeding bivalves	1.8%	8.9%	2.5%
04: cementing epifaunal suspension feeding bivalves	64.0%	50.0%	35.4%
05: nestling epifaunal suspension feeding bivalves	7.7%	3.2%	5.0%
06: shallow infaunal non-siphonate suspension feeding bivalves	11.6%	2.4%	1.9%
07: shallow infaunal siphonate suspension feeding bivalves	5.6%	6.5%	19.9%
08: medium infaunal siphonate suspension feeding bivalves	0.4%	9.7%	12.4%
09: deep infaunal siphonate suspension feeding bivalves	0.7%	-	2.5%
10: shallow infaunal suspension feeding lucinids	1.5%	0.8%	2.5%
11: medium infaunal suspension feeding lucinids	-	-	-
12: epifaunal suspension feeding gastropods	4.1%	15.3%	13.7%
13: vagrant epifaunal grazing gastropods	0.2%	1.6%	0.6%
14: vagrant epifaunal gastropod scavenger/predators	0.4%	-	-
15: vagrant epifaunal boring predatory gastropod	-	-	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	-	-	-

The decreased relative abundance of cementing epifaunal bivalves (guild 04) would be expected with the paleoenvironmental shift from rubbly to muddy bottom. Species of guild 04

require a hard attachment surface on which to cement, and those attachment surfaces should be much more common in a rubbly setting than a muddy one. The increase in relative abundance of siphonate suspension feeding bivalves (guild 07) with a decrease in non-siphonate suspension feeding bivalves was also expected because mantle fusion should allow siphonate forms to handle mud better than non-siphonate forms. The expected increase in the non-tellinid deposit feeders with increasing muddiness did not occur, although there was an increase in the relative abundance of tellinid deposit feeders.

### Lieutenant's Run

The percent abundances of the different guilds at Lieutenant's Run were determined both with all guilds included (Table 6.11) and with *M. congesta* removed (Table 6.12). The Lieutenant's Run locality was located on the landward edge of the Yorktown outcrop belt, and was therefore constantly in the shallowest water, and at closest proximity to the terrestrial source area. Because of this, there was no "transition zone" at Lieutenant's Run. The MBPT samples were all located at the top of the section, but the RBPT and "other" samples were mixed together stratigraphically.

The percent abundance of *M. congesta* in the RBPT and other samples was lower than that in the MBPT samples. The high abundance of *M. congesta* obscures the guild structure of the non-*Mulinia* component of the fauna, and therefore in order to examine the other guilds, *M. congesta* was removed from the analysis, and the percentage recalculated (Table 6.12.)

**Table 6.11** Percent abundance of guilds in different paleocommunity types at LTR.

Guild	RBPT	other	MBPT
01: shallow infaunal deposit feeding bivalves	0.5%	0.4%	0.1%
02: shallow infaunal tellinid deposit feeding bivalves	1.3%	2.0%	0.5%
03: epibyssate suspension feeding bivalves	3.4%	3.9%	1.2%
04: cementing epifaunal suspension feeding bivalves	42.5%	19.3%	30.5%
05: nestling epifaunal suspension feeding bivalves	2.6%	0.9%	1.6%
06: shallow infaunal non-siphonate suspension feeding bivalves	6.9%	25.6%	6.2%
07: shallow infaunal siphonate suspension feeding bivalves	3.9%	8.1%	3.0%
08: medium infaunal siphonate suspension feeding bivalves	5.3%	7.7%	2.5%
09: deep infaunal siphonate suspension feeding bivalves	0.5%	2.5%	0.2%
10: shallow infaunal suspension feeding lucinids	1.3%	4.2%	0.4%
11: medium infaunal suspension feeding lucinids	0.2%	1.2%	0.3%
12: epifaunal suspension feeding gastropods	5.2%	4.7%	3.5%
13: vagrant epifaunal grazing gastropods	0.4%	0.4%	0.4%
14: vagrant epifaunal gastropod scavenger/predators	0.7%	0.7%	1.0%
15: vagrant epifaunal boring predatory gastropod	0.1%	0.4%	0.1%
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	0.8%	0.4%	0.3%
17: <i>M. congesta</i> (opportunist)	24.5%	17.7%	48.2%

Without *M. congesta* in the analysis, the RBPT and MBPT samples at this locality appeared to be remarkably similar to each other (Table 6.12). Both had very similar relative abundances of guild 04 (58.0% and 58.9%), guild 12 (7.1% and 6.8%), and guild 07 (5.3% and 5.8%). Guild 04 in these two groups is composed primarily of *C. congregata*, and the abundances really are quite similar. The main difference between the transition zone and the "other" category and the RBPT and MBPT was the relative abundance of shallow infaunal suspension feeding bivalves, which are much less common in the MBPT and RBPT than in the "other" group. Shallow infaunal lucinids are also more common in the "other" group.

**Table 6.12** Percent abundance of guilds in different paleocommunity types at LTR, *M. congesta* removed from calculation.

Guild	RBPT	other	MBPT
01: shallow infaunal deposit feeding bivalves	0.4%	0.4%	0.3%
02: shallow infaunal tellinid deposit feeding bivalves	1.6%	2.4%	1.0%
03: epibyssate suspension feeding bivalves	4.7%	4.7%	2.3%
04: cementing epifaunal suspension feeding bivalves	58.0%	23.5%	58.9%
05: nestling epifaunal suspension feeding bivalves	3.6%	1.2%	3.0%
06: shallow infaunal non-siphonate suspension feeding bivalves	9.4%	31.1%	12.0%
07: shallow infaunal siphonate suspension feeding bivalves	5.3%	9.8%	5.8%
08: medium infaunal siphonate suspension feeding bivalves	7.2%	9.4%	4.8%
09: deep infaunal siphonate suspension feeding bivalves	0.4%	3.0%	0.5%
10: shallow infaunal suspension feeding lucinids	1.1%	5.1%	0.8%
11: medium infaunal suspension feeding lucinids	0.1%	1.4%	0.5%
12: epifaunal suspension feeding gastropods	7.1%	5.7%	6.8%
13: vagrant epifaunal grazing gastropods	0.3%	0.4%	0.8%
14: vagrant epifaunal gastropod scavenger/predators	0.4%	0.8%	2.0%
15: vagrant epifaunal boring predatory gastropod	-	0.5%	0.3%
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	0.5%	0.5%	0.5%

Other than the relative abundance of *M. congesta*, it is apparent that the RBPT and MBPT samples might have been derived from the same underlying guild distribution. The paleoenvironmental gradient present at the other localities is not present here, so it perhaps should not be surprising that there is not as much difference between the two paleoenvironmental types.

The relationship of the "other" group at Lieutenant's Run to the rest of the data set is somewhat obscure. Some of these samples came from below the RBPT samples, and therefore may be from a paleoenvironmental setting that existed before the conditions that brought about the RBPT were in effect. However, some of the "other" group are sandwiched between RBPT samples, and so there may have been simply paleoenvironmental fluctuations that were responsible for this otherwise unique assemblage.

## Summary

Other than the LTR samples, the relative abundance of the cementing epifaunal suspension feeding bivalve guild (guild 04) tended to decrease as the bottom conditions went from rubbly to muddy, while the *Mulinia* guild tended to increase in relative abundance. The relative abundance of shallow infaunal siphonate suspension feeding bivalves (guild 07) also tended to increase with increased muddiness. The transition zone tended to have a higher relative abundance of the epifaunal suspension feeding gastropod guild. (guild 12). At three localities, the relative abundance of the deposit feeding bivalve guild (guild 01) increased with increased muddiness, although not in KGM samples. At two localities (Kingsmill and Nottoway River), the relative abundance of shallow infaunal non-siphonate suspension feeding bivalves decreased in relative abundance.

## Analysis of Guild Structure within Paleocommunity Types

The same analyses done in chapter 5 for species data was performed for the guild data in order to explore whether or not there is strong recurrence in the relative abundances of the various guilds within samples from the same paleocommunity type, but different localities.

## RBPT

The species richness of the guilds at each locality was tabulated in Table 6.13. Of the 53 species of bivalves present, 24 (45.3%) were shallow burrowing suspension feeders and 16 (30.2%) lived epifaunally. Deposit feeders and all other suspension feeding bivalves accounted for 24.5% of the species richness. Most of the shallow burrowers were either siphonate suspension feeders (22.6%) or non-siphonate suspension feeders (17.0%), with 5.7% of the species richness represented by shallow burrowing lucinids. Of the epifaunal suspension feeding bivalves, 6 (11.3%) of the species attached epibyssally, 5 (9.4%) of the species were cementers, and 5 (9.4%) were nestlers. Of the 18 species of epifaunal suspension feeding bivalves found in all samples, all but 2 of the epibyssate forms are found in the RBPT.

**Table 6.13** Number of species per guild in the RBPT.

<b>Guild</b>	<b>NWR</b>	<b>LTR</b>	<b>KGM</b>	<b>total</b>
01: shallow infaunal deposit feeding bivalves	2	2	2	2
02: shallow infaunal tellinid deposit feeding bivalves	3	3	3	3
03: epibyssate suspension feeding bivalves	6	4	4	6
04: cementing epifaunal suspension feeding bivalves	3	5	5	5
05: nestling epifaunal suspension feeding bivalves	2	3	4	5
06: shallow infaunal non siphonate suspension feeding bivalves	5	8	8	9
07: shallow infaunal siphonate suspension feeding bivalves	9	8	6	12
08: medium infaunal siphonate suspension feeding bivalves	4	4	3	4
09: deep infaunal siphonate suspension feeding bivalves	1	2	1	2
10: shallow infaunal suspension feeding lucinids	-	3	2	3
11: medium infaunal suspension feeding lucinids	1	2	-	2
12: epifaunal suspension feeding gastropods	7	5	6	7
13: vagrant epifaunal grazing gastropods	4	3	3	4
14: vagrant epifaunal gastropod scavenger/predators	10	5	3	15
15: vagrant epifaunal boring predatory gastropod	7	1	1	7
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	2	2	-	2
17: <i>M. congesta</i> (opportunist)	1	1	1	1

The five guilds of gastropods present in the RBPT contained 37 species. The sessile epifaunal gastropods (guild 12) accounted for 18.9% of the species richness, while the four guilds of vagrant gastropods accounted for the other 81.1%. Seven of the 9 species of suspension feeding gastropods recognized from all paleoenvironments in this study were found in one or more samples of the RBPT, and at least 5 of the 9 species were found at each locality. The vagrant epifaunal scavenger/predator guild accounted for 40.5% of the total gastropod species richness, with the two guilds of boring predators accounting for another 24.3% of the species richness. All 9 species of boring snails (guilds 15 and 16) were recovered from at least one of the RBPT localities, although all 9 were recognized together only at the Nottoway River locality, with much lower species richness values for the other 5 localities. Grazers accounted for 10.8% of the species richness overall, and at least 3 of the 4 species of grazers were found at each locality.

**Table 6.14** Percent abundance of guilds of the RBPT. Percentages less than .01% are represented by a dash.

<b>Guild</b>	<b>NWR</b>	<b>LTR</b>	<b>KGM</b>
01: shallow infaunal deposit feeding bivalves	0.3%	0.5%	1.5%
02: shallow infaunal tellinid deposit feeding bivalves	3.4%	1.3%	0.7%
03: epibyssate suspension feeding bivalves	6.7%	3.4%	1.7%
04: cementing epifaunal suspension feeding bivalves	45.6%	42.5%	62.3%
05: nestling epifaunal suspension feeding bivalves	0.8%	2.6%	7.5%
06: shallow infaunal non-siphonate suspension feeding bivalves	12.9%	6.9%	11.3%
07: shallow infaunal siphonate suspension feeding bivalves	3.0%	3.9%	5.5%
08: medium infaunal siphonate suspension feeding bivalves	2.2%	5.3%	0.8%
09: deep infaunal siphonate suspension feeding bivalves	1.0%	0.5%	1.1%
10: shallow infaunal suspension feeding lucinids	-	1.3%	1.5%

11: medium infaunal suspension feeding lucinids	0.1%	0.2%	-
12: epifaunal suspension feeding gastropods	16.4%	5.2%	4.0%
13: vagrant epifaunal grazing gastropods	2.2%	0.4%	0.4%
14: vagrant epifaunal gastropod scavenger/predators	1.9%	0.7%	0.5%
15: vagrant epifaunal boring predatory gastropod	1.6%	0.1%	0.1%
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	2.1%	0.8%	-
17: <i>M. congesta</i> (opportunist)	-	24.5%	1.1%

In terms of percent abundance (Table 6.14), the dominant guild of the RBPT at all localities was the cementing epifaunally attached suspension feeding bivalves, which accounted for between 40-60% of the total abundance. Most of those were specimens of *Chama congregata*, but there were also at least 2 other species in this guild present at every locality, and at two localities, all 5 species in this guild were at least present. The second most abundant guild in LTR samples is the opportunistic guild, represented by *M. congesta*, which account for 25% of the total abundance within LTR samples. Because it was probably not a major faunal component of the normal communities, but rather was most likely abundant only under stressed conditions, it was removed from the data set, and the percent abundances of the non-opportunistic taxa recalculated (Table 6.15).

**Table 6.15** Percent abundance of guilds of the RBPT, with *M. congesta* removed from calculation.

<b>Guild</b>	<b>NWR</b>	<b>LTR</b>	<b>KGM</b>
01: shallow infaunal deposit feeding bivalves	0.1%	0.4%	1.5%
02: shallow infaunal tellinid deposit feeding bivalves	3.4%	1.6%	0.3%
03: epibyssate suspension feeding bivalves	6.8%	4.7%	1.8%
04: cementing epifaunal suspension feeding bivalves	46.3%	58.0%	64.0%
05: nestling epifaunal suspension feeding bivalves	0.6%	3.6%	7.7%
06: shallow infaunal non-siphonate suspension feeding bivalves	13.1%	9.4%	11.6%
07: shallow infaunal siphonate suspension feeding bivalves	3.1%	5.3%	5.6%
08: medium infaunal siphonate suspension feeding bivalves	2.2%	7.2%	0.4%
09: deep infaunal siphonate suspension feeding bivalves	0.9%	0.4%	0.7%
10: shallow infaunal suspension feeding lucinids	-	1.1%	1.5%
11: medium infaunal suspension feeding lucinids	-	0.1%	-
12: epifaunal suspension feeding gastropods	16.7%	7.1%	4.1%
13: vagrant epifaunal grazing gastropods	2.0%	0.3%	0.2%
14: vagrant epifaunal gastropod scavenger/predators	1.8%	0.4%	0.4%
15: vagrant epifaunal boring predatory gastropod	1.5%	-	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	1.6%	0.5%	-

With the removal of *M. congesta* the percent abundances of the remaining guilds should be comparable at all three localities. Other than *M. congesta* the majority of bivalve specimens at Lieutenant's Run are from epifaunal species, including cementers (58.0%), epibyssally attached forms (1.8%), and nestlers (7.7%). Of the infaunal bivalves many of the assigned modern analogs

have been described living in shallow burrows among shell gravel (see Appendix B). Specifically the modern species *Venericardia borealis* (= *Cyclocardia granulata*) and *Astarte undulata* (= *Astarte concentrica*) are found living in rubbly bottoms in the modern ocean. Their analogs at Lt. Run account for 45.9% of the non-*Mulinia* shallow infaunal bivalves.

Numerically, most of the gastropods at Lt. Run are epifaunally attached suspension feeders like *Crepidula costata* (7.1%). More species at Lt. Run belong to the scavenger/predator and boring predator guilds than any other single guild (11 species, 18.0%), although the abundance of these guilds combined is very low (1.2%).

The most numerically abundant species at the Nottoway River was the cementing epifaunal suspension feeding bivalve *C. congregata*. As with the LTR samples, the majority of bivalve specimens are from epifaunal species, including cementers (46.3%), epibyssally attached forms (6.8%), and nestlers (0.6%). Of the infaunal bivalves many of the assigned modern analogs have been described living in shallow burrows among shell gravel (see Appendix B). Specifically the modern species *Venericardia borealis* (= *Cyclocardia granulata*) and *Astarte undulata* (= *Astarte undulata*) are found living in rubbly bottoms in the modern ocean.

Numerically, most of the gastropods at the Nottoway River were epifaunally attached suspension feeders like *Crepidula costata* (16.7%). In terms of species richness, more species at Lt. Run belong to the scavenger/predator and boring predator guilds than any other single guild (19 species, 28.8%), although the abundance of these guilds combined is very low (0.5%).

For the KGM samples, the most numerically abundant species was once again the cementing epifaunal suspension feeding bivalve *C. congregata*. As with the LTR and NWR samples, the majority of bivalve specimens were from epifaunal species, including cementers (64.0%), epibyssally attached forms (1.8%), and nestlers (7.7%). Of the infaunal bivalves many of the assigned modern analogs have been described living in shallow burrows among shell gravel (see Appendix B). Specifically the modern species *Venericardia borealis* (= *Cyclocardia granulata*) and *Astarte undulata* (= *Astarte undulata*) are found living in rubbly bottoms in the modern ocean.

Numerically, most of the gastropods at the Nottoway River were epifaunally attached suspension feeders like *Crepidula costata* (4.1%), although the percent abundance here was lower than that found at the other two localities. The scavenger/predator and boring predator guilds accounted for 12.5% of the overall species richness, but only 0.4% of the total abundance in KGM samples.

In terms of rank percent abundance, all three localities had shallow, non-siphonate suspension feeding bivalves (guild 06) somewhere in the next 3 places. In KGM samples, it is the second most abundant guild followed by nestlers (guild 05). In LTR samples, it was the also the second most abundant guild, followed by medium infaunal suspension feeding bivalves (guild 08) and epifaunal suspension feeding gastropods (guild 12). In the NWR samples, it was the third ranked guild, behind epifaunal suspension feeding gastropods (guild 12). Just by examining the percent abundance at the three localities, there were clearly some difference in the guild structure of the RBPT as expressed at different localities.

### PCA

A PCA was performed on the guild data with *M. congesta* included (Fig. 6.1A). The first principle components axis ordinated samples based primarily on the relative abundance of the cementing epifaunal suspension feeding bivalve guild (guild 04). NWR and KGM samples plotted higher on this axis than most LTR samples. The LTR samples were spread rather evenly along this axis. The second axis ordinated samples based almost exclusively on the relative abundance of *M. congesta*. Since *M. congesta* was only abundant in LTR samples, the LTR samples were separated from the NWR and KGM samples on this axis.

The PCA was also performed on the guild data with *M. congesta* removed in order to determine the relationships among the non-*Mulinia* component of the RBPT guilds (Fig. 6.1B). The first principle axis ordinated samples based on the relative abundance of the cementing epifaunal suspension feeding bivalves (guild 04). With *M. congesta* removed, this axis lost much of its ability to differentiate the different localities since the LTR sample were no longer spread along this axis. The second principle component axis ordinated samples based primarily on the relative abundance of epifaunal suspension feeding gastropods (guild 12). Most NWR samples plotted high on this axis, while most KGM and LTR samples plotted low on this axis. While both analyses separated out the localities somewhat, the separation was not large, which indicated that the guild structure was somewhat similar from locality to locality in the RBPT.

### Correlation Analysis

Analyses of within and between locality values of the correlation matrix were run for the RBPT samples both with *M. congesta* in the data set (Fig. 6.2A), and with *M. congesta* removed from the data set (Fig. 6.2B). The correlation values for within sample comparisons were very

high for each locality in both cases. The between locality comparisons were relatively low for comparisons between the LTR and non-LTR comparisons, but still very high for the KGM versus NWR comparison. With *M. congesta* removed from the data set the mean correlation values for all pairwise comparisons were extremely high (>.915), indicating that the samples were all very similar to each other.

The correlation data was also broken down by locality in order to examine the apparent differences between localities more closely. The distributions of the NWR, LTR, and KGM correlation comparisons for the entire data set can be found in Fig. 6.3, while the distributions with *M. congesta* removed were plotted in Fig. 6.4.

The Lieutenant's Run locality yielded 12 samples which were assigned to the RBPT. The results of comparisons of pairs of LTR samples versus pairs of LTR and non-LTR samples are summarized in Table 6.16.

**Table 6.16** Mean values and significance of difference between correlation coefficients of LTR pairs, and pairs of LTR and non-LTR samples.

	Mean	ANOVA	Mann-Whitney U
LTR vs LTR	.915	-	-
LTR vs KGM	.800	yes (p=.0001)	yes (p=.0001)
LTR vs NWR	.748	yes (p=.0001)	yes (p=.0001)

While the within locality mean correlation value was very high, the between locality comparisons yielded low mean correlation values. The main difference between the LTR and non-LTR samples were the high relative abundance of *M. congesta* in some LTR samples. Without *M. congesta*, much of the apparent dissimilarity between the LTR samples and those from other localities disappears (Table 6.17).

**Table 6.17** Mean values and significance of difference between correlation coefficients of LTR pairs, and pairs of LTR and non-LTR samples, *M. congesta* removed from data set.

	Mean	ANOVA	Mann-Whitney U
LTR vs LTR	.948	-	-
LTR vs KGM	.946	no (p=.7072)	no (p=.8763)
LTR vs NWR	.925	yes (p=.0019)	yes (p=.0004)

The mean correlation values for the non-*Mulinia* component of the LTR samples with either other LTR samples or non-LTR samples were all greater than .900, indicating a high degree of similarity. The LTR versus LTR and LTR versus KGM comparisons were indistinguishable from

each other statistically, and while the mean correlation value of the LTR versus NWR comparison is significantly lower than the LTR versus LTR comparisons, it is still very high.

The Kingsmill locality yielded 6 samples which were assigned to the RBPT. The results of comparisons of pairs of KGM samples versus pairs of KGM and non-KGM samples are summarized in Table 6.18.

**Table 6.18** Mean values and significance of difference between correlation coefficients of KGM pairs, and pairs of KGM and non-KGM samples.

	Mean	ANOVA	Mann-Whitney U
<b>KGM vs KGM</b>	.959	-	-
<b>KGM vs LTR</b>	.800	yes (p=.0001)	yes (p=.0001)
<b>KGM vs NWR</b>	.901	yes (p=.0015)	yes (p=.0001)

The KGM versus NWR comparison yielded a relatively high mean correlation value of .901, and while this mean was significantly lower than the KGM versus KGM mean value of .959, it is still very high. The low correlation value of KGM versus LTR samples was most likely due to the inclusion of *M. congesta* in the analysis. As above, *M. congesta* was removed from the data set and the correlation analysis re-run (Table 6.19).

**Table 6.19** Mean values and significance of difference between correlation coefficients of KGM pairs, and pairs of KGM and non-KGM samples, *M. congesta* removed from data set.

	Mean	ANOVA	Mann-Whitney U
<b>KGM vs KGM</b>	.961	-	-
<b>KGM vs LTR</b>	.946	no (p=.1628)	no (p=.2492)
<b>KGM vs NWR</b>	.915	yes (p=.0002)	yes (p=.0001)

Without *M. congesta*, the mean of the KGM versus LTR comparisons became statistically indistinguishable from the KGM versus KGM mean correlation values. This result confirmed that the LTR and KGM samples were very similar to each other once *M. congesta* was removed, as with the analysis above of the LTR samples. While there was a significant difference in mean correlation values for the KGM versus KGM and KGM versus NWR, the mean correlation values were all very high, once again indicating a high degree of faunal similarity as measured by guilds.

The Nottoway River locality yielded 13 RBPT samples. The results of comparisons of pairs of NWR samples versus pairs of NWR and non-NWR samples are summarized in Table 6.20.

**Table 6.20** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.971	-	-
<b>NWR vs LTR</b>	.748	yes (p=.0001)	yes (p=.0001)
<b>NWR vs KGM</b>	.901	yes (p=.0001)	yes (p=.0001)

As before, the mean correlation values of NWR versus KGM samples was high, although the NWR versus NWR mean correlation value was significantly higher. Also as before, the presence of abundant *M. congesta* in the LTR samples depressed the mean correlation value of that comparison. As before, *M. congesta* was removed from the data set and the analysis re-run (Table 6.21).

**Table 6.21** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples, *M. congesta* removed from data set.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.971	-	-
<b>NWR vs LTR</b>	.925	yes (p=.0001)	yes (p=.0001)
<b>NWR vs KGM</b>	.915	yes (p=.0001)	yes (p=.0001)

The mean correlation value for NWR versus NWR sample was significantly greater than the mean values of NWR versus non-NWR comparisons. However, once again, all correlation values are very high.

The correlation analysis indicates that the guild structure of the RBPT was relatively consistent from locality to locality, once the opportunist *M. congesta* has been removed from the analysis.

### Constancy Analysis

A constancy analysis was performed on the non-*Mulinia* portion of the RBPT data set by pooling all samples within each locality, and determining the within locality constancy, and then repeating that analysis on all samples of the RBPT (Table 6.22).

**Table 6.22** Guild constancy values ( $C_a$ ) for RBPT samples, *M. congesta* removed from the data set.

	samples	$C_a$
<b>NWR</b>	12	.981
<b>LTR</b>	9	.974
<b>KGM</b>	6	.981
<b>all</b>	27	.962

All of the localities had high internal species constancy (.974 - .981). The constancy value for all pooled samples was somewhat lower (.962), but still very high. The constancy analysis therefore confirmed the finding in the correlation analysis that the RBPT is very similar at all localities when the taxa were organized into guilds, and the opportunistic *M. congesta* removed from the data set.

### MANOVA

MANOVAs were performed on the guilds of the RBPT samples, with the *M. congesta* guild removed, for the three localities at which the RBPT was recognized. A MANOVA of all samples grouped by locality revealed that there are differences in the three groups that are significant at the  $p < 0.0001$  level. However, MANOVAs of each localities examined pairwise indicated that there were some similarities (Table 6.23)

**Table 6.23** Significance of differences in samples from different localities of the RBPT, probability values determined by MANOVA.

	KGM	LTR	NWR
<b>KGM</b>	-		
<b>LTR</b>	yes ( $p < .0001$ )	-	
<b>NWR</b>	no ( $p = .1108$ )	no ( $p = .0862$ )	-

While samples from the KGM and LTR localities are statistically different from each other, they are both similar enough to the NWR locality that the null hypothesis that they are in fact the same can not be rejected at the 95% confidence level. As expected from the PCA, correlation analysis, and constancy analysis, the guild structure of the RBPT does appear to recur at different localities, and

so perhaps the Rubbly Bottom Paleocommunity Type constitutes a paleocommunity in the Bennington and Bambach (1996) sense, if guilds are used to define paleocommunities instead of species.

### MBPT

The species richness of the guilds at each locality was tabulated in Table 6.24. Of the 53 species of bivalves present, 25 (47.1%) were shallow burrowing suspension feeders and 15 (28.3%) lived epifaunally. Deposit feeders accounted for 11.3% of the bivalve species richness and all other bivalves accounted for 13.3%. Most of the shallow burrowers were either siphonate suspension feeders (20.8%) or non-siphonate suspension feeders (20.8%), with 5.7% of the bivalve species richness represented by shallow burrowing lucinids. Of the epifaunal suspension feeding bivalves, 6 (11.3%) of the species attached epibyssally, 5 (9.4%) of the species were cementers, and 4 (7.5%) were nestlers.

**Table 6.24** Number of species per guild in the MBPT.

Guild	DYP	NW	BWB	LTR	KG	total
		R			M	
01: shallow infaunal deposit feeding bivalves	2	1	2	1	1	2
02: shallow infaunal tellinid deposit feeding bivalves	4	0	0	2	2	4
03: epibyssate suspension feeding bivalves	4	3	2	4	1	6
04: cementing epifaunal suspension feeding bivalves	5	2	1	5	4	5
05: nestling epifaunal suspension feeding bivalves	3	0	1	2	3	4
06: shallow infaunal non-siphonate suspension feeding bivalves	8	5	0	5	2	11
07: shallow infaunal siphonate suspension feeding bivalves	11	3	3	5	5	11
08: medium infaunal siphonate suspension feeding bivalves	3	3	2	3	2	3
09: deep infaunal siphonate suspension feeding bivalves	2	1	0	1	2	2
10: shallow infaunal suspension feeding lucinids	3	1	1	1	1	3
11: medium infaunal suspension feeding lucinids	0	0	0	2	0	2
12: epifaunal suspension feeding gastropods	7	2	3	6	3	8
13: vagrant epifaunal grazing gastropods	3	1	1	2	1	4
14: vagrant epifaunal gastropod scavenger/predators	11	0	1	5	0	12
15: vagrant epifaunal boring predatory gastropod	6	3	0	1	0	7
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	1	1	1	2	0	2
17: <i>M. congesta</i> (opportunist)	1	1	1	1	1	1
Other	11	4	2	2	3	11

The five guilds of gastropods present in the MBPT contained 33 species. The sessile epifaunal gastropods (guild 12) accounted for 24.2% of the species richness, while the four guilds of vagrant gastropods accounted for the other 75.8%. Eight of the 9 species of suspension feeding gastropods recognized in this study were found in one or more samples of the MBPT, although the number of species found at each locality varied greatly. The vagrant epifaunal scavenger/predator

guild accounted for 36.3% of the total gastropod species richness, with the two guilds of boring predators accounting for another 27.2% . All 9 species of boring snails were recognized at least one of the MBPT localities, although the species richness at any one locality ranged from zero (KGM samples) to 7 (DYP samples). Grazers (guild 13) accounted for 12.2% of the species richness overall, and while this guild was present at all localities, no more than 3 of those species were found at any one locality..

In terms of percent abundance (Table 6.25), the dominant guild of the MBPT at all localities was the opportunistic bivalve *M. congesta*, which accounted for 33.9% - 92.5% of the total abundance.

**Table 6.25** Percent abundance of guilds of the MBPT.

Guild	DYP	NWR	BWB	LTR	KGM
01: shallow infaunal deposit feeding bivalves	6.3%	0.9%	5.7%	0.1%	0.3%
02: shallow infaunal tellinid deposit feeding bivalves	5.2%	-	-	0.5%	1.6%
03: epibyssate suspension feeding bivalves	3.6%	0.3%	0.7%	1.2%	1.3%
04: cementing epifaunal suspension feeding bivalves	6.5%	1.2%	0.9%	30.5%	18.1%
05: nestling epifaunal suspension feeding bivalves	0.4%	-	0.2%	1.6%	2.5%
06: shallow infaunal non-siphonate suspension feeding bivalves	1.1%	1.6%	-	6.2%	1.0%
07: shallow infaunal siphonate suspension feeding bivalves	16.2%	0.2%	2.1%	3.0%	10.2%
08: medium infaunal siphonate suspension feeding bivalves	7.2%	0.3%	0.5%	2.5%	6.3%
09: deep infaunal siphonate suspension feeding bivalves	1.1%	0.1%	-	0.2%	1.3%
10: shallow infaunal suspension feeding lucinids	4.3%	0.3%	3.5%	0.4%	1.3%
11: medium infaunal suspension feeding lucinids	-	-	-	0.3%	-
12: epifaunal suspension feeding gastropods	10.8%	2.2%	2.8%	3.5%	7.0%
13: vagrant epifaunal grazing gastropods	0.4%	-	0.2%	0.4%	0.3%
14: vagrant epifaunal gastropod scavenger/predators	1.7%	-	0.2%	1.0%	-
15: vagrant epifaunal boring predatory gastropod	1.1%	0.2%	-	0.1%	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	0.3%	0.1%	1.4%	0.3%	-
17: <i>M. congesta</i> (opportunist)	33.9%	92.5%	81.6%	48.2%	48.9%

The modern analog of the opportunist *Mulinia congesta* will live in any kind of sediment, but has population explosions at times when the local environmental conditions are very unstable (Calbrese 1970, Levinton and Bambach 1970, Levinton 1970, Andrews 1992) - conditions that would be expected to prevail when the bottom conditions are very muddy, as in the MBPT. This hyper-abundance masked the non-*Mulinia* guild structure, so *M. congesta* was removed from the data set, and the percent abundances of the non-opportunistic taxa recalculated (Table 6.26).

With *M. congesta* removed, it becomes immediately obvious that there is no consistent guild structure to the MBPT as it is expressed at different localities.

**Table 6.26** Percent abundance of guilds of the MBPT, with *M. congesta* removed from calculation.

<b>Guild</b>	<b>DYP</b>	<b>NWR</b>	<b>BWB</b>	<b>LTR</b>	<b>KGM</b>
01: shallow infaunal deposit feeding bivalves	8.2%	11.7%	30.8%	0.3%	0.6%
02: shallow infaunal tellinid deposit feeding bivalves	7.3%	-	-	1.0%	3.1%
03: epibyssate suspension feeding bivalves	5.5%	3.9%	3.8%	2.3%	2.5%
04: cementing epifaunal suspension feeding bivalves	10.3%	16.1%	5.1%	58.9%	35.4%
05: nestling epifaunal suspension feeding bivalves	0.6%	-	1.3%	3.0%	5.0%
06: shallow infaunal non-siphonate suspension feeding bivalves	1.8%	21.1%	-	12.0%	1.9%
07: shallow infaunal siphonate suspension feeding bivalves	25.1%	2.8%	11.5%	5.8%	19.9%
08: medium infaunal siphonate suspension feeding bivalves	10.7%	4.4%	2.6%	4.8%	12.4%
09: deep infaunal siphonate suspension feeding bivalves	1.6%	1.7%	-	0.5%	2.5%
10: shallow infaunal suspension feeding lucinids	6.0%	4.4%	19.2%	0.8%	2.5%
11: medium infaunal suspension feeding lucinids	-	-	-	0.5%	-
12: epifaunal suspension feeding gastropods	17.3%	29.4%	15.4%	6.8%	13.7%
13: vagrant epifaunal grazing gastropods	0.6%	0.6%	1.3%	0.8%	0.6%
14: vagrant epifaunal gastropod scavenger/predators	2.7%	-	1.3%	2.0%	-
15: vagrant epifaunal boring predatory gastropod	1.8%	2.2%	-	0.3%	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	0.5%	1.7%	7.7%	0.5%	-

The most abundant guild in the data set with *M. congesta* removed varied from locality to locality: in DYP samples guild 07 was the most abundant guild; for NWR samples, it was guild 12; in BWB, it was guild 02; in LTR and NWR samples, it was guild 04 - the only time which it was the same guild twice. The most abundant guild in BWB samples (guild 01: shallow infaunal deposit feeding bivalves) is present in relatively high abundance at all localities except for the LTR samples (0.3%) and KGM samples (0.6%). The second most abundant guild in NWR samples (guild 06) was essentially absent from BWB. While some guilds (e.g. guild 11) occurred in low abundance at all localities, the abundances of other guilds varied wildly from locality to locality, and there was no consistent strong guild structure similarity among localities once *M. congesta* was removed from consideration.

### PCA

PCA of the guild data for the MBPT yielded two principle components axes which together account for 94.2% of the variability (Fig. 6.5). The first principle component axis ordinated samples based primarily on the relative abundance of *M. congesta*. KGM, NWR, and BWB samples plotted relatively high on this axis, while the LTR and DYP samples were spread out along this axis. The second principle components axis had high loading values for the shallow infaunal siphonate suspension feeding bivalve guild (guild 07), the epifaunal suspension feeding gastropod guild (guild 12), and the cementing epifaunal suspension feeding bivalve guild (guild

04). DYP and KGM samples, with their high relative abundances of guilds 07 and 12 plotted relatively high on this axis compared to the samples from other localities.

To more fully examine the MBPT, *M. congesta* was removed from the data set, and the PCA re-run. The new PCA required 4 principle components to account for only 88.4% of the variability (Fig. 6.6). With *M. congesta* removed, there was therefore a lot more structure to the data than when all guilds were considered.

Principle component axis one had high positive loadings for guilds 12, 08, and 07, and separated DYP samples from samples from other localities. KGM samples plotted midway up on this axis, while NWR samples all plotted low on this axis. Most BWB samples also had relatively low values on this axis.

Principle component axis two had a high positive loading for the deposit feeding bivalve guild (guild 01) and a negative loading for guild 07. BWB samples, with their high ratio of guild 01 to guild 07 plotted high on this axis. KGM and DYP samples plotted low on this axis, with NWR samples spread out along the axis.

Principle component axis three had a high positive loading for cementing epifaunal suspension feeding bivalves (guild 04), and a high negative loading for guild 07. LTR and DYP samples plotted high on this axis, while samples from other localities plotted low on this axis.

Principle component axis four had high positive loadings for both guild 01 and guild 04, with a high negative loading for epifaunal suspension feeding gastropods (guild 12). NWR samples, with their low relative abundance of guild 12, plotted high on this axis, while KGM and LTR samples plotted relatively low on this axis, and had a relatively high abundance of guild 12. The DYP and BWB samples were distributed along this axis.

In general, the samples from the same locality clustered together in at least one of the PCA plots. The exception is the BWB locality, which did not form tight clusters in any of the bivariate scatter plots. Therefore, other than in BWB samples, there appeared to be at least some similarity in samples from the same locality, even after *M. congesta* was removed from the analysis. However, without *M. congesta*, much of the apparent similarity between localities vanished.

### **Correlation Analysis**

A correlation matrix was determined for the samples of the MBPT using PCA for both the entire guild data set, and the data set with *M. congesta* removed. The correlation values were grouped based on the localities of the two samples in each correlation, and the distribution of these groups determined. The distributions of pairs from the same locality and pairs in which the two members were from different localities is plotted in Figure 6.7.

For the data set that included *M. congesta*, both the within and between locality mean correlation values were relatively high, although nowhere near as high as the values seen in the analysis of the RBPT. The within locality mean correlation value was significantly higher than the between locality mean correlation values according to an ANOVA ( $p=.0282$ ), although not according to the non-parametric Mann-Whitney U test ( $p=.1935$ ). Since the distributions appeared to be non-normal, the Mann-Whitney U result must be given more weight than the ANOVA, so the mean values were not significantly different. With *M. congesta* included in the data set, the between locality similarity was therefore just as great as the within locality similarity.

The distributions of correlation coefficients with *M. congesta* removed tell a very different story. The mean correlation value for the within locality comparisons only drops 10.7%, but the between localities comparisons plummets by 62.7%. The mean correlation values for the within locality comparisons was significantly higher than the between locality comparisons according to both ANOVA ( $p=.0001$ ) and Mann-Whitney U ( $p=.0001$ ) tests. Removing *M. congesta* removed much of the apparent similarity between the MBPT as expressed at different localities.

The correlation analysis data was subdivided into specific match-ups so that each locality could be compared separately for both all guilds (Fig. 6.8) and all guilds except the *M. congesta* guild (Fig. 6.9). For the DYP, BWB, and NWR samples, the match-ups of each with the other 4 localities, and with itself were determined, and ANOVA and Mann-Whitney test performed on the distributions of each sub group. There were only 2 samples of MBPT samples each from LTR and KGM, so these localities could not be analyzed in the same way that they other 3 localities were.

A total of 5 MBPT horizons were sampled at Day's Point. The results of comparisons of pairs of DYP samples versus pairs of DYP and non-DYP samples are summarized in Table 6.27.

**Table 6.27** Mean values and significance of difference between correlation coefficients of DYP pairs, and pairs of DYP and non-DYP samples.

	Mean	ANOVA	Mann-Whitney U
<b>DYP vs DYP</b>	.801	-	-
<b>DYP vs. NWR</b>	.750	yes (p=.0001)	yes (p=.0029)
<b>DYP vs. BWB</b>	.758	yes (p=.0004)	yes (p=.0043)
<b>DYP vs. LTR</b>	.646	yes (p=.0001)	yes (p=.0001)
<b>DYP vs KGM</b>	.795	no (p=.7428)	no (p=.4968)

Other than DYP versus KGM comparisons, DYP versus DYP correlation values were significantly higher than DYP versus non-DYP comparisons. However, all comparisons had mean values greater than .600, and other than the DYP versus LTR comparisons, all were .750 or greater.

