Quantitative approaches and applications to the sequence stratigraphy and biodiversity of Pleistocene – Holocene mollusk communities from the Po plain, Italy and San Salvador Island, the Bahamas

Jacalyn Marie Wittmer

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

Doctor of Philosophy
In
Geosciences

Shuhai Xiao
Michał J. Kowalewski
Daniele Scarponi
Brian W. Romans

February 3rd, 2014
Blacksburg, Virginia

Quantitative approaches and applications to the sequence stratigraphy and biodiversity of Pleistocene – Holocene mollusk communities from the Po plain, Italy and San Salvador Island, the Bahamas

Jacalyn Marie Wittmer

ABSTRACT

The following chapters presented here use modern ecological data and modern marine systems to evaluate past marine depositional settings and the preservation potential of various environments in the geological record.
While the chapters in this dissertation vary in terms of study area, sedimentary systems (carbonate vs. siliciclastic), depositional environment, and organisms, all projects are based on developing and using quantitative models to evaluate the present as a means for understanding the past.

Chapter one focuses on the preservation potential of rocky intertidal environments. The rocky intertidal zone is one of the most poorly preserved fossil-rich environments in the geological record. However in most coastal marine habitats today, it is one of the most diversity rich environments. Chapter one also focuses on the analytical advantages of hierarchical sampling of gastropod communities across San Salvador Island, the Bahamas to quantify community and species level preservation potential in rocky shore environments. Chapters two and three are based on the fossil-rich sedimentary deposits from the Po coastal plain in northeastern Italy. These deposits have been widely studied in terms of their sedimentology and stratigraphy, resulting in a highly resolved sequence stratigraphic architecture. The integration of sequence stratigraphy with paleobiology can enhance our understanding of spatiotemporal biotic patterns recorded in the fossil record. Used in conjunction with the highly-resolved stratigraphic framework, biotic patterns can be used to assess depositional cycles and bathymetry through time. Chapter two integrates sequence stratigraphic patterns and paleoecological data to develop bathymetric models across fossiliferous marine successions of the Po coastal plain, Italy. Chapter three evaluates the modern ecological dataset used to derive the bathymetric models. The last chapter also explores water depth distribution for selected taxa recorded in the Quaternary sediments and observed in present-day habitats. The dissertation research explored here demonstrates that modern ecological systems are essential to evaluating past geologic events. Through direct observation and quantitative analysis, I have learned that modern and fossil communities behave differently depending on environment (e.g. energy, salinity, water depth, etc.). These variables affect the distribution of living organisms today and through my research, delineate fossil distributions through time. With these observations, new questions have arisen about the latitudinal variability of rocky intertidal fossil preservation and extrapolating the quantitative bathymetric models to deeper time intervals. These questions will lead to future endeavors and pointedly add to the field of geology and stratigraphic paleobiology.

DEDICATION

For my husband and daughter.

I also thank my husband, Peter Malinowski, for keeping me grounded and helping me focus on the future when I got overwhelmed with work and couldn't find a way out. Thank you for keeping me sane. And to Rose, thank you for changing my whole entire life for the better, I wouldn't change anything.

I would like to thank my committee members who have been very supportive and patient during my dissertation through research and life changes, especially to Shuhai Xiao for always being there for me. Lastly, I would like to thank my advisor, Michał Kowalewski for being the most patient and supportive person - I deeply appreciate all the guidance and advice he has given me throughout my career.

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

LIST OF TABLES

INTRODUCTION

Paleontologists use modern environments to help understand the past and by doing so, potentially predict future environmental changes. For some marine systems, it is possible to use modern environments, ecological collections, and habitats to aid in understanding of past geological and paleontological settings. The following chapters presented here attempt to use modern ecological data and modern marine systems to evaluate past marine depositional settings and the preservation potential of various types of organisms and environmental settings in the geological record.

While the chapters in this dissertation vary in study area, sedimentary systems (carbonate vs. siliciclastic), depositional environment, and organisms; they are based on developing and using quantitative models to evaluate the present as a ways to understand the past. The following chapters use various multivariate and quantitative techniques to evaluate modern and fossil communities.

Chapter one focuses on the preservation potential of rocky intertidal environments. The rocky intertidal zone is one of the most poorly preserved fossil-rich environments in the geological record. However, in most coastal marine habitats today, it is one of the most diversity rich environments. Chapter one focuses on the analytical advantages of hierarchical sampling of gastropod communities across San Salvador Island, the Bahamas to quantify community and species level preservation potential in rocky shore environments. As the easternmost island in the Bahamian Archipelago, San Salvador Island represents a suitable testing ground to examine the present-day diversity and distribution of rocky intertidal gastropods and to assess their informative value in terms of its potential fossil record. Lithified Pleistocene and Holocene strata were exposed during the most recent glacio-eustatic lowstand creating habitats suitable for

the development of rocky intertidal gastropod-dominated communities. The carbonate rocky outcrops are dominated by pitting, pinnacles, crevices, and solution pans creating a diverse environment for the occupation and potential preservation of gastropod species. This chapter focuses on these habitats and evaluates "preservable" habitat diversity and "less preservable" habitat diversity in relation to their potential for fossilization.

Chapters two and three are based on the fossil-rich Quaternary sedimentary deposits from the Po coastal plain in northeastern Italy. These deposits have been widely studied in terms of their sedimentology and stratigraphy, resulting in a highly resolved sequence stratigraphic architecture. Used in combination with the highly-resolved stratigraphic framework, fossil patterns can be assessed with regard to their lithology, lithofacies, and depositional cycle. These fossil patterns can be quantified using multivariate methods to determine environmental gradients such as water depth, energy, salinity, etc. Chapter two incorporates sequence stratigraphic patterns and ecological data to develop bathymetric (water depth) models via multivariate analyses of fossiliferous marine successions of the Po coastal plain, Italy. Chapter three assesses the modern ecological dataset that was used to construct the high-resolution bathymetric gradient for the Po coastal plain, Italy. The last chapter also explores select taxa and their water depth distribution throughout the Quaternary and into the modern.

CHAPTER 1

Preservation potential and diversity of tropical rocky shore gastropod communities, San Salvador Island, the Bahamas

JACALYN M. WITTMER

1.1 Abstract

This study explores spatial distribution, species diversity, and preservation potential of modern rocky intertidal gastropod communities from the San Salvador Island, Bahamas. Using a hierarchical sampling approach, 17,654 intertidal gastropod specimens representing nine genera and 15 species were recorded from 169 quadrats along 85 transects at 37 sites sampled at ten localities around the island. All localities are dominated by several species of littorinids and neritids. The rank-abundance structure was comparable across all localities, with the same species dominating at all but one locality. The hierarchical sampling scheme revealed a gradual increase in diversity across sampling levels, with most notable increase observed between site level and locality level diversity estimates. Habitat diversity estimates did not vary from bare and exposed surfaces to sheltered pits, crevices, and tide pools. Across energy regimes, there was no meaningful shift in habitat occurrences to more sheltered, protected habitats. Species occurrences in sheltered habitats should augment fossilization potential of those assemblages because, as shown in some paleontological studies, there is evidence of rocky intertidal environments from such settings as tide pools, pits, and crevices. Indeed, when data are restricted to more preservable, sheltered settings only, a good representation of total biodiversity and overall community structure of sampled faunal associations is still retained. Moreover, because the sampled communities appear remarkably homogeneous across and within localities, even a highly fragmentary fossil record (e.g., small area in one locality) would likely collect a substantial fraction of biodiversity and community structure of rocky intertidal communities of the San Salvador Island.

1.2 Introduction

Rocky shore communities have been widely studied by modern community ecologists, with emphasis on diversity, competition and interaction among species, dispersal patterns, latitudinal variability, and geographic disparity (Connell, 1972; Paine, 1977; Paine and Levin, 1981; Branch, 1981; Vermeij, 1987; Foster et al., 1988; Rivadeneira et al., 2002; Noda, 2004; Fraschetti et al., 2005; Nakaoka et al., 2006). Furthermore, comparisons of fossil rocky shore assemblages to their modern counterparts have fueled investigations in reconstructing the environmental history of a given area (Valentine, 1961; Valentine and Lipps, 1963; Valentine, 1989; Lindberg and Lipps, 1996).

Such features of rocky shores as pits, tide pools, and crevices are ideal habitats that mediate abiotic stressors such as energy and desiccation (Minton and Gochfeld, 2001).

Gastropods at San Salvador Island and at other subtropical islands are found to occur in these habitats (Garrity, 1984; Garrity and Levings, 1984; McMahon, 1990; Minton and Gochfeld, 2001). Pits, tide pools, and crevices are not only ideal for rocky intertidal gastropods to occupy, but can be potential sites for fossilization (Johnson, 2006). Evidence of rocky shore habitats can be found in the Ordovician tidal pools from the Trenton Group in Canada (Harland and Pickerill, 1984) and Pleistocene tidal pools containing fossil gastropods from Western Australia (Scott and Johnson, 1993). *In situ* rocky intertidal habitat preservation in the fossil record, however, is not common and fossil rocky shore communities are frequently documented as reworked, transported, and mixed assemblages. Neptunian dikes have been found to trap shells and sediment, preserving a fragment of the diversity like the Pleistocene dikes in Western Australia that is composed of intertidal bivalves and gastropods (Scott and Johnson, 1993). Valentine and Lipps (1963) were able to document mixed fossil rocky communities by analyzing sand lenses from terraces of Anacapa Island near California. Additionally, late Pleistocene rocky shore and shallow intertidal faunal assemblages have been reported in time-averaged beach deposits at San Salvador Island (Hagey, 1988, 1991; Hagey and Mylorie, 1995). In the case of San Salvador Island, these time-averaged deposits retain only a few rocky intertidal taxa, not preserving a complete record of the whole intertidal community.

Such habitats as tide pools, pits, and crevices are not uniformly distributed across rocky shores and the manner in which gastropods occur in these habitats is variable. A hierarchical approach was, therefore, used to assess diversity changes across spatial scales (see also Kowalewski et al., 2002; Layou, 2007) to account for the variability of rocky intertidal habitats. By examining patterns of diversity at different levels, locality (10's of km), site (100's of m), transect (10's of m), and quadrats (< 1 m), the differences in number of gastropod species

collected, if any, can give insight into how preservation potential varies by habitats (Chapman, 1994, 2002; Johnson et al., 2001; Rivadeneira et al., 2002; Noda, 2004; Okuda et al., 2004; Fraschetti et al., 2005).

This study documents the distribution and diversity of rocky intertidal gastropods along the coastlines of San Salvador Island, the Bahamas, looking at their preservation potential based on habitat occurrences at various spatial scales. Intertidal gastropods are a common group of invertebrates used for studying spatiotemporal patterns because of their variable geographic range and, when compared with other rocky shore organisms, a relatively higher potential for fossilization in rocky shore assemblages (Chapman, 1994, 2002; Johnson et al., 2001; Fraschetti et al., 2005; Johnson, 2006). Gastropods were used in this study because the intertidal zone at San Salvador Island is depauperate in other invertebrate species, therefore, generalizations about intertidal communities and overall community diversity cannot be made.

In this paper, I evaluate the preservation potential of rocky intertidal gastropods by observing their habitat distribution and diversity at different spatial scales. Specifically, this study aims to assess quantitatively (1) species richness of the surveyed gastropods at different sampling scales; (2) spatial variation in composition and diversity of gastropod associations; (3) variability in gastropod diversity across habitats, and (4) evaluation of fossilization potential based on the assessment of diversity and faunal composition of gastropod associations occurring in settings that favor preservation.

1.3 Methods

1.3.1 Study area and design

As the easternmost island in the Bahamian Archipelago, San Salvador Island represents a suitable testing ground to examine the present-day diversity and distribution of rocky intertidal gastropods and to assess their informative value in terms of their fossilization. Located in the northern Caribbean, the island is considered a subtropical environment dominated by easterly trade winds originating out of the eastern quadrants. Separated from the Bahamian carbonate shelf, the island is perched on an isolated platform with well-developed Quaternary carbonate successions (Mylroie, 2008). During the glacial maxima (Wisconsinan), exposed lithified Pleistocene and Holocene strata created habitats conducive to development of rocky intertidal gastropod-dominated communities (Williams and Reid, 2004). Pitting, pinnacles, crevices, and solution pans typical of karst features that riddle the intertidal zone dominate the carbonate rocky outcrops (Horwitz and Roberts, 2010). The solution pans tend to be water-filled creating microtide pool habitats that can be frequently rewetted by sea splash and spray or undergo extreme heat and stagnation. The varying karst morphology creates a topographically complex environment for the occupation and potential preservation of gastropod species.

San Salvador Island contains a small microtidal coast that has a clear separation between the high, middle, and low intertidal zones. The higher intertidal zone is classified as a gray zone that is highly pinnacled and rarely rewetted by sea splash. The middle intertidal zone is identified by its high occurrences of rocky features (i.e., tide pools, pits, and crevices) that are ideal habitats for gastropod species. The middle intertidal zone is also classified as a brown zone based on the type of algae present (Kaplan, 1999). The low intertidal zone has higher occurrences of algae and is characterized as a pink zone (Kaplan, 1999). The middle intertidal zone was selected because it contained the habitats that were the focus of this study.

Census of the middle intertidal gastropod species was carried out along the rocky carbonate coastline at 10 localities (Fig. 1). The 10 localities were chosen based on accessibility, availability of rocky carbonate cliffs and beaches, energy settings, and geographic location around the island. Distance between localities varied between 2 km and 20 km with a sufficient coverage of rocky shorelines around the entire island. Within each locality four sites were selected based on the amount of rock coverage within 50 m, sites were chosen if they contained more than 50% rock exposure. Sites were placed parallel to the coastline with each site 50 m long (40 sites in total; Fig. 1C). Each site was separated by 100 –200 m, resulting in coverage of 600 –1000 m per locality, not all localities had the same degree of rock exposure limiting the area covered between sites. The position of each site was determined using a global positioning system (GPS; Garmin) with precisions of 5 to 10 m. Every site was further subdivided into three transects, each transect was five m in length and was assigned along the 50 m at random (12 transects per locality, 120 transects in total: Fig. 1C). Within each transect, four 30 x 30 cm quadrats were placed at random parallel to the coastline in the middle intertidal zone (48 quadrats per locality, 480 quadrats in total) (see Fig. 1C for a detailed illustration of the hierarchical sampling).

Both cliff and shallow rocky outcrops contained the middle intertidal zone with habitats that were the focus of this study. The angle of rock wall for each locality varied from vertical cliff faces, shallow sloping outcrops, to a combination of cliff faces gradually sloping into the sea. The variety of rocky outcrop slopes yielded different degrees of intertidal exposure; for example, shallow sloping outcrops represented low and middle intertidal habitats, whereas vertical cliff faces encompassed high and middle intertidal habitats. The abundance of gastropods, habitat type, and energy regime were determined in the field during low tide in June-

July 2010 for each quadrat. All gastropods (adults and juveniles) within a quadrat were counted and identified at the species level (Table 1). Both adult and juvenile species were combined as total counts.

Taxonomic identification of intertidal gastropods was primarily conducted in the field using Redfern's (2001) guide on Bahamian species. The majority of these intertidal species have identifiable morphological features that make field identifications possible. Species that were not easily identifiable in the field were examined in the laboratory using a binocular microscope to recognize features for accurate identification. Such species as *Echinolittorina ziczac* and *Echinolittorina angustior* have similar morphological characteristics requiring in depth comparison. Body size disparity between the two species was the most straightforward feature to identify them in the field, *E. angustior* (small, 5–17 mm) and *E. ziczac* (large, 15 – 20 mm) (Redfern 2001). Further nomenclatural corrections were conducted after fieldwork to correct for taxonomic discrepancies using Reid (1989), Williams and Reid (2004), and the World Register of Marine Species (Appeltans et al., 2011; www.marinespecies.org).

Physical environmental parameters were documented based on a graded classification scheme at the quadrat level. These parameters were collected to identify possible impact of the physical environment on diversity and taxonomic composition of sampled associations. Habitat type was determined by the specific karst features that riddled the rocky shore; Exposed surfaces: bare, Sheltered surfaces: pitted, tide pool, and crevice. Energy regimes were defined as (1) low, with little to no wave-action quiet and sheltered bays; (2) moderate, with mild wave-action and more exposed rock outcrops; and (3) high, with high wave action and with little to no shelter from destructive processes.

1.3.2 Diversity measures

Quadrats that contained < 30 specimens were removed, reducing the numbers of individuals analyzed from 17,703 to 17,654 specimens. Only 169 of the 420 quadrats, 85 of the 120 transect, and 37 of the 40 sites were retained after the minimum specimen quota was used. Quadrats that contained < 30 individuals were removed because most quadrats under this specimen quota contained few individuals. Confidence intervals were computed for mean species richness at the 95% level to account for uncertainty. Mean richness was evaluated independently for each level (quadrat, transect, site, locality) and for "preservable" and "less preservable" settings (sheltered habitats versus exposed and unprotected habitats). Mean richness was used because it gave an estimate of the expected number of taxa in a community at a given level of sampling (Magurran, 2004). Preservable settings included sheltered surfaces: pits, tide pools, and crevices. Less preservable settings were exposed and bare surfaces that lacked any feature for species to be preserved. Energy settings were not used in the separation between these two groupings because in this study energy did not seem to affect community structure and habitat occurrences (see Fig. 2). Subsampling of data was not preformed because all quadrats were equal in terms of sampling intensity and was standardized when using a hierarchical sampling design (Okuda et al., 2004; Nakaoka et al., 2006).

To examine the complexity of the gastropod communities around San Salvador Island, the logarithm of species abundance was compared to the species rank (Whittaker, 1965; Magurran, 2004). Rank abundance distribution is used to reveal the division between common species and rare species (Hubbel, 2001). The most common species are assigned low ranks and rare species are given higher ranks. Common species display high abundances followed by taxa with moderate to low abundances that create a steep and diminishing curve indicating the low

relative abundance of less common species. Rank abundance distributions are used in many

taphonomic studies showing that skeletonized assemblages can reflect the ecology of the once

living communities (Kidwell, 2001). Rank abundance curves, therefore, were used in this study

to determine what species are most likely to be fossilized at a given locality.

Ranks were treated separately for each locality because not all localities were dominated

by the same species. Although 15 species were sampled, 11 were the maximum number of

species surveyed at any single locality. The rank abundance curves were compared to such

theoretical abundance models as broken-stick (MacArthur, 1957), geometric (Motomura, 1932),

log-series (Fisher et al., 1943), and log Normal (Preston, 1948) using PAST 2.07 (Hammer et al.,

2001) to better understand the assemblages. There are many paleoecological studies that use

these theoretical models to understand the state of death assemblages (Olszewski, 2004; Buzas

and Hayek, 2005; Wagner et al., 2006), and they were used in this study to predict what type of

ecosystem could be preserved if these assemblages were fossilized. Localities were analyzed by

gastropod species abundance via ANOVA using JMP 9.0 (SAS Institute Inc., 2010) and

localities were further compared using Tukey-Kramer HSD (Zar, 1999).

1.3.3 Physical factors on community richness and evenness

Species richness and evenness (Simpson E, Simpson, 1949) were further explored looking at the

impact on habitat preservation in different energy regimes using JMP 9.0 (SAS Institute Inc.,

2010). Species richness and evenness was calculated for all individuals including both adults

and juveniles. Simpson E was calculated as;

$$\text{Simpson's Evenness} = 1 - \sum_{i=1}^{S} p_i^2 = 1 - \lambda$$

where S=richness, p_i= proportion of species i in a sample, and λ= Simpson's dominance index. Evenness measures the abundance distribution of taxa and is a common metric used in paleoecological studies to understand assemblage composition (Powell and Kowalewski, 2002; Olszewski, 2004; Bulinski, 2007). Evenness was primarily used for determining habitat composition, specifically looking at changes in species abundance across tide pools, pits, and crevices. At the quadrat level, species richness and evenness was calculated for the 169 culled quadrats (minimum number of individuals=30) and was grouped by energy type (low, moderate, or high) and habitat (pits, tide pools, and crevices). Confidence limits of 95% were computed to account for the uncertainty around mean species richness and mean evenness separately for habitats in each energy regime.

1.4 Results

1.4.1 Taxonomic composition and variation

A total of 17,703 individuals were counted during the field survey yielding 9 genera and 15 species (Table 1). Quadrats yielded a mean specimen density of 122.9 per square meter with an average of 37 specimens collected per quadrat. Quadrats contained few species with a mean richness of four species, however (Fig. 3). Transects contained five species with an average of 148 specimens collected per transect. Sites contained a mean species richness of six and had an average of 443 individuals counted per site. Localities were composed of a mean species richness of ten with an average of 1,770 individuals per locality with a minimum of 509 individuals surveyed at Fernandez Bay and a maximum of 5,188 individuals at The Gulf locality.

Various species of *Echinolittorina* and *Nerita* comprise the gastropod community in the middle intertidal zone (Table 1). Principal inhabitants of this zone included *E. angustior, E. mespilium*, *E. jamaicensis,* and *E. ziczac* (Fig. 4). Species that had moderate occurrences throughout the study but were not typical middle intertidal dwellers were *E. dilatata, C. muricatus, N. versicolor*, and *N. tessellata*. Both *E. dilatata* and *C. muricatus* prefer higher intertidal settings, whereas *N. versicolor* and *N. tessellata* are more commonly found in lower intertidal habitats. Majority of these upper and lower intertidal species were juveniles with very few adults occurring in the quadrats. Rank abundance curves for most of the localities were dominated by *Echinolittorina* and *Nerita* species occurring in the same order. ANOVA revealed that gastropod assemblages across localities were not equal (p=0.0003), and R^2=0.17 of the variation in localities was explained by species composition (Table 2). A comparison of mean number of species by locality showed that all localities are similar except Fernandez Bay. French Bay and Fernandez Bay were the most similar localities, but French Bay also had comparable composition to the other 8 localities (Table 3). Despite crossing different energy regimes and variable outcrop coverage, the structure of gastropod communities across localities except at Fernandez Bay, is more or less homogeneous.

All but three of the localities have *E. angustior* as the most abundant species followed by either *E. mespilium* or *E. jamaicensis*. The three exceptions include (1) North Point and (2) Rocky Point, where *E. angustior* is ranked as the second most abundant species; and (3) Fernandez Bay, where a different rank abundance structure is observed: these samples are dominated by *N. tessellata,* a species that was not commonly sampled in the other localities (Fig. 4B, E, F). *N. tessellata* dominated over 90% of the quadrats in Fernandez Bay with the other

species that occurred are rare and notably, *E. angustior,* so dominant at other sites, is the third rarest species.

The rank abundance curves were compared to four theoretical abundance models (geometric, log series, broken-stick, log normal) to determine the complexity of the gastropod community structures at each locality (Table 4). For all 10 localities, log normal could not be fitted to the rank abundance curves. All three models, broken-stick, geometric, and log series models correlate to several of the localities, with almost all *p* values lower than 0.05 alpha level.

1.4.2 Sampling intensity

The collections within each sampling level were equal and standardized because of the hierarchical sampling method used in this study. There were five levels that were sampled (quadrat, transect, site, locality, and island) and total diversity was a product of the diversity among quadrats, diversity between transects, diversity between sites, and diversity between localities. At small levels of sampling, transects and sites added 1.3 and 1.5 species to diversity, respectively, to the overall richness curve (Fig. 3). At larger scales, sampling intensity increased by 2.9 species at the locality level (Fig. 3). When the entire island is included, sampling intensity increased with an additional 5.5 more species added to diversity, showing that at the largest scale most of the rare species were captured. When exposed and sheltered habitats were grouped as less preservable and preservable, respectively, and plotted at different sampling levels (Fig. 3B) mean species richness of both preservable and less preservable showed similar diversity at each level of sampling. Compared to total diversity at each sampling level in Figure 3A, diversity in both preservable and less preservable settings are comparable.

1.4.3 Variation across habitat types

Habitat species richness and evenness varied by energy where low-energy environments

contained 26.1% of individuals surveyed with a mean of 4.07 species (Table 5, Fig. 2). In the

low energy localities, pits and crevices contained fewer species when compared to bare and

exposed settings (Fig. 2). Moderate energy environments contained only 17.7% of intertidal

gastropods surveyed with a mean of 3.96 species recovered. Both exposed and sheltered habitats

yielded an average of four species, although sheltered habitats were characterized by less even

assemblages in comparison (Fig. 2, Table 5). High-energy localities were shown to have slightly

lower richness with a mean of 3.60 species. Over half of the individuals from the study (56.2%)

came from high-energy environments. At San Salvador Island, tide pools are common in high-

energy localities and contained highly even communities with such abundant tide pool species as

E. mespilium and *P. pupa*. Habitat diversity and evenness did not vary meaningfully with all

habitats yielding similar species richness and evenness; bare surfaces with mean of 3.9 and

evenness of 0.55, pitted surfaces with a mean of 3.9 and evenness of 0.53, tide pools with a mean

of 3.8 and evenness of 0.5, and crevices with a mean of 3.0 and evenness of 0.65 (Table 5).

1.5 Discussion

1.5.1 Diversity and Abundance

The composition of the gastropod communities at San Salvador Island is dominated by species of

Echinolittorina, and *Nerita*. Both genera are common ecotypes of tropical, subtropical, to

temperate rocky shore systems (Bovbjerg, 1984; Burgett et al., 1987; Lang et al., 1998; Gochfeld

and Minton, 2001; Minton and Gochfeld, 2001; Emson et al,. 2002; Williams and Reid, 2004;

Nakaoka et al., 2006; McClintock et al., 2007; Judge et al., 2009). Species of *Echinolittorina* are

considered to be the most abundant macrofauna of the intertidal zone of tropical to subtropical rocky shores (Williams and Reid, 2004). Two studies based on Jamaican rocky intertidal assemblages, found similar dominant taxa: *C. muricatus, E. angustior, E. dilatata, E. mespilium,* and *E. ziczac* by Lang et al. (1998) and a slightly different structure of *E. dilatata, C. muricatus, E. angustior, E. ziczac,* and *N. versicolor* by Minton and Gochfeld (2001). Although these two studies do not have an identical dominance structure, they both contain the same species that make up the diversity at San Salvador Island.

Because of the small size of San Salvador Island, different levels of diversity are easy to assess by looking at the various levels of sampling intensity. Sampling intensity at smaller scales added one species sequentially from quadrats to sites. The locality level displayed an increase in sampling intensity with almost three species added to the diversity curve. When all species are added at the island level, most of the rare taxa surveyed are included in the diversity counts. These rare species were primarily represented as juveniles with their adult forms occurring more in the high- and low-intertidal zones. In the case of San Salvador Island, the locality level was the best scale of coverage to capture majority of the common intertidal gastropod species found in the data pooled across the entire island. Although the diversity of intertidal gastropods at San Salvador Island is not high in comparison to neighboring islands (i.e. Jamaica *see* Lang et al., 1998; Minton and Gochfeld, 2001), the gradual increase in diversity at larger sampling levels is notable for such a small island (Fig. 3).

The rank abundance curves for each locality fit multiple models, and since this study focuses only on gastropod species, interpretations of the state of these assemblages cannot be determined. None of the models overwhelmingly correlated to the rank abundance distributions and is impractical to conclude which model best fits the gastropod communities at San Salvador

Island at present. A more fruitful approach would involve sampling the entire intertidal community over a period of years to decades to detect changes in assemblage structure or shifts in abundances in response to environmental disturbances (Underwood, 1981; Kennelly and Underwood, 1992; Underwood, 1994).

1.5.2 Assemblage Preservation

Even with a lack of information on the overall intertidal community structure, the differences between gastropod abundance across energy regimes and habitats can illustrate the potential fossilization of these species in subtropical carbonate environments. Intertidal gastropods were found to occur across all localities, energy regimes, and habitats. Despite the fact that both sheltered and exposed habitats have similar diversity and community structure; over half of the gastropod occurrences were in sheltered habitats, which is important for understanding their preservation potential. Across temperate, subtropical, and tropical rocky shore environments, intertidal species of littorinids and neritids occur in protected habitats (Bovbjerg, 1984; Garrity and Levings, 1984; Peckol et al., 1989; Lang et al., 1998; Gochfeld and Minton, 2001; Minton and Gochfeld, 2001; Hohenlohe, 2003; McClintock et al., 2007; Judge et al., 2009). For example, Minton and Gochfeld (2001) performed a census of Jamaican rocky intertidal gastropod communities and observed comparable patterns in diversity and physical controls to this study. They found that gastropods occurred more frequently in pits and crevices and were rarely found in exposed habitats, but had different habitat selection in response to low- and high-energy environments. More species frequented exposed surfaces in high-energy settings leading them to conclude that wave-action had an insignificant effect on the distribution patterns and habitat selection of intertidal species. In this study, gastropods in high- and low-energy localities

occurred across habitats, both exposed and sheltered. For both San Salvador Island and Jamaica, energy does not play a significant role on species distributions within habitats.

