Benthic communities in Atlantic Canada continental shelf basins: Patterns and their influence on ecosystem functions

By

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ABSTRACT

Macrofauna, an abundant and often patchy constituent of benthic soft sediments, alter important processes such as sediment oxygenation and nutrient fluxes. This study links spatial patterns in faunal biodiversity and ecosystem functions. I collected 39 sediment cores from 4 basins within the Gulf of Maine to characterize fauna and sedimentary characteristics. At coarse taxonomic levels (phyla and feeding guild), faunal composition was homogenous across the Gulf of Maine, whereas species-level taxonomy revealed heterogeneous composition and limited species turnover. Of the abiotic variables, all factors varied locally (across sites within basins) but only bottom depth differed significantly regionally. Ecosystem function varied significantly across and within basin, and additional analyses confirmed polychaete biodiversity, as well as abundance, were significant, positive predictors of secondary (microbial) production. Feeding guild biodiversity predicted more ecosystem functions than species or family level groupings, demonstrating that activity and behaviour better predict ecosystem functions in sediments than species diversity.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Horizontal dashed lines and dots indicate mean basin value (dashed line) ± SE (dots). Lower case letters (i.e. a, b, c) indicate significant differences among basins or sediment depths ($p < 0.05$). Star indicates significant differences among sites within a basin. On horizontal axis C = Crowell Basin, G = Georges Basin, J = Jordan Basin, and R = Roseway Basin.

Figure 3.2 Relationship between subsurface bioturbation and whole core polychaete abundance (A), species diversity (B), species richness (C), and species evenness (D). n = 38.

Figure 3.3 Relationship between subsurface bioturbation and polychaete species evenness at surface (A), subsurface (B), and deep (C; [$y = 0.3 * \exp(1.1 * x)$], $R^2 = 0.140$, $p = 0.035$) sediment depths. n = 38. (n/s) indicates non-significance.

Figure 3.4 Relationship between deep bioturbation and whole core polychaete abundance (A), species diversity (B), species richness (C), and species evenness (D). n = 39. (n/s) indicates non-significance.

Figure 3.5 Relationship between deep bioturbation and subsurface polychaete abundance within Crowell (A; [$y = 0.2 + (12.5 / x)$], $R^2 = 0.918$, $p = 0.003$; n = 6), Georges (B; n = 12), Jordan (C; n = 12), and Roseway (D; n = 9) Basins. (n/s) indicates non-significance.

Figure 3.6 Relationship between sediment oxygenation and whole core polychaete abundance (A), species diversity (B), species richness (C), and species evenness (D; [$y = -32.3 + 80.6 * x + -47.7 * x*x$], $R^2 = 0.175$, $p = 0.031$). n = 39. (n/s) indicates non-significance.

Figure 3.7 Relationship between sediment oxygenation and surface polychaete abundance (left panels) and deep polychaete species richness (right panels) within Crowell (A,B; n = 6), Georges (C ([$y = 1.9 + (-11.1 / x)$], $R^2 = 0.341$, $p = 0.046$; n = 12), D), Jordan (E,F; n = 12), and Roseway (G ([$y = 3.9 + -0.52 * \log(x)$], $R^2 = 0.680$, $p = 0.006$; n = 6), H ([$y = -0.4 + 2.5 * x + -0.6 * x*x$], $R^2 = 0.658$, $p = 0.040$; n = 6)) Basins. (n/s) indicates non-significance.

Figure 3.8 Relationship between secondary production and polychaete abundance (A and D; [$y = 3.8 \times 10^8 * \exp(0.01 * x)$], $R^2 = 0.191$, $p = < 0.01$), species diversity (B and E; [$y = 2.2 \times 10^8 * \exp(0.5 * x)$], $R^2 = 0.238$, $p = < 0.01$), and species richness (C and F; [$y = 3.1 \times 10^8 * \exp(0.2 * x)$], $R^2 = 0.169$, $p = < 0.01$) across basins (A, B, C) and sediment depth layers (D, E, F); although neither impacts relationship. n = 39 for each basin and sediment depth.

LIST OF APPENDICES

12), and Roseway (D; n = 9). Measurements from all three sediment depth layers included. (n/s) indicates non-significance.

Appendix H Results from feeding guild biodiversity analyses

Table H1. Summary of two-way ANOVAs (generalized linear model) showing the effect of whole core polychaete feeding guild biodiversity measures and Basin on ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4.

Table H2. Summary of two-way [*three-way] ANOVAs (generalized linear model) showing the effect of polychaete feeding guild biodiversity measures and Basin [*and Sediment Depth] on ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4, Sediment Depth n = 3.

Table H3. Summary of regression analyses for whole core polychaete feeding guild biodiversity measures and ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

Figure H1. Relationship between deep bioturbation and whole core polychaete feeding guild biodiversity measures: diversity (A), richness (B; [$y = 0.1 + 1.1 / x$], $R^2 = 0.124$, $p = 0.028$), and evenness (C). n = 39. (n/s) indicates non-significance.

Figure H2. Relationship between sediment oxygenation and whole core polychaete feeding guild biodiversity measures: diversity (A; [$y = -5.1 + 8.6 * x + -2.7 * x*x$], $R^2 = 0.189$, $p = 0.023$), richness (B; [$y = 1.0 * \exp(0.3 * x)$], $R^2 = 0.100$, $p = 0.049$), and evenness (C). n = 39. (n/s) indicates non-significance.

Table H4. Summary of regression analyses for polychaete feeding guild biodiversity measures and ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

Figure H3. Relationship between subsurface bioturbation and feeding guild diversity at surface (A), subsurface (B; [$y = 1.1 + 0.1 * x + -0.2 * x*x$], $R^2 = 0.220$, $p = 0.013$), and deep (C) sediment depths (n = 38). Relationship between subsurface bioturbation and feeding guild evenness at surface (A; [$y = 1.8 + -0.7 / x$], $R^2 = 0.121$, $p = 0.032$), subsurface (B), and deep (C) sediment depths. n = 38. (n/s) indicates non-significance.

Figure H4. Relationship between sediment oxygenation and polychaete feeding guild diversity at surface (A; [$y = -2.7 + 5.4 * x + -1.7 * x*x$], $R^2 = 0.172$, $p = 0.033$), subsurface (B), and deep (C) sediment depths. n = 39. (n/s) indicates non-significance.

Figure H5. Relationship between secondary production and polychaete feeding guild diversity (A and D; [$y = 2.3 \times 10^8 * \exp(0.8 * x)$], $R^2 = 0.202$, $p = < 0.01$), richness (B and E; [$y = 5.3 \times 10^8 + 9.0 \times 10^6 * x + 1.2 \times 10^8 * x*x$], $R^2 = 0.059$, $p = 0.036$), and evenness (C and F; [$y = -1.8 \times 10^9 + 7.7 \times 10^9 * x + -5.4 \times 10^9 * x*x$], $R^2 = 0.107$, $p = 0.002$) across basins (A, B, C) and

sediment depth layers (D, E, F); although neither impacts relationship. n = 39 for each basin and sediment depth.

CHAPTER I

GENERAL INTRODUCTION

Benthic soft sediments cover ~70% of the seafloor, encompassing the largest ecosystem in the world (Snelgrove 1998). Although much of the sea floor resembles physically homogenous deserts, the biological reality is far different. Studies of benthic communities have intensified since the early 1900's, when Petersen (1913) first described epifaunal and infaunal communities. Publications followed, such as Thorson (1957) and Sanders (1958), proposing links between animals and their sedimentary environments and initiating benthic research on animal-sediment-relationships. The wealth of information collected since the 1950's on marine soft-sediment ecosystems has eliminated the notion of lifeless, barren marine deserts and instead demonstrated rich, diverse, and complex interactive environments (Sanders and Hessler 1969; Grassle 1989; Snelgrove et al. 1997; Snelgrove 1998; Lohrer and Hancock 2004).

Benthic soft sediments house a plethora of marine life, from micro-organisms to large mega-fauna. The dominant groups of infaunal organisms include macrofauna, defined as benthic organisms larger than 300 or 500 μm (e.g. Snelgrove and Smith 2002). This group, typically dominated by marine annelids, molluscs, crustaceans, echinoderms, and other phyla, represents one of the most diverse assemblages on Earth (Snelgrove 1998). Collectively, macrofauna significantly alter their local environments, influencing global cycles (e.g. carbon, nitrogen, and sulphur), secondary production, sediment mixing, and metabolism of pollutants, as they interact with other infaunal groups such as microbial flora and meiofauna (Snelgrove 1998). Polychaetes, in particular, are important constituents of benthic soft-sediment communities, given their ubiquitous distribution across various habitats. They often dominate macrofaunal communities, and are often used as surrogates for macrobenthic community diversity as a result of their high species richness and numerical dominance (Fauchald and Jumars 1979; Hutchings 1998; Ellingsen 2002; Mikac et al. 2011). The feeding and behaviours of these animals create complex relationships with their sediment habitats, sometimes greatly affecting sediment stability and biogeochemical processes via local habitat manipulation (i.e., creating and irrigating burrows). These activities can dramatically alter sediment oxygenation (Painting et al. 2013), bioturbation (Mermillod-Blondin 2011), and secondary productivity (Cole et al. 1988; Muller et al. 1997), among other ecosystem functions.

Benthic communities therefore support a wide range of flora and fauna that strongly influences and regulates ecosystem functions (Kennedy and Jacoby 1997; Barros et al. 2008), creating a critical need to understand linkages between community structure and ecosystem functions. These and other functions (e.g. water purification, carbon remineralisation) maintain a stable and healthy environment, sustaining life and supporting goods and services essential to humanity such as food, recreation and tourism opportunities, waste disposal, and dilution of pollutants (de Groot et al. 2002).

Biological infaunal communities are useful indicators for monitoring the conditions of ecosystems (Kennedy and Jacoby 1997; Barros et al. 2008). One important influence stems from the direct and indirect effects of feeding behaviours of benthic organisms (Snelgrove et al. 1997). For example, grazing and deposit feeding organisms influence primary production because their feeding activities influence nutrient fluxes into the sediments, which in turn, can improve conditions for sedimentary microbes and unicellular algae (Lohrer et al. 2004). Suspension feeders can also influence their immediate environments, generally regulating energy transfer (Diaz and Rosenberg 1995). These organisms can significantly enhance nutrient fluxes from benthic into pelagic environments through sediment mixing and the exchange of solutes (e.g. Marinelli et al. 1998; Norkko et al. 2001).

Infaunal macrofauna are also important sediment irrigators whose burrowing activities and sediment reworking techniques directly regulate the penetration of oxygen into the sediment (Snelgrove et al. 1997). In the absence of macrofauna, factors such as the concentration of oxygen in bottom water, sedimentation of organic matter, grain size, and temperature control penetration of oxygen into the sediment (Diaz and Rosenberg 1995). Generally, in muddy or silt habitats, dissolved oxygen can penetrate only a few millimetres into the sediment through simple physical (molecular) diffusion; however, burrowing and irrigation activities of macrofauna greatly expedite distribution of oxygen into deeper sediment layers. Without infauna and demersal species reworking the sediment, deeper sediment layers typically become anoxic (Revsbech et al. 1980). Dissolved oxygen availability strongly affects respiration rates of macroinvertebrates, especially at low concentrations. Therefore environments with minimal to no sediment

oxygenation support very low numbers of macrofauna and/or are limited to surface sediments. Alterations in oxygen concentrations can also influence rates of bacterial nitrification and denitrification, affecting the renewal of diffusing ammonia and nitrate and potentially altering the nitrogen cycle and ocean productivity (Snelgrove et al. 1997). Microelectrodes and other emerging sensor technologies allow more reliable and precise measurements of sediment oxygenation and respiration rates within marine benthic environments (Diaz and Rosenberg 1995; Glud et al. 1996).

Sediment characteristics, such as grain size and organic content strongly affect the distribution of infauna (e.g. Cacabelos et al. 2009). Decreasing diversity of macrobenthic assemblages with increasing distance from shore was linked to habitat type, which was largely defined by grain size and mud content (Hoey et al. 2004). Numerous other studies have correlated patterns in infaunal communities with sediment grain size but also with sediment depth layers (Holte et al. 2004). Some groups of macrofauna are well known to prefer specific grain sizes (e.g. Cacabelos et al. 2009); however grain size correlates strongly with other key drivers (Snelgrove and Butman 1994). Aside from the distribution of macrofauna, grain size also correlates with organic content. Rapid nutrient regeneration rates and generally higher nutrient concentrations in deeper layers characterize soft sediments in particular when compared with other benthic habitats, and these important nutrient sources fuel primary production (Marinelli et al. 1998). Lower organic content tends to characterize coarser sediments compared to muddier sediments (Oevelen et al. 2009). Other environmental factors, such as hydrodynamic forces and concentration of organic matter, also regulate the formation of benthic sediments and indirectly influence the development of macrofaunal communities. In addition, microbial abundance, food supply, and trophic interactions can also contribute to infaunal community patterns (Snelgrove and Butman 1994).

Measurements of organic matter, including chlorophyll-a distribution within sediments often reflect rates of primary production in overlying waters, transport of material from sedimentation/bioturbation, and alterations in habitats resulting from decomposition or transformation reactions (Sun et al. 1991). Ocean sediments typically contain little chlorophyll-a, but decaying organic matter deposited on the sediment

surface is eventually mixed into deeper sediments through particle reworking (Sun et al. 1991). Chlorophyll-a is widely used as a measure of particle mixing because it is a common pigment in many phytoplankton species and typically occurs only in the uppermost sediment layers, separated into 'bound' (i.e., within cell components) or 'free' forms (Sun et al. 1991). This generally non-conservative tracer can reveal the downward mixing of fresh organic matter, with an average half life of 23 days under oxic conditions (Sun et al. 1993; Maire et al. 2008). Other mineral particles, such as luminophores and radionuclides, are generally used as tracers of sediment reworking when limited organic matter is present (Maire et al. 2008).

To evaluate how an ecosystem functions as a whole unit requires measuring and understanding the individual ecosystem functions that occur within it. Understanding drivers of biodiversity patterns and interconnectivity within the ecosystem is important not only because of the ubiquity of sedimentary environments but also because of the potential implications of biodiversity loss for key regulation functions. Removal of infaunal habitat-forming species can generate habitat homogeneity, creating conditions similar to those after large-scale physical disturbances (Thrush et al. 2006). Benthic environments face numerous threats, spanning from past and present fishing activity to future oil exploration. Baseline information regarding biodiversity and distribution patterns within this region is vital for understanding the patterns and driving factors (Kelly et al. 2010).

The Gulf of Maine, located in the northwest Atlantic, supports productive and valuable commercial fishing grounds (Lapointe 2013). Benthic ecosystems benefit greatly from high primary productivity and the supply of detritus from the pelagic environment, which may vary spatially and temporally depending on environmental conditions. For example, bottom currents greatly dictate benthic sediment type and organic food supply (Gray 1974; Rhoads 1974) but circulation patterns, such as the strong currents found in the Gulf of Maine, can greatly influence other hydrodynamic processes, such as near-bottom flow, thus bringing additional, or less, food (i.e. organic content) to the benthos (Butman 1987; Snelgrove and Butman 1994). Patterns and pelagic processes, such as accumulations (spatially or temporally) of free falling detritus, can impact local variation,

as shown in studies of benthic sediments of the Gulf of Maine by Weissberger et al. (2008) and in Arctic waters by Piepenburg et al. (1997) and Link et al. (2011).

Benthic habitats, particularly in deep waters, are challenging to study because of limited accessibility and limited current knowledge relative to shallow coastal and terrestrial ecosystems (Loreau et al. 2002; Duffy 2003; Naeem 2012). Even with improved technologies that facilitate sampling of the benthos, these environments still limit in situ experiments. Marine environments, and benthic habitats in particular, face increasing anthropogenic pressures that are changing these ecosystems faster than our efforts to understand them (Glover and Smith 2003; Loreau 2007).

This thesis investigates the influence of habitat predictors on the composition of infaunal communities and explores how infauna can influence certain ecosystem functions within benthic marine environments. Chapter 2 examines faunal and environmental variation in space and explores the drivers of regional spatial biodiversity patterns across and within deep basins of the Gulf of Maine. The objectives of this study are to determine: 1) whether faunal composition (macrofaunal abundance, polychaete abundance) and polychaete biodiversity (diversity, richness, and evenness) vary spatially across regional (between basins spanning 100s of kms), local (between sites within basins spanning 10's kms) and vertical spatial scales (cms between sediment depth layers); 2) whether taxonomic (species and family) or functional (feeding guild) resolution of polychaete biodiversity (diversity, richness, and evenness) can explain spatial variation across regional (between basins spanning 100s of kms), local (between sites within basins spanning 10's kms) and vertical spatial scales (cms between sediment depth layers); 3) whether environmental factors (mud content, organic matter, carbon, nitrogen, and chlorophyll concentrations, and bottom depth) vary spatially across regional, local and vertical (i.e. Basin, Site(Basin), Sediment Depth respectively) spatial scales; and 4) whether environmental variables are drivers of faunal spatial patterns. The fourth objective links environmental variation with faunal variation. Based on the previous studies reviewed above that demonstrate the interconnectedness of benthic biota and their abiotic environment, I hypothesize that abiotic and biotic factors will not co-vary across spatial scales, that taxonomic resolution will not influence interpretation of patterns in

infauna, and that correlations between abiotic and biotic factors will not indicate any single strong abiotic driver of biotic variation.

Chapter 3 investigates how biological communities influence ecosystem functions by measuring oxygen penetration into bottom sediments, chlorophyll a concentration within sediment layers, and microbial abundances. The objectives of this study are to determine: 1) if ecosystem function proxies (subsurface and deep bioturbation, sediment oxygenation, and secondary production) vary spatially across local or regional spatial scales; 2) whether polychaete abundance and species biodiversity (i.e., diversity, richness, evenness), predict ecosystem function measures; and 3) whether different taxonomic (species and family) or functional (feeding guild) levels reveal different biodiversity-ecosystem function relationships. I propose that abundance and species biodiversity will predict at least one ecosystem function. I also propose that activity classification (i.e., feeding guild) will predict ecosystem functions more strongly than taxonomic identity (i.e. species). Feeding guilds highlight major differences in feeding behaviour, whereas species taxonomy may reflect relatively modest morphological differences. Feeding guilds also characterize groups of organisms contributing similarly to specific functions (i.e., deposit feeding) whereas taxonomic identity may differentiate organisms that overlap in specific role(s), and thus represent potential redundancy. Overall, this research presents new information about bio-physical interactions within the marine benthos, and examines relationships between biodiversity and ecosystem functions in continental shelf deep basin sediments. This research also adds baseline knowledge on marine biodiversity in Canada's oceans.

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Co-authorship statement

The work described in this thesis was conducted by Ashley Robar with guidance from Paul Snelgrove, Kim Juniper, and Anna Metaxas. Ashley Robar was responsible for field and laboratory data collection and analysis (with assistance by Paul Snelgrove) and contributed to modifications brought to the original design by Paul Snelgrove and Kim Juniper. All chapters were written by Ashley Robar with intellectual and editorial input by Paul Snelgrove, Kim Juniper, and Anna Metaxas. The co-authorship of any publications in the primary literature resulting from this work will reflect the different contributions of those involved.

Chapter II

Benthic biodiversity of basin sediments in the Gulf of Maine: Spatial patterns and drivers

2.1 ABSTRACT

Macrofauna are abundant constituents of benthic soft sediments and their presence and distribution in these habitats can often be patchy. Our study examines variation in benthic infauna, with a detailed focus on polychaetes, as well as their potential response to numerous abiotic factors across multiple spatial scales in soft-sediment basins in the Gulf of Maine. A total of 39 sediment cores were collected from 4 soft-sediment basins (i.e., Crowell, Georges, Jordan, and Roseway) to characterize fauna and sediments. We identified infauna to the lowest taxonomic level possible for polychaetes and to phylum for other taxa, and calculated detailed biodiversity information for polychaetes (i.e. diversity, species richness, evenness). We compared spatial variation in biotic and abiotic factors (mud content, organic matter concentrations and ratios, bottom depth) using univariate analyses and tested abiotic influence on biotic patterns using multivariate analyses. Our results revealed regional (across basins), as well as vertical (i.e. between sediment depth layers) variation in fauna. The only abiotic factor that differed significantly regionally was bottom depth, however, all other abiotic factors varied locally (i.e. across sites within basins). A BIOENV analysis revealed bottom depth as a weak driver of faunal distributions within soft-sediment basins of the Gulf of Maine, a result supported by past studies. We observed fairly homogeneous faunal composition at coarse taxonomic levels (phyla and feeding guild) across the Gulf of Maine, in contrast to more heterogeneous faunal composition at finer taxonomic resolution (species level) with limited species turnover. Whereas previous studies linked biotic patterns to environmental factors, our findings suggest that faunal interactions, as well as select environmental parameters (i.e. water depth), explain regional biotic variation. Most abiotic conditions measured were fairly uniform across regional scales and correlated weakly with biotic measures. Projected seasonal cycles described by previous studies, as well as known oceanographic drivers (i.e., currents), help explain local abiotic variation within the Gulf of Maine. This research demonstrates how the incorporation of multiple spatial and taxonomic scales in the study design, as well as environmental variables, can influence understanding of benthic macrofaunal communities.

2.2 INTRODUCTION

Patterns and relationships within the benthos are challenging to study, given that sediments cover much of the seafloor, and oceans represent ~70% of the Earth's surface (Snelgrove 1998). Most benthic environments also occur at depths requiring large vessels for sampling (Solan et al. 2003; Joydas and Damodaran 2013). With accelerated biodiversity loss from anthropogenic drivers, knowing the identity, quantity, and impacts of animals on their environments in the marine benthos is more important than ever (Tornroos et al. 2014).

Invertebrate fauna such as annelids, crustaceans, echinoderms, and molluscs are often abundant and visible components of soft-sediment environments, where many species exhibit highly mobile planktonic larval stages as well as mobility as juveniles and adults. The large capacity for dispersal presumably contributes to species turnover and patchy distributions, as well as the capacity to colonize newly disturbed environments (e.g. Rosenberg et al. 2002; Norkko et al. 2006). Benthic invertebrates use a variety of dispersal mechanisms to repopulate an area, inhabit new environments, or exchange individuals with another population (i.e. connectivity) (Bradbury and Snelgrove 2001; Valanko et al. 2010). This movement of individuals between communities (i.e. emigration, immigration, recruitment and extirpation) greatly changes local population and community dynamics throughout marine environments and ultimately impacts species turnover, which refers here to the rates at which species composition changes spatially (Snelgrove et al. 1999; Norkko et al. 2001; Valanko 2012).

Documentation and quantification of species distributions and biodiversity patterns at varying spatial and temporal scales help understand the processes that shape benthic communities (Zajac et al. 2003; Carvalho et al. 2005; Hewitt et al. 2010). Benthic sediments can harbour diverse communities of infaunal organisms with naturally patchy distributions, even in areas without obvious environmental heterogeneity (Snelgrove 1999; Lohrer and Hancock 2004). Researchers therefore strive to link community diversity patterns and baseline distribution information across various scales to potential physical, environmental, and biotic drivers, including environmental assessments

conducted before and after natural or un-natural disturbances (Underwood 1994; Hernandez-Arana et al. 2003; Kelly et al. 2010).

Spatial analyses can identify patchiness at scales of a few meters to 100's of kms and thus help to illuminate potential drivers of biodiversity patterns (Morrisey et al. 1992). Building on Jumars (1976) study of spatial scales in deep-sea benthic communities at both large (100 km apart) and small scales (1 km apart), McClain et al. (2011) studied macrofaunal turnover and variability across spatial scales ranging from 1 to 350 m. Furthermore, several studies have combined local (i.e. 10s of kms) and regional (i.e. 100s of kms) spatial approaches (e.g. Bergen et al. 2001; Ellingsen 2002; Preston 2002; Mermillod-Blondin et al. 2003; Carvalho et al. 2005; Rodil et al. 2009) to forecast large-scale biodiversity patterns. Within the Gulf of Maine, several studies (e.g. Weissberger et al. 2008; Kelly et al. 2010; Ellis et al. 2011) assessed biodiversity in specific regions and at varying spatial scales. Weissberger et al. (2008) investigated temporal variation in relationships between benthic communities and sediment nutrients solely within Wilkinson Basin, whereas Kelly et al. (2010) integrated data from multiple Gulf of Maine studies to assess knowledge of diversity, distribution, and abundance of species across different regions. Ellis et al. (2011) compared biodiversity research (i.e., composition, structure and function) approaches from four distinct regions around the world, including the Gulf of Maine to assess how different research communities prioritize needs. Our research investigates wide-scale regional variation across deep basins in the Gulf of Maine to address knowledge gaps with respect to biodiversity patterns across multiple spatial scales and to help understand drivers of sedimentary biodiversity variation across the entire Gulf of Maine region.

Whereas spatial analyses can elucidate benthic community patterns, studies investigating animal-sediment relationships attempt to explain patchy distributions. Loosely defined as interactions between organisms and the sedimentary environment in which they live, animal-sediment relationships may reflect complex and difficult to investigate linkages. Sanders (1958) noted a close association between animals and specific sediment grain size fractions, and linked species distribution and subsequent patchiness with different feeding strategies in different habitats. Subsequent studies

pointed to other sediment features that might determine biotic distribution patterns, such as organic matter availability, quality, and quantity (Whitlatch 1981; Frid et al. 1996; Rodil et al. 2009; Lutz-Collins and Quijon 2014), microbial communities (Alongi 1985; Lopez and Levinton 1987; Kristensen 1988), and fauna and flora interactions (Woodin 1976; Frid et al. 1996; Symons and Arnott 2014). In addition to these food-related drivers, other studies point to physical aspects of the environment such as flow (Warwick and Uncles 1980; Biles et al. 2003), substrate stability (Holland and Dean 1977; Bricelj et al. 1984), water and sediment depth, and latitude (Gagnon and Haedrich 1991; Bergen et al. 2001; Ellingsen 2002; Hernandez-Arana et al. 2003), however, temperature, salinity, primary production, hydrodynamics, and measures of physical and historical disturbance may also play a role (Snelgrove 1998; Cacabelos et al. 2009). Abiotic-biotic relationships often reflect complex interactions between many variables that influence species distributions (Snelgrove and Butman 1994; McArthur et al. 2010), and contribute to discrepancies regarding which factors best explain biodiversity patterns. Macrofaunal organisms themselves can also influence sediment parameters (i.e., effective grain size, organic content) (e.g. Ginsburg and Lowenstam 1958), leading to complex relationships, whereas spatial variables (i.e. bottom depth, latitude, and longitude) can predict, but are not known to directly drive, biotic patterns (McArthur et al. 2010).

Weak correlations between biotic patterns and abiotic or biotic variables suggest that one variable alone does not drive species distributions (Snelgrove and Butman 1994), and feeding strategies alone do not define determine patterns of distribution and co-occurrence (Snelgrove and Butman 1994). Most current research considers numerous physical, chemical, and biological factors working in combination to explain distribution patterns, and uses multivariate approaches to consider combinations of environmental factors, such as grain size, organic matter, pore-water chemistry, microbes, and hydrodynamics (Snelgrove and Butman 1994; Levin et al. 2001; Anderson 2008; Barros et al. 2008).

Species identification, largely based on morphological characteristics, provides the most information about an organism, but requires time, money, and expertise (Olsgard et al. 1997). Researchers have long recognized difficulties with species identification and

have begun to investigate taxonomic sufficiency and assume a degree of species redundancy (Walker 1992; Naeem 1998; O'Connor and Crowe 2005; Dalerum et al. 2012). More commonly, species are grouped at coarser taxonomic levels, such as family or functional group (Clarke and Warwick 1998; Hutchings 1998) to save time or because of a lack of information, and many studies advocate use of coarse taxonomic resolution (genus, family, order, phyla, functional group) to reduce sampling costs or investigate pattern consistency within an ecosystem (Somerfield and Clarke 1995; De Biasi et al. 2003; Quijon and Snelgrove 2006). Olsgard and Somerfield (2000) arrive at a similar conclusion when analysing polychaete families and species to detect influence of pollution on soft-sediment communities. As an increasing number of studies investigate influences of biodiversity on ecosystem functions, focus on animal functions can overshadow biogeographic patterns. As more researchers investigate coarser taxonomic groupings and justify their use to simplify studies on benthic communities, we must recognize the information lost, including undiscovered species and potential change in species composition. Species redundancy (i.e., species performing the same ecosystem function) questions also arise, noting that few studies have addressed this issue and the potential effects of redundant species removal on ecosystem functioning.

This chapter examines faunal and environmental variation and explores the drivers of regional spatial biodiversity patterns across and within deep basins of the Gulf of Maine. The objectives of this study are to determine: 1) whether faunal composition (macrofaunal abundance, polychaete abundance) and polychaete biodiversity (diversity, richness, and evenness) vary spatially across regional (between basins spanning 100s of kms), local (between sites within basins spanning 10's kms) and vertical spatial scales (cms between sediment depth layers); 2) whether taxonomic (species and family) or functional (feeding guild) resolution of polychaete biodiversity (diversity, richness, and evenness) influences spatial variation across regional (between basins spanning 100s of kms), local (between sites within basins spanning 10's kms) and vertical spatial scales (cms between sediment depth layers); 3) whether environmental factors (mud content, organic matter, carbon, nitrogen, and chlorophyll concentrations, and bottom depth) vary spatially across regional, local and vertical (i.e. Basin, Site(Basin), Sediment Depth

respectively) spatial scales; and 4) whether environmental variables contribute to faunal spatial patterns. The fourth objective links environmental variation with faunal variation. We hypothesize that abiotic and biotic factors will not co-vary with spatial scale, that taxonomic or functional resolution will not impact interpretations of patterns in faunal variation, and that variation in biotic factors will not strongly correlate with any single abiotic driver, pointing to one or more abiotic driver of biotic variation.

2.3 MATERIALS AND METHODS

2.3.1 Study area and sampling sites

Benthic samples were collected from four sedimentary basins in the Gulf of Maine (approximate longitude: 71.5 – 63 °W, Latitude: 39.5 - 46 °N), which covers an area of 123,000.6 km^2 located along the eastern coast of North America at the Canada US border (Ellis et al. 2011). The four sampled basins included (Fig. 2.1): Jordan Basin (43° 32'N, 67° 04'W; avg. depth 226 ± 4 [SE] m), Crowell Basin (42° 58'N, 67° 16'W; avg. depth 293 ± 49 m), Georges Basin (42° 27'N, 66° 44'W; avg. depth 348 ± 5 m), and Roseway Basin (43° 10'N, 65° 04'W; avg. depth 173 ± 2 m). Jordan, Crowell, and Georges Basin are located within the Discovery Corridor, a geographic region identified to focus marine biodiversity research (Herder and Van Guelpen 2008; Incze et al. 2010). Roseway Basin is located east of the Discovery Corridor and southeast of Nova Scotia on the Scotian Shelf (Fig. 2.1). These basins were chosen on the basis of generally similar depths and sediment properties conducive to coring and spanning a broad geographic area with contrasting oceanographic conditions for spatial comparison.

Sedimentary infauna was sampled from the Canadian Coast Guard Ship Hudson from July 28 to August 14, 2009 using an Oktopus multicorer fitted with six clear plastic tubes (inner diameter 10 cm, length 1 m). To assess differences across regional and local spatial scales (Fig. 2.2), sediment cores were collected from 13 sites (local scale) across the four basins (regional scale): Jordan (n=4 sites), Crowell (n=2), Georges (n=4), and Roseway (n=3). We collected a total of 39 multi-core drops (3 drops per site), processing 1 core per drop for infauna). Cores generally penetrated to a sediment depth of 15-25 cm, of which we retained only the top 10 cm. All cores were sectioned into three sediment

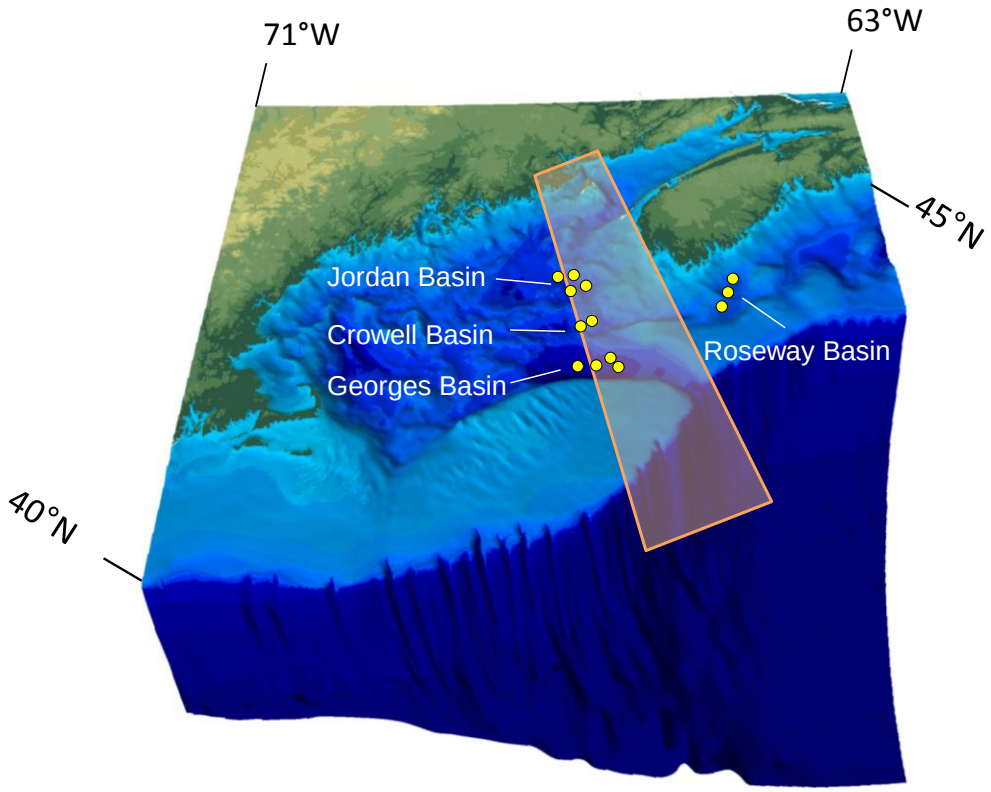

Figure 2.1. Schematic of basin locations sampled within the Gulf of Maine. Yellow dots indicate collection sites of benthic samples (n=13). A total of 39 multicore drops spanned these 13 sites (Jordan [n=12 drops; 4 Sites], Crowell [n=6; 2], Georges [n=12; 4], and Roseway [n=9; 3]). Light orange area indicates boundaries of the Discovery Corridor.

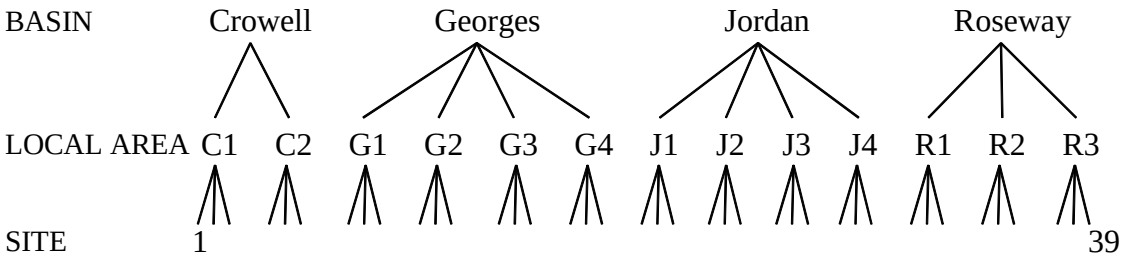

Figure 2.2. Hierarchical nested sampling design. Site is nested within Local Area, which is nested within Basin (unbalanced design). Three replicate cores were collected from each Site.

depth layers (0-2, 2-5, and 5-10 cm). The distance between samples ranged from 1 km (between drops) to 10s of kms (between sites) to 100s of kms (between basins; Appendix Fig. A1).

Most cores were processed quickly onboard the vessel, and any cores not processed immediately were refrigerated at 4 ºC (the approximate seafloor temperature) until they could be processed (typically within 1-2 h). From each drop, 1 core was processed for macrofauna, which was first processed to evaluate sediment oxygenation; oxygen and other ecosystem function-related data are reported in Chapter 3. A 2nd core was designated to measure organic content (food availability and quality), and a 3rd core was used to measure sediment characteristics (mud content) and other geological characteristics. These variables were used to examine how abiotic factors (sediment parameters, availability and quality of organic matter, and bottom depth) influence biodiversity (macrofaunal abundance and polychaete biodiversity) patterns. Each variable was replicated 39 times (once per drop) and analyzed in laboratories at Memorial University (St. John's, Newfoundland and Labrador, Canada).

2.3.2 Macrofaunal collection

Each of the three sediment depth layers (0-2 cm, 2-5 cm, and 5-10 cm) from the 39 cores was rinsed over a 300 µm sieve with filtered seawater. Samples were fixed with 10 % buffered formalin. Instruments were rinsed with filtered seawater between samples to avoid cross contamination. For long-term preservation, macrofaunal samples were transferred into 70 % ethanol at the Ocean Sciences Centre (approximately 4 weeks after collection). Rose Bengal was added a minimum of 24 hours before picking samples to facilitate removal of specimens. Macrofaunal organisms were identified using a dissection microscope and separated into major phyla (Annelida, Arthropoda, Echinodermata, and Mollusca). Polychaetes (phylum Annelida) were further identified into 11 feeding guilds (MacDonald et al. 2010), 36 families and 131 species (Appendix Table E1 and E2).

2.3.3 Collection and analysis of abiotic variables

For determination of mud content (%), we extruded sediment from the core and sliced two 1 cm sections at depths of 0-1 cm and 2-3 cm to determine grain size in surface

and subsurface sediment layers. These sections were chosen to parallel section depths in macrofaunal analysis. Instruments were rinsed with freshwater between samples. On the vessel, samples for grain size and mud content determinations were stored in plastic zip-lock bags and refrigerated (4 ºC) until transport to Memorial University where samples were stored at 4 ºC until processing. To quantify percentage of mud content, 0.25 cm^3 samples of sediment from each depth layer were transferred to plastic centrifuge tubes with 40 mL of 0.05% $NaPO_3$. To determine whether presence of organic matter led to clumping of sediment particles in samples, a subsample (n=5) was treated with 15% peroxide to remove any organic material from the sample. Subsequent comparison showed no difference in average grain size (µm) or mud content (%) between peroxide and non-peroxide treatments, and the peroxide treatment was therefore dropped from the procedure. Samples were agitated for 10 seconds using sonication to disperse clumping particles. Percentage of mud content was determined at Memorial University (Earth Sciences) using a Horiba laser scattering particle size distribution analyzer (partica LA-950). Three measurements were taken for each sample to account for instrument error. The percentage of particles ≤ 62.5 µm was used to quantify mud content for statistical analysis.

Organic carbon and nitrogen concentrations (mg/g), as well as organic matter ratios (C:N), were used to characterize sedimentary organic content. Concentrations were used to quantify food availability, whereas the ratio (C:N) measured food quality. Samples from each core drop were collected (n=39) by subsampling with a modified coring instrument (10-mL syringe with the end cut off to form a uniform barrel for coring; 1 replicate per core). To identify changes in organic content among sediment depth layers, approximately 1 mL (~ 2 grams dry weight) of sediment was removed from each of three depth layers (0-2 cm, 2-5 cm, and 5-10 cm) in each core. Samples were placed onto a sterilized aluminum foil sheet and folded using sterilized forceps. Aluminum foil sheets and forceps were sterilized prior to the field cruise at 400 ºC for 24 hours and rinsed with 95% ethanol, respectively. The samples for organic content (wrapped in aluminum foil) were stored in zip-lock bags at -20 ºC to prevent degradation of organic material prior to processing. All instruments were rinsed thoroughly with

freshwater and wiped dry between sample collections. To quantify organic content, we dried frozen samples at 85 ºC for 24 hours, and ground them with a mortar and pestle prior to removing 2 mg of sediment and placing it in a small tinfoil cup. Using sterilized forceps, we then flattened the tinfoil cup and folded it into a small cylinder. C:N values were determined using a Perkin-Elmer 2400 Series II CHNS/O auto-analyzer at the Ocean Sciences Centre (Memorial University).