Once *M. congesta* was removed from the analysis (Table 6.28) most of the apparent similarity between DYP and non-DYP comparisons disappears. Other than the relatively high .508 mean correlation value for DYP versus KGM samples, the highest mean correlation value for any DYP versus non-DYP comparison set was .270.

**Table 6.28** Mean values and significance of difference between correlation coefficients of DYP pairs, and pairs of DYP and non-DYP samples, *M. congesta* removed.

	Mean	ANOVA	Mann-Whitney U
<b>DYP vs DYP</b>	.718	-	-
<b>DYP vs. NWR</b>	.250	yes (p=.0001)	yes (p=.0001)
<b>DYP vs. BWB</b>	.270	yes (p=.0001)	yes (p=.0001)
<b>DYP vs. LTR</b>	.148	yes (p=.0001)	yes (p=.0001)
<b>DYP vs KGM</b>	.508	yes (p=.0001)	yes (p=.0001)

A total of 5 MBPT samples were collected from the Burwell's Bay locality. The results of comparisons of pairs of BWB samples versus pairs of BWB and non-BWB samples are summarized in Table 6.29.

**Table 6.29** Mean values and significance of difference between correlation coefficients of BWB pairs, and pairs of BWB and non-BWB samples.

	Mean	ANOVA	Mann-Whitney U
<b>BWB vs BWB</b>	.986	-	-
<b>BWB vs DYP</b>	.758	yes (p=.0001)	yes (p=.0001)
<b>BWB vs KGM</b>	.887	yes (p=.0001)	yes (p=.0002)
<b>BWB vs LTR</b>	.777	yes (p=.0001)	yes (p=.0002)
<b>BWB vs NWR</b>	.989	no (p=.4979)	no (p=.3588)

Most correlation values of DYP versus non-DYP samples were relatively high, and are only significantly different from the BWB versus non-BWB samples because of the very high BWB versus BWB mean correlation value.

Once *M. congesta* was removed from the analysis (Table 6.30) most of the apparent similarity between BWB and non-BWB, as well as BWB versus BWB samples disappears. With a BWB versus BWB mean correlation value of .404, the significance of the comparisons to other localities was somewhat irrelevant. The BWB samples had low internal consistency, so the external inconsistency was not as surprising.

**Table 6.30** Mean values and significance of difference between correlation coefficients of BWB pairs, and pairs of BWB and non-BWB samples, *M. congesta* removed.

	Mean	ANOVA	Mann-Whitney U
<b>BWB vs BWB</b>	.404	-	-
<b>BWB vs DYP</b>	.270	yes (p=.0306)	no (p=.0617)
<b>BWB vs KGM</b>	.091	yes (p=.0042)	yes (p=.0216)
<b>BWB vs LTR</b>	.024	yes (p=.0001)	yes (p=.0002)
<b>BWB vs NWR</b>	.394	no (p=.1693)	no (p=.2810)

The Nottoway River locality yielded a total of 4 MBPT samples. The results of comparisons of pairs of NWR samples versus pairs of NWR and non-NWR samples are summarized in Table 6.31.

**Table 6.31** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.994	-	-
<b>NWR vs BWB</b>	.989	no (p=.3178)	no (p=.1616)
<b>NWR vs DYP</b>	.750	yes (p=.0018)	yes (p=.0001)
<b>NWR vs KGM</b>	.887	yes (p=.0013)	yes (p=.0019)
<b>NWR vs LTR</b>	.646	yes (p=.0002)	yes (p=.0019)

With the exception of the NWR versus LTR value, most mean correlation values of NWR versus non-NWR samples are relatively high, and are only significantly different from the NWR versus non-NWR samples because of the very high NWR versus NWR mean correlation value. The NWR versus BWB mean correlation values is high enough that there is no significant difference detectable between it and the NWR versus NWR mean correlation value.

Once again, removal of *M. congesta* from the analysis (Table 6.32) removed most of the apparent similarity between NWR and non-NWR samples, although the NWR versus NWR mean correlation value remained high. While the NWR samples were very similar to each other, even with *M. congesta* removed, they did not have a similar guild structure to that found at other localities.

**Table 6.32** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples, *M. congesta* removed.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.805	-	-
<b>NWR vs BWB</b>	.394	yes (p=.0001)	yes (p=.0004)
<b>NWR vs DYP</b>	.250	yes (p=.0002)	yes (p=.0004)
<b>NWR vs KGM</b>	.329	yes (p=.0006)	yes (p=.0045)
<b>NWR vs LTR</b>	.373	yes (p=.0001)	yes (p=.0019)

Most correlation comparison in the MBPT had high mean correlation values when *M. congesta* is included in the data set. Removing *M. congesta* from the data set did not effect the NWR versus NWR or DYP versus DYP comparisons much, but it dropped the other comparisons drastically. The MBPT within the NWR and DYP samples therefore show strong internal correlations, but the comparisons between localities indicated that all other correlation values were very low, and thus once *M. congesta* was removed from the data set, there was no strong guild structure to the samples from different localities.

### Species Constancy

A constancy analysis was performed for each locality in the MBPT, and for all pooled samples in the MBPT (Table 6.33).

**Table 6.33** Guild constancy ( $C_a$ ) for MBPT samples.

	samples	$C_a$
<b>DYP</b>	5	.998
<b>NWR</b>	4	.996
<b>BWB</b>	5	.931
<b>LTR</b>	2	.990
<b>KGM</b>	2	.994
<b>all</b>	18	.913

As with the RBPT constancy analysis, constancy was higher for groups taken from single localities than from all localities pooled. The constancy values were higher than for the constancy

analysis on the raw data because when the taxonomic data was pooled to make the guilds, the chances of encountering any particular guild is higher than that of encountering any particular species, and thus the guilds tend to have very high occurrence frequencies.

The very high abundance of *M. congesta* in most MBPT samples, coupled with the high occurrence of the small opportunist in all MBPT samples inflated the constancy value for the MBPT samples. A second constancy analysis was run with *M. congesta* removed from the data set (Table 6.34).

**Table 6.34** Guild constancy ( $C_a$ ) for MBPT samples, and species constancy with *M. congesta* removed ( $C_a'$ ).

	samples	$C_a$	$C_a'$	$\Delta C_a$
<b>DYP</b>	5	.998	.996	-.002
<b>NWR</b>	4	.996	.952	-.044
<b>BWB</b>	5	.931	.628	-.293
<b>LTR</b>	2	.990	.980	-.010
<b>KGM</b>	2	.994	.988	-.006
<b>all</b>	18	.913	.803	-.110

As expected, in every case, the constancy value dropped, although in some cases much less than others. Removing *M. congesta* caused the most severe drop in the constancy of BWB samples, indicating that those samples did not contain as consistent a guild structure as the original high constancy value might have indicated. The samples from Burwell's Bay had much lower correlation values than the other localities in the correlation matrix analysis of the non-*Mulinia* component. While all the values dropped, all the locality constancy measures but BWB were still higher than the pooled data set of all MBPT samples.

Other than the BWB samples, the constancy analysis confirmed the results of the PCA analysis and the correlation matrix analysis - there was higher guild constancy within localities than among all pooled localities.

## MANOVA

MANOVAs were performed on the guilds of the MBPT samples from the five localities at which the MBPT was recognized. A MANOVA of all samples grouped by locality revealed that there are differences in the five groups that are significant at the  $p < 0.0001$  level.

MANOVAs were also performed on samples from each pair of localities (BWB and DYP, BWB and KGM, BWB and NWR, DYP and KGM, DYP and NWR, KGM and NWR), which also all yielded difference significant at the  $p < 0.0001$  level. Samples from different localities are dissimilar enough that the null hypothesis that they are the same can be rejected at the 95% confidence level. As expected from the PCA, correlation analysis, and constancy analysis, samples from the MBPT at different localities have statistically dissimilar guild structures, and the Muddy Bottom Paleocommunity Types does not constitute a paleocommunity in the Bennington and Bambach (1996) sense.

### Transition Zone

The species richness of the guilds at each locality was tabulated in Table 6.35. Of the 59 species of bivalves present, 30 (50.8%) were shallow burrowing suspension feeders and 15 (25.4%) lived epifaunally. Deposit feeders accounted for 8.5% of the bivalve species richness and all other bivalves accounted for 15.3%. Most of the shallow burrowers were either siphonate suspension feeders (27.1%) or non-siphonate suspension feeders (18.6%), with 5.1% of the bivalve species richness represented by shallow burrowing lucinids. Of the epifaunal suspension feeding bivalves, 7 (11.9%) of the species attached epibyssally, 5 (8.5%) of the species were cementers, and 3 (5.1%) were nestlers.

**Table 6.35** Number of species per guild in the transition zone.

Guild	DYP	NWR	BWB	LTR	KGM	total
01: shallow infaunal deposit feeding bivalves	2	2	1	2	1	2
02: shallow infaunal tellinid deposit feeding bivalves	3	2	3	3	1	3
03: epibyssate suspension feeding bivalves	2	5	5	6	2	7
04: cementing epifaunal suspension feeding bivalves	1	4	5	5	4	5
05: nestling epifaunal suspension feeding bivalves	0	2	2	3	1	3
06: shallow infaunal non siphonate suspension feeding bivalves	1	7	7	9	1	11
07: shallow infaunal siphonate suspension feeding bivalves	7	7	7	12	4	16
08: medium infaunal siphonate suspension feeding bivalves	3	3	3	4	2	4
09: deep infaunal siphonate suspension feeding bivalves	2	3	2	2	0	3
10: shallow infaunal suspension feeding lucinids	3	2	2	2	1	3
11: medium infaunal suspension feeding lucinids	0	0	0	2	0	2
12: epifaunal suspension feeding gastropods	4	4	6	6	3	7
13: vagrant epifaunal grazing gastropods	2	1	3	3	1	3
14: vagrant epifaunal gastropod scavenger/predators	3	7	6	3	0	12
15: vagrant epifaunal boring predatory gastropod	2	6	4	4	0	8
16: vagrant epifaunal/semi infaunal boring predatory gastropod	0	1	1	2	0	2
17: <i>M. congesta</i> (opportunist)	1	1	1	1	1	1
other	6	8	10	12	4	16

The five guilds of gastropods present in the transition zone contained 32 species. The sessile epifaunal gastropods (guild 12) accounted for 21.9% of the species richness, while the four species of vagrant gastropods accounted for the other 78.1%. The vagrant epifaunal scavenger/predator guild accounted for 20.3% of the total gastropod species richness, with the two guilds of boring predators accounting for another 16.9%. However, the number of species of boring predators varied greatly from locality to locality, from a minimum of no boring gastropods in KGM samples to a maximum of 7 species in NWR samples. Grazers accounted for 5.1% of the species richness overall, and this guild was present at all locality.

In terms of percent abundance (Table 6.36), the dominant guild of the transition zone at some, but not all localities was the opportunistic bivalve *M. congesta*, which accounted for 5.5% - 41.1% of the total abundance.

**Table 6.36** Percent abundance of guilds of the transition zone.

<b>Guild</b>	<b>DYP</b>	<b>NWR</b>	<b>BWB</b>	<b>KGM</b>
01: shallow infaunal deposit feeding bivalves	14.8%	0.4%	0.8%	0.6%
02: shallow infaunal tellinid deposit feeding bivalves	4.4%	1.0%	1.3%	0.6%
03: epibyssate suspension feeding bivalves	2.5%	9.5%	3.9%	7.1%
04: cementing epifaunal suspension feeding bivalves	2.5%	13.2%	9.6%	39.7%
05: nestling epifaunal suspension feeding bivalves	-	0.3%	3.1%	2.6%
06: shallow infaunal non-siphonate suspension feeding bivalves	0.6%	19.4%	2.6%	1.9%
07: shallow infaunal siphonate suspension feeding bivalves	10.1%	2.8%	5.6%	5.1%
08: medium infaunal siphonate suspension feeding bivalves	8.4%	2.1%	7.1%	7.7%
09: deep infaunal siphonate suspension feeding bivalves	4.2%	1.5%	1.3%	-
10: shallow infaunal suspension feeding lucinids	4.4%	0.3%	3.0%	0.6%
11: medium infaunal suspension feeding lucinids	-	-	-	-
12: epifaunal suspension feeding gastropods	3.6%	38.0%	44.9%	12.2%
13: vagrant epifaunal grazing gastropods	0.8%	0.5%	1.9%	1.3%
14: vagrant epifaunal gastropod scavenger/predators	1.3%	1.1%	4.5%	-
15: vagrant epifaunal boring predatory gastropod	0.8%	1.3%	3.1%	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	0.8%	1.8%	1.7%	-
17: <i>M. congesta</i> (opportunist)	41.1%	6.7%	5.5%	20.5%

The hyper-abundance of *M. congesta* in DYP samples, and the high abundance in KGM samples may be masking a fundamental guild structure in the non-*Mulinia* component of the transition zone as expressed at different localities, so *M. congesta* was removed from the analysis and the percentages recalculated (Table 6.37).

**Table 6.37** Percent abundance of guilds of the transition zone, with *M. congesta* removed from the calculation.

<b>Guild</b>	<b>DYP</b>	<b>NWR</b>	<b>BWB</b>	<b>KGM</b>
01: shallow infaunal deposit feeding bivalves	25.2%	0.5%	0.8%	0.8%
02: shallow infaunal tellinid deposit feeding bivalves	7.4%	1.0%	1.4%	0.8%
03: epibyssate suspension feeding bivalves	4.2%	10.2%	4.1%	8.9%
04: cementing epifaunal suspension feeding bivalves	4.2%	14.1%	10.2%	50.0%
05: nestling epifaunal suspension feeding bivalves	-	0.3%	3.3%	3.2%
06: shallow infaunal non-siphonate suspension feeding bivalves	1.0%	20.8%	2.7%	2.4%
07: shallow infaunal siphonate suspension feeding bivalves	17.1%	3.0%	5.9%	6.5%
08: medium infaunal siphonate suspension feeding bivalves	14.2%	2.3%	7.6%	9.7%
09: deep infaunal siphonate suspension feeding bivalves	7.1%	1.6%	1.4%	-
10: shallow infaunal suspension feeding lucinids	7.4%	0.3%	3.2%	0.8%
11: medium infaunal suspension feeding lucinids	-	-	-	-
12: epifaunal suspension feeding gastropods	6.1%	40.8%	47.5%	15.3%
13: vagrant epifaunal grazing gastropods	1.3%	0.6%	2.1%	1.6%
14: vagrant epifaunal gastropod scavenger/predators	2.3%	1.1%	4.8%	-
15: vagrant epifaunal boring predatory gastropod	1.3%	1.4%	3.3%	-
16: vagrant epifaunal/semi-infaunal boring predatory gastropod	1.3%	2.0%	1.8%	-

With *M. congesta* removed, the large difference between the guild structure of the transition zone samples at different localities becomes more glaring. If anything, the abundance of *M. congesta* appeared to have masked the difference between the different localities.

The most abundant guild in DYP samples is the shallow infaunal deposit feeding bivalve guild (guild 01), which accounted for less than 1% of the total abundance at the other 3 localities. The most abundant guild in NWR and BWB samples was the epifaunal suspension feeding gastropod guild (guild 12), which accounted for less than 20% of the total abundance at the other localities. Lest it appear that the NWR and BWB samples were very similar, the next most abundant guild at NWR was the non-siphonate suspension feeding bivalve guild (guild 06), which accounted for only 2.7% of the abundance present in BWB samples. The KGM samples had cementing epifaunal suspension feeding bivalves (guild 04) accounting for half of the abundance, while at the other localities, that guild accounted for less than 15% of the total abundance.

Because the non-*Mulinia* component of the transition zone appeared less structured than the data set with *M. congesta* included, the entire data set was considered in the analyses below. Including *M. congesta* should raise the overall similarity of the various samples, and thus any difference found should be more meaningful than those found in the data set with *M. congesta* removed.

## PCA

PCA of the guild data for the transition zone required four principle components axes to account for 92.7% of the variability (Fig. 6.10). The first principle component axis ordinated samples based primarily on the relative abundance of epifaunal suspension feeding gastropods (guild 12) and cementing epifaunal suspension feeding bivalves (guild 04). NWR and BWB samples, with their very high relative abundance of guild 12 plotted high on this axis. This axis may be recording something about the availability of stable attachment surfaces, since species in both of these guilds require hard attachment surfaces.

*M. congesta* had a high loading value on the second principle components axis. DYP samples, which had a very high relative abundance of *M. congesta* plotted high on this axis, along with one sample each from the Nottoway River and Kingsmill localities. The other samples had a smaller relative abundance of *M. congesta*, and so they plotted low on this axis.

The third principle components axis had a high positive loading for shallow infaunal deposit feeding bivalves (guild 01) and a high negative loading for cementing epifaunal suspension feeding bivalves (guild 04). DYP samples, with their high relative abundance of guild 01, plot high on this axis, while NWR samples, with their high relative abundance of guild 04 plot low on this axis. This axis might be recording something about the substrate conditions. Guild 01 species needed muddy substrate with contained organic detritus on which to feed, while guild 04 species required hard attachment surfaces.

Principle component axis four had high positive loadings for both guild 01 and guild 04. The combination of relatively high abundance of both was found in KGM samples and some DYP samples, but not at any other localities.

In general, samples tended to group by locality in the PCA space on at least one of the principle components axes. Even though there is a lot of variability, samples from the same locality tended to be similar enough to each other to plot in the same portions of the PCA space.

### **Correlation Analysis**

A correlation matrix was determined for the samples of the transition zone using PCA. The correlation values were grouped based on the localities of the two samples in each correlation, and the distribution of these groups determined. The distributions of pairs from the same locality and pairs in which the two members were from different localities were plotted in Figure 6.11. The

correlation values for within locality comparisons were much higher than for between locality comparisons, and the difference in mean was significant according to both ANOVA ( $p=.0001$ ) and Mann-Whitney U ( $p=.0001$ ) tests. The distribution of the between locality comparisons was rather distinctly bimodal, indicating that there may be some underlying structure to the data, which can be examined by breaking the data down further.

The correlation analysis was also performed for each locality individually versus the other localities. Only 3 of the KGM samples belonged to this group, which was probably too small a number to consider separately, since those 3 samples only yielded 3 KGM versus KGM comparisons. However, the analysis was performed, even though the results were most likely suspect. The distributions of correlation values for the DYP, BWB, KGM, and NWR were plotted in Figure 6.12

The bi-modality seen in the distribution of all within and between locality correlations was also seen in the distributions of many of the locality by locality match-ups. Specifically, it was seen in the DYP versus DYP and NWR versus NWR distributions. Because these distributions had a bimodal distribution, the match-ups of DYP versus non-DYP and NWR versus non-NWR were also expected to produce bimodal distributions (since even if they were rather similar to each other, they would be compared to two groups in the DYP and NWR samples), which was in fact the case. In addition, match-ups with KGM samples would also be expected to produce bi-modal or tri-modal distributions because of the small number of KGM samples. The ultimate cause of these distribution patterns, however, remains elusive.

The 11 samples from Day's Point yielded a relatively high mean correlation value of .778 when compared to each other. The results for the comparisons between this mean, and the mean correlation values of DYP and non-DYP samples are summarized in Table 6.38.

**Table 6.38** Mean values and significance of difference between correlation coefficients of DYP pairs, and pairs of DYP and non-DYP samples.

	Mean	ANOVA	Mann-Whitney U
<b>DYP vs DYP</b>	.778	-	-
<b>DYP vs BWB</b>	.009	yes ( $p=.0001$ )	yes ( $p=.0001$ )
<b>DYP vs KGM</b>	.239	yes ( $p=.0001$ )	yes ( $p=.0001$ )
<b>DYP vs NWR</b>	.008	yes ( $p=.0001$ )	yes ( $p=.0001$ )

While the DYP samples are rather similar to each other, they are decidedly dissimilar from the samples from other localities.

The 6 samples from Burwell's Bay yielded a very high mean correlation value of .937 when compared to each other. The results for comparisons between this mean, and the mean correlation values of BWB and non-BWB samples are summarized in Table 6.39.

**Table 6.39** Mean values and significance of difference between correlation coefficients of BWB pairs, and pairs of BWB and non-BWB samples.

	Mean	ANOVA	Mann-Whitney U
<b>BWB vs BWB</b>	.937	-	-
<b>BWB vs DYP</b>	.009	yes (p=.0001)	yes (p=.0001)
<b>BWB vs KGM</b>	.336	yes (p=.0001)	yes (p=.0001)
<b>BWB vs NWR</b>	.771	yes (p=.0001)	yes (p=.0001)

Once again, while the BWB samples showed high internal correlation values, the comparisons with samples from other localities showed that they are rather dissimilar. The BWB and NWR samples did show a somewhat higher mean correlation value than the other correlation values. Both localities have high relative abundances of guild 12, and somewhat similar relative abundances of guild 04, which could account for the high correlation values/

The 10 samples from the Nottoway River yielded a mean correlation value of .826 when compared to each other. The results for comparisons between this mean, and the mean correlation values of NWR and non-NWR samples are summarized in Table 6.40.

**Table 6.40** Mean values and significance of difference between correlation coefficients of NWR pairs, and pairs of NWR and non-NWR samples.

	Mean	ANOVA	Mann-Whitney U
<b>NWR vs NWR</b>	.826	-	-
<b>NWR vs BWB</b>	.771	no (p=.1294)	yes (p=.0001)
<b>NWR vs DYP</b>	.008	yes (p=.0001)	yes (p=.0001)
<b>NWR vs KGM</b>	.356	yes (p=.0001)	yes (p=.0001)

The DYP and KGM samples had very low mean correlation values with NWR samples, and these localities were clearly dissimilar. The relatively high correlation value of NWR versus BWB could not be statistically distinguished from the correlation values of NWR versus NWR. As with the analysis of the BWB samples above, the guild structures of the NWR and BWB samples appeared to be similar to each other.

The 3 samples from Kingsmill yielded a mean correlation value of .551 when compared to each other. With only 3 samples, this mean was not a very robust number. The results for

comparisons between this mean, and the mean correlation values of NWR and non-NWR samples are summarized in Table 6.41.

**Table 6.41** Mean values and significance of difference between correlation coefficients of KGM pairs, and pairs of KGM and non-KGM samples.

	Mean	ANOVA	Mann-Whitney U
<b>KGM vs KGM</b>	..551	-	-
<b>KGM vs BWB</b>	.336	no (p=.2926)	no (p=.3657)
<b>KGM vs DYP</b>	.239	no (p=.1613)	no (= .1978)
<b>KGM vs NWR</b>	.356	no (p=.3384)	no (p=.2871)

All correlation values for the KGM comparisons were low. The lack of significance to the difference in mean correlation values for KGM versus KGM and KGM versus non-KGM matchups was as much due to the low correlation values of the former than high correlation values of the latter.

As expected from the examination of the data and the PCA, the correlation analysis confirmed that there was very little cross-locality guild structure to the transition zone. The guild structure of the BWB and NWR samples, with their high abundances of guild 04, were similar to each other, but highly dissimilar from the other localities. The DYP samples, with their high abundance of guild 01 was completely dissimilar from other localities. The small number of KGM samples made any conclusions about them somewhat suspect, but the KGM samples appeared to also be rather different from transition zone samples from other localities.

### Constancy Analysis

A constancy analysis was performed on the transition zone data set by pooling all samples from each single locality, and determining the within locality constancy, and then repeating that analysis on all sample of the transition zone (Table 6.42).

**Table 6.42** Guild constancy ( $C_a$ ) for transition samples.

	samples	$C_a$
<b>DYP</b>	11	.875
<b>NWR</b>	10	.908
<b>BWB</b>	6	.941
<b>KGM</b>	3	.929
<b>all</b>	30	.766

All localities, including Kingsmill, have rather high constancy values. The constancy metric measures essentially which of the most abundant faunal elements occurred in individual samples, so the high number was not surprising since most guilds that appear at all appear in 2 or 3 of the KGM samples.

The constancy value for all samples combined was lower than for the localities grouped individually. It was however, much higher than the constancy value of .445 calculated from the species data, as were the constancy values of the individual samples. The constancy analysis confirmed the results of the PCA and correlation analysis: samples within individual localities are more similar to each other than to samples from other localities within the transition zone.

### **MANOVA**

MANOVAs were performed on the guild data for transition zone samples from the four localities at which the transition zone was recognized. A MANOVA of all samples grouped by locality revealed that there are differences in the four groups that are significant at the  $p < 0.0001$  level.

MANOVAs were also performed on samples from each pair of localities (BWB and DYP, BWB and KGM, BWB and NWR, DYP and KGM, DYP and NWR, KGM and NWR), which also all yielded difference significant at the  $p < 0.0001$  level. Samples from different localities are dissimilar enough that the null hypothesis that they are the same can be rejected at the 95% confidence level. As expected from the PCA, correlation analysis, and constancy analysis, samples from the transition zone at different localities have statistically dissimilar guild structures, and the transition zone does not constitute a paleocommunity in the Bennington and Bambach (1996) sense.

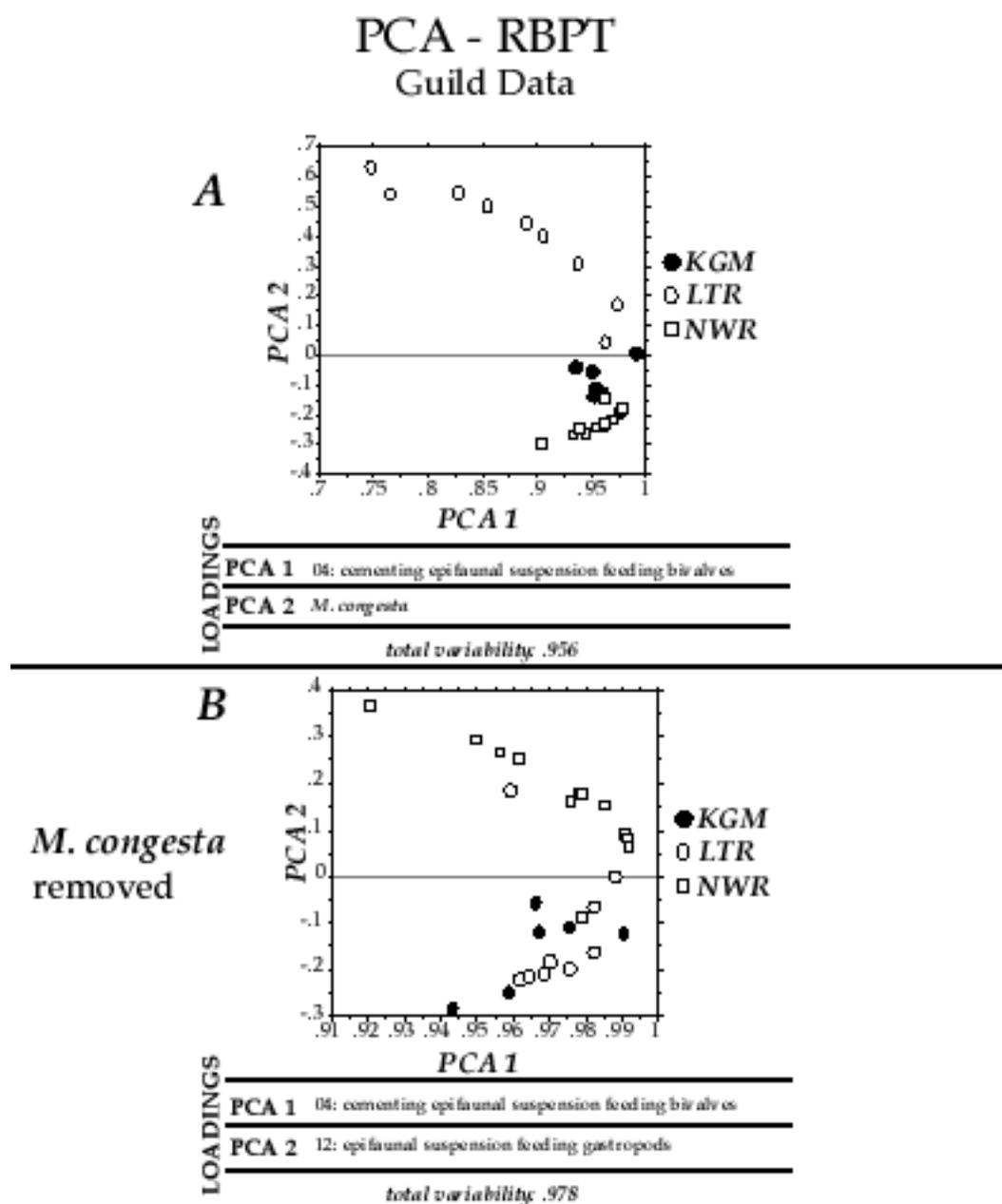
### **Conclusion**

The guild structures of the MBPT and transition zone varied widely from locality to locality. As with the analysis of the taxonomic data, local paleoenvironmental conditions were the strongest controlling factor on the guild structure. There was no consistent guild structure detected even though members of the same guilds were present at almost all localities. The strong ecological interactions predicted by the ecological locking model were not recognizable in the guild structure of the MBPT and transition zone, and therefore ecological locking can not be shown for these Yorktown faunas.

The guild structure of the RBPT recurs with enough similarity to consider it a paleocommunity in the sense of Bennington and Bambach (1996). The species presence and abundance in each guild varied from locality to locality enough that the analysis on the taxonomic data indicated very large differences in the RBPT at different localities. However, the persistence in guild structure indicates that the niche structure was very similar.

The availability of many of the niches in this paleocommunity type was controlled by the rubbliness of the substrata, which in turn was controlled by the high abundance of the bivalve *Chama congregata*. Thus, this appears to have been a biologically mediated system - when environmental conditions changed, and *C. congregata* was no longer present in high abundance, the community type ceased to exist, and thus the paleocommunity type is not found in strata higher in the section. While at first glance this might appear to be evidence for strong species interactions, and thus ecological locking, this is probably not the case. The importance of *C. congregata* to the maintenance of the RBPT was that it supplied rubble to the substrate, and since dead *C. congregata* were just as rubbly as living *C. congregata*, taphonomic feedback (Kidwell and Jablonski 1983, Kidwell 1986) might have been as important as actual interactions between living species. As long as the shells of dead *C. congregata* continued to be added to the sediment, this community type continued to exist. Once dead *C. congregata* shells stopped being supplied to the sediment, and the shells already present were buried, the community type guild structure was no longer viable, and the local communities changed according to the local environmental conditions. Thus, the local paleocommunities of the transition zone differed both from the RBPT and from each other.

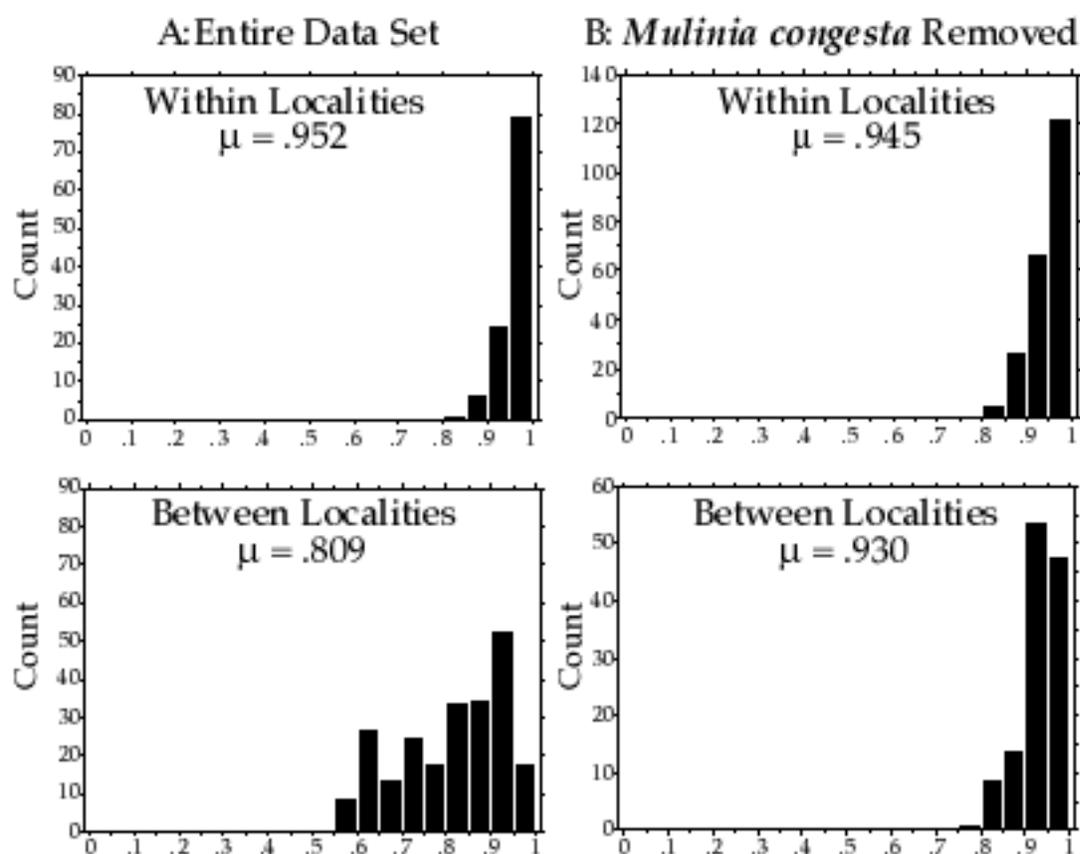
The lack of consistent guild structures within the MBPT and transitions zone, plus the lack of a coordinated response in the local paleocommunities to the paleoenvironmental shift from RBPT to transition zone are not the expected observations for a system in which ecological locking was a major force. Therefore, there is no evidence for ecological locking in the guild structure of the Yorktown fauna. As with the analysis of the taxonomic data, local paleoenvironmental conditions appear to be more important than species interactions for determining local paleocommunities with paleocommunity types.



**Figure 6.1**  
**PCA of RBPT**

Bivariate scatter plots of principle component one and two of the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities. The guilds listed on each axis have the heaviest loading for that axis. (A) All guilds included. (B) *Mulinia congesta* removed from the analysis.

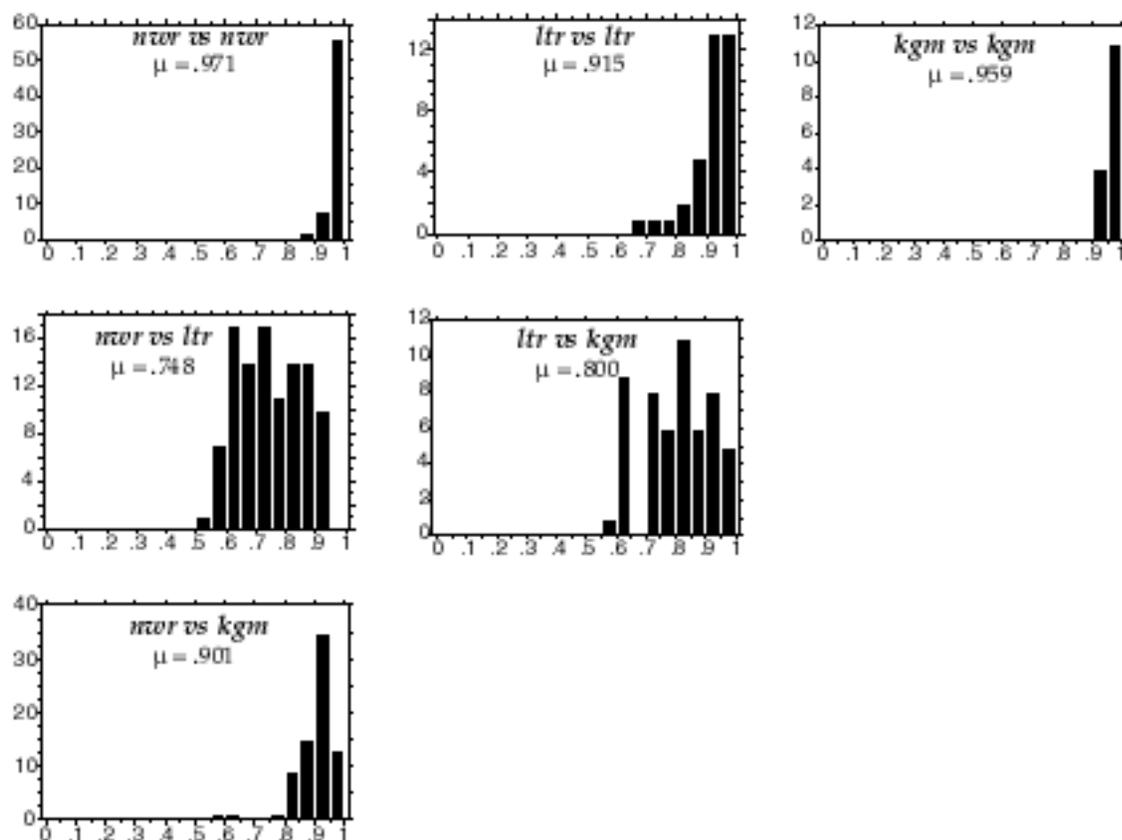
## Correlation Coefficients - RBPT PCA on Guild Data



**Figure 6.2**  
**Correlation values of the RBPT**

Histogram of correlation matchups for pairs of sample from the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The bottom graph in each set contains all pairs of samples from different localities (e.g., KGM vs LTR). (A) All taxa included. (B) *Mulinia congesta* removed from analysis.

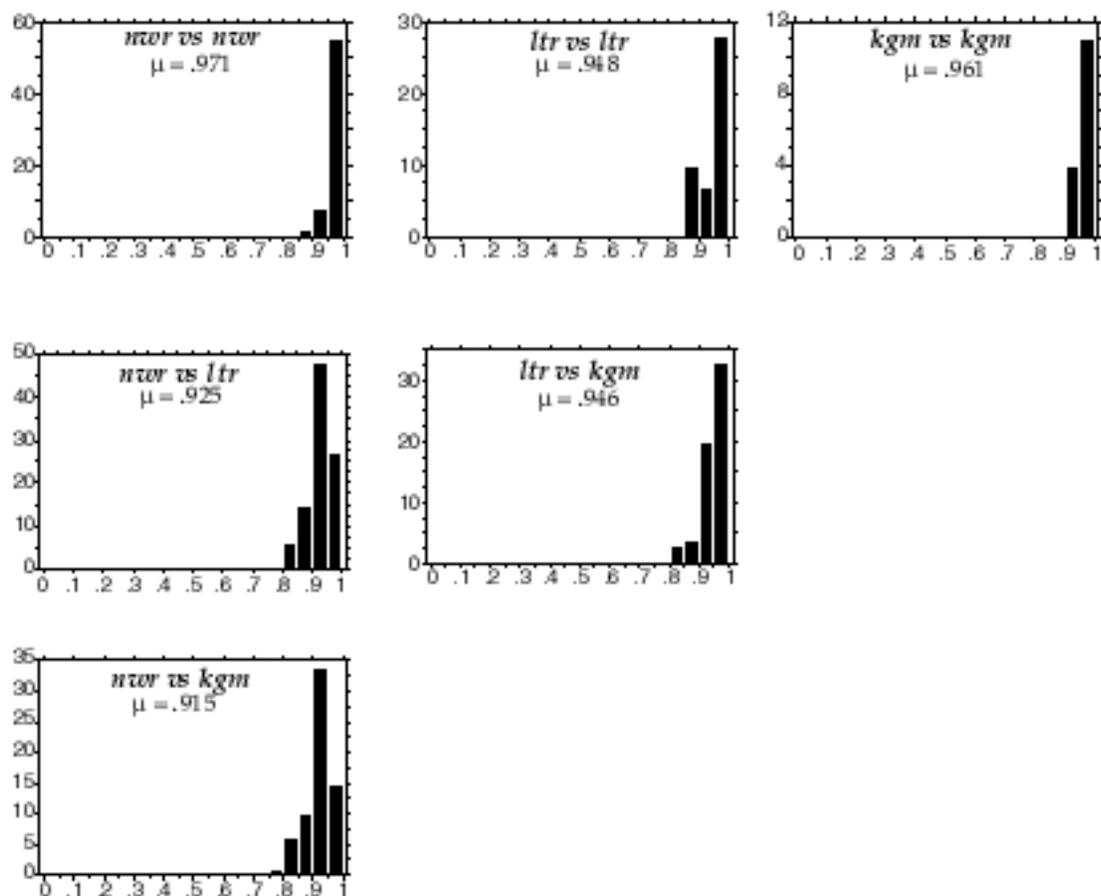
## Correlation Coefficients of RBPT PCA on Guild Data



**Figure 6.3**  
Correlation values of the RBPT at different localities

Histogram of correlation matchups for pairs of sample from the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities.