As Johnson (2006) stated in his review of fossil rocky shore environments, the fauna from these habitats in the fossil record are an ecological fraction of their extant species and the question is whether the same can be said for the rocky intertidal assemblages at San Salvador Island. The Pleistocene rocky intertidal deposits at San Salvador Island have not been well studied and are difficult to locate. A comparison between fossil and modern assemblages is, therefore, not available. A more fruitful approach in discerning the preservation potential of the intertidal assemblages is to compare the diversity estimates attained from this study to other studies focused on fossil rocky shores.

Ordovician fossil rocky shore associations show highly abundant fauna with low diversity of 15 genera (Johnson et al., 1988). The findings from this modern survey suggest a similar pattern of highly abundant intertidal species composed of a few genera. Pleistocene fossil rocky shore studies in Baja California record higher diversity of a maximum of 89 gastropod species and 50 gastropod genera (Valentine and Lipps, 1963; Valentine, 1980; Johnson and Baarli, 1999). These Pleistocene fossil assemblages have greater diversity than the present study because these associations encompassed both shallow and deep marine gastropods. The assemblages were interpreted to be depositional accumulations with a more mixed faunal composition in comparison to the present study.

Hayes et al. (1993) reported different assemblages occurring on the leeward and windward coasts of Isla Requesón, determining that species diversity is not uniformly distributed around an island. This is not the case at San Salvador Island where leeward and windward localities did not have a difference in species distribution. The sampled communities are found

to be homogeneous across and within localities regardless of energy regimes and habitats. Additionally, species richness does not change when preservable and less preservable settings are analyzed separately regardless of the variable distribution of pits, tide pools, and crevices. Such preservable settings as tide pools, pits, and crevices could provide a good representation of the sampled biodiversity in comparison to the overall diversity of San Salvador Island (Fig. 3A).

Categorizing exposed and sheltered habitats based on preservation potential is heavily biased towards species with hard parts. This study focused solely on shelled gastropod species; therefore, this approach is not applicable to species that lack hard parts. Also, these analyses do not take into account additional species washing into preservable habitats producing a mixed assemblage. Mixed fossil rocky shore assemblages are common and can potentially increase the species richness of an assemblage (Hagey, 1991; Scott and Johnson, 1993; Johnson, 2006). In fossil rocky shore deposits, sheltered habitats such as tide pools, pits, and crevices are common sites of preserved assemblages (Harland and Pickerill, 1984; Hagey, 1991; Scott and Johnson, 1993; Valentine and Lipps, 1963). Because these habitats can be preserved and the sampled communities at San Salvador Island appear remarkably similar across and within localities, even a highly fragmentary fossil record (e.g., a site within one locality) would likely represent a fraction of the biodiversity and community structure of the rocky intertidal gastropod community and give insight into the rocky shore diversity.

1.6 Conclusions

The fossilization of rocky intertidal gastropods within habitats is possible and at the smallest level of sampling, the most common gastropod species have the potential to be captured. The overall gastropod diversity at San Salvador Island is low and none of the localities attained all 15

observed species. Localities varied in the number of species collected, but all but one, (Fernandez Bay) was composed of the same dominant species. All habitats that gastropod species occurred in showed similar diversity with species richness and evenness not varying meaningfully by habitat. When species richness and evenness were compared between different energy regimes, there was no substantial change in diversity, indicating that energy across the rocky shores does not impact the assembled diversity. Most noteworthy, when habitats were grouped by preservable and less preservable sites of fossilization there was no evident deviation of mean species richness at different scales from what was observed originally when all samples were analyzed together.

Investigations of rocky shore environments merit further consideration in understanding fossilization at higher latitudes. Such questions as do tropical, subtropical, or temperate rocky shores have comparable fossil records and what environment will likely have rocky shores communities more commonly preserved. These questions could provide more insight into how rocky shore communities can be fossilized and significantly add to our understanding of fossil rocky shores through time.

1.7 References

Appeltans, W., Bouchet, P., Boxshall, G.A., Fauchald, K., Gordon, D.P., Hoeksema, B.W.,
    Poore, G.C.B., van Soest, R.W.M., Stöhr, S., Walter, T.C., Costello, M.J., (eds.), 2011,
    World Register of Marine Species. Accessed at http://www.marinespecies.org on 2011-
    07-27.
Bovbjerg, R.V., 1984, Habitat selection in two intertidal snails, genus *Nerita*: Bulletin of Marine
    Science, v. 34, no. 2, p. 185-196.

Bulinski, K.V., 2007, Analysis of sample-level properties along a paleoenvironmental gradient:

   The behavior of evenness as a function of sample size: Palaeogeography,

   Palaeoclimatology, Palaeoecology, v. 253, no. 3-4, p. 490-508.

Burgett, J.M., Cubit, J.D., Thompson, R.C., 1987, Seasonal growth patterns in the tropical

   littorinid snails *Littorina angulifera* and *Tectarius muricatus*: The Veliger, v. 30, no. 1, p.

   11-23.

Buzas, M.A., and Hayek, L.-A.C., 2005, On richness and evenness within and between

   communities: Paleobiology, v. 31, no. 2, p. 199-220.

Branch, G.M., 1981, The biology of limpets: physical factors, energy flow, and ecological

   interactions: Oceanography and Marine Biology: An Annual Review, v. 19, p. 235-380.

Chapman, M.G., 1994, Small-scale patterns of distribution and size-structure of the intertidal

   littorinid, *Nodilittorina pyramidalis* in New South Wales: Australian Journal of Ecology,

   v. 19, p. 83-95.

Chapman, M.G., 2002, Patterns of spatial and temporal variation of macrofauna under boulders

   in a sheltered boulder field: Australian Ecology.

Connell, J.H., 1972, Community Interactions on Marine Rocky Intertidal Shores: Annual Review

   of Ecology and Systematics, v. 3, p. 169-192.

Emson, R.H., Morritt, D., Andrews, E.B., and Young, C.M., 2002, Life on a hot dry beach:

   behavioral, physiological, and ultrastructural adaptations of the littorinid gastropod

   Cenchritis (*Tectarius*) *muricatus*: Marine Biology, v. 140, p. 723-732.

Fisher, R.A., Corbet, A.S., and William, C.B., 1943, The relation between the number of species

   and the number of individuals in a random sample of an animal population: Journal of

   Animal Ecology, v. 12, p. 42-58.

Foster, M.S., De Vogelaere, A.P.C., Harrold, J.S., Pearse, Thum, A.B., 1988, Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California: Memoirs of the California Academy of Sciences, v. 9, p. 1-45.

Fraschetti, S., Terlizzi, A., Benedetti-Cecchi, L., 2005, Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation: Marine Ecology Progress Series, v. 296, p. 13-29.

Garrity, S.D., 1984, Some Adaptations of Gastropods to Physical Stress on a Tropical Rocky Shore: Ecology, v. 65, no. 2, p. 559-574.

Garrity, S.D., and Levings, S.C., 1984, Aggregation in a tropical neritid: Veliger, v. 27, p. 1-6.

Gochfeld, D.J., and Minton, D.T., 2001, When to move and where to go: Movement behavior of the tropical littorinid *Cenchritis muricatus* (Linnaeus, 1758): Journal of Shellfish Research, v. 20, no. 1, p. 447-452.

Hagey, F.M., 1988, Pleistocene molluscan faunas on San Salvador Island, Bahamas: 1st Keck Research Symposium in Geology Proceedings, v. 1, p. 34-38.

Hagey, F.M., 1991, Pleistocene molluscan assemblages on San Salvador Island, Bahamas: Preliminary investigations and interpretations: Proceedings of the fifth symposium on the geology of the Bahamas, v. 5, p. 103-116.

Hagey, F.M., and Mylroie, J.E., 1995, Pleistocene lake and lagoon deposits, San Salvador Island, Bahamas: Special Paper - Geological Society of America, v. 300, p. 77-90.

Hammer, Ø., Harper, D., Ryan, P., 2001, PAST: Paleontological statistics software for education and data analysis: Palaeontologia Electronica, v. 4, no. 1.

Harland, T.L., and Pickerill, R.F., 1984, Ordovician rocky shoreline deposits - the basal Trenton Group around Quebec City, Canada: Geological Journal, v. 19, p. 271-298.

Hayes, M.L., Johnson, M.E., and Fox, W.T., 1993, Rocky-Shore Biotic Associations and Their Fossilization Potential: Isla Requeson (Baja California Sur, Mexico): Journal of Coastal Research, v. 9, no. 4, p. 944-957.

Hohenlohe, P.A., 2003, Distribution of sister *Littorina* species, I: Tenacity and the wave-exposure gradient: The Veliger, v. 46, no. 2, p. 162-168.

Horwitz, M.H., and Roberts, T.M., 2010, Geomorphic zoning and eogenetic karst on limestones within the supratidal environment: San Salvador, Bahamas: Studia Universitatis Babes-Bolyai, Geologia, v. 55, no. 1, p. 17-27.

Hubbel, S.P., 2001, The unified neutral theory of biodiversity and biogeography, Princeton, Princeton University Press.

Hurlbert, S.H., 1984, Pseudoreplication and the design of ecological field experiments: Ecological Monographs, v. 54, no. 2, p. 187-211.

Johnson, M.E., 2006, Uniformitarianism as a guide to rocky shore ecosystems in the geological record: Canadian Journal of Earth Sciences, v. 43, p. 1119-1147.

Johnson, M.E., Skinner, D.F., and Macleod, K.G., 1988, Ecological zonation during the carbonate transgression of a late Ordovician rocky shore (Northeastern Manitoba, Hudson Bay, Canada): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 65, no. 1-2, p. 93-114.

Johnson, M.E., and Baarli, B.G., 1999, Diversification of rocky-shore biotas through geologic time: Geobios, v. 32, no. 2, p. 257-273.

Johnson, M.P., Allcock, A.L., Pye, S.E., Chambers, S.J., Fitton, D.M., 2001, The effects of dispersal mode on the spatial distribution patterns of intertidal molluscs: Journal of Animal Ecology, v. 70, p. 641-649.

Judge, M.L., Duell, R., Burriesci, L., Moarsi, W., 2009, Life in the supralittoral fringe:

    Microhabitat choice, mobility and growth in the tropical periwinkle *Cenchritis*

    (=*Tectarius*) *muricatus* (Linneaus, 1758): Journal of Experimental Marine Biology and

    Ecology, v. 369, p. 148-154.

Kaplan, E.H., Kaplan, S.L., and Peterson, R.T., 1999, A Field Guide to Southeastern and

    Caribbean Seashores: Cape Hatteras to the Gulf Coast, Florida, and the Caribbean:

    Houghton Mifflin, 480 p.

Kennelly, S.J., and Underwood, A.J., 1992, Fluctuations in the distribution and abundances of

    species in sublittoral kelp forests in New South Wales: Australian Journal of Ecology, v.

    17, p. 367-382.

Kidwell, S.M., 2001, Preservation of species abundance in marine death assemblages: Science,

    v. 294, no. 5544, p. 1091-1094.

Kowalewski, M., Gürs, K., Nebelsick, J.H., Oschmann, W., Piller, W.E., Hoffmeister, A.P.,

    2002, Multivariate hierarchical analyses of Miocene mollusk assemblages of Europe:

    Paleogeographic, paleoecological, and biostratigraphic implications: Geological Society

    of America Bulletin v. 114, p. 239-256.

Lang, R.C., Britton, J.C., Metz, T., 1998, What to do when there is nothing to do: the ecology of

    Jamaican intertidal littorinidae (Gastropoda: Prosobranchia) in repose: Hydrobiologia, v.

    378, p. 161-185

Layou, K.M., 2007, A quantitative null model of additive diversity partitioning: examining the

    response of beta diversity to extinction: Paleobiology, v. 33, p. 116-124..

Lindberg, D.R., and Lipps, J.H., 1996, Reading the chronicle of Quaternary temperate rocky

    shore faunas, *in* Jablonski, D. J., Douglas, H.E., and Lipps, J.H., ed., Evolutionary

    Paleobiology: Chicago, University of Chicago Press, p. 161-184.

MacArthur, R.H., 1957, On the relative abundance of bird species: Proceedings of the National

    Academy of Sciences, v. 43, no. 3, p. 293-295.

Magurran, A.E., 2004, Measuring Biological Diversity, Oxford, Blackwell Science, 256 p.

McClintock, J., Melvin, P., Marion, K., 2007, Movement of periwinkle snails on the rocky

    shores of San Salvador: Bahamas Naturalist and Journal of Science, no. September, p.

    63-68.

McMahon, R.F., 1990, Thermal tolerance, evaporative water loss, air-water oxygen consumption

    and zonation of intertidal prosobranchs: a new synthesis: Hydrobiologia, v. 193, p. 241-

    260.

Minton, D.T., and Gochfeld, D.J., 2001, Is life on the tropical shore really so hard?: the role of

    abiotic factors in structuring a supralittoral molluscan assemblage: Journal of Shellfish

    Research, v. 20, p. 477-483.

Motomura, I., 1932, On the statistical treatment of communities: Zoological Magazine (Tokyo),

    v. 44, p. 379-383.

Mylroie, J.E., 2008, Late Quaternary sea-level position: Evidence from Bahamian carbonate

    deposition and dissolution cycles: Quaternary International, v. 183, no. 1, p. 61-75.

Nakaoka, M., Ito, N., Yamamoto, T., Okuda, T., Noda, T., 2006, Similarity of rocky intertidal

    assemblages along the Pacific coast of Japan: effects of spatial scales and geographic

    distance: Ecological Research, v. 21, p. 425-435.

Noda, T., 2004, Spatial hierarchical approach in community ecology: a way beyond a low predictability in local phenomenon: Population Ecology, v. 46, p. 105-117.

Olszewski, T.D., 2004, A unified mathematical framework for the measurement of richness and evenness within and among multiple communities: Oikos, v. 104, p. 377-387.

Okuda, T., Noda, T., Yamamoto, T., Ito, N., and Nakaoka, M., 2004, Latitudinal gradient of species diversity: multi-scale variability in rocky intertidal sessile assemblages along the Northwestern Pacific coast: Population Ecology, v. 46, no. 2, p. 159-170.

Paine, R.T., 1977, Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory: The Changing Scenes in the Natural Sciences, Philadelphia, Academy of Natural Sciences, p. 245-270.

Paine, R.T., and Levin, A.S., 1981, Intertidal Landscapes: Disturbance and the Dynamics of Pattern: Ecological Monographs, v. 51, no. 2, p. 145-178.

Peckol, P., Guarnagia, S., Fisher, M., 1989, Zonation and behavioral patterns in the intertidal gastropods *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) and *Nerita versicolor* Gmelin, 1791, in the Bahamas: Veliger, v. 32, p. 8-15.

Powell, M.G., and Kowalewski, M., 2002, Increase in evenness and alpha diversity through the Phanerozoic: Comparison of Early Paleozoic and Cenozoic marine fossil assemblages: Geology, v. 30, p. 331-334.

Preston, F.W., 1948, The commonness, and rarity of species: Ecology, v. 29, no. 3, p. 254-283.

Redfern, C., 2001, Bahamian seashells: A thousand species from Abaco, Bahamas: Boca Raton, FL, Bahamianseashells.com, Inc., 280 pp., 124 pls.

Reid, D.G., 1989, The Comparative Morphology, Phylogeny and Evolution of the Gastropod
   Family Littorinidae: Philosophical Transactions of the Royal Society of London. Series
   B, Biological Sciences, v. 324, no. 1220, p. 1-110.

Rivadeneira, M., FernÁndez, M., Navarrete, S., 2002, Latitudinal trends of species diversity in
   rocky intertidal herbivore assemblages: spatial scale and the relationship between local
   and regional species richness: Marine Ecology Progress Series, v. 245, p. 123-131.

SAS Institute, 2010, SAS/IML software, ver. 9.0: Cary, North Carolina, SAS Institute, p. 501.

Scott, J.H., Jr., and Johnson, M.E., 1993, Lateral variation in the geomorphology of a Pleistocene
   rocky coastline at Kalbarri, Western Australia: Journal of Coastal Research, v. 9, p. 1013-
   1025.

Simpson, E.H., 1949, Measurement of diversity: Nature v. 163, p. 688.

Underwood, A.J., 1981, Techniques of analysis of variance in experimental marine biology and
   ecology: Annual review of Oceanography and Marine Biology, v. 19, p. 513-605.

Underwood, A.J., 1994, On Beyond BACI: Sampling Designs that Might Reliably Detect
   Environmental Disturbances: Ecological Applications, v. 4, no. 1, p. 4-15.

Valentine, J.W., and Lipps, J.H., 1963, Late Cenozoic Rocky shore Assemblages from Anacapa
   Island, California: Journal of Paleontology, v. 37, no. 6, p. 1292-1302.

Valentine, J.W., 1961, Paleoecologic molluscan geography of the Californian Pleistocene:
   University of California Publications in Geological Sciences, v. 34, p. 309-442.

Valentine, J.W., 1980, Camalú: A Pleistocene Terrace Fauna from Baja California: Journal of
   Paleontology, v. 54, no. 6, p. 1310-1318.

Valentine, J.W., 1989, How Good was the Fossil Record? Clues from the California Pleistocene:
   Paleobiology, v. 15, no. 2, p. 83-94.

Vermeij, G.J., 1987, The dispersal barrier in the tropical Pacific: implications for molluscan speciation and extinction: Evolution, v. 41, p. 1046-1058.

Wagner, P.J., Kosnik, M.A., Lidgard, S., 2006, Abundance distributions imply elevated complexity of Post-Paleozoic marine ecosystems: Science, v. 314, p. 1289-1292.

Whittaker, R.H., 1965, Dominance and Diversity in Land Plant Communities: Science, v. 147, no. 3655, p. 250-260.

Williams, S.T., and Reid, D.G., 2004, Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*: Evolution, v. 58, no. 10, p. 2227-2251.

Zar, J.H., 1999, Biostatistical analysis: The University of Michigan, Prentice Hall, 663 p.

1.8 Tables and Captions

Table 1.1. List of all rocky intertidal gastropod species with their total number of occurrences at each sampling level and within habitats surveyed.

Genus	Species	Number of individuals	Localities	Sites	Transects	Quadrats	Bare	Pits	Tide pools	Crevices
							Habitats			
Echinolittorina	angustior	8,183	10	34	92	278	3,974	3,173	847	189
Echinolittorina	mespilium	3,991	9	25	53	120	546	1,148	2,215	82
Echinolittorina	dilatata	1,695	10	26	60	152	754	657	282	2
Nerita	versicolor	1,346	10	36	90	247	752	418	115	61
Echinolittorina	jamaicensis	1,225	10	33	78	189	602	444	133	46
Nerita	tessellata	702	9	26	54	119	111	202	150	239
Cenchritis	muricatus	243	5	9	15	30	139	100	4	-
Echinolittorina	ziczac	129	7	15	21	38	89	38	2	-
Nerita	peleronta	97	8	25	41	64	47	26	22	2
Puperita	Pupa	48	2	1	2	3	-	1	47	-
Littoraria	angulifera	26	3	4	5	5	4	22	-	-
Cittarium	pica	13	5	8	8	10	6	3	3	1
Smaragdia	virdis	2	1	1	1	1	-	-	2	-
Stramonita	floridana	2	1	2	2	2	2	-	-	-
Plicopurpura	patula	1	1	1	1	1	-	1	-	-
Total	**15**	**17,703**	**10**	**40**	**120**	**480**	**7,026**	**6,233**	**3,822**	**622**

Table 1.2. ANOVA of gastropod assemblages across localities.

Source of variation	DF	Sum of Squares	Mean Square	F Ratio	p-value	R^2
Locality	9	42.43	4.71	3.75	0.0003***	0.174
Error	160	200.91	1.26			
Total	169	243.35				

Table 1.3. Comparison of locality mean richness using Kramer-Tukey's Honest Significant Difference (HSD).

Locality	n	Mean # of species*		Std Error
Sue Point	24	4.25	a	0.229
North Point	5	4.20	a	0.501
Holiday Track	19	4.00	a	0.257
Grotto Beach	11	3.82	a	0.338
Rocky Point	19	4.47	a	0.257
Fernandez Bay	5	1.80	b	0.501
French Bay	12	3.17	ab	0.323
Rice Bay	17	3.65	a	0.272
Barkers Point	17	3.94	a	0.272
The Gulf	41	3.59	a	0.175

* Means followed by the same letter are not significantly different at the 0.05 level using Kramer-Tukey HSD (Zar, 199).

Table 1.4. Locality level rank abundance distributions compared to theoretical abundance models and to locality community evenness.

		Sue Point	North Point	Holiday Track	Grotto Beach	Rocky Point	Fernandez Bay	French Bay	Rice Bay	Barkers Point	The Gulf
Geometric	*p*	0.004	0.006	0.0009	>0.10	0.02	<0.0001	<0.0001	0.002	<0.0001	0.041
	Chao 2	13.59	12.54	16.32	6.24	11.71	216.4	175.6	15.03	26.86	8.28
Log-Series	*p*	> 0.10	0.003	0.032	>0.10	0.311	<0.0001	<0.0001	>0.10	<0.0001	0.014
	Chao 2	3.64	17.73	12.19	6.3	5.95	56.86	76.82	1.4	27.48	14.23
Broken Stick	*p*	0.002	< 0.0001	0.0002	0.0002	0.001	<0.0001	<0.0001	0.012	<0.0001	<0.0001
	Chao 2	22.58	52.29	28.59	26.83	26.22	126.6	151.5	18.05	69.8	39.1
Log-Normal	*p*	-	-	-	-	-	-	-	-	-	-
	Chao 2	-	-	-	-	-	-	-	-	-	-
Simpson Evenness		0.36	0.27	0.37	0.29	0.30	0.17	0.13	0.37	0.20	0.31

Table 1.5. Species richness and evenness across habitats and energy regimes.

		Exposed	Sheltered		
	Energy	Bare	Pits	Tide pools	Crevices
Mean Richness	Low	4.5	3.6	4.08	2.6
	Moderate	3.5	4.4	4.75	-
	High	3.44	3.85	3.23	-
	All	3.9	3.9	3.8	3
Evenness	All	0.55	0.53	0.5	0.65
Percent Occupation (%)	All	39.7	35.2	21.6	3.5