Samples for measuring chlorophyll-a concentrations (µg/g) were collected from three sediment depth layers (0-2 cm, 2-5 cm, and 5-10 cm) using a modified syringe as described above (1 replicate per core). Surface (0-2 cm) chlorophyll-a concentrations provided a measure of available phytodetrital food on the seafloor, whereas ratios of surface concentrations to concentrations from subsurface (2-5 cm) and deep (5-10 cm) sediment layers approximated bioturbation (see Chapter 3). We removed approximately 1 mL of sediment (~ 2 grams dry weight) from each depth layer (0-2 cm, 2-5 cm, and 5-10 cm) in each core with the modified syringe and placed it in 15 mL Falcon centrifuge tubes. These tubes were completely covered with aluminum foil and stored at -20 ºC to eliminate light exposure that can degrade chlorophyll-a during storage and transport to the laboratory. Instruments were rinsed thoroughly with freshwater between samples and wiped dry. To extract chlorophyll-a from sediment, we added 5 mL of 90% acetone to each tube and incubated it overnight at 4 ºC. The following day, samples were transferred to glass centrifuge tubes and topped with 90% acetone to a final volume of 9 mL. We sealed each tube with Parafilm and centrifuged at 4500 rpm for 5 minutes. The supernatant was poured into a second glass centrifuge tube and diluted by a known factor (410 times) using 90% acetone. Chlorophyll-a concentrations from refrigerated (4 ºC) samples were measured before and after acidification (with 5% HCl) using a Turner Designs 10-AU-005-CE fluorometer at the Ocean Sciences Centre (Memorial University). All glassware was rinsed with two washes of distilled water followed by two washes of 90% acetone between samples.

Bottom depth (m) was recorded using a pinger attached to the multicorer and verified from the CCGS Hudson echo sounder.

2.3.4 Statistical analysis

2.3.4.1 Spatial variation in biotic and abiotic variables (univariate analyses)

We used three-way nested ANOVAs [with factors Basin, Site(Basin), and Sediment Depth] to test for regional (100's kms between basins), local (10's kms between sites within basins), and sediment horizon spatial scale differences in biotic and abiotic variables. Basin sampling encompassed four regions (Crowell, Georges, Jordan, and Roseway Basins) and Site sampling entailed clusters of 3 cores each nested within 2-4 groups within Basin (Crowell [n = 2 sites], Georges [n = 4 sites], Jordan [n = 4 sites], Roseway [n = 3 sites]). To evaluate variability between sediment horizons we included a Sediment Depth factor (surface [0-2 cm], middle [2-5 cm], and deep [5-10 cm]). For variables with no measurements across sediment horizons (i.e. bottom depth), we used two-way nested ANOVAs [with factors Basin and Site(Basin)] to investigate spatial variation.

For each ANOVA, we assessed normality using Shapiro-Wilk's statistics and homogeneity of variance with Levene's test for equality of error variances and by examining graphical distributions of standardized residuals. To resolve problems of non-normal and heteroscedastic data we applied transformations (log, square root, or fourth root) to raw data and reported those transformations within the ANOVA tables below. In cases where transformations homogenized the variance but did not improve non-normal data, we proceeded with the analysis and interpreted the outcome with care, noting that ANOVA is robust to deviations from normality (Underwood 1997). In cases where transformations did not correct heteroscedastic data, we analyzed rank-transformed data and compared the results to the raw data. If the ANOVA results of ranked transformed data were similar to that of the raw data, we proceeded with the raw data analysis, as suggested by Conover and Iman (1981), but when the two results differed we report ranked data results. We then used least-square means multiple comparisons with Bonferonni correction of probabilities to detect differences among levels within a factor for Basin and Sediment Depth. In the event of a significant interaction between factors (i.e. Basin x Sediment Depth), we split the analysis by Sediment Depth to test for spatial scale differences using factors Basin and Site. Basin and Site were considered random factors since they were selected to represent geographic regions rather than specific

locations, whereas Sediment Depth was fixed. A significance threshold of 0.05 was used for all statistical tests, which were conducted using SPSS 22 software.

Measures of biotic factors include total macrofauna abundance, phyla abundance [Annelida, Mollusca, Echinodermata, and Arthropoda], polychaete abundance and polychaete biodiversity (diversity, richness, and evenness). Polychaete biodiversity measures were measured at three taxonomic levels [species, family, and feeding guild]. We calculated diversity using the Shannon-Weiner Index (H'), richness using Margalef's Richness Index (d) and evenness using Pielou's Evenness Index (J'). For faunal analyses we used hierarchical, agglomerative classification employing group-average linking (i.e. CLUSTER analysis) to plot faunal distribution and detect sample similarity across multiple spatial scales. ANOSIM multivariate analyses were used to detect biotic assemblage differences across basins and sediment depth layers using a significance threshold of 0.1% ($p = 0.05$). MDS plots were used to illustrate biotic community patterns with similarity groupings overlaid showing samples with similar biotic compositions. SIMPER multivariate analyses determined which biotic drivers contributed most to sample dissimilarities between factors (Basin and Sediment Depth) and also determined biotic drivers of sample similarities within each factor. Juveniles were excluded from polychaete species analyses because of taxonomic uncertainty. Fourth-root transformations were applied to abundance measures before running multivariate analyses to eliminate dominance of species with higher abundances. Biodiversity calculations, as well as all ANOSIM and SIMPER multivariate analyses, were conducted using PRIMER-E 6.0 software. Abiotic variables included mud content (%), organic matter ratios (C:N), carbon and nitrogen concentrations (mg/g), chlorophyll-a concentrations (μg/g), and bottom depth (m).

2.3.4.2 Influence of abiotic variables on biotic spatial patterns (multivariate analysis)

We further explored the relationship between surface (0-2 cm) biotic communities (macrofauna phyla abundances and polychaete species, family and feeding guild abundances) and abiotic factors (percent mud content, carbon and nitrogen concentrations, C:N, chlorophyll-a concentrations and bottom depth) using the BIOENV procedure (Clarke and Gorley 2006). BIOENV produces Spearman rank correlations

based on resemblance matrixes (Euclidean distance for log transformed environmental variables and Bray-Curtis for fourth root transformed biotic variables) to determine if samples share similar environmental and biotic spatial patterns. BIOENV was preferable to Principal Components Analysis (PCA) given the limited number of abiotic factors (6; Clarke and Gorley 2006). BVSTEP analyses were used to determine which BIOENV correlations were significant. All analyses were conducted with PRIMER 6 software with a significance threshold of 0.1% ($p = 0.05$). We focused on results from the upper sediment horizon (0-2 cm) because of the significant biotic differences between sediment depth layers (see Results Table 2.2 and 2.6).

2.4 RESULTS

2.4.1 Spatial variation in biotic variables

2.4.1.1 Faunal abundance and polychaete biodiversity variation

A total of 5,724 macrofaunal organisms were collected from the top 10 cm of 39 sediment cores and classified into four major phyla: Annelida [67 % of total abundance], Mollusca [19 %], Arthropoda [10 %], and Echinodermata [3 %] (Appendix Table A1). Spatial variation of total macrofauna and phyla abundances were tested using three-way ANOVAs, with factors Basin, Site(Basin), and Sediment Depth. Total macrofaunal abundance differed significantly at the basin scale and across sediment depth layers, but not between sites within basins (Table 2.1). Total macrofaunal abundance was similar in Crowell and Jordan Basin, significantly lower in Georges Basin than all other basins, and significantly higher in Roseway Basin compared to all other basins (Fig. 2.3a). Total abundance in surface sediment layers (0-2 cm) was approximately 4 and 12 times higher than middle (2-5 cm) and deep (5-10 cm) layers, respectively (Fig. 2.3b). Basin differences in total abundance were consistent between sediment depth layers (i.e. no significant interaction between Basin and Sediment Depth factors).

Annelida abundance (67 % of total macrofauna) results were similar to those for total macrofaunal with significant differences at basin scales and across sediment depth layers, but not sites within basins (Table 2.1). Similarly, abundances in Georges Basin

Table 2.1 Summary of three-way ANOVAs (non[1] and rank[2] transformed data) showing the effect of Basin (Crowell, Georges, Jordan, and Roseway), Site (nested within each Basin) and Sediment Depth (0 – 2, 2 – 5, and 5 – 10 cm) on biotic variables. Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

Biotic Variable	Source of Variation		Df	Mean Square	F	Sig.
Total Macrofauna[2]	**Basin**	Hypothesis	3	3911.635	16.656	**0.010**
		Error	4	234.842		
	Site(Basin)	Hypothesis	9	254.393	1.348	0.281
		Error	18	188.710		
	Sediment Depth	Hypothesis	2	48774.243	287.859	< **0.01**
		Error	6	169.438		
	Basin x Sediment Depth	Hypothesis	6	169.158	0.896	0.518
		Error	18	188.710		
	Site(Basin) x Sediment Depth	Hypothesis	18	188.710	1.048	0.419
		Error	78	180.009		
Annelida[2]	**Basin**	Hypothesis	3	5689.660	6.313	**0.016**
		Error	8	901.324		
	Site(Basin)	Hypothesis	9	522.576	2.125	0.083
		Error	18	245.974		
	Sediment Depth	Hypothesis	2	43338.549	69.980	< **0.01**
		Error	6	619.303		
	Basin x Sediment Depth	Hypothesis	6	624.722	2.540	0.058
		Error	18	245.974		
	Site(Basin) x Sediment Depth	Hypothesis	18	245.974	1.230	0.260
		Error	78	200.053		
Mollusca[2]	Basin	Hypothesis	3	2034.121	3.864	0.086
		Error	5	526.466		
	Site(Basin)	Hypothesis	9	243.799	1.074	0.426
		Error	18	226.906		
	Sediment Depth	Hypothesis	2	41447.812	81.989	< **0.01**
		Error	6	505.528		
	Basin x Sediment Depth	Hypothesis	6	509.573	2.246	0.086
		Error	18	226.906		
	Site(Basin) x Sediment Depth	Hypothesis	18	226.906	1.102	0.367
		Error	78	205.897		

Table 2.1. cont.

Biotic Variable	Source of Variation		Df	Mean Square	F	Sig.
Arthropoda[1]	Basin	Hypothesis	3	12.391	12.093	0.967
		Error	0	1.025		
	Site(Basin)	Hypothesis	9	19.638	0.636	0.753
		Error	18	30.894		
	Sediment Depth	Hypothesis	2	2077.601	165.583	**< 0.01**
		Error	6	12.547		
	Basin x Sediment Depth	Hypothesis	6	12.281	0.398	0.871
		Error	18	30.894		
	Site(Basin) x Sediment Depth	Hypothesis	18	30.894	0.997	0.472
		Error	78	30.974		
Echinodermata[2]	Basin	Hypothesis	3	4545.269	4.611	0.070
		Error	5	985.773		
	Site(Basin)	Hypothesis	9	617.923	1.107	0.406
		Error	18	558.367		
	Sediment Depth	Hypothesis	2	17320.748	18.807	**0.002**
		Error	6	920.954		
	Basin x Sediment Depth	Hypothesis	6	926.217	1.659	0.189
		Error	18	558.367		
	Site(Basin) x Sediment Depth	Hypothesis	18	558.367	1.656	0.066
		Error	78	337.118		

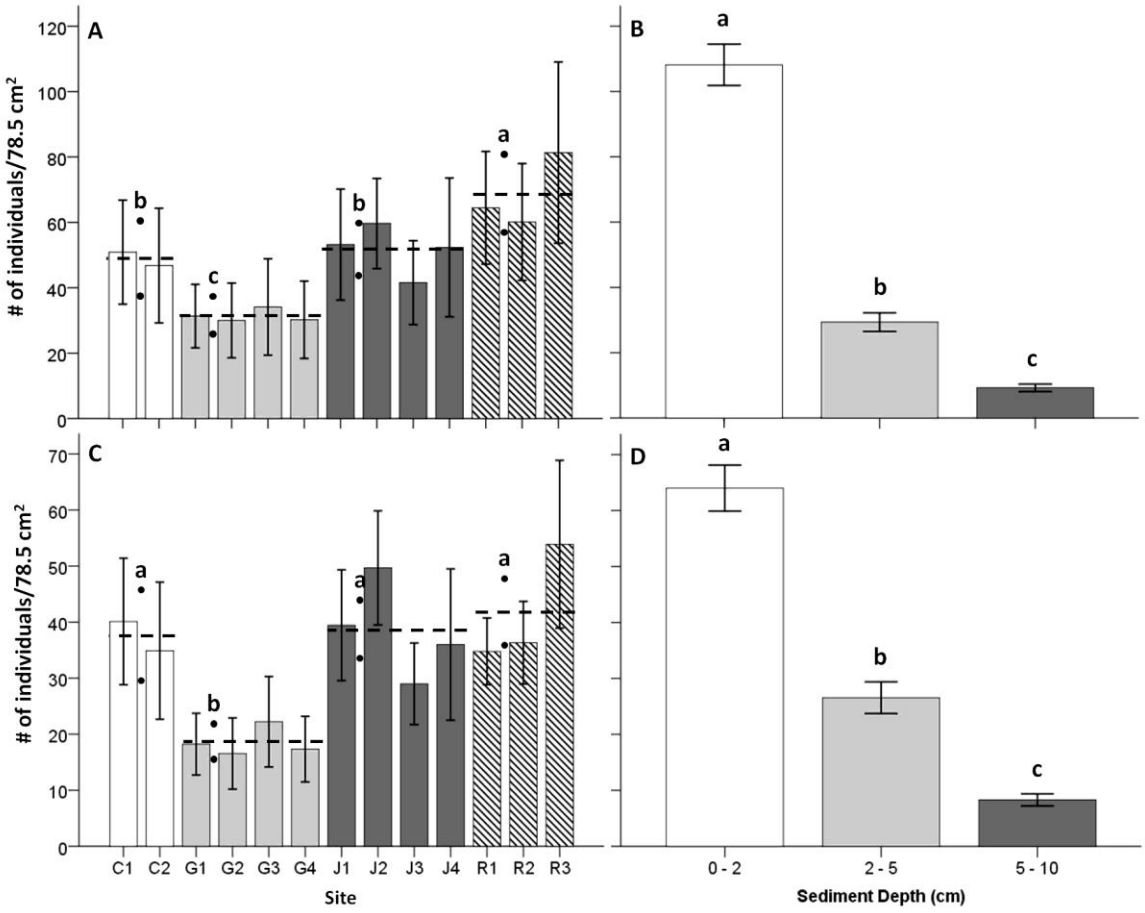

Figure 2.3. Abundance comparisons of total macrofauna (A, B) and Annelida (C, D) across local and regional spatial scales (i.e. Site and Basin respectively; left panels; n = 3 for each bar) and across sediment depth layers (right panels; n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences. On horizontal axis C = Crowell Basin, G = Georges Basin, J = Jordan Basin, and R = Roseway Basin.

were significantly lower compared with all other basins (Fig. 2.3c) and surface sediments had the highest abundances, significantly more than middle or deep sediment layers (Fig. 2.3d). Basin differences were consistent across sediment depth layers. Mollusca, Arthropoda, and Echinodermata abundances did not vary spatially at Basin or Site scales (Appendix Fig. A2a, c, e respectively), however, abundances of each phylum varied significantly across sediment depth layers, with significantly higher abundances in surface sediments than middle and deep sediments (Table 2.2, Appendix Fig. A2b, d, f respectively). Basin similarities were consistent (i.e. invariant) within each sediment depth layer (Table 2.1).

Polychaete abundance and species biodiversity (diversity, richness, and evenness) differed significantly across sediment depth layers (Table 2.2), with significantly higher abundance, diversity, and richness within surface sediment layers (Fig. 2.4) and generally higher evenness in deep sediment layers (Fig. 2.5). Polychaete abundance and species richness also differed significantly across basins (Table 2.2), with significantly lower abundances and species richness in Georges Basin compared to all other basins. No significant differences were found across sites (within basins) for any species biotic measure, except species evenness, which exhibited a significant Site(Basin) and Sediment Depth interaction that indicated inconsistent Site scale differences across sediment depth layers (Table 2.2). Analysis of individual sediment layers revealed significant variation in species evenness between sites within basins (particularly Roseway Basin), but this significant result was limited to just surface sediment layers (Table 2.3; Fig 2.5).

2.4.1.2 Influence of taxonomic resolution on polychaete biodiversity variation

Biodiversity measures from coarser taxonomic groupings (i.e., family and feeding guild, reported in appendices to limit chapter length) also revealed significant variation across sediment depths (Appendix Table B1, B2, and C1), with significantly higher diversity and richness in surface sediments and significantly higher evenness in deep sediments (Appendix Fig. B1, B2, and C1). Family level diversity showed inconsistent Basin differences across sediment depth layers as indicated by a significant interaction between Basin and Sediment Depth (Appendix Table C1). Family evenness showed inconsistent site scale differences across sediment

Table 2.2. Summary of three-way ANOVAs (general linear model) showing the effect of Basin, Site (nested within Basin) and Sediment Depth on polychaete abundance and species biodiversity measures (raw data compared to rank transformed data[1] and rank[2] transformed data). Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

Measurement	Source of Variation		df	Mean Square	F	Sig.
Abundance[2]	**Basin**	Hypothesis	3	5309.560	5.774	**0.018**
		Error	9	919.593		
	Site(Basin)	Hypothesis	9	572.387	2.391	0.055
		Error	18	239.366		
	Sediment Depth	Hypothesis	2	43585.866	74.941	< **0.01**
		Error	6	581.604		
	Basin x Sediment Depth	Hypothesis	6	586.572	2.451	0.066
		Error	18	239.366		
	Site(Basin) x Sediment Depth	Hypothesis	18	239.366	1.166	0.310
		Error	78	205.374		
Diversity[1]	Basin	Hypothesis	3	2.964	5.155	0.051
		Error	5	0.575		
	Site(Basin)	Hypothesis	9	0.322	1.161	0.375
		Error	18	0.278		
	Sediment Depth	Hypothesis	2	20.042	38.044	< **0.01**
		Error	6	0.527		
	Basin x Sediment Depth	Hypothesis	6	0.530	1.911	0.134
		Error	18	0.278		
	Site(Basin) x Sediment Depth	Hypothesis	18	0.278	1.419	0.147
		Error	78	0.196		
Richness[2]	**Basin**	Hypothesis	3	4745.443	6.334	**0.039**
		Error	5	749.151		
	Site(Basin)	Hypothesis	9	382.294	1.027	0.456
		Error	18	372.131		
	Sediment Depth	Hypothesis	2	35631.698	48.347	< **0.01**
		Error	6	737.001		
	Basin x Sediment Depth	Hypothesis	6	740.079	1.980	0.123
		Error	18	373.752		
	Site(Basin) x Sediment Depth	Hypothesis	18	372.692	1.384	0.165
		Error	74	269.271		

Table 2.2. cont.

Measurement	Source of Variation		df	Mean Square	F	Sig.
Evenness[2]	Basin	Hypothesis	3	4382.381	3.456	0.152
		Error	3	1267.989		
	Site(Basin)	Hypothesis	9	1552.241	1.314	0.295
		Error	18	1181.552		
	Sediment Depth	Hypothesis	2	8336.178	9.253	**0.014**
		Error	6	900.881		
	Basin x Sediment Depth	Hypothesis	6	898.628	0.757	0.612
		Error	18	1186.466		
	Site(Basin) x Sediment Depth	Hypothesis	18	1189.270	1.781	**0.045**
		Error	72	667.763		

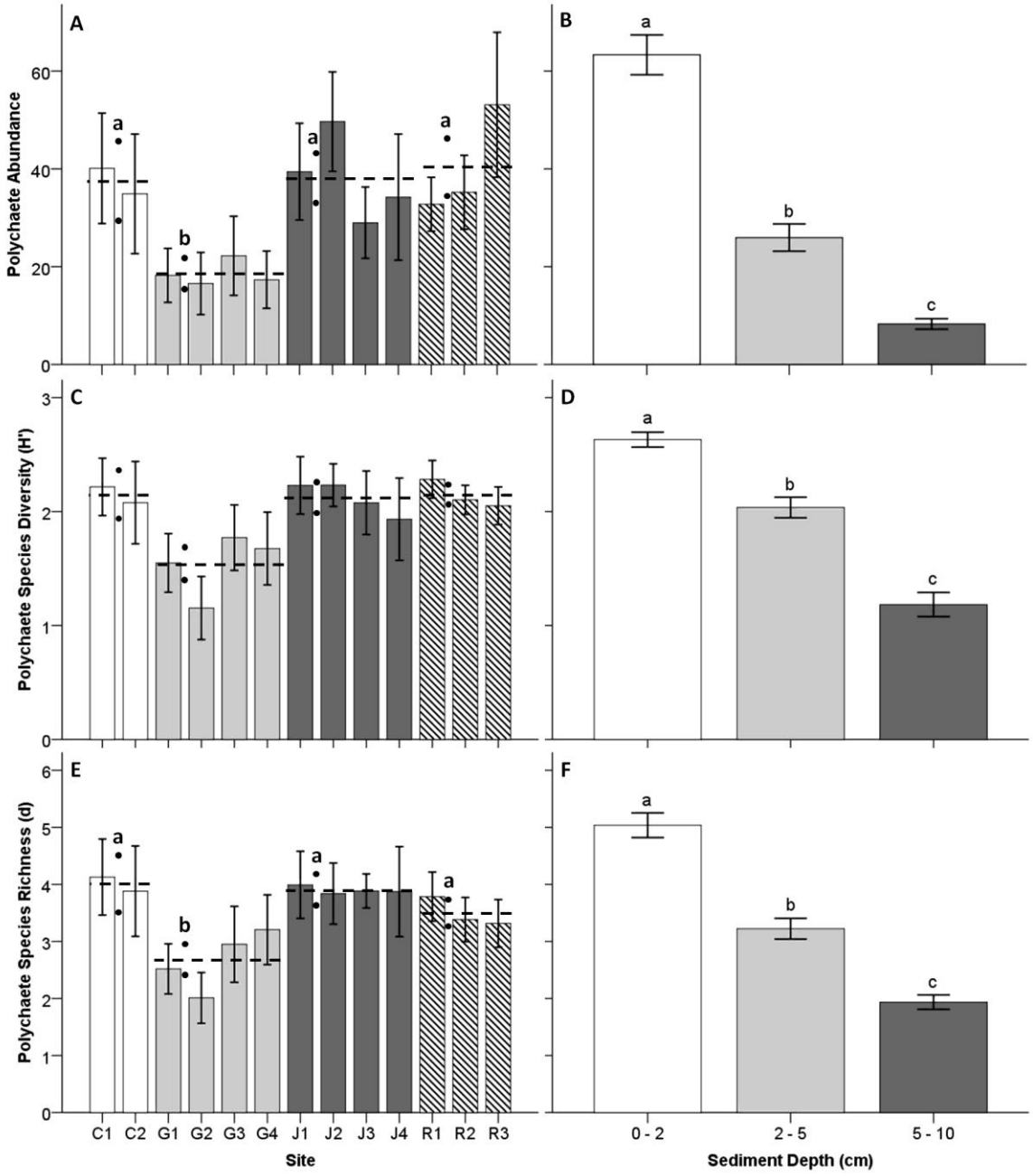

Figure 2.4. Spatial patterns of polychaete abundance (A, B), species diversity (C, D), and species richness (E, F) across local and regional spatial scales (i.e. Site and Basin respectively; left panels; n = 3 for each bar) and across sediment depth layers (right panels; n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences.

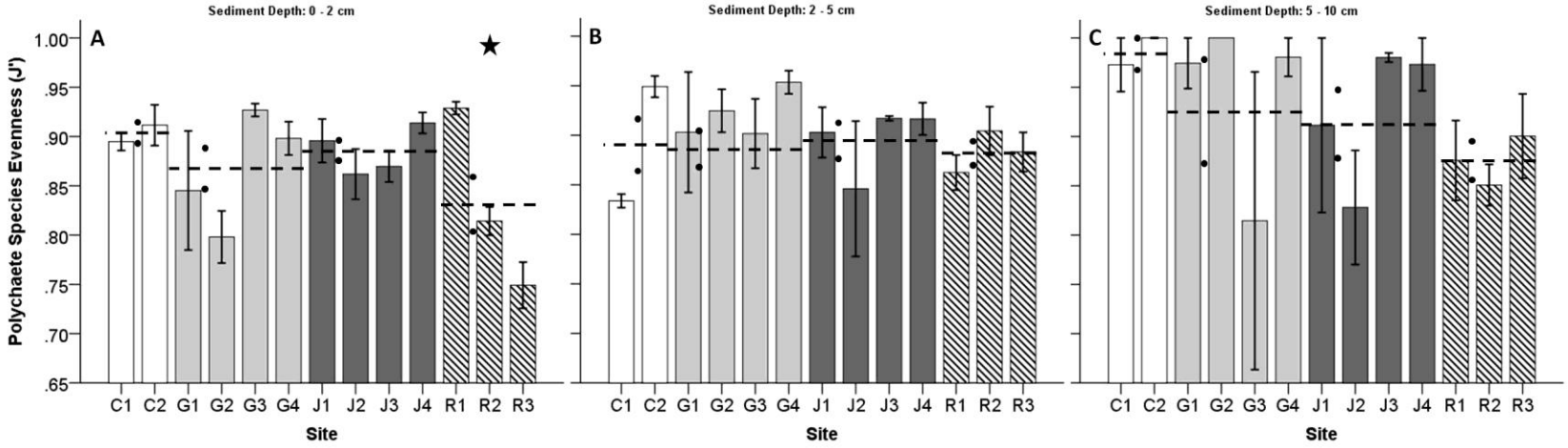

Figure 2.5. Spatial patterns of polychaete species evenness across local and regional spatial scales (i.e. Site and Basin; n = 3 for each bar) and across surface (A, 0 – 2 cm), subsurface (B, 2 – 5 cm), and deep (C, 5 – 10 cm) sediment depth layers. Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Star indicates significant differences among sites within a basin.

Table 2.3. Summary of two-way ANOVAs (fourth root transformed data) separated by Sediment Depth Layer (n = 39) showing the effect of Basin and Site (nested within Basin) on polychaete species evenness. Basin n = 4, Site n = 2-4, Core replicate n = 39.

Sediment Depth (cm)	**Source of Variation**		**df**	**Mean Square**	**F**	**Sig.**
0 - 2	Basin	Hypothesis	3	730.442	0.460	0.717
		Error	9	1588.861		
	Site(Basin)	Hypothesis	9	1588.861	5.060	**< 0.01**
		Error	26	314.026		
2 - 5	Basin	Hypothesis	3	1007.080	0.945	0.459
		Error	9	1065.902		
	Site(Basin)	Hypothesis	9	1065.902	1.511	0.196
		Error	26	705.442		
5 - 10	Basin	Hypothesis	3	4205.036	3.161	0.076
		Error	9	1330.291		
	Site(Basin)	Hypothesis	9	1337.670	1.240	0.327
		Error	20	1078.640		

depth layers as indicated by a significant interaction between Site(Basin) and Sediment Depth (Appendix Table B1). Analysis of individual sediment layers revealed that both family diversity and family evenness varied significantly among sites within basins (Roseway; Georges and Roseway, respectively), however these local scale differences were limited to surface sediment layers (Appendix Table B2). Family diversity also differed significantly across regional (i.e. basin) scales in subsurface (2 – 5 cm) sediment layers (Appendix Table B2). Analyses of feeding guild biodiversity measures (i.e. diversity, richness, and evenness) revealed no significant variation across regional (i.e. basins) or local (i.e. sites within basins) scales (Appendix Table C1).

2.4.1.3 Faunal analysis

Faunal similarities across multiple spatial scales and taxonomic classifications were examined using CLUSTER plots. All samples collected from the Gulf of Maine shared ~80 % of the same macrofauna phyla (Appendix Fig. D1). The majority of samples within Roseway and Georges Basins cluster seperately from most samples in other basins. Generally, samples collected within the same local area (i.e. site) shared high faunal similarities as well. Comparison of polychaetes reveals all samples within the Gulf of Maine shared ~70 % of the same polychaete feeding guilds (Appendix Fig. D2). Again, samples collected from Roseway and Georges Basins are more clearly separated from the other basins, sharing ~80 % and ~70 % similarity, whereas samples within Crowell and Jordan Basin were ~85 % similar. Samples collected from the same local areas (i.e. site) were also clustering indicating high faunal similarity.

Samples share ~53% of the same polychaete families (Appendix Fig. D3). Georges Basin samples were less similar to other samples, with less than 60 % similarity with other samples, whereas samples from Roseway Basin were less than 70 % similar to other samples. Samples collected within the same basin (i.e. neighbouring local areas) were most similar. At higher taxonomic resolution, samples across the Gulf of Maine shared ~25 % of the same polychaete species and exhibited the lowest similarity measured (Appendix Fig. D4). Roseway Basin samples separated from those in other basins, with ~30 % polychaete species similarity to samples from other basins. Samples

collected from the same basin (i.e. 10's kms scale) and the same site (i.e. 1's kms scale) exhibited the highest polychaete similarity.

Further analyses with PRIMER revealed taxonomic drivers of similarities and differences between and within basins, as well as between and within sediment depth layers. At the phylum level, annelids drove sample similarities (37 - 94% similarity) within each basin and sediment depth layer, and surface deposit feeding polychaetes contributed most to sample similarities in basins and sediment depth layers (25 – 47% similarity; Appendix Table D1). Polychaete family and species abundances (or a combination of species as indicated in Appendix Table D1) also contributed to sample similarities within each basin and sediment depth layer (as indicated by their contribution percentages in Appendix Table D1), however, their contributions to sample similarities were much lower (10 – 33% and 11 - 38 % similarity, respectively) compared to contributions based on coarser resolution (phyla and feeding guild levels). Capitellid polychaetes were present in most Crowell Basin samples and also in deep (5 – 10 cm) sediment depth layers throughout the study locations (16 and 33 % sample similarity respectively; Appendix Table D1). Individuals from the family Paraonidae contributed most to sample similarities within Georges Basin (18%) and subsurface (2 – 5 cm) sediment depth layers (20%; Appendix Table D1). In contrast, cossurid polychaetes contributed most to within-basin similiarities for both Jordan (17%) and Roseway Basins (19%; Appendix Table D1). Within the surface (0 – 2 cm) sediment depth layer, spionid polychaetes drove sample similarities (11%; Appendix Table D1). Within each basin and sediment depth ANOSIM analyses identified three polychaete species that contributed most to sample similarities: Capitellidae spp. B, *Prionospio* sp. A, and *Cossura longocirrata*. Capitellidae spp. B was most common in samples from Crowell Basin (13% sample similarity; Appendix Table D1). *Prionospio* sp. A was most common in samples from Georges Basin and also within the surface sediment depth layer (18 and 11% sample similarity respectively; Appendix Table D1). *Cossura longocirrata* was the most common taxon in samples from both Jordan (19%) and Roseway (21%) Basins, as well as subsurface (15%) and deep (38%) sediment depth layers (Appendix Table D1).

Overall, SIMPER analyses revealed that sample dissimilarities (between basins or sediment depth layers) were not driven by a specific phylum, feeding guild, family, or species. For example, whereas the phylum Annelida contributed most to dissimilarities between Georges and Jordan Basin (41%), Mollusca influenced dissimilarities between Crowell and Roseway Basins (38%; Appendix Table D2). No one species contributed more than 8% towards total sample dissimilarities (Appendix Table D2). This result indicated that most species were fairly ubiquitous thoughtout the Gulf of Maine region and/or occurred in very low abundances. Nonetheless, pairwise comparisons revealed signficant differences between some basins and sediment depth layers in terms of community structure, but did not identify a strong driver for these differences.

Although Crowell Basin faunal composition did not differ signficantly from Georges or Jordan Basins, all other basins differed significantly from one another ($p < 0.01$, Appendix Table D2). For example, differences between Georges and Jordan, as well as Georges and Roseway Basins, were primarily driven by annelids (41 and 33% respectively), subsurface deposit feeding guilds (21 and 16%), family Cossuridae (11 and 12%), and the species *Cossura longocirrata* (8 % for both; Appendix Table D2). Another pairwise comparison demonstrated that molluscs and the subsurface meiofaunal predators feeding guild primarily drove differences between Crowell and Roseway Basins (38 and 17% respectively), as well as Jordan and Roseway Basins (34 and 18% respectively; Appendix Table D2), however, family and species drivers of dissimilarities differed. Polychaetes of the family Cossuridae primarily influenced sample dissimilarities between Crowell and Roseway Basins (9% sample dissimilarity), whereas polychaetes of the family Lumbrineridae were most responsible for sample differences between Jordan and Roseway Basins (9 % sample dissimilarity; Appendix Table D2). At the species level, the polychaete Capitellidae spp. A contributed most to sample dissimilarities between Crowell and Roseway Basins, as well as Jordan and Roseway Basins (6 and 5 % sample dissimilarity respectively; Appendix Table D2).

Pairwise comparisons of sediment depth layers revealed significant differences in faunal composition across sediment depth layers ($p < 0.01$, Appendix Table D2). Molluscs primarily drove sample differences between surface and subsurface, as well as

surface and deep sediment depth layers (38 and 33% sample dissimilarity), whereas annelids mainly drove sample dissimilarities between subsurface and deep sediment layers (40 % sample dissimilarity; Appendix Table D2). Surface deposit feeding polychaetes influenced differences between surface and deep, as well as subsurface and deep sediment depth layers (17 and 22% sample dissimilarity respectively), whereas subsurface macrofaunal predators drove differences between surface and subsurface sediment depth layers (16%; Appendix Table D2). Spionid polychaetes and the species *Prionospio* sp. A contributed primarily to sample dissimilarities between surface and subsurface (7 and 4%) as well as surface and deep (8 and 6%) sediment depth layers, whereas differences between subsurface and deep sediment depth layers were driven by polychaetes from the family Paronidae and the species *Cossura longocirrata* (11 and 5%; Appendix Table D2).

2.4.2 Spatial variation in abiotic variables

Analyses of environmental variables (Appendix Table A2) showed that percent mud content varied significantly only within sites and not at basin scales or across sediment depth layers (Table 2.4; Fig. 2.6). Similarly, ratios of organic matter (C:N; measure of food quality) differed significantly within sites, but not at basin scales (Table 2.4; Fig. 2.7a). Organic matter ratios also varied significantly across sediment depth layers, with lower C:N in surface sediments compared with deep sediment layers (Table 2.4; Fig. 2.7b). Carbon concentrations (a measure of food availability) showed inconsistent site scale differences across sediment depth layers, as indicated by a significant Site(Basin) and Sediment Depth interaction (Table 2.4), therefore the analysis was split by Sediment Depth (Table 2.5). Within each sediment depth layer, carbon concentrations varied significantly within sites, but not across basins (Table 2.5; Fig. 2.8). Nitrogen concentrations (also a measure of food availability) varied significantly within site, but not at basin scales or across sediment depth layers (Table 2.4; Fig. 2.7c, d). As with nitrogen concentrations, chlorophyll-a concentrations differed significantly within sites, but not across basins (Table 2.4; Fig. 2.7e). Chlorophyll-a concentrations also varied significantly across sediment depth layers, in that surface layers contained higher concentrations of chlorophyll-a compared to deep layers (Table 2.4; Fig. 2.7f). Bottom

Table 2.4. Summary of three-way [*two-way] nested ANOVAs (non[1] and rank[2] transformed data) showing the effect of Basin, Site (nested within Basin) and Sediment Depth on environmental variables. Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

Environmental Variable	Source of Variation		df	Mean Square	F	Sig.
Mud Content[1]	Basin	Hypothesis	3	992.906	1.293	0.338
		Error	9	768.151		
	Site(Basin)	Hypothesis	9	651.466	4.996	**0.013**
		Error	9	130.394		
	Sediment Depth	Hypothesis	1	457.107	1.863	0.264
		Error	3	245.409		
	Basin x Sediment Depth	Hypothesis	3	247.079	1.895	0.201
		Error	9	130.394		
	Site(Basin) x Sediment Depth	Hypothesis	9	130.394	1.122	0.364
		Error	52	116.188		
Organic Matter Ratio[2]	Basin	Hypothesis	3	4466.373	1.372	0.338
		Error	6	3255.682		
	Site(Basin)	Hypothesis	9	3926.641	4.607	**0.003**
		Error	18	852.230		
	Sediment Depth	Hypothesis	2	2686.810	14.076	**0.004**
		Error	7	190.872		
	Basin x Sediment Depth	Hypothesis	6	181.272	0.213	0.968
		Error	18	852.230		
	Site(Basin) x Sediment Depth	Hypothesis	18	852.230	1.052	0.415
		Error	78	809.778		
Carbon Concentration[2]	Basin	Hypothesis	3	13583.253	1.676	0.242
		Error	9	8105.678		
	Site(Basin)	Hypothesis	9	8195.335	28.302	**< 0.01**
		Error	18	289.567		
	Sediment Depth	Hypothesis	2	315.095	1.566	0.281
		Error	6	201.192		
	Basin x Sediment Depth	Hypothesis	6	199.909	0.690	0.660
		Error	18	289.567		
	Site(Basin) x Sediment Depth	Hypothesis	18	289.567	1.924	**0.026**
		Error	78	150.521		

Table 2.4. cont.

Environmental Variable	Source of Variation		df	Mean Square	F	Sig.
Nitrogen Concentration[1]	Basin	Hypothesis	3	2.685	1.661	0.242
		Error	9	1.617		
	Site(Basin)	Hypothesis	9	1.595	74.049	< **0.01**
		Error	18	0.022		
	Sediment Depth	Hypothesis	2	0.016	0.371	0.705
		Error	6	0.043		
	Basin x Sediment Depth	Hypothesis	6	0.043	1.994	0.120
		Error	18	0.022		
	Site(Basin) x Sediment Depth	Hypothesis	18	0.022	0.876	0.608
		Error	78	0.025		
Chlorophyll-a Concentration[2]	Basin	Hypothesis	3	10134.392	2.173	0.170
		Error	8	4664.128		
	Site(Basin)	Hypothesis	9	4938.314	7.292	< **0.01**
		Error	18	677.181		
	Sediment Depth	Hypothesis	2	2679.320	6.584	**0.029**
		Error	6	406.918		
	Basin x Sediment Depth	Hypothesis	6	402.995	0.595	0.730
		Error	18	677.181		
	Site(Basin) x Sediment Depth	Hypothesis	18	677.181	1.346	0.184
		Error	78	502.991		
***Bottom depth[1]**	**Basin**	Hypothesis	3	1397.688	25.036	< **0.01**
		Error	9	55.826		
	Site(Basin)	Hypothesis	9	55.826	6.035	< **0.01**
		Error	26	9.250		

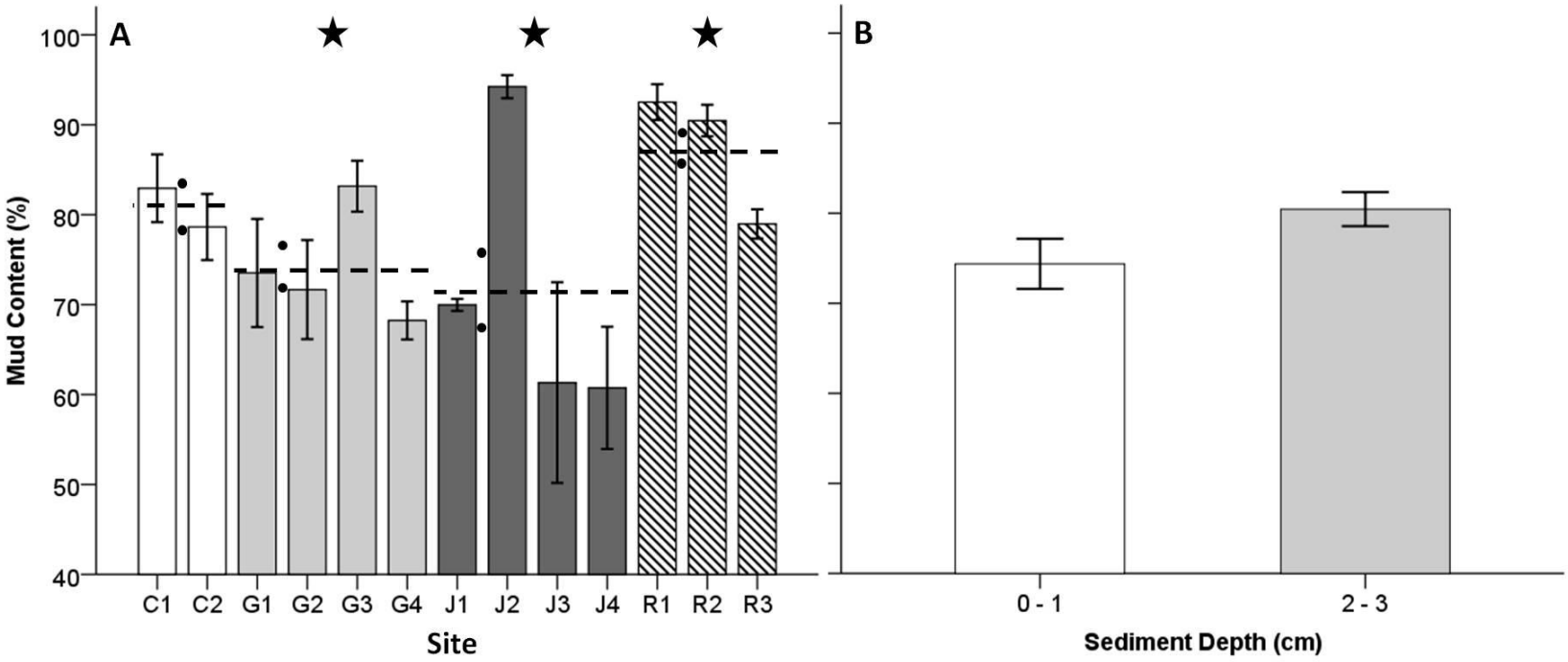

Figure 2.6. Comparison of percent mud content at local and regional spatial scales (i.e. Site and Basin respectively (A); n = 3 for each bar) and across sediment depth layers (B; n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Star indicates significant differences among sites within a basin.