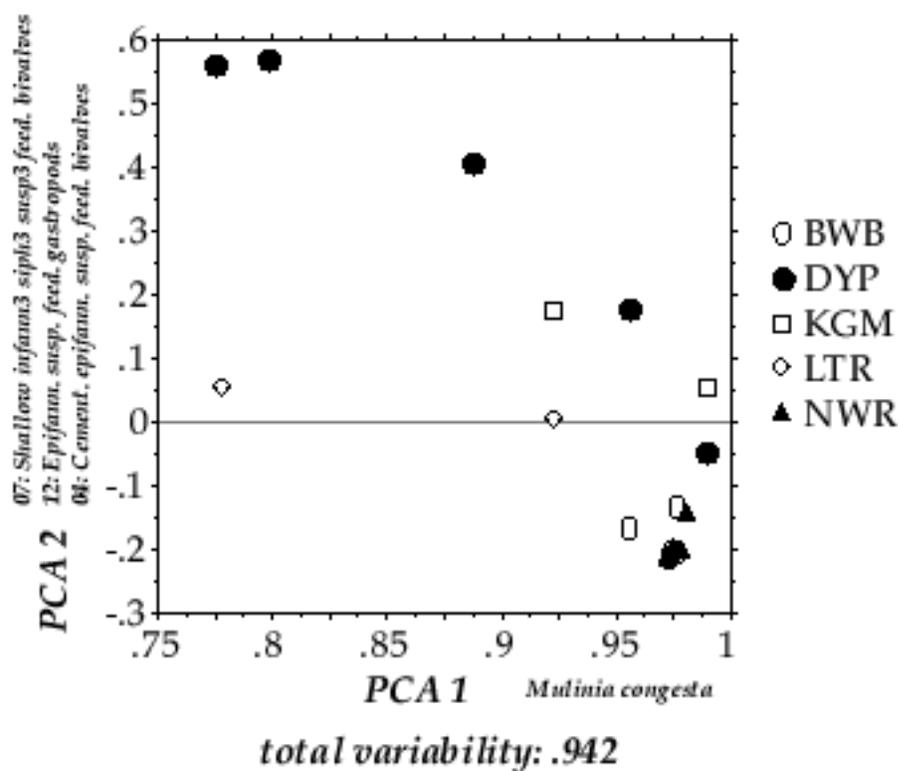
**Correlation Coefficients of RBPT**  
**PCA on Guild Data**  
*M. congesta* removed



**Figure 6.4**  
**Correlation values of the RBPT at different localities**

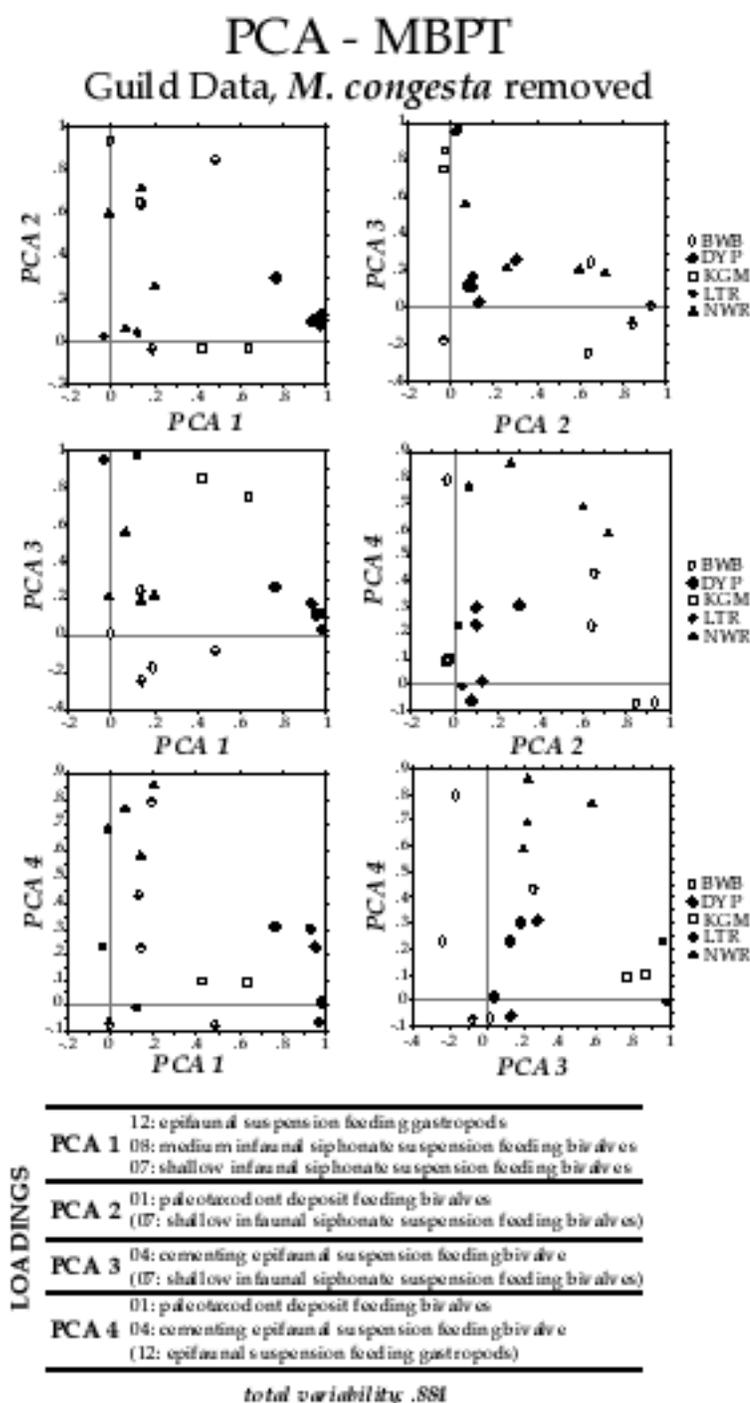
Histogram of correlation matchups for pairs of sample from the RBPT samples from the Nottoway River, Kingsmill, and Lieutenant's Run localities with *Mulinia congesta* removed from the analysis.

## PCA - MBPT Guild Data



**Figure 6.5**  
PCA of MBPT

Bivariate scatter plots of principle component one and two of the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities. The guilds listed on each axis have the heaviest loading for that axis.

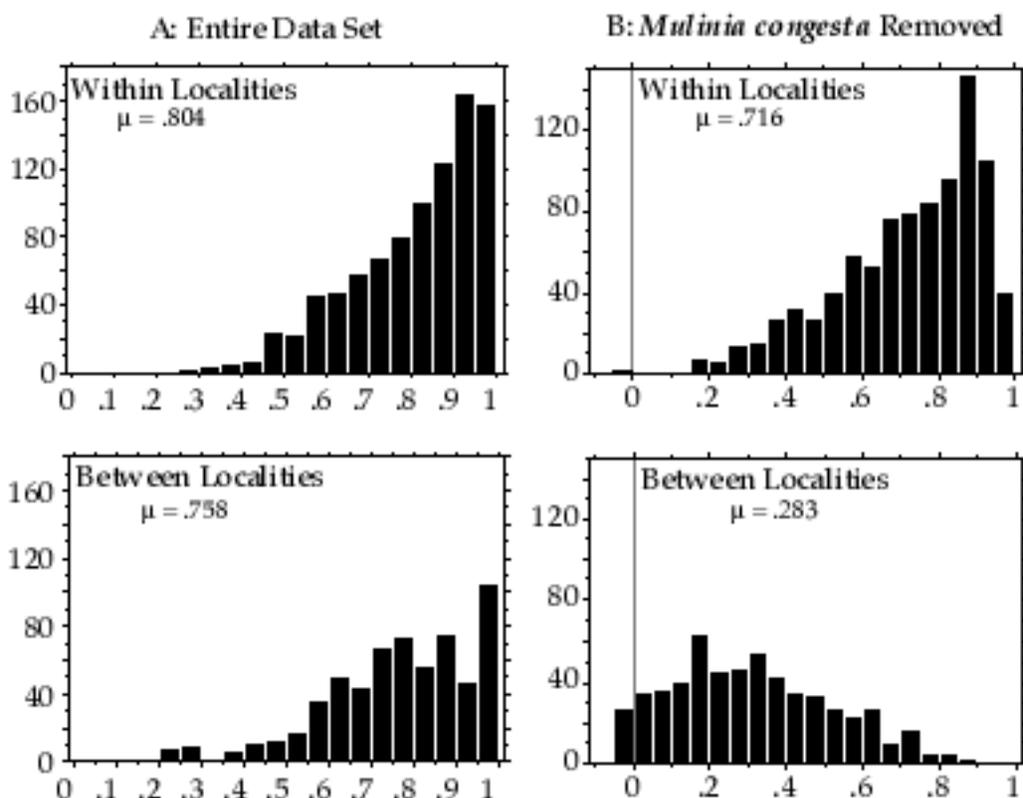


**Figure 6.6**  
PCA of MBPT

Bivariate scatter plots of principle component one, two, three, and four of the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities with *Mulinia congesta* removed from the analysis. The guilds listed on each axis have the heaviest loading for that axis.

## Correlation Coefficients - MBPT

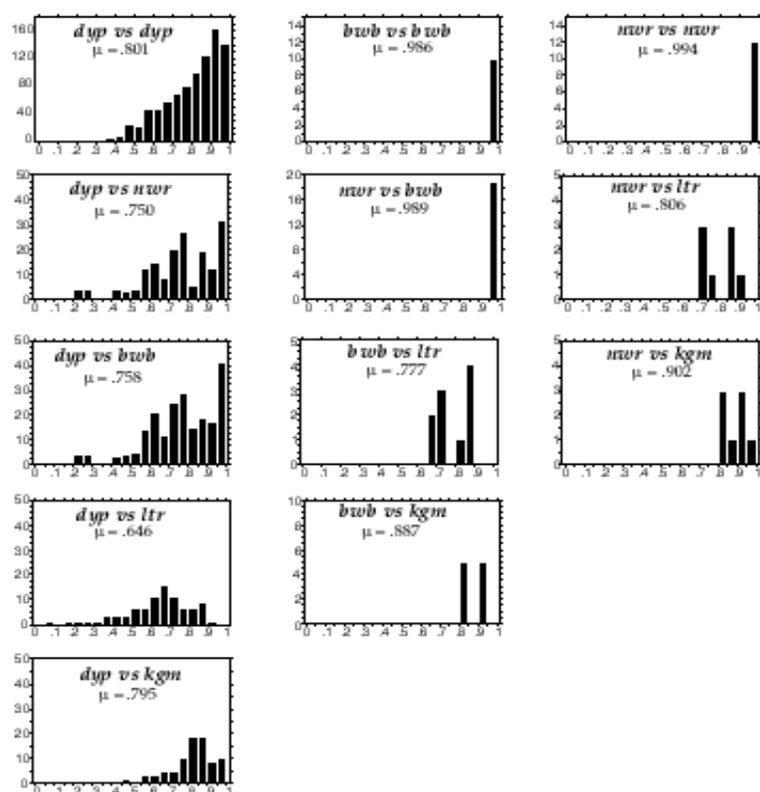
PCA on Guild Data



**Figure 6.7**  
Correlation values of the MBPT

Histogram of correlation matchups for pairs of sample from the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities. The top graph in each set is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The bottom graph in each set contains all pairs of samples from different localities (e.g., KGM vs LTR). (A) All taxa included. (B) *Mulinia congesta* removed from analysis.

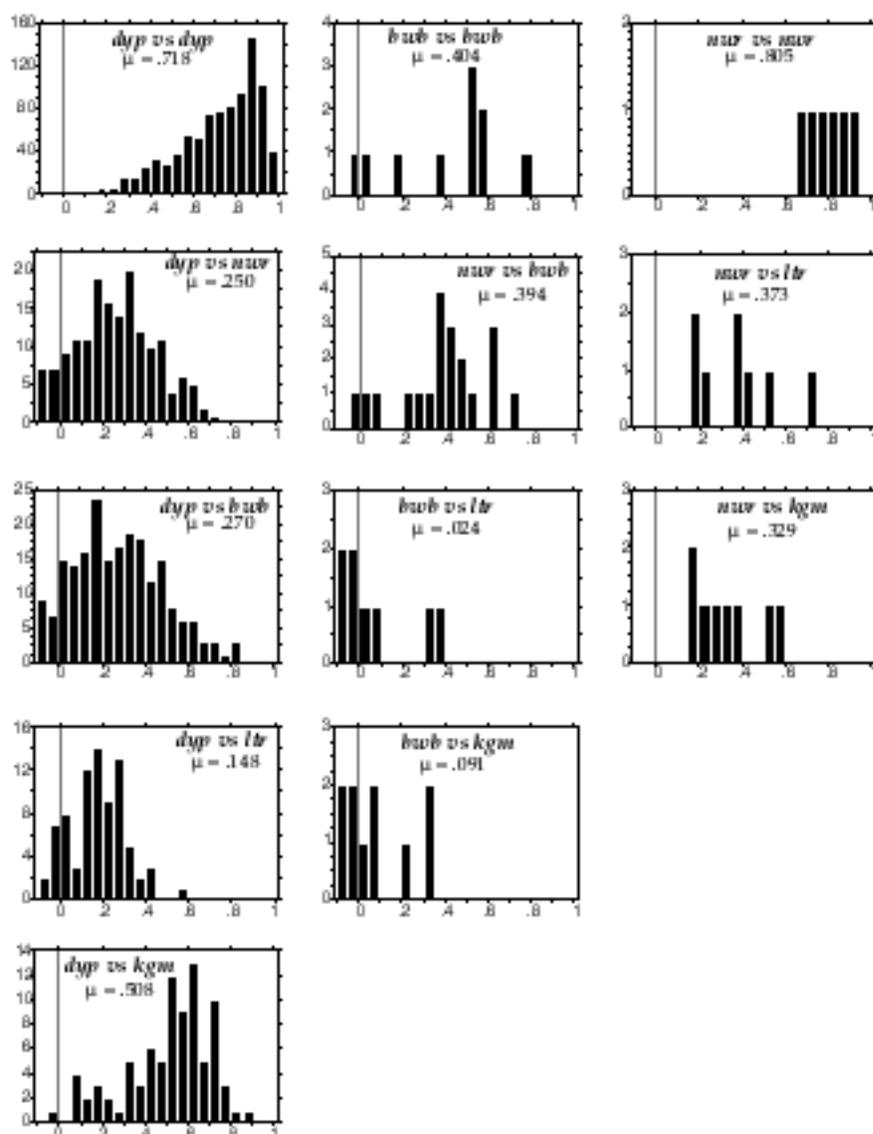
**Correlation Coefficients of MBPT**  
PCA of Guild Data



**Figure 6.8**  
**Correlation values of the MBPT at different localities**

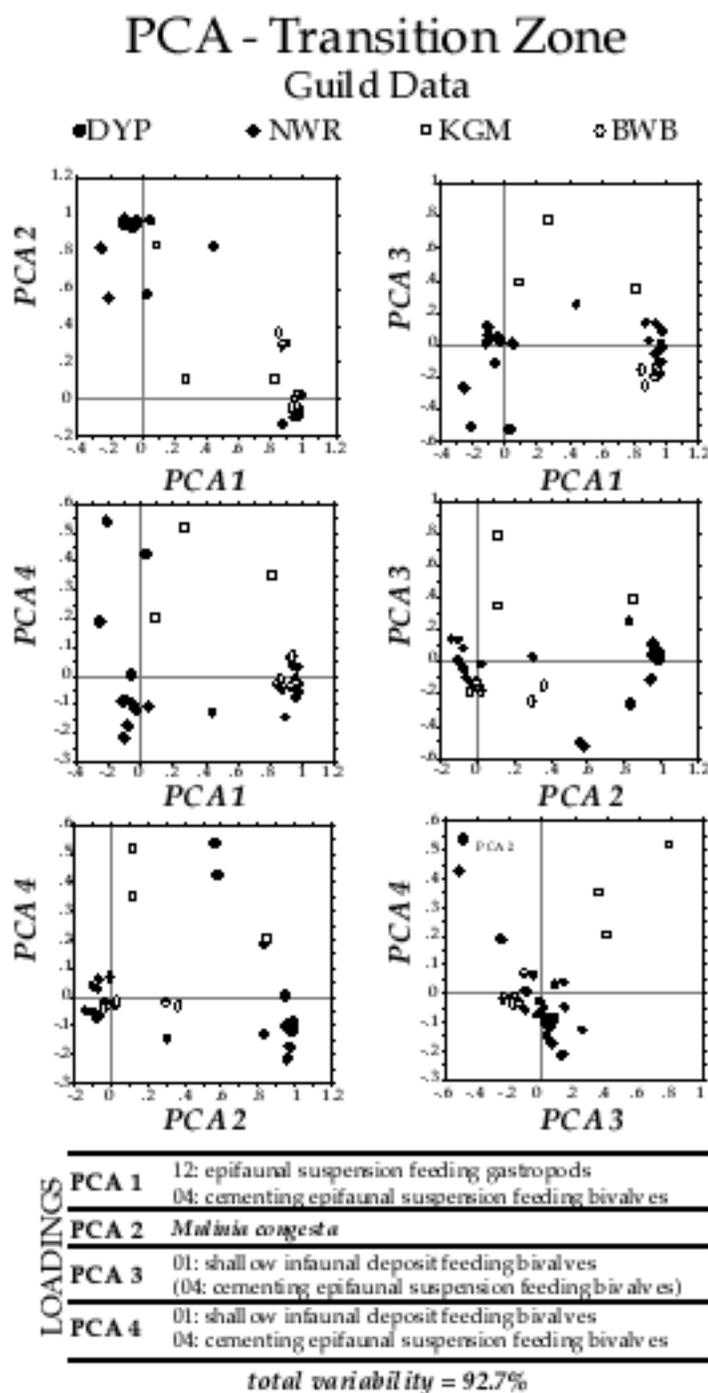
Histogram of correlation matchups for pairs of sample from the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities.

**Correlation Coefficients of MBPT**  
**PCA on Guild Data**  
*(Mulinia congesta removed)*



**Figure 6.9**  
**Correlation values of the MBPT at different localities**

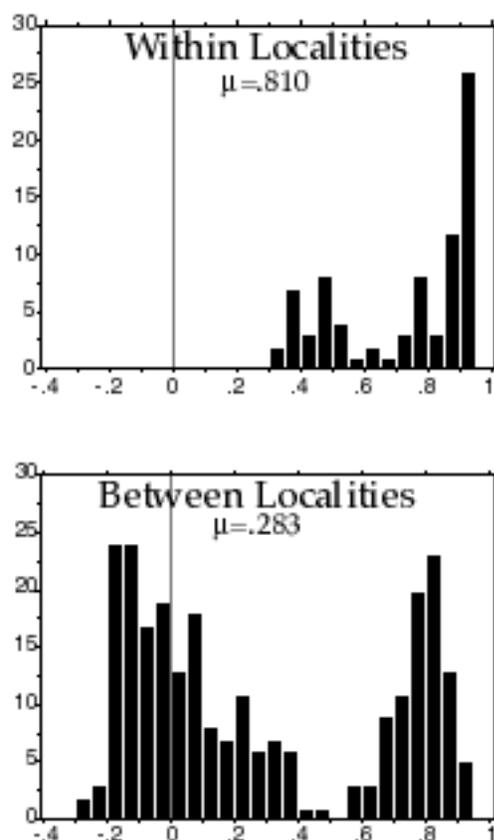
Histogram of correlation matchups for pairs of sample from the MBPT samples from the Burwell's Bay, Day's Point, Nottoway River, Kingsmill, and Lieutenant's Run localities, with *Mulinia congesta* removed from the analysis.



**Figure 6.10**  
**PCA of the Transition Zone**

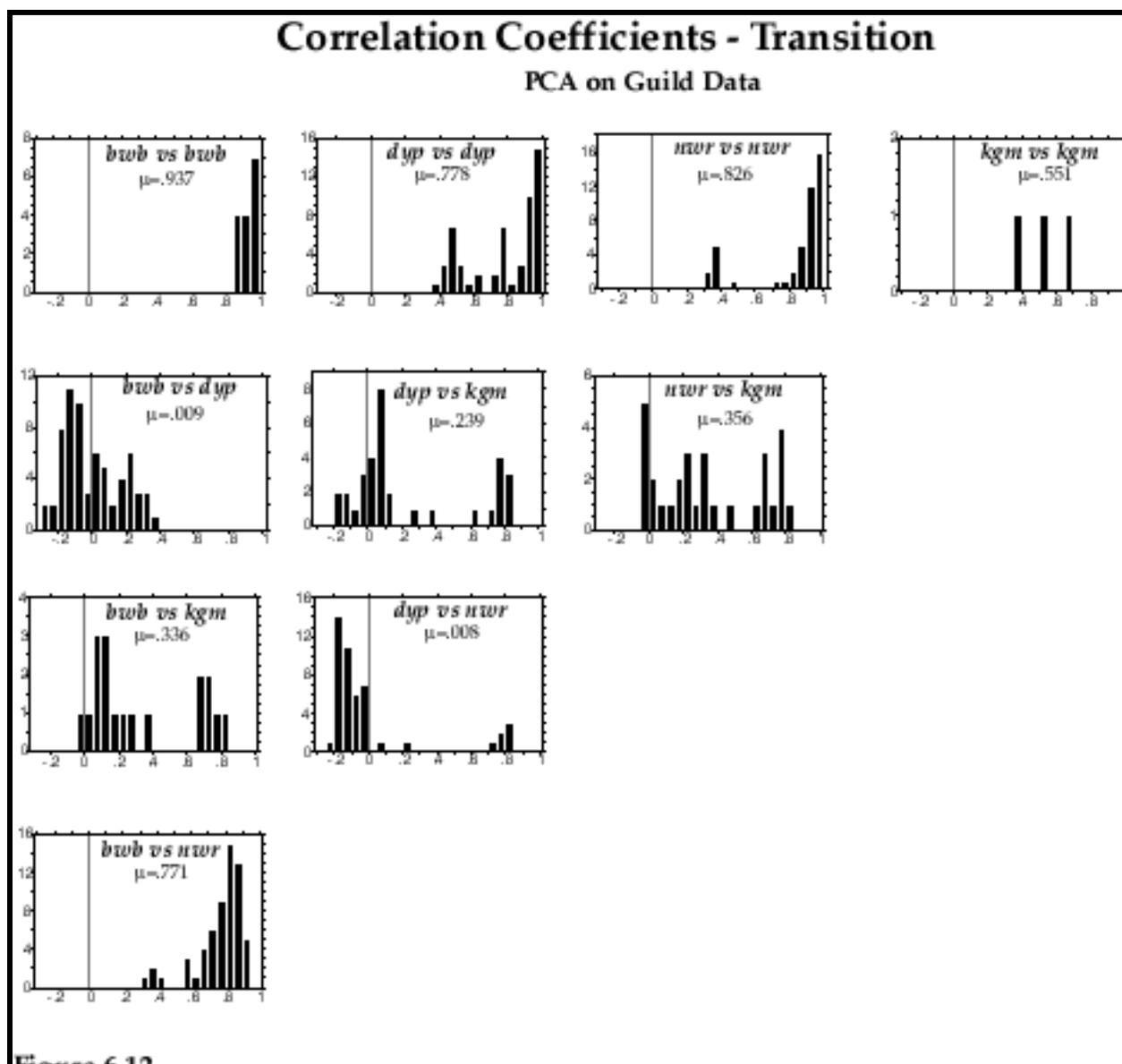
Bivariate scatter plots of principle component one, two, three, and four of the transition zone samples from the Burwell's Bay, Day's Point, Nottoway River, and Kingsmill localities. The guilds listed on each axis have the heaviest loading for that axis.

## Correlation Coefficients - Transition Zone PCA on Guild Data



**Figure 6.11**  
**Correlation values of the Transition Zone**

Histogram of correlation matchups for pairs of sample from the transition zone samples from the Burwell's Day, Day's Point, Nottoway River, and Kingsmill localities. The top graph is the distribution of all pairs of samples from the same locality (e.g., KGM vs KGM). The bottom graph contains all pairs of samples from different localities (e.g., KGM vs NWR).



**Figure 6.12**  
Correlation values of the transition zone at different localities

Histogram of correlation matchups for pairs of sample from the transition zone samples from the Burwell's Bay, Day's Point, Nottoway River, and Kingsmill localities.

## CHAPTER 7: SUMMARY AND CONCLUSIONS

The results of the species accumulation analysis (chapter 3) indicated that the sampling scheme used in this study more than adequately sampled the fauna for the very common and common species. These species account from most of the abundance present in the samples, and thus the sampling scheme adequately samples for paleocommunity analysis performed on relative abundance data.

The analysis of Yorktown diversity (chapter 4) indicated that there was no basin-wide change in fossil assemblage diversity through the changing paleoenvironments of the Rushmere-Morgart's Beach transition. However, diversity measures of fossil assemblages can be heavily affected by the degree of time-averaging, and so the failure to find the expected change in diversity is perhaps not surprising.

Local paleocommunities and paleocommunity types were examined in chapter 5 in order to determine if the strong species interactions expected in the ecological locking model were recognizable in the Yorktown faunas. No recurrent paleocommunities (in the sense of Bennington and Bambach 1996) were found. Samples from the same paleocommunity type at each locality were very similar to each other, and thus the local paleocommunities were consistent within localities. While the same species were found at many localities, they were not found in the same abundances. Samples from different localities were significantly different from each other, and so local paleoenvironmental effects seem to be more important in ordering the local paleocommunities than strong species interactions. Therefore, ecological locking can probably be rejected as a model for recurrence of species in the Yorktown faunas.

The guild structure of local paleocommunities and paleocommunity types was examined in chapter 6. The guild structure was consistent for RBPT at several localities, and this paleocommunity type probably constitutes a paleocommunity in the sense of Bennington and Bambach (1996). However, there was no consistent guild structure in the transition zone or MBPT, so after the paleoenvironmental conditions that allowed for the development of the community type from which RBPT fossil assemblages were derived ceased, the response of the local communities differed from locality to locality, and local control is once again seen in the transition zone and MBPT. The lack of a consistent response to the change in paleoenvironmental conditions is not an expected result in the ecological locking model. In fact, the local response in guild structure through the changing environmental conditions is the opposite of what would be expected from ecological locking. Therefore, the ecological locking model can probably be

discarded as a causal mechanism for the development of ecological structures in the Yorktown fauna.

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## APPENDIX A: Collection localities

### Burwell Bay (BWB)

Sections Sampled: 2

Horizons Sampled Singly: 11

Horizons Sampled In Triplicate: 0

Total Samples: 11

The Burwell Bay locality is on a cutbank on the south bank of the James River. The outcrop is discontinuous, but stretches for several miles along the edge of Burwell Bay. Two sections were sampled between Holly's Point and Burwell Bay, due east of the town of Rushmere (Fig. A.1) (U.S.G.S.: Bacons Castle 7.5 minute quadrangle). The uppermost part of the Rushmere and the entire Morgart's Beach members are exposed at this locality (Fig. A.2).

Further downstream both members are cut out by a large channel cut which is filled in with Moore House sediments.

### Day's Point (DYP)

Sections Sampled: 4

Horizons Sampled Singly: 15

Horizons Sampled In Triplicate: 18

Total Samples: 69

The Day's Point locality is on a cut bank of the south bank of the James River just downstream from Morgart's Beach, and just upstream from the Pagan River (Fig. A.3). While easily accessible by boat, the land is owned by the owners of one of the Smithfield packing plants, and as it is on private property, it is best to obtain permission. From the land side, it can be reached by a relatively well maintained jeep trail. A total of 4 sections were sampled at Day's Point. The uppermost part of the Rushmere Member and the entire Morgart's Beach Member are well exposed at this locality (Fig. A.4).

The locality was heavily eroded during the energetic rainy seasons of the mid- to late-1990s, and is a candidate for erosion control (e.g., rip rap).

### Kingsmill on the James (KGM)

Sections Sampled: 1

Horizons Sampled Singly: 10  
 Horizons Sampled In Triplicate: 1  
 Total Samples: 13

The Kingsmill locality is located in a wash gully approximately one mile downstream from the Kingsmill Marina (Fig. A.5). The entire Yorktown Formation is found at this locality, although the base of the Sunken Meadow Member is not always discernible, and the uppermost Moore House Member is difficult to reach. The exposure of the Rushmere and Morgart's Beach members is superb, with the erosional unconformity at the base of the Morgart's Beach especially well exposed (Fig. A.6).

While the locality would have been a prime candidate for re-sampling, permission from the landowner could not be obtained for a second visit.

### **Lieutenant's Run (LTR)**

Sections Sampled: 4 (2 sets of replicates)  
 Horizons Sampled Singly: 10  
 Horizons Sampled In Triplicate: 6  
 Total Samples: 28

The small stream named Lieutenant's Run flows through Petersburg, Virginia. The Yorktown Formation crops out where the stream flows past A.P. Hill grade school (Fig. A.7). The outcrop is discontinuous, and unlike the erosional cuts on the James and Nottoway Rivers, the individual outcrops in Lieutenant's Run do not exceed approximately a height of 1.5 meters. As the outcrop is located at the landward edge of the Yorktown outcrop belt, only the Rushmere and Morgart's Beach members are present (Fig. A.8).

### **Nottoway River (NWR)**

Sections Sampled: 2  
 Horizons Sampled Singly: 7  
 Horizons Sampled In Triplicate: 7  
 Total Samples: 28

The Yorktown Formation was collected from a locality on the Nottoway River near the town of Delaware, Virginia (Fig. A.9). The outcrop can only be reached by boat, and consists of a

4-5 meter high cutbank, the lower 3 meters of which is composed of Rushmere and Morgart's Beach sediments. Neither of the bounding unconformities is visible at the outcrop (Fig. A.10).

This locality can not be sampled when the Nottoway River is high, and even when the river level is low, the basal portion of the outcrop is frequently flooded. Significant plant and algae growth also obscured the outcrop both times this locality was collected.

Table A.1: Localities and the number of stratigraphic horizons collected.

Abbreviation	Location Name	Member (# of horizons)
BWB-1 and BWB-2	Burwell Bay, near Rushmere, VA	Morgart's Beach (3) Rushmere (3)
DYP-1, DYP-2, DYP-4, DYP-5	Day's Point on the James River	Morgart's Beach (7) Rushmere (3)
KGM-1 through KGM-3	Kingsmill Gully, Kingsmill, VA	Moore House (1) Morgart's Beach (3) Rushmere (8) Sunken Meadow (6)
LTR-1 through LTR-4, LTR-9	Lieutenant's Run, Petersburg, VA	Rushmere (6)
NWR-1 and NWR-2	Nottoway River, VA	Morgart's Beach (1) Rushmere (6)

**Species Occurrence and Abundances**  
**Day's Point**

<b>Sample</b>	<b>Species</b>	<b>Specimens</b>
DYP-1.7	23	179
DYP-1.6	29	118
DYP-1.5	23	215
DYP-1.4	21	207
DYP-1.3	13	61
DYP-1.2	12	34
DYP-1.1	13	40
DYP-2.10	17	97
DYP-2.9	19	87
DYP-2.7	37	282
DYP-2.6	24	180
DYP-2.5	36	239
DYP-2.4	19	250
DYP-2.3	12	62
DYP-2.2	11	27
DYP-4.10A	0	0
DYP-4.10B	28	187
DYP-4.10C	13	93
DYP-4.9A	19	102
DYP-4.9B	22	144
DYP-4.9C	19	125
DYP-4.8A	31	171
DYP-4.8B	28	187
DYP-4.8C	23	108
DYP-4.7A	31	269
DYP-4.7B	33	314
DYP-4.7C	34	300
DYP-4.6A	28	240
DYP-4.6B	31	243
DYP-4.6C	39	356
DYP-4.5A	33	170
DYP-4.5B	31	208
DYP-4.5C	29	153
DYP-4.4A	21	133
DYP-4.4B	25	151
DYP-4.4C	26	204
DYP-4.3A	15	35
DYP-4.3B	12	61
DYP-4.3C	14	69
DYP-4.2A	13	38
DYP-4.2B	9	17
DYP-4.2C	6	10
DYP-4.1B	16	49
DYP-4.1C	18	60

DYP-5.8A	2	2
DYP-5.8B	24	130
DYP-5.8C	19	102
DYP-5.7A	33	264
DYP-5.7B	37	204
DYP-5.7C	34	221
DYP-5.6A	26	209
DYP-5.6B	32	227
DYP-5.6C	35	299
DYP-5.5A	32	161
DYP-5.5B	23	147
DYP-5.5C	31	157
DYP-5.4A	28	196
DYP-5.4B	24	156
DYP-5.4C	31	200
DYP-5.3A	24	120
DYP-5.3B	24	164
DYP-5.3C	29	175
DYP-5.2A	24	101
DYP-5.2B	21	101
DYP-5.2C	19	116
DYP-5.1A	19	45
DYP-5.1B	16	34
DYP-5.1C	12	35

**Burwell's Bay**

<b>Sample</b>	<b>Species</b>	<b>Specimens</b>
BWB-1.7	5	59
BWB-1.6	7	106
BWB-1.5	13	118
BWB-1.4	31	223
BWB-1.3	33	116
BWB-1.2	36	183
BWB-2.6	9	289
BWB-2.5	14	245
BWB-2.4	36	252
BWB-2.3	31	139
BWB-2.2	34	162

## Lieutenant's Run

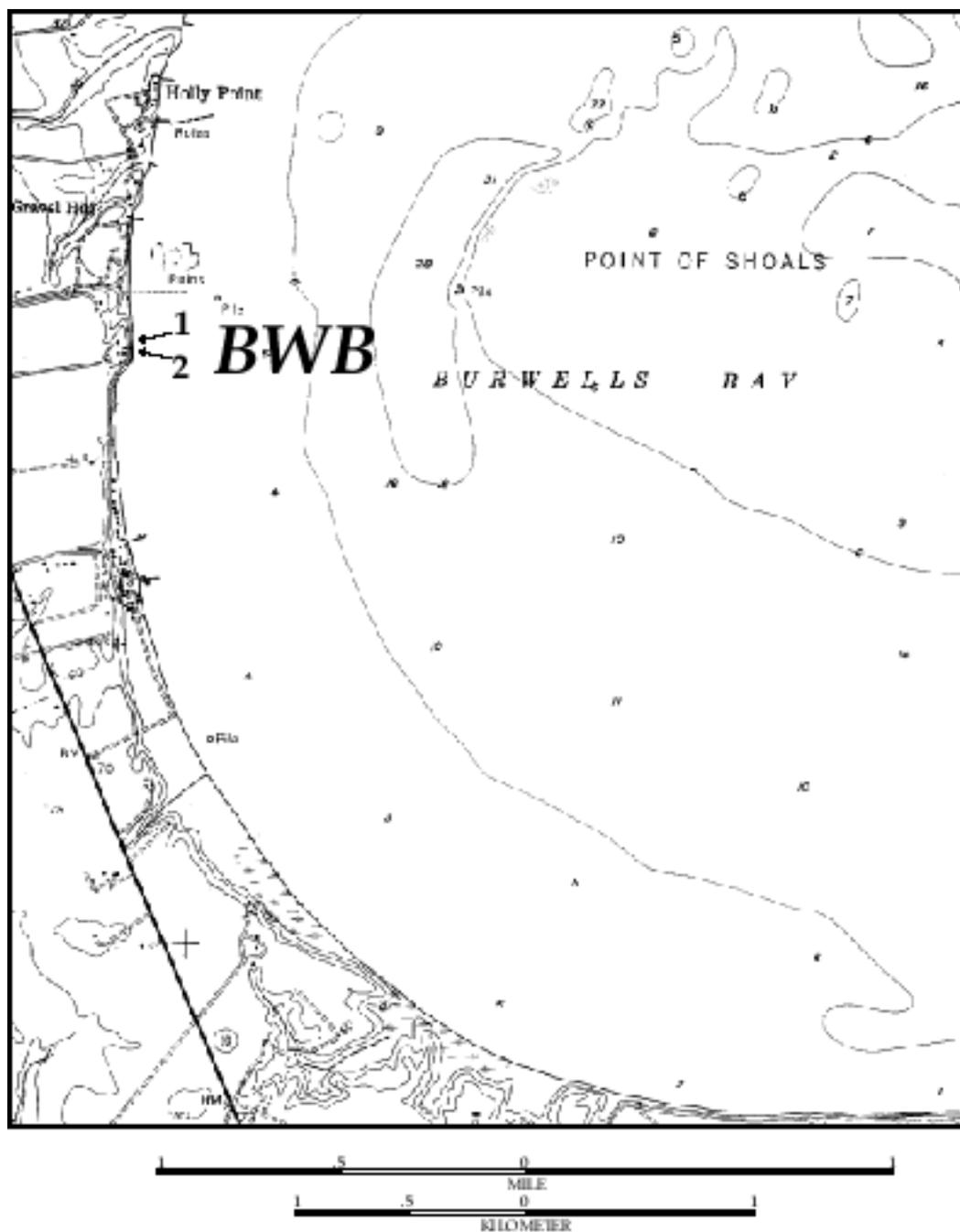
<b>Sample</b>	<b>Species</b>	<b>Specimens</b>
LTR-9.3B	42	276
LTR-9.3C	39	278
LTR-9.2A	42	290
LTR-9.2B	42	268
LTR-9.2C	39	261
LTR-9.1A	33	237
LTR-9.1B	36	199
LTR-9.C	38	222
LTR-7.5A	35	178
LTR-7.5B	37	222
LTR-7.5C	38	236
LTR-7.4A	23	87
LTR-7.4B	25	87
LTR-7.4C	30	118
LTR-7.3A	17	41
LTR-7.3B	12	27
LTR-7.3C	13	26
LTR-4.6	35	930
LTR-4.3	27	99
LTR-3.5	23	287
LTR-3.3	19	127
LTR-2.3	27	287
LTR-2.1	28	232
LTR-1.3	34	326
LTR-1.1	24	131
LTR-1.0	24	268

## River

<b>Sample</b>	<b>Species</b>	<b>Specimens</b>
NWR-1.7	20	359
NWR-1.6	27	133
NWR-1.5	29	162
NWR-1.4	39	271
NWR-1.3	35	198
NWR-1.2	32	222
NWR-2.7A	18	2153
NWR-2.7B	23	1152
NWR-2.7C	20	1035
NWR-2.6A	22	92
NWR-2.6B	19	76
NWR-2.6C	27	194
NWR-2.5A	21	133
NWR-2.5B	23	170
NWR-2.5C	25	170
NWR-2.4A	26	161
NWR-2.4B	20	137
NWR-2.4C	24	161
NWR-2.3A	29	189
NWR-2.3B	30	180
NWR-2.3C	24	180
NWR-2.2A	26	171
NWR-2.2B	35	233
NWR-2.2C	31	244
NWR-2.1A	29	198
NWR-2.1B	29	178
NWR-2.1C	33	203

**Kingsmill**

<b>Sample</b>	<b>Species</b>	<b>Specimens</b>
KGM-3.7	25	232
KGM-3.5	22	120
KGM-3.4	13	70
KGM-3.3	15	98
KGM-3.2	23	159
KGM-2.4	20	367
KGM-2.3	20	199
KGM-1.8	30	227
KGM-1.7A	24	207
KGM-1.7B	27	180
KGM-1.7C	27	216



**Figure A.1**  
**Map of the Burwell's Bay (BWB) locality**

Map of the collection locality at Burwell's Bay. Base map: U.S.G.S. Bacon's Castle 7.5 minute quad range.