1.9 Figure and Figure Captions
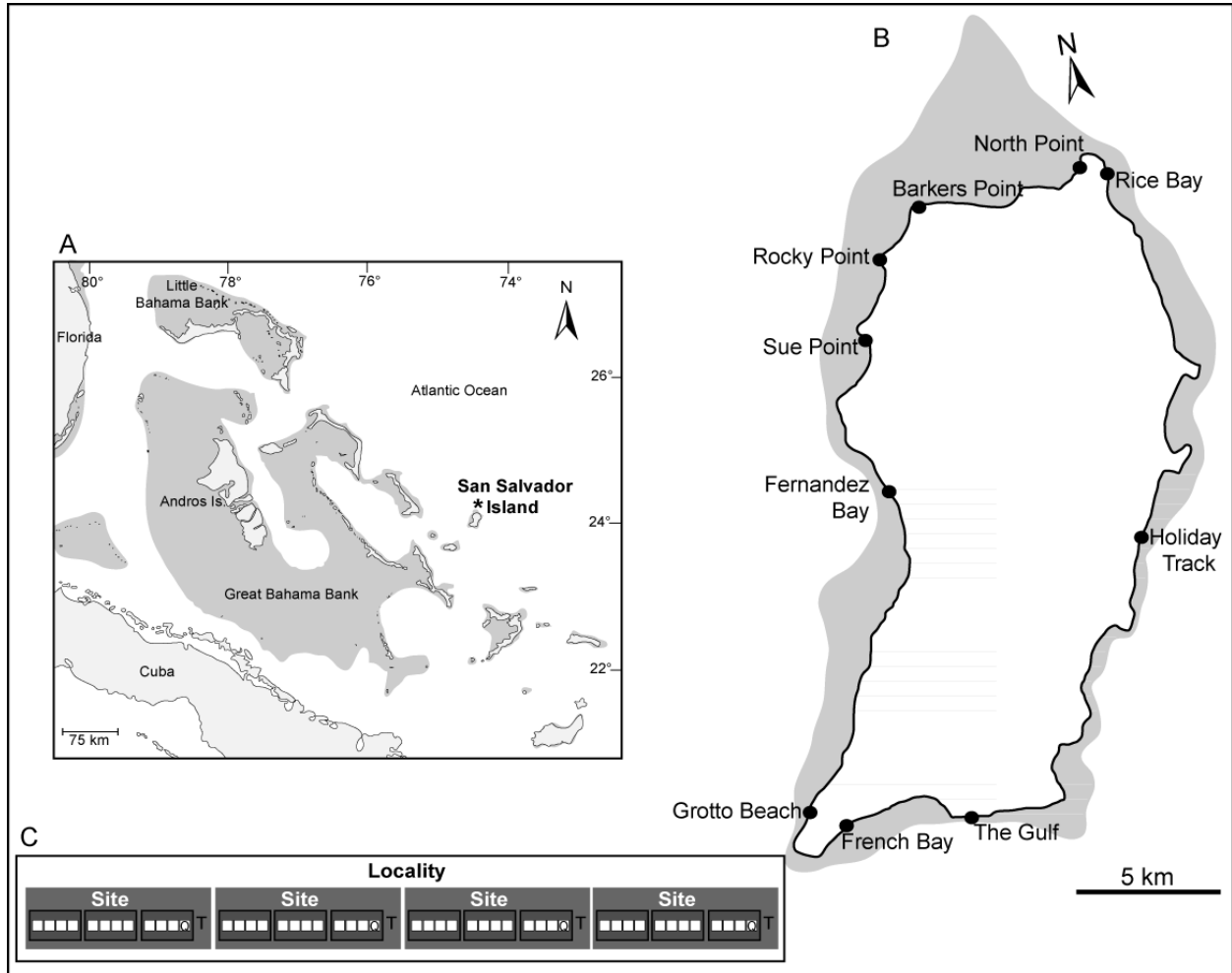
Figure 1.1 Map of the region showing the (A) Caribbean and San Salvador Island (bold and starred). (B) Map of the study area, San Salvador Island, an isolated carbonate platform separated from the Great Bahamas bank (the carbonate platforms are shaded in gray). All 10 localities are identified on the island. (C) Hierarchical sampling scheme shown for one locality following randomized block design (Hurlbert, 1984). Each locality had four, 50 meter sites (large gray box) that were separated into three, five meter transects (black lined box, T) that were further partitioned into four 30x30 cm quadrats (white boxes, Q).
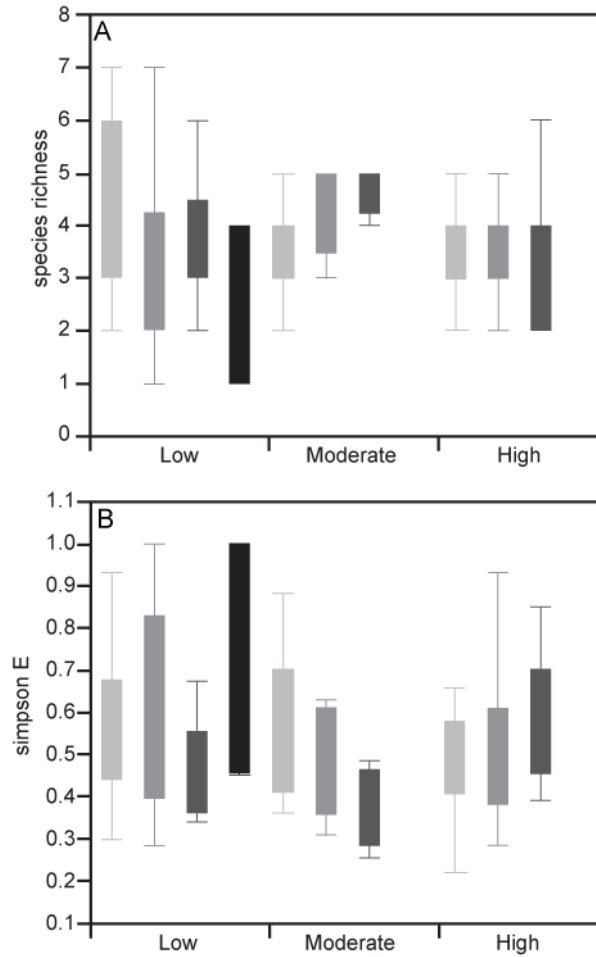
Figure 1.2 Diversity measures for different habitats across energy regimes around the island (high, moderate, and low). A) Species richness. B) Evenness. 95% confidence intervals were calculated around the mean richness and evenness for each habitat in the different energy settings, some confidence limits occurred in the minimum and maximum boxes. Habitats: bare and exposed habitats in light gray, pitted surfaces in medium gray, tide pools in dark gray, and creviced habitats in black. Note that crevices were not present in moderate- and high-energy localities.
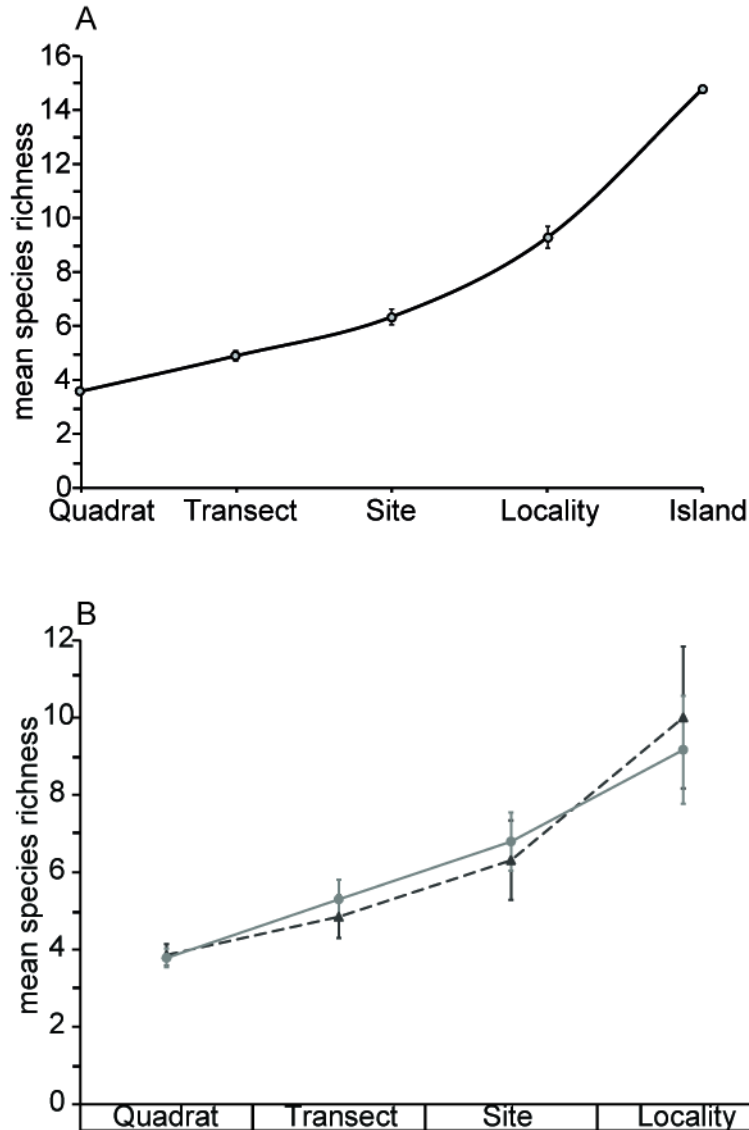
Figure 1.3 A) Mean species richness at all sampling levels with 95% confidence intervals. Sampling intensity increased from the finest level (quadrat) to the largest level, the island. B) Mean species richness at all sampling levels for preservable (light gray circles) and less preservable (dashed triangles) settings with 95% confidence intervals. Preservable settings encompassed species occurring in sheltered habitats such as pits, tide pools, and crevices. Less preservable settings included species occurrences from bare and exposed surfaces.
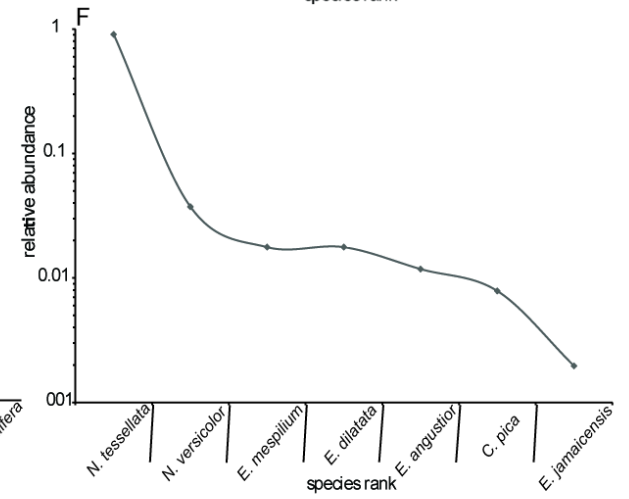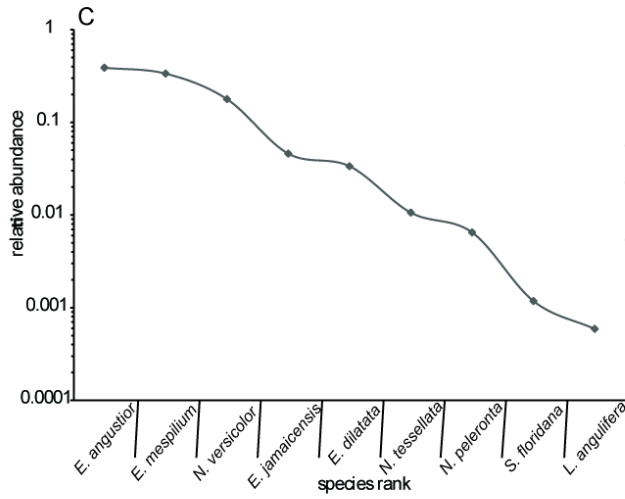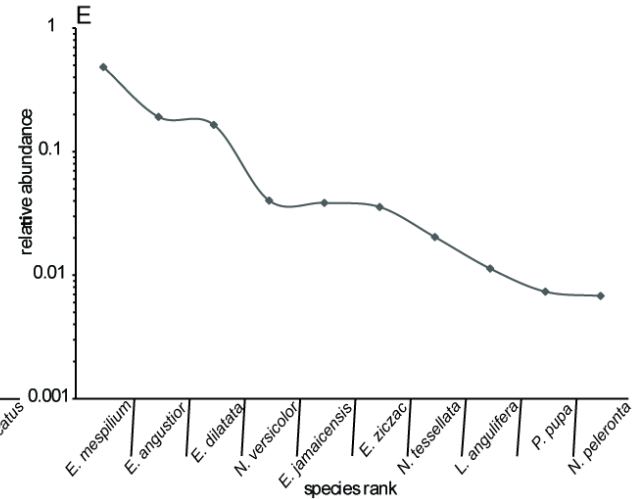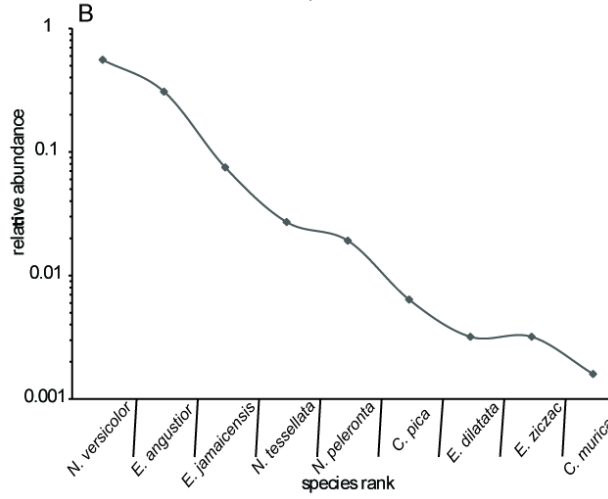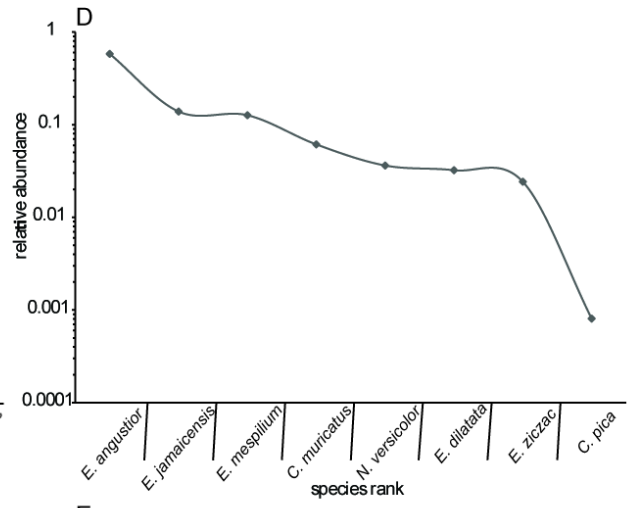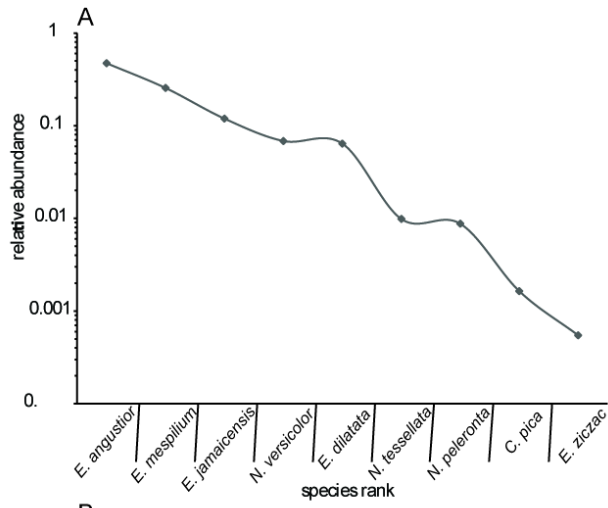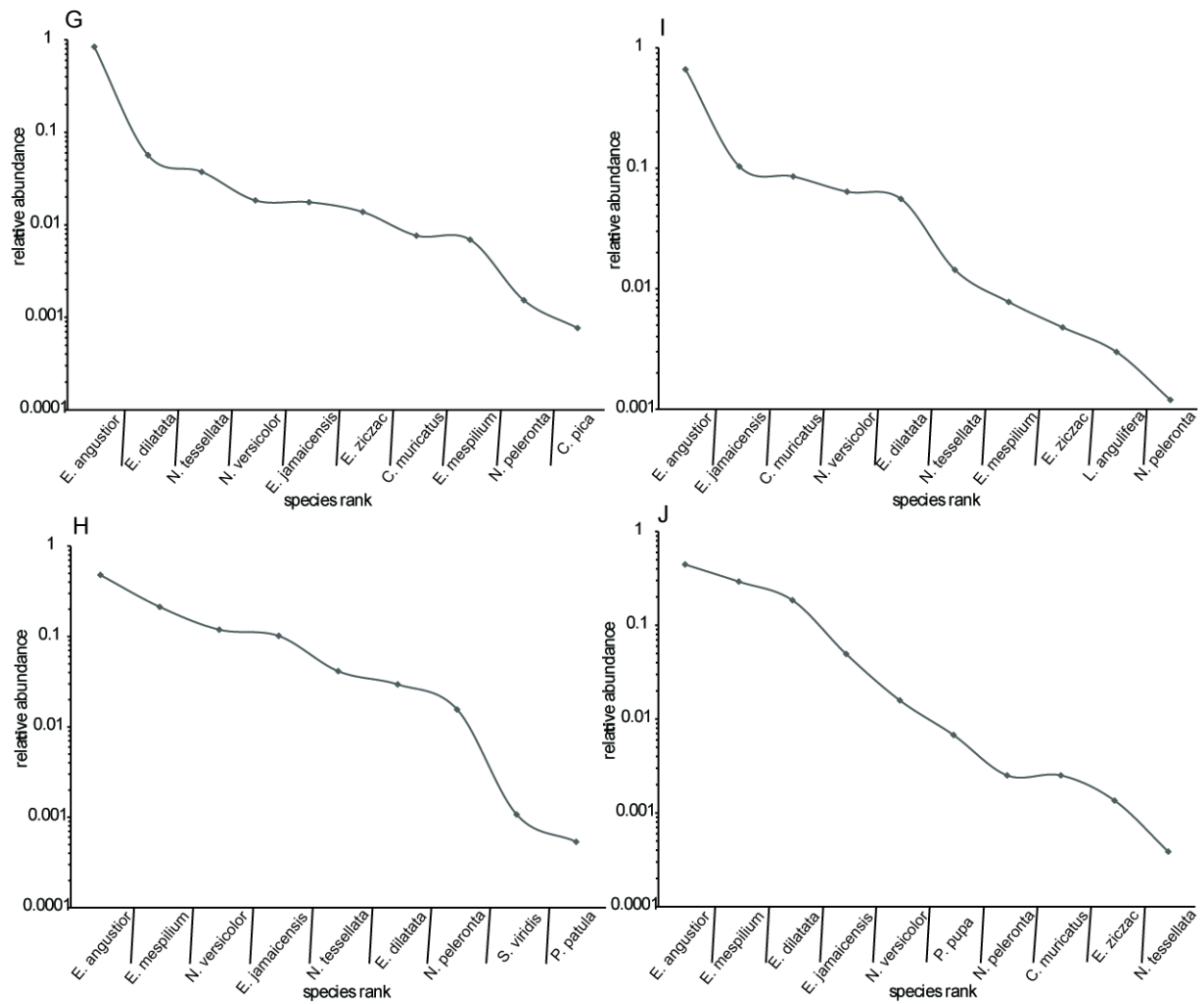
Figure 1.4 Rank abundance curves of intertidal gastropod species at each locality, log transformed. Note a maximum of 11 species are plotted, not 15 species at each locality because the total number of species around the island were not sampled at the locality level. A) Sue Point B) North Point C) Holiday Track D) Grotto Beach E) Rocky Point F) Fernandez Bay G) French Bay H) Rice Bay I) Barkers Point J) The Gulf.

CHAPTER 2

Quantitative Bathymetric Models for Late Quaternary Transgressive-Regressive Cycles of the Po Plain, Italy

JACALYN M. WITTMER, TROY A. DEXTER[1], DANIELE SCARPONI[2], ALESSANDRO AMOROSI[2], & MICHAŁ KOWALEWSKI[1]

[1]Florida Museum of Natural History, University of Florida, Department of Natural History, Museum Road, PO Box 117800, Gainesville, FL 32611

[2] University of Bologna, Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Via Zamboni 67, Bologna, Italy 40126

2.1 Abstract

In marine settings, quantitative bathymetric models can be developed using various water depth proxies, including epibiont distribution, sedimentological features, and the distribution of benthic taxa in time and space. Here, the late Quaternary bathymetric history of the Po coastal plain (Italy) has been reconstructed using mollusk samples from a network of 16 cores. Multiple analytical approaches have been applied in a comparative fashion. A direct ordination approach was used to estimate sample bathymetry using weighted averaging of genera with known preferred depth. Weighted averaging carries an advantage of analytical simplicity and produces direct ordination models expressed in environmentally meaningful units. Indirect ordination methods, based on depth estimates developed using posteriori-calibrated ordination strategies (Correspondence and Detrended Correspondence Analysis calibrated against present-day bathymetric data) yielded results consistent with weighted averaging. Regardless of the choice of analytical methods, mollusk assemblages yielded bathymetric proxies congruent with independent sequence stratigraphic interpretations derived previously for both the late Pleistocene and Holocene transgressive-regressive cycles. The mollusk-derived proxies quantify spatial bathymetric gradients across the basin and local trends in absolute water depth in response to relative changes in sea-level. However, for cores located in the most proximal part of the basin, mollusk-based ordinations failed to provide viable estimates due to inclusion of mixed marine and non-marine mollusk faunas and scarcity of fossiliferous horizons necessary for adequate quantitative sampling. The multiple analytical approaches cross-evaluated in this study consistently suggest that high-resolution quantitative bathymetric estimates can be derived for mollusk samples independent of stratigraphy for fully marine settings. When applied simultaneously to both samples and taxa, these approaches provide a viable strategy for quantifying stratigraphic and paleontological patterns and enhancing interpretations of basin-scale depositional systems.

2.2 Introduction

The field of stratigraphic paleobiology has progressed considerably in the past 20 years: an

increasing integration of sequence stratigraphy and quantitative paleobiology has enhanced our

ability to explore jointly stratigraphic and paleobiological patterns in time and space (Brett 1995;

Holland 1995, 2000; Patzkowsky and Holland 1996; Holland et al. 2001; Scarponi and

Kowalewski 2004; Holland and Patzkowsky 2007; Hendy 2013). In particular, fossil-derived

patterns provide us with an independent assessment of environmental changes potentially

refining and cross-testing sedimentary-based interpretations and models (Holland 2000; Miller et

al. 2001; Peters 2005, 2006; Peters and Heim 2010; Patzkowsky and Holland 2012).

It has been shown that taxonomic composition of assemblages at the basin scale correlate to environmental gradients such as water depth (bathymetry), salinity, energy, substrate, oxygen, or nutrient levels (Funder et al. 2002; Ceregato et al. 2007; Patzkowsky and Holland 2012 and references therein). Also in ecologic studies, bathymetry, which tends to correlate with many other environmental variables, is commonly invoked to describe faunal gradients (e.g. Carney 2005; Olabarria 2006; Konar et al. 2008; Smale 2008, Zuschin et al. 2014) and has been demonstrated as an effective tool for delineating past biotic changes (Holland 2005; Hendy and Kamp 2007). However; other variables can also leave an important or even overriding imprint in the geological record (Lafferty et al. 1994; Redman et al. 2007; Bush and Brame 2010; Huntley and Scarponi, 2012). The focus of this paper is to evaluate water depth as an environmental variable and assess its importance in controlling spatial and temporal ecological patterns within a sequence stratigraphic context.

Changes in water depth along and across sedimentary successions can be estimated using various strategies. Sedimentological features such as grain size, bedding, and sedimentary structures are frequently employed to semi-quantitatively reconstruct bathymetric gradients (Dattilo 1996; Zong and Horton 1999; Holland and Patzkowsky 2007). Epibiont and microendolith distribution can also be used to identify the photic zone (Smrecak 2008 unpub. thesis; Hannon and Meyer 2014). Lastly, macrobenthic marine invertebrates can be used to develop numerical bathymetric-based interpretations of sedimentary successions by means of multivariate ordination analyses (e.g., Holland et al. 2001; Scarponi and Kowalewski 2004; Scarponi and Angeletti 2008). This study focuses primarily on the last of these approaches.

Here we examine the late Quaternary successions of the Po coastal plain that is part of an active sedimentary basin well understood in terms of its sequence stratigraphic architecture and recent sea level history.

Quaternary successions offer a powerful advantage for exploring paleoecological patterns within their sequence stratigraphic framework because samples are dominated by extant taxa with well-understood biology, ecology, biogeography, and taxonomic/phylogenetic affinity. Such paleoecological data can be calibrated against estimates derived from modern environments and provide us with a direct means for testing the accuracy and strength of quantitative paleoecological strategies for resolving depositional environments and outline sequence stratigraphic interpretations of sedimentary successions.

In a pilot study assessing the late Quaternary fossiliferous marine sequences of the Po coastal plain (Italy), Scarponi and Kowalewski (2004) documented a bathymetric gradient from three cores representing a two-dimensional cross-section oblique to the regional depositional profile. These incipient data indicated that paleoecological data coupled with ecological estimates from modern environments can provide a powerful tool for joint stratigraphic paleobiological analyses of Quaternary sedimentary basins. Building on this initial analysis, we undertake here a comprehensive examination of the late Quaternary successions of the southeastern Po coastal plain using a three-dimensional network of cores distributed along and across the depositional profile of the basin. From these cores, we assess the value of an integrated analysis of sequence stratigraphic and quantitative paleoecological patterns. The aim of this project is three-fold: (1) determine the viability of paleoecological data for deriving quantitative estimates of water depth, (2) compare different analytical strategies for deriving such bathymetric estimates, and (3) explore the informative value of this approach for

41

quantifying bathymetric gradients and enhancing stratigraphic interpretations of sedimentary successions.

2.3 Geological Setting

The Po plain, situated in northern Italy, is the emerged surface of a relatively large foreland basin bounded by the Alps to the north and the Apennines to the south (i.e., Po Basin, Fig. 1a). Its rock record includes a thick succession of strongly deformed Pliocene and less tectonically disturbed Pleistocene to Holocene deposits (Pieri and Groppi 1981). The Po Basin geometry has been investigated in detail during the last decades through integration of seismic studies and well-log interpretations aimed at exploration of natural resources. These studies have led to internal subdivision of the Pliocene-Quaternary succession of the Po Basin into a series of 3rd-order depositional sequences. The basal unconformities are well developed at the basin margin, where they mark phases of dramatic basin reorganization generally related to phases of intense tectonic activity (e.g., Gunderson et al. 2011). These unconformities grade basinwards into correlative conformable surfaces.

The uppermost 3rd-order depositional sequence of the Po Basin consists of Middle Pleistocene to Holocene deposits. Based upon magnetostratigraphic data, its lower boundary (0.87 Ma BP according to Muttoni et al. 2007) is close to the Matuyama-Brunhes reversal. This depositional sequence consists of a series of eight vertically stacked, higher (4th)-order depositional cycles, which exhibit distinctive transgressive-regressive trends and reflect a clear glacio-eustatic induced cyclicity (Amorosi et al. 1999; Fig. 1b).

Detailed sedimentological and paleobiological core-based analyses integrated in a well resolved chronostratigraphic framework (amino acid, radiocarbon and pollen) documented the

42

paleogeographic and paleoclimatic development of the Po coastal plain during the latest

Quaternary and its marked relationship with the most recent Quaternary eustatic sea-level

changes. Two prominent stratigraphic markers, corresponding to characteristic wedge-shaped

coastal sand bodies with very similar internal architecture, are recorded beneath the modern

coastal plain at 0-30 m and 100-130 m core depth intervals, respectively. These nearshore to

shallow-marine packages are separated by a thick succession of alluvial deposits. Recent studies

(e.g., Amorosi et al. 2004), have documented that these coastal sands were deposited under a

predominantly glacio-eustatic (100 ky) control during the last two major transgressive pulses and

subsequent sea-level highstands, corresponding to Marine Isotope Stage (MIS) 5e and 1,

respectively (Fig. 1b). In contrast, coastal to alluvial sedimentation took place in a subsiding

setting, during the long phase of sea-level fall between MIS 5d and 2. The deposits and pollen

records recovered from the deepest parts of the cores suggest phases of episodic sedimentation

and widespread erosion in alluvial settings corresponding to - and/or immediately postdating -

the penultimate glacial maximum (i.e., MIS 6).

Rapid climatic change (and subsequent sea-level rise) following the late Middle

Pleistocene glacial maximum induced a rapid landward migration of the depositional

environments. This landward shift of the shoreline is recorded by superposition of the lower

wedge-shaped coastal body onto the glacial continental deposits. In sequence stratigraphic terms,

this unit corresponds to transgressive (TST) and highstand (HST) deposits related to MIS5e.

The overall eustatic sea-level fall documented between ~120 and ~30 ka (MIS 5e/5d

transition to MIS 3/2 transition), induced a forced and generalized downward shift of facies,

documented in the study area by coastal (MIS 5e-5a) to alluvial plain (MIS 4-3) bodies of

variable thickness bounded by clustered erosional surfaces (falling-stage systems tract: FSST)

(Amorosi et al. 2004). Paleosols are also recorded (especially landwards), suggesting fluvial entrenchment during falling sea-level. However, lesser climatic changes and higher frequency pulses punctuated the long-lived erratic FSST and are recorded in the sedimentary succession by relatively continuous, peat-enriched deposits representing primarily lagoon (MIS 5c) to wetland (MIS 5a and 3) depositional settings.

The sedimentary expressions of the Last Glacial Maximum (LGM) and the early phases of the post-LGM transgression (MIS 2) are generally scarce. Channel entrenchment at the MIS 3/2 led to a widespread paleosol development in the study area, whereas the active lowstand sedimentation (LST) was restricted to the adjacent incised valleys. Consequently, in interfluves of the depositional sequence the overlying transgressive surface tends to merge with the sequence boundary (SB).

The ensuing post-glacial dynamics (MIS 1) are manifested in a well-studied and chronologically framed wedge-shaped coastal body (depicting a transgressive-regressive cycle), which shows striking affinity with the late Pleistocene (MIS 5e) one. Hence, the transgressive surfaces (TSs) of MIS 5e and MIS 1 age, which mark facies shifts in more distal parts of the basin while recording important sedimentary hiatuses farther inland (Amorosi et al. 2003 for detailed information), are considerably easier to identify than the other key sequence stratigraphic surfaces.

The lower transgressive deposits record the rapid landward migration of a lagoon-barrier-estuary system, giving way to widespread marginal marine sedimentation in the eastern part of the study area. During the early stages of transgression, the backstepping migration of coastal facies resulted in the development of a characteristic wave ravinement surface, usually enriched in fossils, which divides the transgressive deposits into two wedges thickening in opposite

directions (Fig. 1 in Scarponi and Kowalewski 2004). Across the investigated area, the ravinement surface marks the boundary between the lower TST (marsh and inlet facies associations) and the upper TST (lower shoreface and offshore transition deposits).

During the late phase of fast sea level rise, the shoreline shifted up to ~20/30 km west of its present day position, recording the maximum marine ingression. This stratigraphic interval, developed at peak transgression, includes the maximum flooding surface (MFS). In cores, the MFS marks the turnaround from a deepening-up to a shallowing-up tendency. This surface has no obvious physical expression, and has been identified uniquely on the basis of subtle paleontological features (Scarponi and Kowalewski 2004; Amorosi et al. 2008 and references therein).

From the middle Holocene onwards, the reduced rate of eustatic sea-level rise induced the basinward migration of coastal depositional environments. The basinward shift of facies took place at progressively increasing rates (e.g., Amorosi et al. 2008; Scarponi et al. 2013), as documented by the transition from an aggradational to a distinctive progradational stacking pattern of facies. At relatively distal locations, progradation is expressed in marine deposits by shallowing-upward (i.e., offshore to nearshore or prodelta to delta front) deposits. Landwards, delta plain and coastal plain deposits record a dynamic environmental mosaic of wetlands, fluvial channels and partly emerged lands, where autogenic (e.g., channel avulsion, differential compaction, delta lobe abandonment) and allogenic (higher frequency climatic oscillation) signals are tangled and difficult to decouple.

In summary, a distinctive sequence stratigraphic architecture of the Po plain is well understood in terms of facies architecture, sequence stratigraphic patterns driven by base level

changes, vertical and lateral changes in rates of depositional processes, and the scale of time-averaging affecting paleontological samples.

2.4 Sampling Methods and Datasets

A total of 16 cores were selected based on geographic location and core depth to ensure adequate coverage of both the Holocene and Pleistocene cycles. These cores, were drilled as part of a large multidisciplinary effort also focused on understanding in detail the subsurface stratal patterns of late-Quaternary Po plain deposits (i.e., the new Geologic Map of Italy project, http://www.apat.gov.it/) and evaluate groundwater salinity dynamic in the coastal aquifer near Ravenna (Greggio et al., 2012).

The sequence stratigraphic interpretation of these cored deposits has already been developed based on integrated sedimentological, geochemical, and micropaleontological evidence (Amorosi et al. 2003 and references therein). Various micropaleontological tools (foraminifers, ostracods, and pollen) have been employed to reconstruct depositional environment spatial and temporal development within Po coastal plain deposits, highlighting short term environmental oscillations under a strong glacio-eustatic control (Amorosi et al. 2004). In addition, 11 out of the 16 cores have been time constrained using ^{14}C radiometric dates mainly based on peat layers and ^{14}C-calibrated amino acid racemization dates for ~250 bivalve shells (Scarponi et al. 2013 and references therein).

A total of 611 bulk samples (~375 cm[3] each) were collected from the studied cores with vertical spacing of 4m or less. Samples were dried (24 hours at 45˚C), soaked in ~4% H_2O_2 (≤ 4 hours, depending on lithology), and wet sieved down to 1mm screens. For some samples (massive-clay), this process was repeated at least two times. For each sample, all mollusk

specimens (the most abundant macrofossil group represented in cores) were identified to the species level (when possible) and counted. Less frequent macrobenthic remains (such as serpulids or crustaceans) were noted but not counted. The term specimen is applied here to a complete fossil or a fragment which can be reliably identified as unique individual (e.g., apex for gastropods or umbo for bivalves). In the case of bivalves, each valve or unique fragment was counted as a 0.5 specimen. Along with species counts, the lithology, systems tract, lithofacies, core depth, site altitude, and age (Holocene or Pleistocene) were included for each sample based on well log information stored in the geological cartography database of the Regione Emilia-Romagna and from published (e.g., Amorosi et al. 1999, 2003) and unpublished data (for cores 15-17).

2.4.1 The Po plain Mollusk Dataset

The raw dataset produced from cores included 131,780 specimens of bivalves, gastropods, and scaphopods. The data matrix contained 234 species representing 152 genera of mollusks. All analyses were carried out at the genus level (48% of the genera are represented by only one species) to suppress problems inherent to species-level interpretations, especially considering that taxonomic identification were carried out by multiple researchers. Supplementary multivariate ordination and bathymetric correlations were conducted also at the species level to assess if the species-level data yield results consistent with those derived by genus level analyses (see Appendix).