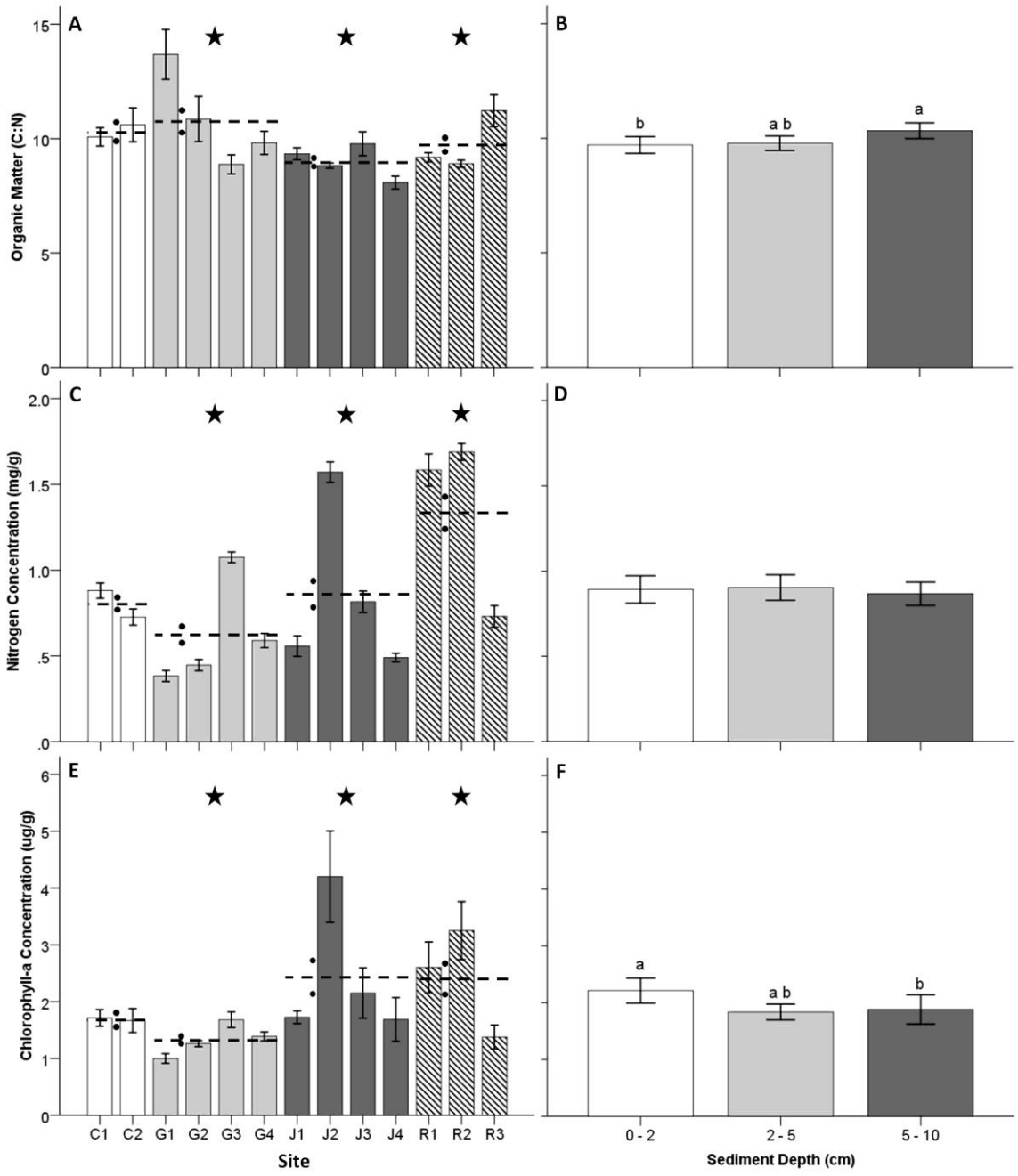

Figure 2.7. Comparison of organic matter ratios (A, B), nitrogen concentration (C, D), and chlorophyll-a concentration (E, F) across local and regional spatial scales (i.e. Site and Basin respectively; left panels; n = 3 for each bar) and across sediment depth layers (right panels; n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences. Star indicates significant differences among sites within a basin.

Table 2.5. Summary of two-way nested ANOVA (rank transformed data) separated by Sediment Depth (n = 39) showing the effect of Basin and Site (nested within Basin) on carbon concentration. Basin n = 4, Site n = 2-4, Core replicate n = 39.

Sediment Depth (cm)	Source of Variation		df	Mean Square	F	Sig.
0 - 2	Basin	Hypothesis	3	6650.803	2.496	0.126
		Error	9	2664.889		
	Site(Basin)	Hypothesis	9	2664.889	13.909	< **0.01**
		Error	26	191.590		
2 - 5	Basin	Hypothesis	3	4198.502	1.362	0.315
		Error	9	3082.528		
	Site(Basin)	Hypothesis	9	3082.528	33.109	< **0.01**
		Error	26	93.103		
5 - 10	Basin	Hypothesis	3	3133.766	1.035	0.422
		Error	9	3027.052		
	Site(Basin)	Hypothesis	9	3027.052	18.140	< **0.01**
		Error	26	166.872		

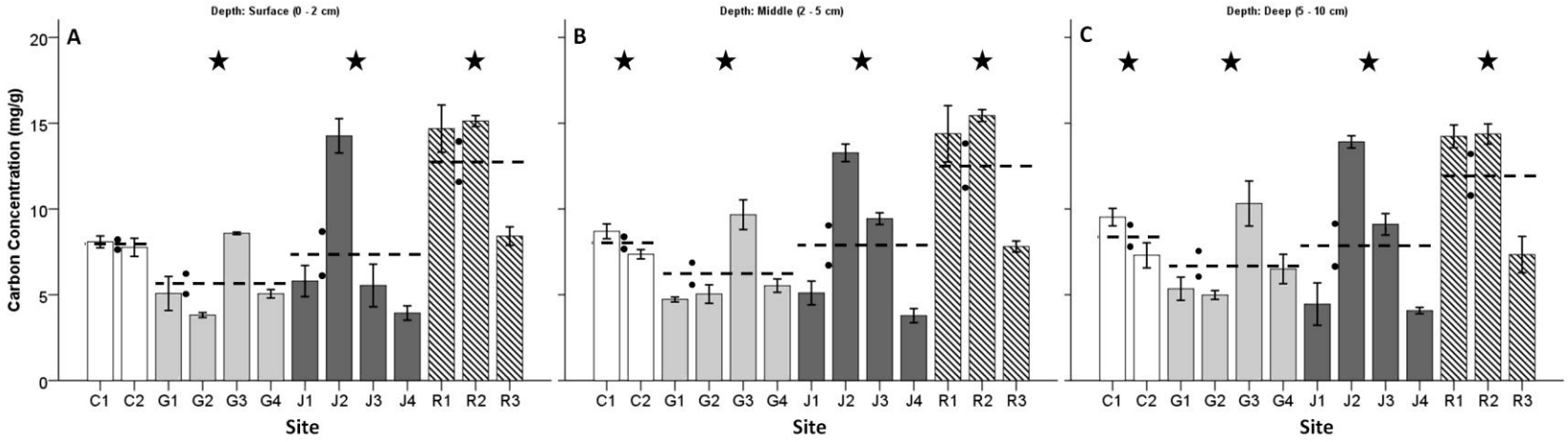

Figure 2.8. Comparison of carbon concentrations across local and regional spatial scales (i.e. Site and Basin respectively; n = 3 for each bar) seperated by Sediment Depths 0-2 (A), 2-5 (B), and 5-10 cm (C). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Star indicates significant differences among sites within a basin.

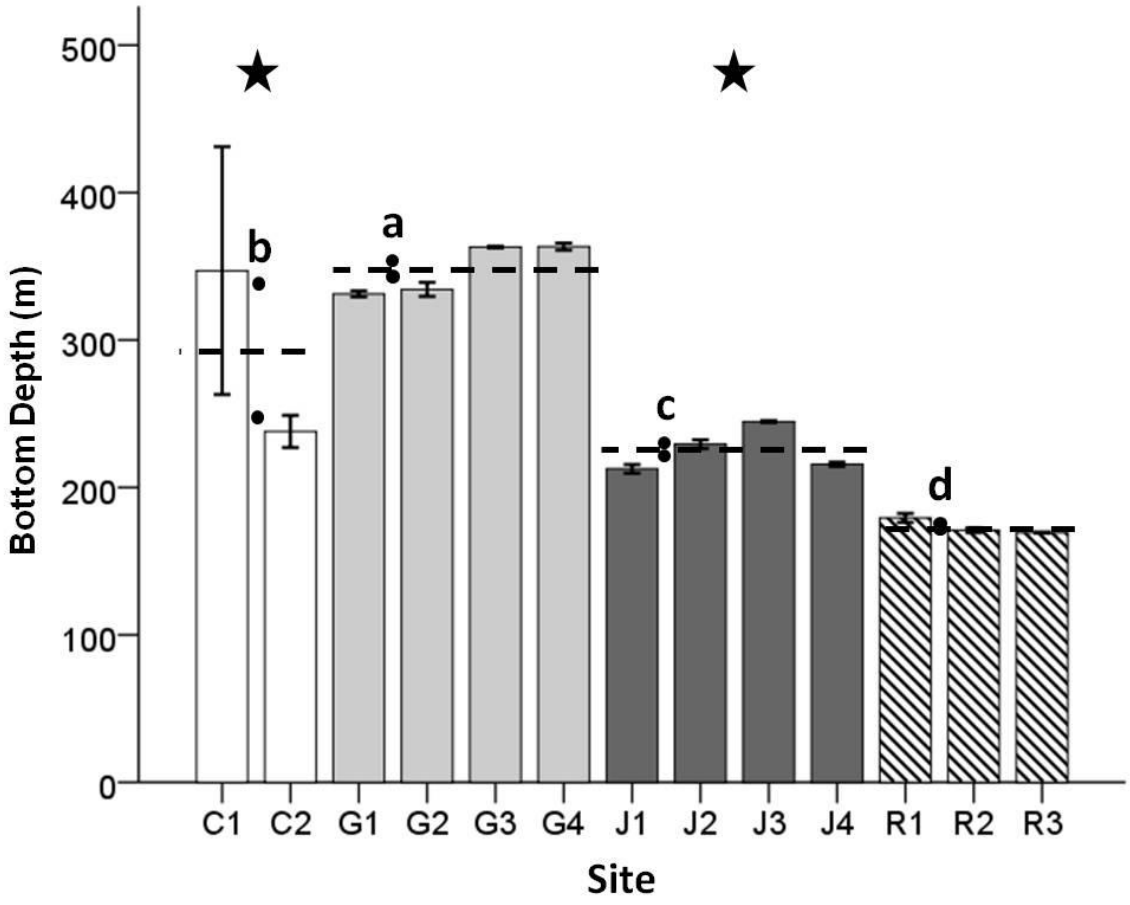

Figure 2.9. Comparison of bottom depth across local and regional spatial scales (i.e. Site and Basin respectively; n = 3 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences. Star indicates significant differences among sites within a basin.

depth differed significantly within sites and across basins (Table 2.4; Fig. 2.9), with the deepest average depth in Georges Basin (348 m) and shallowest average depth in Roseway Basin (173 m). Bottom depth also varied significantly between local areas within Crowell and Jordan Basins while the other two basins showed no local area variation (Fig. 2.9).

2.4.3 Influence of abiotic variables on biodiversity variables

PRIMER analyses of faunal composition (phylum, polychaete species) in surface sediments revealed significant correlations with abiotic variables measured from surface sediments (percent mud content, organic matter ratios, carbon concentrations, nitrogen concentrations, chlorophyll-a concentration, and bottom depth). BIOENV analyses indicated significant, but not strong, correlations between abundances at different levels of taxonomic resolution (i.e. phylum and polychaete species) and abiotic variables. BVSTEP analyses revealed that bottom depth correlated most strongly with abundances from both phylum and polychaete species levels (r_s = 0.363 and 0.547 respectively, Table 2.6). Abundances from higher taxonomic levels (i.e. polychaete family and polychaete feeding guild) also correlated significantly, but not strongly, with abiotic variables, with the combination of organic matter ratio and bottom depth correlating most strongly (r_s = 0.538 and 0.428 respectively, Table 2.6).

2.5 DISCUSSION

Our sediment measurements from the Gulf of Maine addressed four objectives, demonstrating: 1) significant spatial variation in faunal composition and polychaete biodiversity across regional, local and vertical spatial scales; 2) spatial variation at different levels of taxonomic resolution for polychaete biodiversity; 3) significant spatial variation in environmental factors across regional, local and vertical spatial scales; and 4) environmental variables are significant, but weak, predictors of faunal variation irrespective of taxonomic level (species, family, and feeding guild).

Biotic spatial variation: Horizontal

Soft sediment communities in the marine benthos are patchy, but the extent and cause of variation across spatial scales merits further exploration. Studies have

Table 2.6. Correlations from BIOENV analyses comparing environmental (log transformed data[1]) and biotic measures from the surface sediment depth layer (0 – 2 cm). Spearman rank correlation coefficients (r_s) are shown for the top three environmental variable combinations which correlate significantly with faunal distribution patterns tested by BVSTEP analyses ($p < 0.05$). Core replicate n = 39.

Biotic Distribution	**Abiotic Variables**	**r_s**
Macrofaunal Phyla	1- Bottom Depth	0.363
	2- Carbon Concentration[1] + Bottom depth	0.249
	3- Nitrogen Concentration[1] + Bottom depth	0.241
Polychaete Feeding Guild	1- Organic Matter Ratio[1] + Bottom depth	0.428
	2- Organic Matter Ratio[1] + Carbon Concentration[1] + Bottom depth	0.403
	3- Organic Matter Ratio[1] + Nitrogen Concentration[1] + Bottom depth	0.397
Polychaete Family	1- Organic Matter Ratio[1] + Bottom depth	0.538
	2- Bottom depth	0.517
	3- Organic Matter Ratio[1] + Carbon Concentration[1] + Bottom depth	0.475
Polychaete Species	1- Bottom depth	0.547
	2- Organic Matter Ratio[1] + Nitrogen Concentration [1]+ Bottom depth	0.480
	3- Organic Matter Ratio[1] + Carbon Concentration[1] + Bottom depth	0.478

documented heterogeneity in faunal abundance, biomass, and composition on the seafloor, with variation detected across multiple spatial scales from 100's of kms (Schaff et al. 1992; Hernandez-Arana et al. 2003), to 10s of kms (Ramey and Snelgrove 2003; Weissberger et al. 2008), to kms and even metres (Morrisey et al. 1992). Caution must be exercised when describing biotic variation in that variation across one scale could mask variation across another, underscoring the importance of viewing variation across multiple spatial scales (Morrisey et al. 1992).

Our spatial study detected regional faunal variation (across basins; 100's kms apart) in the Gulf of Maine, driven by low faunal abundances and polychaete species richness within Georges Basin. Weissberger et al. (2008) studied Wilkinson Basin (across 10s of kms), a deep basin in the Gulf of Maine similar to basins in our study, and demonstrated biological consistency across temporal scales, ultimately suggesting spatial variation overrides temporal variation. At local scales (across 10s of kms; similar scale as Weissberger et al. 2008) our study revealed minimal faunal variation, with only polychaete species evenness varying locally within surface sediments. Family biodiversity measures (i.e. diversity and evenness) also varied locally but this effect was region dependent (i.e., restricted to within Roseway and Georges Basins). Interestingly, when focused only on cores collected in August (i.e. the same sampling month as our study), Weissberger et al. (2008) reported relatively homogeneous macrofaunal communities within Wilkinson Basin, adding support to our results from Crowell and Jordan Basins. Such results suggest that benthic communities vary across multiple spatial scales within in the Gulf of Maine.

Biotic spatial variation: Influence of taxonomic resolution on polychaete biodiversity variation

In addition to studying biotic patterns across spatial scales, it is necessary to explore patterns at different levels of taxonomic resolution because many studies are limited in time or cost and cannot report multiple levels of taxonomy. Our study investigated spatial variation in macrofauna across four taxonomic levels: phylum, polychaete feeding guild, polychaete family, and polychaete species. As in many studies, annelids (primarily polychaetes) dominated macrofaunal abundances (~70 % of collected macrofauna) (Morrisey et al. 1992; Bergen et al. 2001; Ellingsen 2002; Hernandez-Arana

et al. 2003; Holte et al. 2004) justifying our detailed taxonomic focus on polychaetes to detect ecological patterns. Our study revealed annelids as a major driver of regional sample similarity (i.e. ~37 to ~94 % similarity among samples). Furthermore, as taxonomic detail increased, sample similarity across the Gulf of Maine decreased. All samples shared ~77 % of macrofauna phyla, ~ 68% of polychaete feeding guilds, ~53% of polychaete families, and only ~25% of polychaete species. Overall, differences across samples were not driven by a specific phylum, feeding guild, family, or species, but sample differences increased as taxonomic detail increased punctuating the potential sacrifices of using taxonomic aggregations to determine ecological differences in benthic ecosystems. Jones et al. (2008) stress the importance of species-level identification for bioassessments, but acknowledge that all ecological research does not require species-level identification.

Commonly, coarser taxonomic aggregates (feeding guilds) contributed more to sample similarities (i.e. ~ 60 to ~ 91% similarity among samples), than less aggregated samples (species) which contributed less (i.e. ~ 20 to ~ 49 %). For example, surface deposit feeding polychaetes contributed a large percentage to sample similarities regionally because they occurred in all 39 samples. Furthermore, some families were ubiquitous across most samples; paraonid and capitellid polychaetes occurred in 38 of 39 samples, but they contributed less to sample similarities than feeding guilds. As expected, polychaete species were less ubiquitous at finer taxonomic resolution. The most ubiquitous species, *Prionospio* sp., occurred in 33 of 39 samples; however, collectively species contributed to substantial sample variation (~65 to ~88 %).

While species such as *Cossura longocirrata* (surface deposit feeder), Capitellidae spp. A (subsurface deposit feeder), and Capitellidae spp. B (subsurface deposit feeder) contributed most to regional differences, they were part of a long list of species that drove differences, with each contributing modestly to sample differences (i.e. < 8 %). Clarke and Gorley (2006) state that although faunal investigations commonly look for single drivers of similarity and dissimilarity, uncommon species drive most sample differences rather than one or two dominant species, an assertion our results confirm. In samples containing numerous uncommon species, such as in our study, any one species cannot drive sample

dissimilarities. This is especially true when applying a fourth-root transformation to the data (as we did) which downgrades the importance of abundant species and increases sensitivity to less common species (Clarke and Gorley 2006).

We identified 131 polychaete species with ~ 27 % considered uncommon (i.e. occurring in only/restricted to one sample), as described by Schlacher et al. (1998). Ellingsen (2002) reported similar concentrations of uncommon species across samples from the Norwegian continental shelf (of 508 species, 39% were uncommon/restricted to 1 or 2 sites). Only ~ 4 % of species were abundant and ubiquitous (i.e. occurring in >75 % of samples) throughout our sampling within the Gulf of Maine. Overall, our results confirm spatial variation in the Gulf of Maine across all spatial scales; however, distant samples share as many polychaete species as samples closest in proximity. This observation confirms limited species spatial turnover in the Gulf of Maine.

Biotic spatial variation: Vertical

Infaunal communities vary among sediment depth layers, with most macrofaunal activity in the top few cm (Snelgrove et al. 1997) and decreasing with sediment depth (Mermillod-Blondin et al. 2003). Biogenic structures also occur in higher numbers at sediment surfaces and decrease with depth, paralleling decreasing invertebrate abundances (Mermillod-Blondin et al. 2003). Our study confirms biological variation across sediment depth layers, with surface layers (0 - 2 cm) supporting highest abundances (~ 74 %), diversity, and species richness. Food availability likely explains these differences. Benthic communities, particularly below the photic zone, depend on water column production export as a major food source (Mills 1975; Jorgensen 1983; Smetacek 1984; Beaulieu and Smith 1998; Savenkoff et al. 2000; Gooday 2002), as demonstrated by phytodetritus within macrofaunal gut contents (Thiel et al. 1999).

Within our study, mollusc abundances were particularly high in surface sediments, driving differences between surface and deep layers. Zwarts and Wanink (1989) demonstrated that bivalve size dictates burrowing depth, with smaller individuals congregating near the surface and larger specimens burying deeper. Our samples contained mostly small, juvenile bivalves, resulting in taxonomic difficulties and restrictions in burrowing depths.

The distribution of annelids, particularly polychaetes, also contributed significantly to vertical separation (i.e. most polychaetes found in surface sediments) and echoed horizontal spatial patterns. For example, aggregated polychaete classifications (feeding guilds) contributed most to sample similarities and finer polychaete classifications (species) contributed most to sample dissimilarities. The presence and assumed behaviour of one polychaete species, *Prionospio* sp. A (Family Spionidae), played an important role. This surface deposit feeder was abundant in surface samples and contributed most to species differences across sediment depth layers. Other polychaete feeding behaviour (e.g. capitellids), presumably further contribute to vertical distribution differences because these polychaetes actively burrow below the sediment surface (Fauchauld and Jumars 1979; Hutchings 1998). Some capitellid polychaetes can live in deeper sediments by creating horizontal and vertical burrows up to 15 cm below the surface (Fauchauld and Jumars 1979).

Overall, our study supports the paradigm of lower polychaete abundance and biodiversity in deep sediments than surface and subsurface sediment (e.g. Dauwe et al. 1998; Mermillod-Blondin et al. 2003). Greater food and oxygen availability characterize surface sediments in contrast to deeper layers, as demonstrated by our results showing significantly lower chlorophyll-a concentrations and higher C:N ratios in deeper sediments, and shallower oxygen penetration depth (< 2 cm, see Chapter 3).

Abiotic spatial variation: Horizontal

The four basins in this study were chosen for broad geographic separation but general similarity in sediment type (i.e. soft sediment basins). However, spatial analysis revealed even greater physical similarity between these four basins than expected given the spatial scales involved and the complex circulation within the Gulf of Maine. Cold surface water enters the Gulf from the Nova Scotian Shelf via the Nova Scotia Current, and warmer, denser, saltier water enters at depth through the Northeast Channel (Townsend et al. 2014). Circulation patterns generally move counter-clockwise within the Gulf of Maine, with sub-gyres developing over deep basins such as Georges and Jordan Basins (Townsend et al. 2014). These patterns create an opportunity to test for broad geographic differences in fauna when controlling for seabed composition. Because faunal composition

was generally similar between samples in close and far proximity, local (10s of km) abiotic variation may not impact infaunal distribution as much as we had expected, or abiotic conditions across our study sites were not variable enough to impact benthic communities. Physically, the Gulf of Maine basins sampled in our study differed from one another only in bottom depth, despite large differences in distance from land. We found no strong regional differences in percent mud content, organic matter ratios, carbon concentrations, nitrogen concentrations, or chlorophyll-a concentrations.

In contrast to regional patterns, we detected substantial local variation (i.e. 10s of kms between sites within basins) for each abiotic measure, demonstrating variable habitat characteristics within each basin, with greater variation in some basins than in others. Weissberger et al. (2008) reported similarity in abiotic measures within Wilkinson Basin during August sampling, but also detected strong seasonal variation where August samples reflected an accumulation of settled detritus on the sediment surface. Because we did not sample temporally, we cannot determine how seasonal effects such as blooms contribute to local variation as reported by Weissberger et al. (2008). Other studies assessing sediment characteristics across similar spatial scales also detected local, but not regional variability. For example, Ellingsen (2001) reported uniform abiotic conditions (i.e. water depth and sediment characteristics) across a sampling area spanning 130 x 70 kms along the Norwegian continental shelf. In relatively homogenous environments, such as deep basins of the Gulf of Maine, variability at one scale can mask the variability across another, highlighting the need to study variation across multiple spatial and temporal scales (Morrisey et al. 1992).

Analysis of seafloor abiotic variables, such as organic matter ratios and chlorophyll-a, can describe habitat quality. For example, chlorophyll-a concentrations in surface sediments (0-2 cm) provides a measure of food quantity as organic material sinks from the water column and accumulates on the seafloor (Mills 1975; Jorgensen 1983; Smetacek 1984; Beaulieu and Smith 1998; Savenkoff et al. 2000; Gooday 2002). Carbon and nitrogen concentrations also describes food quality, with low C:N indicating fresh and easily degradable organic material deposited on the seafloor (Banse 1974; Parsons et al. 1984; Grebmeier et al. 1988; Levin et al. 1991).

Within our study, variation in abiotic measures, such as carbon, nitrogen, and chlorophyll-a concentrations, provide information on local food quantity and quality. We observed very high concentrations (chlorophyll-a, carbon, nitrogen) at some sites with Jordan and Roseway Basin compared to other locations within the same basin, indicating areas relatively close together (10's kms) may receive contrasting inputs of organic matter from the water column (Byers et al. 1978). High organic content concentrations, in tandem with low C:N, indicate material sinking quickly to the benthos from the water column (Ambrose and Renaud 1995). Organic matter reaches the benthos via passive detritial rain, remains of plankton/fecal pellets/moults, vertical migrations, or plant debris and animal carcasses (Gage 2003). Studies of benthic sediments from Placentia Bay, NL (Ramey and Snelgrove 2003) and the Northern Seas (Grebmeier et al. 1988; Ambrose and Renaud 1995) use low C:N as indicators of fresh, easily degradable organic material reaching the benthos.

Abiotic spatial variation: Vertical

Compared with surface sediments, deeper sediments (i.e. 5 - 10 cm) had significantly higher C:N ratios and lower chlorophyll-a concentrations, suggesting food limitation in deep sediments of the Gulf of Maine. Typically, low C:N ratios indicate the presence of high quality, fresh food (Ramey and Snelgrove 2003). Sinking water column production accumulates on the sediment surface (Jorgensen 1983; Beaulieu and Smith 1998; Savenkoff et al. 2000; Gooday 2002) and biogenic activities, such as burrowing and feeding, distribute it through the sediment (Rhoads and Young 1970; Fauchauld and Jumars 1979; Hutchings 1998; Diaz et al. 1994). This fresh material disappears quickly in benthic sediments**,** however, as consumers quickly degrade it and chlorophyll-a is broken down into phaeopigments (Shuman and Lorenzen 1975). Our data suggests that deep Gulf of Maine sediments are generally food limited, which limits highest infaunal abundances to the comparatively food-rich surface sediments. Similarities between infaunal and abiotic results could also indicate mixing between surface and subsurface layers with limited mixing into deeper sediment layers. The feeding and movements of infauna directly influence surrounding sediments (e.g. Jumars and Wheatcroft 1989; Diaz et al. 1994;

Schaffner et al. 1997; Mermillod-Blondin and Rosenberg 2006). Subsurface sediments receive more influx from surface feeding, while deeper sediments receive less.

Abiotic influence on biotic spatial variation: Horizontal

Other studies report that physical properties influence biotic distributions, and that many of these properties may act in tandem (Ellingsen 2002; Hernandez-Arana et al. 2003; Holte et al. 2004; Joydas and Damodaran 2013). Ellingsen (2002) reported bottom depth, median grain size, and silt-clay content as the most important environmental influences on faunal patterns. Holte et al. (2004) reported that bottom depth and sediment grain size influenced species community patterns. Our results, nonetheless, suggest limited influence of variation in abiotic factors on horizontal spatial distributions and abundances of macrofauna in Gulf of Maine sediments. Bottom depth and organic matter only weakly correlate with faunal distributions, perhaps reflecting the relatively modest range of those environmental variables encompassed by our sampling sites. For example, although phyla and polychaete species distributions were most strongly associated with bottom depth (i.e. higher abundances at shallower depths), and distribution of polychaete feeding guilds and polychaete families correlated most with a combination of water depth and organic matter ratios (i.e., lower abundances with higher C:N), R^2 values were low in all cases. Compared with other taxonomic groups, Olsgard and Somerfield (2000) reported stronger relationships between polychaetes and environmental variables. We also found correlations between faunal distribution and environmental variables strengthened with increasing taxonomic resolution, particularly with polychaetes, correlating most strongly at polychaete species level. Other studies identified bottom depth as a driving factor of benthic biodiversity patterns (Bergen et al. 2001; Ellingsen 2002; Hernandez-Arana et al. 2003; Holte et al. 2004; Roy et al. 2014), and suggest that depth reflects a cascading effect from changing conditions (e.g. degradation in food quality) that limit food supply to the benthos. Ellingsen (2001 and 2002) and Schlacher et al. (1998) found weak relationships between faunal distribution and environmental parameters across similar spatial scales along the Norwegian continental shelf and coral lagoons from Fiji, respectively. These results imply potential factors other than abiotic variables measured in our study, such as

larval settlement or biological interactions, influence local variation in benthic structure and distribution.

Regardless of location, sediment type (i.e. grain size) and bottom depth correlate most strongly with biodiversity patterns (Gagnon and Haedrich 1991; Bergen et al. 2001; Ellingsen 2002). Although previous studies point to grain size measures (such as mud content, average grain size, median grain size, silt/clay content) as important drivers of biotic distributions (Gagnon and Haedrich 1991; Ellingsen 2002; Hernandez-Arana et al. 2003; Holte et al. 2004; Van Hoey et al. 2004), our study found no such linkage. One major difference between our study and these previous studies is the uniformly high mud percentages (~75 %) in our Gulf of Maine sediments, compared to low mud percentages (under 50 %) and wide ranges in sediment characteristics from other studies. The uniformly muddy sediments sampled in our study from Gulf of Maine basins may not vary sufficiently to influence faunal distributions.

Evidence of environmental effects on benthic biota over multiple spatial scales continues to accumulate (Ellingsen 2002), including our study which demonstrates little effect of geographic distance on faunal similarity over 100s of km when other environmental variables are held largely constant. Determining cause and effect relationships within marine environments remains difficult and requires extensive strategies combining field and laboratory research (Snelgrove and Butman 1994). Regardless, environmental changes resulting from increasing anthropogenic pressures add urgency to investigating links between abiotic factors and biotic spatial patterns.

Abiotic influence on biotic spatial variation: Vertical

Macrofaunal position within sediment depth layers largely reflects food distribution. Fauchald and Jumars (1979) documented that macrofauna can feed in the water column, surface sediments, or within the sediment, indicating that metabolic requirements largely dictates where an animal spends most of its time. Benthic habitats receive food as it falls from the water column and accumulates at the sediment surface. Surface (0-2 cm) chlorophyll-a concentrations provide a measure of available phytodetrital food on the seafloor as organic material sinks from the water column (Mills 1975; Jorgensen 1983; Smetacek 1984; Beaulieu and Smith 1998; Savenkoff et al. 2000; Gooday

2002). Our results support vertical differences in that we found higher abundances and biodiversity (except evenness) in surface sediments, paralleling an abundance of food indicated by high chlorophyll-a concentrations, as well as regional homogeneity in chlorophyll-a and organic matter ratios, throughout the Gulf of Maine. The presence of specific feeding guilds also provides additional support for high concentrations of food in surface sediments across the Gulf of Maine. For example, surface deposit feeding polychaetes dominate surface sediments and drive high similarity among samples throughout the Gulf of Maine grouped by feeding guild (~78 %).

Limitations to study/Further exploration

Spatial studies are important for determining biotic distributions, yet require caution. The nested design of our study eliminates issues of pseudoreplication (Morrisey et al. 1992), however, the number of replicates limited our conclusions. Our study showcased biodiversity across broad regional (100's kms) and local (10's kms) geographic areas. Despite collecting and analyzing cores from smaller spatial scales (kms), we were limited from analyzing variation at this scale because of insufficient replication. We could showcase faunal turnover and sample similarities across the Gulf of Maine, but additional research on small-scale variation (e.g. microscale patchiness) could provide information on whether differences in benthic communities result from natural patchiness, assemblage shifts, or external variables (Morrisey et al. 1992). Reporting smaller-scale variation, if any exist, in abiotic factors and benthic biological distributions could further clarify natural abiotic and biotic patches within the region.

Our study also lacked a temporal component, which could provide information regarding seasonal influences within the Gulf of Maine. We lacked the resources for this type of study and depended on Weissberger et al. (2008) for temporal information, noting they found no significant temporal influence on polychaete distributions within Wilkinson Basin, ultimately concluding that spatial variation outweighs seasonal influences. Limitations also exist with feeding guild classifications as there is flexibility of feeding modes within species and especially within families (Macdonald et al. 2010). This can make accurately assigning guilds very difficult, especially for species where little to no information is available.

Ultimately, biological measures varied primarily across regional (i.e. basin) scales, while abiotic measures varied across local (i.e. sites within basins) scales. Abiotic factors within these basins did not strongly influence faunal distribution at the scales examined, suggesting factors other than those we measured, such as larval settlement and microscale patchiness, may have greater influence on spatial distribution. Moreover, the limited range of some potentially important environmental drivers (organic matter supply or water depth) encompassed by our sampling may have been insufficient to result in biotic changes. These similarities may have contributed to limited faunal turnover across Gulf of Maine basins, as indicated by high sample similarities. Polychaete species, nonetheless, showed some spatial turnover, driven largely by high percentages of uncommon species. Food likely limits vertical distributions of fauna, as indicated by higher abundances and diversity in surface sediments.

This research demonstrates how examining various spatial scales can influence understanding of benthic macrofaunal communities and highlights surprisingly weak influences of abiotic factors on macrofaunal community spatial patterns. The taxonomic data from this research advances the inventory of marine species collected from the Discovery Corridor and furthers knowledge of benthic biological communities and interactions with the abiotic environment within the Gulf of Maine.

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Chapter III

Influence of polychaete abundance and biodiversity on ecosystem functions in Gulf of Maine sediments

3.1 ABSTRACT

Presence, distribution, and activities of infaunal organisms can greatly influence soft-sediment ecosystems by altering important processes such as sediment oxygenation and nutrient fluxes. Interest and concern regarding the impact of biodiversity on ecosystem functions in marine ecosystems has increased, particularly in light of increasing anthropogenic pressures. Our study investigated biodiversity-ecosystem function relationships within deep soft-sediments across deep basins within the Gulf of Maine. Our primary objectives were to investigate variation in ecosystem functions across multiple spatial scales, to determine whether polychaete biodiversity or abundance could predict key functions within the ecosystem, and to investigate the influence of taxonomic resolution on biodiversity-ecosystem function relationships. We collected 39 sediment cores from 4 soft sediment basins (Crowell, Georges, Jordan, and Roseway) throughout the Gulf of Maine and identified infaunal polychaetes to the lowest possible taxonomic level and other taxa to phylum, calculating additional information for polychaetes (abundance and biodiversity measures). Ecosystem functions (bioturbation, sediment oxygenation, and secondary production) were quantified using proxy measurements (chlorophyll-a concentration, oxygenation penetration, and prokaryote abundance respectively). Our study determined that ecosystem functions varied significantly across regional (across basins) and local (across sites within basins) spatial scales. We also confirmed significant predictive relationships between polychaete biodiversity and ecosystem function proxies within basin soft sediments. Specifically, all measures of polychaete biodiversity, as well as abundance, positively predicted secondary (microbial) production. Biodiversity measures grouped by feeding guild predicted more ecosystem functions than species or family taxonomic levels, demonstrating that groupings based on activity and behaviour of infaunal animals better predicts ecosystem functions than species level taxonomy within soft sediments.

3.2 INTRODUCTION

Ecosystem functions in the global ocean maintain environments that sustain life and support goods and services essential to humanity such as food, recreation and tourism opportunities, waste disposal, and dilution of pollutants (de Groot et al. 2002). Examples of ecosystem functions within marine benthic ecosystems include, but are not limited to, sediment oxygenation (Painting et al. 2013), productivity (Cole et al. 1988; Muller et al. 1997), and bioturbation (Mermillod-Blondin 2011), which results from biological activity within the sediment and can greatly impact sediment biogeochemistry and induce changes in energy and matter.

Some infaunal organisms can act as "ecosystem engineers", altering the physicochemical landscape at local scales (such as effective grain size, organic matter, and oxygen concentrations) and stimulating microbial growth around burrows (Aller and Aller 1986; Jones et al. 1994; Duffy et al. 2001; Mermillod-Blondin and Rosenberg 2006; Nogaro et al. 2009; Lohrer et al. 2013). For example, conveyer-belt deposit feeders (Mulsow and Landrum 1995) can generate movement of sediment by ingesting material from depth and depositing waste at the sediment surface (Robbins 1986). Burrowing polychaetes (Woodin 1976), as well as suspension-feeding brittle stars (Boon and Duineveld 1998) and bivalves frequently mix sediments through movement and burial into deeper sediment layers. Given their wide distributions and diverse feeding forms, infaunal animals therefore can potentially impact ecosystem stability and functions within their habitat.

Infaunal movement and feeding behaviour can mix, or bioturbate, sediments. This biogenic mixing of sediment (Boon and Duineveld 1998; Solan et al. 2004) enhances fluxes of nutrients and dissolved gases across the sediment-water interface (Marinelli et al. 1998; Belley et al. 2010). Bioturbation also facilitates breakdown and/or burial of organic matter, as well as movement of sediment particles, inextricably tying bioturbation to sediment mixing. For example, the pigment chlorophyll-a, which sinks from the water column and accumulates on the seafloor as decomposing phytodetritus (Sun et al. 1991; Ingalls et al. 2000), can be used as a tracer of fresh organic matter within sediments and thus, an effective proxy for bioturbation (Stephens et al. 1997; Green et al. 2002; Maire et

al. 2008). The presence of chlorophyll below the sediment surface therefore represents recent sediment mixing, primarily driven by feeding and burrowing activities of infaunal organisms (Boon and Duineveld 1998).

Activities of infaunal organisms can also oxygenate sediments, a process vital for many organisms (Diaz and Rosenberg 1995), and which allows recruitment into deeper sediment layers (Levin and Gage 1998). Particularly in fine mud, sediments limit oxygen diffusion to only a few millimeters below the sediment-water interface (Revsbech et al. 1980). For example, burrow irrigation behaviour of a common lugworm can increase the oxygen concentration within burrows up to 80 % saturation as well as oxygenate neighbouring sediment up to distances of 0.7 mm (Timmermann et al. 2006).

Whereas natural infaunal activities (e.g. burrowing, irrigation) promote oxygen penetration into otherwise oxygen-poor deeper sediment layers, their activities can also stimulate growth of microbial communities around their burrows as a direct result of increased oxygen and waste deposits (Aller 1985; Aller and Aller 1986; Mermillod-Blondin et al. 2003; Mermillod-Blondin et al. 2004). Ubiquitous microbes play a major role in regulating secondary production within benthic environments, including carbon remineralisation, organic matter degradation, and nutrient recycling (Velji and Albright 1986; Alongi 1994; Jiang 2007; Pusceddu et al. 2007). Microbial abundance, therefore, indirectly characterises benthic productivity. Within benthic environments, researchers typically quantify productivity (e.g. nutrient regeneration or recycling) with incubation experiments and measurements of nutrient fluxes across the sediment-water interface over time (Marinelli et al. 1998; Link et al. 2013). These incubation experiments, however, require specially designed equipment, and potentially generate containment artefacts (Marinelli et al. 1998; Jarvis et al. 2001; Almroth et al. 2009). Alternatively, abundances of organisms that regulate secondary productivity (i.e., microbes) offer an indirect measure of productivity, assuming that higher microbial abundance generally corresponds to higher nutrient cycling and carbon fixation (e.g. Danovaro et al. 2008), assuming other key drivers, such as sediment grain size, are relatively comparable.

Numerous recent studies have addressed the impact of living organisms on ecosystem functions in both marine (Lohrer 2004; Waldbusser et al. 2004; Danovaro et al.

2008) as well as non-marine (Loreau et al. 2001; Loreau 2007; Poisot et al. 2013) systems. These initial studies generally suggest positive relationships between biodiversity and ecosystem functions; however, the pattern of these relationships generates considerable debate (Naeem et al. 2002). Initial investigations of biodiversity-ecosystem relationships from terrestrial environments (Naeem et al. 1994; Tilman et al. 1997; Tilman 1999; Tilman et al. 2001; Eisenhauer et al. 2012) paved the way for marine studies (e.g. Crowe et al. 2013) and offer insights on the generalities of relationships. Some data suggest exponential relationships between diversity and function (Danovaro et al. 2008), whereas others report parabolic to linear relationships (Loreau et al. 2001; Bond et al. 2002; Gessner et al. 2004), potentially reflecting the spatial scales of different studies. The consistency of this relationship across faunal groups and the specific influences of abiotic factors remain unclear.