# Burwell's Bay (BWB)

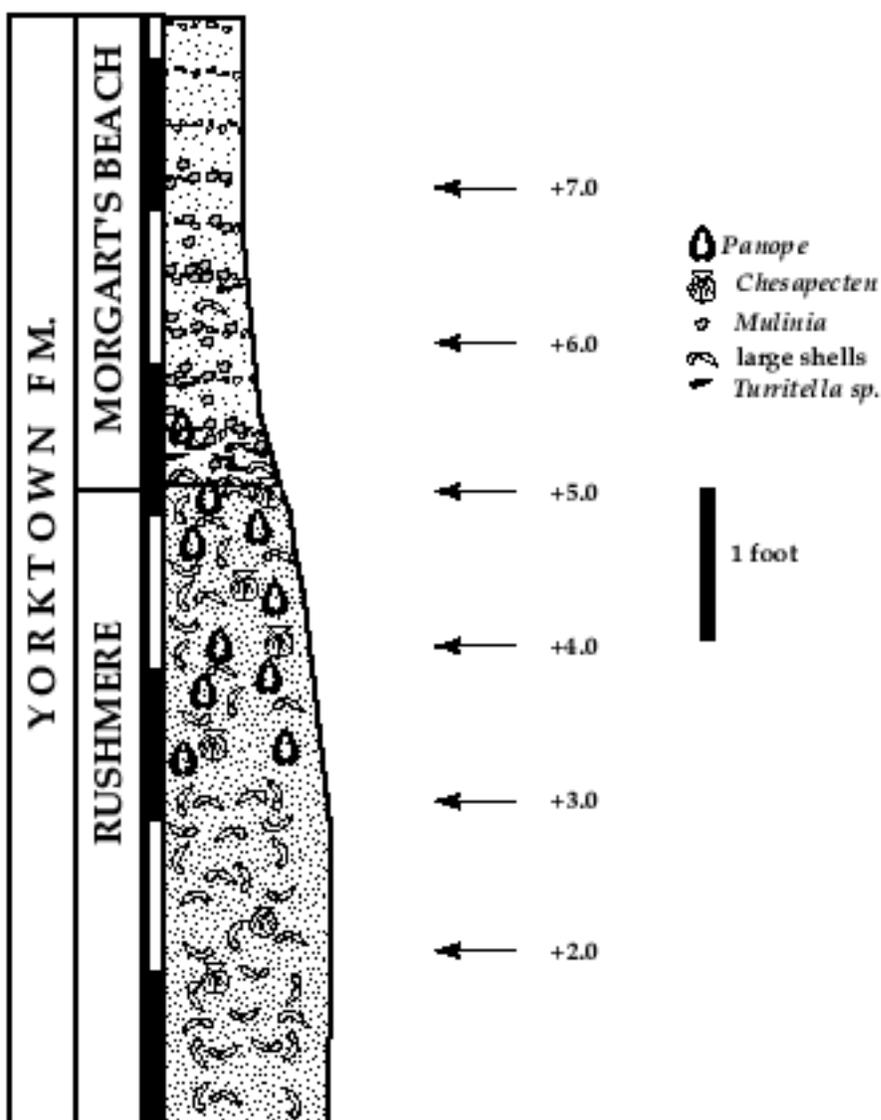
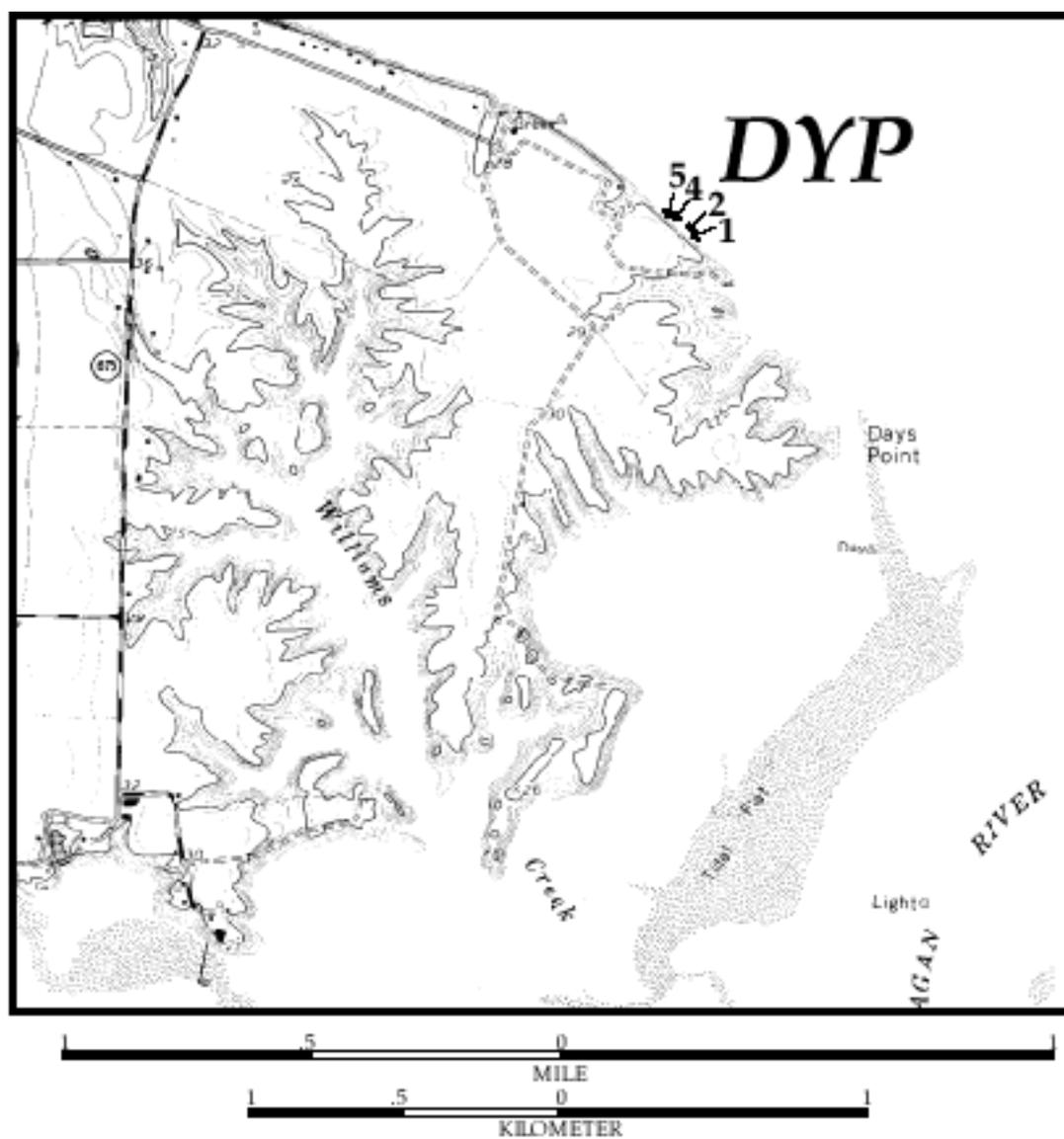


Figure A.2  
BWB Section

Stratigraphic section at Burwell's Bay showing stratigraphic horizons collected.



**Figure A.3**  
**Map of the Day's Point (DYP) locality**

Map of the collection locality at Day's Point. Base map: U.S.G.S. Mulberry Island 7.5 minute quadrangle.

# Day's Point (DYP)

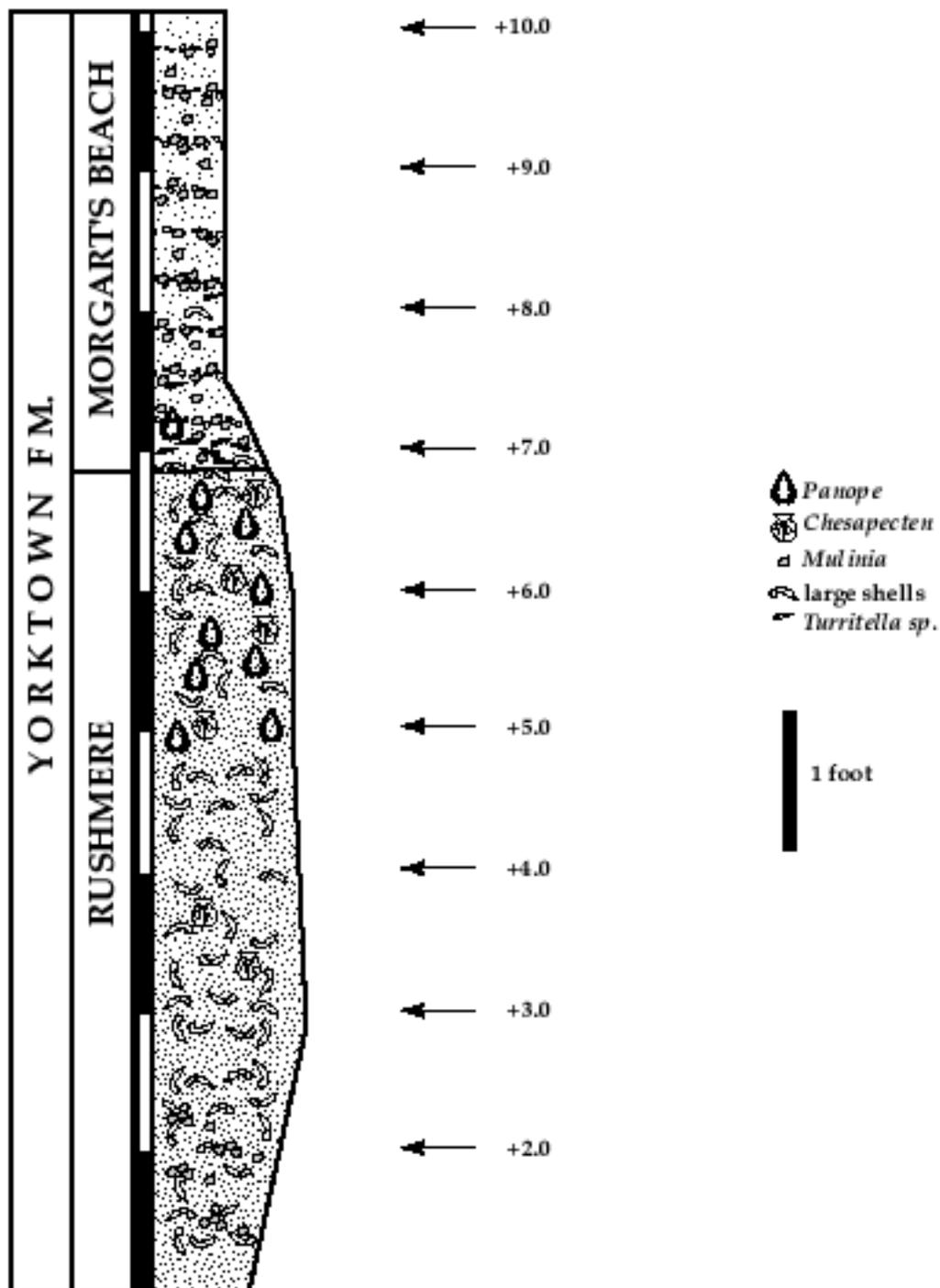
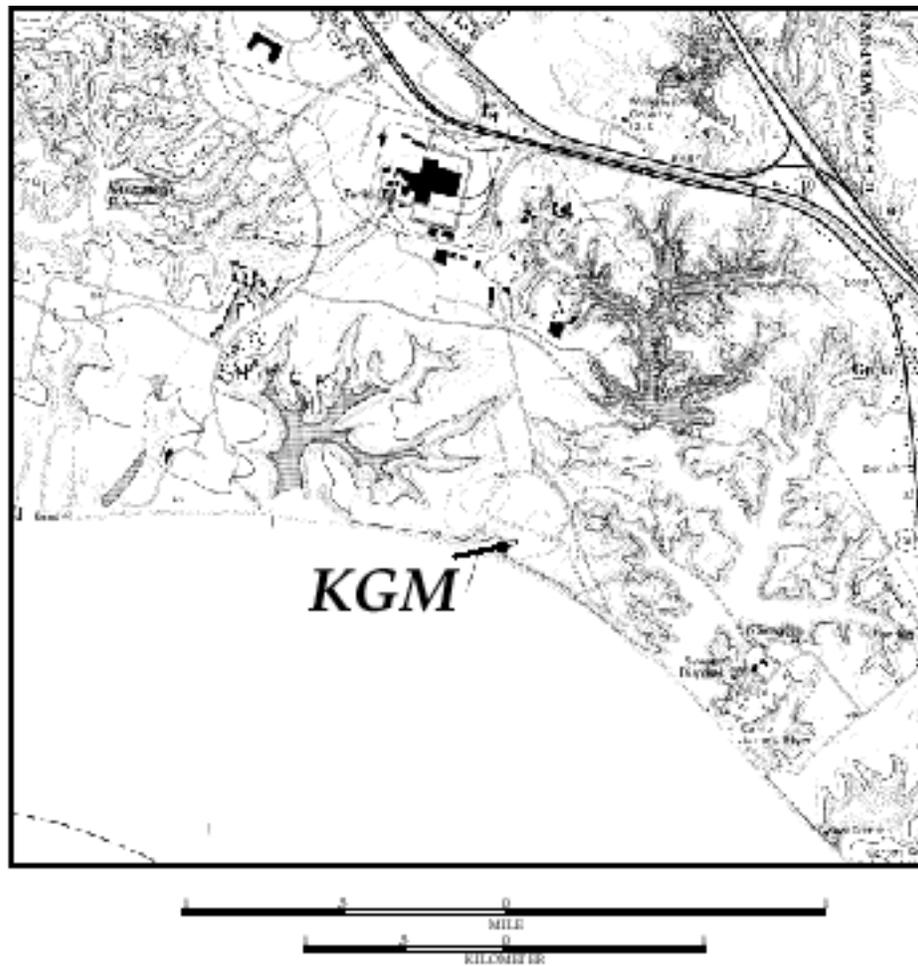


Figure A4  
DYP Section

Stratigraphic section at Day's Point showing stratigraphic horizons collected.



**Figure A.5**  
**Map of the Kingsmill (KGM) locality**

Map of the collection locality at Kingsmill on the James. Base map: U.S.G.S. Hog Island 7.5 minute quadrangle.

## Kingsmill (pg. 1)

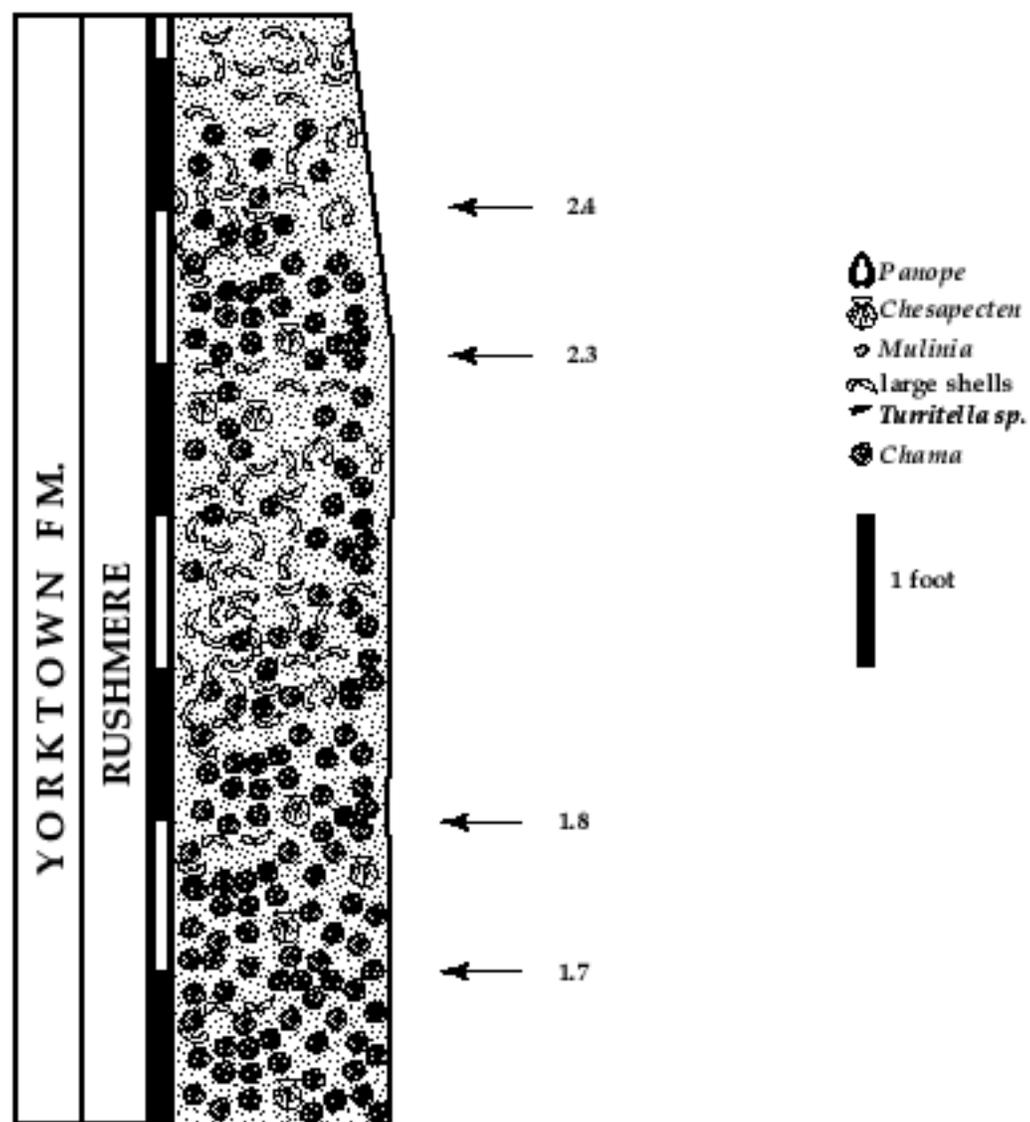
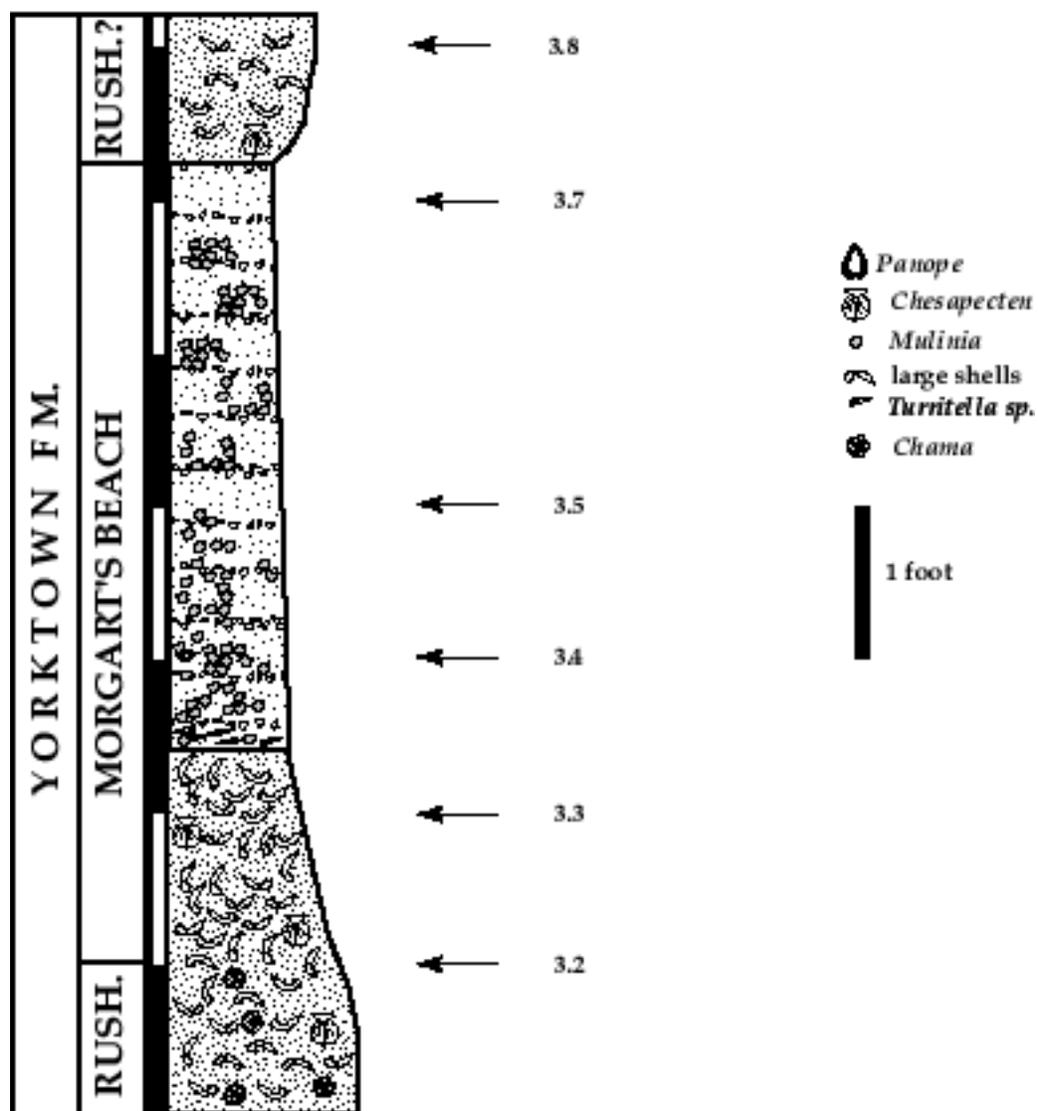


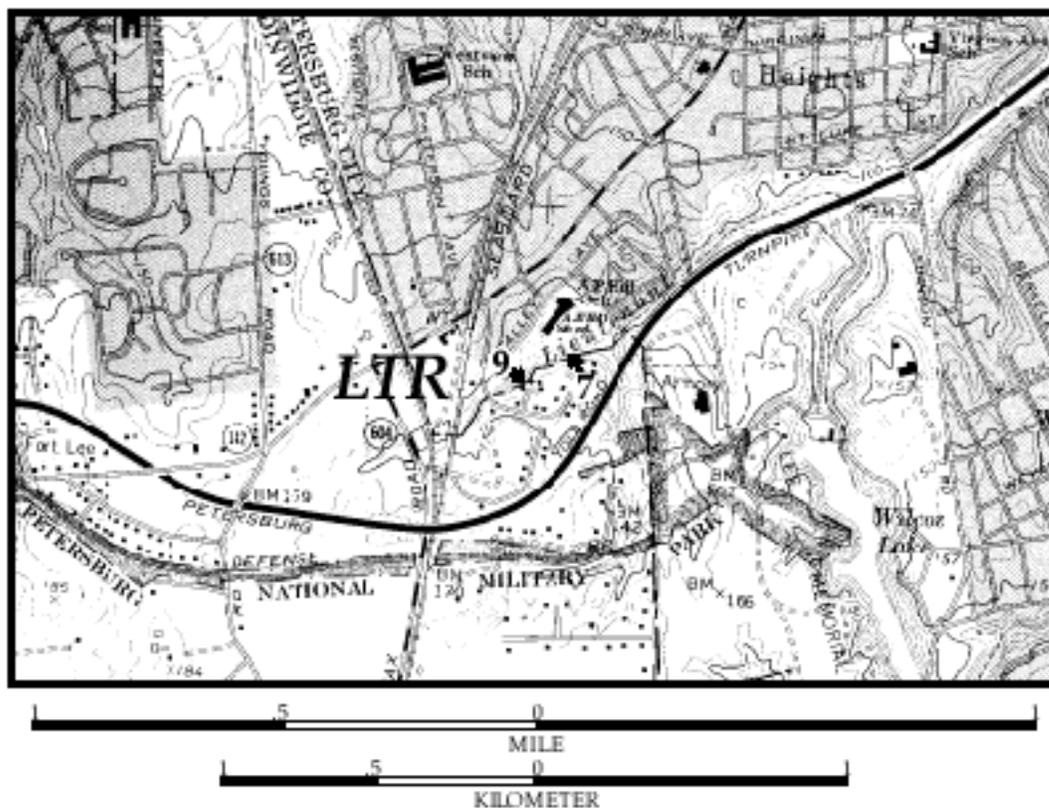
Figure A.6  
KGMSection

Stratigraphic section at Kingmill showing stratigraphic horizons collected. Figure continues on next page.

## Kingsmill (pg. 2)



## Lieutenant Run (LTR)



**Figure A.7**  
**Map of the Lieutenant's Run (LTR) locality**

Map of the collection locality at Lieutenant's Run. Base map: U.S.G.S. Petersburg 7.5 minute quadrangle.

# Lieutenant's Run (LTR)

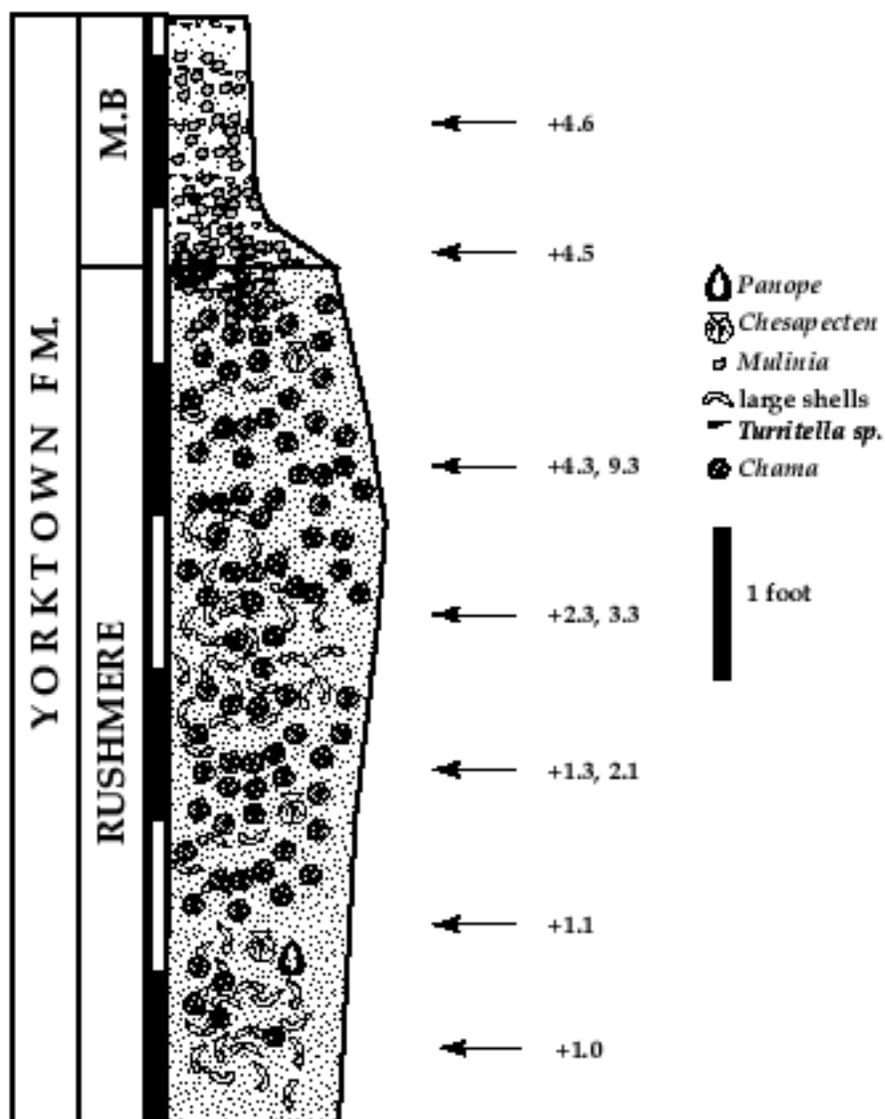
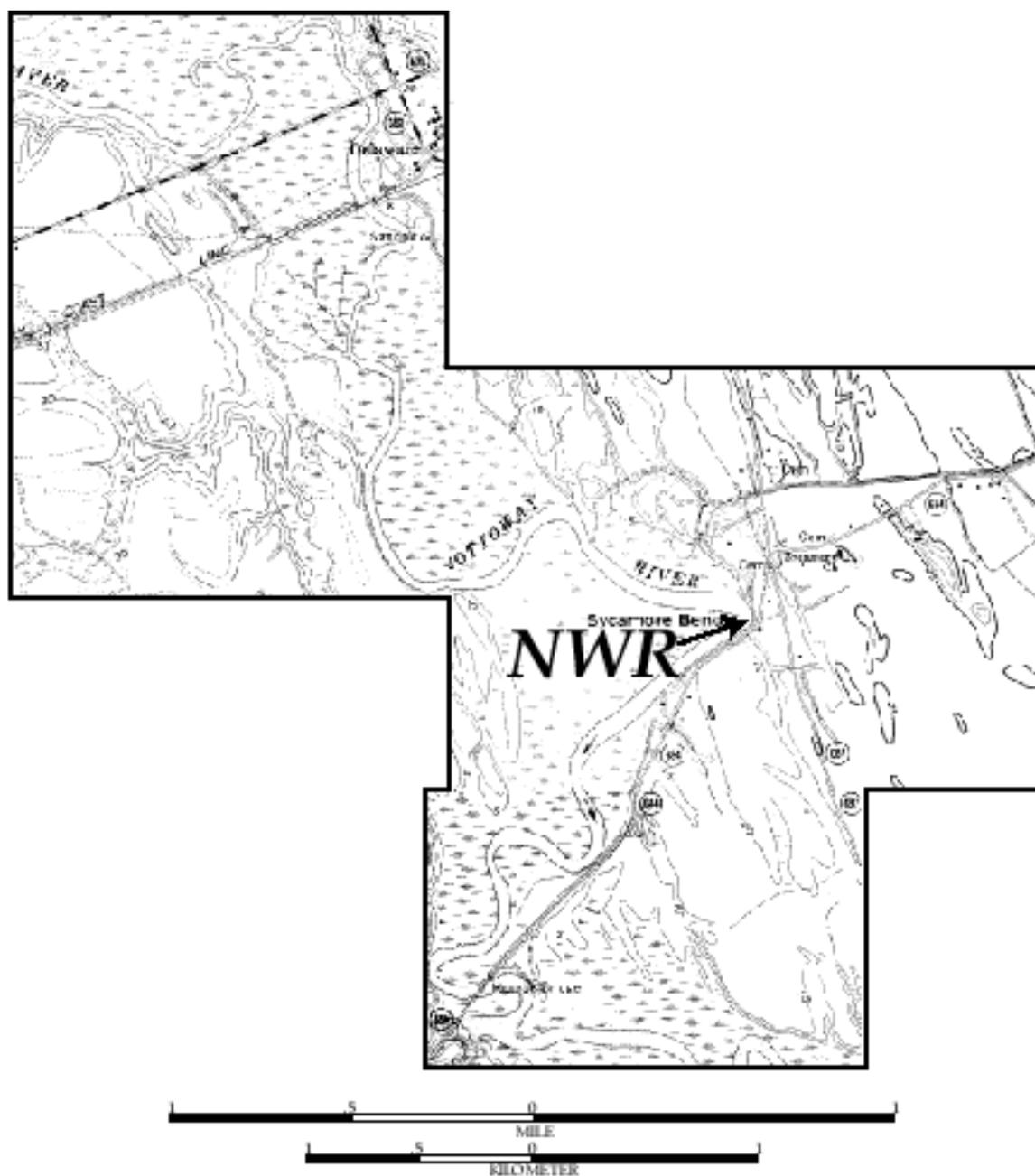


Figure A.8  
LTR Section

Stratigraphic section at Lieutenant's Run showing stratigraphic horizons collected.



**Figure A.9**  
**Map of the Nottoway River (NWR) locality**

Map of the collection locality at the Nottoway River Base maps: U.S.G.S. Courtland 7.5 minute quadrangle, U.S.G.S. Franklin 7.5 minute quadrangle, U.S.G.S. Riverdale 7.5 minute quadrangle.

# Nottoway River (NWR)

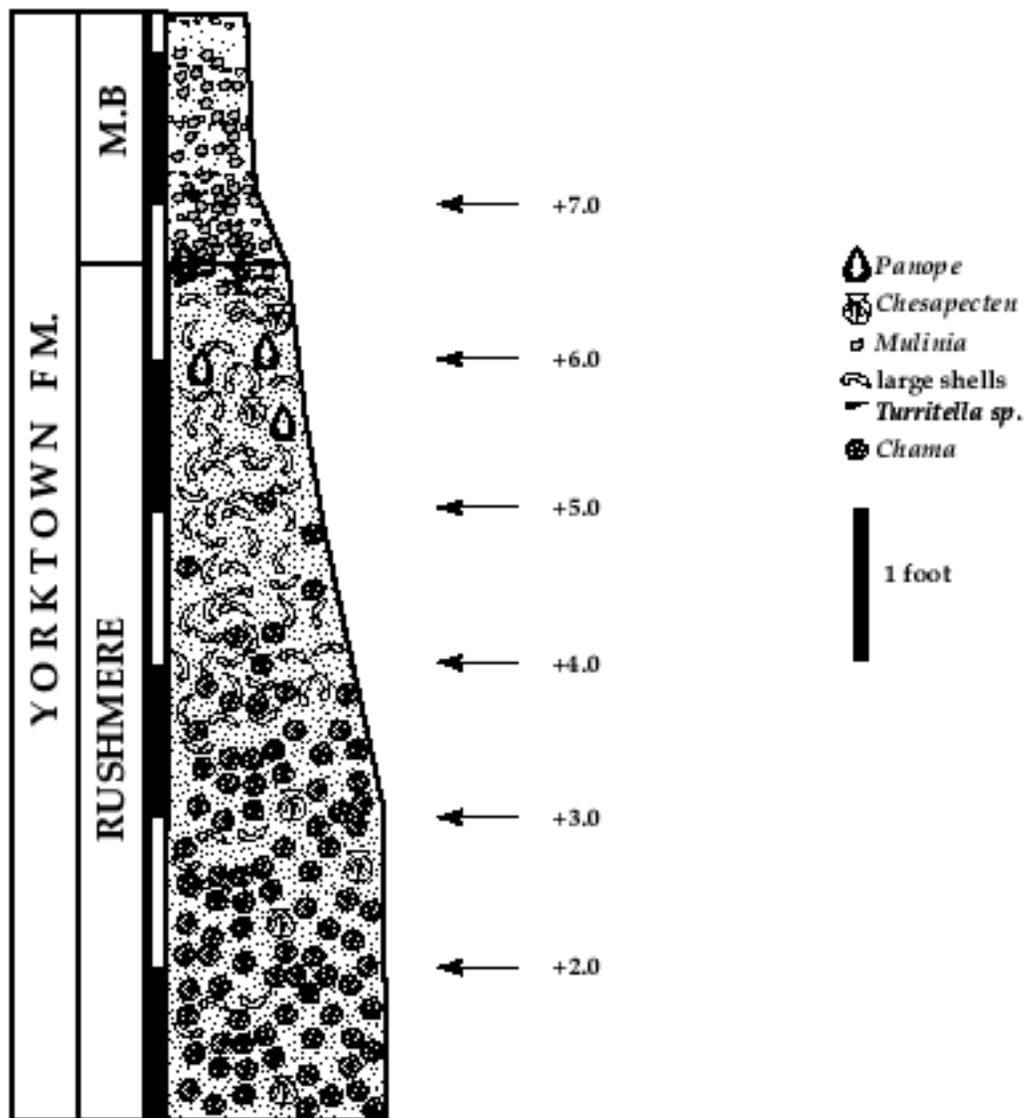


Figure A.10  
NWR Section

Stratigraphic section at the Nottoway River showing stratigraphic horizons collected.

## APPENDIX B: SYSTEMATICS

### Systematics

The systematics of the organisms presented has the following format:

Higher order classification:

**Subclass PALAEOTAXODONTA** Korobkov, 1954  
**Order NUCULOIDEA** Dall, 1889  
**Superfamily NUCULACEA** Gray, 1824  
**Family NUCULIDAE** Gray, 1824

Common name of family:

**NUT CLAMS**

Classification of genus and species:

**Genus *Nucula*** Lamarck 1799, Mem. Soc. H. N. Paris, 87.  
*Nucula proxima* (Say)

Number of samples (s), and total abundances (n) of this sample in the Yorktown data set:  
s=33. n=53

Descriptions of species in the literature, sometimes, but not always, including the first description, and including at least one reference with a good illustration and/or description of the species. For species assigned to a genus, but with no specific species designation, a reference with a description and/or illustration of other species of the genus is included:

- 1820 *Nucula obliqua* Say, Am. Jour. Sci., 1st ser. vol 2: 40.
- 1943 *Nucula proxima* (Say) Gardner, U.S.G.S. Paper 199-A: 19-20,
- 1987 *Nucula proxima* (Say). Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 134, pl 1.
- 1993 *Nucula proxima* (Say). Campbell, Virginia Div. Min. Res. Publ. 127: 18-19.

The life habit as inferred from function morphology, taxonomic affinity, and the life habit of a modern analog:

**Life habit:** infaunal deposit feeder

A modern analog was assigned to each species. For extant species, the modern species was assigned as the modern analog. For extinct species in an extant genus, a living species with a similar morphology within that genus was usually assigned. For extinct genera, a species in a genus in the same family, with a similar morphology was assigned:

**Modern analog:** *Nucula proxima* Say (Atlantic Nut Clam). Maine-Florida, sheltered bays and harbors, mud. Most abundant nut shell in near shore areas. (Morris 1975). Muddy substrata in sheltered subtidal conditions

(Stanley 1970); sandy mud bottom (Andrews 1992), large colonies in mud in moderately deep water (Jacobson and Emerson 1971).

## Class BIVALVIA Linné, 1758

**Subclass PALAEOTAXODONTA** Korobkov, 1954

**Order NUCULOIDEA** Dall, 1889

**Superfamily NUCULACEA** Gray, 1824

**Family NUCULIDAE** Gray, 1824

### NUT CLAMS

**Genus *Nucula*** Lamarck 1799, Mem. Soc. H. N. Paris, 87.

*Nucula proxima* (Say)

s=33. n=53

- 1820 *Nucula obliqua* Say, Am. Jour. Sci., 1st ser. vol 2: 40.  
 1943 *Nucula proxima* Say Gardner, U.S.G.S. Paper 199-A: 19-20,  
 1987 *Nucula proxima* Say. Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 134, pl  
 1.  
 1993 *Nucula proxima* Say. Campbell, Virginia Div. Min. Res. Publ. 127: 18-19.

**Life habit:** infaunal deposit feeder

**Modern analog:** *Nucula proxima* Say (Atlantic Nut Clam). Maine-Florida, sheltered bays and harbors, mud. Most abundant nut shell in near shore areas. (Morris 1975). Muddy substrata in sheltered subtidal conditions (Stanley 1970); sandy mud bottom (Andrews 1992), large colonies in mud in moderately deep water (Jacobson and Emerson 1971), often common in muddy or gravelly situations near shore, Gulf of St. Lawrence to South Carolina (Crowder 1959).

**Superfamily NUCULANACEA** H. & A. Adams, 1858

**Family NUCULANIDAE** H. & A. Adams, 1858

### ELONGATE NUT CLAMS

**Genus *Yoldia*** Moeller 1842, Index Moll. Groenl. 18; 1842, Naturhist. Tidsskrift 4(1): 91.

*Yoldia laevis* (Say) Conrad

s=94, n=874

- 1862 *Yoldia laevis* Conrad: Acad. Nat. Sci. Philad. Proc. 1862, 14: 581.  
 1943 *Yoldia laevis* Conrad. Gardner, U.S.G.S. Paper 199-A: 20-21, pl. 1.  
 1993 *Yoldia laevis* Conrad. Campbell, Virginia Div. Min. Res. Publ. 127: 19.