In addition to LST deposits, also proximal (up-dip) cores included a large portion of alluvial samples. These samples are dominated by freshwater and terrestrial genera that likely respond to different environmental drivers with respect to the marine ones. Consequently, all

analyses below are restricted to samples dominated by lagoon or marine genera. The removal of

freshwater and terrestrial taxa (which account for less than 2% of specimens in the dataset), did

not reduce the number of samples and specimens in a substantial way, but only the number of

genera.

Also, to minimize analytical volatility and remove statistical outliers due to small sample size, all

singletons (genera occurring in one sample only) and all small samples (n<20 specimens after the

removal of singletons) were excluded.

The criteria applied resulted in a minor loss of specimens and a substantial loss of

exceedingly rare genera and inadequately small samples (Fig. 2) especially from

alluvial/continental depositional environments. Indeed all LST (and great part of FSST) samples

were removed from the culled dataset. The final dataset used in all subsequent analyses includes

297 samples, 128,603 specimens, and 196 species grouped in 104 genera.

2.4.2 Independent Ecological Estimates of Preferred Species and Genus Depths

We obtained present-day water depth estimates of extant genera from the New Technologies

Energy and Environment Agency (ENEA) Italian mollusk census database

(http://www.santateresa.enea.it/wwwste/malaco/home.htm; Table 1). The ENEA census is part

of a coordinated effort from multiple surveys that catalogued their collections of the

Mediterranean mollusks and made them publicly available. The ENEA database included

information such as locality (latitude/longitude), collection methods (dredging, immersion, etc.),

water depth (meters), substrate (sandy, rocky, muddy, etc.), and the number of individuals

collected both live and dead. These data were used to acquire independent quantitative estimates

of the preferred water depth for genera commonly found in the core material. Calculated water

depths for individual species for each genus were based on samples from the ENEA dataset that had three or more live specimens in the collection suggesting their presence in the sampled location was not due to transport. The counts for both live and dead specimens were combined for each collection that met this criterion and the total numbers of individuals from all the available samples with their respective collected depths were recorded.

Hence, for each species retrieved in the Po plain deposits, its preferred bathymetry was estimated (via ENEA database), as the specimen-weighted average depth. The genus-level water depth [EG] was then calculated by averaging species-level estimates. Thus, for genera represented by only one species, species depth and EG are equivalent. We obtained EG estimates for 24 genera (represented by 44 species) that were most common in the core material (Table 1).

2.5 Analytical Methods

The final Po plain dataset (see above) represents a large multivariate data matrix suitable for development of quantitative environmental estimates applicable to core samples included in the dataset. Based on initial analyses of three cores (Scarponi and Kowalewski 2004), we postulate that bathymetry is the primary correlative of variation in faunal composition across the sampled cores. Here, we employ a series of multivariate strategies to evaluate this hypothesis using a large dataset derived from a 3D-network of core samples. In addition, this hypothesis is further tested by means of ecological estimates of preferred species and genus depths derived independently using present-day bathymetric data (see ENEA dataset above).

Multiple strategies can be employed to develop a bathymetric model suitable for interpreting different tract of facies in a sequence stratigraphic perspective. Here, we focus on two analytical techniques: weighted averaging and a posteriori ordination.

2.5.1 Weighted Averaging

Weighted averaging, a precursor to Correspondence Analysis (CA), is a direct one-dimensional ordination strategy (Hill 1973; McCune and Grace 2002), where external environmental information is used to ordinate samples or taxa. In this particular case, genus preferred bathymetry attributes are employed to develop sample-level paleoenvironmental (water depth) estimates. Here, the average water depth of a Po plain sample is computed by considering all genera present in that sample for which EG estimates (=genus preferred depths via relevant species-level estimates from the ENEA dataset) are available (Table 2, Fig. 3). The estimated sample depth via weighted averaging [S-WA] is computed as the mean EG of the above mentioned genera weighted by the number of specimens per genus. For example, if a sample contains four genera with EG estimates, the sample depth is estimated using EG values of the four taxa (e.g., -5.58, -0.33, -2.86, and -13.16 m) weighted by the number of specimens of those genera present in that core sample (e.g., 150, 10, 28, and 56). In this example, the resulting sample depth (S-WA) expressed in meters would be -6.79 m. The advantages of this strategy are its analytical simplicity and derivation of a univariate ordination function that is a linear combination of variables (taxa) expressed in environmentally meaningful units. In the case of our data, the obvious drawback of the approach is the partial use of specimen counts describing a given sample (i.e., if a sample is dominated by genera for which EG estimates are not available, the sample depth estimates can be unreliable). Although the EG estimates are available for the most common genera, some samples are affected by this problem here and their position along the ordination axes may be inaccurate. Weighted averaging also allows for a reciprocal derivation of genus scores from S-WA scores. The preferred genus depth [G-WA] is then

computed as a specimen-weighted average of S-WA scores of all samples from which the

targeted genus has been retrieved (see Table 2). This approach is somewhat circular because S-

WA values were derived from EG estimates. However this redundancy allows for testing the

robustness of sample depth estimates and for estimating G-WA depth estimates for all genera in

the dataset (even if it should be reliable only for genera that nowadays peaks in the range of

depositional environments recorded by studied Po plain deposits). Note that for the 24 genera

with modern depth information, G-WA and EG values should correlate highly – a low

correlation would indicate that the 24 genera are insufficient to generate a robust depth estimates

and/or the range of depositional environments (i.e., species) recorded in the Po plain datasets is

not strongly overlapping with those recorded by the ENEA marine dataset (i.e., ENEA dataset is

not representative of the Po plain dataset). Finally, we note here that this approach is analytically

related to, but not synonymous with, Correspondence Analysis (CA), an indirect ordination

approach which can be computed by iterative reciprocal averaging of samples and taxa starting

from arbitrary score configurations (Gauch 1982). The fundamental difference is that the

weighted averaging, as employed here, is based on external environmental scores (preferred

genus water depth in this case), whereas CA represents an unconstrained (indirect) approach,

where ordination is obtained from sample-versus-taxa similarities without *a priori* constraints

given by external variables.

2.5.2 Indirect ordination approaches

Initially, three indirect (unconstrained) ordination procedures often used with compositional data

(e.g., Holland et al. 2001; Miller et al. 2001; Olszewski and Patzkowsky 2001; Kowalewski et al.

2002; Holland 2005; Zuschin et al. 2006; Holland and Patzkowsky 2007; Ivany et al. 2009;

Zuschin et al. 2011; Ayoub-Hannaa et al. 2013; Hendy 2013, Zuschin et al. 2014) were applied

to the relative abundance matrix: correspondence analysis, detrended correspondence analysis

(DCA), and nonparametric multidimensional scaling (NMDS - using the Bray-Curtis

dissimilarity measure). All three methods produced comparable ordinations and strong *post-hoc*

correlations with independent EG estimate of genus preferred depth. We report here results from

DCA only. Although DCA suffers from multiple drawbacks (Beals 1984; Kenkel and Orlóci

1986; Minchin 1987; Wartenberg et al. 1987; Jackson and Somers 1991; McCune and Grace

2002), it is often effective in reducing an arch effect (Hill and Gauch 1980), especially when

distribution of taxa is overwhelmingly controlled by a single gradient, which is likely the case

here (Scarponi and Kowalewski 2004), as also indicated by a strong "arch effect" observed in the

CA ordinations of the Po plain dataset (see below). This method has been used successfully in

numerous studies comparing stratigraphic and paleoecological data (see references in

Patzkowsky and Holland 2012). Like DCA, the NMDS ordinations displayed a reduced arch

effect, whereas CA produced ordinations with a strong arch effect that was evident in both the

genus and sample ordinations.

  Paleontological statistics software package (PAST 2.07: Hammer et al. 2001) was used to

obtain DCA scores using default settings with detrending 'on' and 26 segments selected, the

number of first axis segments that are rescaled to counteract arch effect. Relative abundance

values were log-transformed using the "downweight" option to minimize distortion of very

abundant genera (Hammer et al. 2001). Statistical analysis software (SAS® and SAS/IML®)

was used to create the relative abundance data matrix, and to perform supplementary tests (SAS

Institute Inc. 2002). Bathymetric calibrations were calculated using Ordinary Least Squares

(OLS) of DC1 scores against several types of depth estimates for sample and genera derived

from the EG values for the 24 common genera in the Po plain dataset (Table 2). For sample

depth, depth-calibrated scores (S-DC) can be derived regressing DC1 scores against S-WA

estimates obtained by weighted averaging (see above). For genera, depth-calibrated scores (EG-

DC) can be similarly derived using original EG estimates obtained from ENEA. Alternatively,

genus depth estimates (G-DC) can be derived using G-WA scores . The depth-calibrated indirect

ordination can be then cross-evaluated against direct ordination estimates derived by weighted

averaging discussed above.

2.5.3 Cross-correlations of bathymetric models

The use of multiple strategies allows us to derive partly redundant estimates of sample depth (S-

WA vs. S-DC) and genus depth (G-WA vs. G-DC). The latter can be also contrasted against EG

depth estimates derived from the ENEA database either directly (EG) or indirectly (EG-DC).

This redundancy allows for multiple cross-assessments of consistency of bathymetric estimates

derived using different analytical strategies and for assessing relative biases across the

bathymetric models (Table 2). Ideally, calculated water depths via weighted averaging (S-WA)

should correlate tightly with DC1 calibrated water depths (S-DC) and yield quantitatively

consistent depth estimates. Similarly, the two genus-level calibrations (EG-DC and G-DC)

should result in equivalent DC1 calibrated depth estimates congruent with direct ecological

estimates from modern genera (G-WA). For sample and genus-level estimates, high pairwise

correlations and similar absolute depth estimates are desired across all the models.

2.6 Results

2.6.1 Weighted Averaging

Genus depth (EG) estimates from ENEA and the Po plain dataset (G-WA) predict comparable

water depth r^2=0.96, n=24, p<0.0001 (Fig. 4). The G-WA parameter slightly overestimates water

depth relative to the EG parameter. However, this offset is relatively minor (<1m), indicating

that the two metrics provide a reasonably consistent estimate of the preferred genus depth. In

Fig. 4, the few more notable departures (these can exceed 1m, but are all below 5m) of individual

genera from EG vs. G-WA regression line are observed. These can be explained as the result of

differences in species representing those genera in the ENEA versus Po plain datasets. For

example, the preferred depth of genus *Abra* based on its abundance in Po plain samples is G-

WA=-2.8m, whereas the ENEA based estimate is EG=-7.1m. This relatively high offset reflects

the different proportional weight of *A. segmentum*, a brackish species, that is rare in the ENEA

marine dataset (only six occurrences out of 135 used in the computation) but abundant in the Po

plain dataset (*A. segmentum* is very common with 1,138 occurrences out of 3,120).

Water depth estimates of Pleistocene and Holocene samples based on direct ordination

display a left skewed distribution with shallow-water samples ~0 to -4m dominating the dataset

(Fig. 5). The Pleistocene sub-dataset has a limited number of samples (n=44), producing a less

pronounced left skewed depth pattern compared to the Holocene. Depth distributions grouped by

sequence stratigraphic position reflect the generalized water depth for each depositional

sequence (Fig. 6). FSST samples include primarily shallow-water sites and maximum flooding

samples span a relative wide range of depths (-2m to -16m). TST samples array across the depth

gradient with a greater number of samples occurring around endpoints at -15m and -3m in depth,

suggesting a possible bimodal distribution. The bimodal distribution can be a result of variable

sampling intensity of cores across the study area and potential differential preservation within the

network of cores. The left skewed distribution of the HST samples can be explained by shallow-

water samples (~0 to -4m) dominating the dataset because the HST here is generally represented by fast stacking of thick sand bodies subject to low compaction, resulting in an overrepresentation of shallow-water sites in the data (see also Scarponi et al. 2013; Holland and Christie 2013).

2.6.2 Indirect gradient analysis

DCA ordination of mollusk genera from the Po plain dataset revealed a wedge-shaped distribution of taxa, with an increasing range of DC2 scores toward low DC1 score values (Fig. 7). The wedge-shaped pattern may be due to distortions related to detrending (as seen in Bush and Brame 2010), but it may also capture additional environmental information, as appears to be the case for Po plain mollusk associations (Scarponi and Kowalewski, 2004). For the lowest DC1 scores (0-120), the DC2 scores of genera vary widely (from -176 to 695). As DC1 scores increase, the variation along the DC2 axis gradually decreases (Fig. 7). The distribution of the 24 common extant genera (Table 1) along DC1 suggest that genera are ordinated by water depth, with shallowest-water taxa (e.g., *Heleobia*, *Lentidium* or *Donax*) having lower DC1 scores and increasingly deeper water taxa (e.g., *Turritella*, *Euspira*, or *Antalis*) having higher DC1 scores. To evaluate this relation, the DC1 scores were evaluated against the two depth proxies (ENEA (EG) and Po plain (G-WA)) using OLS (Fig. 7, insets). For both genus depth estimators, the DC1 scores are a robust linear predictor of depth, indicating that the primary gradient observed in the ordination of genera is water depth (and/or its environmental correlatives). For the ENEA water depth estimate, DC1 is a linear predictor with a model error (root mean square error: RMSE) of 2.6 m (r^2 =0.82, n=24, p <0.0001; Fig. 7, inset A). For G-WA depth estimate, the DC1 scores perform comparably well (r^2=0.81, n=24, p <0.0001; Fig. 7, inset B) with a model error of 2.8 m.

DCA ordinations at the species-level displayed a weaker association between DC1 scores and the EG water depth estimates (r^2 =0.41, see Appendix).

When samples are plotted in the same coordinate system that was used above for genera (Fig. 7), they also form a wedge-shaped ordination pattern; although samples with low DC1 scores are decidedly bimodal in terms of their DC2 scores forming two distinct sample clusters (Fig. 8). Depth estimates of the ordinated samples derived by weighted averaging of the ecological data (S-WA) range from ~0m to ~18m. Compared to the given genus-level analyses above, deeper water samples have high DC1 scores and shallower water samples have low DC1 scores. Samples with low DC1 scores (<140) and high DC2 scores (>250) represent brackish-shallow water environments such as lagoonal and back-barrier deposits. Samples with both low DC1 scores and low DC2 scores (<250) represent outer lagoon to shallow marine samples suggesting that variation along DC2 axis may represent salinity and energy (as suggested by Scarponi and Kowalewski 2004). DC1 scores also appear to be a good predictor of sample water depth estimates (S-WA) derived by direct ordination via weighted averaging of EG (Fig. 8, inset): r^2=0.92, n=264, p <0.0001. Sample DC1 scores produce depth estimates to the nearest 1.3 m (Fig. 8 inset). Samples with estimated depths deeper than -5 meters display a tight linear correlation, but residuals for samples with low DC1 scores (shallower than -5m) are more variable. Overall, S-WA depths correlate tightly with DC1 scores.

A majority of the studied cores yield samples that vary substantially in DC1 scores reflecting both shallowing and deepening trends through time (Fig. 9A). Proximal cores generally represent shallower settings and do not capture deeper environments present in more distal cores. When the ordination of samples is coded by age, both the Pleistocene and Holocene samples cover the entire depth gradient along axis 1 (Fig. 9B). In assessment of sequence

stratigraphic patterns, both TST and HST samples spread across DC1 and occur in both DC2 clusters (Fig. 9C). Samples identified as MFS/MFZ spread across DC1 and have intermediate DC2 scores for both landward and seaward cores. FSST samples have low DC1 scores because they represent nearshore environments limiting the extent of FSST samples along the depth gradient. There is no distinct separation of HST and TST samples (via MFZ) along DC1 because cores range across the depositional profile, mixing TST and HST samples from sites with different proximity to the regional depocenter.

2.6.3 Cross evaluation of calibrated bathymetric models

Water depth estimates of genera derived by a direct EG-constrained approach (G-WA) show a high correlation with those obtained by the unconstrained and calibrated approach (i.e., G-DC), thus indicating that the two approaches estimate water depth for the selected 24 taxa in a concordant manner (Fig. 10A). The calibrated DC1 sample depths (S-DC) are comparable to the weighted averaged sample depths (S-WA) indicating that the analyses are also consistent for sample estimates (Fig. 10B, Table 3).

Although the different metrics used here correlate tightly, they produce somewhat different absolute depth values for genera and samples (i.e., they are somewhat offset relative to each other with genus depths estimates more widespread than sample depths for DC1; Fig. 10). This is understandable as samples are a combination of genera, hence bathymetry estimates of samples will tend to show a restricted range depth, unless samples at both ends record only the shallowest/deepest genus.

Depth calibrations of sample-level S-DC and genus-level EG-DC ((or G-DC; Fig. 11B)(i.e., the approach developed in Scarponi and Kowalewski, 2004)) were compared using

intervals of 100 for the DC1 scores (Fig. 11); similar results are produced with both models, with S-DC slightly overestimating depths relative to the other approach (Fig.11). At shallow DC1 scores =100, EG-DC (or G-DC) and S-DC calibrations produced depths with a difference smaller than 1.6 meters: -3.5m (3.0m) and -5.1m, respectively (Fig. 11). With higher DC1 scores (DC1=400), the difference between the two metrics is slightly more pronounced, with the two calibrations being within 2.3 meters of each other: -17.9m (-17.8m) and 15.6m, respectively (Fig. 11). Hence with DC1 scores ranging from 0 to 400, EG-DC and G-DC depth estimates produce a wider depths gradient (EG-DC: from +1.2 to -17.9m or G-DC: from +1.9 to -17.8m) when compared to S-DC depth estimates (-1.6 to -15.6m).

2.6.4 Bathymetric models and their applications to sequence stratigraphy

S-WA and S-DC depth estimates (see equations in Table 2) were calculated for each sample and the resultant water depth estimates were plotted stratigraphically (Fig. 12). Both parameters showed similar depth trends displaying gradual deepening-upward followed by shallowing-upward depth signals. S-WA and S-DC are slightly offset compared to each other in both Pleistocene and Holocene cores with S-DC estimating slightly deeper depths than S-WA except in Core #3 from the Pleistocene where S-WA estimates deeper depths during maximum flooding (fig 12B). The stratigraphic plots of bathymetrically related trends delineate and match the independent and expected sequence stratigraphic interpretations available for the Pleistocene and Holocene succession of Po plain (Fig. 1). However, unlike Core #3, cores from proximal settings generally are less easy to be interpret, either showing substantial stratigraphic disagreements with sequence stratigraphic interpretations (Fig. 12C) or revealing more complicated patterns than suggested by the regional sequence stratigraphic model (Fig. 12D).

Water depths based on S-DC estimates of independently derived MFS plotted by core (Fig. 13), show slight offsets in maximum water depths relative to each other across the Po plain deposits. Southern cores range in maximum water depths from seven to 12 meters (Fig. 13B) followed by a deeper water signal in northern cores with maximum water depths of 12 to 16 meters at peak transgression (Fig. 13A).

2.7 Discussion

The water depth estimates derived from genus and sample based bathymetric models are mutually consistent and generally agree with the sequence stratigraphic interpretations of the Po coastal plain (with few exceptions in very proximal areas). However, their utility may be more limited when applied to sedimentary basins in which fossil samples are dominated by either extinct genera or extant genera with poorly understood ecology and bathymetric distribution. The approaches worked well here because late Quaternary mollusk assemblages preserved in Po plain deposits have remained remarkably unchanged over the present and last interglacial (Scarponi and Kowalewski 2007). Nevertheless, the results affirm the general notion that in marine systems, bathymetry and depth-related variables can represent an overriding control on species composition. This indicates that indirect ordination approaches may provide a successful indirect proxy of depth (without absolute depth calibration) also when applied to older sedimentary basins (e.g., Holland et al. 2001; Hendy 2013).

An additional limitation, specific to the direct ordination approach, is its limited reliability for samples dominated by genera for which EG estimates are not available. In the case of our data, only one sample in the culled marine dataset did not contain any of the 24 taxa with EG water depth estimates and was not used in any of the analyses. Six of the 297 samples

included only one genus of the 24 genera along with other minor taxa, but these samples represented primarily very proximal cores (back-barrier and estuarine facies). For samples affected by this problem their position along the ordination depth axis may be substantially inaccurate. In this case or in case studies where the lack of ecological data at taxa level could hamper paleoenvironmental reconstructions, a correlation analysis between indirect and direct derived ordination estimates (Fig. 10) can improve the paleoenvironmental accuracy of poorly defined samples and/or genera.

The results also highlight limitations of the proposed approach to identify bathymetric gradients. Ordinations of landward cores show mixed paleoenvironmental trends likely resulting from the influence of environmental variables that do not correlate strongly with bathymetry, such as variation in salinity or water energy across shallow water settings. Coastal/back-barrier habitats that vary notably in salinity and water energy are thus particularly problematic to use for bathymetric reconstructions. The non-bathymetric sources of variations are particularly noticeable in figure 8, where samples with comparable DC1 scores separate into clusters along DC2, suggesting different salinity and energy regimes. This DC2 interpretation is consistent with microfaunistic and sedimentary inferences independently obtained for the same units (Amorosi et al. 1999, 2003).

The spatiotemporal scale of analysis may also limit the importance of bathymetric gradients. Redman et al. (2007; see also Grill and Zuschin 2001) found that at small spatiotemporal scales, water depth becomes less relevant for controlling ordination gradients. Instead, life mode appears to be more appropriate at controlling variation from site to site, based on microhabitat change. These local heterogeneities may have also contributed to variability across landward cores observed in the bathymetric analyses of the Po plain samples.

Another important caveat to the proposed approach is the confounding role of pooling

data obtained along the regional depositional profile. Pooling of data from proximal and distal

cores can mask stratigraphic signals that are discernible in 2D cross-sections parallel or

perpendicular to the depositional profile of the basin. For example, Scarponi and Kowalewski

(2004), using an array of three cores that did not differ dramatically in their location relative to

the regional depocenter of the Po Basin, were able to recognize a distinct stratigraphic signal

overprinting the ordination patterns, with TST, HST, and MFZ samples behaving in a predictable

manner. However, when the ordination is based on a 3D network of cores encompassing both

distal and proximal settings, the sequence stratigraphic signals become obscured (Fig. 9C). The

indistinct pattern arising when samples are grouped by systems tracts is caused by pooling sites

along the depositional profile, where proximal MFZ samples plot together with late HST samples

from more distal samples, and so on. Moreover, deepening and shallowing-upward trends based

on water depth estimates are less clear or obscured in part of the most proximal cores, possibly

adding to the lack of separation between HST and TST samples in the ordinations (Fig. 9C). For

example, in figure 12, the transgressive regressive pattern is recognizable, however, MFS does

not equate to core maximum water depth estimates which is not necessarily because of a problem

with the curves but could be a misinterpretation of the previously defined sequence stratigraphic

pattern. The stratigraphic context becomes more discernible when analyses are restricted to an

array of cores (e.g., cores 4, 5, and 6) parallel to the shoreline and equidistant to the depocenter

(Fig. 14A). In this case, and similar to the findings of Scarponi and Kowalewski (2004), HST

and TST samples ordinate consistent with their sequence stratigraphic interpretations (Fig. 14A).

Unlike the ordination pattern encompassing all samples (Fig. 9C), sample DCA scores from the

initial ordination plotted solely for cores 4-6 display TST samples with low to intermediate DC1

and DC2 scores. HST samples occur from intermediate to high DC1 and DC2 scores demonstrating a noticeable separation between HST and TST. This separation indicates that cores sampled parallel to the coastline recover distal settings dominated by marine samples. In contrast, an ordination of a transverse transect of cores that include both proximal and distal settings produce ordination patterns where the separation between systems tracts becomes blurred (Fig. 14B). Both TST and HST samples overlap across DC1 and DC2 as seen in figure 9C.

Although the Po plain dataset contains an extensive number of samples from different systems tracts and various depths, shallow-water HST samples dominate the dataset (Fig. 6). During the HST, net accumulation rates are relatively high and include more frequent depositional events compared to the other systems tracts of the Po plain (Scarponi et al. 2013). The presence of numerous depositional events and thick sedimentary packages allow for an increased deposition and preservation of shallow-water fauna, possibly creating a bias in our dataset for shallow-water samples. The dominance of shallow-water samples is consistent with recent modeling predictions of Holland and Christie (2013).

Despite the above caveats, the bathymetric ordination models can be potentially applied to various stratigraphic and paleobiologic settings. The coupling of bathymetric models with stratigraphy allows for tracking of changes in relative sea level through time and space (Holland et al. 2001; Miller et al. 2001; Scarponi and Kowalewski 2004, 2007; Hendy 2013). The previous models focused on preferred water depths of extant genera (EG) to quantify regional bathymetric gradients (Scarponi and Kowalewski 2004; Scarponi and Angeletti 2008; Hendy 2013). However, the multi-ordination approach proposed here allows for cross-validation of different bathymetric models against each other and against the independently established sequence

stratigraphic interpretations. Posteriori calibrated sample depth estimates (S-DC) can be contrasted against estimated sample depth estimates (S-WA) to determine which model is most effective in explaining relative water levels. These models can be further applied to compare direction of regional depositional gradients and flooding across the basin, particularly in the Quaternary because of the well-known sea level fluctuations. In addition, these models can aid in the development of paleobathymetric maps that can estimate quantitative changes in water depth. Paleobathymetric maps can show gradual deepening and shallowing-upward trends at multiple time slices to illustrate regional changes in environment and habitat within a given study area.

2.8 Conclusion

In this study we have developed multiple quantitative ordination models to assess the regional bathymetry across a stratigraphically well-resolved area of the Po plain basin (Italy). The ordination models were consistent in estimating water depth during the most recent geological history of the Po coastal plain and reaffirmed that multivariate analyses of fossil samples can (1) aid in evaluating high-resolution transgressive-regressive cycles by defining temporal water level changes at fine resolution; (2) track maximum flooding across a basin by identifying maximum water depth through a 3D network of cores; and (3) explore the spatial behavior of taxa by tracking their preferred depth distributions through time.

2.9 References

Amorosi, A., Colalongo, M. L., Fusco, F., Pasini, G., and Fiorini, F. 1999. Glacio-eustatic
    Control of Continental–Shallow Marine Cyclicity from Late Quaternary Deposits of the
    Southeastern Po Plain, Northern Italy. Quaternary Research 52(1):1-13.

Amorosi, A., Centineo, M. C., Colalongo, M. L., Pasini, G., Sarti, G., and Vaiani, S. C. 2003. Facies Architecture and Latest Pleistocene–Holocene Depositional History of the Po Delta (Comacchio Area), Italy. The Journal of Geology 111(1):39-56.

Amorosi, A., Colalongo, M. L., Fiorini, F., Fusco, F., Pasini, G., Vaiani, S. C., and Sarti, G. 2004. Palaeogeographic and palaeoclimatic evolution of the Po Plain from 150-ky core records. Global and Planetary Change 40(1-2):55-78.

Amorosi, A., Dinelli, E., Rossi, V., Vaiani, S. C., and Sacchetto, M. 2008. Late Quaternary palaeoenvironmental evolution of the Adriatic coastal plain and the onset of Po River Delta. Palaeogeography, Palaeoclimatology, Palaeoecology 268 (1-2):80-90.

Ayoub-Hannaa, W., Huntley, J. W., and Fürsich, F. T. 2013. Significance of Detrended Correspondence Analysis (DCA) in palaeoecology and biostratigraphy: A case study from the Upper Cretaceous of Egypt. Journal of African Earth Sciences 80 (0):48-59.

Beals, E. W. 1984. Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14:1-55.

Brett, C. E. 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. Palaios 10:597-616.

Bush, A. M. and Brame, R. I. 2010. Multiple paleoecological controls on the composition of marine fossil assemblages from the Frasnian (Late Devonian) of Virginia, with a comparison of ordination methods. Paleobiology 36:573-591.

Carney, R. S. 2005. Zonation of deep biota on continental margins. Oceanography and Marine Biology: An Annual Review 43:211-278.

Ceregato, A., Raffi, S., and Scarponi D. 2007. The circalittoral/bathyal paleocummunities in the Middle Pliocene of Northern Italy: The case of the Korobkovia oblonga-Jupiteria concava paleo community type. Geobios 40:555-572.

Dattilo, B. F. 1996. A quantitative paleoecological approach to high-resolution cyclic and event stratigraphy: The Upper Ordivician Miamitown shale in the type Cincinnatian. Lethaia 29:21-37.

Funder, S., Demidov, I., and Yelovicheva, Y. 2002. Hydrography and mollusc faunas of the Baltic and the White Sea-North Sea seaway in the Eemian: Palaeogeography, Palaeoclimatology, Palaeoecology 184:275–304.

Gauch, H. G. 1982. Multivariate analysis in community ecology, Cambridge Studies in Ecology. New York: Cambridge University Press. 298 p.

Greggio, N., Mollema, P., Antonellini, M., and Gabbianelli, G. 2012. Irrigation management in coastal zones to prevent soil and groundwater salinization. In Resource Management for Sustainable Agriculture, edited by V. Abrol.