Influences from abiotic factors (e.g. bottom currents) can also impact ecosystem functions by altering local conditions, such as grain size and supply of organic matter. For example, Schallenberg et al. (1989) showed localized upwelling increased organic matter flux to the seafloor stimulating increased bacterial abundance, and Biles et al. (2003) illustrated that flow can modify ecosystem functions via influence on particular animals, such as polychaetes. Most likely, some combination of biotic and abiotic factors influences ecosystem functions, with infaunal organisms potentially amplifying abiotic effects. Further investigations are needed to understand linkages in benthic soft-sediment ecosystems and identify which factors most influence the delivery of key ecosystem functions and the specific roles that benthic infauna may play (Snelgrove et al. 2014).

To date, most studies of biodiversity-ecosystem function relationships have been primarily experimental; manipulating diversity to test impacts on ecosystem function (Schwartz et al. 2000; O'Connor and Crowe 2005). Many of these experimental/manipulative studies are laboratory based with a few small-scale *in situ* studies (Waldbusser et al. 2004; O'Connor and Crowe 2005; Jiang 2007), often working in simplified or low diversity, shallow (often intertidal) systems that may not easily translate to more diverse and less physically dominated subtidal ecosystems. Few of these studies explore whether patterns vary across different spatial scales. Results from small-scale *in*

situ studies cannot necessarily be scaled up because they cannot account for many environmental factors (Morrisey et al. 1992; Thrush et al. 2006; Snelgrove et al. 2014). A few meta-analyses have examined *in situ* large-scale biodiversity-ecosystem function relationships; however these studies focused on specific faunal groups. For example, Danovaro et al. (2008) demonstrated a positive exponential relationship between nematode diversity and deep-sea ecosystem functions. These large-scale *in situ* studies are crucial because they help in evaluating whether laboratory experiments can sufficiently represent natural systems and also confirm whether biodiversity-ecosystem function relationships persist across spatial scales (Srivastava and Vellend 2005) and trophic groups (Snelgrove et al. 2014).

Although biodiversity-ecosystem function studies have focused primarily on species-level comparisons, an emerging body of literature expands beyond traditional diversity metrics (i.e. species diversity or species richness; Garcia and Martinez 2012) to consider other forms of diversity, such as phylogenetic or functional diversity (Bengtsson 1998; Duffy et al. 2001; Bolam et al. 2002; Cadotte et al. 2012) and genotypic richness and dissimilarity (Jousset et al. 2011). These alternative approaches provide further insight into the complex linkages between faunal groups and functions.

Despite a rich body of research on the Gulf of Maine ecosystem (Link et al. 2011; Methratta and Link 2012; Cook and Auster 2013; Hernandez et al. 2013; Wahle et al. 2013), and additional studies on factors shaping spatial and temporal community patterns (Rowe et al. 1975; Weissberger et al. 2008; Kelly et al. 2010), few studies have addressed biodiversity-ecosystem function relationships (though see Johnson et al. (2011) for pelagic ecosystems). Chapter 2 demonstrated significant variations in sedimentary communities across different basins within the Gulf of Maine system, and that water depth was the primary driver of these differences, whereas here we evaluate whether marine ecosystem functions vary from local to regional scales within the Gulf of Maine, and investigate whether benthic macrofaunal communities influence, and potentially drive variation in functions. Specifically, we quantified key ecosystem functions (bioturbation, sediment oxygenation, and secondary production as inferred from prokaryote abundance) to determine whether polychaete biodiversity (diversity, richness, evenness, and abundance)

measured at three levels of taxonomic resolution (species, family, feeding guild) could predict measures of ecosystem functions.

The objectives of this study are to determine if: 1) ecosystem function proxies (subsurface and deep bioturbation, sediment oxygenation, and secondary production) vary spatially across local (between sites within basins spanning 10's kms) or regional (between basins spanning 100s of kms) spatial scales; 2) whether polychaete abundance and species biodiversity (i.e. diversity, richness, evenness), predict ecosystem function measures; and 3) whether different taxonomic (species and family) or functional (feeding guild) levels reveal different biodiversity-ecosystem function relationships. We propose that abundance as well as any species biodiversity measure may predict ecosystem functions. We also propose that activity classification (i.e. feeding guild) would be a stronger predictor of ecosystem functions than taxonomic identity (i.e. species). Feeding guilds highlight major differences in feeding behaviour, whereas species taxonomy may reflect relatively modest morphological differences. Feeding guilds also characterize groups of organisms contributing similarly to specific functions (i.e. deposit feeding) whereas taxonomic identity may differentiate organisms that overlap in specific role(s), and thus represent redundancy.

3.3 MATERIALS AND METHODS

3.3.1 Study area and sampling sites

Samples were collected from four soft-sediment basins in the Gulf of Maine (approximate longitude: 71.5 - 63 W, Latitude: 39.5 – 46 N): Jordan Basin (43° 32'N, 67° 04'W), Crowell Basin (42° 58'N, 67° 16'W), Georges Basin (42° 27'N, 66° 44'W), and Roseway Basin (43° 10'N, 65° 04'W). Depth of sample collection ranged from 169 to 515 m. All four basins were chosen because of their soft-sediment properties and similar depths, which allowed coring for spatial and cross-scale comparisons.

Benthic sampling occurred from July 28 to August 14, 2009 on the Canadian Coast Guard Ship Hudson using a multi-corer fitted with six clear plastic tubes (1 m long x 10 cm in diameter). We collected multi-cores from 13 sites distributed among the basins: Jordan (n=4), Crowell (n=2), Georges (n=4), and Roseway (n=3) to assess differences

across local (Sites) and regional (Basin) spatial scales. In total, we collected 39 multi-core drops (3 drops per site). We designated one core per drop for measurement of sediment oxygenation using an oxygen microprofiling system, which was then processed for macrofauna. A second core was designated for measurement of sediment characteristics, which included organic content (food availability and quality) and ecosystem function proxies (secondary production and bioturbation).

3.3.2 Collection and analysis of ecosystem functions

Chlorophyll-a measurements were obtained by subsampling the core designated for sediment characterization with a modified coring instrument (10-mL syringe with the end cut off to form a uniform barrel for coring and vertical alignment of samples). To quantify mixing throughout sediment depth layers, approximately 1 mL of sediment (~ 2 grams dry weight) was removed from three depth layers (0-2 cm, 2-5 cm, and 5-10 cm) in each core using our modified coring instrument as described above (1 replicate per core). Samples were placed in 15 mL Falcon centrifuge tubes, fully covered with aluminum foil, and stored at -20 ºC; this procedure eliminated light exposure and prevented chlorophyll-a degradation. Instruments were rinsed thoroughly with freshwater and dried between samples. To extract chlorophyll-a from sediment, we added 5 mL of 90% acetone to each tube and incubated it overnight at 4 ºC. The following day, samples were transferred to glass centrifuge tubes and topped with 90% acetone to a final volume of 9 mL. With the top sealed with Parafilm, samples were centrifuged at 4500 rpm for 5 minutes. The supernatant from each sample was poured into a second glass centrifuge tube and diluted by a known factor (410 times) using 90% acetone. Chlorophyll-a concentrations, from refrigerated (4 ºC) samples were measured before and after acidification with 5% HCl using a Turner Designs 10-AU-005-CE fluorometer. Glassware was rinsed twice between samples with distilled water followed by 90% acetone rinses. We used chlorophyll-a as a marker in the sediment to measure bioturbation (Sun et al. 1991; Maire et al. 2008). Ratios were calculated by dividing subsurface layer concentrations by surface layer concentrations, therefore increases in the ratio indicate an increased sediment mixing, and vice versa. We defined subsurface bioturbation as the ratio of chlorophyll-a in middle

depth layers (2-5 cm) to surface depth layers (0-2 cm), and deep bioturbation as the ratio of chlorophyll-a in deep depth layers (5-10 cm) to surface depth layers (0-2 cm).

We quantified oxygen penetration depths to quantify sediment oxygenation using a UNISENSE oxygen micro-electrode probe. Prior to use, we placed the probe in an oxygen saturated control (distilled water bubbled with an air stone) for 2 hours to de-polarize the sensor. Upon signal stabilization, the probe was calibrated in the oxygen saturated solution and in an anoxic solution (mixture of sodium hydroxide and sodium ascorbate). To profile the cores, we positioned the probe at the sediment surface by visual observation through the transparent core tube. We programmed the probe to measure oxygen concentration (in µmol/L) at 0.05 cm (500 µm) intervals to a depth of 3.5 cm (35,000 µm), using UNISENSE control software. Profiles were replicated three times in each core to account for small-scale variation and identify extreme outliers (e.g. active burrows, instrument error). Between cores, instruments were rinsed with freshwater and the probe re-calibrated to ensure accurate data collection. We then processed the data from sediment profiles to remove invalid measurements associated with signal interference, and to highlight features such as spikes in oxygen concentrations that may have resulted from macrofaunal burrows. The depth of anoxia (0 µmol L^{-1}, or a stable signal), was defined as the oxygen penetration depth, and was therefore our proxy for sediment oxygenation.

Prokaryotic abundance was used as a proxy variable for secondary production where abundance represented activity (production) within a given area at a given time, assuming that higher microbial abundance equates to higher nutrient and carbon cycling (e.g. measures of secondary production). Samples were collected with cut-off 10 mL syringes similar to those used for CHN and chlorophyll-a samples (1 replicate per core). To determine the distribution of prokaryotic populations within the sediment layers, we generally followed the protocol outlined by Danovaro (2009). Approximately 1 mL (~ 2 grams) of sediment was extracted from each depth layer in each core (0-2 cm, 2-5 cm and 5-10 cm). Each 1 mL sample was placed in 10 mL of 4 % formalin to fix samples during shipment to the laboratory. Instruments were rinsed with freshwater between samples.

Before filtering and counting cells, the samples required a three-step dilution and separation of cells from the sediment particles. The first dilution occurred onboard ship (1

mL of sediment added to 10 mL of 4% formalin), followed by serial dilutions (1/550) with filtered formalin to achieve an optimal dilution. To separate prokaryotic cells from sediment particles, samples were shaken vigorously by hand for 2 minutes and allowed to settle for 5 minutes. This technique proved more effective than shorter (1 minute) and longer settlement times (10 minutes). After dilution and cell separation, 2 mL of the serial dilution was further diluted with 3 mL of 4 % formalin and added to a glass tower attached to a vacuum pump, along with 200 µL of filtered Acridine Orange stain. After staining the prokaryotic cells for 2 minutes, the solution (0.0018 mL of original 1 mL sediment sample) was filtered through a 0.2 µm polycarbonate filter using a vacuum pump.

The filter was then fixed to a microscope slide using immersion oil (type A) and examined under a microscope (to ensure proper staining) prior to storing at -20 ºC until it could be counted. Between samples, we rinsed all equipment with a wash cycle of 90% acetone, distilled water, 5% HCl, then two final rinses with filtered distilled water. Prokaryotic cells on the filters were enumerated using epifluorescence microscopy by examining several fields of view under oil immersion until a minimum of 400 prokaryotic cells were counted. Field of view counts were averaged to obtain the approximate number of prokaryotic cells per field of view. The equations used to calculate prokaryotic abundance are:

1) cells on a filter = {(average # of cells counted per grid)*[(vacuum tower area/(ocular grid length)^2)) / ((# of boxes in a grid)/(# of boxed counted))]}

2) cells/g = {((cells on filter)x(diluted subsample filtered)) / (dry weight of 1 mL sample)}

We standardized prokaryotic abundances (cells/g of sediment) for statistical analysis and determined abundances for each sediment depth layer (0-2, 2-5, and 5-10 cm).

3.3.3 Collection and analysis of polychaetes

The abundance, distribution, and diversity of polychaetes were evaluated for the three sediment depth layers (0-2 cm, 2-5 cm, and 5-10 cm). Each section was processed on a 300 µm sieve, fixed with 10% buffered formalin, and then transferred to 70% ethanol. We determined total abundance of polychaetes and also identified each individual to the lowest taxonomic level possible which was generally to species. Polychaetes accounted for ~70 % of total macrofaunal abundances and because we were unable to identify some

other phyla to species level we chose to focus on polychaetes for the analyses presented here. We assessed diversity using Shannon-Wiener diversity, Margalef richness, and Pielou's evenness. Each diversity measure was calculated for species, family, and feeding guild taxonomic levels using PRIMER-E software. We assigned feeding guilds to polychaetes based on Macdonald et al. (2010), and removed juveniles from calculations of species biodiversity measures (diversity, richness, and evenness) because of ambiguity of taxonomic assignment. Abundance and biodiversity measures were analyzed for each individual sediment depth layer, as well as whole core, to determine if impacts on ecosystem function were localized to a specific depth layer or at a larger (i.e. whole core) scale.

3.3.4 Statistical analysis

3.3.4.1 *Spatial variation in ecosystem functions*

Separate two-way ANOVAs with factors Basin (Crowell, Georges, Jordan, Roseway) and Site(Basin) were used to test for regional (100's kms between basins) and local (10's kms between sites) spatial scale differences in ecosystem function proxies (subsurface and deep bioturbation (subsurface:surface chl-a (µg/g); deep:surface chl-a (µg/g)), sediment oxygenation (cm), and whole core secondary production (cells/g)). A three-way ANOVA with factors Basin (Crowell, Georges, Jordan, Roseway), Site(Basin) and Sediment Depth (0 - 2, 2 - 5, and 5 - 10 cm) was used to determine spatial variation in secondary production.

For each ANOVA, we assessed assumptions of normality with Shapiro-Wilk's statistics; for homogeneity of variance we used Levene's test for equality of error variances and graphical distributions of standardized residuals. Transformations (log or square root) were applied to the raw data to resolve issues of non-normal and heteroscedastic data. In cases of non-normality we proceeded with ANOVAs because they are robust to deviations from normality (Underwood 1997). In cases when data transformations did not correct heteroscedasticity, we analyzed rank-transformed data and compared results to the raw data (Conover and Iman 1981). We used least-square means multiple comparisons with Bonferonni correction of probabilities to detect differences among levels within each factor. If an interaction term was significant (e.g. Basin x

Sediment Depth), the analyses were split by Sediment Depth to test for spatial differences across factors Basin and Site(Basin). Basin and Site were considered random factors since they were selected to represent geographic regions rather than specific locations, whereas Sediment Depth was fixed. A significance threshold of 0.05 was used in all statistical tests and analyses were conducted using SPSS 19 software.

3.3.4.2 *Effect of polychaete on ecosystem function measurements*

We used two-way ANOVAs (generalized linear models) with Biotic Measure (Abundance, Diversity, Richness, Evenness) as a continuous factor and Basin (Crowell, Georges, Jordan, and Roseway) as a categorical factor to determine how polychaete abundance and biodiversity (diversity, richness, and evenness) at each of three taxonomic levels (species, family, feeding guild) influences ecosystem function proxies (subsurface and deep bioturbation, sediment oxygenation, secondary production). We used three-way ANOVAs (generalized linear models) with Biotic Measure (Abundance, Diversity, Richness, Evenness) as a continuous factor, and categorical factors, Basin (Crowell, Georges, Jordan, and Roseway), and Sediment Depth (0 - 2, 2 - 5, 5 - 10 cm), to test patterns in ecosystem functions measured across sediment depths (e.g. secondary production). These ANOVAs were conducted to determine whether biodiversity-ecosystem function relationships varied across categorical factors (to test interaction terms between polychaete Biotic Measures and categorical factors Basin or Sediment Depth). If an interaction was significant the analysis was split by the categorical factor. In the absence of a significant interaction we dropped the categorical factors (and respective interaction terms) from the model. Regression analyses were then used to test for potential relationships between polychaete biotic measures (abundance or diversity metrics) and ecosystem function proxies. Curve estimations were used to test for linear versus nonlinear associations between variables. We accepted the statistically significant model with the highest coefficient of determination (R^2) as the optimal model. A significance threshold of 0.05 was used for all statistical tests, which were conducted using SPSS 19 software.

3.4 RESULTS

3.4.1 Spatial variation in ecosystem functions

Analysis of data using two-way ANOVAs showed no significant spatial variation in either subsurface or deep bioturbation across basins or sites (Table 3.1; Fig. 3.1a, b respectively). Sediment oxygenation differed significantly at Basin scale, but not at the Site scale (Table 3.1; Fig. 3.1c). The deepest oxygen penetration occurred within Crowell Basin (1.9 cm; Appendix Table A3), compared to the shallowest oxygen penetration in Jordan Basin (1.3 cm; Appendix Table A3; LS means, $p = 0.02$; Table 3.1; Fig. 3.1c).

Secondary production (i.e., prokaryote abundance) was the only ecosystem function proxy quantified across three sediment horizons, therefore analyses were conducted for each individual depth layer. A three-way ANOVA (with Basin, Site(Basin), and Sediment Depth as factors) demonstrated significant spatial variation at local spatial scales (i.e. Sites within Georges and Jordan Basins) and across sediment depth layers, but not across regional scales (i.e. Basin; Table 3.1; Fig. 3.1e). Surface (0 – 2 cm) prokaryote abundance (9.88E+08 cells/g; Appendix Table A3) was significantly greater than in middle (6.46E+08 cells/g; Appendix Table A3) and deep layers (5.45E+08 cells/g; Appendix Table A3; LS means, $p < 0.01$; Table 3.1; Fig. 3.1f). Non-significant interactions between factors (Basin and Site by Sediment Depth; Table 3.1) indicated consistency in patterns.

3.4.2 Influence of polychaetes (abundance and species biodiversity) on ecosystem functions

We found no significant relationships between whole core (i.e. 0 - 10 cm) polychaete biotic measures (abundance and species diversity metrics) and subsurface bioturbation (Table 3.2; Fig. 3.2). When investigating individual sediment depth layers, however, we found significant relationships between polychaete species diversity and subsurface bioturbation (Table 3.3). In particular, species evenness was a significant positive predictor of subsurface bioturbation within deep sediments (5 - 10 cm; $R^2 = 0.140$; $p = 0.035$; Table 3.3; Fig.3.3c). No significant relationships were evident within surface or subsurface sediment depths (0 - 2 and 2 - 5 cm; Table 3.3; Fig.3.3a, b).

As with subsurface bioturbation, we observed no significant relationships between whole core polychaete biotic measures (abundance and species diversity metrics) and deep

Table 3.1. Summary of two-way [three-way] ANOVAs showing the effect of Basin (Crowell, Georges, Jordan, Roseway) and Site (nested within Basin) [and Sediment Depth (0-2, 2-5, 5-10 cm)] on ecosystem function proxies. EF denotes ecosystem function: SB denotes shallow bioturbation (subsurface:surface chl-a (µg/g), DB denotes deep bioturbation (deep:surface chl-a (µg/g), SO denotes sediment oxygenation (cm), and SP denotes secondary production (cells/g). Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

EF	Source of Variation		df	Mean Square	F	Sig.
SB[1]	Basin	Hypothesis	3	0.1	1.2	0.359
		Error	9	0.1		
	Site(Basin)	Hypothesis	9	0.1	1.3	0.304
		Error	25	0.1		
DB[2]	Basin	Hypothesis	3	0.1	3.8	0.053
		Error	9	0.0		
	Site(Basin)	Hypothesis	9	0.0	0.8	0.642
		Error	26	0.0		
SO[1]	**Basin**	Hypothesis	3	0.6	5.5	**0.020**
		Error	9	0.1		
	Site(Basin)	Hypothesis	9	0.1	1.2	0.347
		Error	26	0.1		
SP[2]	Basin	Hypothesis	3	9720.8	2.1	0.161
		Error	10	4571.9		
	Site(Basin)	Hypothesis	9	4339.7	22.8	< **0.01**
		Error	18	190.0		
	Sediment Depth	Hypothesis	2	8856.6	21.1	**0.002**
		Error	6	418.9		
	Sediment Depth x Site(Basin)	Hypothesis	18	190.0	0.3	0.993
		Error	78	545.0		
	Sediment Depth x Basin	Hypothesis	6	422.3	2.2	0.088
		Error	18	190.0		

1. Raw data (compared to rank transformed data)
2. Rank transformed data

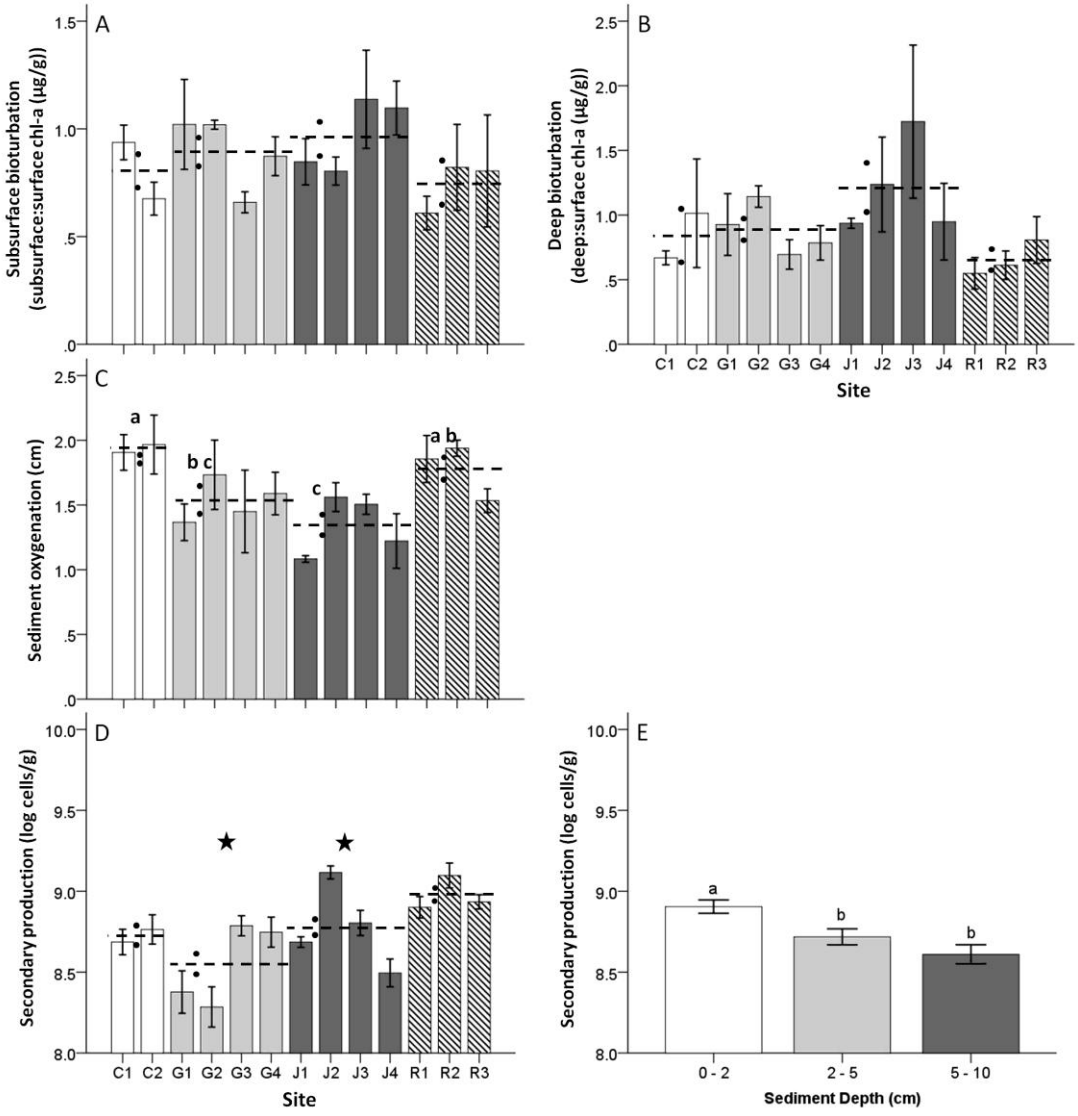

Figure 3.1. Spatial variation in subsurface bioturbation (A), deep bioturbation (B), sediment oxygenation (C), and secondary production (D) at regional and local scales (i.e. Basin and Site respectively; mean ± SE; n = 3 for each bar), as well as secondary production across sediment depth horizons (E; n = 39 for each bar). Horizontal dashed lines and dots indicate mean basin value (dashed line) ± SE (dots). Lower case letters (i.e. a, b, c) indicate significant differences among basins or sediment depths ($p < 0.05$). Star indicates significant differences among sites within a basin. On horizontal axis C = Crowell Basin, G = Georges Basin, J = Jordan Basin, and R = Roseway Basin.

Table 3.2. Summary of regression analyses for whole core polychaete biotic measures (abundance and species biodiversity) on ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

EF	Biotic Measure	Regression	R^2	Sig.
SB	Abundance	Exponential	0.084	0.077
	Diversity	Quadratic	0.042	0.475
	Richness	Quadratic	0.042	0.475
	Evenness	Exponential	0.007	0.618
DB	Abundance	Quadratic	0.092	0.177
	Diversity	Quadratic	0.020	0.700
	Richness	Quadratic	0.036	0.515
	Evenness	Exponential	0.001	0.847
SO	Abundance	Inverse	0.058	0.139
	Diversity	Quadratic	0.075	0.246
	Richness	Quadratic	0.103	0.140
	Evenness	**Quadratic**	**0.175**	**0.031**

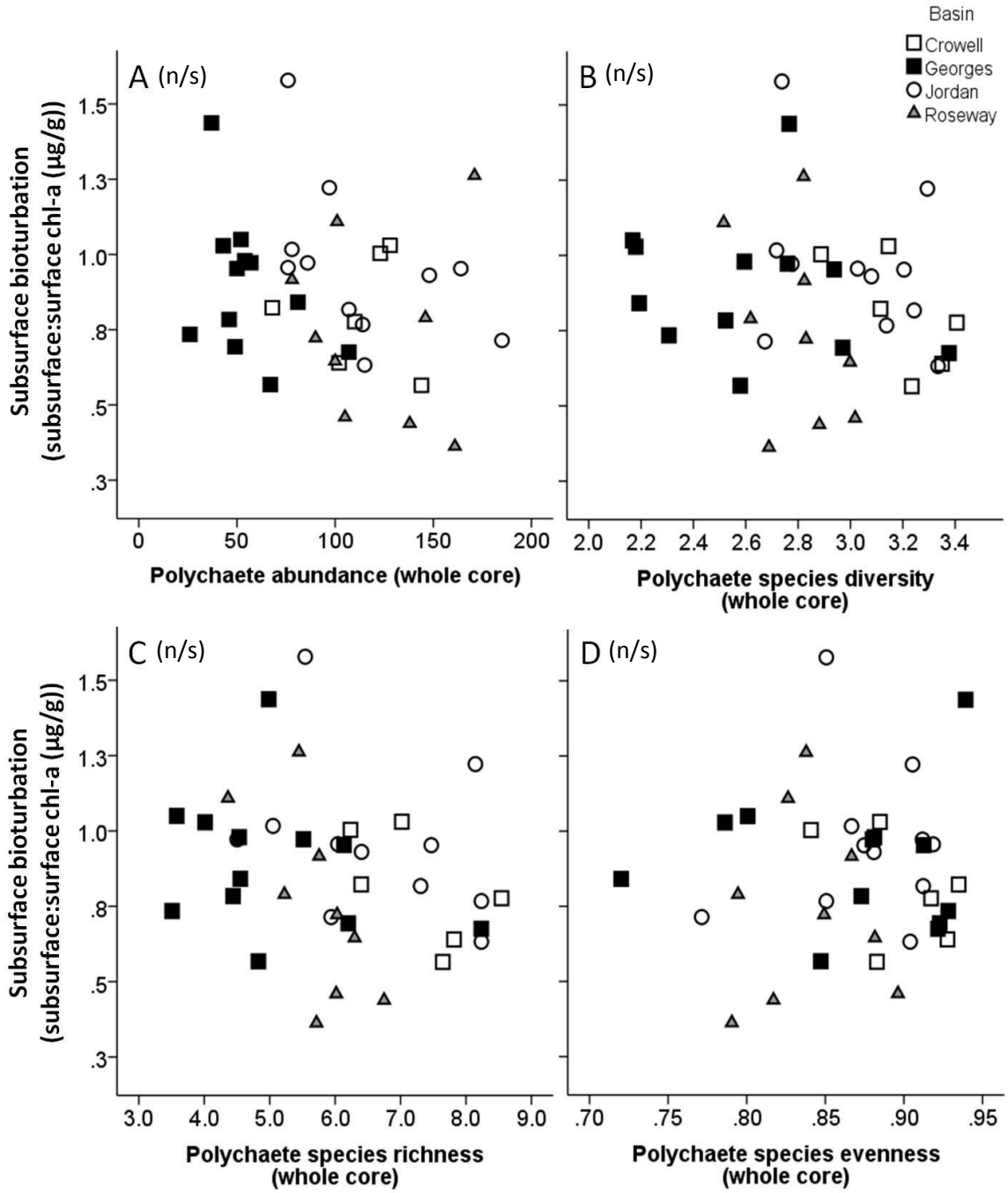

Figure 3.2. Relationships between subsurface bioturbation and whole core polychaete abundance (A), species diversity (B), species richness (C), and species evenness (D). n = 38. (n/s) indicates non-significance.

Table 3.3. Summary of regression analyses for polychaete biotic measures (abundance and species diversity) and ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

Ecosystem Function	Biotic Measure	Sediment Depth (cm)	Regression	R^2	Sig.	
SB	Abundance	0 – 2	Exponential	0.061	0.134	
		2 – 5	Quadratic	0.085	0.212	
		5 – 10	Quadratic	0.045	0.444	
	Diversity	0 – 2	Quadratic	0.070	0.281	
		2 – 5	Inverse	0.083	0.079	
		5 – 10	Quadratic	0.008	0.875	
	Richness	0 – 2	Quadratic	0.070	0.281	
		2 – 5	Inverse	0.083	0.079	
		5 – 10	Quadratic	0.008	0.875	
	Evenness	0 – 2	Quadratic	0.054	0.376	
		2 – 5	Quadratic	0.020	0.701	
		5 – 10	**Exponential**	**0.140**	**0.035**	
DB	**Abundance**	0 – 2	Quadratic	0.004	0.922	
		2 – 5	**Inverse**	**0.918**	**0.003**	**Crowell**
			Logarithmic	0.235	0.111	Georges
			Quadratic	0.098	0.629	Jordan
			Quadratic	0.029	0.916	Roseway
		5 – 10	Quadratic	0.084	0.205	
	Diversity	0 – 2	Exponential	0.020	0.393	
		2 – 5	Exponential	0.042	0.212	
		5 – 10	Linear	0.053	0.159	
	Richness	0 – 2	Exponential	0.042	0.210	
		2 – 5	Exponential	0.035	0.253	
		5 – 10	Quadratic	0.014	0.802	

Table 3.3. cont.

Ecosystem Function	Biotic Measure	Sediment Depth (cm)	Regression	R^2	Sig.	
DB	Evenness	0 – 2	Quadratic	0.039	0.490	
		2 – 5	Quadratic	0.035	0.530	
		5 – 10	Quadratic	0.040	0.542	
SO	**Abundance**	**0 – 2**	Quadratic	0.723	0.146	Crowell
			Inverse	**0.341**	**0.046**	**Georges**
			Quadratic	0.066	0.734	Jordan
			Logarithmic	**0.680**	**0.006**	**Roseway**
		2 – 5	Quadratic	0.005	0.921	
		5 – 10	Quadratic	0.149	0.054	
	Diversity	0 – 2	Quadratic	0.073	0.255	
		2 – 5	Quadratic	0.017	0.739	
		5 – 10	Exponential	0.013	0.495	
	Richness	0 – 2	Inverse	0.022	0.366	
		2 – 5	Quadratic	0.050	0.399	
		5 – 10	Quadratic	0.351	0.523	Crowell
			Linear	0.296	0.104	Georges
			Inverse	0.189	0.210	Jordan
			Quadratic	**0.658**	**0.040**	**Roseway**
	Evenness	0 – 2	Quadratic	0.040	0.480	
		2 – 5	Quadratic	0.020	0.695	
		5 – 10	Linear	0.026	0.375	
***SP**	**Abundance**	Whole core	**Exponential**	**0.191**	**< 0.01**	
	Diversity	Whole core	**Exponential**	**0.238**	**< 0.01**	
	Richness	Whole core	**Exponential**	**0.169**	**< 0.01**	
	Evenness	Whole core	Quadratic	0.172	0.266	Crowell
			Quadratic	0.016	0.784	Georges
			Exponential	**0.172**	**0.015**	**Jordan**
			Quadratic	0.038	0.630	Roseway

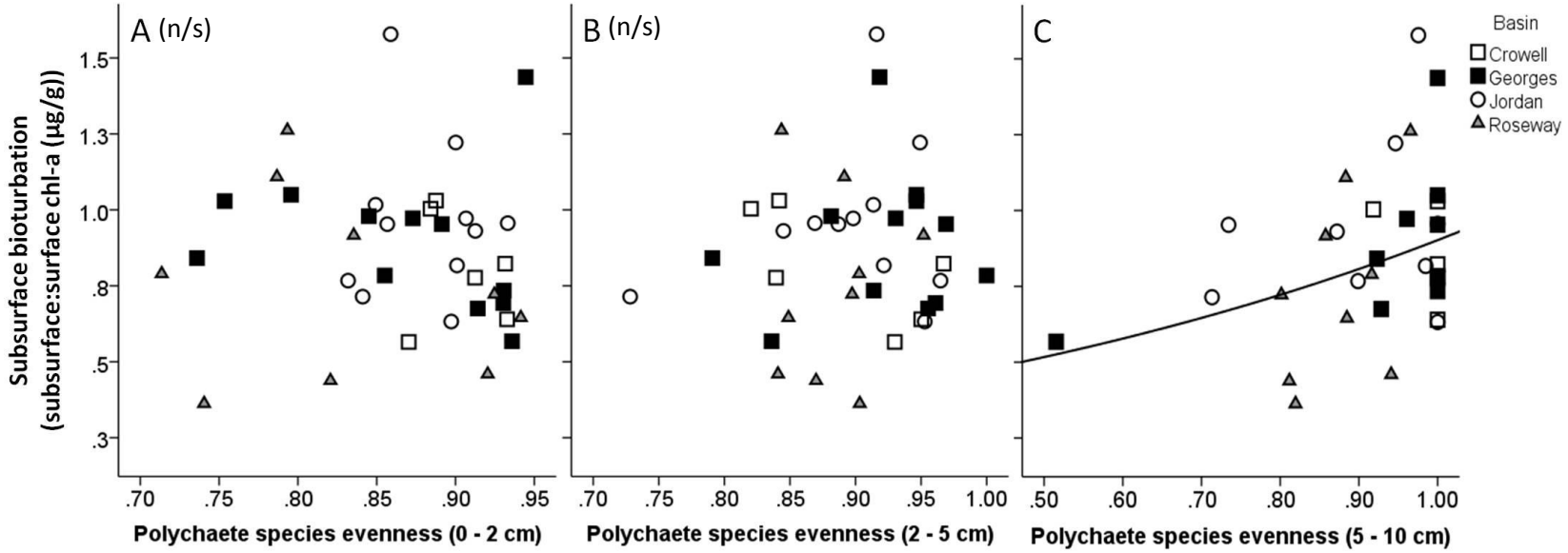

Figure 3.3. Relationship between subsurface bioturbation and polychaete species evenness at surface (A), subsurface (B), and deep (C; [y = 0.3 * exp(1.1 * x)], $R^2 = 0.140$, p = 0.035) sediment depths. n = 38. (n/s) indicates non-significance.

bioturbation (Table 3.2; Fig. 3.4). Although examination of individual sediment depth layers revealed a significant relationship between subsurface polychaete abundance and deep bioturbation, this relationship varied across basins (as indicated by a significant interaction between factors Basin and Biotic Measure; Table 3.4). Further investigation showed that subsurface polychaete abundance was a strong negative predictor of deep bioturbation only within Crowell Basin ($R^2 = 0.918$; $p = 0.003$; Table 3.3; Fig.3.5a).

Polychaete species evenness was the only significant predictor of sediment oxygenation, in whole core measurements (quadratic relationship, Table 3.2; Fig. 3.6d). Comparisons within sediment depths were non- significant (Table 3.3), demonstrating that this relationship with species evenness was restricted to whole core parameters only. Analysis within sediment depths did, nonetheless, demonstrate other relationships with sediment oxygenation. Polychaete abundance and species richness were both significant predictors of sediment oxygenation, but relationships were inconsistent across basins (Table 3.4). In Georges Basin only, polychaete abundance was a significant positive predictor of oxygen penetration depth within surface sediments ($R^2 = 0.341$; $p = 0.046$; Table 3.3; Fig.3.7c), whereas we observed a negative relationship in surface sediments of Roseway Basin ($R^2 = 0.680$; $p = 0.006$; Table 3.3; Fig.3.7g). In deep sediments within Roseway Basin species richness was also a significant positive predictor of sediment oxygenation (quadratic relationship, $R^2 = 0.658$; $p = 0.040$; Table 3.3; Fig.3.7h). No significant relationships were evident between polychaete biotic measures (abundance and species diversity) and sediment oxygenation within the other two basins (i.e. Crowell and Jordan).

When testing relationships between prokaryote abundances and polychaete biotic measures we analyzed whole core prokaryote abundance (i.e., pooled across sediment depths as no interactions were found between factors Sediment Depth and Basin or Biotic Measure, Table 3.4), which increased detection power of spatial patterns with biodiversity measures. Positive significant relationships were evident in each case when testing effects of polychaete abundance, species diversity, and species richness on secondary production (Table 3.3; Fig.3.8). Species evenness was also significantly related to secondary

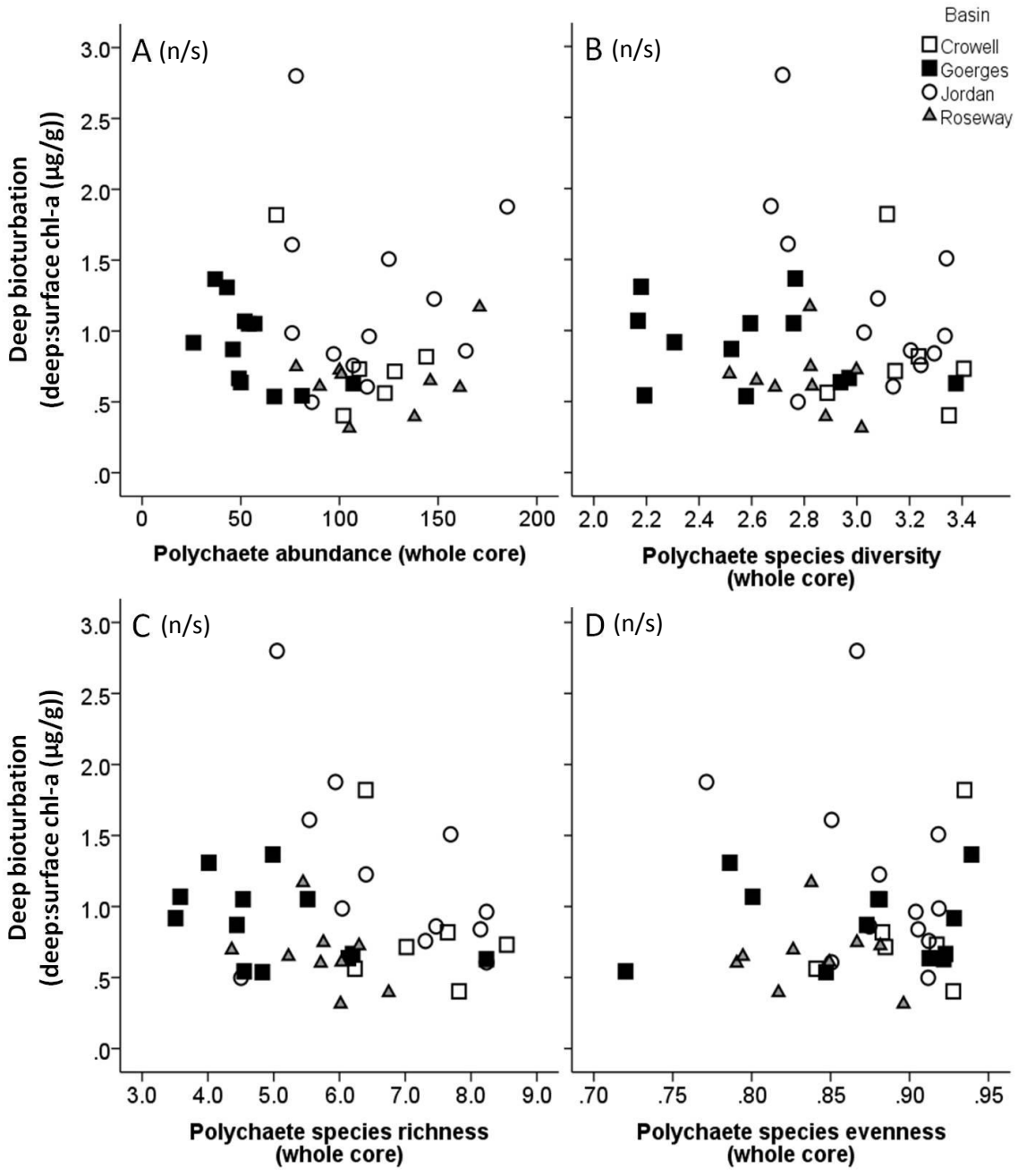

Figure 3.4. Relationship between deep bioturbation and whole core polychaete abundance (A), species diversity (B), species richness (C), and species evenness (D). n = 39. (n/s) indicates non-significance.