**Life habit:** siphonate infaunal deposit feeder

**Modern analog:** *Yoldia myalis* Couthouy (Oval Yoldia). Labrador to Massachusetts, moderately shallow water, muds. (Morris 1975). *Yoldia limatula* Say (File Yoldia). muddy substrata in sheltered subtidal conditions, in Long Island Sound reached maximum abundance in 40% silt/clay (Stanley 1970), in clean sand and sandy mud in water deep enough to require dredging (Jacobson and Emerson 1971), Arctic Ocean to Puget Sound (Oldroyd 1924). Nova Scotia to North Carolina, in mud, muddy sand, shallow water (Rehder 1995), active species, able to crawl or leap, common in shallow water, Labrador to North Carolina (Crowder 1959).

**Subclass PTERIOMORPHA** Beurlen, 1944

**Order ARCOIDA** Stoliczka, 1871

**Superfamily ARCACEA** Lamarck, 1809

**Family ARCIDAE** Lamarck 1809**ARK SHELLS**

**Genus *Scapharca*** Gray 1847. Proc. Zool. Soc. London 15: 198, 206.

*Scapharca scalariais* (Conrad)

s=2, n=2

1843 *Arca scalaris* Conrad, A.N.S.P. vol. 1, p. 324.

1845 *Arca scalaris* Conrad, Foss. Tert. Form, pg, 59, pl. 31, fig. 1.

**Life habit:** epibyssate suspension feeder

**Modern analog:** *Anadara brasiliiana* (= *Arca incongrua* Say) Lamarck (Incongruous Ark). North Carolina to Brazil, moderately shallow water, gravelly bottoms, in sand (Rehder 1995) relatively common species in West Indies, in about 30 feet of water depth (Humphrey 1975), offshore and in shallow water (Andrews 1992). *Anadara chemnitzii* Phil. South Florida to West Indies, moderately shallow water, gravelly bottoms. (Morris 1975), offshore in shallow water, infaunal (Andrews 1992). Also *Anadara multicostata* Sow. California-Galapagos (mostly Pacific coast of Mexico), moderately shallow water (Morris 1962).

**Family NOETIIDAE** Stewart 1830

**Genus *Noetia*** Gray 1840, Syn. Cont. Brit. Mus. (42 ed.): 151.

*Noetia incile* (Say)

s=54, n=192

1822 Say, Acad. Nat. Sci. Phil., 1st ser., 5: 207-221.

1993 *Noetia incile* (Say). Campbell, Virginia Div. Min. Res. Publ. 127: 20.

**Life habit:** nestling epibyssate suspension feeder

**Modern analog:** *Barbatia gradata* (Brod. and Sowerby), Gulf of Mexico to Peru, shallow water, rocky shores (Morris 1966). *Arca zebra* (Turkey Wing) Sawinson, Florida to Puerto Rico, attached to rocks and coral colonies, nestled in shallow crevices, but always exposed, never burrowing (Stanley 1970).

**Subfamily STRIARCINAE** MacNeil, 1938

**Genus *Striarca*** Conrad 1863, Proc. Acad. Nat. Sci. Philad. 14: 290.

*Striarca centenaria* (Say)

s=6, n=52

1824 Say. Jour. Acad. Nat. Sci. Phil., IV(1):124-155, pl. vii-xii.

1993 *Striarca centenaria* (Say). Campbell, Virginia Div. Min. Res. Publ. 127: 20.

**Life habit:** nestling epibyssate suspension feeder

**Modern analog:** *Barbatia tenera* C.B. Adams (Doc Bale's Ark). South Florida to West Indies, moderately shallow water. (Morris 1975), attaches to the undersides of rocks (Stanley 1970), offshore, epibyssate nestler (Andrews 1992).. *Barbatia candida* Helbling (Bright Ark, White Bearded Ark). North Carolina to Brazil, attached to stones or in crevices, shallow water (Rehder 1995), on rocks beyond low tide, epibyssate nestler (Andrews 1992).

**Superfamily LIMOPSACEA** Dall, 1895  
**Family GLYCYMERIDIDAE** Newton, 1922

**BITTERSWEETS**

**Genus *Glycymeris*** da Costa 1778, Brit. Conch. 168.  
***Glycymeris americana*** (Defrance) Dall  
 s=43, n=167

- 1826 *Pectunculus americanus* Defrance: 225.  
 1898 *Glycymeris americana* (Defrance). Dall, Wagner Free Inst. Trans. 3(4): 609.  
 1943 *Glycymeris americana* (Defrance). Gardner, U.S.G.S. Paper 199-A: 27-28, pl. 1.  
 1987 *Glycymeris americana* (Defrance). Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 137, pl 2.  
 1993 *Glycymeris americana* (Defrance). Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 21.

**Life habit:** shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Glycymeris americana* Defrance (American Bittersweet). Virginia to Texas, moderately shallow water (Morris 1975), uncommon, found in moderately shallow to deep water from North Carolina to Florida and Texas (Romashko 1998).

***Glycymeris subovata*** Say  
 (= *Costagygymeris subovata* (Say) Ward 1992)  
 s=2, n=2

- 1824 *Glycymeris subovata* Say, Acad. Nat. Sci. Phil. 1st ser., 5: 207-221.  
 1993 *Glycymeris subovata* Say. Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 21.

**Life habit:** shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Glycymeris americana* Defrance (American Bittersweet). Virginia to Texas, moderately shallow water. (Morris 1975).

**Order MYTILOIDA** Ferussac, 1822  
**Superfamily MYTILACEA** Rafinesque, 1815  
**Family MYTILIDAE** Rafinesque, 1815

**MUSSELS**

**Genus *Modiolus*** Lamarck 1799, Mem. Soc. H. N. Paris, 87.  
***Modiolus* sp.**  
 s=25, n=28

**Life habit:** shallow infaunal byssate suspension feeder

**Modern analog:** *Modiolus americanus* Leach (= *M. tulipa* Lam.) (Tulip Mussel). North Carolina to West Indies, moderately shallow water. (Morris 1975). Inhabits mostly sandy subtidal grass mats, also found in clean sand (Stanley 1970), very common attached to thick algae or mossy rocks in 1-10 feet water depth (Humphrey 1975), often in crevices, or burrowed into soft substrata, to depths of 60 m (Fish and Fish 1996).

**Genus *Mytilus*** Linné 1758, Syst. Nat. (ed. 10): 704.  
***Mytilus* sp.**  
 s=2, n=2

**Life habit:** epibyssate suspension feeder

**Modern analog:** *Mytilus edulis* Linnaeus (Common Blue Mussel). Greenland to South Carolina, Alaska to California, Europe, intertidal. (Morris 1975). Prefers rocky intertidal zone, but can form clumps on any hard substrate (Stanley 1970). Found attached to hard surface, and on soft

sediments in estuaries, can tolerate salinities as low as 4 o/oo (Fish and Fish 1996), very abundant, found in crowded colonies attached to tocks, wharves, by strong bussal threads (Romashko 1998).

**Order OSTREIODA** Férussac 1822  
**Superfamily OSTREOIDEA** Rafinesque 1815  
**Family GRYPHAEIDAE** Vyalov 1936  
**Subfamily PYCNODONTINAE** Stenzel 1959  
**Genus *Pycnodonte*** Fischer de Waldheim 1835  
*Pycnodonte* sp. Fisher 1835  
s=23, n=201

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Crassostrea virginica* (Eastern Oyster). Gulf of St. Lawrence to the Gulf of Mexico and the West Indies, hard or soft substrates (Rehder 1995), usually abundant only in areas of low salinity which limits starfish and other predators. Brackish bays and estuaries, cemented epifaunal (Andrews 1992).

**Family OSTREIDAE** Rafinesque 1815  
**Subfamily OSTREINAE** Rafinesque 1815  
**Genus *Ostrea*** Linné 1758  
*Ostrea sculpturata* Conrad 1840  
(=*Conradostrea sculpturata* of Ward and Blackwelder 1987)  
s=124, n=1760

1840 *Ostrea sculpturata* Conrad. Am. Jour. Sci. & Arts 39: 387-388.

1993 *Ostrea sculpturata* Conrad. Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 27.

**Life habit:** epifaunal, cementing suspension feeder

**Modern analog:** *Crassostrea virginica* (Eastern Oyster). Gulf of St. Lawrence to the Gulf of Mexico and the West Indies, hard or soft substrates (Rehder 1995), usually abundant only in areas of low salinity which limits starfish and other predators. Brackish bays and estuaries, cemented epifaunal (Andrews 1992).

***Ostrea raveneliana*** Tuomey and Holmes 1855  
s=17, n=40

1824 *Ostrea raveneliana* Tuomey and Holmes. Pliocene Fossils of South Carolina: 21, pl. 4.

**Life habit:** epifaunal, cementing suspension feeder

**Modern analog:** *Crassostrea virginica* (Eastern Oyster). Gulf of St. Lawrence to the Gulf of Mexico and the West Indies, hard or soft substrates (Rehder 1995), usually abundant only in areas of low salinity which limits starfish and other predators. Brackish bays and estuaries, cemented epifaunal (Andrews 1992). A deeper water oyster would probably better be a better modern analog for this species.

**Order PTERIODA** Newell 1965.  
**Suborder PTERIINA** Newell 1965.  
**Superfamily PECTINACEA** Rafinesque 1815  
**Family PECTINIDAE** Rafinesque 1815

## SCALLOPS

**Genus *Carolinapecten*** Ward and Blackwelder 1987. Smith. Contr. Paleo. 61: 141.

***Carolinapecten eboreus*** (Conrad)

s=59, n=167

- 1833 *Pecten eboreus*. Conrad. Am. Jour. Arts & Sci. 23: 341.  
 1987 *Carolinapecten eboreus* (Conrad). Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 141-142, pl 6,7.  
 1993 *Carolinapecten eboreus* (Conrad). Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 24.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Argopecten gibbus* (Calico Scallop). North Carolina to Gulf of Mexico, Cuba to Puerto Rico, on sand in shallow water (Rehder 1995); common around Jamaica, found in shallow water on eel grass beds (Humphrey 1975)

**Genus *Chesapecten*** Ward and Blackwelder 1975, U.S. U.S.G.S. Paper 861: 7.

***Chesapecten jeffersonius*** (Say)

s=2, n=5

- 1824 *Pecten jeffersonius* Say. Acad. Nat. Sci. Phil. Jour. 4:133, pl. 9.  
 1987 *Chesapecten jeffersonius* (Say). Gibson, Smith. Contr. to Paleobiology 61: 69-71, pl. 21-23.  
 1993 *Chesapecten jeffersonius* (Say). Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 25.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Pecten ziczac* (Zigzag Scallop), North Carolina to Brazil, in sand or mud, nestles in soft sand or mud, strong swimmer (Rehder 1995), common, prefers calm, protected, shallow water on eel grass (Humphrey 1975).

***Chesapecten madisonius*** (Say)

s=111, n=538

- 1824 *Pecten madisonius* Say. Acad. Nat. Sci. Phil. Jour. 4:134.  
 1975 *Chesapecten madisonius* (Say). Ward and Blackwelder, 16-18, pl. 6, 7.  
 1987 *Chesapecten madisonius* (Say). Gibson, Smith. Contr. to Paleobiology 61: 73-76, pl. 21-23.  
 1993 *Chesapecten madisonius* (Say). Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 25.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Pecten ziczac* (Zigzag Scallop), North Carolina to Brazil, in sand or mud, nestles in soft sand or mud, strong swimmer (Rehder 1995), common, prefers calm, protected, shallow water (Humphrey 1975).

***Chesapecten septenarius*** (Say)

s=1, n=1

- 1824 *Pecten septenarius* Say, Acad. Nat. Sci. Phil. Jour. 4:136, pl. 9.  
 1987 *Chesapecten septenarius* Gibson, Smith. Contr. to Paleobiology 61: 61-73, pl. 21-23.  
 1993 *Chesapecten septenarius* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 25.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Pecten ziczac* (Zigzag Scallop), North Carolina to Brazil, in sand or mud, nestles in soft sand or mud, strong swimmer (Rehder 1995), common, prefers calm, protected, shallow water, on eel grass (Humfrey 1975).

**Family PLICATULIDAE** Watson, 1930

**KITTEN'S PAWS**

**Genus *Plicatula*** Lamarck 1801, Syst. Anim. S. Vert. 132.

*Plicatula marginata* Say 1824

s=50, n=700

1824 *Plicatula marginata* Say, Acad. Nat. Sci. Philad. Jour. 1st. ser., vol. 4: 136.

1943 *Plicatula marginata* Gardner, U.S.G.S. Paper 199-A: 40, pl. 11.

1987 *Plicatula marginata* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 143, pl 7.

1993 *Plicatula marginata* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 26.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Plicatula gibbosa* Lamarck (Kitten's Paw). North Carolina to West Indies, intertidal. (Morris 1975) attached to rocks or shells, shallow water (Rehder 1995), abundant in 1 foot water depth attached to objects along the harbor side of the Palisadoes, in deeper water elsewhere (Humfrey 1975), offshore on banks, cemented epifaunal (Andrews 1992).

**Superfamily ANOMIACEA**

**Family ANOMIIDAE** Rafinesque 1815

**JINGLE SHELLS**

**Genus *Anomia*** Linné 1758, Syst. Nat. (10th Ed.): 700.

*Anomia simplex* d'Orbigny

s=11, n=16

1842 *Anomya simplex* d'Orbigny, Mollusca 1: pl. 28, figs 31-33.

1987 *Anomia simplex* d'Orbigny, Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 143, pl 7.

1993 *Anomia simplex* d'Orbigny, Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 26.

**Life habit:** epibyssate suspension feeder

**Modern analog:** *Anomia simplex* Orbigny (Common Jingle Shell). Nova Scotia to West Indies, shallow water (Morris 1975). Attached to pebbles, cobbles, shell debris on firm substrata, restricted to shallow subtidal with moderate current flow (Stanley 1970) on rocks, shells, logs, boats, and piers, from near low-tide line to water 30', common in 3 feet water depth attached to rocks, shells, or any other firm substrate (Humfrey 1975), hypersaline oyster or rock reef, close epibyssate attachment (Andrews 1992), attached to any solid submerged object, preferring stones and dead or live shells (Jacobson and Emerson 1971). (=A. *ephippium* ?) abundant on stones, oysters, dead shells and other solid objects in shallow water (Crowder 1959).

**Genus *Pododesmus*** Philippi 1837

*Pododesmus* sp.

s=2, n=4

**Life habit:** epibyssate suspension feeder

**Modern analog:** *Anomia simplex* Orbigny (Common Jingle Shell). Nova Scotia to West Indies, shallow water (Morris 1975). Attached to pebbles, cobbles, shell debris on firm substrata, restricted to shallow subtidal with moderate current flow (Stanley 1970). *Pododesmus rudis* Broderip (False Jingle Shell) found attached to bottoms of boats in shallow water, also attached to rocks, shells and other firm substrata (Humphrey 1975); on rocks in inlet-influenced areas (Andrews 1992).

**Subclass HETERODONTA** Cox 1960

**Order VENEROIDA** H. & A. Adams, 1856

**Superfamily LUCINACEA** Fleming, 1828

**Family LUCINIDAE** Fleming, 1828

**LUCINE SHELLS**

**Genus *Stewartia*** Olsson and Harbison 1953, Acad. Nat. Sci. Philad., Mono. 8: 82.

*Stewartia anodonta* (Say 1824)

s=14, n=24

1987 *Stewartia anodonta floridana* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 145-146, pl 9.

**Life habit:** moderately deep infaunal lucinid suspension feeder

**Modern analog:** *Anodontia alba* Linneaus (Buttercup Lucine). North Carolina to West Indies, shallow water (Morris 1962) in sand (Rehder 1995) common in 3-15 feet of water in sandy areas (Humphrey 1975), inlet-influenced areas, bay margins, hypersaline lagoons, infaunal (Andrews 1992). *Pseudomiltha floridana* Conrad (Florida Lucina), Western Florida to Texas, open bays and inlet-influenced areas, infaunal (Andrews 1992).

**Genus *Parvilucina*** Dall 1901, Proc. U. S. Natl. Mus. 23: 806.

*Parvilucina multilineatus* (Tuomey and Holmes)

s=90, n=365

1903 *Parvilucina multilineatus* Tuomey and Holmes Dall, Wagner Free Inst. Sci. Trans. 3(6): 1384.

1943 *Parvilucina multilineatus* Gardner, U.S.G.S. Paper 199-A: 78-79, pl. 13.

1987 *Phacoides (Parvilucina) multilineata* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 146, pl 9.

**Life habit:** shallow infaunal lucinid suspension feeder

**Modern analog:** *Lucina multilineatus* Tuomey and Holmes. North Carolina to Florida, shallow water. = *Parvilucina multilineata* Holmes (Many-Lined Lucine). Virginia to Florida Keys, Caribbean, in sand and mud, shallow water (Rehder 1995), offshore and inlet areas, infaunal (Andrews 1992). *Parvilucina nassula* (Woven Lucine = *Phacoides nassula*, *Lucina nassula*) North Carolina to Florida, Belize, British Honduras, Greater Antilles, in sand, 1-2000' water depth (Rehder 1995).

**Genus *Divalinga*** Chavan 1951, Bull. Inst. Roy. Sci. Nat. Belg. 27(18): 6.

*Divalinga quadrisulcata* d'Orbigny 1842.

s=5, n=6

1993 *Divalinga quadrisulcata* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 28.

**Life habit:** moderately deep infaunal lucinid suspension feeder

**Modern analog:** *Divaricella quadrisulcata* Orbigny (Cross-Hatched Lucine). Massachusetts to West Indies, moderately shallow water (Morris 1975) in sand (Rehder 1995), occurs live in about 6 feet of water in sand (Humfrey 1975), deeper offshore water (Jacobson and Emerson 1971), common in moderately shallow water (Romashko 1998).

**Subfamily LUCININAE** Fleming, 1828

**Genus *Lucinisca*** Dall 1901, Proc. U.S. natl. Mus. 23: 805.

*Lucinisca cribrarius* (Say) Dall 1903  
s=67, n=278

- 1824 *Lucina cribraria* Say, Acad. Nat. Sci. Phil. Jour., 1st ser., 4: 147, pl. 13, fig. 1.  
1903 *Phacoides (Lucinisca) cribrarius* Dall, Wagner Free Inst. Sci. Trans. 3(6): 1372.  
1943 *Phacoides (Lucinisca) cribrarius* (Say) Dall, Gardner, U.S.G.S. Paper 199-A: 77-78, pl. 13.  
1993 *Lucinisca cribrarius* (Say) Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 28.

**Life habit:** shallow infaunal lucinid suspension feeder

**Modern analog:** (*Parvi*)*Lucina nuttalli* Conrad (Nuttall's Lucine). Monterey, California to Mexico, moderately shallow water, (Morris 1966) in sand (Rehder 1995).. *Phacoides muricatus* (Spengler), muddy substrata in subtidal, sheltered conditions (Stanley 1970) abundant in sandy areas (Humfrey 1975). *Parvilucina nassula* (Woven Lucine), North Carolina to Florida, Belize, British Honduras, Greater Antilles, in sand, 1-2000' water depth (Rehder 1995) =*Phacoides nassula*, *Lucina nassula*.

**Genus *Ctena*** Morch 1860. Malak. Bl., 7: 201.

*Ctena speciosa* (Rogers & Rogers 1837) Gardner 1943  
s=10, s=20

- 1943 *Ctena speciosa* (Rogers and Rogers) Gardner, U.S.G.S. Paper 199-A: 75, pl. 13, fig. 33.  
1993 *Ctena speciosa* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 28.

**Life habit:** shallow infaunal lucinid suspension feeder

**Modern analog:** *Ctena bella* Conrad. Pacific, moderately shallow water (Morris 1962).

**Family UNGULINIDAE** H. & A. Adams 1857

**DIPLODON SHELLS**

**Genus *Diplodonta*** Bronn, 1831. Ergeb. nat. Reisen, 2:484, 1831, Italiens tert. Gebilde, ix-xii, 96.

*Diplodonta leana* Dall 1900  
s=9, n=15

- 1900 *Diplodonta leana* Dall, Wagner Free Inst. Sci. Trans., 3(5): 1187.  
1943 *Diplodonta leana* Gardner, U.S.G.S. Paper 199-A: 80, pl. 14.

*Diplodonta* sp.A  
s=4, n=9

*Diplodonta* sp.B

s=3, n=3

**Life habit:** shallow infaunal lucinid suspension feeder**Modern analog:** *Diplodonta necliformis* Wagner. Florida to West Indies, shallow water or *Diplodonta punctuata* Say (Common Atlantic Diplodon). North Carolina to West Indies, moderately shallow water (Morris 1975) in sand (Rehder 1995), common in 3-12 feet of water, usually found on soft sand or mud (Humphrey 1975).**Superfamily CHAMACEA** Blainville, 1825**Family CHAMIDAE** Blainville, 1825**JEWEL BOX CLAMS****Genus *Chama*** Linné 1758, Syst, Nat. (ed. 10): 691.***Chama congregata*** Conrad 1833

s=75, n=3224

1833 Conrad, Am. Jour. Sci. &amp; Arts, 23: 339-346.

1993 *Chama congregata* Conrad, Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 30.**Life habit:** epifaunal cementing suspension feeder**Modern analog:** *Chama pellucida* Broderip (Clear Jewel Box) Oregon to Baja California, moderately shallow water. (Morris 1966), common attached to rocks and pilings in shallow to moderately deep water, Oregon to Peru (Romashko 1998). *Chama congregata* Conrad (Little Corrugated Jewel Box). North Carolina to Bermuda, Texas, Brazil, on rocks and other hard surfaces (Rehder 1995), relatively common in 1-50 feet of water depth, in rocky areas (Humphrey 1975), offshore on calcareous banks, cemented epifaunal (Andrews 1992). Right valve commonly transported (Humphrey 1975, Andrews 1992)**Genus *Pseudochama*** Odhner 1917, K. svenska VetenskAkad. Handl., 52(16): 28.***Pseudochama corticosa*** (Conrad) Gardner

s=9, n=14

1833 *Chama corticosa* Conrad, Am. Jour. Sci., 1st ser. 23:341.1943 *Pseudochama corticosa* (Conrad) Gardner, U.S.G.S. Paper 199-A: 89, pl. 13.**Life habit:** epifaunal cementing suspension feeder**Modern analog:** *Pseudochama exogyra* Conrad (Pacific Left-Handed Jewel Box). Oregon to Baja California, moderately shallow water. (Morris 1966). *Psuedochama radians* (Lamarck) (Atlantic Left-Handed Jewel Box). North Carolina to Brazil, on rocks and other hard surfaces in shallow water (Rehder 1995) relatively common in 1-50 feet of water depth attached to hard substrata, including mangrove roots (Humphrey 1975), offshore on calcareous banks, cementing epifaunal (Andrews 1992).**Superfamily GALEOMMATACEA** Gray 1840**Family KELLIIDAE** Forbes & Hanley 1848**COIN CLAMS****Genus *Bornia*** Phillipi, 1836, Eum. Moll. Sicililae, 1:13.***Bornia triangula*** Dall

s=5, n=6

- 1904 *Bornia triangula* Dall, Glenn, Maryland Geol. Survey, Miocene, p. 330, pl. 88, figs. 9a, 9b.  
 1943 *Bornia triangula* Gardner, U.S.G.S. Paper 199-A: 82-83, pl. 14.  
 1987 *Bornia triangula* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 148, pl 12.

**Life habit:** nestling epifaunal suspension feeder

**Modern analog:** *Kellia suborbicularis*. (North Atlantic Kellia) Labrador to New York, British Columbia to Panama, also Europe, attached to dead shells, algae, and rock crevices from near low-tide mark to 400' (Rehder 1995).

**Superfamily CARDITACEA** Fleming, 1820  
**Family CARDITIDAE** Fleming, 1820  
**Subfamily CARDITAMERINAE** Chavan, 1969

**CARDITA CLAMS**

**Genus *Carditamera*** Conrad 1838, Fossils of the medial Tertiary of the United States: 11.

***Carditamera arata*** Conrad 1838  
 s=16, n=42

- 1838 *Carditamera arata* Conrad, Fossils of the medial Tertiary of the United States: 11.  
 1943 *Carditamera arata* Gardner, U.S.G.S. Paper 199-A: 69, pl. 15.  
 1987 *Carditamera arata* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 149, pl 14.  
 1993 *Carditamera arata* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 33.

**Life habit:** nestling epibyssate non-siphonate suspension feeder

**Modern analog:** *Cardita floridana* Conrad (Broad Ribbed Cardita) Conrad. Florida to Texas, shallow water. (Morris 1975) in sand and mud in shallow water (Rehder 1995), inlet-influenced areas and hypersaline lagoons, infaunal (Andrews 1992).

**Genus *Pteromeris*** Conrad 1862, Acad. Nat. Sci. Philad. Proc. 1862, 14: 290.

***Pteromeris perplana*** (Conrad)  
 s=7, n=14

- 1841 *Cardita perplana* Conrad, Am. Jour. Sci., ser. 1., 41:347, pl. 2, fig. 16.  
 1943 *Glans (Pteromeris) perplana* Gardner, U.S.G.S. Paper 199-A: 72-73, pl. 13.  
 1987 *Pteromeris perplana* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 150, pl 14.  
 1993 *Pteromeris perplana* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 34.

**Life habit:** Shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Venericardia perplana* Conrad. North Carolina to Florida, moderately shallow water. (Morris 1975). *Pleuromeris tridentata* (Three Toothed Cardita), North Carolina to Florida Keys, on sand or rubble in 9-45 feet water depth (Rehder 1995)

**Genus *Cyclocardia*** Conrad 1867, Amer. Jour. Conch. 3: 191.

***Cyclocardia granulata*** (Say)  
 s=66, n=1241

- 1824 *Venericardia granulata* Say, Jour. Acad. Nat. Sci. Phil., 1sr ser.: 142, pl. 12, fig. 1.  
 1987 *Cyclocardia granulata* (Say) Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 150, pl 14.

1993 *Cyclocardia granulata* (Say) Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 34.

**Life habit:** shallow infaunal suspension feeder

**Modern analog:** *Venericardia borealis* Conrad (Cod Clam). Artic Ocean to Cape Hatteras, moderately shallow water (Morris 1975). *Cyclocardia borealis* (Northern Cardita). Labrador to North Carolina, in sand, gravel, and rubble (Rehder 1995), deep off-shore waters (Jacobson and Emerson 1971), occurs in offshore waters, but dead shells commonly cast upon the beach, Labrador to New Jersey (Crowder 1959).

**Superfamily** CARDIACEA Lamarck 1809

**Family** CARDIIDAE Lamarck 1809

## COCKLES

**Genus** *Chesacardium* Ward 1992

*Chesacardium acutilaqueatum*

s=31, n=51

**Life habit:** shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Dinocardium robustum* Sol. (Giant Atlantic Cockle), Virginia to Texas, moderately shallow water (Morris 1975) in sand and mud, shallow water (Rehder 1995), common in moderately shallow water or washed up on shore from Virginia to Florida to Texas (Romashko 1998).=*Laevicardium robustum* Lightfoot, close to shore in inlet-influenced areas (Andrews 1992).

**Superfamily** MACTRACEA Lamarck, 1809

**Family** MACTRIDAE Lamarck, 1809

**Subfamily** MACTRINAE Lamarck, 1809

## SURF CLAMS

**Genus** *Mulinia* Gray 1837, Proc. Zool. Soc. London 4(46): 104; Gray 1837, Mag. Nat. Hist. 2: 335, 375.

*Mulinia congesta* (Conrad) Dall 1898

s=117, n=11,282

1833 *Mactra congesta* Conrad, Am. Jour. Sci., 1st ser. 23: 340.

1898 *Mulinia congesta* (Conrad), Dall, Wagner Free Inst. Sci. Trans. 3(4): 900.

1943 *Mulinia congesta* (Conrad) Gardner, U.S.G.S. Paper 199-A: 113-114, pl. 23.

1987 *Mulinia congesta* (Conrad) Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 154 (in discussion of *M. lateralis*).

1993 *Mulinia congesta* (Conrad) Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 38.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Mulina lateralis* Say (Dwarf Surf Clam, Coot Clam, Duck Clam). Maine to Florida and Texas, shallow water. (Morris 1975). Lagoonal, tolerates large range of salinities and substrate types, but not found in clean, shifting sand (Stanley 1970), huge numbers in muddy bottoms of bays around New York (Jacobson and Emerson 1971), clayey sediments in every type of assemblage, infaunal, most abundant and ubiquitous bivalves on Texas coast due to ability to withstand wide range of salinities, juveniles thin and opalescent coming ashore in vast numbers in winter months (Andrews 1992), particularly abundant in spring months, especially in hypersaline or low salinity bays (Fotheringham and Brunenmeister 1989)

**Genus *Leptmaetra***  
***Leptmaetra dolombus*** (Conrad) Ward 1992  
s=10, n=17

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Mactra fragilia* (= *fragilis*) Gmelin (Atlantic Mactra, Fragile Surf Clam). North Carolina to Texas, West Indies, shallow water. (Morris 1975). Intertidal and shallow subtidal, restricted to grassy bottoms and sandy substrata (Stanley 1970), reasonably common in 5 feet of water depth (Humfrey 1975), open-bay margins, infaunal (Andrews 1992).

**Genus *Hemimaetra***  
***Hemimaetra duplinensis*** (Dall 1898)  
s=21, n=29

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Mactra fragilis* (Fragile Atlantic Mactra). North Carolina to Brazil, in sand in shallow water (Rehder 1995).

**Genus *Spisula*** Gray 1837, Mag. Nat. Hist. (N.S.) 1: 372.  
***Spisula similis*** (Say) Gardner  
s=13, n=19

1822 *Mactra similis* Say. Acad. Nat. Sci. Phil. Jour., 1st ser., 2: 309.

1943 *Spisula (Hemimaetra) similis* (Say) Gardner, U.S.G.S. Paper 199-A: 111, pl. 22.

1987 *Spisula similis* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 154, pl 18.

***Spisula* sp.A**  
s=1, n=1

***Spisula* sp.B**  
s=1, n=1

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Spisula solidissima* Dillwyn (Atlantic Surf Clam). Nova Scotia to South Carolina, moderately shallow water. (Morris 1975). Lives on medium to coarse grained shifting sands (Stanley 1970) just beneath surface in sand, mud, or gravel (Rehder 1995), inlet-influenced areas, infaunal (Andrews 1992), in sand subtidally, slow burrower (Jacobson and Emerson 1971), common, found sand in moderately shallow water from Nova Scotia to Florida (Romashko 1998).

**Superfamily SOLENACEA** Lamarck, 1809  
**Family CULTELLIDAE** Davies, 1935  
**Genus *Ensis*** Schumacher 1817, Essai Vers Test., 47, 143.  
***Ensis directus***  
s=84, n=182

**Life habit:** deep infaunal siphonate suspension feeder

**Modern analog:** *Ensis directus* Conrad (Atlantic Jackknife Clam). Labrador to Florida, intertidal, extremely rapid burrower in sand bars. (Morris 1975) in sand intertidally (Rehder 1995), in sand and mud in shallow water in bays (Jacobson and Emerson 1971). =? *Ensis minor* Dall (Small Jackknife Cam) fairley common in intertidal zone, Florida to Texas (Romashko 1998).

**Superfamily ASTARTACEA**  
**Family ASTARTIDAE** d'Orbigny, 1844

## Subfamily ASTARINAE d'Orbigny, 1844

## ASTARTIDS

**Genus *Astarte*** Sowerby 1816, Min. Conch. 2: 85, (pl. 137).

*Astarte undulata* Say 1824

s=82, n=454

- 1824 *Astarte undulata* Say, Acad. Nat. Sci. Philadelphia Jour., 1st. ser., vol. 4: 150.  
 1943 *Astarte (Ashtarotha) undulata* Gardner, U.S.G.S. Paper 199-A: 57-59, pl. 12.  
 1993 *Astarte undulata* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 35.

**Life habit:** shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Astarte undulata* Gould (Waved Astarte). Labrador to Maryland, moderately shallow water. (Morris 1975), the modern species has a colder water distribution that than expected for the ancient species. *Astarte undata* Gould, prefers coarse substrate (up to gravelly), slow burrower (Stanley 1970), shallow water, Gulf of St. Lawrence to Long Island Sound (Crowder 1959).

*Astarte concentrica* Conrad 1834

s=24, n=149

- 1834 *Astarte concentrica* Conrad, Acad. Nat. Sci. Philadelphia Jour., 1st. ser., vol. 4: 133.  
 1943 *Astarte (Ashtarotha) concentrica* Gardner, U.S.G.S. Paper 199-A: 59-60, pl. 12.  
 1987 *Astarte concentrica* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 151, pl 16.  
 1993 *Astarte concentrica* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 34-35.

**Life habit:** shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Astarte subaequilatera* Sowerby. Labrador to Florida, 80-180 feet deep. (Morris 1975)

## Superfamily CRASSATELLACEA Ferussac, 1822

## Family CRASSATELLIDAE Férussac 1822

## Subfamily CRASSATELLINAE Férussac 1822

## CRASSATELLIDS

**Genus *Marvacrassatella*** Ward and Blackwelder 1987, Smith. Contr. to Paleobiology 61: 151-152, pl 1.

*Marvacrassatella undulata*

s=82, n=38

- 1993 *Eucrassatella undulata* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 35.

**Life habit:** medium infaunal non-siphonate suspension feeder

**Modern analog:** *Eucrassatella speciosa* A.Adams (= *Crassatella gibbesii* Toumey and Holmes, Gibb's Clam). North Carolina to West Indies, moderately shallow water. (Morris 1975).

**Genus *Crassinella*** Guppy 1874.

*Crassinella lunulata* (Conrad) Dall

s=25, n=38

- 1834 *Astarte lunulata* Conrad, Acad. Nat. Sci. Phil. Jour., 1st ser. 7:133.  
 1932 *Crassinella lunulata* Dall. Mansfield, Florida Geol. Survey Bull. 8, p. 82, pl. 15, fig. 6.  
 1943 *Crassinella lunulata* (Conrad) Dall, Gardner, U.S.G.S. Paper 199-A: 62-63, pl. 19.  
 1987 *Crassinella lunulata* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 153, pl 16.  
 1993 *Crassinella lunulata* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 36.

**Life habit:** shallow infaunal non-siphonate suspension feeder

**Modern analog:** *Crassinella lunulata* Conrad (Lunate Crassinella). Florida, Bahamas, West Indies, shallow water and *Crassinella mastracea* Linsley. Massachusetts to New York. (Morris 1975) in sand, or mud with rubble, shallow water (Rehder 1995), inlet-influenced areas and channels on shelly bottom, infaunal (Andrews 1992).

**Superfamily TELLINACEA** Blainville, 1814

**Family TELLINIDAE** Blainville, 1814

**TELLINS**

**Genus *Macoma*** Leach 1819, in Ross, Voy Discov. Baffin's Bay (4to), App. 2, lxii.

*Macoma virginiana* (Conrad) Dall

s=72, n=181

- 1840 *Tellina lusoria* Conrad, Fossils of the Medial Tertiary of the U.S: 35, pl. 19, fig. 3.  
 1900 *Macoma virginiana* Conrad, Wagner Free Inst. Sci. Trans. 3(5): 1048.  
 1943 *Macoma virginiana* (Conrad) Dall, Gardner, U.S.G.S. Paper 199-A: 98-100, pl. 17.  
 1993 *Macoma virginiana* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 41.

**Life habit:** shallow infaunal tellinid siphonate deposit feeder

**Modern analog:** *Macoma tenta* Say. Prince Edward Island to Florida, Gulf of Mexico, West Indies, shallow water (Morris 1975) in sand (Rehder 1995), common in muddy areas, 5-20 feet water depth (Humfrey 1975), open-bay margins, shallow hypersaline lagoons, infaunal (Andrews 1992), on muddy bay bottoms in shallow water (Jacobson and Emerson 1971), occurs in muddy bays, Cape Cod to Florida and West Indies (Crowder 1959).

**Family SEMELIDAE** Stoliczka, 1870

**SEMELES**

**Genus *Abra*** Lamarck 1818, Anim. s. Vert. 5: 492.

*Abra subreflexa* (Conrad)

s=66, n=268

- 1834 *Amphidesma subreflexa* Conrad, Acad. Nat. Sci. Phil. Jour., 1st ser.7:133.  
 1863 *Abra subreflexa* Conrad, Acad. Nat. Sci. Philadelphia Proc. 1862: 574.  
 1943 *Abra subreflexa* (Conrad) Conrad, Gardner, U.S.G.S. Paper 199-A: 103-104, pl. 17.  
 1993 *Abra subreflexa* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 42.

**Life habit:** shallow infaunal siphonate deposit feeder

**Modern analog:** *Abra aequalis* (Common Atlantic Abra). North Carolina to Brazil, in sand and mud in shallow water (Rehder 1995), widely distributed in northern Gulf of Mexico (Fotheringham and Brunenmeister 1989).

**Genus *Semele*** Schumacher 1817, Essai Vers Test., 53, 165.

***Semele* sp.A**  
s=91, n=248

**Life habit:** shallow infaunal siphonate deposit feeder

**Modern analog:** *Semele proficua* Pulteney (Common Atlantic Semele, White Atlantic Semele). North Carolina to Brazil, in sand, shallow water (Rehder 1995), relatively in shallow water (Humfrey 1975), open-bay centers, inlet areas, near shore, infaunal (Andrews 1992).

**Genus *Cumingia*** Sowerby 1833.

***Cumingia tellinoides*** (Conrad)  
s=1, n=1

1831 *Mactra tellinoides* Conrad, Am. Jour. Sci., ser. 1, 23:258, pl.11, figs. 2, 3.

1987 *Cumingia tellinoides* Conrad. Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 156, pl 21.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Cumingia tellinoides* Conrad (Tellin-Like Cumingia). Shallow water (1-4 meter) in muddy, medium sand, found in narrow tidal channels (Stanley 1970) Nova Scotia to Florida, in mud, very shallow water (Rehder 1995), bay margins, high-salinity bays, inlet areas, infaunal (Andrews 1992).

**Superfamily GLOSSACEA** Gray 1847

**Family GLOSSIDAE** Gray 1847

**Genus *Glossus*** Poli 1795, Test. Sicil. 2: 112.

***Glossus* sp.**  
s=1, n=1

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Glossus hummanus* (check European distribution).

**Superfamily VENERACEA** Rafinesque, 1815

**Family VENERIDAE** Rafinesque, 1815

**Subfamily CHIONINAE** Frizzell, 1936

## VENUS CLAMS

**Genus *Chione*** Megerle von Muhlfield 1811, Mag. Ges. Nat. Fr. Berlin 5: 51.

***Chione cribraria*** (Conrad) Dall  
s=5, n=7

1843 *Venus cribraria* Conrad, Acad. Nat. Sci. Phil. Proc., ser. 1: 310.

1903 *Chione cribraria* Conrad, Dall, Wagner Free Inst. Sci. Trans. 3(6): 1292.

1943 *Chione (Chione) cribraria* (Conrad) Dall, Gardner, U.S.G.S. Paper 199-A: 128.

1987 *Chione cribraria* (Conrad) Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 158, pl 23.

1993 *Chione cribraria* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 44.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Chione intapurpurea* Conrad (Lady-in-Waiting Venus). North Carolina to West Indies, moderately shallow water. (Morris 1975), near shore 3.6-21.6 meters, infaunal (Andrews 1992), common, North Carolina to Florida, Gulf states, West Indies (Romashko 1998).