Grill, B., and Zuschin, M. 2001. Modern shallow - to deep-water bivalve death assemblages in the Red Sea - Ecology and biogeography. Palaeogeography, Palaeoclimatology, Palaeoecology 16:75-96.

Gunderson, K., Pazzaglia, F., Anastasio, D., Kodama, K., Frankel, K., Ponza, A., Berti, C., Smith, D., Tanen, B., and O'Neil M., Along-strike partitioning of shortening on thrust-related folds, Northern Apennine mountain front, Italy. Geophysical Research Abstracts, 13.

Hammer, Ø., Harper, D., and Ryan, P. 2001. PAST: Paleontological statistics software for education and data analysis. Palaeontologia Electronica 4(1).

Hannon, J. S. and Meyer, D. L. 2014. Microendolithic structures from the Fort Payne Formation (Lower Mississippian), Kentucky and Tennessee: Implications for the paleoenvironment of carbonate mud-mounds. Palaeogeography, Palaeoclimatology, Palaeoecology 393: 20-29.

Hendy, A. J. W. 2013. Spatial and stratigraphic variation of marine paleoenvironments in the middle-upper Miocene Gatun formation, Isthmus of Panama. Palaios:210-227.

Hendy, A. J. W. and Kamp, P. J. J. 2007. Paleoecology of late Miocene-early Pliocene sixth-order glacioeustatic sequences in the Manutahi-1 core, Wanganui-Taranaki Basin, New Zealand. Palaios 22:325-337.

Hill, M. O. 1973. Reciprocal Averaging: An Eigenvector Method of Ordination. Journal of Ecology 61(1):237-249.

Hill, M. O., and Gauch, H. G. 1980. Detrended Correspondence Analysis: An Improved Ordination Technique. Vegetatio 42:47-58.

Holland, S. M. 1995. The stratigraphic distribution of fossils. Paleobiology 21:92-109.

Holland, S. M. 2000. The quality of the fossil record - a sequence stratigraphic perspective. *In* Erwin, D. H. and Wings, S. L. eds. Deep time: Paleobiology's perspective. The Paleontological Society, Lawrence, Kansas:148-168.

Holland, S. M. 2005. The signatures of patches and gradients in ecological ordinations. Palaios 20:573-580.

Holland, S. M., Miller, A. I., Meyer, D. L., and Dattilo, B. F. 2001. The detection and importance of subtle biofacies within a single lithofacies: The Upper Ordovician Kope Formation of the Cincinnati, Ohio Region. Palaios 16(3):205-217.

Holland, S. M., and Patzkowsky, M. E. 2004. Ecosystem structure and stability: Middle Upper

      Ordovician of central Kentucky, USA. Palaios 19:316-331.

Holland, S. M., and Patzkowsky, M. E. 2007. Gradient ecology of a biotic invasion: Biofacies of

      the type Cincinnatian series (Upper Ordovician), Cincinnati, Ohio region, USA. Palaios

      22:392-407.

Holland, S. M. and Christie, M. 2013. Changes in area of shallow siliciclastic marine habitat in

      response to sediment deposition: implications for onshore-offshore palebiologic patterns.

      Paleobiology 39 (4):511-524.

Huntley, J. W. and Scarponi, D. 2012. Evolutionary and ecological implications of trematode

      parasitism of modern and fossil northern Adriatic bivalves. Paleobiology, 38 (1): 40-51.

Ivany, L. C., Brett, C. E., Wall, H. L. B., Wall, P. D., and Handley, J. C. 2009. Relative

      taxonomic and ecologic stability in Devonian marine faunas of New York State: A test of

      coordinated stasis. Paleobiology 35 (4):499-524.

Jackson, D. A. and Somers, K. M. 1991. Putting things in order: The ups and downs of detrended

      correspondence analysis. American Naturalist 137:704-712.

Kenkel, N. C. and Orlóci, L. 1986. Applying metric and nonmetric multidimensional scaling to

      ecological studies: Some new results. Ecology 67:919-928.

Konar, B., Iken, K., and Edwards, M. 2008. Depth-stratified community zonation patterns on

      Gulf of Alaska rocky shores. Marine Ecology 30:63-73.

Kowalewski, M., Gürs, K., Nebelsick, J. H., Oschmann, W., Piller, W. E., and Hoffmeister, A. P.

      2002. Multivariate hierarchical analyses of Miocene mollusk assemblages of Europe:

      Paleogeographic, paleoecological, and biostratigraphic implications. Geological Society

      of America Bulletin 114:239-256.

Lafferty, A., Miller, A. I., and Brett, C. E. 1994. Comparative spatial variability in faunal composition along two Middle Devonian paleoenvironmental gradients. Palaios 9:224-236.

McCune, B. and Grace, J.B. 2002. Analysis of ecological communities. MJM software, Gleneden Beach, Oregon, USA: 304.

Miller, A. I., Holland, S. M., Meyer, D. L., and Dattilo, B. F. 2001. The Use of Faunal Gradient Analysis for Intraregional Correlation and Assessment of Changes in Sea-Floor Topography in the Type Cincinnatian. The Journal of Geology 109(5):603-613.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69:89-107.

Muttoni, G., Ravazzi, C., Breda, M., Laj, C., Kissel, C., Mazaud, A., Pini, R., and Garzanti, E. 2007. Magnetostratigraphic dating of an intensification of glacial activity in the southern Italian Alps during Marine Isotope Stage 22. Quaternary Research 67:161-173.

Olabarria, C. 2006. Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from northeastern Altantic. Biodiversity and Conservation 15:3685-3702.

Olszewski, T. D., Patzkowsky, M. E. 2001. Measuring recurrence of marine biotic gradients: A case study from the Pennsylvanian-Permian midcontinent. Palaios 16:444-460.

Patzkowsky, M. E., and Holland, S. M. 1996. Extinction, invasion, and sequence stratigraphy: Patterns of faunal change in the Middle and Upper Ordovician of the eastern United States. *In* Witzke, B. J., Ludvigson, G. A., and Day, J. E., eds. Paleozoic Sequence Stratigraphy: Views from the North American Craton. Geological Society of America Special Paper 306:131-142.

Patzkowsky, M. E., and Holland, S. M. 2012. Stratigraphic Paleobiology: Understanding the distribution of fossil taxa in time and space. The University of Chicago Press, Chicago:259.

Peters, S. E. 2005. Geologic constraints on the macroevolutionary history of marine animals. Proceedings of the National Academy of Sciences 102:12326-12331.

Peters, S. E. 2006. Genus extinction, origination, and the duration of sedimentary hiatuses. Paleobiology 32:387-407.

Peters, S. E., and Heim, N. A. 2010. The geological completeness of paleontological sampling in North America. Paleobiology 36 (1):61-79.

Pieri, M., and Groppi, G. 1981. Subsurface geological structure of the Po Plain, Italy. Roma, Consiglio Nazionale delle Ricerche Pubblicazioni:1-23

Redman, C. M., Leighton, L. R., Schellenberg, S. A., Gale, C. N., Nielsen, J. L., Dressler, D. L., and Klinger, M. K. 2007. Influence of spatiotemporal scale on the interpretation of paleocommunity structure: lateral variation in the Imperial formation of California. Palaios 22 (6):630-641.

SAS Institute Inc. 2002. SAS/IML Software, ver. 9.0: SAS Institute. Cary, North Carolina:501.

Scarponi, D., and Kowalewski, M. 2004. Stratigraphic paleoecology: Bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. Geology 32(11):989-992.

Scarponi, D., and Kowalewski, M. 2007. Sequence stratigraphic anatomy of diversity patterns: Late Quaternary benthic mollusks of the Po Plain, Italy. Palaios 22:296-305.

Scarponi, D., and Angeletti, L. 2008. Integration of palaeontological patterns in the sequence
stratigraphy paradigm: a case study from Holocene deposits of the Po Plain (Italy):
GeoActa 7:1–13.

Scarponi, D., Kaufman, D., Amorosi, A., and Kowalewski, M. 2013. Sequence stratigraphy and
the resolution of the fossil record. Geology 41(2):239-242.

Smale, A. B. 2008. Continuous benthic community change along a depth gradient in antarctic
shallows: Evidence of patchiness but not zonation. Polar Biology 31:189-198.

Smrecak, T. A. 2008. Toward an Epibiofacies Model: A Comparison of Depth-Related Epibiont
Gradients in the Cincinnatian (Late Ordovician) and Present-Day, University of
Cincinnati.

Wartenberg, D., Ferson, S., Rohlf, F.J. 1987. Putting things in order: A critique of detrended
correspondence analysis. American Naturalist 129:434-448.

Zong, Y., and Horton, B.P. 1999. Diatom-based tidal-level transfer functions as an aid in
reconstructing Quaternary history of sea-level movements in the U.K. Journal of
Quaternary Science 14:153-167.

Zuschin, M., Harzhauser, M., and Sauermoser, K. 2006. Patchiness of local species richness and
its implication for large-scale diversity patterns: an example from the middle Miocene of
the Paratethys. Lethaia 39 (1):65-80.

Zuschin, M., Harzhauser, M., Mandic O. 2007. The stratigraphic and sedimentologic framework
of fine-scale faunal replacements in the middle Miocene of the Vienna basin (Austria).
Palaios 22:285-295.

Zuschin, M. Harzhauser, M., and Mandic, O. 2011. Disentangling palaeodiversity signals from a
biased sedimentary record: an example from the Early to Middle Miocene of Central

Paratethys Sea. *In* McGowan, A. J., and Smith, AB., eds. Comparing the Geological and

Fossil Records: Implications for Biodiversity Studies. London: Geological Society

Special Publications 358:123-139.

Zuschin, M., Harzhauser, M., Hengst, B., Mandic, O., and Roetzel, R. 2014. Long-term

ecosystem stability in an Early Miocene estuary. Geology 42 (1): 7-10.

2.10 Tables and Captions

Table 2.1. List of 24 genera used in this study with their estimated mean water depths from the ENEA dataset and rank abundance in the Po plain dataset.

Genus	Rank	# of individuals in fossil samples	# of species	EG (m)
Lentidium	1	84373	1	-2.86
Heleobia	2	10542	1	-0.95
Varicorbula	3	6027	1	-13.51
Chamelea	4	5363	1	-7.71
Abra	5	3120	1	-7.14
Spisula	6	2398	6	-6.60
Turritella	7	2355	3	-18.26
Tellina	8	1903	1	-11.66
Donax	9	1683	3	-1.36
Bittium	10	1424	3	-4.91
Cerastoderma	11	1037	4	-0.326
Nassarius	12	902	3	-6.99
Dosinia	13	710	1	-5.58
Antalis	14	647	5	-19.24
Bela	16	458	1	-6.93
Nucula	17	388	2	-19.37
Kurtiella	18	364	1	-13.14
Glycymeris	19	326	1	-7.67
Pitar	22	251	2	-16.68
Acanthocardia	23	242	1	-9.54
Euspira	24	239	1	-19.24
Acteon	27	149	4	-8.00
Fustiaria	28	137	1	-15.76
Mimachlamys	36	66	1	-14.89

Table 2.2. Different types of depth estimates of samples and genera used to develop bathymetric models for the Po plain dataset.

Depth Estimator	Datasets Used	Derivation	Scope	Comments	Equation
EG : Preferred genus depth	ENEA	Weighted averaging of species level data	24 genera	Direct estimates from the Adriatic Sea	$EG = \frac{\sum_{i=1}^{n}(D_i * SP_s)}{N_s}$
S-WA : Sample depth by Weighted Averaging	Po plain and ENEA	Weighted averaging of EG estimates	All samples	Weighted averaging of samples	$S\text{-}WA = \frac{\sum_{i=1}^{n}(EG_i * G_s)}{N_{EG}}$
G-WA : Preferred genus depth by Weighted Averaging	Po plain and ENEA	Weighted averaging of S-WA estimates	All genera	Reciprocal estimates by weighted averaging of sample depth (S-WA)	$G\text{-}WA = \frac{\sum_{i=1}^{n}(S-WA_i * G_s)}{N_g}$
S-DC : Sample depth by posteriori calibration	Po plain and ENEA	DCA	All samples	Posteriori calibration of DC1 scores using S-WA estimates	$S\text{-}DC = (-0.0351 * DC_s) - 1.5575$
EG-DC : Preferred Genus depth by posteriori calibration	ENEA	DCA	24 genera	Posteriori calibration of DC1 scores using EG depth estimates	$EG\text{-}DC = (-0.0479 * DC_g) + 1.2479$
G-DC: Preferred Genus depths by posteriori calibration	Po plain and ENEA	DCA	All genera	Posteriori calibration of DC1 scores using G-WA estimates	$G\text{-}DC = (-0.0493 * DC_g) + 1.9042$

NOTE. –

D = Depth of selected species within a sample

SP_s = Number of specimens of a given species within a sample

N_s = Total number of specimens of the given species in the entire ENEA dataset

[*]After filtering samples with < three live specimens of a given genus (see Methods)

G_s = Number of specimens of a given genus within a sample

N_{EG} = Total number of specimens in a sample with EG depths from the Po plain dataset
N_g = Total number of specimens for a selected genus in the entire Po plain dataset
DC_g = DC1 ordination scores for genera
DC_s = DC1 ordination scores for samples

Table 2.3. Correlation coefficients of depth estimates

| Depth Estimates	n	Pearson's r	r^2	95% Confidence Intervals	p (α=0.05)
G-WA vs. G-DC	24	0.90	0.81	0.69, 0.93	0.0001
S-WA vs. S-DC	264	0.96	0.92	0.90, 0.94	0.0001
G-DC vs. EG-DC	24	1	1	0.99, 1.00	0.0001
G-DC vs. S-DC	5	1	1	0.99, 1.00	0.0175

2.11 Figures and Figure Captions
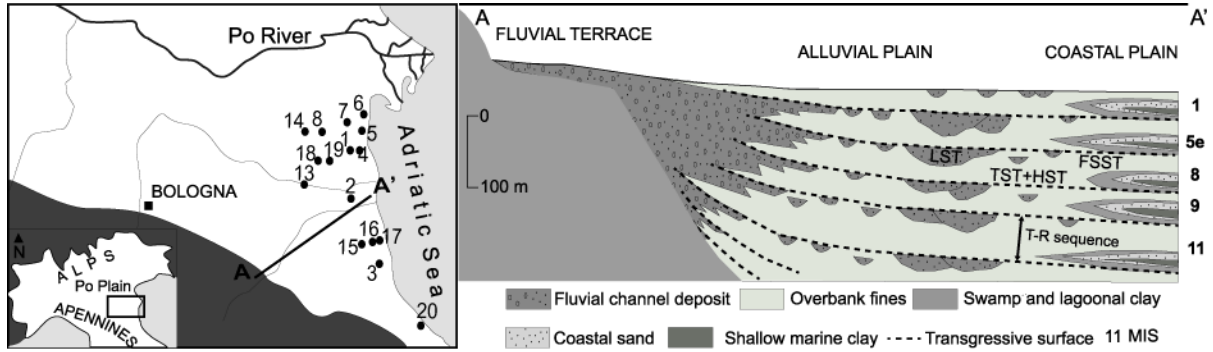
Figure 2.1. Map of the study area (left) and geological cross section (right) of the uppermost deposits of the Po coastal plain. Localities indicated by black circles. Geological cross-section along a plane defined by localities 6, 7, and 8 with the cores occurring below sea level because the region is dramatically lower than the surrounding area. LST/FSST=lowstand and falling stage systems tracts; TST=transgressive systems tract; HST=highstand systems tract; s.l.=sea level. Scale 1:50,000.
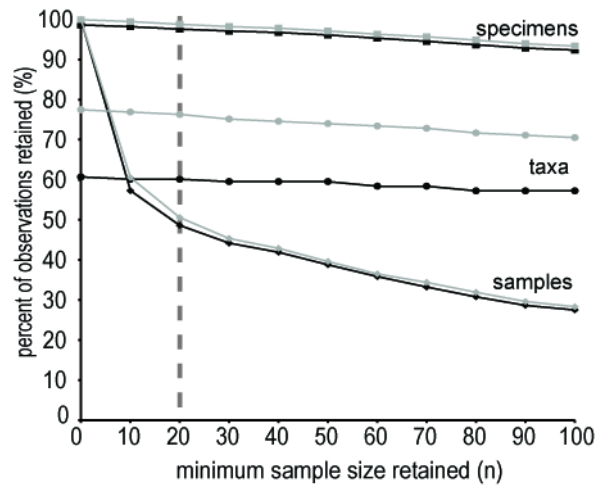
Figure 2.2. The effect of removal of small samples, singletons, and non-marine taxa on the percentage of information retained. The loss of information for the Po plain culled data, with no singletons and no non-marine taxa (black), is only slightly more pronounced than that observed for the raw data (gray) when considering specimens and samples. There is a dramatic separation between the datasets at the taxon level; where with the removal of non-marine taxa and singletons greatly reduce the dataset. All final analyses were based on the marine dataset with samples that contained at least 20 specimens. Dashed line indicates the final dataset.
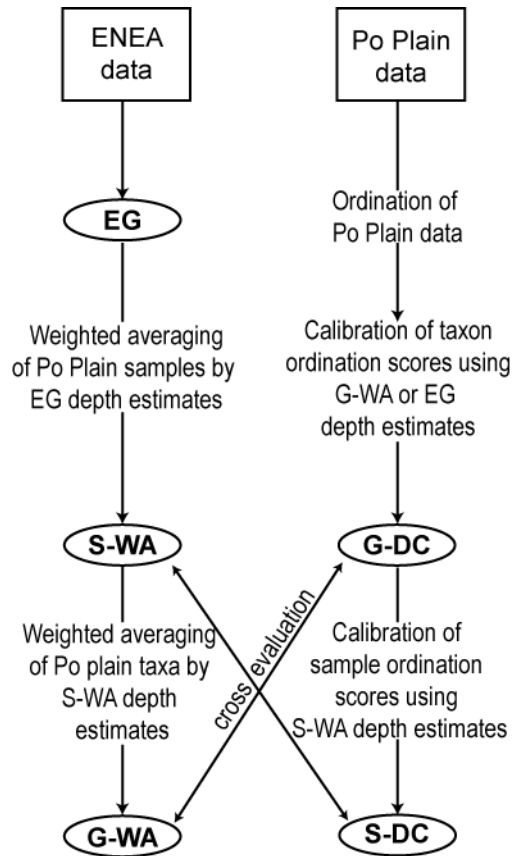
Figure 2.3. Flowchart illustrating the process of estimating water depth using multiple approaches based on the ecological (ENEA) and Po plain datasets. Squared segments represent data matrices and circled segments indicate calculable depth estimates. See Table 2 for explanation of acronyms.
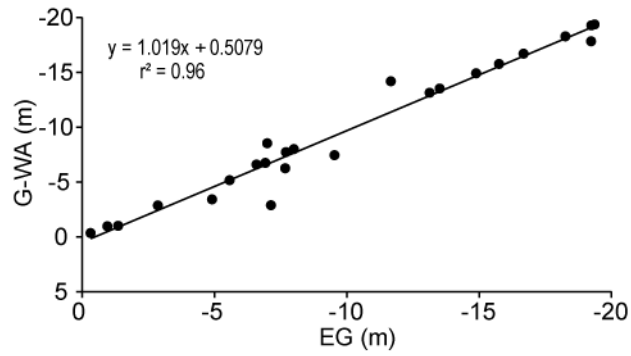
Figure 2.4. Bivariate plot of the weighted average water depth estimates for 24 genera using preferred water depths from the ENEA website (EG) and the Po plain dataset (G-WA). An ordinary least squares regression model (gray line and numbers in the upper left corner), indicates that G-WA is an excellent predictor of EG.
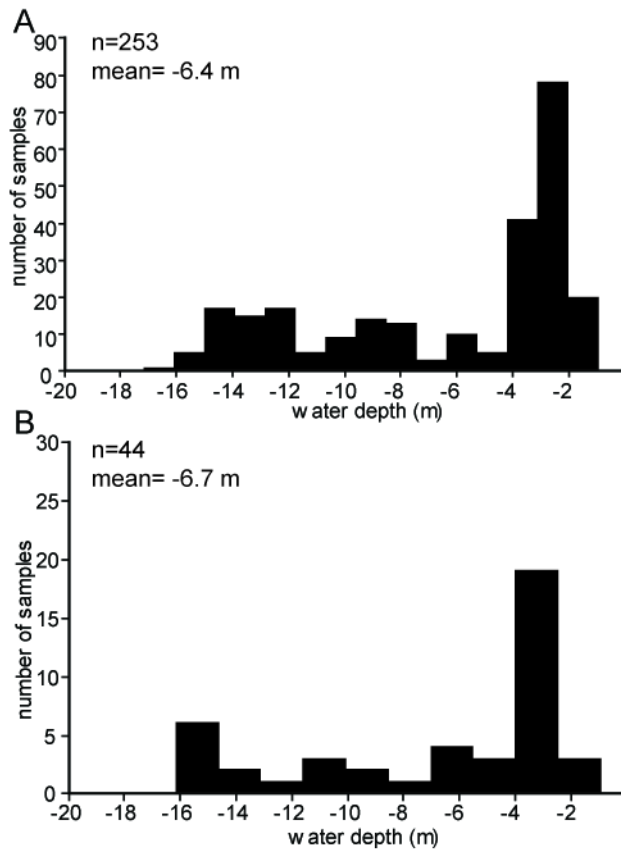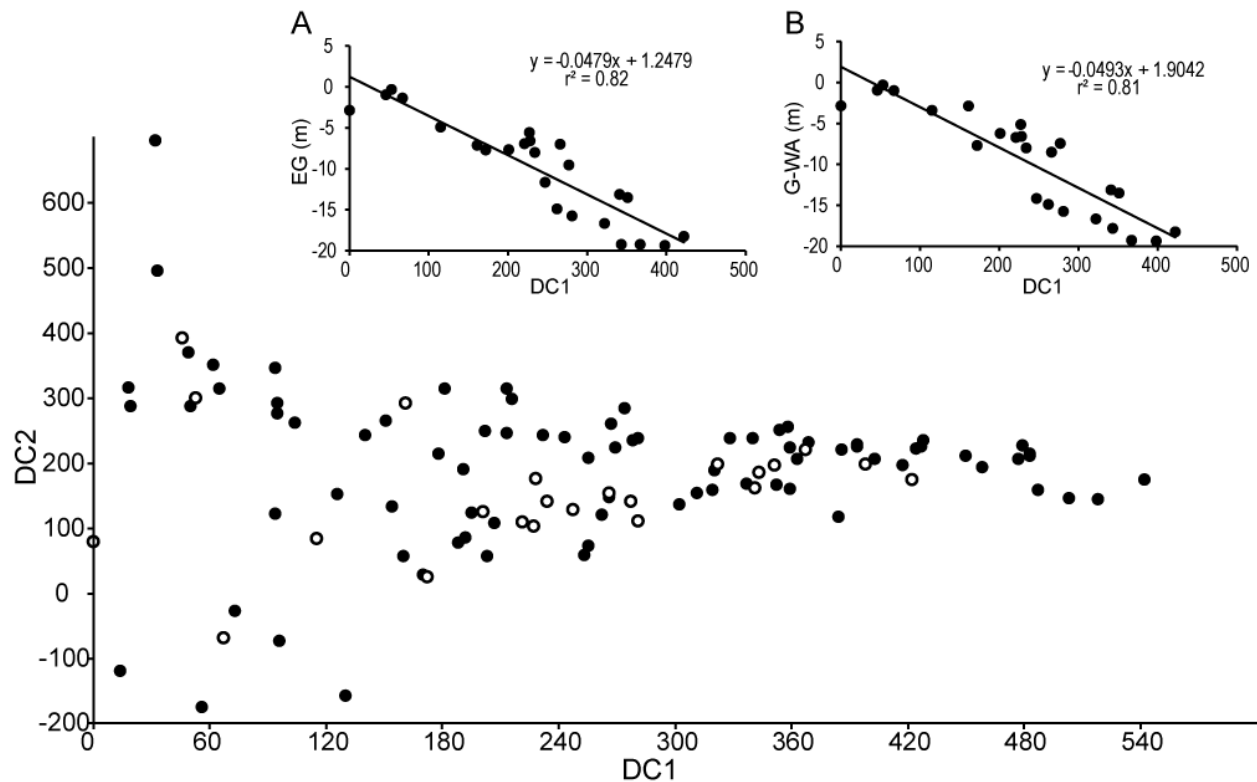
**Figure 2.5.** Distribution of sample water depths (S-WA). A) Holocene, B) Pleistocene.
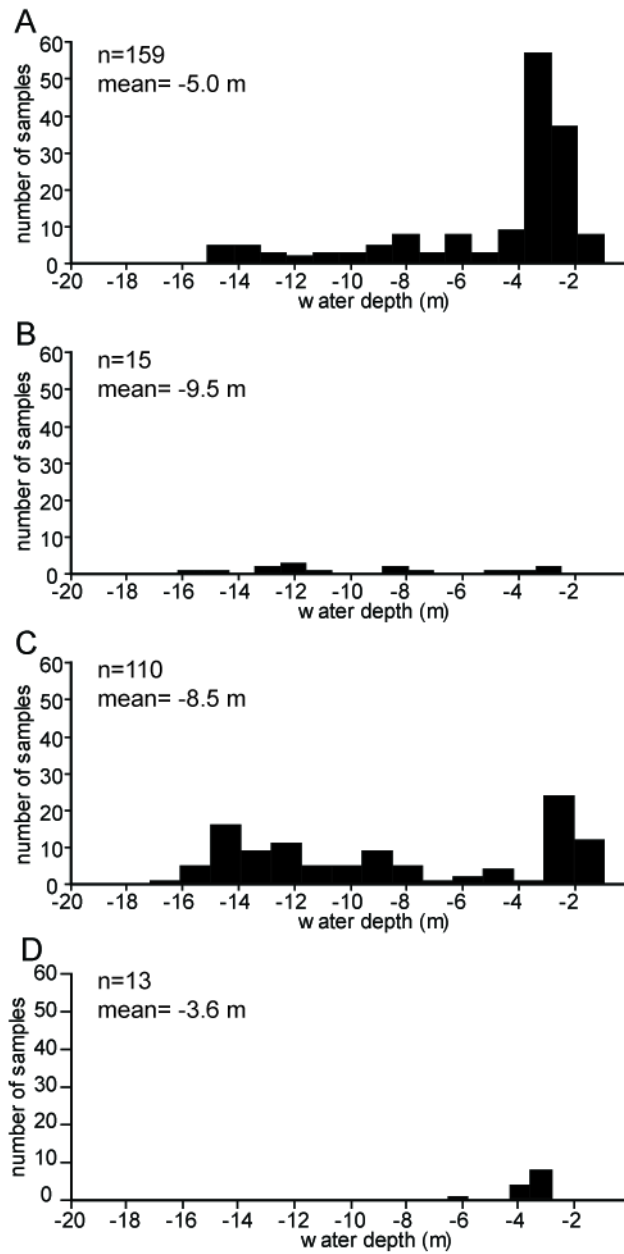
Figure 2.6. Distribution of sample water depths (S-WA) grouped by highstand systems tract (A); maximum flooding zone (B); transgressive systems tract (C); and falling stage systems tract (D).