Table 3.4. Results from two-way [*three-way] ANOVAs (generalized linear model) showing the effect of polychaete biotic measure (abundance and species diversity) and Basin [*and Sediment Depth] on ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4, Sediment Depth n = 3.

			Abundance (N)			**Diversity (H')**			**Richness (d)**			**Evenness (J')**		
EF	**Sediment Depth (cm)**	**Source of Variation**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**
SB	**0 – 2**	Biotic Measure x Basin	2.0	3	0.570	4.7	3	0.194	4.7	3	0.194	0.1	3	0.990
		Biotic Measure	2.4	1	0.124	**5.3**	**1**	**0.021**	**5.3**	**1**	**0.021**	0.3	1	0.608
		Basin	3.4	3	0.329	4.5	3	0.209	4.5	3	0.209	0.1	3	0.996
	2 – 5	Biotic Measure x Basin	2.1	3	0.547	1.0	3	0.796	1.0	3	0.796	2.2	3	0.536
		Biotic Measure	3.0	1	0.084	**4.7**	**1**	**0.031**	**4.7**	**1**	**0.031**	0.0	1	0.979
		Basin	3.3	3	0.349	1.2	3	0.756	1.2	3	0.756	2.0	3	0.576
	5 – 10	Biotic Measure x Basin	4.6	3	0.207	6.3	3	0.098	6.3	3	0.098	2.7	3	0.438
		Biotic Measure	0.6	1	0.439	**4.1**	**1**	**0.044**	**4.1**	**1**	**0.044**	0.3	1	0.602
		Basin	7.1	3	0.069	**9.1**	**3**	**0.028**	**9.1**	**3**	**0.028**	3.0	3	0.397
DB	**0 – 2**	Biotic Measure x Basin	2.7	3	0.434	3.5	3	0.325	2.7	3	0.440	3.0	3	0.387
		Biotic Measure	1.4	1	0.239	3.5	1	0.061	**6.6**	**1**	**0.010**	0.0	1	0.925
		Basin	5.8	3	0.122	4.9	3	0.178	4.8	3	0.185	3.4	3	0.330
	2 – 5	**Biotic Measure x Basin**	**8.4**	**3**	**0.038**	2.0	3	0.571	1.7	3	0.638	5.6	3	0.136
		Biotic Measure	3.7	1	0.054	1.9	1	0.166	2.4	1	0.124	0.1	1	0.772
		Basin	2.7	3	0.438	3.3	3	0.354	2.9	3	0.403	6.3	3	0.100

Table 3.4. cont.

EF	Sediment Depth (cm)	Source of Variation	Abundance (N)			Diversity (H')			Richness (d)			Evenness (J')		
			χ^2	df	Sig.	χ^2	df	Sig.	χ^2	df	Sig.	χ^2	df	Sig.
DB	5 – 10	Biotic Measure x Basin	2.9	3	0.402	1.9	3	0.604	0.6	3	0.907	3.5	3	0.326
		Biotic Measure	0.7	1	0.410	0.2	1	0.694	0.0	1	0.927	1.4	1	0.230
		Basin	3.6	3	0.305	5.5	3	0.137	1.2	3	0.758	4.5	3	0.214
SO	**0 – 2**	**Biotic Measure x Basin**	**11.3**	**3**	**0.010**	1.9	3	0.598	1.0	3	0.790	2.8	3	0.420
		Biotic Measure	2.0	1	0.161	0.1	1	0.706	0.3	1	0.561	0.7	1	0.397
		Basin	**15.1**	**3**	**0.002**	2.0	3	0.577	2.1	3	0.562	2.7	3	0.448
	2 – 5	Biotic Measure x Basin	1.0	3	0.796	1.1	3	0.777	1.3	3	0.725	1.4	3	0.701
		Biotic Measure	0.3	1	0.572	0.1	1	0.809	0.1	1	0.712	0.3	1	0.600
		Basin	**7.9**	**3**	**0.048**	1.7	3	0.636	2.2	3	0.522	1.0	3	0.803
	5 – 10	**Biotic Measure x Basin**	4.7	3	0.199	4.8	3	0.189	**8.2**	**3**	**0.042**	1.3	3	0.720
		Biotic Measure	1.7	1	0.195	0.0	1	0.898	0.1	1	0.704	0.4	1	0.552
		Basin	**14.9**	**3**	**0.002**	**14.4**	**3**	**0.002**	**11.3**	**3**	**0.010**	1.9	3	0.595
SP	n/a	Biotic Measure x Basin x Sediment Depth	6.1	6	0.407	3.3	6	0.765	5.8	6	0.444	4.0	6	0.683
		Biotic Measure x Basin	1.4	3	0.698	5.2	3	0.157	2.4	3	0.490	**13.9**	**3**	**0.003**
		Biotic Measure x Sediment Depth	3.1	2	0.211	0.2	2	0.914	0.5	2	0.766	0.2	2	0.916
		Basin x Sediment Depth	2.9	6	0.826	2.6	6	0.854	4.0	6	0.681	3.7	6	0.716

Table 3.4. cont.

EF	Sediment Depth (cm)	Source of Variation	Abundance (N)			Diversity (H')			Richness (d)			Evenness (J')		
			χ^2	df	Sig.	χ^2	df	Sig.	χ^2	df	Sig.	χ^2	df	Sig.
SP	n/a	Biotic Measure	0.4	1	0.506	2.0	1	0.160	2.4	1	0.121	0.7	1	0.412
		Basin	3.5	3	0.324	5.6	3	0.133	5.2	3	0.161	**15.2**	**3**	**0.002**
		Sediment Depth	4.5	2	0.106	0.2	2	0.918	0.3	2	0.844	0.2	2	0.883

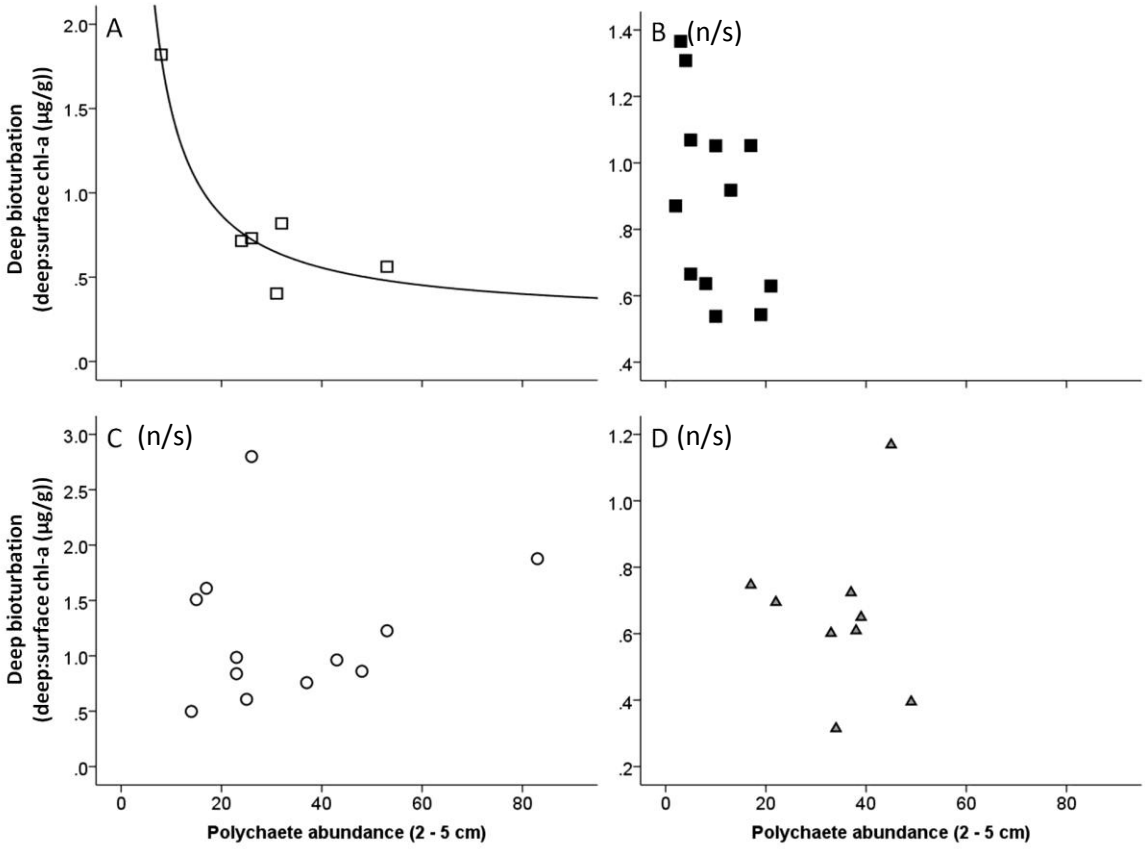

Figure 3.5. Relationship between deep bioturbation and subsurface polychaete abundance within Crowell (A; [$y = 0.2 + (12.5 / x)$], $R^2 = 0.918$, $p = 0.003$; $n = 6$), Georges (B; $n = 12$), Jordan (C; $n = 12$), and Roseway (D; $n = 9$) Basins. (n/s) indicates non-significance.

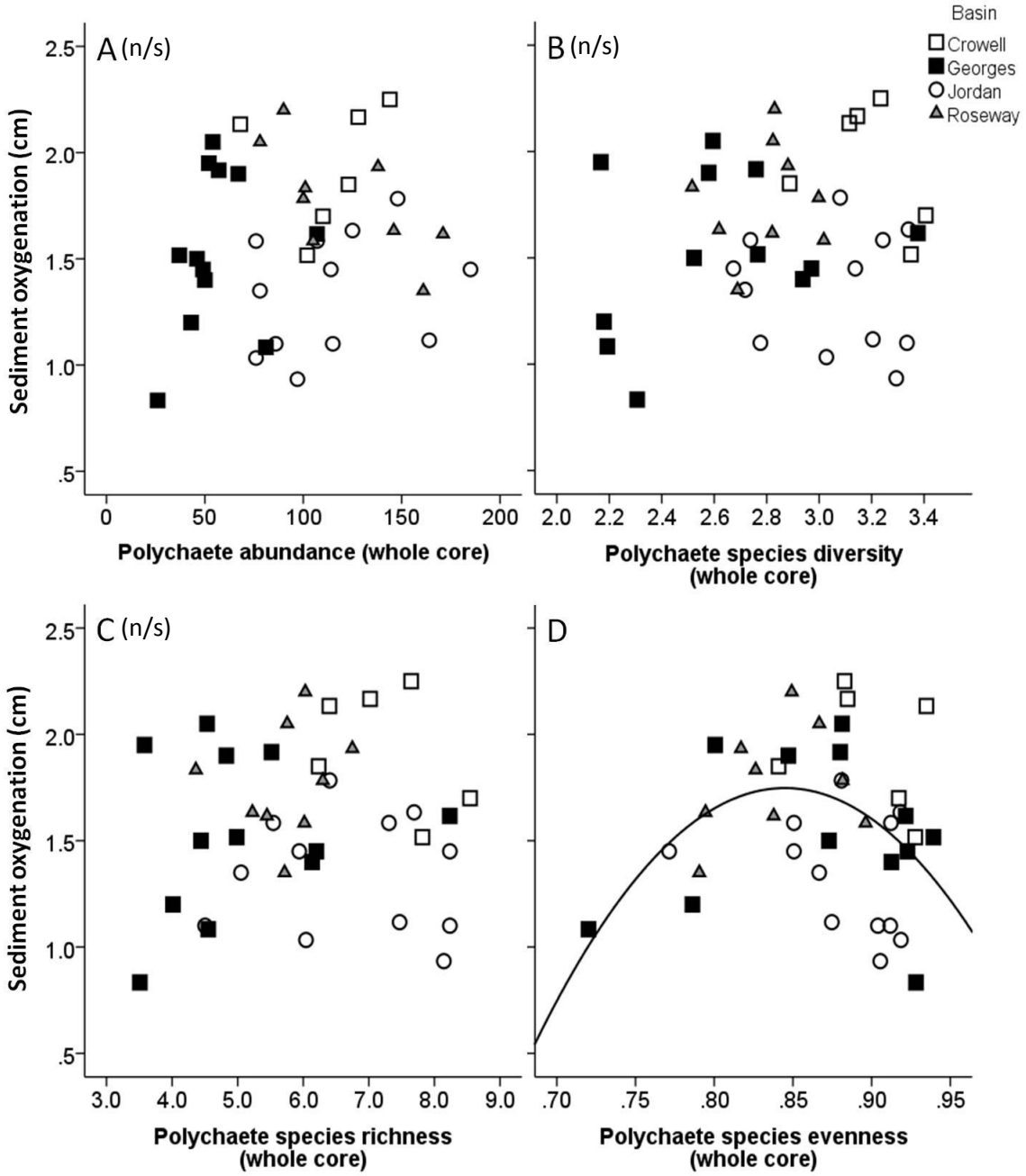

Figure 3.6. Relationship between sediment oxygenation and whole core polychaete abundance (A), species diversity (B), species richness (C), and species evenness (D; [y = -32.3 + 80.6 * x + -47.7 * x*x], $R^2 = 0.175$, $p = 0.031$). n = 39. (n/s) indicates non-significance.

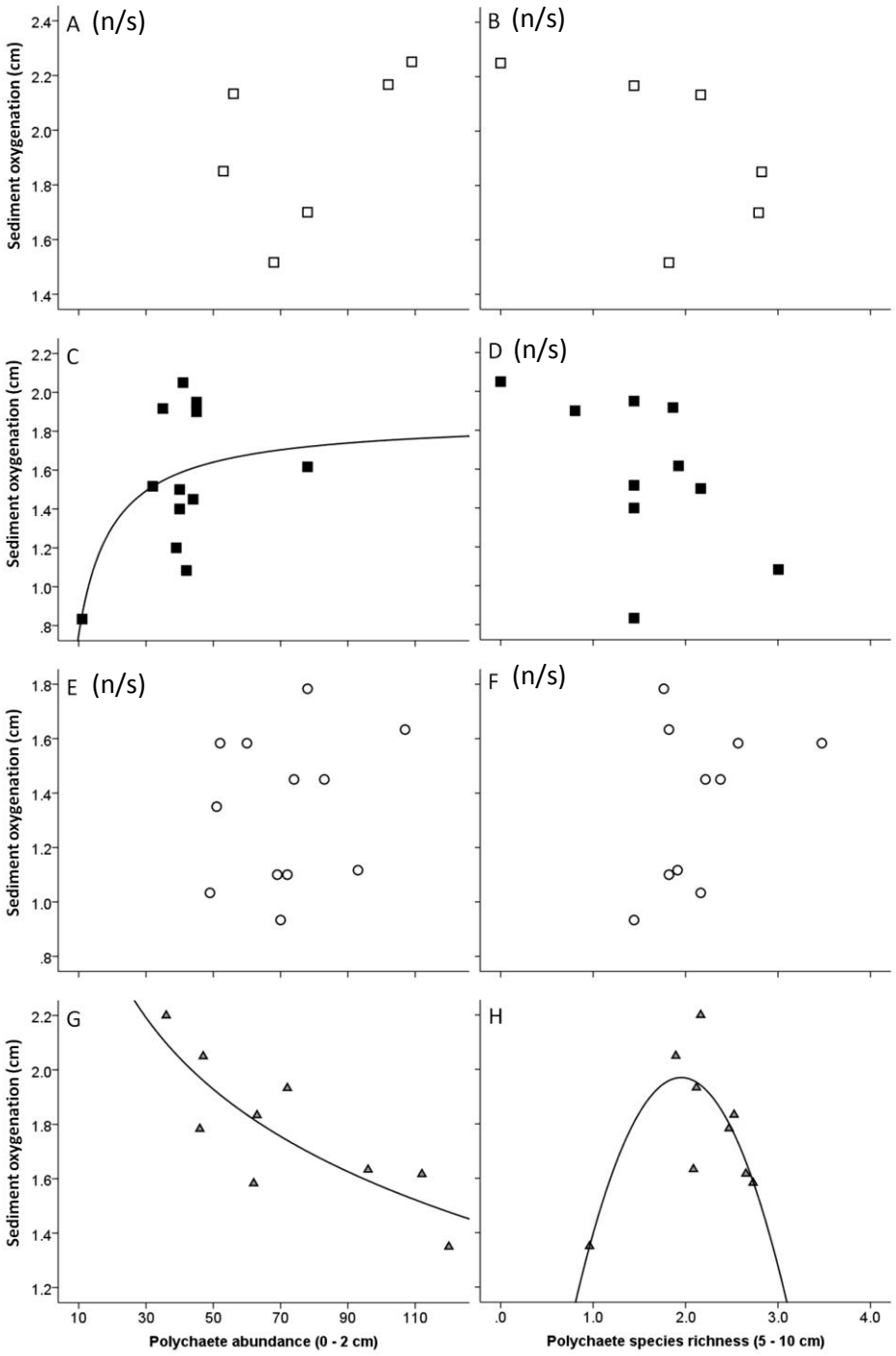

Figure 3.7. Relationship between sediment oxygenation and surface polychaete abundance (left panels) and deep polychaete species richness (right panels) within Crowell (A,B; n = 6), Georges (C ([y = 1.9 + (-11.1 / x)], R^2 = 0.341, p = 0.046; n = 12), D), Jordan (E,F; n = 12), and Roseway (G ([y = 3.9 + -0.52 * log(x)], R^2 = 0.680, p = 0.006; n = 9), H ([y = -0.4 + 2.5 * x + -0.6 * x*x], R^2 = 0.658, p = 0.040; n = 6) Basins. (n/s) indicates non-significance.

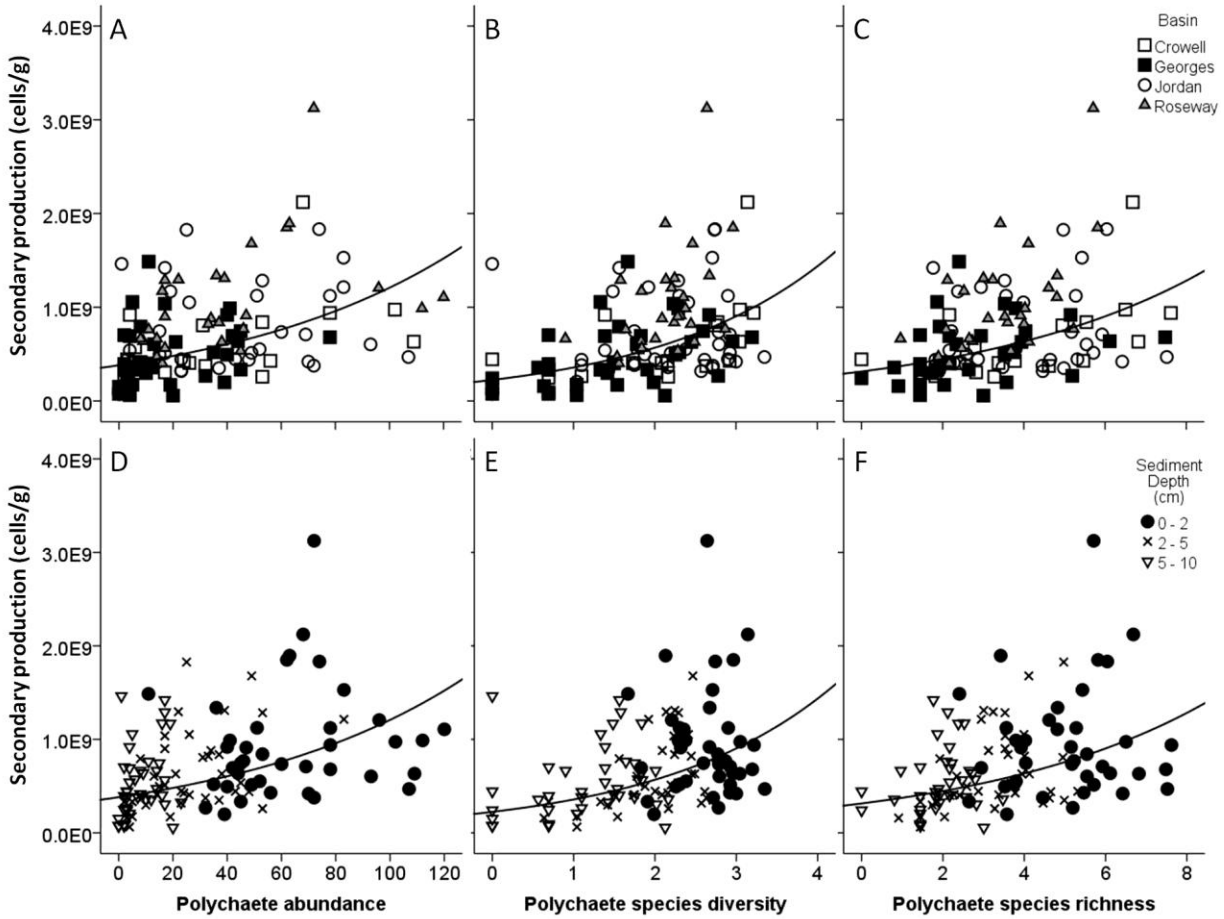

Figure 3.8. Relationship between secondary production and polychaete abundance (A and D; [$y = 3.8 \times 10^8 * \exp(0.01 * x)$], $R^2 = 0.191$, $p = < 0.01$), species diversity (B and E; [$y = 2.2 \times 10^8 * \exp(0.5 * x)$], $R^2 = 0.238$, $p = < 0.01$), and species richness (C and F; [$y = 3.1 \times 10^8 * \exp(0.2 * x)$], $R^2 = 0.169$, $p = < 0.01$) across basins (A, B, C) and sediment depth layers (D, E, F); although neither impacts relationship. n = 39 for each basin and sediment depth.

production, however, results varied across basins (as indicated by a significant interaction between Biotic Measure and Basin; Table 3.4). Separate analyses for each basin revealed a negative relationship between species evenness and prokaryote abundance, but only in Jordan Basin (Table 3.3; Fig.3.9c). Diversity proved to be the strongest predictor of prokaryote abundance ($R^2 = 0.238$; $p = < 0.01$; Table 3.3; Fig.3.8b, e).

3.4.3 Influence of taxonomic (species, family) and functional (feeding guild) level on biodiversity-ecosystem function relationships

Examination of biodiversity measures at coarser taxonomic (i.e., Family) and functional (i.e., Feeding Guild) levels revealed significant relationships with some ecosystem function measures, however, few of these relationships coincided with species level relationships. At the family level, we found a significant, and generally negative, relationship between whole core richness and deep bioturbation ($R^2 = 0.211$; $p = 0.014$; Appendix Table G3; Fig. G1); the relationship dissolved when analysing individual sediment depths (Appendix Table G4). Family level analyses also revealed significant relationships between all biodiversity measures (i.e. diversity, richness, and evenness) and secondary production (pooled across sediment depths), however, these relationships varied across basins (as indicated by a significant interaction between Basin and Biodiversity; Appendix Table G2). Family level diversity was a significant predictor of secondary production in all basins except Jordan ($R^2 = 0.448$, 0.238, and 0.254; $p = 0.012$, 0.003, and 0.030; Appendix Table G4; Fig. G2; Crowell, Georges, and Roseway respectively). Positive relationships were also evident between family level richness and secondary production, but only in Crowell and Roseway Basins ($R^2 = 0.440$ and 0.379; $p = 0.013$ and 0.003; Appendix Table G4; Fig. G3, respectively). In contrast, evenness related negatively with secondary production, but only in Jordan Basin ($R^2 = 0.238$; $p = 0.003$; Appendix Table G4; Fig. G4).

At the feeding guild level, we found significant biodiversity-ecosystem function relationships across whole core parameters and at individual sediment depths. While we found no significant relationships between whole core feeding guild diversity measures

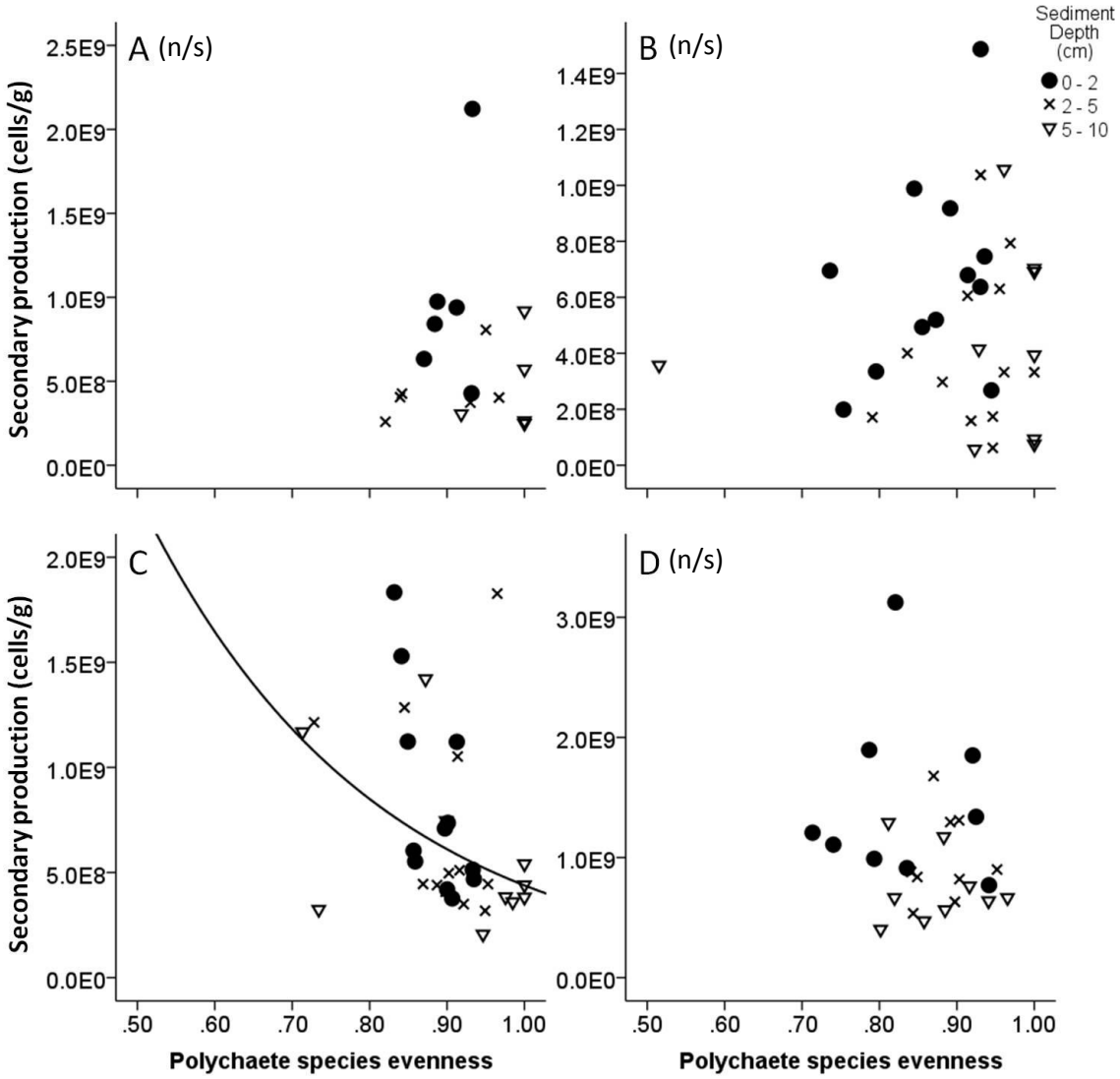

Figure 3.9. Relationship between secondary production and polychaete species evenness within Crowell (A; n = 6), Georges (B; n = 12), Jordan (C; [$y = 1.2 \times 10^{10} * \exp(-3.3 * x)$], $R^2 = 0.172$, $p = 0.015$; n = 12), and Roseway (D; n = 9). Measurements from all three sediment depth layers included. (n/s) indicates non-significance.

and subsurface bioturbation (Appendix Table H3), analyses of individual sediment depths showed that diversity related negatively to subsurface bioturbation in subsurface (2-5 cm) sediment layers and evenness in surface (0-2 cm) sediment layers related positively with subsurface bioturbation (R^2 = 0.220 and 0.121; p = 0.013 and 0.032 respectively; Appendix Table H4; Fig. H3).

Whole core feeding guild richness was a negative predictor of deep bioturbation (R^2 = 0.124; p = 0.028; Appendix Table H3; Fig. H1); however, as with family level analyses this relationship dissolved when analysing individual sediment depths (Appendix Table G4). Whole core feeding guild diversity and richness were both positive predictors of sediment oxygenation (R^2 = 0.189 and 0.100; p = 0.023 and 0.049; Appendix Table H3; Fig. H2). Further investigation of individual sediment horizons dissolved the richness relationship, but revealed a significant, and generally positive, relationship between feeding guild diversity and sediment oxygenation but within surface layers only (R^2 = 0.172; p = 0.033; Appendix Table H4; Fig. H4).

As with species and family level analyses, all measures of feeding guild biodiversity (i.e. diversity, richness, and evenness) were significantly, and positively, related to secondary production pooled across depth layers (R^2 = 0.202, 0.059, and 0.107; p = < 0.01, 0.036, and 0.002; Appendix Table H4; Fig. H5).

A summary of the biodiversity-ecosystem function relationships across taxonomic levels showed that feeding guild diversity related most strongly with ecosystem functions (9 significant relationships), followed by species level diversity (6 relationships), then family level diversity (4 relationships) and abundance (3 relationships; Table 3.5).

3.5 DISCUSSION

Our measurements of sediments from the Gulf of Maine addressed three objectives, demonstrating: 1) significant spatial variation in ecosystem function proxies (i.e. sediment oxygenation and secondary production) across regional and local spatial scales; 2) significant biodiversity-ecosystem function relationships; and 3) polychaete biotic measures (abundance and biodiversity) are significant predictors of ecosystem

Table 3.5. Summary of regression analyses showing significant polychaete biodiversity-ecosystem function relationships at three taxonomic levels (species, family, feeding guild). WC indicates whole core analyses. 0-2, 2-5 or 5-10 indicates specific sediment depth layers. More than one relationship [i.e. quadratic (+) / quadratic (+)] indicates significant basin variation. Core replicate n = 39 (except for SB n = 38).

Taxonomic Level	Biodiversity Measure	Ecosystem Function	Relationship
Species	Evenness $_{WC}$	SO	Quadratic (-)
	Evenness (5-10 cm)	SB	Exponential (+)
	Richness (5-10 cm)	SO	Quadratic (-)
	Diversity	SP	Exponential (+)
	Richness	SP	Exponential (+)
	Evenness	SP	Exponential (+)
Family	Richness $_{WC}$	DB	Quadratic (+)
	Diversity	SP	Quadratic (+) / Exponential (+) / Quadratic (+)
	Richness	SP	Quadratic (+) / Quadratic (+)
	Evenness	SP	Exponential (-)
Feeding Guild	Richness $_{WC}$	DB	Inverse (-)
	Diversity $_{WC}$	SO	Quadratic (-)
	Richness $_{WC}$	SO	Exponential (+)
	Diversity (2-5 cm)	SB	Quadratic (-)
	Evenness (0-2 cm)	SB	Inverse (+)
	Diversity (0-2 cm)	SO	Quadratic (-)
	Diversity	SP	Exponential (+)
	Richness	SP	Quadratic (+)
	Evenness	SP	Quadratic (-)

functions, irrespective of measure (abundance, diversity, richness, and evenness) or taxonomic level (species, family, and feeding guild).

EF spatial variation (horizontal)

Our study demonstrated significant variation in ecosystem function measures across multiple spatial scales (both horizontal and vertical) within the Gulf of Maine, but only sediment oxygenation (i.e., oxygen penetration) varied significantly regionally (i.e., across basins). These results are the first to indicate such patterns in deep shelf sediments of the Gulf of Maine, but support other findings of variation of oxygen penetration in marine sediments detected in Mediterranean coastal seabeds (Ziebis et al. 1996). Our study found the deepest oxygen penetration (up to 1.9 cm, in Crowell Basin), was 30% deeper than the shallowest oxygen penetration depth in Jordan Basin. In comparison, studies of shallow coastal areas report oxygen penetration usually no deeper than 5 mm (Revsbech et al. 1980; Anderson and Helder 1987). Understanding sediment surface topography, sediment permeability, and sediment surface flow velocities could provide further insight into observed regional variations in oxygen penetration (Ziebes et al. 2006).

Gulf of Maine basin sediments were high in mud content (< 60%; Chapter 2) diminishing the possible contribution of diffusive oxygen penetration and increasing support for the importance of infaunal sediment reworking. Our results may therefore be best explained by spatial variation in faunal composition across regional and local spatial scales. Previous studies have demonstrated deeper oxygen penetration induced by macrofaunal activity, in particular, burrowing macrofauna that irrigate their burrows and transport water, and thus oxygen, to greater depths (Revsbech et al. 1980; Timmermann et al. 2006). In Gulf of Maine sediments, we detected regional variation (i.e., across basins) for total macrofaunal and annelid abundance, as well as polychaete species diversity and richness (Chapter 2). Although oxygen penetration was shallowest in Jordan Basin (1.3 cm), faunal abundances and biodiversity measures were not significantly lower compared to other basins in the Gulf of Maine (Chapter 2). The surface deposit feeder, *Cossura longocirrata*, dominates Jordan Basin and may further explain shallow oxygen

penetration within Jordan Basin, noting the potential contribution of other physical factors such as grain size.

While our study did not demonstrate regional variation (i.e. across basins) with bioturbation measures or secondary production, we detected significant local-scale variation (i.e. across sites within each basin) in secondary production (i.e. prokaryote abundance). Bacteria are known to be important players in nutrient recycling and degradation (Alongi 1994) and previous work that links bacteria and organic carbon (i.e. chlorophyll-a) indicated that organic matter input can enhance bacterial production (van Duyl et al. 1993). Related research within the Gulf of Maine, showed concentrations of carbon, nitrogen, and chlorophyll-a varied locally within basin sediments (Chapter 2), which may link to the local variability in prokaryote abundances indicated by our results. Faunal abundance and distribution could also explain local variation in prokaryote abundance, given that polychaete burrows are known to promote bacterial growth (Alongi 1985; Aller and Aller 1986). Interestingly, we found prokaryote abundances varied locally within Georges and Jordan Basins, but showed elsewhere (Chapter 2), that polychaete evenness at species and family levels, as well as polychaete family diversity varied locally (i.e. across sites within basins), but only in specific basins. Each of these biodiversity measures varied locally within Roseway Basin, however, polychaete family evenness also varied locally within Georges Basin (Chapter 2), showing a similar pattern to the local scale variation in prokaryote abundances. Within Jordan Basin, local variation in prokaryote abundance resembles local variation in organic concentrations, particularly of carbon, nitrogen and chlorophyll-a, as well as mud content (Chapter 2). Ultimately, these two examples lend support to previous studies that show polychaetes and organic matter influence bacteria (Aller and Aller 1986; van Duyl et al. 1993).

EF spatial variation (vertical)

Secondary production varied significantly between sediment depth layers. For example, prokaryote abundances were higher in surface layers compared to subsurface and deep layers. The vertical patterns of prokaryote abundance in benthic sediments reflect patterns reported by Sahm and Berninger (1998). Throughout the Gulf of Maine region, higher abundances and biodiversity measures of all macrofaunal taxa in surface (0

– 2 cm) sediment layers than in subsurface layers (Chapter 2), echoes a commonly reported result and confirms that food and oxygen availability strongly dictate vertical distribution patterns (Snelgrove et al. 1997).

Spatial influence on Biodiversity-EF relationships (species level)

Spatial scale can strongly influence biodiversity-ecosystem function relationships. Bond et al. (2002) suggested that examination of relationships at local and regional scales may reveal contrasting patterns, likely resulting from local patchiness; their meta-analysis of multiple studies documented parabolic and linear relationships at local and regional scales, respectively. To date, terrestrial experiments overwhelmingly dominate biodiversity-ecosystem function relationship studies (i.e. Naeem et al. 1994; Tilman et al. 1997; Hector et al. 1999; Petchey et al. 2004; Fitter et al. 2005; Schmitz 2009), with the majority of studies demonstrating positive biodiversity-ecosystem function relationships (i.e. species richness and plant biomass). For example, Eisenhauer et al. (2012) demonstrated positive complementary biodiversity-ecosystem function relationships at local scales using plant and decomposer diversity. Recent studies are beginning to examine biodiversity-ecosystem function patterns within marine habitats (i.e. Wall 1999; O'Connor and Crowe 2005; Loreau 2007; Shelley et al. 2008). For example, Danovaro et al. (2008) demonstrated positive exponential relationships occurring between nematode diversity and prokaryote carbon production. These studies allow us to evaluate whether these relationships transcend terrestrial and aquatic environments.

We generally found positive biodiversity-ecosystem function associations. For example, as with polychaete abundance, species diversity and richness were exponentially positive predictors of secondary production (i.e. prokaryote abundance). Polychaetes are known to stimulate bacterial growth around their burrows (Alongi 1985; Aller and Aller 1986; Mermillod-Blondin et al. 2004), thus explaining this observation. These patterns also echo exponential positive relationships between nematode functional diversity and prokaryote biomass within deep- sea sediments reported by Danovaro et al. (2008). In some instances we found significant negative biodiversity-ecosystem function associations but most were regionally dependent. For example, polychaete abundance negatively predicted sediment oxygenation but only within Roseway Basin. These results

could stem from pressures of local factors, such as habitat homogenization or removal of large infaunal, which can drive negative relationships within specific regions (Thrush et al. 2006). Nonetheless, co-variation in these factors rather than cause and effect relationships may contribute to these patterns.

The presence of particular species, combinations of species, or loss of a species can also dramatically alter activities and thereby influence ecosystem function performance both on land (Hooper et al. 2005) and in marine seafloor sediments (Lohrer et al. 2004; Thrush et al. 2006). Numerous studies show that infaunal organisms, particularly polychaetes, significantly impact their surrounding geochemical environments (Mermillod-Blondin and Rosenberg 2006; Weissberger et al. 2008; Nogaro et al. 2009). For example, in benthic sediments, high abundances of burrowing or bioturbating infauna can increase subsurface bioturbation (i.e., sediment mixing) and facilitate sediment oxygenation (Mermillod-Blondin 2011). In our study, we found weak links between polychaete species biodiversity and sediment mixing between depth layers, which suggests that biodiversity-sediment mixing (i.e., bioturbation) relationships in our study were limited to specific sediment layers and basins. For example, subsurface bioturbation increased with increased polychaete species evenness within deep sediment layers (5 – 10 cm), indicating more sediment mixing occurred between surface and subsurface sediment layers when a heterogeneous mix of polychaetes were found within deep sediment layers. An explanation for increased sediment mixing could be the presence of capitellid polychaetes, found within the deepest sediment layers (5 – 10 cm) throughout the Gulf of Maine region (Chapter 2). Capitellidae are deposit feeders that typically build extensive burrows into deep sediment layers, but can also be highly mobile near surface sediments when required (Fauchald and Jumars 1979). In contrast to this pattern, within Crowell Basin, we found a negative relationship between deep bioturbation and polychaete abundance within subsurface sediment layers (2 – 5 cm). One explanation may be that increased subsurface abundance corresponds to limited activity in deeper sediments, thereby reducing the mixing of deeper sediments. Another explanation may be high abundances of paraonids (Family Paraonidae) found within subsurface layers throughout Gulf of Maine sediments (Chapter 2). These primarily

surface deposit feeding polychaetes can create spiral burrows extending into deeper sediment layers, but the majority of their activity (i.e., feeding) focuses on sediment surfaces (Fauchald and Jumars 1979). The dominance of paraonids in subsurface layers within the Gulf of Maine (Chapter 2), with their activity focused at the surface, may correspond to limited bioturbation in deeper sediment layers. Numerous laboratory studies demonstrate the effectiveness of polychaetes as bioturbators (Marinelli 1994; Mulsow and Landrum 1995; Weissberger et al. 2008); these findings motivated our field study and support the relationships we found between polychaete biodiversity and bioturbation proxies.