*Chione grus* (Holmes) Dall  
s=1, n=1

- 1858 *Tapes grus* Holmes, Post-Pliocene fossils of South Carolina: 37, pl. 7, fig. 5.  
1903 *Chione (Timoclea) grus* Holmes, Dall, Wagner Free Inst. Sci. Trans. 3(6): 1299.  
1943 *Chione (Chione) grus* (Holmes) Dall, Gardner, U.S.G.S. Paper 199-A: 128-129, pl. 19.  
1987 *Chione grus*, Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 158, pl 23.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Chione grus* Holmes (Gray Pygmy Venus). South Carolina to Florida, moderately shallow water. (Morris 1975), North Carolina to Florida, Texas, sand and sandy mud, shallow water (Rehder 1995), offshore in intermediate shelf assemblage, sand and shell bottoms, infaunal (Andrews 1992). In crevices on artificial reefs (Fotheringham and Brunemeister 1989).

**Genus *Mercenaria*** Schumacher 1817, Essai Vers Test., 45: 135.  
*Mercenaria campechiensis* Conrad 1832  
s=46, n=228

- 1838 *Venus rileyi* Conrad. Fossils of the medial Tertiary of the U.S.: 9, pl. 6, fig. 1.  
1943 *Venus (Mercenaria) campechiensis* Conrad. Gardner, U.S.G.S. Paper 199-A: 130-133, pl. 23.  
1993 *Mercenaria campechiensis* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 43-44.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Mercenaria mercenaria* Linné (Northern Quahog). Gulf of St. Lawrence to Florida, shallow water and *Mercenaria campechiensis* Gmelin (Southern Quahog). Virginia to Texas. (Morris 1975). Commonly shallow subtidal to intertidal, various substrata, usually on bare bottoms, but very tolerant. In sand or mud in bays or inlets (Rehder 1995), offshore, open bays and inlet-influences areas, infaunal (Andrews 1992).

**Subfamily DOSINIINAE** Deshayes, 1835  
**Genus *Dosinia*** Scopoli 1777, Intr. Hist. Nat. 399.  
*Dosinia acetabulum* (Conrad) Conrad  
s=103, n=846

- 1832 *Artemis acetabulum* Conrad, Fossil shells of the Tertiary formations of North America: 20, pl. 6, fig. 1.  
1894 *Dosinia acetabulum* Conrad, Conrad, Whitfield, U.S.G.S. Mono. 24: 73.  
1943 *Dosinia (Dosinidia) acetabulum* (Conrad) Conrad, Gardner, U.S.G.S. Paper 199-A: 120-122, pl. 11.  
1993 *Dosinia acetabulum* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 46.

**Life habit:** medium infaunal siphonate suspension feeder

**Modern analog:** *Dosinia elagans* Conrad (Elegant *Dosinia*, Elegant Venus). West Florida to Texas, shallow water. (Morris 1975). Lives on moderately exposed sand flats (Stanley 1970), offshore, infaunal (Andrews 1992), common in Gulf states (Romashko 1998).

**Subfamily PITARINAE** Stewart 1930**Genus *Pitar*** Romer 1857, Krit. Untersuch, Venus, 15.*Pitar sayana* Conrad 1833

s=12, n=44

1993 *Pitar sayana* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 45.***Pitar* sp. B**

s=2, n=6

**Life habit:** shallow infaunal siphonate suspension feeder**Modern analog:** *Pitar alternatus* Gulf of California to Peru, moderately shallow water. (Morris 1966). *Pitar fulminata* (Lightning Venus). North Carolina to Brazil, in mud and sand, shallow water (Rehder 1995), common in mud or sand in 10-40 feet of water depth, within *Thalassia* beds (Humfrey 1975).**Genus *Macrocallista*** Meek 1876. Rep. U.S. geol. surv. Terr. (Hayden), 9:179.*Macrocallista reposta* (Conrad) Dall

s=10, n=25

1834 *Cytherea reposta* Conrad, Acad. Nat. Sci. Phil. Jour., 1st ser., 7:132.1903 *Macrocallista reposta* Conrad, Dall, Wagner Free Inst. Sci. Trans., 3(6):1252.1943 *Macrocallista reposta* (Conrad) Dall, Gardner, U.S.G.S. Paper 199-A: 123, pl. 19.**Life habit:** infaunal siphonate suspension feeder**Modern analog:** *Macrocallista maculata* Linné (Calico Clam). North Carolina to Brazil, shallow water. (Morris 1975) in sand (Rehder 1995), relatively common in mud or sand, in about 6 feet water depth (Humfrey 1975).**Subfamily GEMMINAE** Dall 1902**Genus *Gemma*** Deshayes 1853, Cat. Conch. Coll. Brit. Mus. 1:112.*Gemma magna* Dall

s=17, n=71

1903 *Gemma magna* Dall, Wagner Free Inst. Sci. Trans. 3(6): 1330.1943 *Gemma magna* Dall, Gardner, U.S.G.S. Paper 199-A: 135-137, pl. 19.1987 *Gemma magna* Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 158, pl 22.1993 *Gemma magna* Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 46.**Life habit:** infaunal siphonate suspension feeder**Modern analog:** *Gemma gemma* Totten (Amethyst Gem Clam). Nova Scotia to Florida and Texas, shallow water. (Morris 1975) and Bahamas, on sand or mud flats intertidally (Rehder 1995), common in most bays around New York, living in sand from just below the high water mark to the deeper waters offshore (Jacobson and Emerson 1971).**Family PETRICOLIDAE** Deshayes 1839**PETRICOLIDS****Genus *Petricola*** Lamarck 1801, Syst. Anim. s. Vert., 121.*Petricola grinelli* Olsson

s=4, n=4

- 1914 *Petricola (Claudiconcha) grinelli*, Olsson, . Bull. Am. Paleontology, 5(24): 16, pl. 4, figs 7-10.  
 1943 *Petricola (Rupellaria) grinelli* Olsson, Gardner, U.S.G.S. Paper 199-A: 117, pl. 15.

**Life habit:** mudboring suspension feeder

**Modern analog:** *Petricola pholadiformis* Lamarck (False Angel Wing). Prince Edward Island to Florida, Gulf of Mexico, intertidal, mudbanks - burrows into peat, mud, or stiff clay (Morris 1975). Lower intertidally (Rehder 1995), open-bay margins, inlet influenced areas, near shore in clay banks, infaunal (Andrews 1992), bores in clay, limestone, coral rock, tidal zone and shallow water, common south of Cape Cod boring in clay, Gulf of California to Texas (Crowder 1959), common in intertidal zone, Canada to Florida, Gulf of Mexico, West Indies, introduced to Washington and California (Romashko 1998).

**Genus *Pleiorytis*** Conrad 1862. Proc. Acad. nat. Sci. Philad. 14:286.

*Pleiorytis centenaria* (Conrad) Conrad

s=6, n=6

- 1833 *Pleiorytis centernaria* Conrad, Am. Jour. Sci., 1st. ser., 23:341.  
 1943 *Pleiorytis centenaria* (Conrad) Conrad, Gardner, U.S.G.S. Paper 199-A: 118, pl. 15.

**Life habit:** boring suspension feeder

**Modern analog:** *Petricola lapicida* (Gmelin) (Boring Petricola). Bermuda, south Florida, West Indies, bores into coral rock (Morris 1975), boring in coral rock in very shallow water (Andrews 1992, Rehder 1995), coral borer, 1-20 feet wherever coral is found (Humfrey 1975).

**Order MYOIDA** Stoliczka, 1870  
**Suborder MYINA** Stoliczka, 1870  
**Superfamily MYACEA** Lamarck, 1809  
**Family CORBULIDAE** Lamarck, 1818  
**Subfamily CORBULINAE** Gray 1823

**LITTLE BASKET (OR BOX) CLAMS**

**Genus *Corbula*** Bruguière 1797, Encycl. Meth. (Tabl. Vers.) 2: pl. 230; Lamarck 1799, Mem. Soc. H. N. Paris 89.

*Corbula retusa* Garder 1944  
s=95, n=487

- 1943 *Corbula (Carycorbula) conradi retusa* Gardner, U.S.G.S. Prof. Paper 199-A: 140, pl. 23.  
1993 *Corbula retusa* Gardner, Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 47-48

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Corbula contracta* Say (Contracted Corbula, Contracted Basket Clam or Box Clam). Massachusetts to West Indies, shallow water (Morris 1975) in sand or mud, has very short siphons (Rehder 1995). *Corbula caribaea* d'Orbigny (Caribbean Corbula), North Carolina, Florida, West Indies, Surinam to Brazil, muddy bottoms in bays and offshore (Andrews 1992), in shallow water in bays and Long Island Sound (Jacobson and Emerson 1971).

*Corbula inaequalis* Say 1824  
s=105, n=738

- 1993 *Corbula inaequalis* Say, Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 48.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Corbula contracta* Say (Contracted Corbula, Contracted Basket Clam or Box Clam). Massachusetts to West Indies, shallow water (Morris 1975) in sand or mud, has very short siphons (Rehder 1995). *Corbula caribaea* d'Orbigny (Caribbean Corbula), North Carolina, Florida, West Indies, Surinam to Brazil, muddy bottoms in bays and offshore (Andrews 1992), in shallow water in bays and Long Island Sound (Jacobson and Emerson 1971).

*Corbula cuneata* Say 1824  
s=84, n=630

- 1993 *Corbula cuneata* Say, Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 47.

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Corbula contracta* Say (Contracted Corbula, Contracted Basket Clam or Box Clam). Massachusetts to West Indies, shallow water (Morris 1975) in sand or mud, has very short siphons (Rehder 1995). *Corbula caribaea* d'Orbigny (Caribbean Corbula), North Carolina, Florida, West Indies, Surinam to Brazil, muddy bottoms in bays and offshore (Andrews 1992), in shallow water in bays and Long Island Sound (Jacobson and Emerson 1971).

**Superfamily HIATELLACEA** Gray, 1824  
**Family HIATELLIDAE** Gray, 1824

**HIATELLIDS**

**Genus Panopeaa** Menard 1807. Ann. Mus. Hist. Nat. Paris 9(50-51): 135.

*Panopeaa reflexa* Say 1824

s=34, n=74

1993 *Panopeaa reflexa* Say, Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 48.

**Life habit:** deep infaunal siphonate suspension feeder

**Modern analog:** *Panopeaa bitruncata* Conrad. North Carolina to Florida, moderately shallow water (Morris 1975), very uncommon (Romashko 1998) and *Panopeaa generosa* Gould (Geoduck Clam). Alaska to Baja California, moderately shallow water, up to 3 feet deep in mud (Morris 1962). *Panopeaa abrupta* (= *Panopeaa generosa*) low intertidal to subtidal bays, sloughs, estuaries (water depth to 360 feet), most abundant 30-60 feet water depth, below mean low tide mark, burrows in variety of substrates including soft mud, pea gravel, and stable mud or sand bottoms, up to 40 living specimens per square yard of seafloor in prime habitat (Gordon 1996).

**Genus Saxicava**

*Saxicava* sp.

s=16, n=23

**Life habit:** nestling epifaunal siphonate suspension feeder

**Modern analog:** *Hiatella artica* Linne (Arctic Saxicava). Arctic Ocean to the West Indies to Panama, byssally attached nestler in crevices and old bore holes in shallow water (Rehder 1995), inlet areas, hypersaline lagoons, offshore, boring infaunal, nestling and boring habits cause great shape and sculpture variation (Andrews 1992), common to depths of 50 m, bores into soft rock or nestles in crevices and pre-existing burrows (Fish and Fish 1996), sometimes found on holdfast of algae living offshore (Jacobson and Emerson 1971).

**Subclass ANOMALODESMATA** Dall, 1889  
**Order PHOLADOMYOIDA** Newell, 1965  
**Superfamily PANDORACEA** Rafinesque, 1815  
**Family PANDORIDAE** Rafinesque, 1815

**PANDORIDS**

**Genus *Pandora*** Bruguière 1797, Encycl. Meth. (Tabl. Vers.) 2: pl. 250.

***Pandora* sp.A**  
s=61, n=109

***Pandora* sp.B**  
s=2, n=2

***Pandora* sp.C**  
s=1, n=1

**Life habit:** shallow infaunal siphonate suspension feeder

**Modern analog:** *Pandora arenosa* Conrad (Sand Pandora). North Carolina to Florida, shallow water. (Morris 1975) in sand, shallow water (Rehder 1995). *Pandora trilineata* Say (Say's Pandora) Cape Hatteras to Florida, Texas, Inlet areas, open-sound and lagoon centers in clayey sediment (Andrews 1992).

**Family PERIPLOMATIDAE** Dall 1895

**Genus *Cochlodesma*** Couthouy 1839, Boston Jour. Nat. Hist. 2(2): 170.

***Cochlodesma antiqua*** Conrad 1873  
s=6, n=7

1873 Conrad, Verrill, Invertebrate animals of Vineyard Sound, U.S. Comm. Fish and Fisheries Rept.: 673.

1993 *Cochlodesma antiqua* Conrad (= *Cochlodesma emmonsii* of Ward and Blackwelder 1987) Campbell, Virginia Div. Min. Res. Publ. 127:, Virginia Div. Min. Res. Publ. 127: 51.

**Life habit:** unknown

**Modern analog:**

**Family THRACIIDAE** Stoliczka 1870

**THRACHIA**

**Genus *Thracia*** Leach 1824. in Blainville, Dict. Sci. nat., 32:347, 1825, Man. Malacol., 564, 1827, Man. Malacol. (planches), 600, pl. 76, fig. 7.

***Thracia conradi*** Couthouy 1832  
s=1, n=1

1839 *Thracia conradi* Couthouy, Boston Jour. Nat. Hist. 2:153, pl. 4, fig. 2.

1943 *Thracia conradi* Couthouy, Gardner, U.S.G.S. Paper 199-A: 43, pl. 10.

**Life habit:** deep infaunal suspension feeder

**Modern analog:** *Thracia conradi* Couthouy. Nova Scotia to Long Island, moderately deep water (Morris 1975) Labrador Sound to Long Island Sound in muddy sand, shallow water (13'-90'), burrows 5.5-10' deep (Rehder 1995).

**Class GASTROPODA Cuvier 1797**  
**Subclass PROSOBRANCHIA Milne Edwards 1848**

**ORDER ARCHAEGASTROPODA Thiele 1925**  
**Superfamily FISSURELLACEA Fleming 1822**  
**Family FISSURELLIDAE Fleming 1822**

**KEYHOLE LIMPETS**

*Diodora catelliformis* Rogers and Rogers 1837  
s=14, n=16

1993 *Diodora catelliformis* Rogers and Rogers. Campbell, Virginia Div. Min. Res. 127: 53.

**Life habit:** epifaunal mobile grazer

**Modern analog:** *Diodora cayennensis* Lamarack (Cayenne Keyhole Limpet, Little Key Hole Limpet), Maryland to Brazil, shallow water to intertidal (Morris 1975), on and among rocks (Rehder 1995), intertidal to moderately deep water, attached epifaunally mainly on undersides of rocks, jetties (Andrews 1992).

*Diodora redimicula* (Say)  
s=7, n=7

1948 *Diodora redimicula* (Say). Gardner, U.S.G.S Prof. Paper 199-B: 182, pl. 24, fig. 23, 24.

1993 *Diodora redimicula* (Say). Campbell, Virginia Div. Min. Res. 127: 53.

**Life habit:** epifaunal mobile grazer

**Modern analog:** *Diodora cayennensis* Lamarack (Cayenne Keyhole Limpet, Little Key Hole Limpet), Maryland to Brazil, shallow water to intertidal (Morris 1975), on and among rocks (Rehder 1995), intertidal to moderately deep water, attached epifaunally mainly on undersides of rocks, jetties (Andrews 1992).

**Superfamily TROCHIACEA Rafinesque 1815**  
**Family TROCHIDAE Rafinesque 1815**

**TOP SHELLS**

**Genus** *Calliostoma* Swainson 1840. Treatise on Malacology:218, 219, 351.

*Calliostoma mitchelli* (Conrad)  
s=32, n=52

1948 *Calliostoma mitchelli* (Conrad). Gardner. U.S.G.S. Prof. Paper 199-B: 184, pl. 26, fig. 19, 23.

1993 *Calliostoma mitchelli* (Conrad). Campbell, Virginia Div. Min. Res. 127: 54-55.

*Calliostoma virginicum* (Conrad)  
s=18, n=22

1875 *Zizyphinus virginicus* Conrad. North Carolina Geol. Surv. Rept. 1: App. A, p. 22, fig. 4

1948 *Calliostoma virginicum* (Conrad). Gardner. U.S.G.S. Prof. Paper 199-B: 185, pl. 26, fig. 12.

1993 *Calliostoma virginicum* (Conrad). Campbell, Virginia Div. Min. Res. 127: 55-56.

**Life habit:** epifaunal mobile grazer

**Modern analog:** *Calliostoma pulchrum* C.B. Adams (Beautiful Top Shell). North Carolina to West Indies, moderately shallow water; or *Callistoma psyche* Dall. Cape Hatteras to Florida moderately deep water (Morris 1975) on rocks (Rehder 1995). Relatively common in 6-20 foot water under rocks in sandy areas (Humphrey 1975).

## ORDER MESOGASTROPODA

Superfamily CERITHIACEA Fleming 1822

Family TURRITELLIDAE Lamarck 1799.

## TURRET OR SCREW SHELLS

**Genus *Turritella*** Lamarck 1799. Soc. histoire nat. Paris Mem.: 74.***Turritella* sp.**

s=117, n=n/a

**Life habit:** shallow burrowing epifaunal suspension feeder**Modern analog:** *Turritella acropora* Dall. (Boring Turret Shell), North Carolina to West Indies, moderately shallow water (Morris 1975); dredged from moderately shallow water (Romashko 1998). *Turritella variegata* (Linne 1758) (Variegated Turret Shell) common in West Indies, in shallow water, on mud or sand, mainly in protected area (Humphrey 1975).

## Family VERMICULARIDAE

## WORM SHELLS

**Genus *Serpulorbis******Serpulorbis granifera*** (Say 1824)

s=12, n=n/a

1824 *Serpulorbis graniforma* Say 1824. Jour. Acad. Nat. Sci. 4(2): 154, pl. 8, fig. 4.1993 *Serpulorbis graniforma* Say. Campbell, Virginia Div. Min. Res. 127: 58.**Life habit:** epifaunal suspension feeder**Modern analog:** *Vermicularia spirata* Phillipi (West Indian Worm Shells, Common Worm Shell). Massachusetts to West Indies, shallow water, often found with sponges or other colonial marine animals (Rehder 1995), intertidal, attached to rocks, in mud, in bays (Andrews 1992). *Serpulorbis riisei* Morch (Riise's Worm Shell) commonly found attached to solid objects in shallow water (Humphrey 1975).

Superfamily EPITONIACEA Berry 1910

Family EPITONIIDAE Berry 1910

WENTLETRAPS  
(Spiral Staircases)**Genus *Epitonium*** Röding 1798. Mus. Boltenianum (2):91.***Epitonium* sp.**

s=1, n=1

1993 Campbell, Virginia Div. Min. Res. 127: 66-67.

**Life habit:** vagrant epifaunal scavenger/predator**Modern analog:** *Epitonium novangliae* Couthouy (Couthouy's Wentletrap, New England Wentletrap). Virginia, West Indies, south to Brazil, moderately shallow water (Morris 1975) on sand or gravel (Rehder 1995). Relatively common in sand and under rocks, at about 25 feet, also dredged from deep water (Humphrey 1975), epifaunal offshore, common in beach drift (Andrews 1995).

**Superfamily CREPIDULACEA (=CALYPTRAECEA)  
Family CREPIDULIDAE**

**CUP AND SAUCER SNAILS**

**Genus *Crucibulum*** Schumacher 1817.

*Crucibulum grandis* Say 1884

s=14, n=38

1824 *Calyptera grandis* Say 1824. Jour. Acad. Nat. Sci. Phil.: 130. pl. 7, fig. 6.

1993 *Crucibulum grandis* Say, Campbell, Virginia Div. Min. Res. 127: 70.

*Crucibulum leanum* Campbell 1993

s=36, n=65

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Crucibulum auricula* (Gmelin) (West Indian Cup and Saucer Shell), South Florida to West Indies, moderately shallow water (Morris 1975) attached to rocks or other shells in 3-20 feet (Humfrey 1975).. *Crucibulum striatum* (Striate Cup and Saucer) Southern Canada to Florida, on rocks and dead shells in water 15-1000' (Rehder 1995).

1993 *Crucibulum leanum* Campbell, Virginia Div. Min. Res. 127: 70.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Crucibulum auricula* (Gmelin) (West Indian Cup and Saucer Shell), South Florida to West Indies, moderately shallow water (Morris 1975) attached to rocks or other shells in 3-20 feet (Humfrey 1975).. *Crucibulum striatum* (Striate Cup and Saucer) Southern Canada to Florida, on rocks and dead shells in water 15-1000' (Rehder 1995).

*Crucibulum scutellum* Wood 1828

s=24, n=51

1993 *Crucibulum scutellum* Wood, Campbell, Virginia Div. Min. Res. 127: 70.

**Life habit:** epifaunal suspension feeder

**Modern analog:** *Crucibulum auricula* (Gmelin) (West Indian Cup and Saucer Shell), South Florida to West Indies, moderately shallow water (Morris 1975) attached to rocks or other shells in 3-20 feet (Humfrey 1975).. *Crucibulum striatum* (Striate Cup and Saucer) Southern Canada to Florida, on rocks and dead shells in water 15-1000' (Rehder 1995).

**SLIPPER SNAILS  
(Boat Shells)**

**Genus *Crepidula*** Lamarck 1799.

*Crepidula costata* (Morton 1830)

s=112, n=1445

1791 *Patella aculeata* Gmelin, Olsson and Harbinson, Systema naturae per regna tria natura. Editio decimo tertia, aucta, reformata 1(6):3693.

1953 *Crepidula (Bostrycapulus) aculeata* (Gmelin), Acad. Nat. Sci. Phil. Mono 5:280.

1987 *Crepidula aculeata* (Gmelin) Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 171-172, pl 37.

1993 *Crepidula aculeata* (Gmelin), Campbell, Virginia Div. Min. Res. 127: 71.

*Crepidula adunca* Sowerby 1825

s=1, n=1

1993 *Crepidula adunca* Sowerby, Campbell, Virginia Div. Min. Res. 127: 71.**Life habit:** epifaunal suspension feeder**Modern analog:** *Crepidula aculeata* (Gmelin) (Spiny Slipper Snail, Thorny Slipper). North Carolina to West Indies, Pacific, shallow water. (Morris 1975), on rocks and other hard objects in shallow water (Rehder 1995). Attached to hard substrata in 1-16 feet water depth (Humfrey 1975).*Crepidula plana* Say 1822

s=26, n=64

1822 *Crepidula plana* Say, Jour. Acad. Nat. Sci. Phil. 1st ser. 5(2):226.1987 *Crepidula plana* Say, Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 172, pl 38.1993 *Crepidula plana* Say, Campbell, Virginia Div. Min. Res. 127: 71.**Life habit:** attached epifaunal suspension feeder**Modern analog:** *Crepidula plana* Say (Eastern White Slipper Snail, Flatboat Shell, Flat Slipper Shell). North Carolina to West Indies, Pacific, shallow water. (Morris 1975), on rocks and other hard objects in shallow water (Rehder 1995) in 3-50 feet water depth attached to shells, particularly the opercula of *Fasciolaria* and *Murex* (Humfrey 1975), epifaunal, intertidal to moderate depths (Andrews 1995). Living within the apertures of dead shells, shallow to offshore, Maine to Texas (Crowder 1959).*Crepidula* sp.A

s=3, n=5

**Life habit:** attached epifaunal suspension feeder**Modern analog:** *Crepidula plana* Say (Eastern White Slipper Snail). North Carolina to West Indies, Pacific, shallow water. (Morris 1975), on rocks and other hard objects in shallow water (Rehder 1995) in 3-50 feet water depth attached to shells, particularly the opercula of *Fasciolaria* and *Murex* (Humfrey 1975), epifaunal, intertidal to moderate depths (Andrews 1995).

## Superfamily NATICACEA Gray 1840

## Family NATICIDAE Gray 1840

## MOON SNAILS

Genus *Lunatia* Gray 1847*Lunatia heros* (Say)

s=45, n=97

1822 *Natica heros* Say, Jour. Acad. Nat. Sci. Phil. 1st ser. 5(2): 248.1974 *Lunatia heros* (Say), Abbott, American Seashells: 155, fig. 1690.1987 *Lunatia heros* (Say), Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 172, pl 38.**Life habit:** infaunal (burrowing) boring scavenger/predator**Modern analog:** *Lunatia heros* (Say) (Common Northern Moon Snail). Gulf of St. Lawrence to North Carolina, sand and mud flats (Morris 1975). Shallow bays and estuaries, Cape Cod to

Gulf of Mexico (MacGinitie and MacGinitie 1949). Sandy regions, shallow to offshore, Labrador to Virginia (Crowder 1959).

**Genus *Polinices*** Montfort 1810

***Polinices duplicata*** (Say)

s=5, n=7

1822 *Natica heros* Say, Jour. Acad. Nat. Sci. Phil. 1st ser. 5(2): 247.

1892 *Polinices (Natica) heros* (Say), Dall, Trans. Wagner Free Inst.: 368.

1987 *Polinices duplicata* (Say), Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 172, pl 38.

**Life habit:** infaunal (burrowing) boring scavenger/predator

**Modern analog:** *Polinices duplicatus* (Say) (Callused Moon Snail, Double Moon Snail), Massachusetts to Florida, and the Gulf of Mexico, sand and mud flats (Morris 1975). infaunal, shallow water of Gulf of Mexico and bays (Andrews 1995), commonly found on sand and mud flats (Romashko 1998).

**Superfamily TONNACEA**

**Family FICIDAE** Meek 1864

**TUN SHELLS**

**Genus *Ficus*** Röding 1798, Mus. Boltenianum(2):148.

***Ficus papyratia*** Smith

s=4, n=5

1907 *Ficus papyratia caloosahatchiensis* Smith, Acad. Nat. Sci. Phil. Proc: 212.

1948 *Ficus papyratia caloosahatchiensis* (Smith), Gardner, U.S.G.S Prof. Paper 199-B: 127-218, pl. 29.

**Life habit:** vagrant epifaunal scavenger/predator (echinoderms)

**Modern analog:** *Ficus communis* Röding 1798 (Common Fig Shell). North Carolina to Gulf of Mexico, moderately deep water (Morris 1975) in sand (Rehder 1995).

**Superfamily ARCHITECTONICACEA**

**Family ARCHITECTONICIDAE** Gray 1850

**SUNDIALS**

**Genus *Architectonica*** Röding 1798. Mus. Boltenianum (2):78. = *Solarium* Lamarck 1799. Soc. histoire. nat. Paris Mem.:74.

***Architectonica nupera*** (Conrad) Conrad

s=3, n=3

**Life habit:** unknown, probably predatory/scavenger

**Modern analog:** *Architectonica nobilis* Röding (Common American Sundial). North Carolina to Texas, West Indies, shallow water (Morris 1975) in sand (Rehder 1995), in sand at 35 feet at Montenegro Bay, Kingston harbor and Ocho Rios (Humfrey 1975), along shore with sea pansies, epifaunal (Andrews 1992), fairly common in shallow water in sand (Romashko 1998).

**Order NEOGASTROPODA**  
**Superfamily MURICEA Rafinesque 1815**

**Family COLUMBELLIDAE Swainson 1845**

**DOVE SHELLS**

**Genus *Anachis*** Adams & Adams, Genera Recent Mollusca 1:184.

***Anachis* sp.**

s=3, n=3

1993 Campbell, Virginia Div. Min. Res. 127: 77.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Anachis avara* (Say) (Greedy Dove Snail). New Jersey to Florida, shallow water (Morris 1975) on eel grass near low-tide line, on stones in deeper water (Rehder 1995), in bays and Long Island Sound, frequently inhabited by smaller hermit crabs (Jacobson and Emerson 1971).

**Genus *Mitrella*** Risso 1826, Histoire naturelle des principales productions de l'Europe meridionale 4:247.

***Mitrella gardnerae*** Olsson and Harbinson

s=9, n=13

1953 *Anachis (Alia) gardnerae* Olsson & Harbinson 1953. Acad. Nat. Sci. Phil. Mono. 8: 236, pl. 38.

1987 *Anchis gardnerae* Olsson and Harbinson, Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 174, pl 40.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Mitrella albella* C.B. Adams. South Florida, moderately shallow water (Morris 1975). *Mitrella ocellata* (White-spotted Dove Shell), southeast Florida to Northern Brazil, under rocks, in sand or mud at low tide line (Rehder 1995). *Mitrella lunata* Say (Lunar Dove Snail) frequently found on clumps of seaweed (Jacobson and Emerson 1971).

**Family NASSARIIDAE Iredale 1916**

**DOG WHELKS**

**Genus *Nassarius*** Dumeril 1806

***Nassarius* sp.**

s=4, n=5

1993 Campbell, Virginia Div. Min. Res. 127: 82-83.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Nassarius albus* (Say) (Variable Dog Whelk, White Basket Shell). North Carolina to West Indies, shallow water (Morris 1975) on sand (Rehder 1995) common in water 1-60 feet deep, often partially buried in mud or sand (Humfrey 1975).

**Genus *Uzita*** Adams & Adams 1853. General Recent Mollusca 1:20.

***Uzita* sp.**

s=1, n=1

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Nassarius albus* (Say) (Variable Dog Whelk, White Basket Shell). North Carolina to West Indies, shallow water (Morris 1975) on sand (Rehder 1995) common in water 1-60 feet deep, often partially buried in mud or sand (Humfrey 1975).

### Family FASCIOLARIDAE

#### SPINDLE SHELLS

**Genus *Fusinus*** Rafinesque 1815

*Fusinus exilis* (Conrad)

s=33, n=58

1832 *Fusinus exilis* Conrad, Fossil shells of the Tertiary formation of North America 2(1): 17, pl. 3.

1948 *Fusinus exilis* (Conrad), Gardner, U.S.G.S Prof. Paper 199-B: 255, pl. 32.

1993 *Fusinus exilis* (Conrad), Campbell, Virginia Div. Min. Res. 127: 85-86.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Fusinus ambustus* (Gould), Gulf of California, moderately shallow water (Morris 1966)

### Family MELONGENIDAE Gill 1867

#### CROWN CONCHS

**Genus *Busycon*** Röding 1798

*Busycon* sp.

s=7, n=9

1993 Campbell, Virginia Div. Min. Res. 127: 81-82.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Busycon canaliculatum* (Linnaeus) (Channeled Whelk) Massachusetts to Florida, shallow water (Morris 1975) on sand or mud (Rehder 1995), in shallow water in Long Island Sound, and in bays (Jacobson and Emerson 1971), found in sand and mud in intertidal zone to just below low-tide line, Massachusetts to northern Florida, introduced to California (Romashko 1998).

**Genus *Lyrosoma*** Röding 1798.

*Lyrosoma sulcosa* Conrad 1830

s=3, n=4

1993 *Lyrosoma sulcosa* Conrad, Campbell, Virginia Div. Min. Res. 127: 83.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:**

### Family BUCCINIDAE

#### WHELKS

**Genus *Ptychosalpinx*** Gill 1867, Am. Jour. Conch. 3:153.

*Ptychosalpinx multirugata* (Conrad)

s=12, n=22

- 1841 *Buccinum multirugata* Conrad, Am. Jour. Sci., 1st Ser. 41:345.  
 1867 *Ptychosalpinx multirugata* (Conrad), Gill, Am. Jour. Conchology 3:154.  
 1948 *Ptychosalpinx multirugata* (Conrad) Conrad, Gardner, U.S.G.S Prof. Paper 199-B: 235, pl. 32.  
 1993 *Ptychosalpinx multirugata* (Conrad), Campbell, Virginia Div. Min. Res. 127: 80-81.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Ptychosalpinx globulus* (Dall 1829), Florida Straits, Bahamas (check distribution pattern in literature).

### Superfamily MURICACEA Rafinesque 1815

#### Family THAIDIDAE

**Genus *Ecphora*** Conrad 1843.

*Ecphora quadricostata* Say 1824

s=27, n=29

- 1993 *Ecphora quadricostata* Say, Campbell, Virginia Div. Min. Res. 127: 81.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:**

#### Family MURICIDAE

#### MUREX SHELLS

**Genus *Eupleura*** Adams & Adams 1853, Gen. Rec. Moll. 1:107.

*Eupleura caudata* (Say)

s=27, n=33

- 1822 *Rancellia caudata* Say, Acad. Nat. Sci. Phil. Jour., 1st series(2): 236.  
 1858 *Eupleura caudata* (Say), Holmes, Post-Pleiocene fossils of South Carolina: 62, pl. 10, fig. 3.  
 1948 *Eupleura caudata* (Say), Gardner, U.S.G.S Prof. Paper 199-B: 222, pl. 29.  
 1987 *Eupleura caudata* (Say), Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 174, pl. 39.  
 1993 *Eupleura caudata* (Say), Campbell, Virginia Div. Min. Res. 127: 76.

**Life habit:** vagrant epifaunal boring scavenger/predator

**Modern analog:** *Eupleura caudata* (Say) (Thick Lipped Oyster Drill). Massachusetts to Florida, shallow water (Morris 1975) on and near oyster beds (Rehder 1995), among oysters (Jacobson and Emerson 1971), lives near low tide level, and in shallow water, Cape Cod to west Florida (Crowder 1959).

**Genus *Scalaspira*** Conrad 1862.

*Scalaspira strumosa* Conrad 1830

s=5, n=6

- 1993 *Scalaspira strumosa* Conrad, Campbell, Virginia Div. Min. Res. 127: 74.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Urosalpinx perrugata* (Conrad), West Florida, shallow water, (Morris 1975). Prefer to prey on oysters (Rogers 1937) *Urosalpinx cinerea* (Atlantic Oyster Drill). Nova Scotia, intertidally among oyster bed rubble (Rehder 1995), found wherever oysters are common (Jacobson and Emerson 1971).

**Genus *Urosalpinx*** Stimpson 1865, Am. Jour. Conch. 1:58.

*Urosalpinx stimpsoni* Gardner

s=15, n=20

1948 *Urosalpinx stimpsoni* Gardner, U.S.G.S Prof. Paper 199-B: 224, pl. 31.

1987 *Urosalpinx stimpsoni* Gardner, Ward and Blackwelder, Smith. Contr. to Paleobiology 61: 173, pl 39.

*Urosalpinx trossula* (Conrad)

s=4, n=4

1832 *Fusus trossulus* Conrad, Fossils of the Tertiary formation of North America: 18, pl. 3, fig. 5.

1890 *Urosalpinx trossula* (Conrad), Dall, Wagner Free Inst. Sci. Trans. 3(1):148, pl. 7, fig. 12.

1948 *Urosalpinx trossula* (Conrad) Gardner, U.S.G.S Prof. Paper 199-B: 223, pl. 31.

1993 *Urosalpinx trossula* (Conrad), Campbell, Virginia Div. Min. Res. 127: 76.

*Urosalpinx* sp.

(=*Fusinus rappahockensis* of Gardner 1948)

s=2, n=2

**Life habit:** vagrant epifaunal boring scavenger/predator

**Modern analog:** *Urosalpinx perrugata* (Conrad), West Florida, shallow water, (Morris 1975). Prefer to prey on oysters (Rogers 1937) *Urosalpinx cinerea* (Atlantic Oyster Drill). Nova Scotia, intertidally among oyster bed rubble (Rehder 1995), found wherever oysters are common (Jacobson and Emerson 1971), very common on oyster beds, Massachusetts Bay to Florida, Pacific Coast (Crowder 1959).

**Genus *Pterorhytis*** Fischer 1884.

*Pterorhytis umbrifera*

s=7, n=7

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Pterorhytis nuttalli*

**Family OLIVIDAE** Latreille 1825

## OLIVE SHELLS

**Genus *Oliva*** Martyn 1786. Universal conchologist 3: pl. 111.

*Oliva canaliculata* H.C. Lea 1843

s=5, n=10

1843 *Oliva canaliculata* H.C. Lea 1843. Amer. Phil. Soc.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Oliva reticularis* Lamarck (Netted Olive), common in 2-40 feet of water depth, in mud and sand (Humfrey 1975). *Oliva sayana* Ravenel (Lettered Olive), North Carolina to

Florida, Gulf of Mexico, West Indies, Brazil, infaunal in inlets and offshore (Andrews 1992), in shallow to moderately shallow water, in sand (Romashko 1998).

**Family MARGINELLIDAE** Fleming 1828

**MARGIN SHELLS**

**Genus *Marginella*** Lamarck 1799. Soc. histoire nat. Paris mem.: 70.

***Marginella denticulata*** Conrad

s=1, n=1

1948 *Marginella (Serrata) denticulata* Conrad?, Gardner, U.S.G.S Prof. Paper 199-B: 275-276, pl. 38.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Marginella denitculata* Conrad, North Carolina to West Indies, shallow water (Morris 1975).

**Genus *Dentimargo*** Cossman 1899.

***Dentimargo aureocincta*** Stearns 1872

s=1, n=2

1993 *Dentimargo aureocincta* Stearns, Campbell, Virginia Div. Min. Res. 127: 90.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:**

**Family TURRIDAE** H. & A. Adams

**TURRID SHELLS**

**Genus *Pyrgospira*** McLean 1971.

***Pyrgospira tricatendaria*** (Conrad 1834)

s=6, n=8

1993 *Pyrgospira tricatendaria* (Conrad), Campbell, Virginia Div. Min. Res. 127: 96.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Pyrgospira ostreacum* (Oyster Turrid). North Carolina to the Virgin Islands, on sand and rubble in shallow water, produces toxin to kill prey (Rehder 1995).

**Genus "*Drillia* "**

***Drillia* sp. A**

s=19, n=24

***Drillia* sp. B**

s=13, n=16

1948 Gardner, U.S.G.S Prof. Paper 199-B: 265, pl. 37. (description of genus)

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Inodrilla aepynota* (Dall), North Carolina to Florida, moderately deep water or *Drilla cydia* Bartsch, Florida to West Indies, moderately shallow water (Morris 1975), uncommon, occurs in about 25 feet of water depth (Humfrey 1975).

**Superfamily TERE BriACEA**  
**Family TERE BriDAE** H.&A. Adams

**Genus *Terebra*** Bruguiere 1789. Encyclopedie methodology, Histoires naturelle des vers 1:XV.  
*Terebra carolinensis* Conrad  
s=2, n=3

1841 Conrad 1841. Am. Jour. Sci. 1st ser., 41:345.

1993 *Terebra carolinensis* Conrad, Campbell, Virginia Div. Min. Res. 127: 93 (Morris 1975).

***Terebra* sp. A**  
s=11, n=14

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Terebra protexta* Conrad (Fine-Ribbed Auger), North Carolina to West Indies, Texas, moderately shallow water (Morris 1975), uncommon in 10 feet in mud or sand, dredged from 800+ feet (Humfrey 1975), infaunal, offshore in 1.8-90 meters water depth, inlet areas (Andrews 1995), inhabits shallow warm seas (Rogers 1937). *Terebra dislocata* Say (Common American Auger). Virginia to the West Indies, in sand low tide to shallow water (Rehder 1995), inlet areas, infaunal, can be found under bulges of sand at low tides (Andrews 1992), in sand in shallow water (Romashko 1998).

**Superfamily VOLUTACEA** Rafinesque 1815  
**Family VOLUTIDAE** Rafinesque 1815

**VOLUTES**

**Genus *Scaphella*** Swainson 1832. Zoological illustrations, 2nd series 2: pl. 87.  
*Scaphella* sp.  
s=1, n=1

1993 Campbell, Virginia Div. Min. Res. 127: 87.

**Life habit:** vagrant epifaunal scavenger/predator

**Modern analog:** *Scaphella gouldiana* (Dall), North Carolina to West Indies, deep water (Morris 1975), uncommon, found in deep water (Romashko 1998).