Figure 2.7. Detrended correspondence analysis of genera (black circles) with the 24 genera used for bathymetric analysis (open circles). Deeper water genera have high DC1 scores and comparable DC2 scores and shallow marine-brackish genera have low DC1 scores and variable DC2 scores. Eigenvalues for DC1: 0.76, DC2: 0.44; Percent variance for DC1: 57.7%, DC2: 19.6% however percentage of explained variance of DCA axes is suspect due to detrending and rescaling (Patzkowsky and Holland 2012). Insets: A) Ordinary least squares regression for DC1 scores and EG depth estimates based on ENEA data, B) Ordinary least squares regression for DC1 scores and G-WA depth estimates derived from paleontological data using weighted averaging.
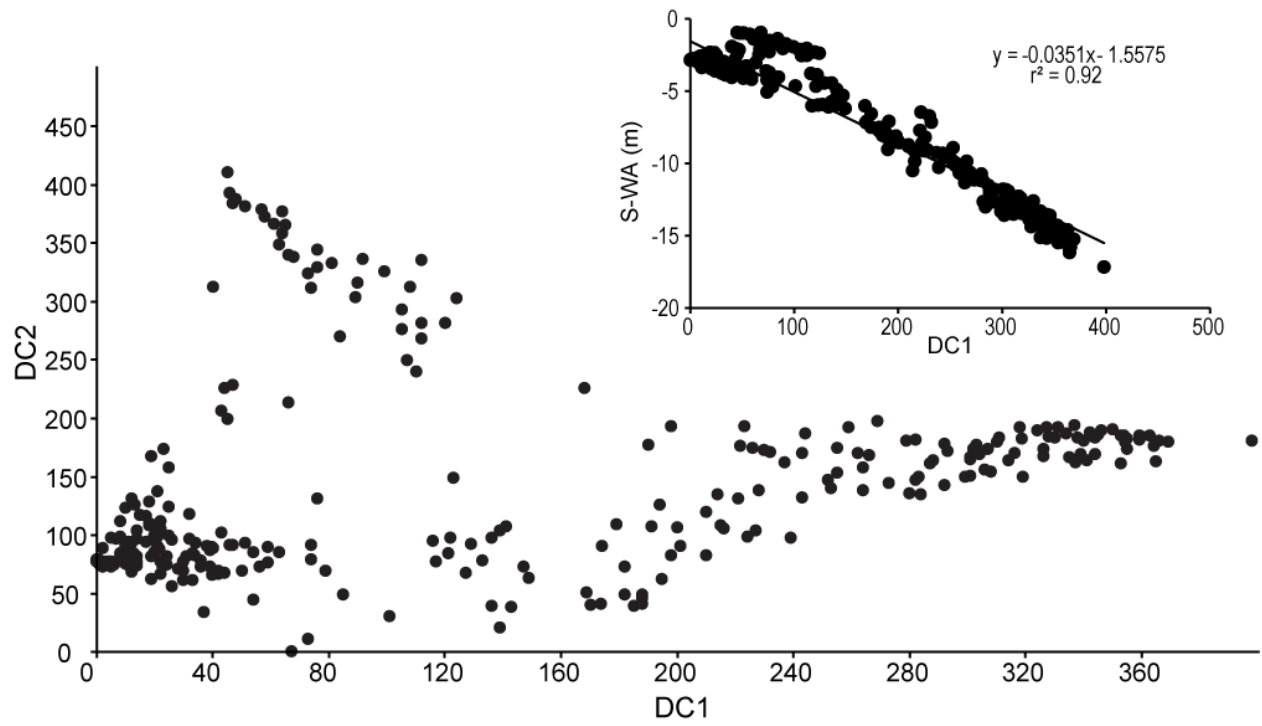
Figure 2.8. Detrended correspondence analysis of samples, n=297. Inset: Scatter plot of sample water depth estimates graphed against sample DC1 scores, n=297, RMSE=1.27m.
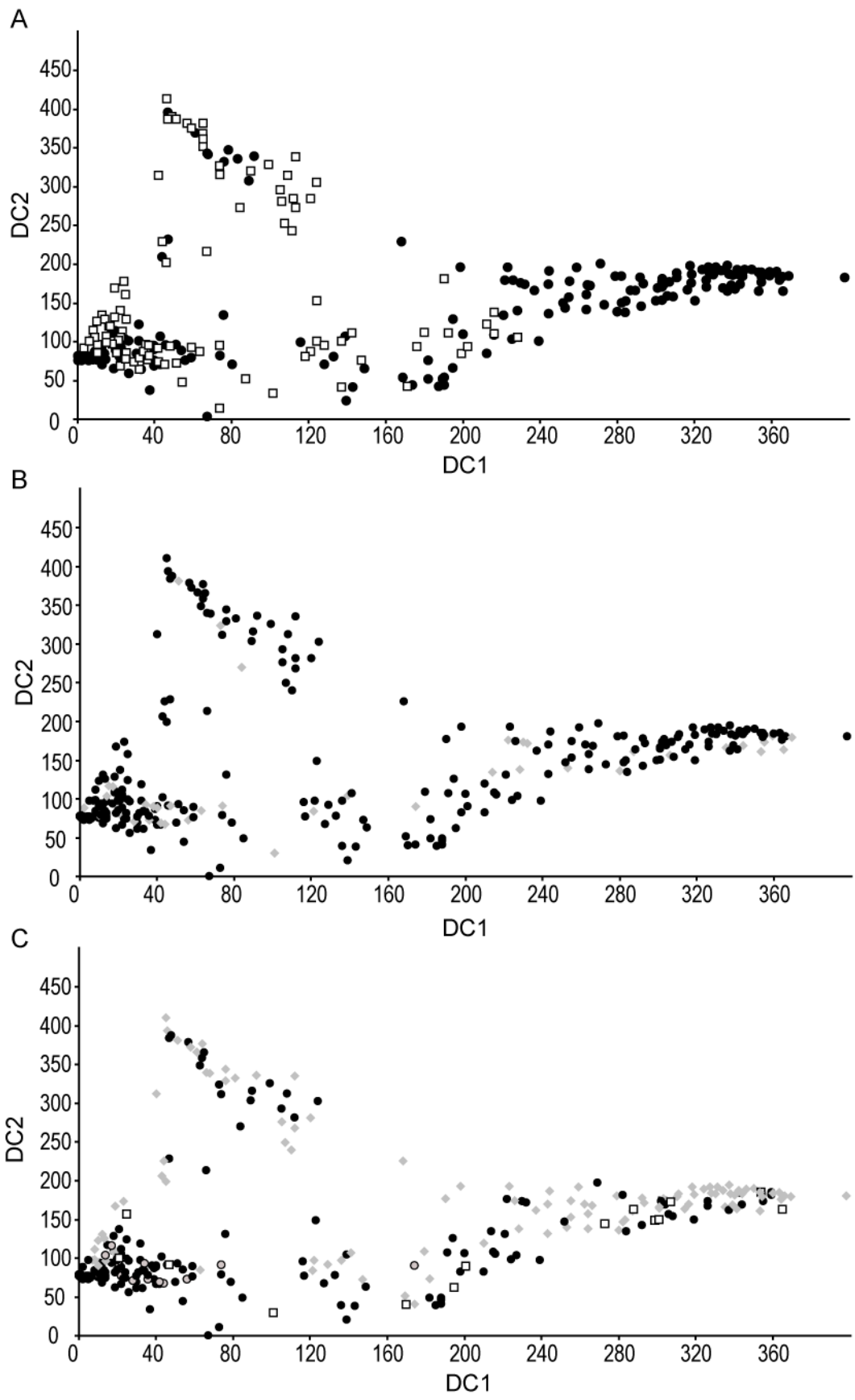
Figure 2.9. Detrended correspondence analysis of samples, n=297. A) Position along depositional profile: proximal cores in white squares: 8, 13-15, 18-20 whereas distal cores in black circles: 1-7, 16, 17; B) Age: Pleistocene (gray diamonds) and Holocene (black circles); and C) Sequence-stratigraphic position: FSST marked by gray circles; TST marked by gray diamonds; MFZ marked by open squares; HST marked by black circles.
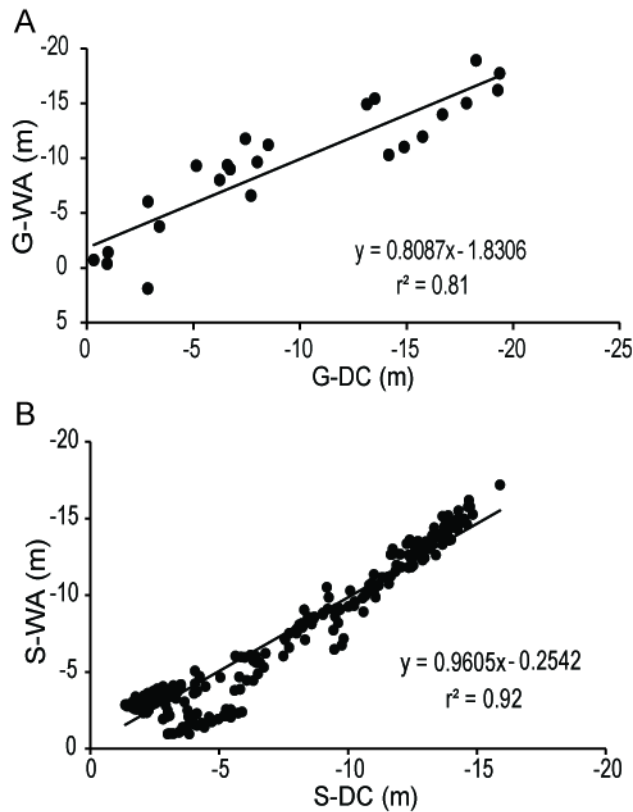
Figure 2.10. Scatter plot of estimated and calibrated water depths. A) Comparison of genus level estimated water depths to DCA calibrated genus water depths of the 24 taxa. B) Comparison of S-WA estimated water depths to DCA calibrated S-DC.
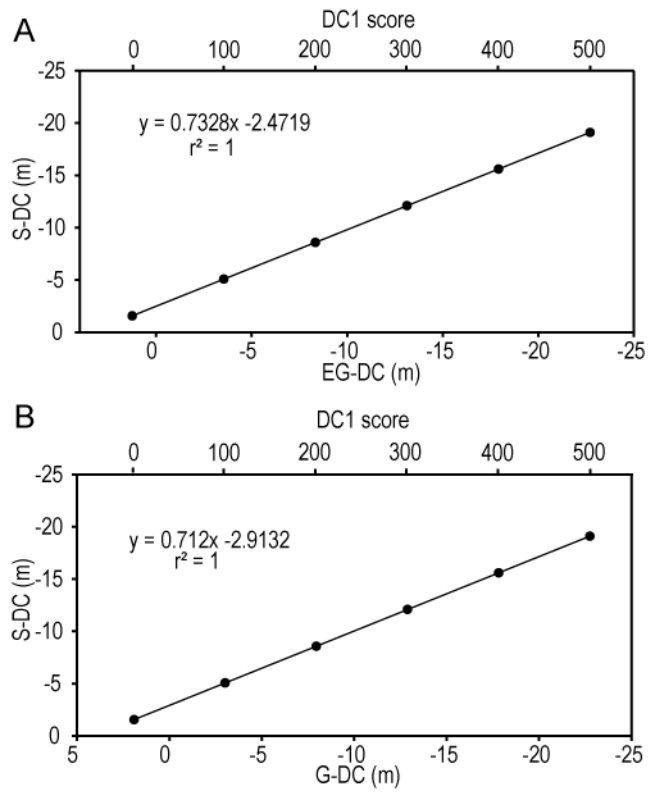
Figure 2.11. Bivariate plot of DC1 calibrated depths. A) Comparison of S-DC and EG-DC depth estimates for DC1 scores. Comparison of S-DC and G-DC depth estimates for DC1 scores.
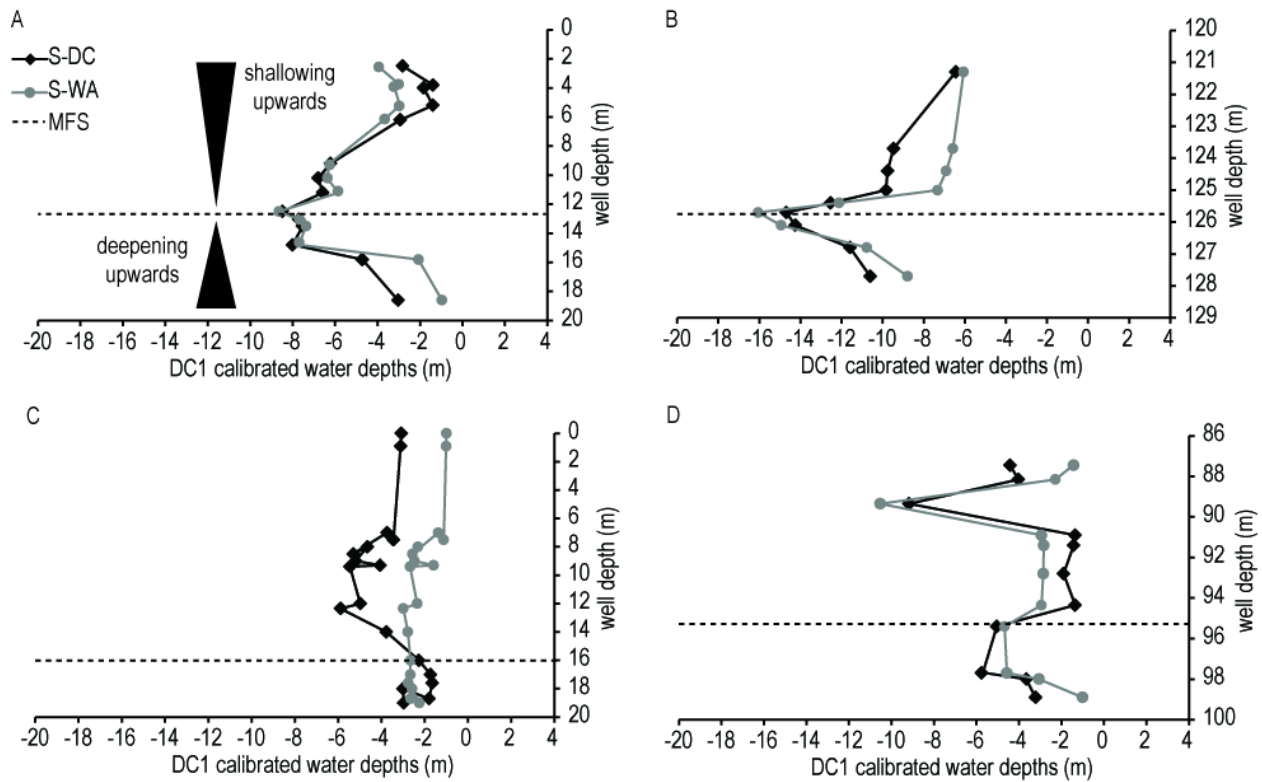
Figure 2.12. Stratigraphic patterns in DC1 calibrated water depths based on sample and genus-level estimators. Maximum flooding shown based on independent sequence stratigraphic interpretations (e.g., Amorosi et al. 2003 and 2004). Examples of distal cores: A) Holocene transgressive-regressive cycle of locality 3. B) Pleistocene transgressive-regressive cycle of core 3. Examples of proximal cores: C) Holocene transgressive-regressive cycle of core 8. D) Pleistocene transgressive-regressive cycle of core 13.
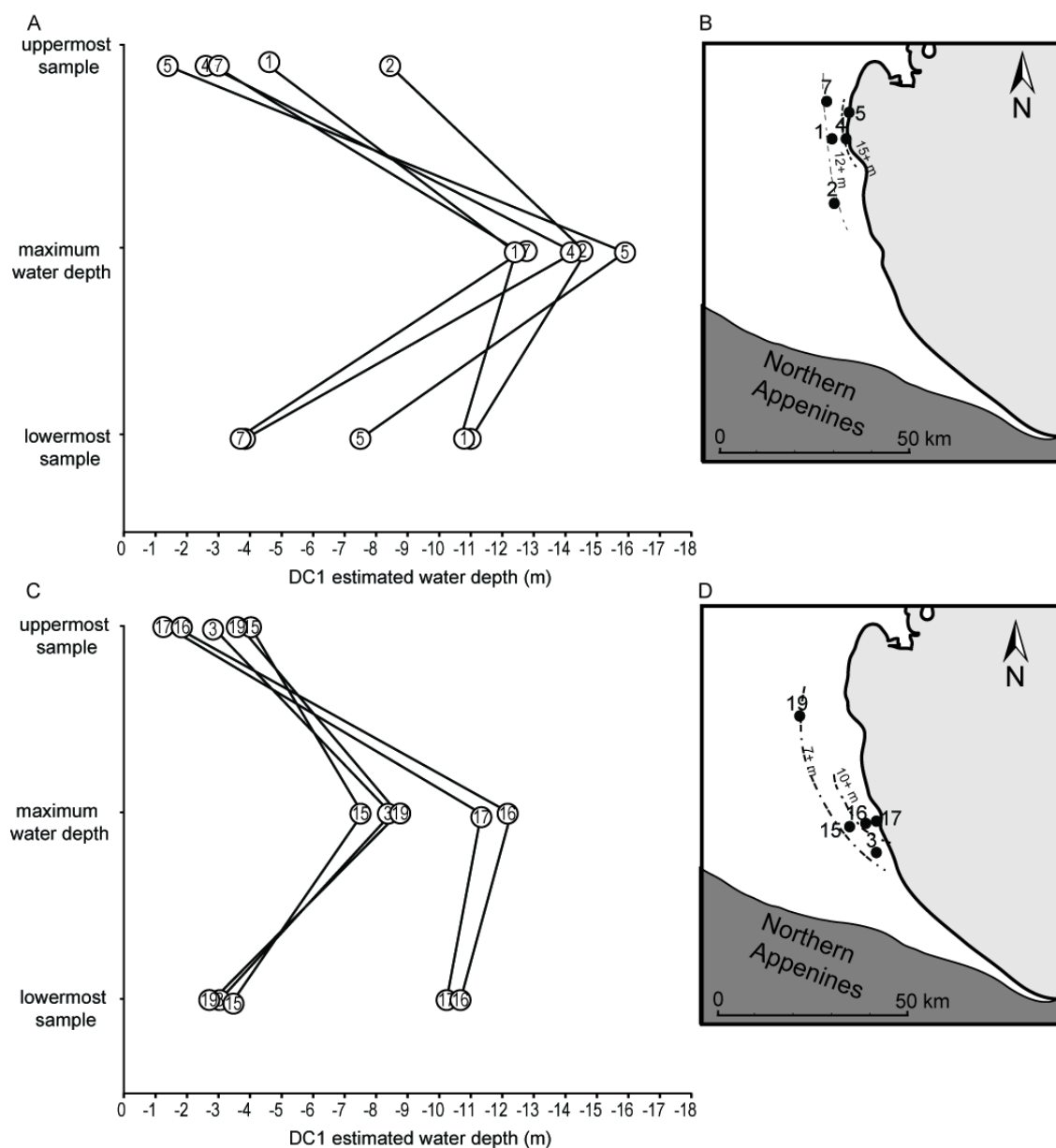
Figure 2.13. Comparison of maximum flooding zones and surfaces from S- DC estimated depths for the Holocene. A) DC1 estimated maximum water depths plotted from five northern cores. B) Map of northern Holocene cores and contour lines of their estimated maximum water depth. C) DC1 estimated maximum water depths plotted from five southern cores. D) Map of southern Holocene cores and contour lines of their estimated maximum water depth.
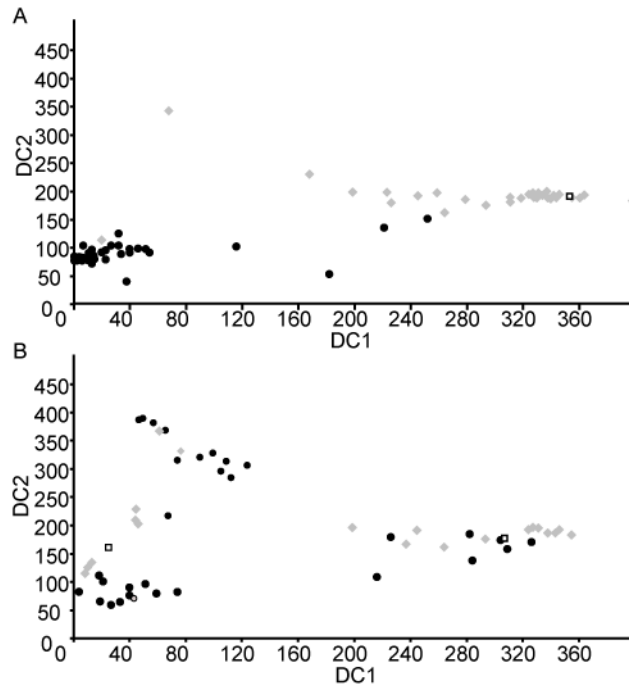
Figure 2.14. Detrended correspondence analysis of samples plotted by sequence stratigraphic interpretation. A) Parallel transect: cores 4, 5, and 6, B) Transverse transect: cores 6, 7, and 8. TST samples marked by gray diamonds; HST samples marked by black circles; FSST sample marked by gray circle; and MFS/MFZ samples marked by open squares.

CHAPTER 3

Comparison of bathymetric distributions of mollusks from modern environments and late Quaternary sedimentary record: Assessing the ecological fidelity of the fossil record of extant mollusks

JACALYN M. WITTMER

3.1 Abstract

The late Quaternary bathymetric history of the Po coastal plain (Italy) reconstructed from mollusk-rich samples were derived from independent ecological estimates of extant taxa and their water depth from the Mediterranean and Adriatic Sea. In this chapter, I assess the modern ecological dataset that was used to construct the high-resolution bathymetric gradient for the Po coastal plain, Italy. Multiple analytical approaches were applied to the Po plain and modern ecological data, a direct ordination approach was used to estimate sample bathymetry using weighted averaging of genera with known preferred depth. Detrended Correspondence Analysis of genera from the Po plain dataset ordinated based on water depth, demonstrating that water depth describes the primary axis of variation. DCA of the modern ecological data revealed an unclear gradient along the first axis with water depth correlated to the secondary axis. Multiple variables influence the environmental gradient in the modern ecological dataset employed to estimate the bathymetric gradient of the Quaternary Po plain deposits. Collection methods, substrate, and spatial scale are variables, and all these factors may potentially affect quantitative estimates of the distribution of taxa along the gradient. Despite the unclear gradient analysis of the modern ecological data, genera and their water depth distributions can be compared through time. Sample water depth frequency distributions for individual taxa of the Holocene sediments were compared against those observed in modern environments. A slight offset in distribution patterns was observed due to differences in depositional profiles represented by the two data sources.

3.2 Introduction

Quantitative paleontologists use today's marine systems to unlock questions about the past. Using modern settings and taxa to aid in the interpretation and reconstruction of fossil communities and sedimentary successions has been successful in stratigraphic paleobiology. In the field of stratigraphic paleobiology, fossil-derived patterns are used to provide us with an independent assessment of environmental changes potentially refining and cross-testing sedimentary-based interpretations and models (Holland 2000; Miller et al. 2001; Peters 2005, 2006; Peters and Heim 2010; Patzkowsky and Holland 2012). It has been shown in various studies (including Chapter 2 above) that taxonomic composition of assemblages at the basin scale correlate to environmental gradients such as water depth (bathymetry), salinity, energy, substrate, oxygen, or nutrient levels (Funder et al. 2002; Ceregato et al. 2007; Patzkowsky and Holland 2012 and references therein). Also, in ecological studies, bathymetry is commonly used to describe faunal gradients (e.g. Carney 2005; Olabarria 2006; Konar et al. 2008; Smale 2008) and has been demonstrated as an effective tool for delineating past biotic changes (Holland 2005; Hendy and Kamp 2007).

The focus of this paper is to assess the modern ecological data used to derive water depth estimates for the Po plain dataset and determine the fidelity of water depth distributions of certain taxa through time. In Chapter two, macrobenthic marine invertebrates were used to develop numerical bathymetric-based interpretations of sedimentary successions by means of multivariate ordination analyses based on the preferred water depth of extant taxa (e.g., Holland et al. 2001; Scarponi and Kowalewski 2004; Scarponi and Angeletti 2008). Here, we examine and compare the mollusk-rich sedimentary successions of the Po coastal plain and present-day mollusk communities from the Mediterranean and Adriatic Sea. The analyses in Chapter two are

based on the assumption that Quaternary successions offer a powerful advantage for exploring paleoecological patterns within their sequence stratigraphic framework because samples are dominated by extant taxa with well-understood biology, ecology, biogeography, and taxonomic/phylogenetic affinity. This chapter will determine whether such paleoecological data can be calibrated against estimates derived from modern environments and provide us with a direct means for testing the accuracy and strength of quantitative paleoecological strategies for resolving depositional environments and enhancing sequence stratigraphic interpretations of sedimentary successions.

3.2 Geological Setting

The Po plain, situated in northern Italy, is the emerged surface of a relatively large foreland basin bounded by the Alps to the north and the Apennines to the south (i.e., Po Basin, Fig. 1a). Its rock record includes a thick succession of strongly deformed Pliocene and less tectonically disturbed Pleistocene to Holocene deposits (Pieri and Groppi 1981). The Po Basin geometry has been investigated in detail during the last decades through integration of seismic studies and well-log interpretations aimed at exploration of natural resources. These studies have led to internal subdivision of the Pliocene-Quaternary succession of the Po Basin into a series of 3rd-order depositional sequences. *The stratigraphic architecture and system tracts are described in detail in Chapter two and are not discussed further here.*

3.4 Sampling Methods and Datasets

A total of 16 cores were selected based on geographic location and core depth to ensure adequate coverage of both the Holocene and Pleistocene cycles. These cores, were drilled as part of a large

multidisciplinary effort also focused on understanding in detail the subsurface stratal patterns of late-Quaternary Po plain deposits (i.e., the new Geologic Map of Italy project, http://www.apat.gov.it/) and evaluate groundwater salinity dynamic in the coastal aquifer near Ravenna (Greggio et al., 2012).

The sequence stratigraphic interpretation of these cored deposits has already been developed based on integrated sedimentological, geochemical, and micropaleontological evidence (Amorosi et al. 2003 and references therein). Various micropaleontological tools (foraminifers, ostracods, and pollen) have been employed to reconstruct depositional environment spatial and temporal development within Po coastal plain deposits, highlighting short term environmental oscillations under a strong glacio-eustatic control (Amorosi et al. 2004). In addition, 11 out of the 16 cores have been time constrained using ^{14}C radiometric dates mainly based on peat layers and ^{14}C-calibrated amino acid racemization dates for ~250 bivalve shells (Scarponi et al. 2013 and references therein).

A total of 611 bulk samples (~375 cm[3] each) were collected from the studied cores with vertical spacing of 4m or less. Samples were dried (24 hours at 45˚C), soaked in ~4% H_2O_2 (≤ 4 hours, depending on lithology), and wet sieved down to 1mm screens. For some samples (massive-clay), this process was repeated at least two times. For each sample, all mollusc specimens (the most abundant macrofossil group represented in cores) were identified to the species level (when possible) and counted. Less frequent macrobenthic remains (such as serpulids or crustaceans) were noted but not counted. The term specimen is applied here to a complete fossil or a fragment which can be reliably identified as unique individual (e.g., apex for gastropods or umbo for bivalves). In the case of bivalves, each valve or unique fragment was counted as a 0.5 specimen. Along with species counts, the lithology, systems tract, lithofacies,

core depth, site altitude, and age (Holocene or Pleistocene) were included for each sample based on well log information stored in the geological cartography database of the Regione Emilia-Romagna and from published (e.g., Amorosi et al. 1999, 2003) and unpublished data (for cores 15-17).

3.4.1 The Po plain Mollusk Dataset

The raw dataset produced from cores included 131,780 specimens of bivalves, gastropods, and scaphopods. The data matrix contained 234 species representing 152 genera of mollusks. All analyses were carried out at the genus level (48% of the genera are represented by only one species) to suppress problems inherent to species-level interpretations, especially considering that taxonomic identifications was carried out by multiple researchers. Supplementary multivariate ordination and bathymetric correlations were conducted also at the species level to assess if the species-level data yield results consistent with those derived by genus level analyses (see supplementary material).

In addition to LST deposits, also proximal (up-dip) cores included a large portion of alluvial samples. These samples are dominated by freshwater and terrestrial genera that likely respond to different environmental drivers with respect to the marine ones. Consequently, all analyses below are restricted to samples dominated by lagoon or marine genera. The removal of freshwater and terrestrial taxa (that in the dataset account for less than 2%), did not reduce the number of samples and specimens in a substantial way, but only the number of genera. Also, to minimize analytical volatility and remove statistical outliers due to small sample size, all singletons, (genera occurring in one sample only), and all small samples (n<20 specimens after

the removal of singletons) were excluded. The final dataset used in all subsequent analyses includes 297 samples, 128,603 specimens, and 196 species grouped in 104 genera.

3.4.2 Independent Ecological Dataset.

We obtained present-day water depth estimates of 24 extant genera from the New Technologies Energy and Environment Agency (ENEA) Italian mollusk census database (http://www.santateresa.enea.it/wwwste/malaco/home.htm; table 1). The ENEA census is part of a coordinated effort from multiple surveys that catalogued their collections of the Mediterranean mollusks and made them publicly available. The ENEA database included information such as locality (latitude/longitude), collection methods (dredging, immersion, etc.), water depth (meters), substrate (sandy, rocky, muddy, etc.), and the number of individuals collected both live and dead. These data were used to acquire independent quantitative estimates of the preferred water depth for genera commonly found in the core material. Calculated water depths for individual species for each genus were based on samples from the ENEA dataset that had three or more live specimens in the collection suggesting their presence in the sampled location was not due to transport. The counts for both live and dead specimens were combined for each collection that met this criterion and the total numbers of individuals from all the available samples with their respective collected depths were recorded. Collections used to calculate water depths for individual species were from both Mediterranean and Adriatic seas ranging from 0m to -100m in depth.

Hence, for each species retrieved in the Po plain deposits, its preferred bathymetry was estimated (via ENEA database), as the specimen-weighted average depth. The genus-level water depth [EG] was then calculated by averaging species-level estimates. Thus, for genera

represented by only one species, species depth and EG are equivalent. We obtained EG estimates for 24 genera—grouping 44 species, that were most common in the core material (table 1, see Chapter two for further explanation of water depth calculations).