When burrowing and feeding polychaetes mix sediments, they also facilitate oxygen influx into sediment layers by creating and irrigating burrows and through their feeding activities (e.g. Timmermann et al. 2006). Polychaetes move oxygen into their burrows by ventilating them, and oxygen can then seep through most burrow walls, oxygenating surrounding sediments (Wenzhofer and Glud 2004; Timmermann et al. 2006). We found significant relationships between diversity and sediment oxygenation, however, the relationships varied across regional scales (i.e., different shaped relationships for different basins). Polychaete abundance significantly predicted sediment oxygenation, but only within surface (0 – 2 cm) sediment layers and relationships varied among basins. Faunal differences within each basin may explain contrasting patterns. For example, although we observed significantly lower overall abundances and diversity metrics in Georges Basin, the predominant species *Prionospio* sp. (Family Spionidae; Chapter 2) builds burrows and can be highly mobile (Fauchald and Jumars 1979); both activities can enhance sediment oxygenation. In contrast, a mobile surface deposit feeder, *Cossura longocirrata* (Family Cossuridae) dominates Roseway Basin; this polychaete primarily occupies surface sediment layers, and is thus unlikely to oxygenate deeper sediments (Fauchald and Jumars 1979). Furthermore, research by Waldbusser et al. (2004), investigating links between oxygen fluxes and deposit-feeding polychaetes, also suggested that differences in sediment oxygen fluxes likely result from species-specific feeding, burrowing behaviours, and species-related interactions. Ieno et al. (2006), who studied infaunal species diversity impacts on nutrient generation and bioturbation, also

found that species identity, density, and species-specific traits influenced responses. Species-specific traits were also found to override species richness and functional biodiversity when investigating ecosystem function links (Norling et al. 2007). These findings further support our conclusion that the presence of particular species can greatly impact regional patters within the Gulf of Maine.

Secondary production (i.e., prokaryote abundance) provides the strongest biodiversity-ecosystem function link within our study, acknowledging the possibility of co-variation in these variables and/or a disconnect between microbial abundance and production. Secondary production significantly increased with increases in abundance and species biodiversity (i.e., diversity and richness). Similar positive relationships were also reported for nematode (functional) diversity and prokaryote biomass in deep-sea sediments from several regions around the world (Danovaro et al. 2008). Polychaetes are known to stimulate bacterial and meiofaunal growth near their burrows in field studies (Nova Scotian Rise (Aller and Aller 1986)) and laboratory experiments (Alongi 1985); possibly as a result of expulsion of organic waste and oxygenation of the sediments surrounding burrows (Aller 1985; Alongi 1985). Our results, supported by these previous studies, suggest that increased polychaete biodiversity increases prokaryote abundance, resulting in increased secondary production activities (carbon fixation and nutrient cycling) in the Gulf of Maine.

We observed a significant negative correlation with secondary production, but only in Jordan Basin. Within this basin, highly variable supply of organic matter may influence prokaryote abundances (Chapter 2). Taxonomic resolution offers another potential explanation. Evenness describes heterogeneity within a community, and increased evenness often indicates increased diversity and richness (Bulla 1994; Warwick and Clarke 1995; Magurran 2004). However, with species level taxonomic resolution, increased evenness indicates a heterogeneous mix of morphologically different species, but not necessarily a mix of activities (indicative of increased functional diversity). Different species could belong to the same feeding/functional group and perform similar activities, arguably resulting in species redundancy. For example, two polychaete species, *Capitella capitata* (Family: Capitellidae) and *Scalibregma inflatum* (Family:

Scalibregmatidae), are morphologically different species that occupy the same feeding/functional group (i.e., subsurface deposit feeder; MacDonald et al. 2010). Thus, different species may perform similar functions and potentially influence ecosystem functions in a similar way. Alternatively, animals with similar morphologies can also perform different activities. Polychaetes encompass a wide variety of feeding/functional groups with different species performing different activities, such as burrowing or motility, with varied impacts on the local environment (MacDonald et al. 2010).

Taxonomic influence on Biodiversity-EF relationships

Species redundancy (Snelgrove et al. 1997; Naeem 1998; Fonseca and Ganade 2001; Wellnitz and Poff 2001) and whether ecosystem function studies require species level taxonomy has generated considerable discussion in recent years (O'Connor and Crowe 2005; Bertrand et al. 2006; Waldbusser and Marinelli 2006; Kirwan et al. 2009). Indeed, some researchers argue that an organism's function or activity outweighs morphological differences when relating diversity to ecosystem functions (Bengtsson et al. 1998; Waldbusser and Marinelli 2006). Feeding guilds "simplify" diversity compared to finer taxonomic resolution levels (species) because they group individuals that exhibit similar activities (e.g. feeding behaviour), as opposed to morphological differences that characterize species-level identification. Ultimately, our study supports this generalization given that we observed additional significant, albeit weak (low R^2 values), relationships between ecosystem functions and animal feeding guild, rather than with more detailed (i.e. species level) taxonomic characterization. Previous studies examining taxonomic influence on ecosystem functions generally support our findings, pointing to higher occurrence of relationships between ecosystem functions and functional characteristics than with morphological classifications (Waldbusser and Marinelli 2006; Caliman et al. 2007; Tornroos et al. 2014). We also hypothesized that biodiversity measures would predict more ecosystem functions than abundance, which also proved true. Previous studies (Hooper and Vitousek 1997; McGrady-Steed et al. 1997; Emmerson et al. 2001; Paine 2002; Hooper et al. 2012) add support and demonstrate the importance of an organisms' identity. Interestingly, the strongest predictors (i.e. highest R^2 value) of ecosystem functions were abundance, followed by species biodiversity measures,

however, these relationships were restricted to a specific basin, as well as a specific depth layer, signifying that localized environmental factors could affect results.

Although the biodiversity-ecosystem function relationships we found varied in direction and strength, we can generalize some patterns across taxonomic levels. Abundance, diversity, and richness negatively predicted bioturbation (subsurface and deep mixing), while evenness positively predicted bioturbation but only in specific sediment layers, indicating high abundance and foraging activities reduced sediment mixing into deeper sediment layers. All biotic measures (abundance, diversity, richness, and evenness) positively predicted sediment oxygenation, indicating higher biodiversity links to deeper oxygen penetration; abundance was a notable exception, showing regional influences (positive in one basin, negative in another). Finally, abundance, diversity, and richness positively and exponentially predicted secondary production, whereas evenness negatively predicted secondary production in most cases.

Although our study documents spatial variation in ecosystem functions and demonstrates benthic biodiversity-ecosystem function relationships within the Gulf of Maine, our proxy measurements of ecosystem functions may underestimate linkages with biodiversity. For example, our use of chlorophyll-a concentrations as a tracer of bioturbation offers a coarse proxy that may be less sensitive than more direct measures. In addition to direct measurement of bioturbation using techniques such as radioisotopes or luminophores (De Backer et al. 2011), other measurements of ecosystem function (e.g. nutrient fluxes [Rasheed et al. 2006; Shelley el al. 2008]), in parallel with experimental approaches such as oxygen consumption in incubation experiments) may further clarify these relationships.

Our research addresses polychaete biodiversity-ecosystem function relationships, however, consideration of mega, macro, meio, and microfauna and more trophic levels may improve prediction of key ecosystem functions. Feeding and burrowing, in bivalves (Marinelli and Williams 2003; Thrush et al. 2006), amphipods (Mermillod-Blondin et al. 2005; De Backer et al. 2011), and echinoderms (Covich et al. 2004; Lohrer et al. 2005; Gilbert et al. 2007) can also contribute significantly to bioturbation in some environments. Another factor worth considering is biomass which can also have great

influence over certain ecosystem functions, such as bioturbation (Clough et al. 1997) and oxygen penetration (Norkko et al. 2013). In summary, our study demonstrates significant predictive relationships between polychaete biodiversity and ecosystem function proxies in deep soft-sediment habitats, however, feeding guild classifications are better predictors of ecosystem function than species level taxonomy.

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CHAPTER IV

SUMMARY

Benthic sediments cover more of Earth's surface than all other habitats combined (Snelgrove 1998). They house a plethora of marine life, from micro-organisms to large mega-fauna, any number of which are useful tools for monitoring conditions of ecosystems (Barros et al. 2008). It is imperative that we continue to research these environments in which our understanding is limited, especially as increasing anthropogenic pressures change these ecosystems faster than we can understand them (Glover and Smith 2003; Loreau 2007). The intent of this study was to describe faunal spatial patterns and relationships with abiotic factors as well as key ecosystem functions within benthic soft-sediments of the Gulf of Maine. Our study also explored the importance of taxonomic resolution and examined faunal impacts at different scales.

Chapter 2 focused on spatial patterns, uncovering regional faunal variations and local abiotic variations. This research from the Gulf of Maine addressed four objectives and demonstrated: 1) significant spatial variation in faunal composition and polychaete biodiversity across regional, local and vertical spatial scales; 2) spatial variation at different levels of taxonomic resolution for polychaete biodiversity; 3) significant spatial variation in environmental factors across regional, local and vertical spatial scales; and 4) environmental variables are significant, but weak, predictors of faunal variation irrespective of taxonomic level (species, family, and feeding guild).

Specifically, we detected lower abundances and polychaete richness in Georges Basin than in the other basins, and only polychaete species evenness and family biodiversity measures (i.e. diversity and evenness) varied at local scales. Comparison of vertical distribution patterns showed higher abundances and biodiversity within surface sediments. Overall, sample differences increased as taxonomic detail increased, punctuating the potential sacrifices of using taxonomic aggregations to determine ecological differences in benthic ecosystems. Across regional scales, only bottom depth different significantly across basins, but within each basin, all abiotic measures varied locally. Furthermore, correlative analyses exposed weak links between fauna and some environmental parameters (i.e., water depth and organic matter), ultimately suggesting the factors measured within our study were not sole drivers of faunal patterns. Overall, this

research demonstrates how examining various spatial and taxonomic scales, as well as environmental variables, can influence and increase our understanding of benthic macrofaunal communities.

Chapter 3 investigated biodiversity-ecosystem function relationships within deep soft-sediments across basins within the Gulf of Maine. Our measurements of sediments from the Gulf of Maine addressed three objectives and demonstrated: 1) significant spatial variation in ecosystem function proxies (i.e. sediment oxygenation and secondary production) across regional and local spatial scales;, 2) significant biodiversity-ecosystem function relationships; and 3) polychaete biotic measures (abundance and biodiversity) were significant predictors of ecosystem functions, irrespective of measure (abundance, diversity, richness, and evenness) or taxonomic level (species, family, and feeding guild).

Specifically, oxygen penetration varied regionally across the Gulf of Maine, with the shallowest penetration in Jordan Basin. The only variable showing significant local-scale variation was secondary production, which also differed significantly between sediment layers, with higher prokaryote abundances in surface sediments. We also confirmed significant predictive relationships between polychaete biodiversity and ecosystem function proxies within basin soft sediments. Specifically, all measures of polychaete biodiversity, as well as abundance, positively predicted secondary production. Biodiversity measures grouped by feeding guild predicted more ecosystem functions than species or family taxonomic levels demonstrating that groupings based on activity and behaviour of infaunal animals better predicts ecosystem functions than species level taxonomy within soft sediments.

Understanding benthic communities requires examining species distributions and biodiversity patterns at varying spatial and temporal scales. Exploring drivers of spatial patterns is a helpful step to understanding how benthic communities interlink with function. Noting that variation at one level can mask variation at another level (i.e. pseudoreplication) careful consideration must be used when conducting spatial analyses. Factors other than those we investigated might have influenced both faunal and abiotic spatial patterns. For example, larval settlement or biological interactions can greatly influence faunal spatial patterns, whereas seasonal fluxes could explain local scale

variations in abiotic variables; we did not test these effects. Other studies, such as Weissberger et al. (2008), detected local-scale variations in a soft-sediment basin within the Gulf of Maine similar to those within our study. Their study reported seasonal changes, reflecting spring and fall phytoplankton blooms, leading to local-scale variations in abiotic measures (Weissberger et al. 2008). Our study also focused primarily on polychaetes, due to time and financial constraints, however, future research could expand on our results by examining a broader range of faunal groups.

Ultimately, this study examined faunal patterns and potential drivers of pattern and function at various spatial and taxonomic scales. We also explored faunal links to ecosystem functions within benthic soft-sediment habitats. These functions, which help to maintain stable and healthy environments, sustain life and support goods and services essential to humanity (e.g. food, recreation and tourism opportunities, waste disposal, and dilution of pollutants; de Groot et al. 2002). As anthropogenic impacts increasingly alter benthic environments so does the urgency in exploring and determining links between fauna and their environments. This type of knowledge can also contribute to compiling a more complete species inventory and investigating the balance between marine conservation and sustainable utilization of marine resources in focal study areas such as the Discovery Corridor.

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APPENDIX A - Maps and summary tables of biotic and abiotic measurements

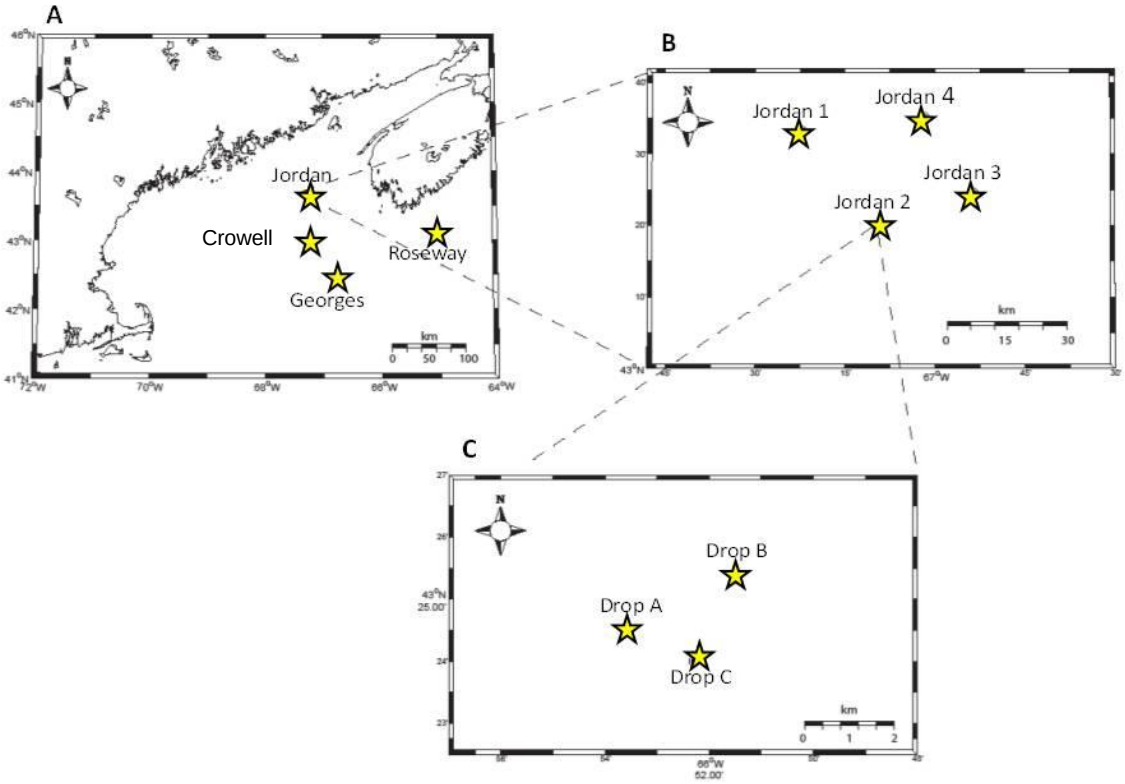

Figure A1. Charts showing scales of benthic sampling: **A)** Basins within the Gulf of Maine (100's of kms) showing regional spatial scale. **B)** Sites within each Basin (10's of kms) showing local spatial scale. **C)** Triplicate multicore drops within each site (kms between drops).

Table A1. Summary of mean abundances and standard error for total macrofauna and for each phylum collected from four sedimentary basins. Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

Biotic Variable	Sediment Depth (cm)	Crowell (n = 6)		Georges (n = 12)		Jordan (n = 12)		Roseway (n = 9)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Total Macrofauna	0 - 2	109.2	14.3	73.6	7.9	110.9	8.1	150.0	11.6
	2 - 5	29.7	6.5	14.8	3.4	35.0	6.1	41.0	3.8
	5 - 10	7.7	2.2	5.8	2.0	9.2	2.5	14.9	1.3
Annelida	0 - 2	77.7	10.5	41.0	4.5	72.8	5.3	73.9	10.6
	2 - 5	29.0	6.5	9.8	2.0	34.0	6.1	37.4	3.3
	5 - 10	5.8	2.5	5.0	1.8	8.8	2.3	13.7	1.3
Mollusca	0 - 2	12.8	2.1	11.3	1.9	21.0	1.9	64.4	3.4
	2 - 5	0.2	0.2	1.7	1.1	0.3	0.2	2.7	1.0
	5 - 10	0.7	0.5	0.1	0.1	0.2	0.1	0.8	0.6
Arthropoda	0 - 2	15.5	3.9	13.9	2.6	14.2	3.3	11.2	1.6
	2 - 5	0.3	0.2	2.3	1.9	0.3	0.1	0.9	0.2
	5 - 10	1.2	0.6	0.4	0.2	0.2	0.2	0.4	0.3
Echinodermata	0 - 2	3.2	1.2	7.4	1.7	3.0	0.8	0.4	0.3
	2 - 5	0.2	0.2	1.1	0.5	0.4	0.2	0.0	0.0
	5 - 10	0.0	0.0	0.3	0.2	0.0	0.0	0.0	0.0

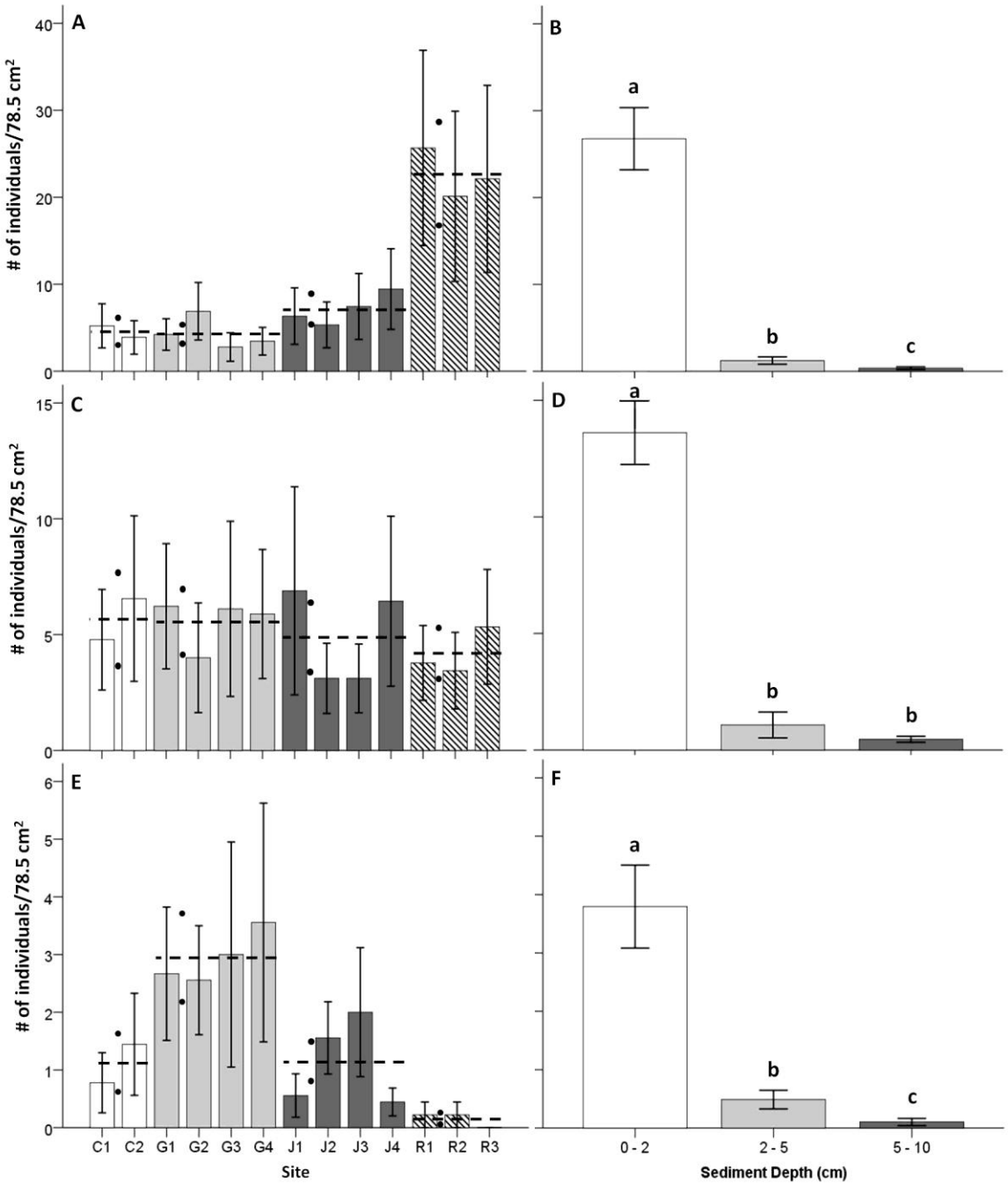

Figure A2. Abundance comparisons of Mollusca (A, B), Arthropoda (C, D), and Echinodermata (E, F) across local and regional spatial scales (i.e. Site and Basin respectively; left panels; n = 3 for each bar) and across sediment depth layers (right panels; n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences.

Table A2. Summary of means and standard error for environmental variables collected from four sedimentary basins. Basin n = 4, Site n = 2-4, Sediment Depth n = 1-3, Core replicate n = 39.

Environmental Variable	Sediment Depth (cm)	Crowell (n = 6)		Georges (n = 12)		Jordan (n = 12)		Roseway (n = 9)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Mud content (%)	0 - 1	82.27	2.58	67.99	2.78	66.91	7.51	87.60	2.76
	2 - 3	79.30	5.26	80.31	3.23	76.23	4.33	87.04	2.62
Organic matter (C:N (mg/g))	0 - 2	9.47	0.31	11.23	1.09	8.66	0.20	9.23	0.30
	2 - 5	11.09	1.26	10.21	0.65	8.86	0.35	9.58	0.55
	5 - 10	10.45	0.30	10.98	0.91	9.50	0.42	10.50	0.75
Carbon concentration (mg/g)	0 - 2	7.92	0.32	5.63	0.61	7.39	1.34	12.74	1.24
	2 - 5	8.03	0.41	6.24	0.67	7.90	1.20	12.55	1.37
	5 - 10	8.41	0.70	6.79	0.77	7.89	1.30	11.98	1.30
Nitrogen concentration (mg/g)	0 - 2	0.84	0.02	0.57	0.09	0.86	0.16	1.41	0.16
	2 - 5	0.77	0.11	0.64	0.08	0.88	0.13	1.38	0.19
	5 - 10	0.80	0.06	0.67	0.10	0.84	0.14	1.22	0.17
Chlorophyll-a concentration (µg/g)	0 - 2	2.01	0.29	1.51	0.15	2.24	0.39	3.26	0.71
	2 - 5	1.57	0.19	1.26	0.07	2.30	0.31	2.17	0.34
	5 - 10	1.49	0.19	1.23	0.09	2.78	0.80	1.81	0.21
Bottom depth (m)	n/a	292.50	49.36	348.00	4.95	225.58	4.12	173.22	1.93

Table A3. Summary of mean abundances and standard error for ecosystem function proxy variables collected from each sedimentary basin. EF denotes ecosystem function: SB denotes shallow bioturbation (subsurface:surface chl-a (µg/g)), DB denotes deep bioturbation (deep:surface chl-a (µg/g)), SO denotes sediment oxygenation (cm), and SP denotes secondary production (cells/g). Basin n = 4, Site n = 2-4, Sediment Depth n = 1-3, Core replicate n = 39 (except for SB n = 38).

	Sediment	Crowell (n = 6)		Georges (n = 12)		Jordan (n = 12)		Roseway (n = 9)	
EF	Depth (cm)	Mean	SE	Mean	SE	Mean	SE	Mean	SE
SB	2 - 5 : 0 – 2	0.81	0.09	0.89	0.07	*0.96	*0.08	0.74	0.12
DB	5 - 10 : 0 – 2	0.84	0.22	0.89	0.09	1.21	0.17	0.66	0.10
SO	0 - 3.5	1.94	0.09	1.53	0.09	1.34	0.07	1.78	0.07
SP	0 – 2	9.90E+08	7.67E+03	6.64E+08	3.98E+03	8.32E+08	4.70E+03	1.47E+09	6.39E+03
	2 – 5	4.46E+08	3.61E+03	4.16E+08	4.15E+03	7.33E+08	5.20E+03	9.88E+08	3.89E+03
	5 – 10	4.59E+08	4.89E+03	3.59E+08	4.81E+03	6.26E+08	5.44E+03	7.37E+08	3.70E+03

Table A4. Summary of two-way ANOVAs (generalized linear model) showing the effect of whole core polychaete biotic measures (abundance and species diversity) and Basin on ecosystem functions (EF). Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4.

		Abundance (N)			**Diversity (H')**			**Richness (d)**			**Evenness (J')**		
EF	**Source of Variation**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**
SB	Biotic Measure x Basin	1.9	3	0.591	2.2	3	0.522	2.2	3	0.522	0.7	3	0.863
	Biotic Measure	2.0	1	0.162	**5.2**	**1**	**0.023**	**5.2**	**1**	**0.023**	0.2	1	0.678
	Basin	2.9	3	0.405	2.3	3	0.519	2.3	3	0.519	0.7	3	0.876
DB	Biotic Measure x Basin	4.8	3	0.189	4.1	3	0.251	1.0	3	0.806	6.9	3	0.076
	Biotic Measure	3.1	1	0.078	3.1	1	0.079	**4.9**	**1**	**0.027**	0.0	1	0.891
	Basin	4.3	3	0.231	5.6	3	0.130	3.0	3	0.392	7.5	3	0.059
SO	Biotic Measure x Basin	5.9	3	0.116	2.0	3	0.581	1.7	3	0.627	1.9	3	0.594
	Biotic Measure	0.2	1	0.622	0.1	1	0.789	0.0	1	0.890	0.1	1	0.804
	Basin	**9.6**	**3**	**0.023**	2.0	3	0.573	2.2	3	0.527	1.7	3	0.636

APPENDIX B - Results of polychaete family spatial analyses

Table B1. Summary of three-way ANOVAs (fourth root plus non[1] and rank[2] transformed data) showing the effect of Basin, Site (nested within Basin) and Sediment Depth on polychaete family biodiversity measures. Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

Biodiversity Measurement	Source of Variation		df	Mean Square	F	Sig.
Diversity[2]	Basin	Hypothesis	3	3241.466	2.601	0.149
		Error	6	1246.051		
	Site(Basin)	Hypothesis	9	425.209	1.149	0.381
		Error	18	369.999		
	Sediment Depth	Hypothesis	2	42033.706	35.649	< **0.01**
		Error	6	1179.096		
	Basin x Sediment Depth	Hypothesis	6	1190.841	3.218	**0.025**
		Error	18	369.999		
	Site(Basin) x Sediment Depth	Hypothesis	18	369.999	1.466	0.126
		Error	78	252.331		
Richness[1]	Basin	Hypothesis	3	1.762	2.466	0.185
		Error	5	0.715		
	Site(Basin)	Hypothesis	9	0.458	1.091	0.415
		Error	18	0.420		
	Sediment Depth	Hypothesis	2	33.109	49.080	< **0.01**
		Error	6	0.675		
	Basin x Sediment Depth	Hypothesis	6	0.677	1.602	0.204
		Error	18	0.422		
	Site(Basin) x Sediment Depth	Hypothesis	18	0.421	1.531	0.103
		Error	74	0.275		
Evenness[1]	Basin	Hypothesis	3	0.012	1.514	0.384
		Error	3	0.008		
	Site(Basin)	Hypothesis	9	0.012	1.518	0.214
		Error	18	0.008		
	Sediment Depth	Hypothesis	2	0.021	5.860	**0.036**
		Error	6	0.004		

Table B1. cont.

Biodiversity Measurement	Source of Variation		df	Mean Square	F	Sig.
Evenness[1]	Basin x Sediment Depth	Hypothesis	6	0.004	0.439	0.843
		Error	18	0.008		
	Site(Basin) x Sediment Depth	Hypothesis	18	0.008	1.856	**0.034**
		Error	72	0.004		

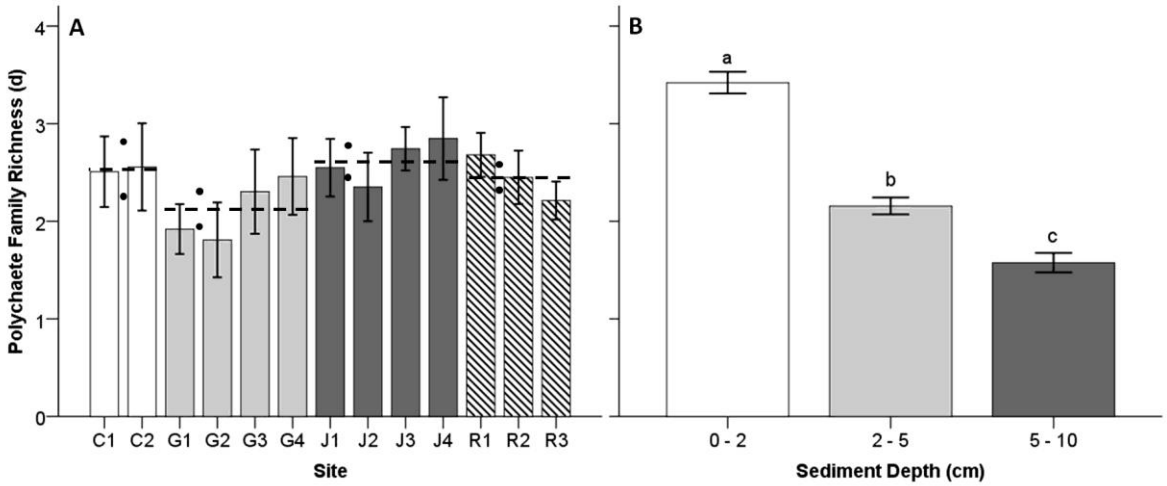

Figure B1. Spatial patterns of polychaete species richness across local and regional spatial scales (i.e. Site and Basin respectively; left panel (A); n = 3 for each bar) and across sediment depth layers (right panel (B); n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences.

Table B2. Summary of three-way ANOVAs (fourth root plus non[1] and rank[2] transformed data) showing the effect of Basin, Site (nested within Basin) on polychaete family biodiversity measures separated by Sediment Depth. Basin n = 4, Site n = 2-4, Core replicate n = 39.

Biodiversity Measure	Sediment Depth (cm)	Source of Variation		df	Mean Square	F	Sig.
Diversity[2]	**0 - 2**	Basin	Hypothesis	3	1115.806	2.079	0.173
			Error	9	536.617		
		Site(Basin)	Hypothesis	9	536.617	2.694	**0.023**
			Error	26	199.154		
	2 - 5	**Basin**	Hypothesis	3	3503.058	10.465	**0.003**
			Error	9	334.728		
		Site(Basin)	Hypothesis	9	334.728	1.332	0.269
			Error	26	251.372		
	5 - 10	Basin	Hypothesis	3	1004.284	3.418	0.066
			Error	9	293.861		
		Site(Basin)	Hypothesis	9	293.861	0.959	0.494
			Error	26	306.468		
Evenness[1]	**0 - 2**	Basin	Hypothesis	3	0.007	0.631	0.613
			Error	9	0.010		
		Site(Basin)	Hypothesis	9	0.010	7.029	< **0.01**
			Error	26	0.001		
	2 - 5	Basin	Hypothesis	3	0.003	0.661	0.597
			Error	9	0.005		
		Site(Basin)	Hypothesis	9	0.005	1.991	0.082
			Error	26	0.002		
	5 - 10	Basin	Hypothesis	3	0.008	0.662	0.595
			Error	9	0.013		
		Site(Basin)	Hypothesis	9	0.013	1.201	0.347
			Error	20	0.011		

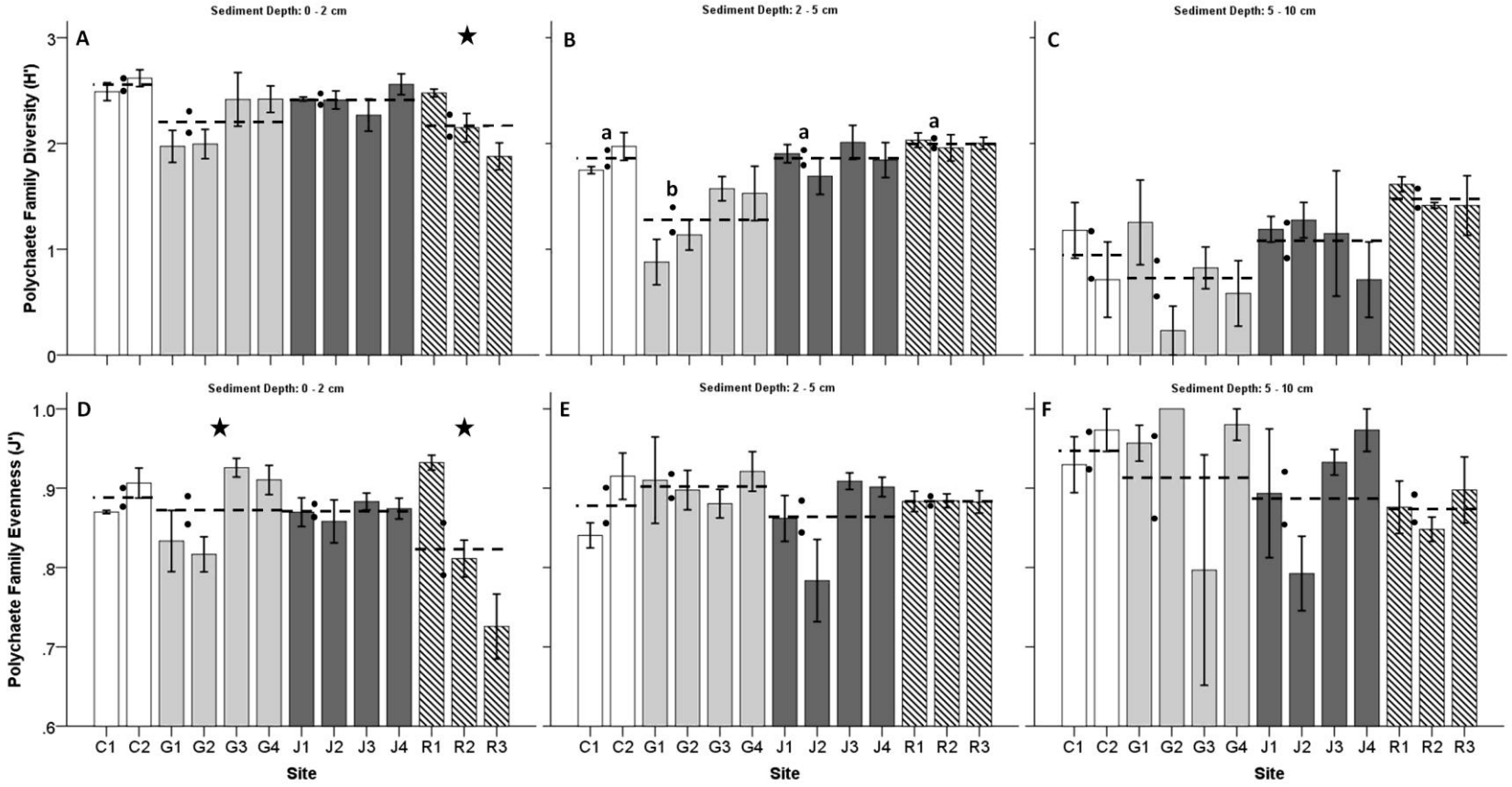

Figure B2. Spatial patterns of polychaete family diversity (A, B, C) and evenness (D, E, F) across local and regional spatial scales (i.e. Site and Basin; n = 3 for each bar) at surface (A and D; 0 – 2 cm), subsurface (B and E; 2 – 5 cm), and deep (C and F; 5 – 10 cm) sediment depth layers. Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences. Star indicates significant differences among sites within a basin.

APPENDIX C - Results of polychaete feeding guild spatial analyses

Table C1. Summary of three-way ANOVAs (fourth root plus non[1] and rank[2] transformed data) showing the effect of Basin, Site (nested within Basin) and Sediment Depth on polychaete feeding guild biodiversity measures. Basin n = 4, Site n = 2-4, Sediment Depth n = 3, Core replicate n = 39.

Biodiversity Measurement	Source of Variation		df	Mean Square	F	Sig.
Diversity[2]	Basin	Hypothesis	3	3186.843	3.698	0.079
		Error	6	861.754		
	Site(Basin)	Hypothesis	9	684.299	1.645	0.176
		Error	18	416.065		
	Sediment Depth	Hypothesis	2	33730.560	57.076	**< 0.01**
		Error	6	590.980		
	Basin x Sediment Depth	Hypothesis	6	593.519	1.427	0.259
		Error	18	416.065		
	Site(Basin) x Sediment Depth	Hypothesis	18	416.065	0.876	0.608
		Error	78	474.882		
Richness[1]	Basin	Hypothesis	3	0.168	0.853	0.507
		Error	7	0.197		
	Site(Basin)	Hypothesis	9	0.177	2.289	0.063
		Error	18	0.077		
	Sediment Depth	Hypothesis	2	1.550	16.269	**0.004**
		Error	6	0.095		
	Basin x Sediment Depth	Hypothesis	6	0.095	1.255	0.328
		Error	17	0.076		
	Site(Basin) x Sediment Depth	Hypothesis	18	0.077	0.454	0.969
		Error	74	0.170		
Evenness[1]	Basin	Hypothesis	3	0.075	1.942	0.206
		Error	8	0.038		
	Site(Basin)	Hypothesis	9	0.020	1.807	0.135
		Error	18	0.011		
	Sediment Depth	Hypothesis	2	0.177	6.051	**0.036**
		Error	6	0.029		

Table C1. cont.

Biodiversity Measurement	Source of Variation		df	Mean Square	F	Sig.
Evenness[1]	Basin x Sediment Depth	Hypothesis	6	0.029	2.606	0.053
		Error	18	0.011		
	Site(Basin) x Sediment Depth	Hypothesis	18	0.011	0.987	0.484
		Error	72	0.011		

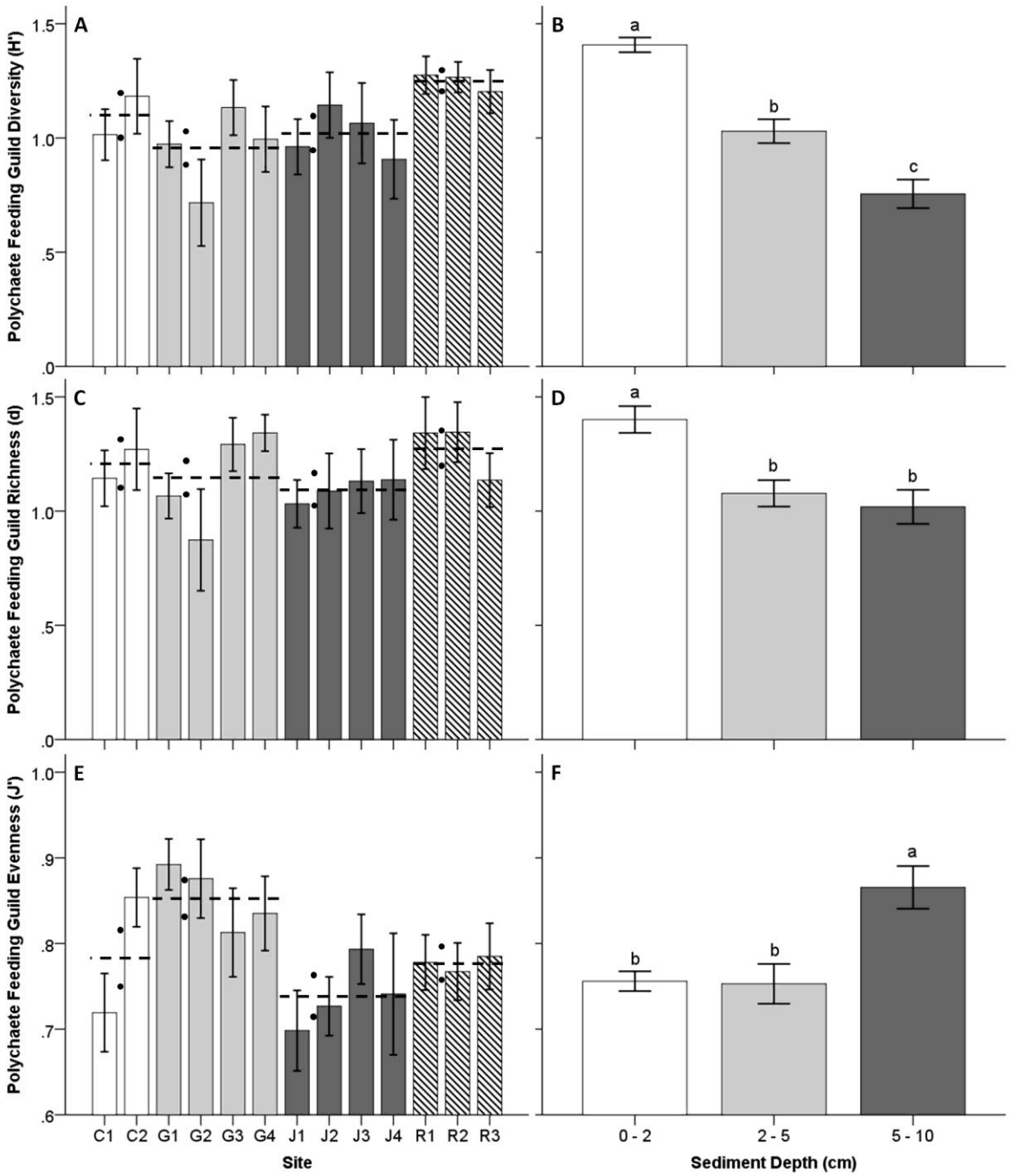

Figure C1. Spatial patterns of polychaete feeding guild diversity (A, B), richness (C, D), and evenness (E, F) across local and regional spatial scales (i.e. Site and Basin respectively; left panels; n = 3 for each bar) and across sediment depth layers (right panels; n = 39 for each bar). Error bars show ± 1 SE. Dashed lines indicate basin averages with dots showing ± 1 SE. Lower case letters indicate significant differences.