**Superfamily CANCELLARIACEA**  
**Family CANCELLARIIDAE** Forbes and Hanley 1853

**NUTMEG SHELLS**

**Genus *Cancellaria*** Lamarck 1799. Soc. histoire nat. Paris mem.: 71.  
*Cancellaria rotunda* Dall  
s=1, n=1

1892 *Cancellaria conradiana* Dall var. *rotunda* Dall. Wagner Free Inst. Trans. 3(2): 224.

1948 *Cancellaria rotunda* Dall, Gardner, U.S.G.S Prof. Paper 199-B: 264, pl. 38.

1993 *Cancellaria rotunda* Dall, Campbell, Virginia Div. Min. Res. 127: 89.

**Life habit:** vagrant epifaunal [grazer (Rogers 1937)] scavenger/predator

**Modern analog:** *Cancellaria reticulata* Linnaeus (Common Nutmeg). North Carolina to Florida, shallow water (Morris 1975) and Texas to Brazil, in sand among turtle grass (Rehder 1995) in 15-

30 feet of water depth (Humfrey 1975), found in shallow water, Cape Hatteras to Florida (Crowder 1959), common in sand (Romashko 1998).

**SUBCLASS HETEROBRANCHIATA**  
**ORDER PYRAMIDELLOIDA** Gray 1840  
**Superfamily PYRAMIDELLACEA** Gray 1840  
**Family PYRAMIDELLIDAE** Gray 1840

**Genus *Longchaeus*** Morch 1875.  
***Longchaeus suturalis*** H.C. Lea 1843  
s=4, n=4

1993 *Longchaeus suturalis* H.C. Lea, Campbell, Virginia Div. Min. Res. 127: 100.

**Life habit:** unknown, possibly parasitic

**Modern analog:** *Pyramidella candida* (Morch), North Carolina to Florida, Gulf of Mexico, West Indies, moderately deep water (Morris 1975). *Pyramidella (Longchaeus) crenulata* (Holmes 1859) (Notched Pyram), South Carolina to Florida, epifaunal ectoparasitic in inlets and hypersaline lagoons (Andrews 1992), *Pyramidella dolobrata* Lamarck (Giant Atlantic Pyram), common, found in sand and shallow water, Florida to West Indies (Romashko 1998).

**Class SCAPHOPODA**  
**Order DENTALIOIDA**  
**Family DENTALIIDAE**

**TUSK SHELLS**

**Genus *Dentalium*** Lamarck 1758  
***Dentalium* sp.**  
s=99, n=n/a

**Life habit:** infaunal predator

**Modern analog:** *Dentalium texasianum* Philippi 1849 (Texas Tusk), North Carolina to Yucatan, Texas, open-bay margins, inlets, channel in stiff clay sediment, semi-infaunal (Andrews 1992).

**Class POLYPLACOPHORA**

**CHITONS**

**Unidentified chiton** (One or two chiton species)  
s=6, n=n/a

**Life habit:** epifaunal grazer

**Modern analog:** n/a

**Phylum BRACHIOPODA**  
**Class INARTICULATA**  
**Order ACROTRETIDA**

**Unidentified acrotreterid**  
s=19, n=n/a

**Life habit:** attached epifaunal filter feeder  
**Modern analog:** n/a

### Order LINGULIDA

**Unidentified lingulid** (probably *Glottidia*)  
 s=9, n=n/a

**Life habit:** shallow infaunal filter feeder  
**Modern analog:** n/a

## Phylum BRYOZOA

**Unidentified bryozoans** (cheilostome and cyclostome bryozoan species)

s=106, n=n/a

**Life habit:** attached epifaunal suspension feeder  
**Modern analog:** n/a

## Phylum ARTHROPODA

### Superclass CRUSTACEA

### Class CIPPIPIDIA

#### Order Thoracia

#### Suborder Balanomorpha

**Unidentified barnacle species**  
 s=145, n=n/a

**Life habit:** attached epifaunal suspension feeder  
**Modern analog:** n/a

### Class MALACOSTRACA

#### Order DECAPODA

**Unidentified decapods** (mostly claws)  
 s=145, n=n/a

**Life habit:** vagrant epifaunal scavenger/predator  
**Modern analog:** n/a

## Phylum ECHINODERMATA

### Class ECHINOIDEA

**Unidentified echinoids** (mostly spines and plater)  
 s=145, n=n/a

**Life habit:** full marine, various life habits  
**Modern analog:** n/a

## Systematic Summary

### Phylum Mollusca

#### Class Bivalvia

##### Subclass Palaeotaxodonta

##### Order Nuculoidea

##### Superfamily Nuculacea

##### Family Nuculidae (Nut Clams)

##### Genus *Nucula*

*Nucula proxima* (s=33, n=53)

##### Superfamily Nuculanacea

##### Family Nuculanidae (Elongate Nut Clams)

##### Genus *Yoldia*

*Yoldia laevis* (s=94, n=874)

##### Subclass Pteriomorpha

##### Order Arcoida

##### Superfamily Arcacea

##### Family Arcidae (Ark Shells)

##### Genus *Scapharca*

*Scapharca scalariais* (s=2, n=2)

##### Family Noetiidae

##### Genus *Noetia*

*Noetia incile* (s=54, n=192)

##### Genus *Striarca*

*Striarca centenaria* (s=6, n=52)

##### Superfamily Limopsacea

##### Family Glycymerididae (Bittersweets)

##### Genus *Glycymeris*

*Glycymeris americana* (s=43, n=167)

*Glycymeris subovata* (s=2, n=2)

##### Order Mytiloida

##### Superfamily Mytilacea

##### Family Mytilidae (Mussels)

##### Genus *Modiolus*

*Modiolus* sp. (s=25, n=28)

##### Genus *Mytilus*

*Mytilus* sp. (s=2, n=2)

##### Order Ostreioda

##### Superfamily Ostreoidea

##### Family Gryphaeidae

##### Genus *Pycnodonte*

*Pycnodonte* sp. (s=23, n=201)

##### Family Ostreidae

##### Genus *Ostrea*

*Ostrea sculpturata* (s=124, n=1760)

*Ostrea raveneliana* (s=17, n=40)

##### Order Pterioda

##### Superfamily Pectinacea

##### Family Pectinidae (Scallops)

##### Genus *Carolinapecten*

*Carolinapecten eboreus* (s=59, n=167)

##### Genus *Chesapecten*

*Chesapecten jeffersonius* (s=2, n=5)

- Chesapecten madisonius* (s=111, n=538)
- Chesapecten septenarius* (s=1, n=1)
- Family Plicatulidae (Kitten's Paws)
  - Genus *Plicatula*
    - Plicatula marginata* (s=50, n=700)
- Superfamily Anomiacea
  - Family Anomiidae (Jingle Shells)
    - Genus *Anomia*
      - Anomia simplex* (s=11, n=16)
    - Genus *Pododesmus*
      - Pododesmus* sp. (s=2, n=4)
- Subclass Heterodonta
  - Order Veneroida
    - Superfamily Lucinacea
      - Family Lucinidae (Lucine Shells)
        - Genus *Stewartia*
          - Stewartia anodonta* (s=14, n=24)
        - Genus *Parvilucina*
          - Parvilucina multilineatus* (s=90, n=365)
        - Genus *Divalinga*
          - Divalinga quadrisulcata* (s=5, n=6)
        - Genus *Lucinisca*
          - Lucinisca cribrarius* (s=67, n=278)
        - Genus *Ctena*
          - Ctena speciosa* (s=10, s=20)
      - Family Ungulinidae (Diplodon Shells)
        - Genus *Diplodonta*
          - Diplodonta leana* (s=9, n=15)
          - Diplodonta* sp.A (s=4, n=9)
          - Diplodonta* sp.B (s=3, n=3)
    - Superfamily Chamacea
      - Family Chamidae (Jewel Box Clams)
        - Genus *Chama*
          - Chama congregata* (s=75, n=3224)
        - Genus *Pseudochama*
          - Pseudochama corticosa* (s=9, n=14)
    - Superfamily Galeommatacea
      - Family Kelliidae (Coin Clams)
        - Genus *Bornia*
          - Bornia triangula* (s=5, n=6)
    - Superfamily Carditacea
      - Family Carditidae(Cardita Clams)
        - Genus *Carditamera*
          - Carditamera arata* (s=16, n=42)
        - Genus *Pteromeris*
          - Pteromeris perplana* (s=7, n=14)
        - Genus *Cyclocardia*
          - Cyclocardia granulata* (s=66, n=1241)
    - Superfamily Cardiacea
      - Family Cardiidae (Cockles)
        - Genus *Chesacardium*
          - Chesacardium acutilaqueatum*(s=31, n=51)
    - Superfamily Mactracea
      - Family Mactridae(Surf Clams)

- Genus *Mulinia*
  - Mulinia congesta* (s=117, n=11,282)
- Genus *Leptmaetra*
  - Leptmaetra dolomus* (s=10, n=17)
- Genus *Hemimaetra*
  - Hemimaetra duplinensis* (s=21, n=29)
- Genus *Spisula*
  - Spisula similis* (s=13, n=19)
  - Spisula* sp.A (s=1, n=1)
  - Spisula* sp.B (s=1, n=1)
- Superfamily Solenacea
  - Family Cultellidae
    - Genus *Ensis*
      - Ensis directus* (s=84, n=182)
- Superfamily Astartacea
  - Family Astartidae(Astartids)
    - Genus *Astarte*
      - Astarte undulata* (s=82, n=454)
      - Astarte concentrica* (s=24, n=149)
- Superfamily Crassatellacea
  - Family Crassatellidae (Crassatellids)
    - Genus *Marvacrassatella*
      - Marvacrassatella undulata* (s=82, n=38)
    - Genus *Crassinella*
      - Crassinella lunulata* (s=25, n=38)
- Superfamily Tellinacea
  - Family Tellinidae (Tellins)
    - Genus *Macoma*
      - Macoma virginiana* (s=72, n=181)
  - Family Semelidae (Semele)
    - Genus *Abra*
      - Abra subreflexa* (s=66, n=268)
    - Genus *Semele*
      - Semele* sp.A (s=91, n=248)
    - Genus *Cumingia*
      - Cumingia tellinoides* (s=1, n=1)
- Superfamily Glossacea
  - Family Glossidae
    - Genus *Glossus*
      - Glossus* sp. (s=1, n=1)
- Superfamily Veneracea
  - Family Veneridae(Venus Clams)
    - Genus *Chione*
      - Chione cribraria* (s=5, n=7)
      - Chione grus* (s=1, n=1)
    - Genus *Mercenaria*
      - Mercenaria campechiensis* (s=46, n=228)
    - Genus *Dosinia*
      - Dosinia acetabulum* (s=103, n=846)
    - Genus *Pitar*
      - Pitar sayana* (s=12, n=44)
      - Pitar* sp. B (s=2, n=6)
    - Genus *Macrocallista*
      - Macrocallista reposta* (s=10, n=25)

- Genus *Gemma*
  - Gemma magna* (s=17, n=71)
- Family Petricolidae (Petricolids)
  - Genus *Petricola*
    - Petricola grinelli* (s=4, n=4)
  - Genus *Pleiorytis*
    - Pleiorytis centenaria* (s=6, n=6)
- Order Myoida
  - Suborder Myina
    - Superfamily Myacea
      - Family Corbulidae (Little Basket (Or Box) Clams)
        - Genus *Corbula*
          - Corbula retusa* (s=95, n=487)
          - Corbula inaequalis* (s=105, n=738)
          - Corbula cuneata* Say 1824 (s=84, n=630)
      - Superfamily Hiatellacea
        - Family Hiatellidae (Hiatellids)
          - Genus *Panopeaa*
            - Panopeaa reflexa* (s=34, n=74)
          - Genus *Saxicava*
            - Saxicava* sp. (s=16, n=23)
  - Subclass Anomalodesmata
    - Order Pholadomyoida
      - Superfamily Pandoracea
        - Family Pandoridae (Pandorids)
          - Genus *Pandora*
            - Pandora* sp.A (s=61, n=109)
            - Pandora* sp.B (s=2, n=2)
            - Pandora* sp.C (s=1, n=1)
        - Family Periplomatidae
          - Genus *Cochlodesma*
            - Cochlodesma antiqua* (s=6, n=7)
        - Family Thraciidae (Thrachia)
          - Genus *Thracia*
            - Thracia conradi* (s=1, n=1)
  - Class Gastropoda**
    - Subclass Prosobranchia
      - Order Archaeogastropoda
        - Superfamily Fissurellacea
          - Family Fissurellidae (Keyhole Limpets)
            - Genus *Diodora*
              - Diodora catelliformis* (s=14, n=16)
              - Diodora redimicula* (s=7, n=7)
          - Superfamily Trochiacea
            - Family Trochidae (Top Shells)
              - Genus *Calliostoma*
                - Calliostoma mitchelli* (s=32, n=52)
                - Calliostoma virginicum* (s=18, n=22)
          - Order Mesogastropoda
            - Superfamily Cerithiacea
              - Family Turritellidae (Turret or Screw Shells)
                - Genus *Turritella*
                  - Turritella* sp. (s=117, n=n/a)
              - Family Vermicularidae (Worm Shells)

- Genus *Serpulorbis*
  - Serpulorbis graniforma* (s=12, n=n/a)
- Superfamily Epitoniacea
  - Family Epitoniidae (Wentletraps)
    - Genus *Epitonium*
      - Epitonium* sp. (s=1, n=1)
- Superfamily Crepidulacea
  - Family Crepidulidae (Cup And Saucer Snails)
    - Genus *Crucibulum* Schumacher 1817.
      - Crucibulum grandis* (s=14, n=38)
      - Crucibulum leanum* (s=36, n=65)
      - Crucibulum scutellum* (s=24, n=51)
    - Genus *Crepidula* Lamarck 1799.
      - Crepidula costata* (s=112, n=1445)
      - Crepidula adunca* (s=1, n=1)
      - Crepidula plana* (s=26, n=64)
      - Crepidula* sp.A (s=3, n=5)
- Superfamily Naticacea
  - Family Naticidae (Moon Snails)
    - Genus *Lunatia*
      - Lunatia heros* (s=45, n=97)
    - Genus *Polinices*
      - Polinices duplicata* (s=5, n=7)
- Superfamily Tonnacea
  - Family Ficidae (Tun Shells)
    - Genus *Ficus*
      - Ficus papyratia* (s=4, n=5)
- Superfamily Architectonicacea
  - Family Architectonicidae (Sundials)
    - Genus *Architectonica*
      - Architectonica nupera* (s=3, n=3)
- Order Neogastropoda
  - Superfamily Muriacea
    - Family Columbelloidea (Dove Shells)
      - Genus *Anachis*
        - Anachis* sp. (s=3, n=3)
      - Genus *Mitrella*
        - Mitrella gardnerae* (s=9, n=13)
    - Family Nassariidae (Dog Whelks)
      - Genus *Nassarius*
        - Nassarius* sp. (s=4, n=5)
      - Genus *Uzita*
        - Uzita* sp. (s=1, n=1)
    - Family Fasciolaridae (Spindle Shells)
      - Genus *Fusinus*
        - Fusinus exilis* (s=33, n=58)
    - Family Melongenidae (Crown Conchs)
      - Genus *Busycon*
        - Busycon* sp. (s=7, n=9)
      - Genus *Lyrosoma*
        - Lyrosoma sulcosa* (s=3, n=4)
    - Family Buccinidae (Whelks)
      - Genus *Ptychosalpinx*
        - Ptychosalpinx multirugata* (s=12, n=22)

- Superfamily Muricacea
  - Family Thaididae
    - Genus *Ecphora*
      - Ecphora quadricostata* (s=27, n=29)
  - Family Muricidae (Murex Shells)
    - Genus *Eupleura*
      - Eupleura caudata* (s=27, n=33)
    - Genus *Scalaspira*
      - Scalaspira strumosa* (s=5, n=6)
    - Genus *Urosalpinx*
      - Urosalpinx stimpsoni* (s=15, n=20)
      - Urosalpinx trossula* (s=4, n=4)
      - Urosalpinx* sp.(s=2, n=2)
    - Genus *Pterorhytis*
      - Pterorhytis umbrifera* (s=7, n=7)
  - Family Olividae (Olive Shells)
    - Genus *Oliva*
      - Oliva canaliculata* (s=5, n=10)
  - Family Marginellidae (Margin Shells)
    - Genus *Marginella*
      - Marginella denticulata* (s=1, n=1)
    - Genus *Dentimargo*
      - Dentimargo aureocincta* (s=1, n=2)
  - Family Turridae (Turrid Shells)
    - Genus *Pyrgospira*
      - Pyrgospira tricateneria* (s=6, n=8)
    - Genus "*Drillia* "
      - Drillia* sp. A (s=19, n=24)
      - Drillia* sp. B (s=13, n=16)
- Superfamily Terebriacea
  - Family Terebridae
    - Genus *Terebra*
      - Terebra carolinensis* (s=2, n=3)
      - Terebra* sp. A (s=11, n=14)
- Superfamily Volutacea
  - Family Volutidae (Volutes)
    - Genus *Scaphella*
      - Scaphella* sp. (s=1, n=1)
- Superfamily Cancellariacea
  - Family Cancellariidae (Nutmeg Shells)
    - Genus *Cancellaria* (s=1, n=1)
- Subclass Heterobranchiata
  - Order Pyramidelloida
    - Superfamily Pyramidellacea
      - Family Pyramidellidae
        - Genus *Longchaeus*
          - Longchaeus suturalis* (s=4, n=4)
- Class Scaphopoda**
  - Order Dentalioida
    - Family Dentaliidae
      - Genus *Dentalium*
        - Dentalium* sp. (s=99, n=n/a)
- Class Polyplacophora**
  - Order Dentalioida

1 or 2 species of unidentified chiton (s=6, n=n/a)

**Phylum Brachiopoda**

**Class Inarticulata**

Order Acrotretida

unidentified acrotretid (s=19, n=n/a)

Order Lingulida

unidentified lingulid (s=9, n=n/a)

**Phylum Bryozoa**

unidentified cheilostome and cyclostomes (s=106, n=n/a)

**Phylum Arthropoda**

**Superclass Crustacea**

**Class Cirripedia**

Order Thoracia

Suborder Balanomorpha

unidentified barnacle species (s=145, n=n/a)

**Class Malacostraca**

Order Decapoda

Suborder Balanomorpha

unidentified decapod species, mostly claws (s=145, n=n/a)

**Phylum Echinodermata**

**Class Echinoidea**

unidentified echinoid species, mostly spines and plates (s=145, n=n/a)

## APPENDIX C: DIVERSITY MEASUREMENTS

### Species Richness Indices

Most simple species richness indices are ratios of species recognized per specimens counted, although few use raw numbers. Most incorporate some form of logarithmic transformation of the number of specimens, and thus contain an implicit assumption of a non-linear relationship between species present and specimens counted.

Margalef's Diversity Index:

$$DMg = (S-1)/\ln(N)$$

is one of the simpler measures of species richness (Magurran 1988). It is simply the total number of species (S) divided by the natural log of the total number of specimens.

### Log Series Species Abundance Models

When displaying species abundance data, neo-ecologists frequently use a power function for the number of specimens within each species. A log base of 2 is popular, where each bin contains double the number of specimens than the next lower bin

(Magurran 1988). Log base 3 was popular in the 1930s through the 1950s, but has since gone out of style (Williams 1964, Magurran 1988). My data is probably best viewed in log base 10 (Fig. C.1), in which the bins, or "octaves", contain species organized as such

- Octave I** - "rare" 1-10 individuals per species
- Octave II** - "uncommon" 11-100 individuals per species
- Octave III** - "common" 101-1000 individuals per species
- Octave IV** - "very common" 1001-10,000 individuals per species

The pattern of distribution within these octaves fits that expected for the log series model (namely that the majority of species will be found in the first octave) better than the log normal distribution (Magurran 1988). When the rank-abundance data is plotted for the Yorktown species, the distribution and abundance of Yorktown species also seems to fit the log series model better than the other popular models, although perhaps the log normal model would fit as well. The log series model is rather robust, and the properties of the diversity measure  $\alpha$  is such that it is a good measure of diversity even for distributions that do not strictly fit the log series distribution (Magurran 1988).

Various mathematical models have been used to examine the underlying distribution of species within ecologic systems to gain a fuller understanding of diversity. One of the first successful models was that of Fisher et al (1943) in which they fit large empirical data sets to log series functions. The method was expanded and clarified by Williams (1964). The log series distribution of a sample with  $n$  species takes the form:

$$\alpha x, \alpha x^2/2, \alpha x^3/3, \dots \alpha x^n/n$$

$\alpha x$  = number of individuals represented by 1 individual

$\alpha x^2/2$  = number of individuals represented by 2 individuals, etc.

The term  $\alpha$  is therefore a measure of diversity related to the number of species and their abundance by the following relationship:

$$\alpha = N(1-x)/x$$

The value  $x$  can be determined mathematically for any given distribution, or estimated by using the procedure outlined in Williams (1964). Estimation seems to be the preferred procedure in the ecologic literature (Magurran 1988, Stiling 1999).

### **Shannon-Weiner Index**

The Shannon-Weiner index:

$$H' = -[\sum[(p_i)\ln(p_i)]]$$

was derived not from biological data, but from information theory, and contains the assumption that the specimens are sampled from an "infinitely large" underlying population (Magurran 1988). As written, it also contains the troubling assumption that all species present are sampled. The degree of error increases with the proportion of species which are not sampled.

### **Simpson's Dominance Index**

Simpson's dominance index:

$$\begin{aligned} D &= \sum[(N_i(N_i-1)/N(N-1))] \\ &= \sum[(p_i)(N_i-1)/(N-1)] \end{aligned}$$

is one of several diversity indices that does not include an assumption about the underlying distribution of species abundances, and is therefore a "non-parametric" index (Magurran 1988). It is essentially the sum of the squared proportional abundances of the various species.

### **Berger-Parker Dominance Index**

At first glance, the Berger-Parker dominance index:

$$d = N_{\max}/N$$

appears to be an overly simplistic diversity/dominance measurement. It is simply the proportional abundance of the most abundant species in a sample. The index is completely independent of the

number of species, and while influenced by sample size, it is directly related only to the relative abundance of the most abundant species. Less diverse samples should have higher dominance values than more diverse samples, as long as the change in diversity is not the result of an increased incorporation of very low abundance species. While disdained by some (e.g., Stiling 1999) as too simplistic, for my data, the Berger-Parker dominance index correlates very well with the Simpson dominance index, and the two dominance measurements therefore appear to give at least consistent results.

### Burwell's Bay (BWB)

$N_{\max}/N$

#### Analysis of Variance Table

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | .39548       | .39548       | 32.73103  |
| Within groups  | 9   | .10874       | .01208       | p = .0003 |
| Total          | 10  | .50423       |              |           |

Model II estimate of between component variance = .07029

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| transition | 6      | .41848 | .08309     | .03392      |
| MBPT       | 5      | .79928 | .13622     | .06092      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | -.3808      | .15059*      | 32.73103*       | 5.7211     |

### Shannon H'

#### Analysis of Variance Table

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | 3.30702      | 3.30702      | 5.63622   |
| Within groups  | 9   | 5.2807       | .58674       | p = .0416 |
| Total          | 10  | 8.58772      |              |           |

Model II estimate of between component variance = .49872

| Group:     | Count: | Mean:   | Std. Dev.: | Std. Error: |
|------------|--------|---------|------------|-------------|
| transition | 6      | 2.25841 | .51061     | .20846      |
| MBPT       | 5      | 1.15724 | .99713     | .44593      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | 1.10117     | 1.04939*     | 5.63622*        | 2.37407    |

### Simpson D

#### Analysis of Variance Table

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | .96915       | .96915       | 54.2567   |
| Within groups  | 9   | .16076       | .01786       | p = .0001 |
| Total          | 10  | 1.12992      |              |           |

Model II estimate of between component variance = .1744

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| transition | 6      | .85902 | .03962     | .01617      |
| MBPT       | 5      | .2629  | .19552     | .08744      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | .59612      | .1831*       | 54.2567*        | 7.36591    |

**William's  $\alpha$   
Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | 316.74828    | 316.74828    | 364.3051  |
| Within groups  | 9   | 7.82513      | .86946       | p = .0001 |
| Total          | 10  | 324.57341    |              |           |

Model II estimate of between component variance = 57.91112

| Group:     | Count: | Mean:    | Std. Dev.: | Std. Error: |
|------------|--------|----------|------------|-------------|
| transition | 6      | 12.97283 | .92598     | .37803      |
| MBPT       | 5      | 2.19596  | .94046     | .42059      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | 10.77688    | 1.27743*     | 364.3051*       | 19.08678   |

**Day's Point (DYP)**N<sub>max</sub>/N**Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:  |
|----------------|-----|--------------|--------------|----------|
| Between groups | 1   | .01036       | .01036       | .51415   |
| Within groups  | 64  | 1.28908      | .02014       | p = .476 |
| Total          | 65  | 1.29943      |              |          |

Model II estimate of between component variance = -.00036

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| transition | 19     | .35715 | .13829     | .03173      |
| MBPT       | 47     | .32948 | .14332     | .02091      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | .02767      | .07709       | .51415          | .71704     |

**Shannon H'****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | 5.26577      | 5.26577      | 13.86521  |
| Within groups  | 8   | 3.03826      | .37978       | p = .0058 |
| Total          | 9   | 8.30403      |              |           |

Model II estimate of between component variance = 1.01791

| Group:     | Count: | Mean:   | Std. Dev.: | Std. Error: |
|------------|--------|---------|------------|-------------|
| transition | 4      | 2.59584 | .17703     | .08852      |
| MBPT       | 6      | 1.1146  | .76736     | .31328      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | 1.48124     | .91744*      | 13.86521*       | 3.7236     |

**Simpson D****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | .02442       | .02442       | 1.52216   |
| Within groups  | 64  | 1.02665      | .01604       | p = .2218 |
| Total          | 65  | 1.05107      |              |           |

Model II estimate of between component variance = .00031

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| transition | 19     | .76454 | .12015     | .02756      |
| MBPT       | 47     | .80702 | .12911     | .01883      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | -.04248     | .06879       | 1.52216         | 1.23376    |

**William's  $\alpha$** **Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 1   | 59.47824     | 59.47824     | 10.17012  |
| Within groups  | 64  | 374.29334    | 5.84833      | p = .0022 |
| Total          | 65  | 433.77157    |              |           |

Model II estimate of between component variance = 1.98184

| Group:     | Count: | Mean:   | Std. Dev.: | Std. Error: |
|------------|--------|---------|------------|-------------|
| transition | 19     | 6.71259 | 1.9678     | .45144      |
| MBPT       | 47     | 8.80924 | 2.57325    | .37535      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| T vs. M     | -2.09665    | 1.31354*     | 10.17012*       | 3.18906    |

**Kingsmill (KGM)**N<sub>max</sub>/N**Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | .0091        | .00455       | .22559    |
| Within groups  | 9   | .18149       | .02017       | p = .8024 |
| Total          | 11  | .19059       |              |           |

Model II estimate of between component variance = -.00416

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| RBPT       | 6      | .4831  | .16206     | .06616      |
| transition | 3      | .4381  | .12627     | .0729       |
| MBPT       | 3      | .42073 | .09561     | .0552       |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. T     | .04499      | .22718       | .1004           | .4481      |
| C vs. M     | .06237      | .22718       | .1929           | .62114     |
| T vs. M     | .01737      | .26232       | .01123          | .14985     |

**Shannon H'****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | .09672       | .04836       | .26165    |
| Within groups  | 9   | 1.66351      | .18483       | p = .7754 |
| Total          | 11  | 1.76023      |              |           |

Model II estimate of between component variance = -.03639

| Group:     | Count: | Mean:   | Std. Dev.: | Std. Error: |
|------------|--------|---------|------------|-------------|
| RBPT       | 6      | 2.06638 | .54315     | .22174      |
| transition | 3      | 1.96901 | .266       | .15358      |
| MBPT       | 3      | 2.21983 | .15322     | .08846      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. T     | .09737      | .68778       | .05129          | .32029     |
| C vs. M     | -.15345     | .68778       | .12739          | .50477     |
| T vs. M     | -.25082     | .79418       | .25527          | .71452     |

**William's  $\alpha$** **Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | 1.46853      | .73426       | .17173    |
| Within groups  | 9   | 38.48066     | 4.27563      | p = .8449 |
| Total          | 11  | 39.94918     |              |           |

Model II estimate of between component variance = -.94436

| Group:     | Count: | Mean:   | Std. Dev.: | Std. Error: |
|------------|--------|---------|------------|-------------|
| RBPT       | 6      | 6.22418 | 2.11885    | .86502      |
| transition | 3      | 6.26504 | 1.82242    | 1.05218     |

|             |             |              |                 |            |
|-------------|-------------|--------------|-----------------|------------|
| MBPT        | 3           | 7.04477      | 2.16687         | 1.25104    |
| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
| C vs. T     | -.04087     | 3.30796      | .00039          | .02795     |
| C vs. M     | -.82059     | 3.30796      | .15749          | .56123     |
| T vs. M     | -.77972     | 3.8197       | .10665          | .46183     |

**Lieutenant's Run (LTR)** $N_{\max}/N$ **Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:  |
|----------------|-----|--------------|--------------|----------|
| Between groups | 2   | .03157       | .01579       | 1.98831  |
| Within groups  | 25  | .19849       | .00794       | p = .158 |
| Total          | 27  | .23006       |              |          |

Model II estimate of between component variance = .00116

| Group: | Count: | Mean:  | Std. Dev.: | Std. Error: |
|--------|--------|--------|------------|-------------|
| RBPT   | 9      | .30551 | .09107     | .03036      |
| MBPT   | 1      | .35714 | •          | •           |
| other  | 18     | .24331 | .08816     | .02078      |

| Comparison:    | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|----------------|-------------|--------------|-----------------|------------|
| C vs. M        | -.05163     | .19346       | .15109          | .54972     |
| RBPT vs. other | .0622       | .07493       | 1.46196         | 1.70995    |
| MBPT vs. other | .11383      | .18856       | .7731           | 1.24346    |

**Shannon H'****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | .69187       | .34593       | 2.95504   |
| Within groups  | 25  | 2.92664      | .11707       | p = .0705 |
| Total          | 27  | 3.6185       |              |           |

Model II estimate of between component variance = .03391

| Group: | Count: | Mean:   | Std. Dev.: | Std. Error: |
|--------|--------|---------|------------|-------------|
| RBPT   | 9      | 2.42775 | .31412     | .10471      |
| MBPT   | 1      | 2.35268 | •          | •           |
| other  | 18     | 2.7471  | .35457     | .08357      |

| Comparison:    | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|----------------|-------------|--------------|-----------------|------------|
| C vs. M        | .07507      | .74286       | .02166          | .20815     |
| RBPT vs. other | -.31935     | .28771*      | 2.61351         | 2.28627    |
| MBPT vs. other | -.39442     | .72405       | .62947          | 1.12202    |

**Simpson D****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | .02268       | .01134       | 2.6229    |
| Within groups  | 25  | .10806       | .00432       | p = .0925 |
| Total          | 27  | .13074       |              |           |

Model II estimate of between component variance = .00104

| Group: | Count: | Mean:  | Std. Dev.: | Std. Error: |
|--------|--------|--------|------------|-------------|
| RBPT   | 9      | .811   | .06625     | .02208      |
| MBPT   | 1      | .79284 | •          | •           |
| other  | 18     | .86819 | .06551     | .01544      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. M     | .01816      | .14275       | .03435          | .26211     |
| C vs.O      | -.05718     | .05529*      | 2.2695          | 2.13049    |
| M vs. O     | -.07535     | .13913       | .62216          | 1.11549    |

**William's  $\alpha$   
Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | 56.07474     | 28.03737     | 2.71003   |
| Within groups  | 25  | 258.64492    | 10.3458      | p = .0861 |
| Total          | 27  | 314.71966    |              |           |

Model II estimate of between component variance = 2.62097

| Group: | Count: | Mean:    | Std. Dev.: | Std. Error: |
|--------|--------|----------|------------|-------------|
| RBPT   | 9      | 8.81272  | 3.60598    | 1.20199     |
| MBPT   | 1      | 8.28426  | •          | •           |
| other  | 18     | 11.70667 | 3.01584    | .71084      |

| Comparison:    | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|----------------|-------------|--------------|-----------------|------------|
| C vs. M        | .52845      | 6.98355      | .01215          | .15586     |
| RBPT vs. other | -2.89396    | 2.70472*     | 2.42852         | 2.20387    |
| MBPT vs. other | -3.42241    | 6.80672      | .53628          | 1.03564    |

**Nottoway River (NWR)** $N_{\max}/N$ **Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | .85449       | .42724       | 96.59057  |
| Within groups  | 24  | .10616       | .00442       | p = .0001 |
| Total          | 26  | .96065       |              |           |

Model II estimate of between component variance = .05096

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| RBPT       | 11     | .40728 | .04206     | .01268      |
| transition | 12     | .35716 | .06879     | .01986      |
| MBPT       | 4      | .87766 | .11018     | .05509      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. T     | .05012      | .0573        | 1.62996         | 1.80552    |
| C vs. M     | -.47038     | .08015*      | 73.36415*       | 12.11315   |
| T vs. M     | -.5205      | .07926*      | 91.87462*       | 13.55541   |

**Shannon H'****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | 9.9914       | 4.9957       | 115.38972 |
| Within groups  | 24  | 1.03906      | .04329       | p = .0001 |
| Total          | 26  | 11.03046     |              |           |

Model II estimate of between component variance = .59694

| Group:     | Count: | Mean:   | Std. Dev.: | Std. Error: |
|------------|--------|---------|------------|-------------|
| RBPT       | 11     | 2.40149 | .12665     | .03819      |
| transition | 12     | 2.30696 | .16211     | .0468       |
| MBPT       | 4      | .64419  | .44331     | .22166      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. T     | .09452      | .17928       | .59219          | 1.08829    |
| C vs. M     | 1.7573      | .25077*      | 104.61508*      | 14.46479   |
| T vs. M     | 1.66278     | .24796*      | 95.79225*       | 13.8414    |

**Simpson****Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | 1.36346      | .68173       | 151.36993 |
| Within groups  | 24  | .10809       | .0045        | p = .0001 |
| Total          | 26  | 1.47155      |              |           |

Model II estimate of between component variance = .08163

| Group:     | Count: | Mean:  | Std. Dev.: | Std. Error: |
|------------|--------|--------|------------|-------------|
| RBPT       | 11     | .73972 | .037       | .01116      |
| transition | 12     | .83671 | .05167     | .01492      |
| MBPT       | 4      | .17041 | .14723     | .07362      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. T     | -.09699     | .05782*      | 5.99434*        | 3.46247    |
| C vs. M     | .56931      | .08088*      | 105.55069*      | 14.52933   |
| T vs. M     | .66631      | .07998*      | 147.86612*      | 17.19687   |

**William's  $\alpha$   
Analysis of Variance Table**

| Source:        | DF: | Sum Squares: | Mean Square: | F-test:   |
|----------------|-----|--------------|--------------|-----------|
| Between groups | 2   | 136.69486    | 68.34743     | 17.68692  |
| Within groups  | 24  | 92.74302     | 3.86429      | p = .0001 |
| Total          | 26  | 229.43788    |              |           |

Model II estimate of between component variance = 7.77252

| Group:     | Count: | Mean:    | Std. Dev.: | Std. Error: |
|------------|--------|----------|------------|-------------|
| RBPT       | 11     | 10.44327 | 2.28972    | .69038      |
| transition | 12     | 9.4821   | 1.8286     | .52787      |
| MBPT       | 4      | 3.73205  | 1.08526    | .54263      |

| Comparison: | Mean Diff.: | Fisher PLSD: | Scheffe F-test: | Dunnett t: |
|-------------|-------------|--------------|-----------------|------------|
| C vs. T     | .96118      | 1.69374      | .68605          | 1.17136    |
| C vs. M     | 6.71123     | 2.36913*     | 17.09485*       | 5.8472     |
| T vs. M     | 5.75005     | 2.34266*     | 12.83407*       | 5.06637    |



## APPENDIX D Supplementary Tables

### Bivalve Color Scheme:

**Paleotaxondonta**  
**Pteriomorpha and Oysters**  
**Pterioda**  
**Heterdonta**  
**Myoida**  
**Anomalodesmata**

### Bivalve Life Habits

| taxon                              | habitat             | feeding type                |
|------------------------------------|---------------------|-----------------------------|
| <i>Nucula proxima</i>              | infaunal            | deposit feeder              |
| <i>Yoldia laevis</i>               | infaunal            | siphonate deposit feeder    |
| <i>Scapharca scalariais</i>        | epibyssate          | suspension feeder           |
| <i>Noetia incile</i>               | nestling epibyssate | suspension feeder           |
| <i>Striarca centenaria</i>         | nestling epibyssate | suspension feeder           |
| <i>Glycymeris americana</i>        | shallow infaunal    | suspension feeder           |
| <i>Glycymeris subovata</i>         | shallow infaunal    | suspension feeder           |
| <i>Modiolus sp.</i>                | epibyssate          | suspension feeder           |
| <i>Mytilus sp.</i>                 | epibyssate          | suspension feeder           |
| <i>Pycnodonte sp.</i>              | epibyssate          | suspension feeder           |
| <i>Ostrea sculpturata</i>          | cementing epifaunal | suspension feeder           |
| <i>Ostrea raveliniana</i>          | cementing epifaunal | suspension feeder           |
| <i>Carolinapecten eboreus</i>      | epibyssate          | suspension feeder           |
| <i>Chesapeake septenarius</i>      | epibyssate          | suspension feeder           |
| <i>Chesapeake madisonius</i>       | epibyssate          | suspension feeder           |
| <i>Plicatula marginata</i>         | cementing epifaunal | suspension feeder           |
| <i>Anomia simplex</i>              | epibyssate          | suspension feeder           |
| <i>Pododesmus sp.</i>              | epibyssate          | suspension feeder           |
| <i>Stewartia anodonta</i>          | medium infaunal     | lucinid suspension feeder   |
| <i>Parvilucina multilineatus</i>   | shallow infaunal    | lucinid suspension feeder   |
| <i>Divalinga quadrisulcata</i>     | medium infaunal     | lucinid suspension feeder   |
| <i>Luciniscia cribrarius</i>       | shallow infaunal    | lucinid suspension feeder   |
| <i>Ctena speciosa</i>              | shallow infaunal    | lucinid suspension feeder   |
| <i>Diplodonta leana</i>            | nestling            | suspension feeder           |
| <i>Diplodonta sp. A</i>            | nestling            | suspension feeder           |
| <i>Diplodonta sp. B</i>            | nestling            | suspension feeder           |
| <i>Chama congregata</i>            | cementing epifaunal | suspension feeder           |
| <i>Pseudochama corticosa</i>       | cementing epifaunal | suspension feeder           |
| <i>Bornia triangula</i>            | nestling            | suspension feeder           |
| <i>Carditermera arata</i>          | nestling epibyssate | suspension feeder           |
| <i>Pteromeris perplana</i>         | shallow infaunal    | suspension feeder           |
| <i>Cyclocardia granulata</i>       | shallow infaunal    | suspension feeder           |
| <i>Chesacardium aquelitactreum</i> | shallow infaunal    | suspension feeder           |
| <i>Mulina congesta</i>             | shallow infaunal    | siphonate suspension feeder |
| <i>Leptomacra dolombus</i>         | shallow infaunal    | siphonate suspension feeder |
| <i>Hemimacra duplinensis</i>       | shallow infaunal    | siphonate suspension feeder |

|                                  |                    |                             |
|----------------------------------|--------------------|-----------------------------|
| <i>Spisula similis</i>           | shallow infaunal   | siphonate suspension feeder |
| <i>Spisula sp. A</i>             | shallow infaunal   | siphonate suspension feeder |
| <i>Spisula sp. B</i>             | shallow infaunal   | siphonate suspension feeder |
| <i>Ensis directus</i>            | deep infaunal      | siphonate suspension feeder |
| <i>Astarte undulata</i>          | shallow infaunal   | suspension feeder           |
| <i>Astarte concentrica</i>       | shallow infaunal   | suspension feeder           |
| <i>Marvacrassatella undulata</i> | medium infaunal    | suspension feeder           |
| <i>Crassinella lunulata</i>      | shallow infaunal   | suspension feeder           |
| <i>Macoma virginiana</i>         | shallow infaunal   | deposit feeder              |
| <i>Abra subreflexa</i>           | shallow infaunal   | siphonate suspension feeder |
| <i>Semele sp.A</i>               | shallow infaunal   | siphonate suspension feeder |
| <i>Cumingia tellenoides</i>      | shallow infaunal   | siphonate suspension feeder |
| <i>Glossus sp.</i>               | shallow infaunal   | siphonate suspension feeder |
| <i>Chione cribrarius</i>         | shallow infaunal   | siphonate suspension feeder |
| <i>Chione grus</i>               | shallow infaunal   | siphonate suspension feeder |
| <i>Mercenaria campechiensis</i>  | medium infaunal    | siphonate suspension feeder |
| <i>Dosinia acetabulum</i>        | medium infaunal    | siphonate suspension feeder |
| <i>Pitar sayana</i>              | shallow infaunal   | siphonate suspension feeder |
| <i>Pitar sp. B</i>               | shallow infaunal   | siphonate suspension feeder |
| <i>Macrocallista reposta</i>     | medium infaunal    | siphonate suspension feeder |
| <i>Gemma magna</i>               | shallow infaunal   | siphonate suspension feeder |
| <i>Petricola grinelli</i>        | mud boring         | suspension feeder           |
| <i>Pleiorythis centenaria</i>    | rock boring        | suspension feeder           |
| <i>Corbula retusa</i>            | shallow infaunal   | siphonate suspension feeder |
| <i>Corbula inaequalis</i>        | shallow infaunal   | siphonate suspension feeder |
| <i>Corbula cuneata</i>           | shallow infaunal   | siphonate suspension feeder |
| <i>Panopea reflexa</i>           | deep infaunal      | siphonate suspension feeder |
| <i>Saxicava sp.</i>              | nestling epifaunal | siphonate suspension feeder |
| <i>Pandora sp. A</i>             | shallow infaunal   | siphonate suspension feeder |
| <i>Pandora sp. B</i>             | shallow infaunal   | siphonate suspension feeder |
| <i>Pandora sp. C</i>             | shallow infaunal   | siphonate suspension feeder |
| <i>Cochlodesma antiqua</i>       | ?                  | ?                           |
| <i>Thracia conradi</i>           | deep infaunal      | siphonate suspension feeder |