3.5 Analytical Methods

Based on the analyses in Chapter two, bathymetry is the primary correlative of variation in faunal composition across the sampled cores. Here, we employed the multivariate strategies invoked in Chapter two to compare the Po plain bathymetric model and water depth estimates to the modern ENEA dataset.

ENEA sample water depths used in the subsequent analyses are directly from the collections used to calculate EG estimates. We focused on samples that contained the 24 extant taxa, no other collections were included in the following analyses from the ENEA dataset. To adequately compare the ENEA and Po plain sample water depths, we removed samples that occurred in water depths greater than -30m for following analyses to cover similar depositional environments. For the Po plain data, genus preferred bathymetry attributes are employed to develop sample-level paleoenvironmental (water depth) estimates. The average water depth of a Po plain sample is computed by considering all genera present in that sample for which EG estimates (=genus preferred depths via relevant species-level estimates from the ENEA dataset) are available (see Chapter two for detailed analyses). The estimated sample depth via weighted averaging [S-WA], is computed as the mean EG of the above mentioned genera weighted by the number of specimens per genus.

Detrended Correspondence Analysis (DCA) was applied to the relative abundance matrix for both the Po and ENEA dataset (see Chapter two for detailed discussion on the ordination

procedures). Paleontological statistics software package (PAST 2.07: Hammer et al. 2001) was

used to obtain DCA scores using default settings with detrending 'on' and 26 segments selected,

the number of first axis segments that are rescaled to counteract arch effect. Relative abundance

values were log-transformed using the "downweight" option to minimize distortion of very

abundant genera (Hammer et al. 2001). Statistical analysis software (SAS® and SAS/IML®)

was used to create the relative abundance data matrix, and to perform supplementary tests (SAS

Institute Inc. 2002). Bathymetric calibrations were calculated using ordinary least squares (OLS)

of DC1 scores against several types of depth estimates for sample and genera derived from the

EG values for the 24 common genera in the Po plain and ENEA dataset.

3.6 Results

3.6.1 Water depth distributions

Water depth estimates (S-WA) of Pleistocene and Holocene Po plain samples based on direct

ordination display a left skewed distribution with shallow-water samples ~0 to -4m dominating

the dataset (Fig. 2). The Pleistocene sub-dataset has a limited number of samples (n=44),

producing a less pronounced left skewed depth pattern compared to the Holocene (Fig. 2B).

ENEA sample water depths including all water depths (> -30m) display a pronounced left

skewed distribution with majority of samples occurring in less than -30 meters but some samples

are as deep as -112m (Fig. 3A). Reducing the ENEA dataset to samples less than -30 meters in

water depth (~100 deep-water samples removed), the sub-dataset displays a less pronounced left

skewed depth pattern with shallow-water samples ~0 to -3m dominating the dataset (Fig. 3B).

Sample depth distributions of taxa from the Holocene to the modern yield somewhat

different frequency distribution patterns (Fig. 4). Concentrating on select genera: *Nassarius,*

Abra, and *Tellina*, the frequency of sample water depths from the ENEA collections were compared to Po plain samples containing the selected genera (Po plain sample water depths used S-WA depth estimates obtained from Chapter two, see for explanation of calculations). *Nassarius* depth distributions display a left skewed pattern in the ENEA dataset (Fig. 4A,B) with most samples ranging from 0 to -16m, similar to the Holocene S-WA distribution of *Nassarius* samples. However, despite the abundant shallow-water samples at -1 to -4m, there is a significant amount of Holocene samples containing *Nassarius* at depths slightly deeper (-12m to -16m) compared to the modern. In the modern data, there are limited *Abra* samples compared to the Holocene, yet water depth distribution of samples are comparable with the bulk of samples at 0 to -4m and -7m to -16m (Fig. 4C,D). *Tellina* sample water depth distribution in the Holocene display a right skewed distribution with majority of deeper water *Tellina* samples at -12m to -16m (Fig. 4E,F). Compared to the modern, samples containing *Tellina* occur across the gradient from 0 to -30m with a greater volume of samples at 0 to -4m, -12m, and -20m.

3.6.2 Gradient analysis

DCA ordination of mollusk genera from the Po plain dataset revealed a wedge-shaped distribution of taxa, with an increasing range of DC2 scores toward low DC1 score values (Fig. 5). The wedge-shaped pattern may be due to distortions related to detrending (as seen in Bush and Brame 2010), but it may also capture additional environmental information, as appears to be the case for Po plain mollusk associations (Scarponi and Kowalewski, 2004). For the lowest DC1 scores (0-120), the DC2 scores of genera vary widely (from -176 to 695). As DC1 scores increase, the variation along the DC2 axis gradually decreases (Fig. 5). The distribution of the 24 common extant genera (table 1) along DC1 suggest that genera are ordinated by water depth,

with shallowest-water taxa (e.g., *Heleobia*, *Lentidium* or *Donax*) having lower DC1 scores and increasingly deeper water taxa (e.g., *Turritella*, *Euspira*, or *Antalis*) having higher DC1 scores. To evaluate this relation, the DC1 scores were evaluated against the depth proxy from ENEA (EG) using OLS (Fig. 5, inset). The DC1 scores are a robust linear predictor of depth, indicating that the primary gradient observed in the ordination of genera is water depth (and/or its environmental correlatives). DC1 is a linear predictor with a model error (root mean square error: RMSE) of 2.6 m (r^2=0.82, n=24, *p* <0.0001; Fig. 5).

DCA ordination of the 24 taxa from the ENEA dataset produced a less clear ordination pattern compared to the Po plain data. Majority of taxa distributed along medial DC1 scores (240 to 360) and across DC2 scores (0 to 540) with a few taxa spread across DC1 (0 to 600) and at low DC2 scores (0 to 180) creating a T-shaped pattern (Fig. 6A). The 24 extant genera do not appear to correspond to the primary axis of variation (DC1), unlike the Po plain data. However, ordination of DC2 and DC3 reveal a broad distribution of taxa across DC2 scores (0 to 600) and across DC3 (0 to 400; Fig. 6B). The distribution of the 24 taxa across DC2 reveals a subtle separation of shallow water taxa occurring at lower DC2 scores (e.g., *Donax or Lentidium*) and increasingly deeper water taxa at higher DC2 scores (e.g., *Pitar, Euspira, or Antalis*). To determine if the secondary axis correlates to water depth, DC2 scores were evaluated against the 24 EG water depth estimates using OLS (Fig. 7). The DC2 scores are effective linear predictors of water depth, indicating that water depth is the secondary gradient of variation in the ordination of the 24 extant genera, RMSE = 2.3m (r^2=0.69, n=24, *p* <0.0001; Fig. 7). Ordinary Least Squares was performed with DC1 scores and EG from the 24 taxa with no correlation (r^2=0.008, *p*=0.69).

3.7 Discussion

Through the collection of modern (ENEA) water depth estimates we were able to construct and evaluate a bathymetric gradient for the Po coastal plain, demonstrated in Chapter two. Using modern ecological data is useful for delineating water depth across a sedimentary basin (Scarponi and Kowalewsk 2004, Chapter two), however, there are a few caveats with using the ENEA database. The Po coastal plain deposits are restricted to a small portion of the onshore – offshore gradient (i.e. back-barrier to transitional to shelf environment, maximum extent of -30m) compared to the ENEA collection of mollusks that encompasses the shoreface to inner shelf environment (up to -60m) and all the way out to the outer shelf (-100m). Calculated water depth estimates from ENEA come from a wider portion of the onshore gradient, potentially over-estimating S-WA and making comparisons problematic. Reducing the ENEA dataset to samples from 0 to -30m allows us to better compare water depth coverage, demonstrated in Figure 3. To amend the over-estimation of S-WA, the calculation of EG, G-WA, and S-WA water depths have to be computed using the restricted ENEA dataset of 0 to -30m. This effort was not taken in this paper but will be attempted in upcoming analyses.

Although the ENEA collections based on the 24 extant genera do not demonstrate a bathymetric gradient along DC1, the spatiotemporal scale of analysis may also limit the evaluation of the bathymetric gradient. Redman et al. (2007; see also Grill and Zuschin 2001) found that at small spatiotemporal scales, water depth becomes less relevant for controlling ordination gradients. Instead, life mode and grain size appear to be more appropriate at controlling variation from site to site, based on microhabitat change. These local heterogeneities may have impacted the ordination pattern. Multiple variables in the ENEA dataset are likely affecting composition and distribution of taxa across depositional environment, such as

inconsistent methods for collection of samples (dredging, bucket collection, fishing with nets) could have impacted the results we see here. Additionally, the ENEA data used to create the ordination are based on only 24 genera and we did not include other taxa that occur in the Adriatic and Mediterranean Sea that could potentially aid in the ordination analyses.

3.8 Conclusion

Despite the unclear gradient analysis of the modern ecological data, genera and their water depth distributions can be compared through time. Using modern ecological data to quantitatively assess fossil collections is advantageous but requires prudence. Further assessment of the ENEA data is needed to examine the differences in coverage of depositional environments, overestimation of S-WA, and to improve the models and applications for aiding in the interpretation of sequence stratigraphic models and sedimentary successions.

3.9 References

Amorosi, A., Colalongo, M. L., Fusco, F., Pasini, G., and Fiorini, F. 1999. Glacio-eustatic
Control of Continental–Shallow Marine Cyclicity from Late Quaternary Deposits of the
Southeastern Po Plain, Northern Italy. Quaternary Research 52(1):1-13.

Amorosi, A., Centineo, M. C., Colalongo, M. L., Pasini, G., Sarti, G., and Vaiani, S. C. 2003.
Facies Architecture and Latest Pleistocene–Holocene Depositional History of the Po
Delta (Comacchio Area), Italy. The Journal of Geology 111(1):39-56.

Amorosi, A., Colalongo, M. L., Fiorini, F., Fusco, F., Pasini, G., Vaiani, S. C., and Sarti, G.
2004. Palaeogeographic and palaeoclimatic evolution of the Po Plain from 150-ky core
records. Global and Planetary Change 40(1-2):55-78.

Amorosi, A., Dinelli, E., Rossi, V., Vaiani, S. C., and Sacchetto, M. 2008. Late Quaternary
palaeoenvironmental evolution of the Adriatic coastal plain and the onset of Po River
Delta. Palaeogeography, Palaeoclimatology, Palaeoecology 268 (1-2):80-90.

Carney, R. S. 2005. Zonation of deep biota on continental margins. Oceanography and Marine
Biology: An Annual Review 43:211-278.

Ceregato, A. Raffl, S., and Scarponi, D. 2007. The circalittoral/bathyal paleocommunities in the
Middle Pliocene of Northern Italy: The case of the Korobkovia oblonga-Jupiteria
concave paleo community type. Geobios 40:555-572.

Funder, S., Demidov, I., and Yelovicheva, Y. 2002. Hydrography and mollusc faunas of the
Baltic and the White Sea-North Sea seaway in the Eemian: Palaeogeography,
Palaeoclimatology, Palaeoecology 184:275–304.

Greggio, N., Mollema, P., Antonellini, M., and Gabbianelli, G. 2012. Irrigation management in
coastal zones to prevent soil and groundwater salinization. In Resource Management for
Sustainable Agriculture, edited by V. Abrol.

Grill, B., and Zuschin, M. 2001. Modern shallow - to deep-water bivalve death assemblages in
the Red Sea - Ecology and biogeography. Palaeogeography, Palaeoclimatology,
Palaeoecology 16:75-96.

Gunderson, K., Pazzaglia, F., Anastasio, D., Kodama, K., Frankel, K., Ponza, A., Berti, C.,
Smith, D., Tanen, B., and O'Neil M., Along-strike partitioning of shortening on thrust-related
folds, Northern Apennine mountain front, Italy. Geophysical Research Abstracts, 13.

Hendy, A. J. W. and Kamp, P. J. J. 2007. Paleoecology of late Miocene-early Pliocene sixth-
order glacioeustatic sequences in the Manutahi-1 core, Wanganui-Taranaki Basin, New
Zealand. Palaios 22:325-337.

Holland, S. M. 2000. The quality of the fossil record - a sequence stratigraphic perspective. *In* Erwin, D. H. and Wings, S. L. eds. Deep time: Paleobiology's perspective. The Paleontological Society, Lawrence, Kansas:148-168.

Holland, S. M. 2005. The signatures of patches and gradients in ecological ordinations. Palaios 20:573-580.

Holland, S. M., Miller, A. I., Meyer, D. L., and Dattilo, B. F. 2001. The detection and importance of subtle biofacies within a single lithofacies: The Upper Ordovician Kope Formation of the Cincinnati, Ohio Region. Palaios 16(3):205-217.

Konar, B., Iken, K., and Edwards, M. 2008. Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. Marine Ecology 30:63-73.

Miller, A. I., Holland, S. M., Meyer, D. L., and Dattilo, B. F. 2001. The Use of Faunal Gradient Analysis for Intraregional Correlation and Assessment of Changes in Sea-Floor Topography in the Type Cincinnatian. The Journal of Geology 109(5):603-613.

Muttoni, G., Ravazzi, C., Breda, M., Laj, C., Kissel, C., Mazaud, A., Pini, R., and Garzanti, E. 2007. Magnetostratigraphic dating of an intensification of glacial activity in the southern Italian Alps during Marine Isotope Stage 22. Quaternary Research 67:161-173.

Olabarria, C. 2006. Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from northeastern Altantic. Biodiversity and Conservation 15:3685-3702.

Patzkowsky, M. E., and Holland, S. M. 2012. Stratigraphic Paleobiology: Understanding the distribution of fossil taxa in time and space. The University of Chicago Press, Chicago:259.

Peters, S. E. 2005. Geologic constraints on the macroevolutionary history of marine animals. Proceedings of the National Academy of Sciences 102:12326-12331.

Peters, S. E. 2006. Genus extinction, origination, and the duration of sedimentary hiatuses. Paleobiology 32:387-407.

Peters, S. E., and Heim, N. A. 2010. The geological completeness of paleontological sampling in North America. Paleobiology 36 (1):61-79.

Pieri, M., and Groppi, G. 1981. Subsurface geological structure of the Po Plain, Italy. Roma, Consiglio Nazionale delle Ricerche Pubblicazioni:1-23

Redman, C. M., Leighton, L. R., Schellenberg, S. A., Gale, C. N., Nielsen, J. L., Dressler, D. L., and Klinger, M. K. 2007. Influence of spatiotemporal scale on the interpretation of paleocommunity structure: lateral variation in the Imperial formation of California. Palaios 22 (6):630-641.

SAS Institute Inc. 2002. SAS/IML Software, ver. 9.0: SAS Institute. Cary, North Carolina:501.

Scarponi, D., and Kowalewski, M. 2004. Stratigraphic paleoecology: Bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. Geology 32(11):989-992.

Scarponi, D., and Angeletti, L. 2008. Integration of palaeontological patterns in the sequence stratigraphy paradigm: a case study from Holocene deposits of the Po Plain (Italy): GeoActa 7:1–13.

Scarponi, D., Kaufman, D., Amorosi, A., and Kowalewski, M. 2013. Sequence stratigraphy and the resolution of the fossil record. Geology 41(2):239-242.

Smale, A. B. 2008. Continuous benthic community change along a depth gradient in antartic shallows: Evidence of patchiness but not zonation. Polar Biology 31:189-198.

3.10 Tables and Captions

Table 3.1. List of 24 genera used in this study with their estimated mean water depths from the ENEA dataset and rank abundance in the Po plain dataset.

| Genus	Rank	# of individuals in fossil samples	# of species	EG (m)
Lentidium	1	84373	1	-2.86
Heleobia	2	10542	1	-0.95
Varicorbula	3	6027	1	-13.51
Chamelea	4	5363	1	-7.71
Abra	5	3120	1	-7.14
Spisula	6	2398	6	-6.60
Turritella	7	2355	3	-18.26
Tellina	8	1903	1	-11.66
Donax	9	1683	3	-1.36
Bittium	10	1424	3	-4.91
Cerastoderma	11	1037	4	-0.326
Nassarius	12	902	3	-6.99
Dosinia	13	710	1	-5.58
Antalis	14	647	5	-19.24
Bela	16	458	1	-6.93
Nucula	17	388	2	-19.37
Kurtiella	18	364	1	-13.14
Glycymeris	19	326	1	-7.67
Pitar	22	251	2	-16.68
Acanthocardia	23	242	1	-9.54
Euspira	24	239	1	-19.24
Acteon	27	149	4	-8.00
Fustiaria	28	137	1	-15.76
Mimachlamys	36	66	1	-14.89

## 3.11 Figures and Figure Captions
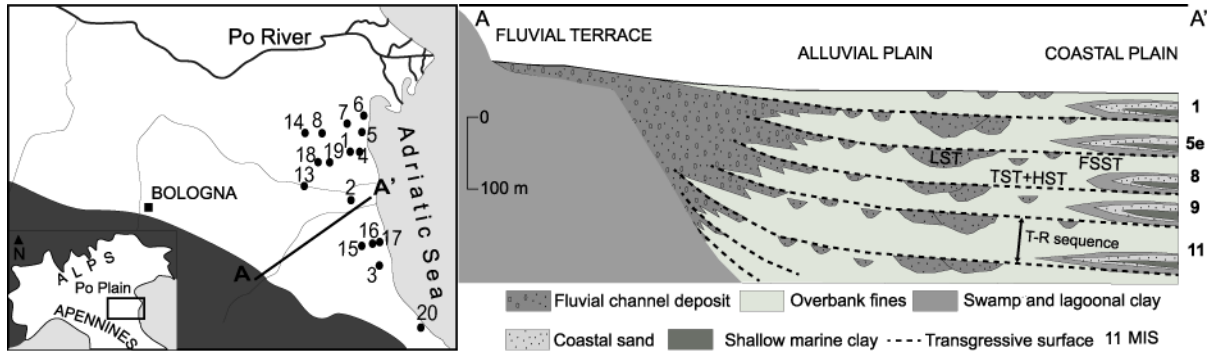
Figure 3.1. Map of the study area (left) and geological cross section (right) of the uppermost deposits of the Po coastal plain. Localities indicated by black circles. Geological cross-section along a plane defined by localities 6, 7, and 8 with the cores occurring below sea level because the region is dramatically lower than the surrounding area. LST/FSST=lowstand and falling stage systems tracts; TST=transgressive systems tract; HST=highstand systems tract; s.l.=sea level. Scale 1:50,000.
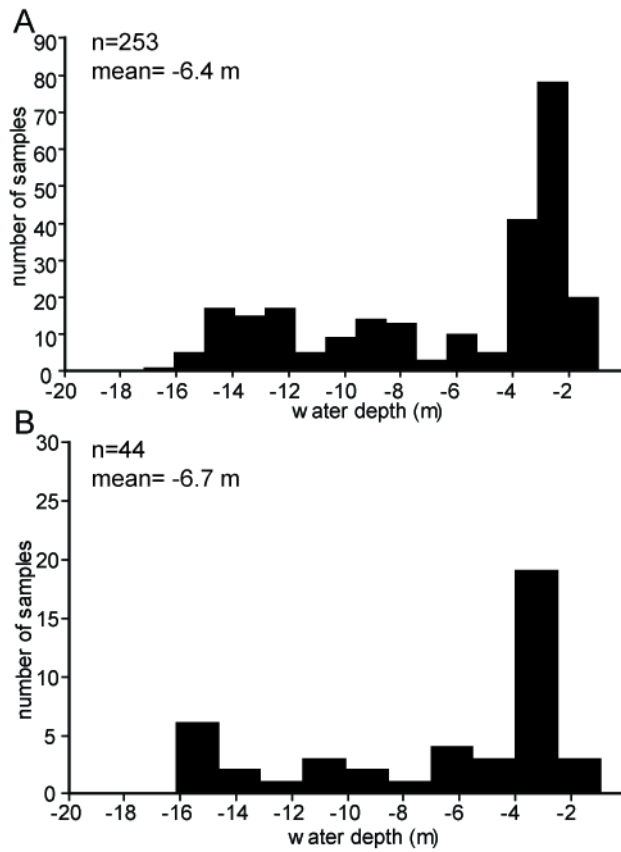
Figure 3.2. Distribution of sample water depths (S-WA) from the Po coastal plain. A) Holocene, B) Pleistocene.
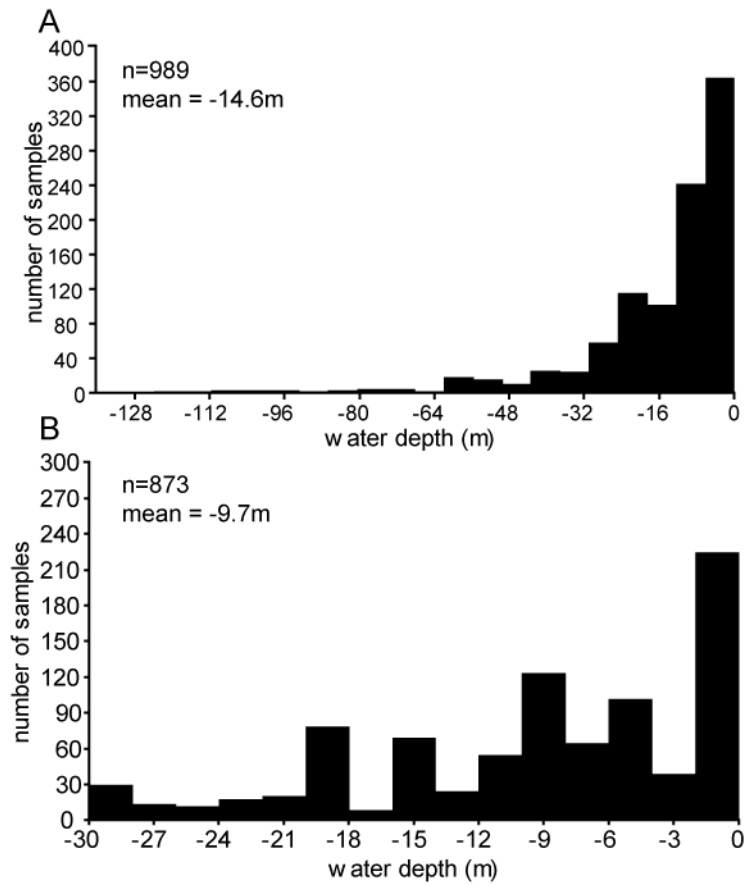
Figure 3.3. Distribution of sample water depths from the ENEA database. A) All water depths from the ENEA. B) Reduced ENEA data with sample water depth distributions from 0 to -30m.
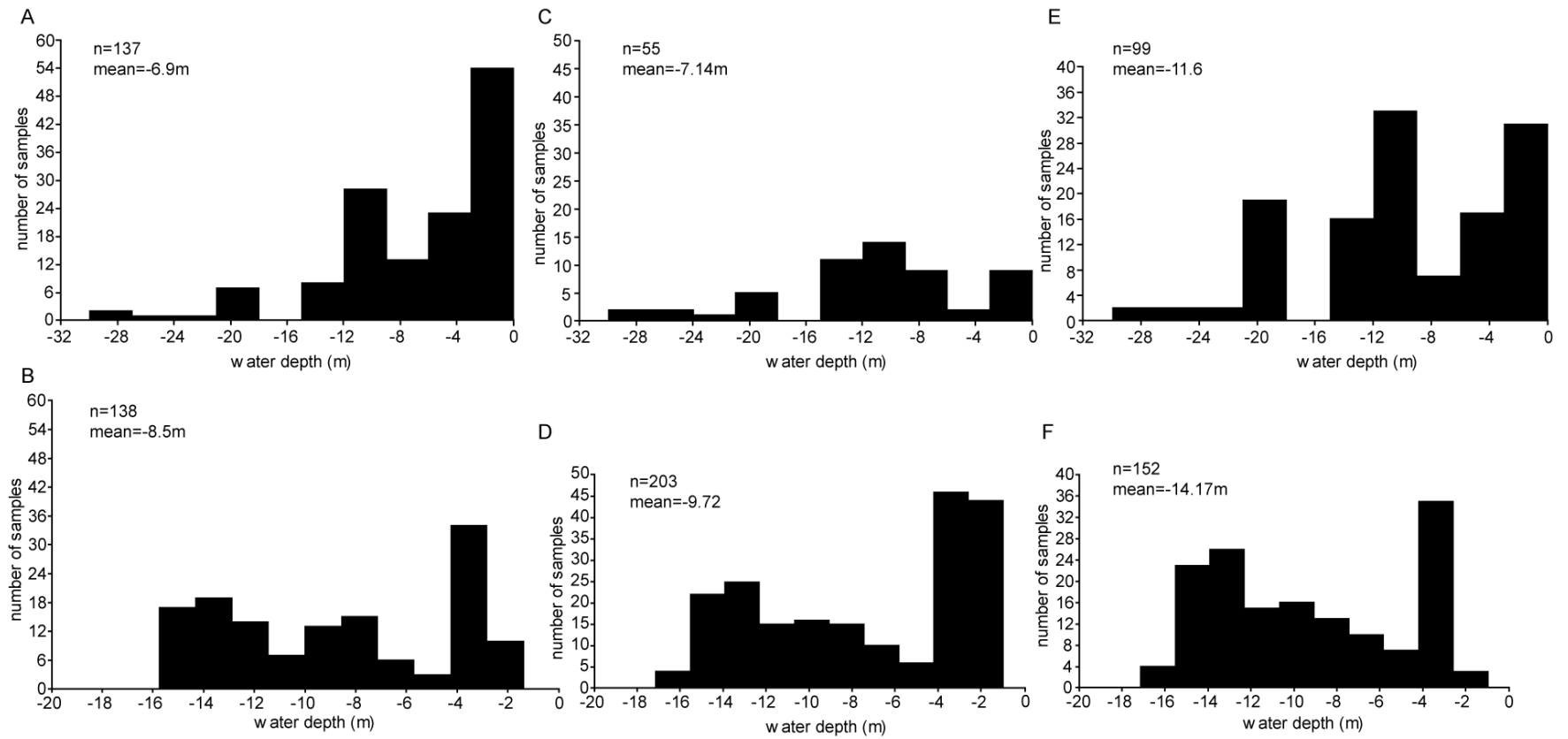
Figure 3.4. Distribution of sample water depths. A) *Nassarius* sample water depths from ENEA. B) *Nassarius* sample water depths from the Po plain data. C) *Abra* sample water depths from ENEA. D) *Abra* sample water depths from the Po plain data. E) *Tellina* sample water depths from ENEA. F) *Tellina* sample water depths from the Po plain data.
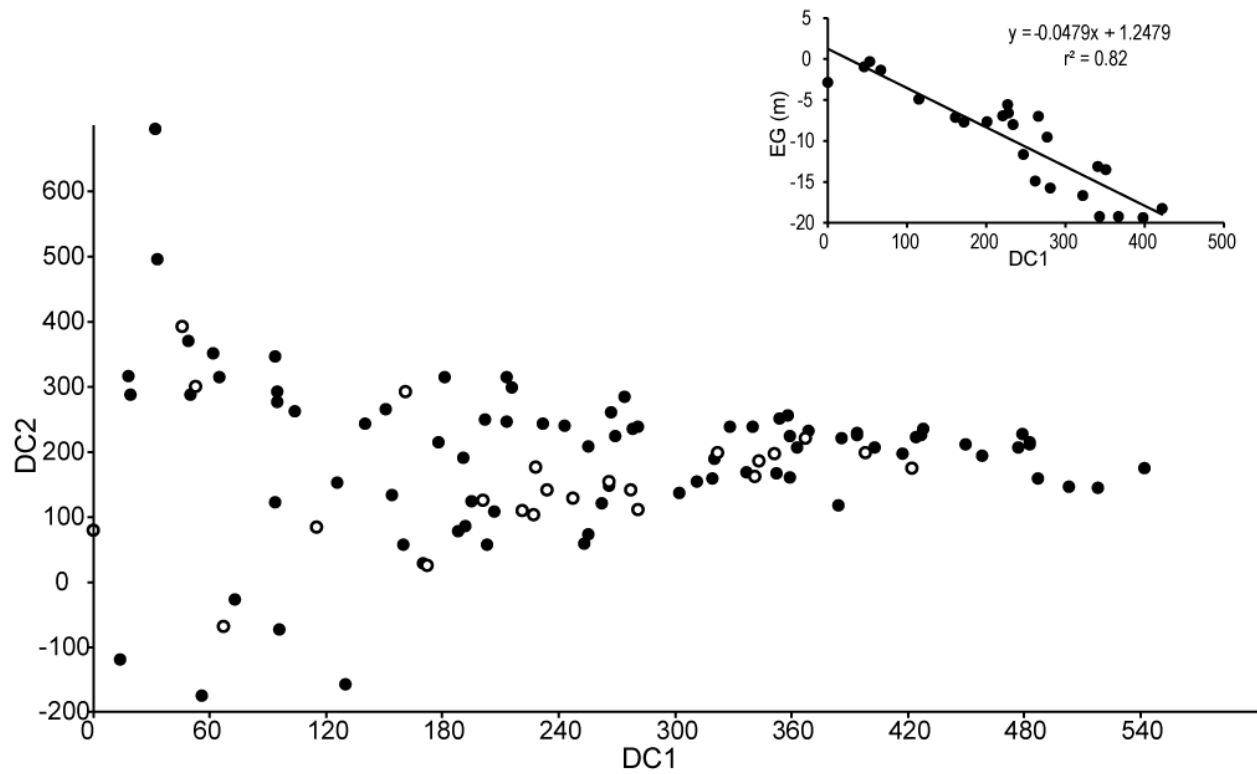
Figure 3.5. Detrended correspondence analysis of genera (black circles) with the 24 genera used for bathymetric analysis (open circles) from the Po plain dataset. Deeper water genera have high DC1 scores and comparable DC2 scores and shallow marine-brackish genera have low DC1 scores and variable DC2 scores. Insets: Ordinary least squares regression for DC1 scores and EG depth estimates based on ENEA data.
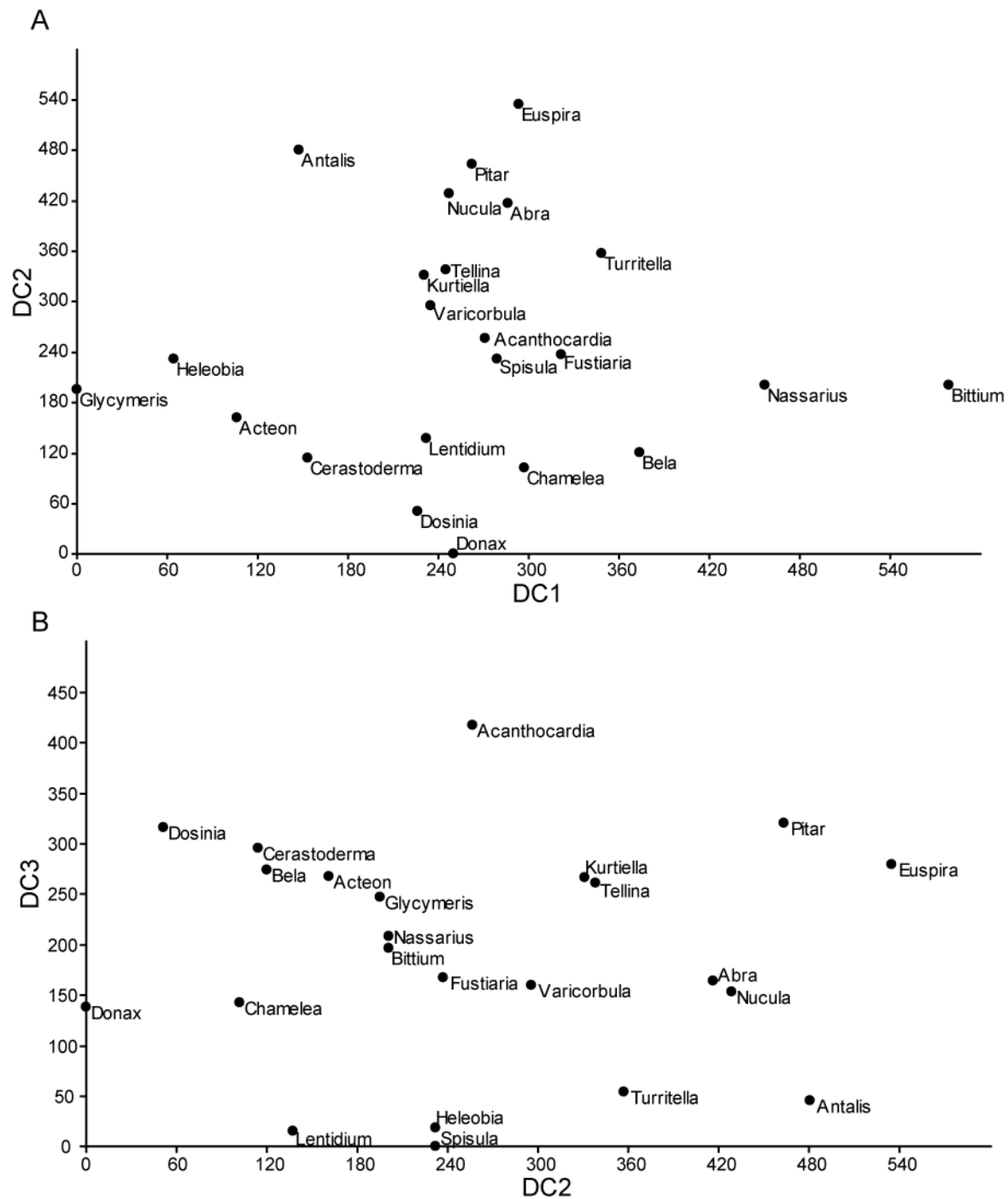
Figure 3.6. Detrended correspondence analysis of genera from the ENEA database with the 24 genera (labeled) used for bathymetric analysis. A) Ordination of DC1 and DC2; no gradient visible. B) Ordination of DC2 and DC3, along DC2 a subtle bathymetric gradient is recognizable.
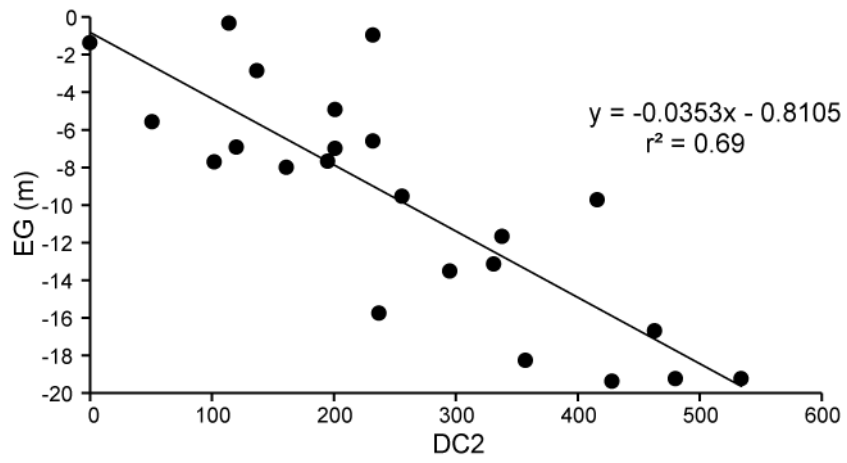
Figure 3.7. Ordinary least squares regression of ENEA ordination DC2 scores and EG depth estimates.