APPENDIX D - Results from PRIMER faunal analyses

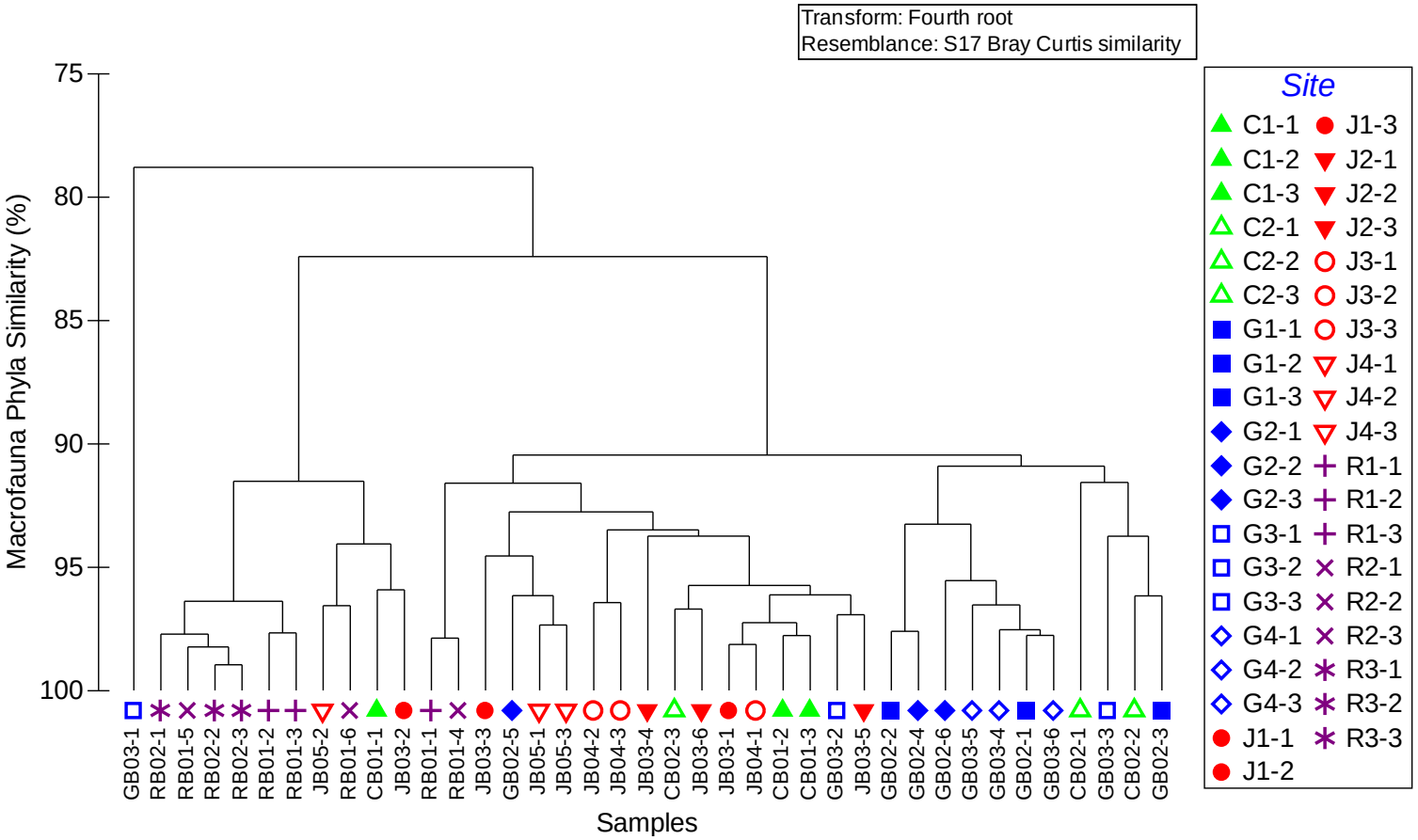

Figure D1. Cluster plot showing similarity of **macrofauna phyla** among whole core samples across basins (colour and letter coded: Green & C = Crowell; Blue & G = Georges; Red & J = Jordan; Purple & R = Roseway), local areas within basins (symbol and number coded: 1 to 4 local areas in each basin), and sites within local areas within basins (number coded: three sites in each local area). Basin n = 4, Local Area n = 2-4, Site n = 3, Core replicate n = 39.

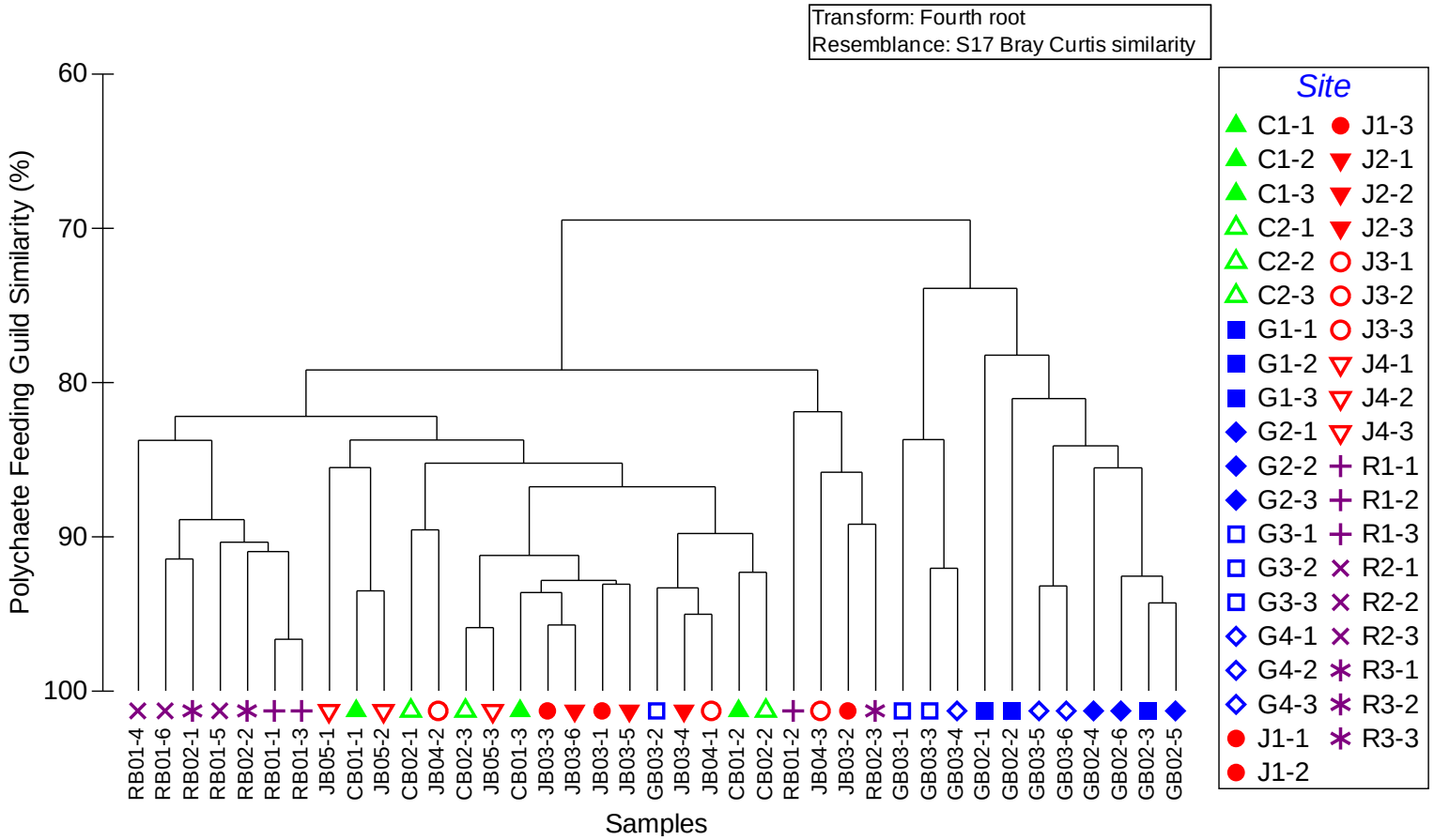

Figure D2. Cluster plot showing similarity of **polychaete feeding guilds** among whole core samples across basins (colour and letter coded: Green & C = Crowell; Blue & G = Georges; Red & J = Jordan; Purple & R = Roseway), local areas within basins (symbol and number coded: 1 to 4 local areas in each basin), and sites within local areas within basins (number coded: three sites in each local area). Basin n = 4, Local Area n = 2-4, Site n = 3, Core replicate n = 39.

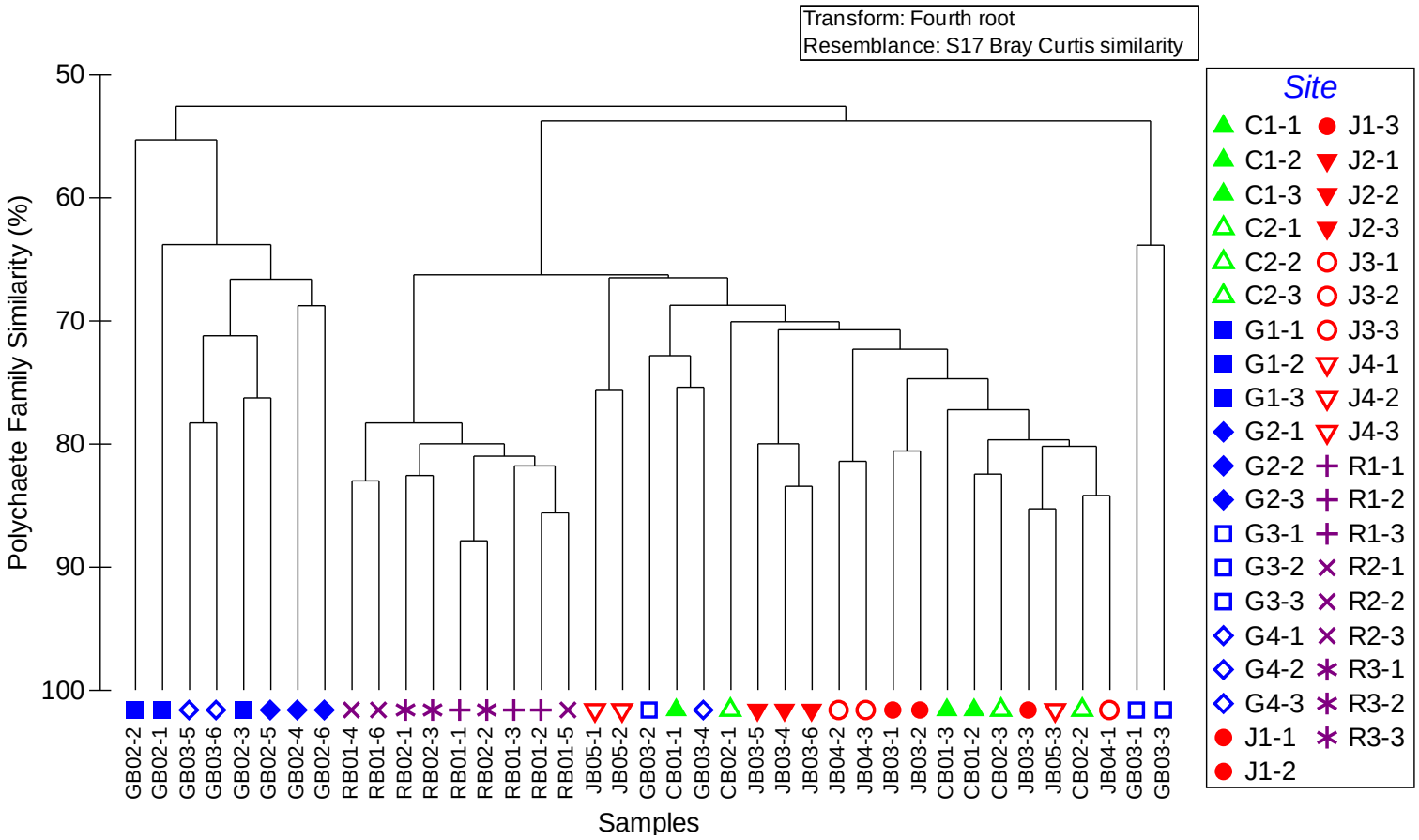

Figure D3. Cluster plot showing similarity of **polychaete families** among whole core samples across basins (colour and letter coded: Green & C = Crowell; Blue & G = Georges; Red & J = Jordan; Purple & R = Roseway), local areas within basins (symbol and number coded: 1 to 4 local areas in each basin), and sites within local areas within basins (number coded: three sites in each local area). Basin n = 4, Local Area n = 2-4, Site n = 3, Core replicate n = 39.

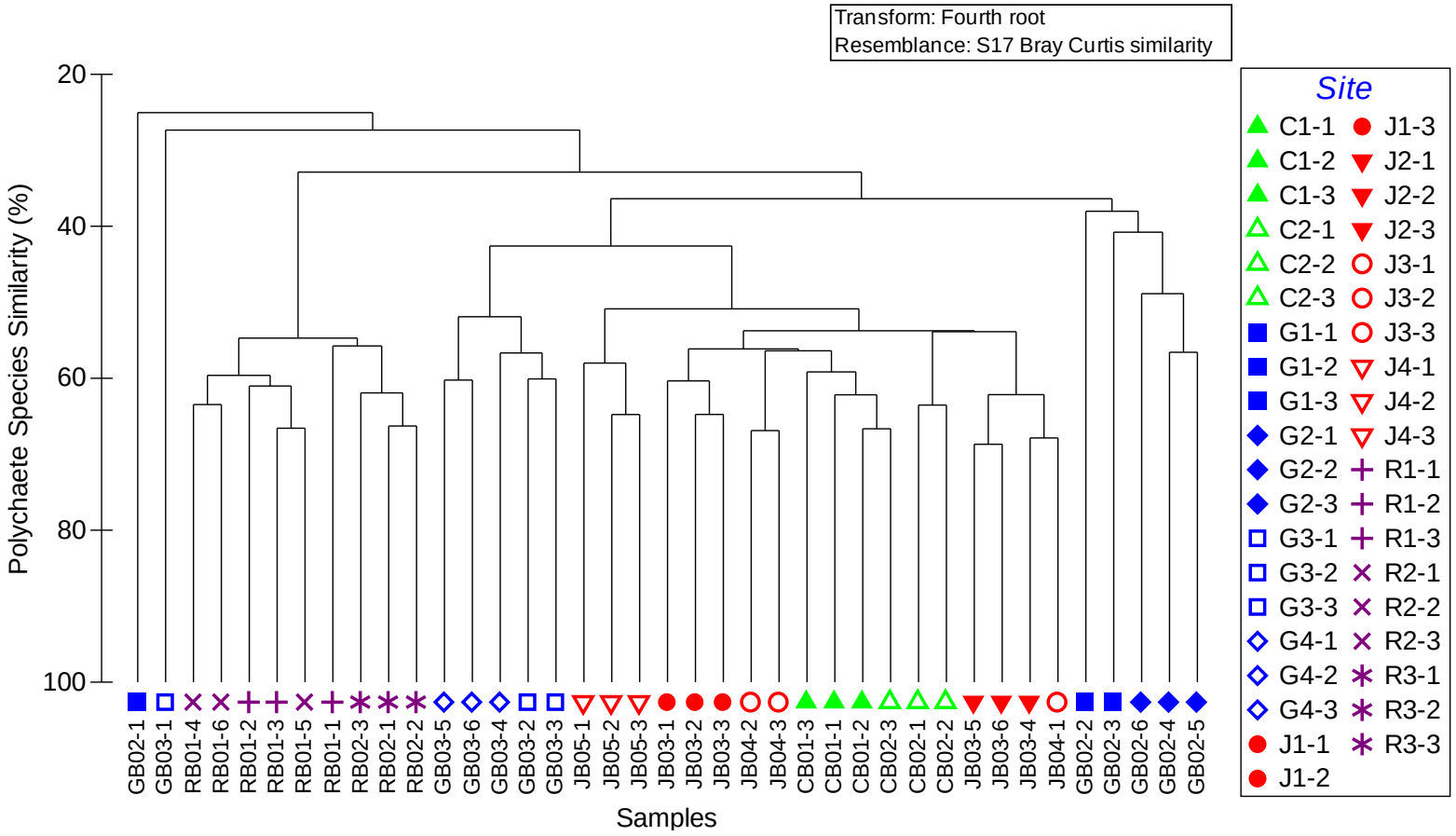

Figure D4. Cluster plot showing similarity of **polychaete species** among whole core samples across basins (colour and letter coded: Green & C = Crowell; Blue & G = Georges; Red & J = Jordan; Purple & R = Roseway), local areas within basins (symbol and number coded: 1 to 4 local areas in each basin), and sites within local areas within basins (number coded: three sites in each local area). Basin n = 4, Local Area n = 2-4, Site n = 3, Core replicate n = 39.

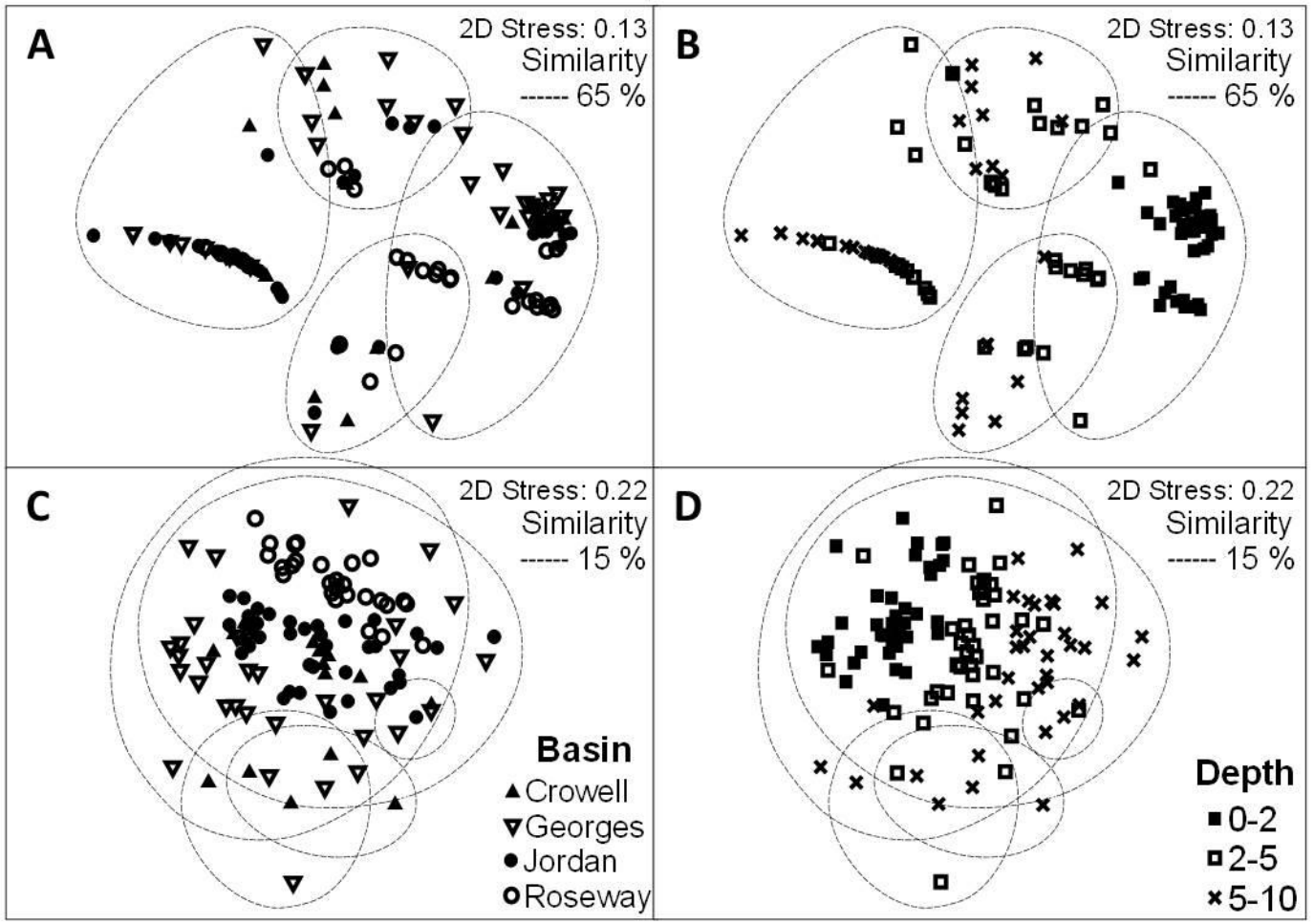

Figure D5. MDS ordination showing faunal similarity across basins (left panels) and sediment depths (right panels) for total macrofauna (A, B) and polychaete species (C, D). Basin n = 4, Sediment Depth n = 3, Core replicate n = 39.

Table D1. Analysis of biotic similarities from samples within each basin and sediment depth layer showing drivers contributing to sample similarities. Basin n = 4, Sediment Depth n = 3, Core replicate n = 39.

Basin/Sediment Depth Variable	Biotic Variable	Total Similarity	Drivers of Similarity	Similarity Contribution (%)
Crowell	Macrofaunal phyla	76.2	Annelida	70.1
			Arthropoda	14.7
	Polychaete feeding guild	59.8	SR-De	34.7
			SS-De	24.9
	Polychaete family	49.3	Capitellidae	16.3
			Cirratulidae	12.8
	Polychaete species	35.3	Capitellidae spp. B	12.5
			Cossura longocirrata	10.0
			Tharyx sp. B	8.6
Georges	Macrofaunal phyla	66.6	Annelida	60.6
			Arthropoda	16.3
			Mollusca	11.8
	Polychaete feeding guild	50.8	SR-De	43.5
			SS-De	19.1
	Polychaete family	33.4	Paraonidae	18.3
			Spionidae	12.7
	Polychaete species	20.0	*Prionospio* sp. A	18.3
			Paramphinome jeffreysii	7.4

Table D1. cont.

Basin/Sediment Depth Variable	Biotic Variable	Total Similarity	Drivers of Similarity	Similarity Contribution (%)
Jordan	Macrofaunal phyla	76.3	Annelida	73.0
			Mollusca	11.5
	Polychaete feeding guild	67.0	SR-De	38.3
			SS-De	28.9
	Polychaete family	54.7	Cossuridae	16.6
			Capitellidae	15.7
	Polychaete species	38.1	*Cossura longocirrata*	19.4
			Capitellidae spp. A	8.3
Roseway	Macrofaunal phyla	83.9	Annelida	64.6
			Mollusca	20.7
	Polychaete feeding guild	75.1	SR-De	34.0
			SS-De	23.8
	Polychaete family	65.7	Cossuridae	18.5
			Capitellidae	13.2
	Polychaete species	48.8	*Cossura longocirrata*	20.7
			Capitellidae spp. A	13.7
0-2	Macrofaunal phyla	90.9	Annelida	37.1
			Mollusca	28.3
			Arthropoda	23.6
	Polychaete feeding guild	78.1	SR-De	27.5

Table D1. cont.

Basin/Sediment Depth Variable	Biotic Variable	Total Similarity	Drivers of Similarity	Similarity Contribution (%)
0-2	Polychaete feeding guild	78.1	SS-De	17.5
			SS-Pr-mac	14.4
	Polychaete family	63.8	Spionidae	10.8
			Cirratulidae	8.7
			Sabellidae	7.9
	Polychaete species	44.4	*Prionospio* sp. A	11.0
			Sabellidae spp. A	5.8
			Meiodorvillea minuta	5.5
			Pseudoscalibregma parvum	5.2
2-5	Macrofaunal phyla	71.9	Annelida	82.0
	Polychaete feeding guild	65.1	SR-De	46.3
			SS-De	25.3
	Polychaete family	50.0	Paraonidae	20.0
			Cirratulidae	16.3
	Polychaete species	33.4	*Cossura longocirrata*	15.3
			Capitellidae spp. A	8.5
			Levinsenia sp. A	8.4
5-10	Macrofaunal phyla	60.2	Annelida	93.7
	Polychaete feeding guild	43.4	SR-De	46.8
			SS-De	35.8

Table D1. cont.

Basin/Sediment Depth Variable	Biotic Variable	Total Similarity	Drivers of Similarity	Similarity Contribution (%)
5-10	Polychaete family	32.4	Capitellidae	33.1
	Polychaete species	22.6	*Cossura longocirrata*	37.5

Table D2. Analysis of biotic dissimilarities between basins and sediment depth layers showing drivers contributing to sample dissimilarities. R statistic and significance values tested with analysis of similarity (ANOSIM). Sample statistic tested against Global R statistic with 999 permutations; Basin n = 4, Sediment Depth n = 3, Core replicate n = 39. Significance (bolded values) indicates which sample comparisons are significantly different (i.e. sample statistic deviates significantly from the Global R statistic).

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
Crowell & Georges	Macrofaunal phyla	30.5	Annelida	30.5	0.027	0.327
			Arthropoda	29.1		
			Mollusca	20.6		
	Polychaete feeding guild	47.9	SS-De	17.8	0.048	0.226
			SR-De	16.9		
			SR-He-mic	12.6		
			SS-Pr-mac	12.5		
			SS-Pr-mei	12.0		
			SR-Pr-mei	9.8		
	Polychaete family	62.6	Capitellidae	11.4	-0.014	0.529
			Cossuridae	9.8		
			Paraonidae	8.8		
	Polychaete species	78.5	Capitellidae spp. B	7.7	0.030	0.308
			Cossura longocirrata	6.4		
			Paramphinome jeffreysii	4.0		
			Capitellidae spp. A	3.9		
			Tharyx sp. B	3.6		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
Crowell & Jordan	Macrofaunal phyla	23.7	Arthropoda	33.6	0.018	0.334
			Annelida	28.8		
			Mollusca	23.8		
	Polychaete feeding guild	36.4	SS-De	17.3	0.038	0.252
			SR-De	16.8		
			SR-He-mic	14.3		
			SS-Pr-mac	12.1		
			SS-Pr-mei	11.0		
			EP-Su	10.6		
	Polychaete family	49.3	Capitellidae	10.0	0.058	0.186
			Cossuridae	9.8		
			Paraonidae	7.9		
	Polychaete species	65.3	Capitellidae spp. B	6.3	0.079	0.132
			Cossura longocirrata	6.1		
			Capitellidae spp. A	5.8		
			Levinsenia sp. A	3.5		
			Aricidea nolani	3.0		
			Tharyx sp. B	2.9		
Georges & Jordan	Macrofaunal phyla	31.1	Annelida	40.9	0.422	< **0.01**
			Arthropoda	21.8		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
Georges	Macrofaunal phyla	31.1	Echinodermata	21.1	0.422	< **0.01**
& Jordan	Polychaete feeding guild	48.5	SS-De	20.5	0.328	< **0.01**
			SR-De	18.8		
			SS-Pr-mac	13.6		
			SS-Pr-mei	11.1		
			EP-Su	10.7		
			SS-Om-mic	8.5		
	Polychaete family	64.7	Cossuridae	11.3	0.510	< **0.01**
			Capitellidae	10.7		
			Cirratulidae	7.7		
	Polychaete species	79.1	*Cossura longocirrata*	7.9	0.768	< **0.01**
			Capitellidae spp. A	6.0		
			Capitellidae spp. B	4.6		
			Levinsenia sp. A	4.4		
			Paramphinome jeffreysii	3.9		
			Tharyx sp. B	3.6		
Crowell	Macrofaunal phyla	25.1	Mollusca	38.2	0.161	< **0.01**
& Roseway			Arthropoda	29.8		
			Annelida	20.7		
	Polychaete feeding guild	36.6	SS-Pr-mei	17.2	0.268	< **0.01**

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
Crowell & Roseway	Polychaete feeding guild	36.6	SR-De	13.3	0.268	< **0.01**
			SS-De	13.1		
			SR-He-mic	12.5		
			SS-Pr-mac	11.4		
			EP-Su	11.2		
			SS-Om-mic	9.9		
	Polychaete family	49.3	Cossuridae	9.2	0.324	< **0.01**
			Lumbrineridae	8.6		
			Capitellidae	7.9		
			Paraonidae	7.1		
	Polychaete species	75.5	Capitellidae spp. A	5.6	0.331	< **0.01**
			Cossura longocirrata	5.1		
			Capitellidae spp. B	4.1		
			Lumbrineris sp. C	4.0		
			Levinsenia sp. A	3.4		
			Euchone sp. A	3.1		
			Chaetozone anasimus	3.0		
Georges & Roseway	Macrofaunal phyla	33.5	Annelida	33.4	0.362	< **0.01**
			Mollusca	26.6		
			Echinodermata	20.3		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
Georges & Roseway	Polychaete feeding guild	51.6	SS-De	15.7	0.400	< **0.01**
			SR-De	14.9		
			SS-Pr-mei	14.2		
			EP-Su	13.1		
			SS-Pr-mac	11.7		
			SR-He-mic	9.9		
			SS-Om-mic	9.1		
	Polychaete family	66.5	Cossuridae	12.0	0.382	< **0.01**
			Capitellidae	8.8		
			Lumbrineridae	7.6		
	Polychaete species	83.6	*Cossura longocirrata*	8.2	0.425	< **0.01**
			Capitellidae spp. A	6.2		
			Lumbrineris sp. C	4.7		
			Levinsenia sp. A	4.1		
			Chaetozone anasimus	3.7		
Jordan & Roseway	Macrofaunal phyla	24.9	Mollusca	34.1	0.322	< **0.01**
			Annelida	27.9		
			Arthropoda	24.4		
	Polychaete feeding guild	33.6	SS-Pr-mei	18.2	0.218	< **0.01**
			EP-Su	13.4		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
Jordan & Roseway	Polychaete feeding guild	33.6	SR-He-mic	13.0	0.218	< **0.01**
			SS-De	12.7		
			SR-De	11.5		
			SS-Pr-mac	10.9		
			SS-Om-mic	9.8		
	Polychaete family	45.2	Lumbrineridae	8.8	0.237	< **0.01**
			Capitellidae	7.1		
			Maldanidae	7.0		
			Cossuridae	6.8		
	Polychaete species	69.3	Capitellidae spp. A	4.5	0.547	< **0.01**
			Lumbrineris sp. C	4.2		
			Cossura longocirrata	3.7		
			Euchone sp. A	3.4		
			Levinsenia sp. A	3.3		
			Capitellidae spp. B	3.3		
			Chaetozone anasimus	3.2		
			Monticellina sp. A	3.1		
0-2 & 2-5	Macrofaunal phyla	40.7	Mollusca	37.7	0.740	< **0.01**
			Arthropoda	29.7		
			Echinodermata	18.3		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
0-2 & 2-5	Polychaete feeding guild	39.3	SS-Pr-mac	16.3	0.453	< **0.01**
			SR-He-mic	15.2		
			EP-Su	14.8		
			SS-Om-mic	12.3		
			SS-Pr-mei	10.4		
			SR-De	9.1		
			SS-De	8.6		
	Polychaete family	57.6	Spionidae	6.9	0.609	< **0.01**
			Scalibregmatidae	6.4		
			Ampharetidae	6.0		
			Syllidae	5.9		
			Sabellidae	5.6		
	Polychaete species	74.5	*Prionospio* sp. A	4.4	0.598	< **0.01**
			Pseudoscalibregma parvum	3.4		
			Nereimyra sp. A	3.1		
			Prosphaerosyllis sp. A	2.9		
			Sabellidae spp. A	2.9		
			Meiodorvillea minuta	2.6		
			Ampharete finmarchica	2.5		
			Capitellidae spp. A	2.5		
			Maldanidae spp. A	2.4		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
0-2 & 2-5	Polychaete species	74.5	*Tharyx* sp. B	2.3	0.598	< **0.01**
0-2 & 5-10	Macrofaunal phyla	59.6	Mollusca	33.2	0.779	< **0.01**
			Arthropoda	27.3		
			Annelida	22.6		
	Polychaete feeding guild	60.7	SR-De	16.8	0.569	< **0.01**
			SS-Pr-mac	14.9		
			SS-Om-mic	14.1		
			EP-Su	12.5		
			SR-He-mic	12.2		
			SS-De	10.5		
	Polychaete family	77.3	Spionidae	8.3	0.635	< **0.01**
			Cirratulidae	6.4		
			Scalibregmatidae	6.3		
			Ampharetidae	6.2		
	Polychaete species	87.8	*Prionospio* sp. A	5.5	0.643	< **0.01**
			Pseudoscalibregma parvum	3.6		
			Protodorvillea minuta	3.5		
			Nereimyra sp. A	3.2		
			Ampharete finmarchica	3.1		
			Sabellidae spp. A	3.0		

Table D2. cont.

Pairwise Comparison	Biotic Variable	Total Dissimilarity	Drivers of Dissimilarity	Dissimilarity Contribution (%)	R Statistic	Sig.
0-2 & 5-10	Polychaete species	87.8	*Prosphaerosyllis* sp. A	3.0	0.643	< **0.01**
			Maldanidae spp. A	3.0		
2-5 & 5-10	Macrofaunal phyla	39.1	Annelida	39.4	0.201	< **0.01**
			Arthropoda	24.2		
			Mollusca	20.3		
	Polychaete feeding guild	51.2	SR-De	22.2	0.208	< **0.01**
			SS-De	17.3		
			SS-Pr-mei	14.5		
			SS-Pr-mac	13.7		
			SS-Om-mic	10.9		
			SR-Pr-mei	7.1		
	Polychaete family	65.4	Paraonidae	10.7	0.224	< **0.01**
			Cirratulidae	10.4		
			Capitellidae	8.8		
	Polychaete species	77.9	*Cossura longocirrata*	5.2	0.245	< **0.01**
			Capitellidae spp. A	5.0		
			Levinsenia sp. A	5.0		
			Tharyx sp. B	4.9		
			Capitellidae spp. B	4.3		
			Lumbrineris sp. C	4.2		

APPENDIX E - Taxonomic classification

Table E1. Taxonomic list showing polychaete species (135 including juveniles), families (37) and feeding guilds (11).

Species	Family	Feeding Guild
Aberranta sp. A	Aberrantidae	SR-De
Ampharete finmarchica	Ampharetidae	SR-De
Ampharetidae spp. A	Ampharetidae	SR-De
Ampharetidae spp. B (juvenile)	Ampharetidae	SR-De
Auchenoplax crinita	Ampharetidae	SR-De
Ampharete sp. A	Ampharetidae	SR-De
Amage auricula	Ampharetidae	SR-De
Anobothrus gracilis	Ampharetidae	SR-De
Paramphinome jeffreysii	Amphinomidae	SS-Pr-mac
Aphroditidae spp. A	Aphroditidae	SS-Pr-mac
Apistobranchus sp. A	Apistobranchidae	SR-De
Capitellidae spp. A	Capitellidae	SS-De
Capitellidae spp. B	Capitellidae	SS-De
Capitellidae spp. C	Capitellidae	SS-De
Capitellidae spp. D	Capitellidae	SS-De
Capitellidae spp. E	Capitellidae	SS-De
Capitellidae spp. F	Capitellidae	SS-De
Capitellidae spp. G	Capitellidae	SS-De
Capitellidae spp. H	Capitellidae	SS-De
Capitellidae spp. I	Capitellidae	SS-De
Capitellidae spp. J	Capitellidae	SS-De
Dysponetus pygmaeus	Chrysopetalidae	SR-Pr-mei
Chaetozone anasimus	Cirratulidae	SR-De
Aphelochaeta sp. A	Cirratulidae	SR-De
Tharyx sp. A	Cirratulidae	SR-De
Cirratulidae spp. A	Cirratulidae	SR-De
Tharyx sp. B	Cirratulidae	SR-De
Monticellina sp. A	Cirratulidae	SR-De
Cirratulidae spp. B	Cirratulidae	SR-De
Cossura longocirrata	Cossuridae	SR-De
Dorvilleidae spp. A	Dorvilleidae	SS-Om-mic
Meiodorvillea minuta	Dorvilleidae	SS-Om-mic

Table E1. cont.

Species	Family	Feeding Guild
Protodorvillea sp. A	Dorvilleidae	SS-Om-mic
Dorvilleidae spp. B	Dorvilleidae	SS-Om-mic
Brada villosa	Flabelligeridae	SR-De
Brada inhabilis	Flabelligeridae	SR-De
Diplocirrus longisetosus	Flabelligeridae	SR-De
Glycera sp. A	Glyceridae	SS-Pr-mac
Glycera sp. B	Glyceridae	SS-Pr-mac
Nereimyra sp. A	Hesionidae	SS-Pr-mac
Hesionidae spp. A	Hesionidae	SS-Pr-mac
Lumbrineris sp. A	Lumbrineridae	SS-Pr-mei
Lumbrineris sp. B	Lumbrineridae	SS-Pr-mei
Lumbrineris sp. C	Lumbrineridae	SS-Pr-mei
Lumbrineris sp. D	Lumbrineridae	SS-Pr-mei
Lumbrineris sp. E (juvenile)	Lumbrineridae	SS-Pr-mei
Lumbrineris fragilis	Lumbrineridae	SS-Pr-mei
Lumbrineris sp. F	Lumbrineridae	SS-Pr-mei
Ninoë sp. A	Lumbrineridae	SS-Pr-mei
Maldanidae spp. A	Maldanidae	SS-De
Maldanidae spp. B	Maldanidae	SS-De
Maldanidae spp. C	Maldanidae	SS-De
Maldanidae spp. D	Maldanidae	SS-De
Maldanidae spp. E	Maldanidae	SS-De
Maldanidae spp. F	Maldanidae	SS-De
Maldanidae spp. G	Maldanidae	SS-De
Maldanidae spp. H	Maldanidae	SS-De
Maldanidae spp. I	Maldanidae	SS-De
Maldanidae spp. J	Maldanidae	SS-De
Maldanidae spp. K	Maldanidae	SS-De
Maldanidae spp. L	Maldanidae	SS-De
Maldanidae spp. M	Maldanidae	SS-De
Maldanidae spp. N	Maldanidae	SS-De
Nephtys incise	Nephtyidae	SS-Pr-mac
Aglaophamus circinata	Nephtyidae	SS-Pr-mac
Ceratocephale sp. A	Nereididae	SR-Om-mic

Table E1. cont.

Species	Family	Feeding Guild
Nereididae spp. A	Nereididae	SR-Om-mic
Ceratocephale loveni	Nereididae	SR-Om-mic
Nereididae spp. B (juvenile)	Nereididae	SR-Om-mic
Ophelina sp. A	Opheliidae	SS-De
Scoloplos sp. A	Orbiniidae	SS-De
Galathowenia sp. A	Oweniidae	SR-De
Galathowenia sp. B	Oweniidae	SR-De
Aricidea nolani	Paraonidae	SR-De
Aricidea quadrilobata	Paraonidae	SR-De
Paraonidae spp. A	Paraonidae	SR-De
Aricidea (Allia) sp. A	Paraonidae	SR-De
Aricidea sp. A	Paraonidae	SR-De
Paraonidae spp. B	Paraonidae	SR-De
Levinsenia sp. A	Paraonidae	SR-De
Paraonidae spp. C	Paraonidae	SR-De
Paraonidae spp. D	Paraonidae	SR-De
Pholoe sp. A	Pholoidae	SS-Pr-mac
Pholoe sp. B	Pholoidae	SS-Pr-mac
Metaxypsamma sp. A	Pholoidae	SS-Pr-mac
Phyllodoce sp. A	Phyllodocidae	SR-Sc-mac
Phyllodoce sp. B	Phyllodocidae	SR-Sc-mac
Phyllodocidae spp. A	Phyllodocidae	SR-Sc-mac
Phyllodocidae spp. B	Phyllodocidae	SR-Sc-mac
Ancistrosyllis groenlandica	Pilargidae	SR-Pr-mei
Pilargidae spp. A	Pilargidae	SR-Pr-mei
Eunoe sp. A	Polynoidae	SS-Pr-mac
Antinoella sp. A	Polynoidae	SS-Pr-mac
Sabellidae spp. A	Sabellidae	EP-Su
Jasmineria sp. A	Sabellidae	EP-Su
Euchone incolor	Sabellidae	EP-Su
Sabellidae spp. B	Sabellidae	EP-Su
Sabellidae spp. C	Sabellidae	EP-Su
Euchone sp. A	Sabellidae	EP-Su
Pseudoscalibregma parvum	Scalibregmatidae	SS-De

Table E1. cont.