## Bivalve Life Habits

| <b>Taxon</b>                      | <b>Habitat</b>      | <b>Feeding Type</b>         |
|-----------------------------------|---------------------|-----------------------------|
| <i>Nucula proxima</i>             | infaunal            | deposit feeder              |
| <i>Yoldia laevis</i>              | infaunal            | siphonate deposit feeder    |
| <i>Macoma virginiana</i>          | shallow infaunal    | tellinid deposit feeder     |
| <i>Macoma cookei</i>              | shallow infaunal    | tellinid deposit feeder     |
| <i>Divalinga quadrisulcata</i>    | medium infaunal     | lucinid suspension feeder   |
| <i>Stewartia anodonta</i>         | medium infaunal     | lucinid suspension feeder   |
| <i>Ctena speciosa</i>             | shallow infaunal    | lucinid suspension feeder   |
| <i>Lucinisca cribrarius</i>       | shallow infaunal    | lucinid suspension feeder   |
| <i>Parvilucina multilineatus</i>  | shallow infaunal    | lucinid suspension feeder   |
| <i>Abra subreflexa</i>            | shallow infaunal    | siphonate suspension feeder |
| <i>Chione cribrarius</i>          | shallow infaunal    | siphonate suspension feeder |
| <i>Chione grus</i>                | shallow infaunal    | siphonate suspension feeder |
| <i>Corbula cuneata</i>            | shallow infaunal    | siphonate suspension feeder |
| <i>Corbula inaequalis</i>         | shallow infaunal    | siphonate suspension feeder |
| <i>Corbula retusa</i>             | shallow infaunal    | siphonate suspension feeder |
| <i>Cumingia tellenoides</i>       | shallow infaunal    | siphonate suspension feeder |
| <i>Gemma magna</i>                | shallow infaunal    | siphonate suspension feeder |
| <i>Hemimacra duplinensis</i>      | shallow infaunal    | siphonate suspension feeder |
| <i>Leptomacra dolomus</i>         | shallow infaunal    | siphonate suspension feeder |
| <i>Mulina congesta</i>            | shallow infaunal    | siphonate suspension feeder |
| <i>Pandora</i> sp. A              | shallow infaunal    | siphonate suspension feeder |
| <i>Pandora</i> sp. B              | shallow infaunal    | siphonate suspension feeder |
| <i>Pandora</i> sp. C              | shallow infaunal    | siphonate suspension feeder |
| <i>Pitar sayana</i>               | shallow infaunal    | siphonate suspension feeder |
| <i>Pitar</i> sp. B                | shallow infaunal    | siphonate suspension feeder |
| <i>Semele similis</i>             | shallow infaunal    | siphonate suspension feeder |
| <i>Semele</i> sp. A               | shallow infaunal    | siphonate suspension feeder |
| <i>Semele</i> sp. B               | shallow infaunal    | siphonate suspension feeder |
| <i>Spisula similis</i>            | shallow infaunal    | siphonate suspension feeder |
| <i>Spisula</i> sp. A              | shallow infaunal    | siphonate suspension feeder |
| <i>Spisula</i> sp. B              | shallow infaunal    | siphonate suspension feeder |
| <i>Petricola grinelli</i>         | mud boring          | siphonate suspension feeder |
| <i>Dosinia acetabulum</i>         | medium infaunal     | siphonate suspension feeder |
| <i>Macrocallista reposta</i>      | medium infaunal     | siphonate suspension feeder |
| <i>Marcocrassatella undulata</i>  | medium infaunal     | siphonate suspension feeder |
| <i>Mercenaria campechiensis</i>   | medium infaunal     | siphonate suspension feeder |
| <i>Ensis directus</i>             | deep infaunal       | siphonate suspension feeder |
| <i>Panopea reflexa</i>            | deep infaunal       | siphonate suspension feeder |
| <i>Thracia conradi</i>            | deep infaunal       | siphonate suspension feeder |
| <i>Chama congregata</i>           | cementing epifaunal | suspension feeder           |
| <i>Ostrea raveliniana</i>         | cementing epifaunal | suspension feeder           |
| <i>Ostrea sculpturata</i>         | cementing epifaunal | suspension feeder           |
| <i>Plicatula marginata</i>        | cementing epifaunal | suspension feeder           |
| <i>Pseudochama corticosa</i>      | cementing epifaunal | suspension feeder           |
| <i>Anomia simplex</i>             | epibyssate          | suspension feeder           |
| <i>Carolinapecten eboreus</i>     | epibyssate          | suspension feeder           |
| <i>Chesapeakecten madisonius</i>  | epibyssate          | suspension feeder           |
| <i>Chesapeakecten septenarius</i> | epibyssate          | suspension feeder           |
| <i>Modiolus</i> sp. A             | epibyssate          | suspension feeder           |

|                                   |                     |                             |
|-----------------------------------|---------------------|-----------------------------|
| <i>Mytilus</i> sp. A              | epibyssate          | suspension feeder           |
| <i>Placopecten clintonius</i>     | epibyssate          | suspension feeder           |
| <i>Pycnodonte</i> sp.             | epibyssate          | suspension feeder           |
| <i>Scapharca scalariais</i>       | epibyssate          | suspension feeder           |
| <i>Saxicava</i> sp. A             | nestling epifaunal  | siphonate suspension feeder |
| <i>Bornia triangula</i>           | nestling            | suspension feeder           |
| <i>Diplodonta leana</i>           | nestling            | suspension feeder           |
| <i>Diplodonta</i> sp. A           | nestling            | suspension feeder           |
| <i>Diplodonta</i> sp. B           | nestling            | suspension feeder           |
| <i>Carditermera arata</i>         | nestling epibyssate | suspension feeder           |
| <i>Noetia incile</i>              | nestling epibyssate | suspension feeder           |
| <i>Striarca centenaria</i>        | nestling epibyssate | suspension feeder           |
| <i>Astarte concentrica</i>        | shallow infaunal    | suspension feeder           |
| <i>Astarte undulata</i>           | shallow infaunal    | suspension feeder           |
| <i>Chesacardium aquelatctreum</i> | shallow infaunal    | suspension feeder           |
| <i>Crassinella lunulata</i>       | shallow infaunal    | suspension feeder           |
| <i>Cyclocardia granulata</i>      | shallow infaunal    | suspension feeder           |
| <i>Glycymeris americana</i>       | shallow infaunal    | suspension feeder           |
| <i>Glycymeris subovata</i>        | shallow infaunal    | suspension feeder           |
| <i>Pteromeris perplana</i>        | shallow infaunal    | suspension feeder           |
| <i>Cochlodesma antiqua</i>        | ?                   | ?                           |
| <i>Pleiorythis centenaria</i>     | ?                   | ?                           |

### Bivalve Modern Analogs

| species                          | modern analog                   | water depth   | substrate  | habitat             | feeding type              |
|----------------------------------|---------------------------------|---|--|---------------------|---------------------------|
| <i>Nucula proxima</i>            | <i>Nucula proxima</i>           | sheltered subtidal  | mud  | infaunal            | deposit feeder            |
| <i>Yoldia laevis</i>             | <i>Yoldia limatula</i>          | shallow water (4-100')  | mud, muddy sand  | infaunal            | siphonate deposit feeder  |
| <i>Scapharca scalariais</i>      | <i>Anadara brasiliana</i>       | shallow water (0-30')   | gravelly bottoms, in sand                                    | epibyssate          | suspension feeder         |
| <i>Noetia incile</i>             | <i>Arca zebra</i>               | shallow water (0-20')   | rocks and coral colonies, nestled in shallow crevices        | nestling epibyssate | suspension feeder         |
| <i>Striarca centenaria</i>       | <i>Barbatia candida</i>         | shallow water (2-15')   | attached to stones or in crevices                            | nestling epibyssate | suspension feeder         |
| <i>Glycymeris americana</i>      | <i>Glycymeris americana</i>     | moderately shallow water  |  | shallow infaunal    | suspension feeder         |
| <i>Glycymeris subovata</i>       | <i>Glycymeris americana</i>     | moderately shallow water  |  | shallow infaunal    | suspension feeder         |
| <i>Modiolus</i> sp.              | <i>Modiolus americanus</i>      | moderately shallow water (1-18')                                  | sandy subtidal grass mats, also found in clean sand          | epibyssate          | suspension feeder         |
| <i>Mytilus</i> sp.               | <i>Mytilus edulis</i>           | intertidal  | prefers rubble, but can attach to any hard substrate         | epibyssate          | suspension feeder         |
| <i>Pycnodonte</i> sp.            |                                 |   |  | epibyssate          | suspension feeder         |
| <i>Ostrea sculpturata</i>        | <i>Crassostrea virginica</i>    | usually abundant only in areas of low salinity (10-40')           | hard or soft substrates                                      | cementing epifaunal | suspension feeder         |
| <i>Ostrea raveneliana</i>        |                                 |   |  | cementing epifaunal | suspension feeder         |
| <i>Carolinapecten eboreus</i>    | <i>Argopecten gibbus</i>        | shallow water (5-300')  | on sand  | epibyssate          | suspension feeder         |
| <i>Chesapecten septenarius</i>   | <i>Pecten ziczac</i>            | protected or calm water (3-200')                                  | nestles in soft sand or mud, strong swimmer                  | epibyssate          | suspension feeder         |
| <i>Chesapecten madisonius</i>    | <i>Pecten ziczac</i>            | protected or calm water (3-200')                                  | nestles in soft sand or mud, strong swimmer                  | epibyssate          | suspension feeder         |
| <i>Plicatula marginata</i>       | <i>Plicatula gibbosa</i>        | intertidal/ shallow water (0-300')                                | attached to rocks or shells                                  | cementing epifaunal | suspension feeder         |
| <i>Anomia simplex</i>            | <i>Anomia simplex</i>           | restricted to shallow subtidal with moderate current flow (0-30') | Attached to pebbles, cobbles, shell debris on firm substrata | epibyssate          | suspension feeder         |
| <i>Pododesmus</i> sp.            | <i>Anomia simplex</i>           | restricted to shallow subtidal with moderate current flow (0-30') | Attached to pebbles, cobbles, shell debris on firm substrata | epibyssate          | suspension feeder         |
| <i>Stewartia anodonta</i>        | <i>Anodonta alba</i>            | shallow water (3-100')  | in sand  | medium infaunal     | lucinid suspension feeder |
| <i>Parvilucina multilineatus</i> | <i>Parvilucina multilineata</i> | shallow water (2-600')  | in sand and mud  | shallow infaunal    | lucinid suspension feeder |

|                                     |                                  |                                    |   |                     |                             |
|-------------------------------------|----------------------------------|------------------------------------|---|---------------------|-----------------------------|
| <i>Divalinga quadrisulcata</i>      | <i>Divaricella quadrisulcata</i> | moderately shallow water (6-300')  | in sand   | medium infaunal     | lucinid suspension feeder   |
| <i>Lucinisca cribrarius</i>         | <i>Parvilucina nassula</i>       | moderately shallow water (1-2000') | in sand   | shallow infaunal    | lucinid suspension feeder   |
| <i>Ctena speciosa</i>               | <i>Ctena bella</i>               | moderately shallow water           |   | shallow infaunal    | lucinid suspension feeder   |
| <i>Diplodonta leana</i>             | <i>Diplodonta punctuata</i>      | moderately shallow water (6-750')  | in sand   | nestling            | suspension feeder           |
| <i>Diplodonta</i> sp.A              | <i>Diplodonta punctuata</i>      | moderately shallow water (6-750')  | in sand   | nestling            | suspension feeder           |
| <i>Diplodonta</i> sp.B              | <i>Diplodonta punctuata</i>      | moderately shallow water (6-750')  | in sand   | nestling            | suspension feeder           |
| <i>Chama congregata</i>             | <i>Chama congregata</i>          | shallow water (1-50')              | on rocks and other hard surfaces  | cementing epifaunal | suspension feeder           |
| <i>Pseudochama corticosa</i>        | <i>Pseudochama radians</i>       | shallow water (0-250')             | on rocks and other hard surfaces  | cementing epifaunal | suspension feeder           |
| <i>Bornia triangula</i>             | <i>Kellia suborbicularis</i>     | shallow water (0-400')             | attached to dead shells, algae, and rock crevices                                     | nestling            | suspension feeder           |
| <i>Carditamera arata</i>            | <i>Cardita floridana</i>         | shallow water (3-25')              | in sand and mud   | nestling epibyssate | suspension feeder           |
| <i>Pteromeris perplana</i>          | <i>Pleuromeris tridentata</i>    | shallow water (9-45')              | on sand or rubble   | shallow infaunal    | suspension feeder           |
| <i>Cyclocardia granulata</i>        | <i>Cyclocardia borealis</i>      | moderately shallow water (15-750') | in sand, gravel, and rubble   | shallow infaunal    | suspension feeder           |
| <i>Chesacardium aequilactreatum</i> | <i>Dinocardium robustum</i>      | shallow water (0-100')             | in sand and mud   | shallow infaunal    | suspension feeder           |
| <i>Mulinia congesta</i>             | <i>Mulina lateralis</i>          | shallow water. lagoonal (0-55')    | usually mud and muddy sand, tolerates large range of salinities and substrata         | shallow infaunal    | siphonate suspension feeder |
| <i>Leptomacra dolomus</i>           | <i>Macra fragilia</i>            | Intertidal and shallow subtidal    | restricted to grassy bottoms and sandy substrata                                      | shallow infaunal    | siphonate suspension feeder |
| <i>Hemimacra duplinensis</i>        | <i>Macra fragilis</i>            | shallow water (30-150')            | in sand   | shallow infaunal    | siphonate suspension feeder |
| <i>Spisula similis</i>              | <i>Spisula solidissima</i>       | moderately shallow water (0-140')  | medium to coarse grained shifting sands, just beneath surface in sand, mud, or gravel | shallow infaunal    | siphonate suspension feeder |
| <i>Spisula</i> sp.A                 | <i>Spisula solidissima</i>       | moderately shallow water (0-140')  | medium to coarse grained shifting sands, just beneath surface in sand, mud, or gravel | shallow infaunal    | siphonate suspension feeder |
| <i>Spisula</i> sp.B                 | <i>Spisula solidissima</i>       | moderately shallow water (0-140')  | medium to coarse grained shifting sands, just beneath surface in sand, mud, or gravel | shallow infaunal    | siphonate suspension feeder |

|                                   |                                 |   |   |                  |                             |
|-----------------------------------|---------------------------------|---|---|------------------|-----------------------------|
| <i>Ensis directus</i>             | <i>Ensis directus</i>           | intertidal                              | extremely rapid burrower in sand bars   | deep infaunal    | siphonate suspension feeder |
| <i>Astarte undulata</i>           | <i>Astarte undulata</i>         | moderately shallow water                | prefers coarse substrate (up to gravelly)   | shallow infaunal | suspension feeder           |
| <i>Astarte concentrica</i>        | <i>Astarte subaequilatera</i>   | (80-180')                               |   | shallow infaunal | suspension feeder           |
| <i>Marvaccrassatella undulata</i> | <i>Eucrassatella speciosa</i>   | moderately shallow water                |   | medium infaunal  | suspension feeder           |
| <i>Crassinella lunulata</i>       | <i>Crassinella lunulata</i>     | shallow water                           |   | shallow infaunal | suspension feeder           |
| <i>Macoma virginiana</i>          | <i>Macoma tenta</i>             | shallow water (35-120')                 | in sand   | shallow infaunal | deposit feeder              |
| <i>Abra subreflexa</i>            | <i>Abra aequalis</i>            | shallow water (6-120')                  | in sand and mud   | shallow infaunal | siphonate suspension feeder |
| <i>Semele</i> sp.A                | <i>Semele proficua</i>          | shallow water (0-36')                   | in sand   | shallow infaunal | siphonate suspension feeder |
| <i>Cumingia tellinoides</i>       | <i>Cumingia tellinoides</i>     | shallow water (0-60')                   | in muddy, medium sand, found in narrow tidal channels   | shallow infaunal | siphonate suspension feeder |
| <i>Glossus</i> sp.                |                                 |   |   | shallow infaunal | siphonate suspension feeder |
| <i>Chione cribraria</i>           | <i>Chione intepurpurea</i>      | moderately shallow water                |   | shallow infaunal | siphonate suspension feeder |
| <i>Chione grus</i>                | <i>Chione grus</i>              | shallow water (6-60')                   | sand and sandy mud  | shallow infaunal | siphonate suspension feeder |
| <i>Mercenaria campechiensis</i>   | <i>Mercenaria campechiensis</i> | Commonly shallow subtidal to intertidal | various substrata, usually on bare bottoms, but very tolerant. In sand or mud in bays or inlets | medium infaunal  | siphonate suspension feeder |
| <i>Dosinia acetabulum</i>         | <i>Dosinia elagans</i>          | shallow water, lower intertidal         | moderately exposed sand flats   | medium infaunal  | siphonate suspension feeder |
| <i>Pitar sayana</i>               | <i>Pitar fulminata</i>          | shallow water (10-100')                 | in mud and sand   | shallow infaunal | siphonate suspension feeder |
| <i>Pitar</i> sp. B                | <i>Pitar fulminata</i>          | shallow water (10-100')                 | in mud and sand   | shallow infaunal | siphonate suspension feeder |
| <i>Macrocallista reposta</i>      | <i>Macrocallista maculata</i>   | shallow water (6-60')                   | in sand   | medium infaunal  | siphonate suspension feeder |
| <i>Gemma magna</i>                | <i>Gemma gemma</i>              | intertidal                              | on sand or mud flats  | shallow infaunal | siphonate suspension feeder |
| <i>Petricola grinelli</i>         | <i>Petricola pholadiformis</i>  | shallow water, lower intertidal         | burrows into peat, mud, or stiff clay   | mud boring       | suspension feeder           |

|                              |                           |                                  |  |                    |                             |
|------------------------------|---------------------------|----------------------------------|--|--------------------|-----------------------------|
| <i>Pleiorytis centenaria</i> | <i>Petricola lapicida</i> | shallow water (1-20')            | boring in coral rock                                     | shell boring       | suspension feeder           |
| <i>Corbula retusa</i>        | <i>Corbula contracta</i>  | shallow water (12-90')           | in sand or mud   | shallow infaunal   | siphonate suspension feeder |
| <i>Corbula inaequalis</i>    | <i>Corbula contracta</i>  | shallow water (12-90')           | in sand or mud   | shallow infaunal   | siphonate suspension feeder |
| <i>Corbula cuneata</i>       | <i>Corbula contracta</i>  | shallow water (12-90')           | in sand or mud   | shallow infaunal   | siphonate suspension feeder |
| <i>Panopea reflexa</i>       | <i>Panopea generosa</i>   | moderately shallow water (0-50') | in mud and sandy mud in bays                             | deep infaunal      | siphonate suspension feeder |
| <i>Saxicava</i> sp           | <i>Hiatella artica</i>    | shallow water (0-600')           | byssally attached nestler in crevices and old bore holes | nestling epifaunal | siphonate suspension feeder |
| <i>Pandora</i> sp.A          | <i>Pandora arenosa</i>    | shallow water (0-120')           | in sand  | shallow infaunal   | siphonate suspension feeder |
| <i>Pandora</i> sp.B          | <i>Pandora arenosa</i>    | shallow water (0-120')           | in sand  | shallow infaunal   | siphonate suspension feeder |
| <i>Pandora</i> sp.C          | <i>Pandora arenosa</i>    | shallow water (0-120')           | in sand  | shallow infaunal   | siphonate suspension feeder |
| <i>Cochlodesma antiqua</i>   |                           |                                  |  | ?                  | ?                           |
| <i>Thracia conradi</i>       | <i>Thracia conradi</i>    | shallow water (13-90')           | muddy sand   | deep infaunal      | siphonate suspension feeder |

## Gastropod Color Scheme:

Archaeogastropods

Mesogastropods

Neogastropods

Other

## Gastropod Life Habits

| taxon                                   | habitat           | feeding type              |
|---|-------------------|---------------------------|
| <i>Strombiformis</i> sp                 | epifaunal         | ?                         |
| <i>Carinorbis</i> <i>lyra</i>           | epifaunal         | ?                         |
| <i>Lunatia</i> <i>heros</i>             | vagrant infaunal  | boring scavenger/predator |
| <i>Polinices</i> <i>duplicata</i>       | vagrant infaunal  | boring scavenger/predator |
| <i>Ephora</i> <i>quadricostata</i> .    | vagrant epifaunal | boring scavenger/predator |
| <i>Eupleura</i> <i>caudata</i>          | vagrant epifaunal | boring scavenger/predator |
| <i>Scalaspira</i> <i>strumosa</i>       | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx</i> <i>stimpsoni</i>      | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx</i> <i>trossula</i>       | vagrant epifaunal | boring scavenger/predator |
| <i>Boreotrophon</i> sp.                 | vagrant epifaunal | boring scavenger/predator |
| <i>Pterorytis</i> <i>umbrier</i>        | vagrant epifaunal | boring scavenger/predator |
| <i>Diodora</i> <i>carolinensis</i>      | vagrant epifaunal | grazer                    |
| <i>Diodora</i> <i>catelliformis</i>     | vagrant epifaunal | grazer                    |
| <i>Diodora</i> <i>redimicula</i>        | vagrant epifaunal | grazer                    |
| <i>Calliostoma</i> <i>mitchelli</i>     | vagrant epifaunal | grazer                    |
| <i>Calliostoma</i> <i>virginicum</i>    | vagrant epifaunal | grazer                    |
| <i>Littorina</i> <i>irrorata</i>        | vagrant epifaunal | grazer                    |
| <i>Longchaeus</i> <i>suturalis</i>      | unknown           | possibly parasitic        |
| <i>Epitonium</i> sp.                    | vagrant epifaunal | scavenger/predator        |
| <i>Ficus</i> <i>papyratia</i>           | vagrant epifaunal | scavenger/predator        |
| <i>Architectonica</i> <i>nupera</i>     | vagrant epifaunal | scavenger/predator        |
| <i>Anachis</i> sp.                      | vagrant epifaunal | scavenger/predator        |
| <i>Strombina</i> <i>anomala</i>         | vagrant epifaunal | scavenger/predator        |
| <i>Mitrella</i> <i>gardnerae</i>        | vagrant epifaunal | scavenger/predator        |
| <i>Nassarius</i> sp.                    | vagrant epifaunal | scavenger/predator        |
| <i>Uzita</i> sp.                        | vagrant epifaunal | scavenger/predator        |
| <i>Fusinus</i> <i>exilis</i>            | vagrant epifaunal | scavenger/predator        |
| <i>Hesperisternia</i> <i>filicata</i>   | vagrant epifaunal | scavenger/predator        |
| <i>Busycon</i> sp.                      | vagrant epifaunal | scavenger/predator        |
| <i>Lyrosoma</i> <i>sulcosa</i>          | vagrant epifaunal | scavenger/predator        |
| <i>Ptychosalpinx</i> <i>multirugata</i> | vagrant epifaunal | scavenger/predator        |
| <i>Urosalpinx</i> sp.                   | vagrant epifaunal | scavenger/predator        |
| <i>Oliva</i> <i>canaliculata</i>        | vagrant epifaunal | scavenger/predator        |
| <i>Oliva</i> sp.                        | vagrant epifaunal | scavenger/predator        |
| <i>Marginella</i> <i>denticulata</i>    | vagrant epifaunal | scavenger/predator        |
| <i>Dentimargo</i> <i>aureocincta</i>    | vagrant epifaunal | scavenger/predator        |
| <i>Pyrghospira</i> <i>tricatenaria</i>  | vagrant epifaunal | scavenger/predator        |
| <i>Cerodrilla</i> <i>simpsoni</i>       | vagrant epifaunal | scavenger/predator        |
| <i>Drilla</i> sp. A                     | vagrant epifaunal | scavenger/predator        |
| <i>Drilla</i> sp. B                     | vagrant epifaunal | scavenger/predator        |
| <i>Sedilia</i> <i>bella</i>             | vagrant epifaunal | scavenger/predator        |
| <i>Conus</i> <i>marylandicus</i>        | vagrant epifaunal | scavenger/predator        |

|                              |                   |                    |
|------------------------------|-------------------|--------------------|
| <i>Scaphella sp.</i>         | vagrant epifaunal | scavenger/predator |
| <i>Cancellaria rotunda</i>   | vagrant epifaunal | scavenger/predator |
| <i>Terebra carolinensis</i>  | vagrant epifaunal | scavenger/predator |
| <i>Turritella sp.</i>        | sessile epifaunal | suspension feeder  |
| <i>Sepulorbis graniforma</i> | sessile epifaunal | suspension feeder  |
| <i>Crucibulum grandis</i>    | sessile epifaunal | suspension feeder  |
| <i>Crucibulum leanum</i>     | sessile epifaunal | suspension feeder  |
| <i>Crucibulum scutellum</i>  | sessile epifaunal | suspension feeder  |
| <i>Crepidula costata</i>     | sessile epifaunal | suspension feeder  |
| <i>Crepidula adunca</i>      | sessile epifaunal | suspension feeder  |
| <i>Crepidula plana</i>       | sessile epifaunal | suspension feeder  |

## Gastropod Life Habits

| taxon                            | habitat           | feeding type              |
|----------------------------------|-------------------|---------------------------|
| <i>Diodora catelliformis</i>     | vagrant epifaunal | grazer                    |
| <i>Diodora redimicula</i>        | vagrant epifaunal | grazer                    |
| <i>Calliostoma mitchelli</i>     | vagrant epifaunal | grazer                    |
| <i>Calliostoma virginicum</i>    | vagrant epifaunal | grazer                    |
| <i>Turritella</i> sp.            | sessile epifaunal | suspension feeder         |
| <i>Sepulorbis graniforma</i>     | sessile epifaunal | suspension feeder         |
| <i>Epitonium</i> sp.             | vagrant epifaunal | scavenger/predator        |
| <i>Crucibulum grandis</i>        | sessile epifaunal | suspension feeder         |
| <i>Crucibulum leanum</i>         | sessile epifaunal | suspension feeder         |
| <i>Crucibulum scutellum</i>      | sessile epifaunal | suspension feeder         |
| <i>Crepidula costata</i>         | sessile epifaunal | suspension feeder         |
| <i>Crepidula adunca</i>          | sessile epifaunal | suspension feeder         |
| <i>Crepidula</i> sp.A            | sessile epifaunal | suspension feeder         |
| <i>Crepidula plana</i>           | sessile epifaunal | suspension feeder         |
| <i>Lunatia heros</i>             | vagrant infaunal  | boring scavenger/predator |
| <i>Polinices duplicata</i>       | vagrant infaunal  | boring scavenger/predator |
| <i>Ficus papyratia</i>           | vagrant epifaunal | scavenger/predator        |
| <i>Architectonica nupera</i>     | vagrant epifaunal | scavenger/predator        |
| <i>Anachis</i> sp.               | vagrant epifaunal | scavenger/predator        |
| <i>Mitrella gardnerae</i>        | vagrant epifaunal | scavenger/predator        |
| <i>Nassarius</i> sp.             | vagrant epifaunal | scavenger/predator        |
| <i>Uzita</i> sp.                 | vagrant epifaunal | scavenger/predator        |
| <i>Fusinus exilis</i>            | vagrant epifaunal | scavenger/predator        |
| <i>Busycon</i> sp.               | vagrant epifaunal | scavenger/predator        |
| <i>Lyrosoma sulcosa</i>          | vagrant epifaunal | scavenger/predator        |
| <i>Ptychosalpinx multirugata</i> | vagrant epifaunal | scavenger/predator        |
| <i>Ecphora quadricostata.</i>    | vagrant epifaunal | boring scavenger/predator |
| <i>Eupleura caudata</i>          | vagrant epifaunal | boring scavenger/predator |
| <i>Scalaspira strumosa</i>       | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx stimpsoni</i>      | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx trossula</i>       | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx</i> sp.            | vagrant epifaunal | scavenger/predator        |
| <i>Pterorhytis umbrifier</i>     | vagrant epifaunal | boring scavenger/predator |
| <i>Oliva canaliculata</i>        | vagrant epifaunal | scavenger/predator        |
| <i>Marginella denticulata</i>    | vagrant epifaunal | scavenger/predator        |
| <i>Dentimargo aureocincta</i>    | vagrant epifaunal | scavenger/predator        |
| <i>Pyrgospira tricatendaria</i>  | vagrant epifaunal | scavenger/predator        |
| <i>Drilla</i> sp. A              | vagrant epifaunal | scavenger/predator        |
| <i>Drilla</i> sp. B              | vagrant epifaunal | scavenger/predator        |
| <i>Terebra carolinensis</i>      | vagrant epifaunal | scavenger/predator        |
| <i>Terebra</i> sp.A              | vagrant epifaunal | scavenger/predator        |
| <i>Scaphella</i> sp.             | vagrant epifaunal | scavenger/predator        |
| <i>Cancellaria rotunda</i>       | vagrant epifaunal | scavenger/predator        |
| <i>Longchaeus suturalis</i>      | unknown           | possibly parasitic        |

## Gastropod Modern Analogs

| species                       | modern analog               | water depth                         | substrate   | habitat           | feeding type              |
|-------------------------------|-----------------------------|-------------------------------------|---|-------------------|---------------------------|
| <i>Diodora catelliformis</i>  | <i>Diodora cayennensis</i>  | shallow water to intertidal (0-90') | on and among rocks  | vagrant epifaunal | grazer                    |
| <i>Diodora redimicula</i>     | <i>Diodora cayennensis</i>  | shallow water to intertidal (0-90') | on and among rocks  | vagrant epifaunal | grazer                    |
| <i>Calliostoma mitchelli</i>  | <i>Calliostoma pulchrum</i> | moderately shallow water            | on rocks  | vagrant epifaunal | grazer                    |
| <i>Calliostoma virginicum</i> | <i>Calliostoma pulchrum</i> | moderately shallow water            | on rocks  | vagrant epifaunal | grazer                    |
| <i>Turritella</i> sp.         | <i>Turritella acropora</i>  | moderately shallow water            |   | sessile epifaunal | suspension feeder         |
| <i>Sepulorbis graniforma</i>  | <i>Vermicularia spirata</i> | shallow water                       | often found with sponges or other colonial marine animals, attached to hard substrata | sessile epifaunal | suspension feeder         |
| <i>Epitonium</i> sp.          | <i>Epitonium novangliae</i> | moderately shallow water (0-500')   | on sand or gravel   | vagrant epifaunal | scavenger/predator        |
| <i>Crucibulum grandis</i>     | <i>Crucibulum striatum</i>  | shallow water (15-1100')            | on rocks and dead shells  | sessile epifaunal | suspension feeder         |
| <i>Crucibulum leanum</i>      | <i>Crucibulum striatum</i>  | shallow water (15-1100')            | on rocks and dead shells  | sessile epifaunal | suspension feeder         |
| <i>Crucibulum scutellum</i>   | <i>Crucibulum striatum</i>  | shallow water (15-1100')            | on rocks and dead shells  | sessile epifaunal | suspension feeder         |
| <i>Crepidula costata</i>      | <i>Crepidula aculeata</i>   | shallow water                       | on rocks, shells, and other hard objects  | sessile epifaunal | suspension feeder         |
| <i>Crepidula adunca</i>       | <i>Crepidula aculeata</i>   | shallow water                       | on rocks, shells, and other hard objects  | sessile epifaunal | suspension feeder         |
| <i>Crepidula</i> sp.A         | <i>Crepidula aculeata</i>   | shallow water                       | on rocks, shells, and other hard objects  | sessile epifaunal | suspension feeder         |
| <i>Crepidula plana</i>        | <i>Crepidula plana</i>      | intertidal                          | inside large shells or on rocks, shells, or other hard objects                        | sessile epifaunal | suspension feeder         |
| <i>Lunatia heros</i>          | <i>Lunatia heros</i>        | Shallow bays and estuaries          | sand and mud flats  | vagrant infaunal  | boring scavenger/predator |
| <i>Polinices duplicata</i>    | <i>Polinices duplicatus</i> | shallow water                       | sand and mud flats  | vagrant infaunal  | boring scavenger/predator |
| <i>Ficus papyraria</i>        | <i>Ficus communis</i>       | moderately deep water (0-120')      | in sand   | vagrant epifaunal | scavenger/predator        |

|                                  |                               |                                |  |                   |                           |
|----------------------------------|-------------------------------|--------------------------------|--|-------------------|---------------------------|
| <i>Architectonica nupera</i>     | <i>Architectonica nobilis</i> | shallow water                  | in sand  | vagrant epifaunal | scavenger/predator        |
| <i>Anachis</i> sp.               | <i>Anachis avara</i>          | shallow water                  | on eel grass near low-tide line, on stones in deeper water | vagrant epifaunal | scavenger/predator        |
| <i>Mitrella gardnerae</i>        | <i>Mitrella ocellata</i>      | at low tide line               | under rocks, in sand or mud                                | vagrant epifaunal | scavenger/predator        |
| <i>Nassarius</i> sp.             | <i>Nassarius albus</i>        | shallow water (0-100')         | on sand  | vagrant epifaunal | scavenger/predator        |
| <i>Uzita</i> sp.                 | <i>Nassarius albus</i>        | shallow water (0-100')         | on sand  | vagrant epifaunal | scavenger/predator        |
| <i>Fusinus exilis</i>            | <i>Fusinus ambustus</i>       | moderately shallow water       |  | vagrant epifaunal | scavenger/predator        |
| <i>Busycon</i> sp.               | <i>Busycon canaliculatum</i>  | intertidal to shallow subtidal | on sand or mud   | vagrant epifaunal | scavenger/predator        |
| <i>Lyrosoma sulcosa</i>          |                               |                                |  | vagrant epifaunal | scavenger/predator        |
| <i>Ptychosalpinx multirugata</i> |                               |                                |  | vagrant epifaunal | scavenger/predator        |
| <i>Ephora quadricostata</i>      |                               |                                |  | vagrant epifaunal | boring scavenger/predator |
| <i>Eupleura caudata</i>          | <i>Eupleura caudata</i>       | shallow water                  | on and near oyster beds                                    | vagrant epifaunal | boring scavenger/predator |
| <i>Scalaspira strumosa</i>       |                               |                                |  | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx stimpsoni</i>      | <i>Urosalpinx cinerea</i>     | intertidal                     | among oyster bed rubble                                    | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx trossula</i>       | <i>Urosalpinx cinerea</i>     | intertidal                     | among oyster bed rubble                                    | vagrant epifaunal | boring scavenger/predator |
| <i>Urosalpinx</i> sp.            | <i>Urosalpinx cinerea</i>     | intertidal                     | among oyster bed rubble                                    | vagrant epifaunal | scavenger/predator        |
| <i>Pterorhytis umbrifera</i>     |                               |                                |  | vagrant epifaunal | boring scavenger/predator |
| <i>Oliva canaliculata</i>        |                               |                                |  | vagrant epifaunal | scavenger/predator        |
| <i>Marginella denticulata</i>    | <i>Marginella denitculata</i> | shallow water                  |  | vagrant epifaunal | scavenger/predator        |
| <i>Dentimargo aureocincta</i>    |                               |                                |  | vagrant epifaunal | scavenger/predator        |
| <i>Pyrgospira tricatenaia</i>    | <i>Pyrgospira ostreacum</i>   | shallow water                  | on sand and rubble   | vagrant epifaunal | scavenger/predator        |
| <i>Drilla</i> sp. A              | <i>Drilla cydia</i>           | moderately shallow water       |  | vagrant epifaunal | scavenger/predator        |
| <i>Drilla</i> sp. B              | <i>Drilla cydia</i>           | moderately shallow water       |  | vagrant epifaunal | scavenger/predator        |
| <i>Terebra carolinensis</i>      | <i>Terebra dislocata</i>      | low tide to shallow water      | in sand  | vagrant epifaunal | scavenger/predator        |

|                             |                               |                           |                            |                   |                    |
|-----------------------------|-------------------------------|---------------------------|----------------------------|-------------------|--------------------|
| <i>Terebra</i> sp. A        | <i>Terebra dislocata</i>      | low tide to shallow water | in sand                    | vagrant epifaunal | scavenger/predator |
| <i>Scaphella</i> sp.        | <i>Scaphella gouldiana</i>    | deep water                |                            | vagrant epifaunal | scavenger/predator |
| <i>Cancellaria rotunda</i>  | <i>Cancellaria reticulata</i> | shallow water             | in sand among turtle grass | vagrant epifaunal | scavenger/predator |
| <i>Longchaeus suturalis</i> | <i>Pyramidella candida</i>    | moderately deep water     |                            | unknown           | possibly parasitic |

**VITA**  
**Gwen M. Daley**

Gwen M. Daley was born on November 24th, 1968 in Illinois. After graduating from Glenbard West High School in Glen Ellyn, Illinois, she attended the University of Chicago, where she received a B.A. in the Geophysical Sciences from the College of the University of Chicago in 1990. In the summer between her undergraduate and graduate education, she worked as an interpretive ranger for the National Park Service at Florissant Fossil Beds National Monument in Florissant, Colorado. Having developed an interest in the history of life, she received an M.S. in Geology from the University of Cincinnati in 1993, and served a summer internship with Amoco's West Africa Regional Project in Houston. She came to the Virginia Tech Department of Geological Sciences in order to pursue a doctoral degree. After completing her Ph.D., she will continue her paleontological research in academia.