CONCLUDING REMARKS

The paleontological investigations in these three chapters target both modern and past biota-rich environments to better understand the preservation of a range of habitat types and evaluate the importance of using fossil-rich succession to interpret environmental gradients such as bathymetry. The research in these chapters aims to use the present as a key for understanding the past and to further aid in understanding recent ecosystem changes.

Summaries of the main findings from each chapter are presented here:

Chapter 1: The hierarchical sampling scheme used to evaluate the rocky intertidal communities revealed a gradual increase in diversity across sampling levels, with most notable increase observed between site level and locality level diversity estimates. Across energy regimes and habitat types (sheltered and exposed), there was no meaningful shift in diversity or occurrences. Species occurrences in sheltered habitats should augment fossilization potential of those assemblages because, as shown in some paleontological studies, which indicate that some sub-habitats from rocky intertidal environments, from such settings as tide pools, pits, and crevices, are occasionally preserved in the rock record. In fact, when data are restricted to more preservable, sheltered settings, a good representation of total biodiversity and overall community structure of sampled faunal associations is still retained. Moreover, because the sampled communities appear remarkably homogeneous across and within localities, even a highly fragmentary fossil record (e.g., small area in one locality) would likely collect a substantial fraction of biodiversity and community structure of rocky intertidal communities of the San Salvador Island. The fossilization of rocky intertidal gastropods within habitats is possible and, at the smallest level of sampling, the most common gastropod species have the potential to be

captured.   Investigations of rocky shore environments merit further consideration in understanding fossilization of these environments through time.

Chapter 2: By using the abundant mollusks available in a wide network of cores from the Po Basin, we were able to quantitatively estimate water depth from extant taxa and their preferred water depths for individual samples. In doing so, I have successfully applied several quantitative models towards sedimentological-based sequence stratigraphic interpretations and create bathymetric estimates across the Quaternary marine successions of the Po coastal plain. The mollusk-derived proxies quantify spatial bathymetric gradients across the basin and local trends in absolute water depth in response to relative changes in sea-level. However, for cores located in the most proximal part of the basin, mollusk-based ordinations failed to provide viable estimates due to inclusion of mixed marine and non-marine mollusk faunas and scarcity of fossiliferous horizons necessary for adequate quantitative sampling. The multiple analytical approaches cross-evaluated in this study consistently suggest that high-resolution quantitative bathymetric estimates can be derived for mollusk samples independent of stratigraphy for fully marine settings. When applied simultaneously to both samples and taxa, these approaches provide a viable strategy for quantifying stratigraphic and paleontological patterns and enhancing interpretations of basin-scale depositional systems.

Chapter 3: Multiple variables influence the environmental gradient in the modern ecological dataset employed to estimate the bathymetric gradient of the Quaternary Po plain deposits. Collection methods, substrate, and spatial scale are variables, and all these factors may potentially affect quantitative estimates of the distribution of taxa along the gradient. Despite the unclear gradient analysis of the modern ecological data, genera and their water depth distributions can be compared through time. Sample water depth frequency distributions for

114

individual taxa of the Holocene sediments were compared against those observed in modern environments. A slight offset in distribution patterns was observed due to differences in depositional profiles represented by the two data sources.

The dissertation research explored here demonstrates that modern ecological systems are essential to evaluating past geologic events. Through direct observation and quantitative analysis, I have learned that modern and fossil communities behave differently depending on environment (e.g. energy, salinity, water depth, etc.). These variables affect the distribution of living organisms today and through my research, delineate fossil distributions through time. With these observations, new questions have arisen about the latitudinal variability of rocky intertidal fossil preservation and extrapolating the quantitative bathymetric models to deeper time intervals. These questions will lead to future endeavors and pointedly add to the field of geology and stratigraphic paleobiology.

Appendix A. Sequence stratigraphic information of all 16 cores used in the study after Amorosi et al. 2003 (cores 5-8), Amorosi et al. 2005 (core 14). Original labels of cores collected by Amorosi and others are also included, such as 205 S7 for Core 7. Please note that in the studies by Amorosi and others, depth is below sea level (and somewhat inaccurate), here we report core depth. Lithological abbreviations: c=clay, s=silt, sd=sand, and g=gravel. System tract abbreviations: HST=highstand systems tract, TST=transgressive systems tract, LST=lowstand systems tract, FSST=falling stage systems tract, MFS=maximum flooding surface, and MFZ=maximum flooding zone. Sequence boundaries are denoted as SB, transgressive surfaces as TS, and wave ravinement surfaces as WRS (dashed line).
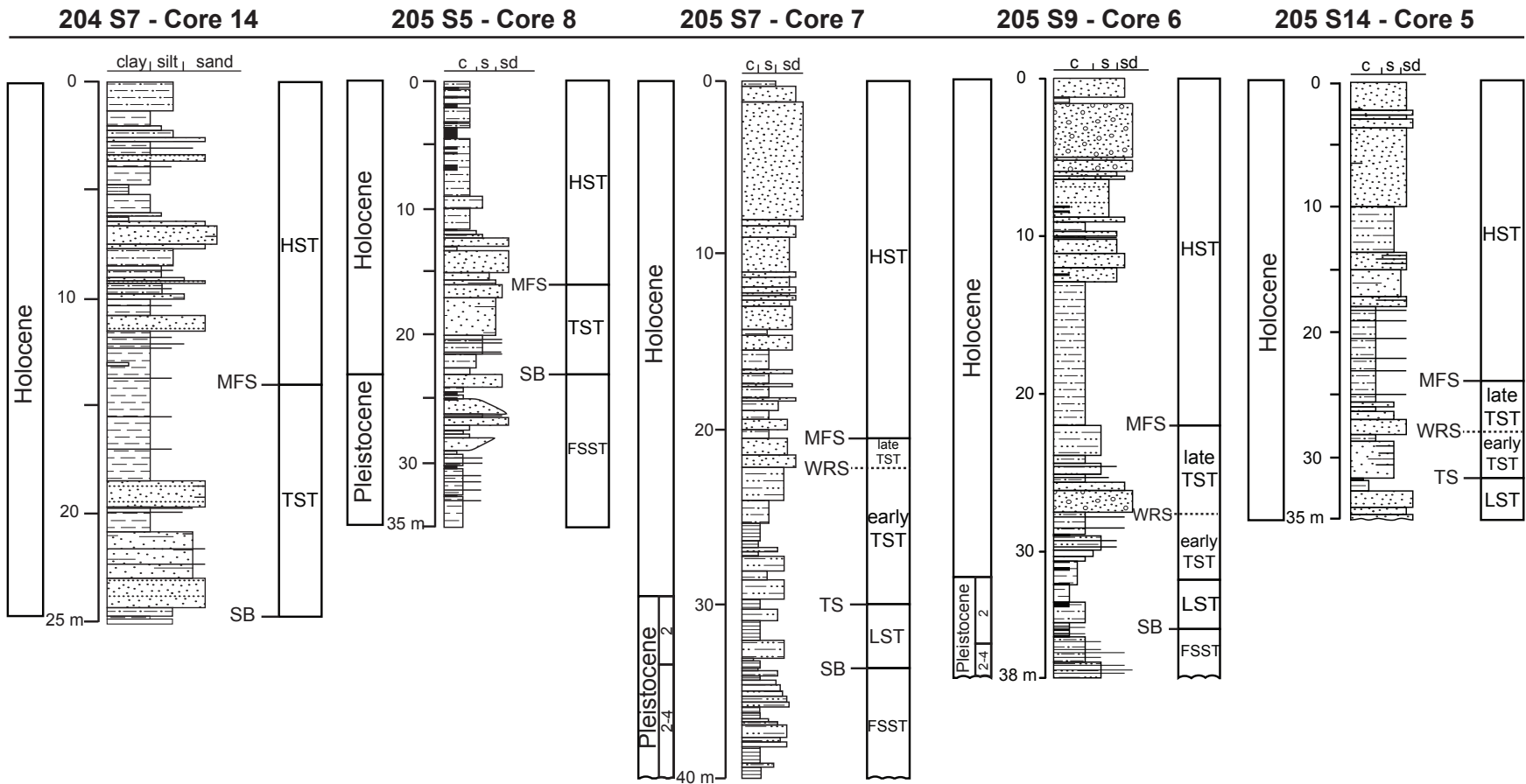
Appendix A continued. Sequence stratigraphic information after Amorosi et al. 2003. For extensive cores, only sample intervals are shown, such as Core 1.


205 S1 - Core 18

205 S2 - Core 19

205 S10 - Core 1

205 S4 - Core 4
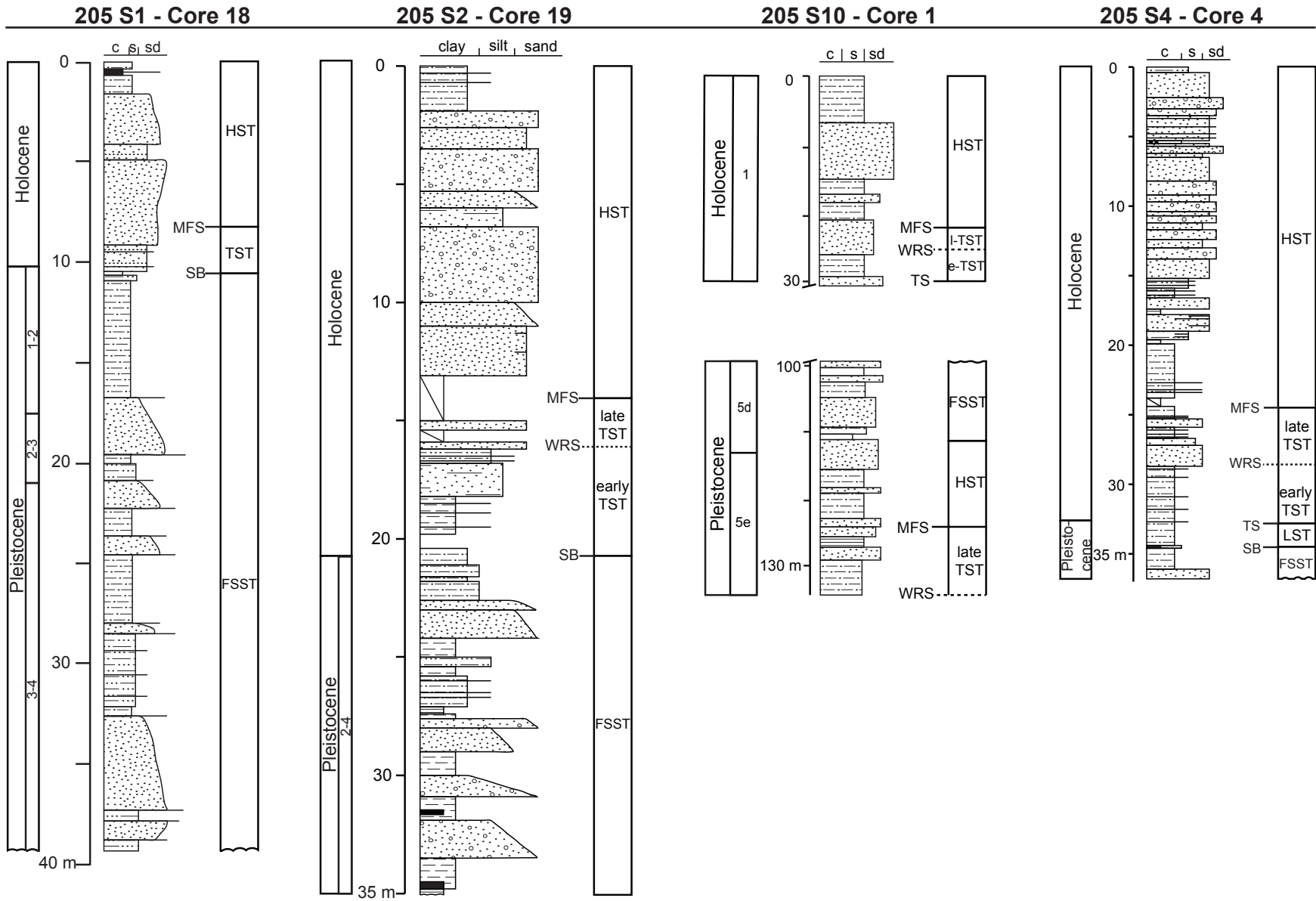
Appendix A continued. Sequence stratigraphic information after Amorosi et al. 2004 and Greggio et al. 2012.

Appendix A continued. Sequence stratigraphic information after Amorosi et al. 2004.

119
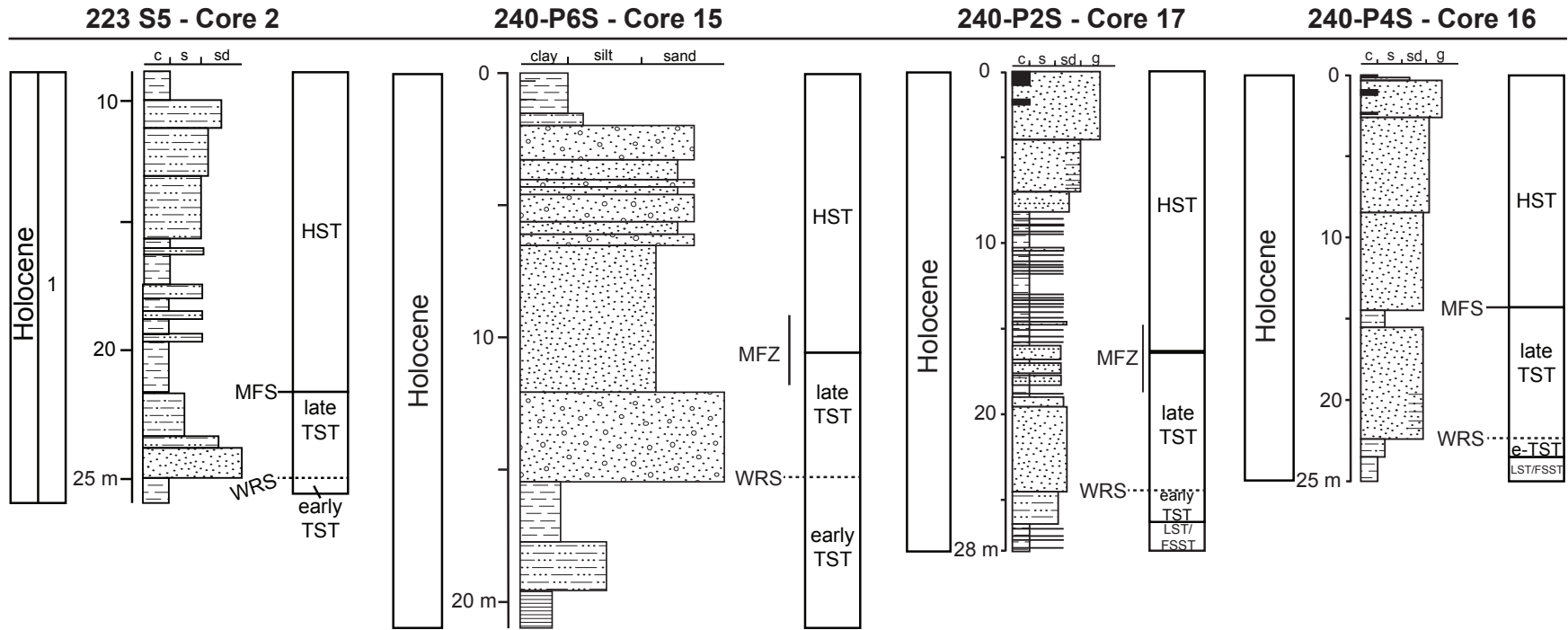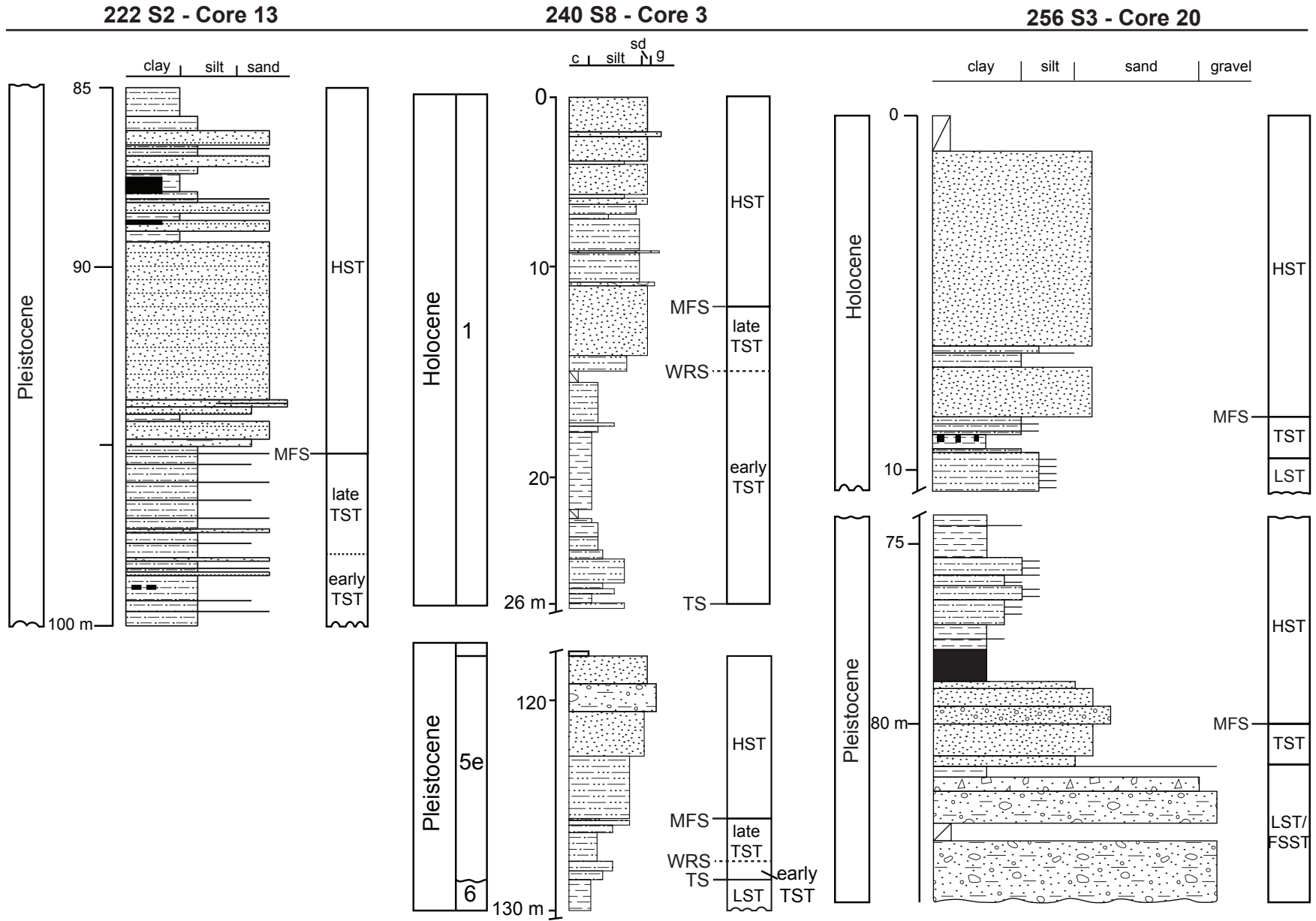
Appendix B. Detrended Correspondence Analysis of species from the Po plain. Ordination by species displays a wedge-shaped pattern with deeper water genera at high DC1 scores and medial DC2 scores. Shallow marine-brackish genera have low DC1 scores and spread across DC2.
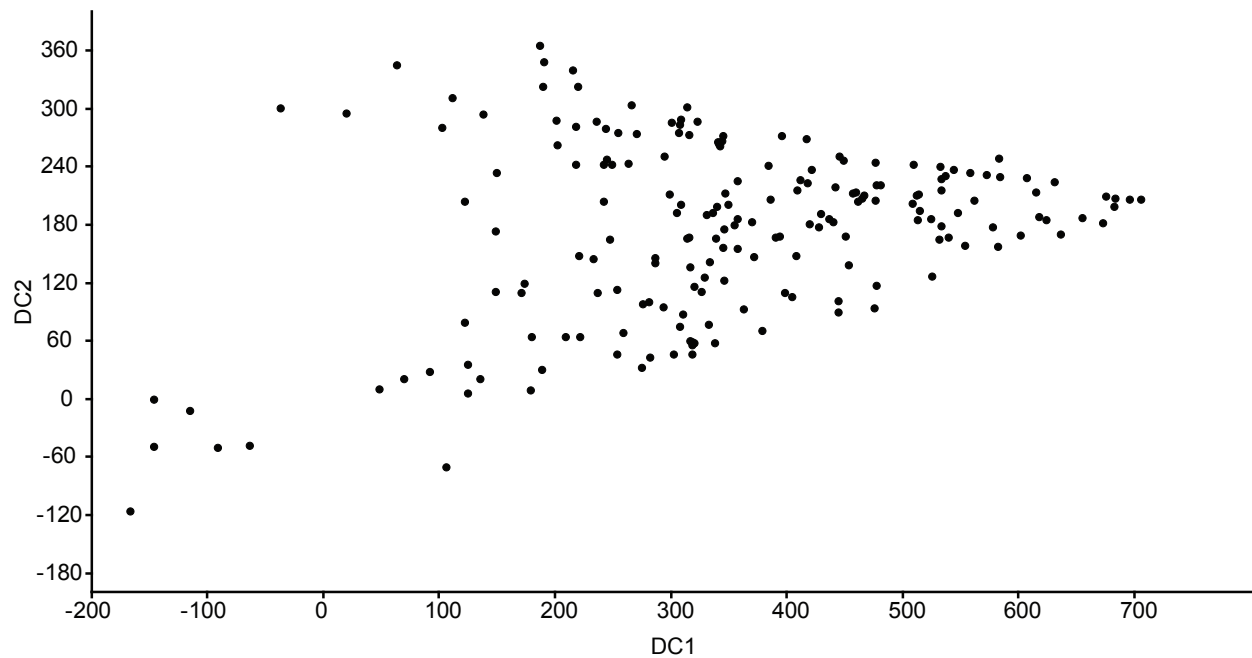
Appendix C. Bivariate plot of species ordination DC1 scores versus EG water depth estimates, n=44. The correlation between DC1 and water depth as the main environmental gradient is weaker compared to the genus level ordination in Figure 7 with an r² of 0.41.

$$y = -0.0326x + 2.2497$$
$$r^2 = 0.41$$