Species	Family	Feeding Guild
Lipobranchius sp. A	Scalibregmatidae	SS-De
Scalibregma inflatum	Scalibregmatidae	SS-De
Scalibregmatidae spp. A	Scalibregmatidae	SS-De
Serpulidae spp. A	Serpulidae	EP-Su
Sphaerodoropsis sp. A	Sphaerodoridae	SR-Dt
Sphaerodorium sp. A	Sphaerodoridae	SR-Dt
Sphaerodoridium sp. A	Sphaerodoridae	SR-Dt
Sphaerodoropsis sp. B	Sphaerodoridae	SR-Dt
Sphaerodoridae spp. A	Sphaerodoridae	SR-Dt
Sphaerodoropsis longipalpa	Sphaerodoridae	SR-Dt
Prionospio sp. A	Spionidae	SR-De
Spiophanes kroyeri	Spionidae	SR-De
Spiophanes sp. A	Spionidae	SR-De
Spionidae spp. A	Spionidae	SR-De
Sternaspis scutata	Sternaspidae	SS-De
Streptosyllis sp. A	Syllidae	SR-He-mic
Exogone (Exogone) verugera	Syllidae	SR-He-mic
Prosphaerosyllis sp. A	Syllidae	SR-He-mic
Syllidae spp. A	Syllidae	SR-He-mic
Artacama proboscidea	Terebellidae	SR-De
Streblosoma sp. A	Terebellidae	SR-De
Pista sp. A	Terebellidae	SR-De
Lysilla loveni	Terebellidae	SR-De
Terebellidae spp. A (juvenile)	Terebellidae	SR-De
Streblosoma sp. B	Terebellidae	SR-De
Streblosoma sp. C	Terebellidae	SR-De
Polycirrinae spp. A	Terebellidae	SR-De
Leaena sp. A	Terebellidae	SR-De
Amphitrite sp. A	Terebellidae	SR-De
Polycirrus sp. A	Terebellidae	SR-De
Terebellides stroemii	Trichobranchidae	SR-De
Trichobranchus gracialis	Trichobranchidae	SR-De
Trichobranchidae spp. A	Trichobranchidae	SR-De
Trochochaeta sp. A	Trochochaetidae	SR-De

Table E1. cont.

Species	Family	Feeding Guild
Uncispionidae spp. A	Uncispionidae	SR-De

Table E2. Descriptions of feeding guild abbreviations (see MacDonald et al. 2010 in Chapter 2).

Code	Description
SR-De	surface deposit
SS-Pr-mac	subsurface predator macrofauna
SS-De	subsurface deposit
SR-Pr-mei	surface predator meiofauna
SS-Pr-mei	subsurface predator meiofauna
SS-Om-mic	subsurface omnivore microbial
SR-Sc-mac	surface scavengar macrofauna
SR-Om-mic	surface omnivore microbial
EP-Su	epibenthic suspension
SR-Dt	surface detritivore
SR-He-mic	surface herbivore microbial

APPENDIX F – Non-significant results from species biodiversity analyses

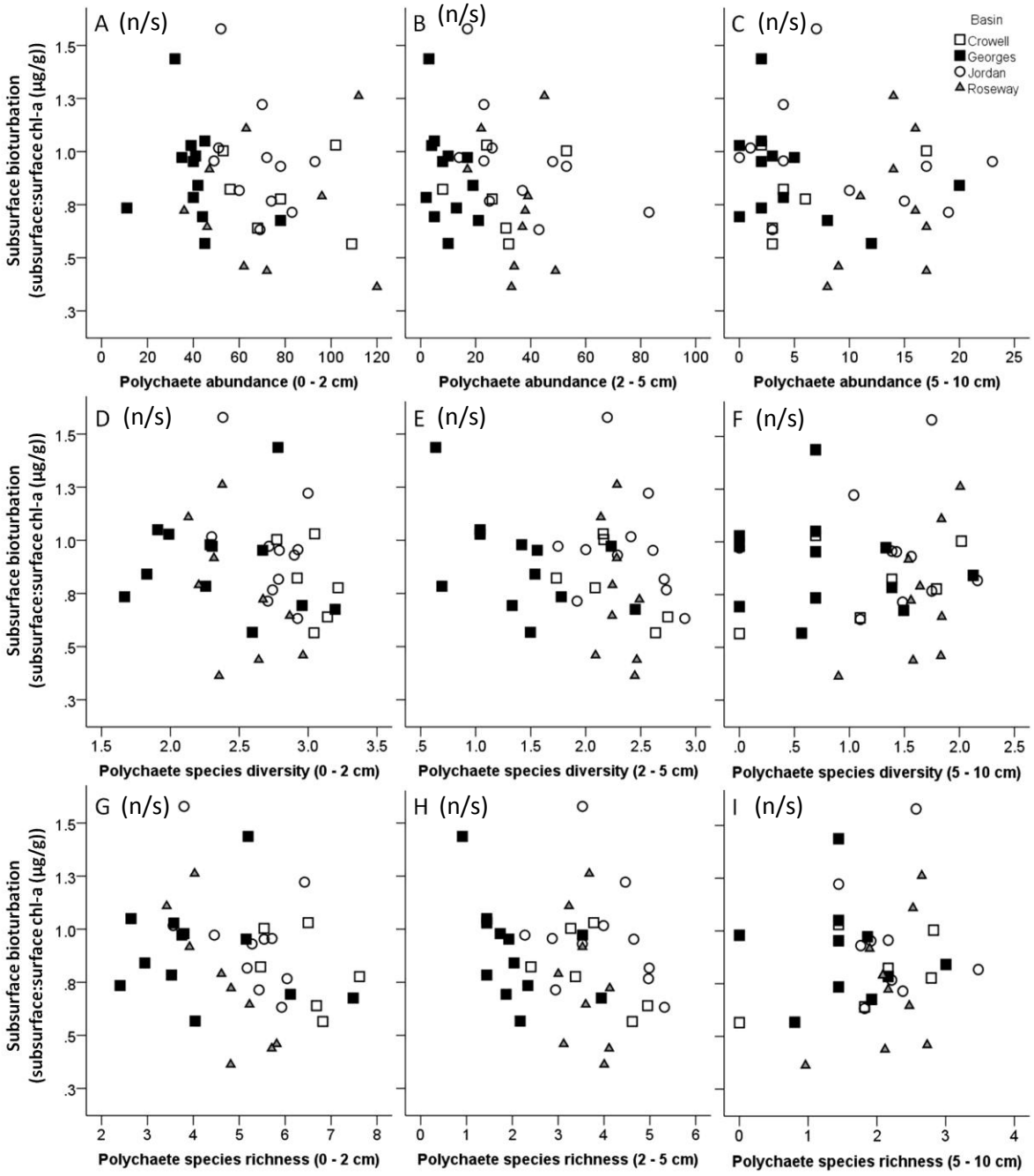

Figure F1. Relationship between subsurface bioturbation and polychaete species biodiversity measures: abundance (A, B, C), diversity (D, E, F), and richness (G, H, I) across surface (A, D, G), subsurface (B, E, H), and deep (C, F, I) sediment layers. n = 38. (n/s) indicates non-significance.

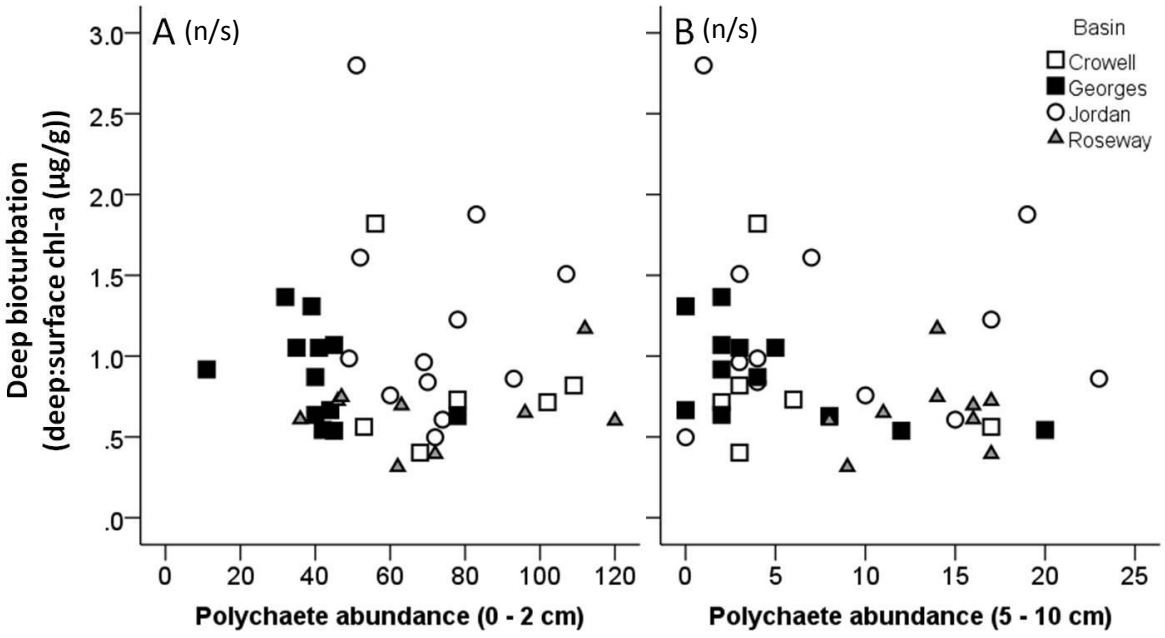

Figure F2. Relationship between deep bioturbation and abundance across surface (A) and deep (B) sediment layers. n = 39. (n/s) indicates non-significance.

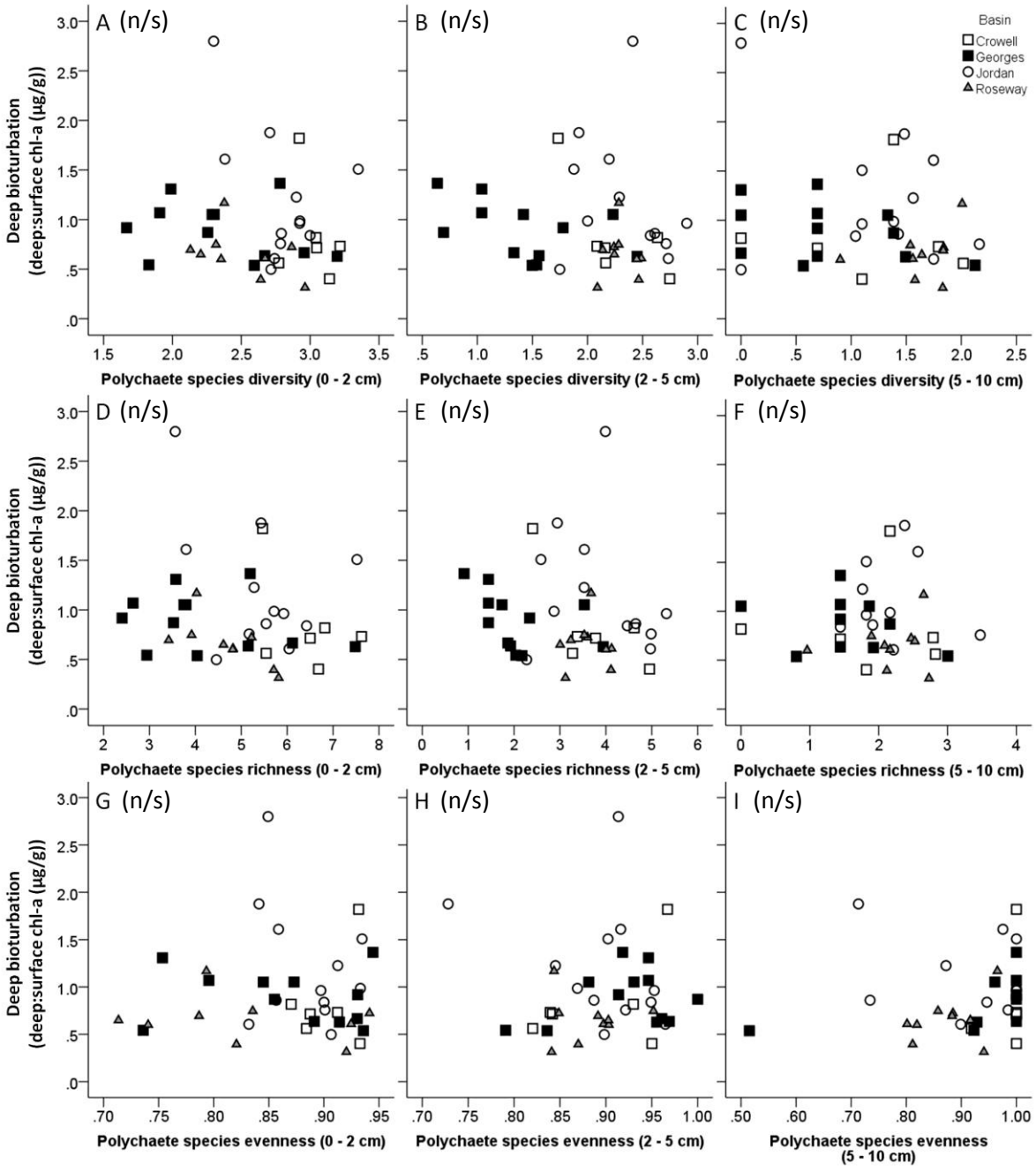

Figure F3. Relationship between deep bioturbation and polychaete species biodiversity measures: diversity (A, B, C), richness (D, E, F) and evenness (G, H, I) across surface (A, D, G), subsurface (B, E, H), and deep (C, F, I) sediment layers. n = 39. (n/s) indicates non-significance.

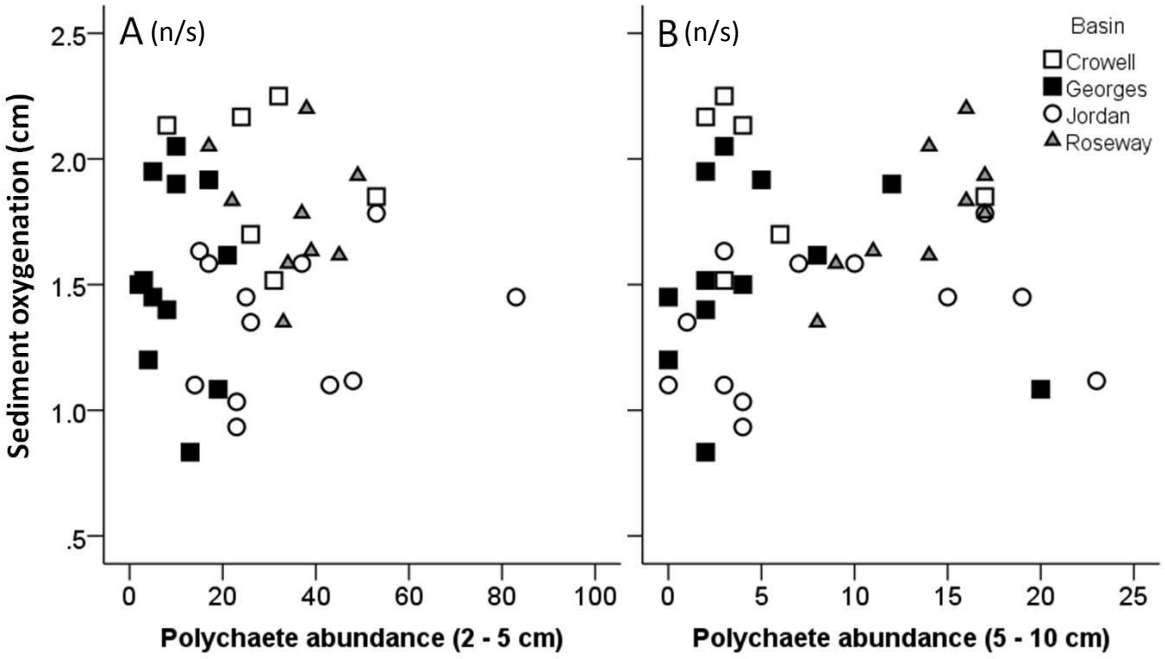

Figure F4. Relationship between sediment oxygenation and polychaete abundance across subsurface (A), and deep (B) sediment layers. n = 39. (n/s) indicates non-significance.

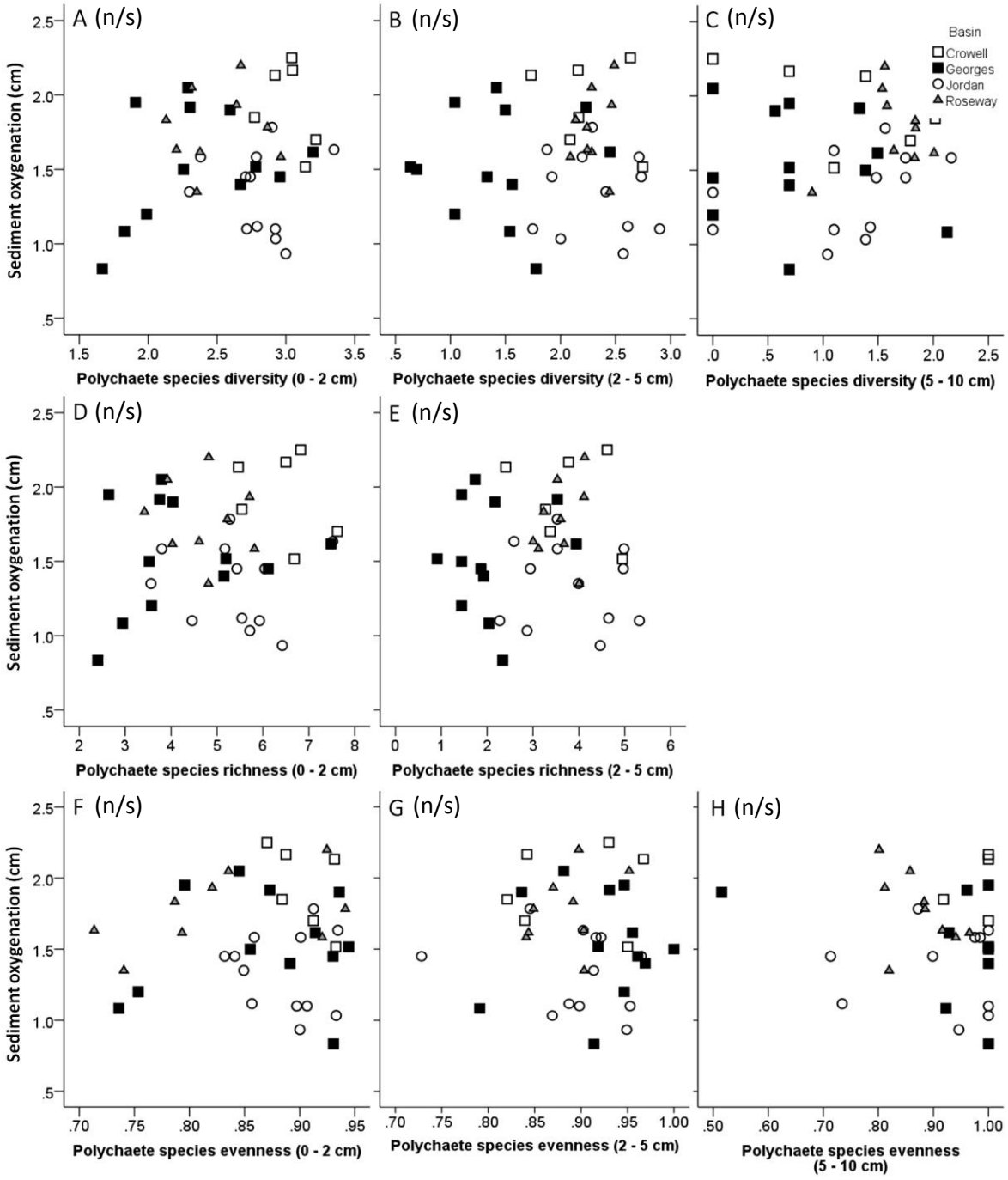

Figure F5. Relationship between sediment oxygenation and polychaete species biodiversity measures: diversity (A, B, C), richness (D, E), and evenness (F, G, H) across surface (A, D, F), subsurface (B, E, G), and deep (C, H) sediment layers. n = 39. (n/s) indicates non-significance.

APPENDIX G – Results from family biodiversity analyses

Table G1. Summary of two-way ANOVAs (generalized linear model) showing the effect of whole core polychaete **family** biodiversity measures and Basin on ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4.

		Diversity (H')			**Richness (d)**			**Evenness (J')**		
EF	**Source of Variation**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**
SB	Basin x Biodiversity	2.1	3	0.543	3.6	3	0.313	4.5	3	0.209
	Biodiversity	2.4	1	0.118	6.5	1	0.011	0.1	1	0.813
	Basin	1.8	3	0.614	2.2	3	0.535	4.3	3	0.231
DB	Basin x Biodiversity	4.5	3	0.213	5.2	3	0.157	0.5	3	0.926
	Biodiversity	2.4	1	0.122	2.8	1	0.093	0.5	1	0.494
	Basin	5.7	3	0.128	7.7	3	0.053	0.3	3	0.953
SO	Basin x Biodiversity	3.6	3	0.305	4.5	3	0.214	1.1	3	0.777
	Biodiversity	0.2	1	0.671	0.0	1	0.831	0.4	1	0.514
	Basin	3.8	3	0.279	5.1	3	0.163	1.1	3	0.775

Table G2. Summary of two-way [*three-way] ANOVAs (generalized linear model) showing the effect of polychaete **family** biodiversity measures and Basin [*and Sediment Depth] on ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4, Sediment Depth n = 3.

			Diversity (H')			**Richness (d)**			**Evenness (J')**		
EF	**Sediment Depth (cm)**	**Source of Variation**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**
SB	0 - 2	Biodiversity x Basin	1.2	3	0.760	2.1	3	0.554	0.6	3	0.902
		Biodiversity	5.9	1	0.015	5.9	1	0.015	1.5	1	0.227
		Basin	1.2	3	0.749	1.1	3	0.783	0.7	3	0.867
	2 - 5	Biodiversity x Basin	3.2	3	0.359	3.5	3	0.323	1.9	3	0.600
		Biodiversity	3.8	1	0.051	3.0	1	0.085	0.0	1	0.876
		Basin	2.4	3	0.486	2.1	3	0.544	1.6	3	0.664
	5 - 10	Biodiversity x Basin	3.9	3	0.272	0.9	3	0.836	2.8	3	0.419
		Biodiversity	2.5	1	0.113	0.9	1	0.354	1.6	1	0.203
		Basin	6.2	3	0.102	2.0	3	0.581	3.2	3	0.358
DB	0 - 2	Biodiversity x Basin	6.4	3	0.093	5.0	3	0.172	0.4	3	0.934
		Biodiversity	6.0	1	0.014	5.5	1	0.019	0.0	1	0.997
		Basin	8.3	3	0.041	7.9	3	0.047	0.4	3	0.947
	2 - 5	Biodiversity x Basin	1.5	3	0.693	0.7	3	0.867	6.1	3	0.107
		Biodiversity	2.9	1	0.087	0.8	1	0.370	0.3	1	0.601
		Basin	2.8	3	0.428	2.0	3	0.575	6.8	3	0.079

Table G2. cont.

EF	Sediment Depth (cm)	Source of Variation	Diversity (H')			Richness (d)			Evenness (J')		
			χ^2	df	Sig.	χ^2	df	Sig.	χ^2	df	Sig.
DB	5 - 10	Biodiversity x Basin	1.8	3	0.610	0.9	3	0.816	2.3	3	0.505
		Biodiversity	0.3	1	0.560	0.8	1	0.360	0.1	1	0.754
		Basin	5.8	3	0.122	3.1	3	0.376	3.2	3	0.363
SO	0 - 2	Biodiversity x Basin	2.9	3	0.404	3.8	3	0.282	2.7	3	0.447
		Biodiversity	0.1	1	0.799	0.2	1	0.660	0.1	1	0.722
		Basin	3.5	3	0.325	4.6	3	0.203	2.8	3	0.431
	2 - 5	Biodiversity x Basin	1.2	3	0.754	1.0	3	0.791	0.5	3	0.909
		Biodiversity	0.6	1	0.434	0.0	1	0.969	0.0	1	0.902
		Basin	1.7	3	0.637	1.4	3	0.715	0.3	3	0.967
	5 - 10	Biodiversity x Basin	4.5	3	0.209	7.5	3	0.057	0.7	3	0.862
		Biodiversity	0.1	1	0.741	2.5	1	0.117	0.8	1	0.382
		Basin	13.4	3	0.004	9.9	3	0.019	0.9	3	0.815
SP	n/a	Biodiversity x Basin x Sediment Depth	5.3	6	0.509	4.8	6	0.569	3.3	6	0.765
		Biodiversity x Basin	**10.8**	**3**	**0.013**	**10.9**	**3**	**0.012**	**8.4**	**3**	**0.039**
		Biodiversity x Sediment Depth	1.1	2	0.579	**8.8**	**2**	**0.012**	2.6	2	0.268
		Basin x Sediment Depth	6.1	6	0.410	4.9	6	0.551	3.3	6	0.773
		Biodiversity	2.1	1	0.151	1.2	1	0.275	0.1	1	0.755
		Basin	10.5	3	0.015	13.1	3	0.004	9.2	3	0.027
		Sediment Depth	0.8	2	0.678	5.7	2	0.058	2.0	2	0.367

Table G3. Summary of regression analyses for whole core polychaete **family** biodiversity measures and ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

EF	Biodiversity Measure	Regression	R^2	Sig.
SB	Diversity	Quadratic	0.052	0.392
	Richness	Quadratic	0.100	0.159
	Evenness	Quadratic	0.018	0.726
DB	Diversity	Quadratic	0.036	0.515
	Richness	**Quadratic**	**0.211**	**0.014**
	Evenness	Inverse	0.006	0.646
SO	Diversity	Quadratic	0.120	0.101
	Richness	Quadratic	0.059	0.332
	Evenness	Quadratic	0.084	0.204

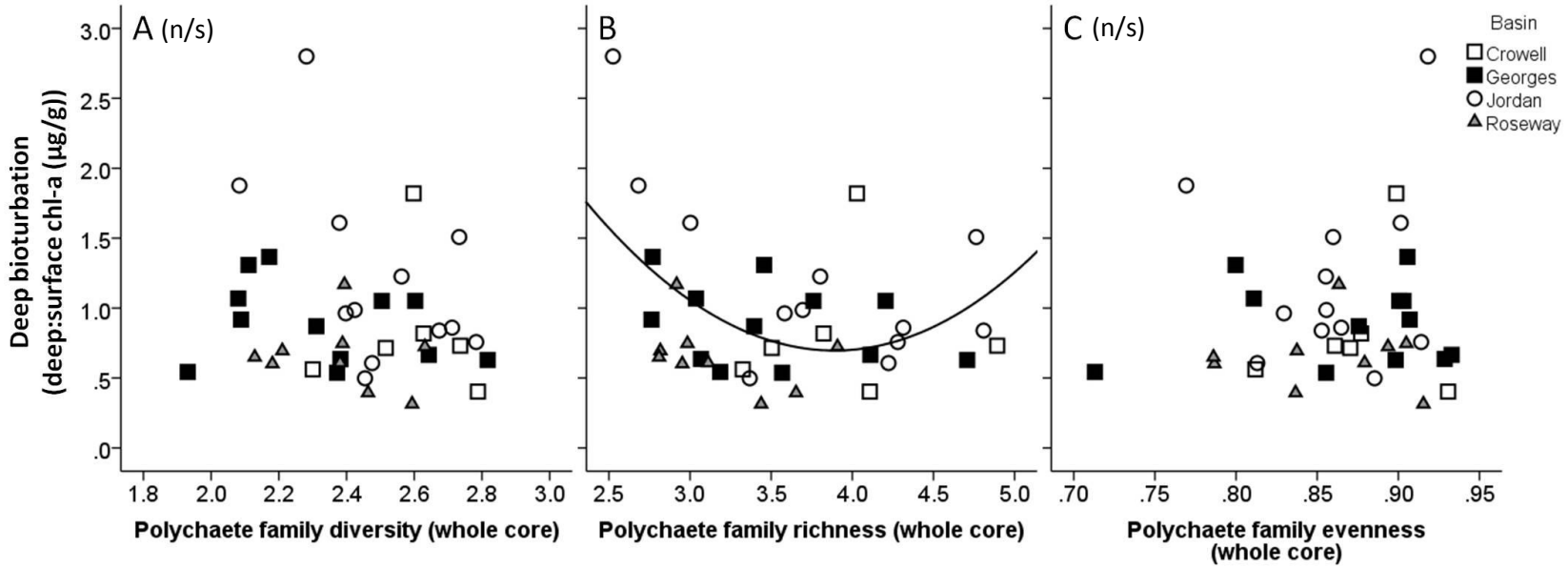

Figure G1. Relationship between deep bioturbation and whole core polychaete **family** biodiversity measures: diversity (A), richness (B; [y = 7.6 + -3.5 * x + 0.5 * x*x], R^2 = 0.211, p = 0.014), and evenness (C). n = 39. (n/s) indicates non-significance.

Table G4. Summary of regression analyses for polychaete **family** biodiversity measures and ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

EF	Biodiversity Measure	Sediment Depth (cm)	Regression	R^2	Sig.
SB	Diversity	0 - 2	Quadratic	0.139	0.072
		2 - 5	Inverse	0.082	0.082
		5 - 10	Exponential	0.003	0.746
	Richness	0 - 2	Quadratic	0.086	0.207
		2 - 5	Quadratic	0.134	0.081
		5 - 10	Quadratic	0.021	0.720
	Evenness	0 - 2	Quadratic	0.158	0.050
		2 - 5	Quadratic	0.022	0.677
		5 - 10	Exponential	0.108	0.067
DB	Diversity	0 - 2	Quadratic	0.061	0.323
		2 - 5	Exponential	0.059	0.138
		5 - 10	Quadratic	0.077	0.236
	Richness	0 - 2	Quadratic	0.071	0.264
		2 - 5	Exponential	0.036	0.248
		5 - 10	Exponential	0.035	0.279
	Evenness	0 - 2	Quadratic	0.083	0.212
		2 - 5	Quadratic	0.118	0.104
		5 - 10	Exponential	0.022	0.140
SO	Diversity	0 - 2	Quadratic	0.029	0.585
		2 - 5	Linear	0.009	0.575
		5 - 10	Exponential	0.003	0.731
	Richness	0 - 2	Quadratic	0.018	0.715
		2 - 5	Quadratic	0.035	0.527
		5 - 10	Quadratic	0.133	0.101

Table G4. cont.

EF	Biodiversity Measure	Sediment Depth (cm)	Regression	R^2	Sig.	
SO	Evenness	0 - 2	Quadratic	0.009	0.844	
		2 - 5	Quadratic	0.011	0.813	
		5 - 10	Exponential	0.041	0.258	
***SP**	**Diversity**	Whole Core	**Quadratic**	**0.448**	**0.012**	**Crowell**
		Whole Core	**Exponential**	**0.238**	**0.003**	**Georges**
		Whole Core	Exponential	0.042	0.233	Jordan
		Whole Core	**Quadratic**	**0.254**	**0.030**	**Roseway**
	Richness	Whole Core	**Quadratic**	**0.440**	**0.013**	**Crowell**
		Whole Core	Quadratic	0.167	0.059	Georges
		Whole Core	Inverse	0.009	0.590	Jordan
		Whole Core	**Quadratic**	**0.379**	**0.003**	**Roseway**
	Evenness	Whole Core	Quadratic	0.156	0.305	Crowell
		Whole Core	Quadratic	0.014	0.808	Georges
		Whole Core	**Exponential**	**0.238**	**0.003**	**Jordan**
		Whole Core	Exponential	0.031	0.378	Roseway

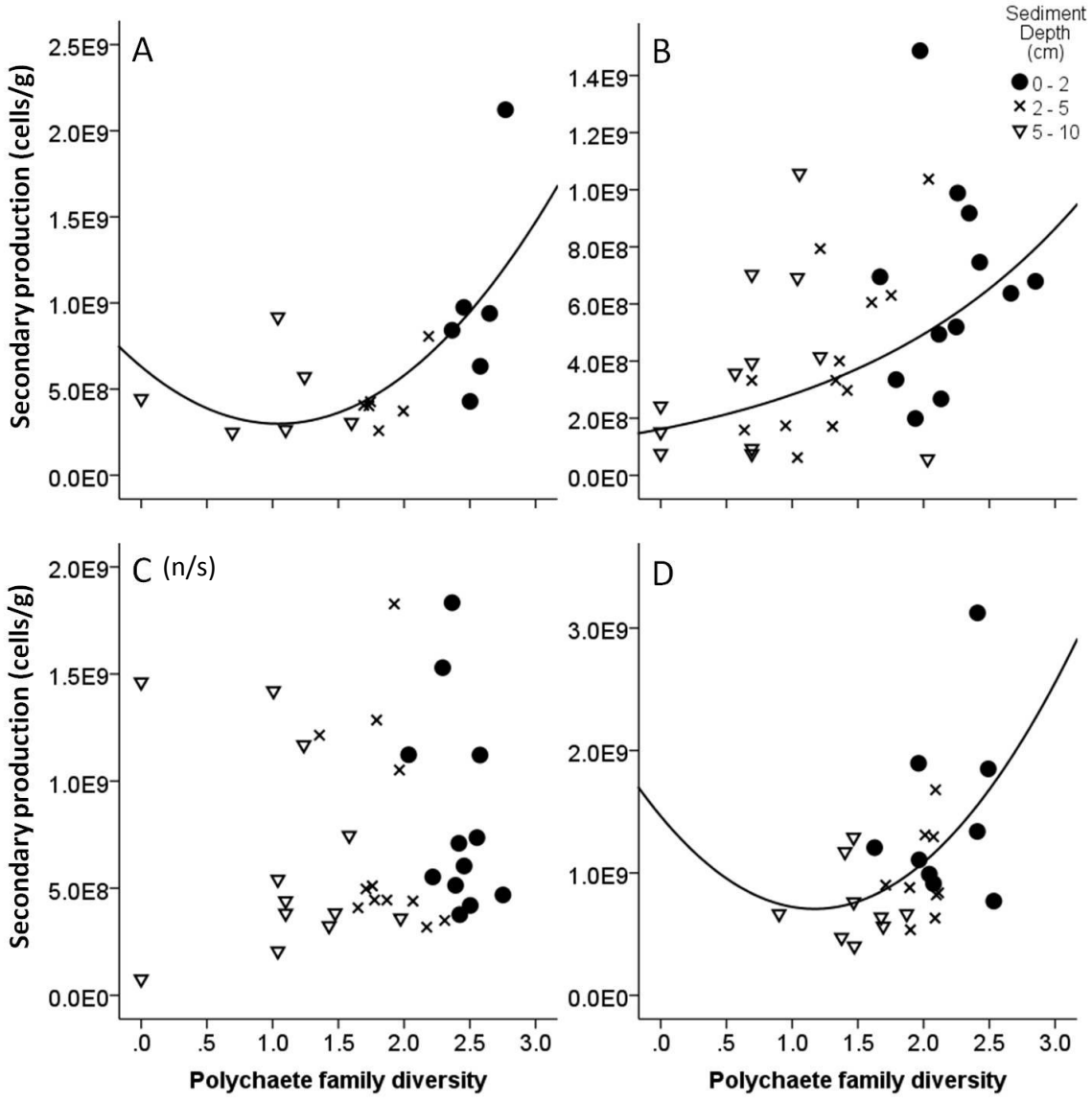

Figure G2. Relationships between secondary production and polychaete **family** diversity (A; [y = 6.3 x 10^8 + -6.4 x 10^8 * x + 3.1 x 10^8 * x*x], R^2 = 0.448, p = 0.012, D; [y = 1.6 x 10^8 * exp(0.6 * x)], R^2 = 0.238, p = 0.003, G, J; [y = 1.5 x 10^9 + -1.3 x 10^9 * x + 5.5 a 10^8 * x*x], R^2 = 0.254, p = 0.030) within Crowell (A; n = 6), Georges (B; n = 12), Jordan (C; n = 12), and Roseway (D; n = 9). Measurements from all three sediment depth layers included. (n/s) indicates non-significance.

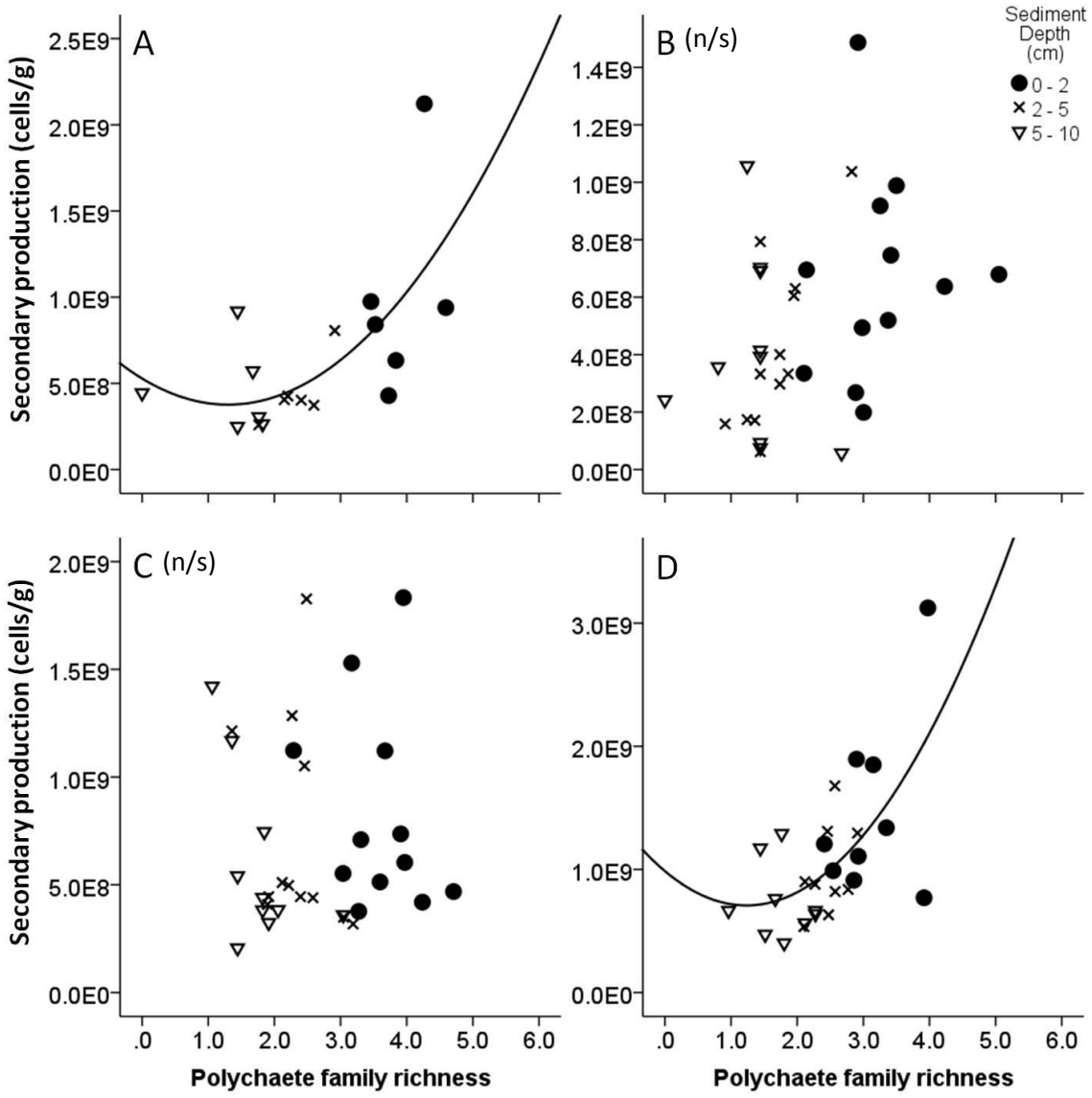

Figure G3. Relationships between secondary production and polychaete **family** richness (A; [$y = 5.3 \times 10^8 + -2.3 \times 10^8 * x + 9.0 \times 10^7 * x*x$], $R^2 = 0.440$, $p = 0.013$, B, C, D; [$y = 9.9 \times 10^8 + -4.5 \times 10^8 * x + 1.8 \times 10^8 * x*x$], $R^2 = 0.379$, $p = 0.003$) within Crowell (A; n = 6), Georges (B; n = 12), Jordan (C; n = 12), and Roseway (D; n = 9). Measurements from all three sediment depth layers included. (n/s) indicates non-significance.

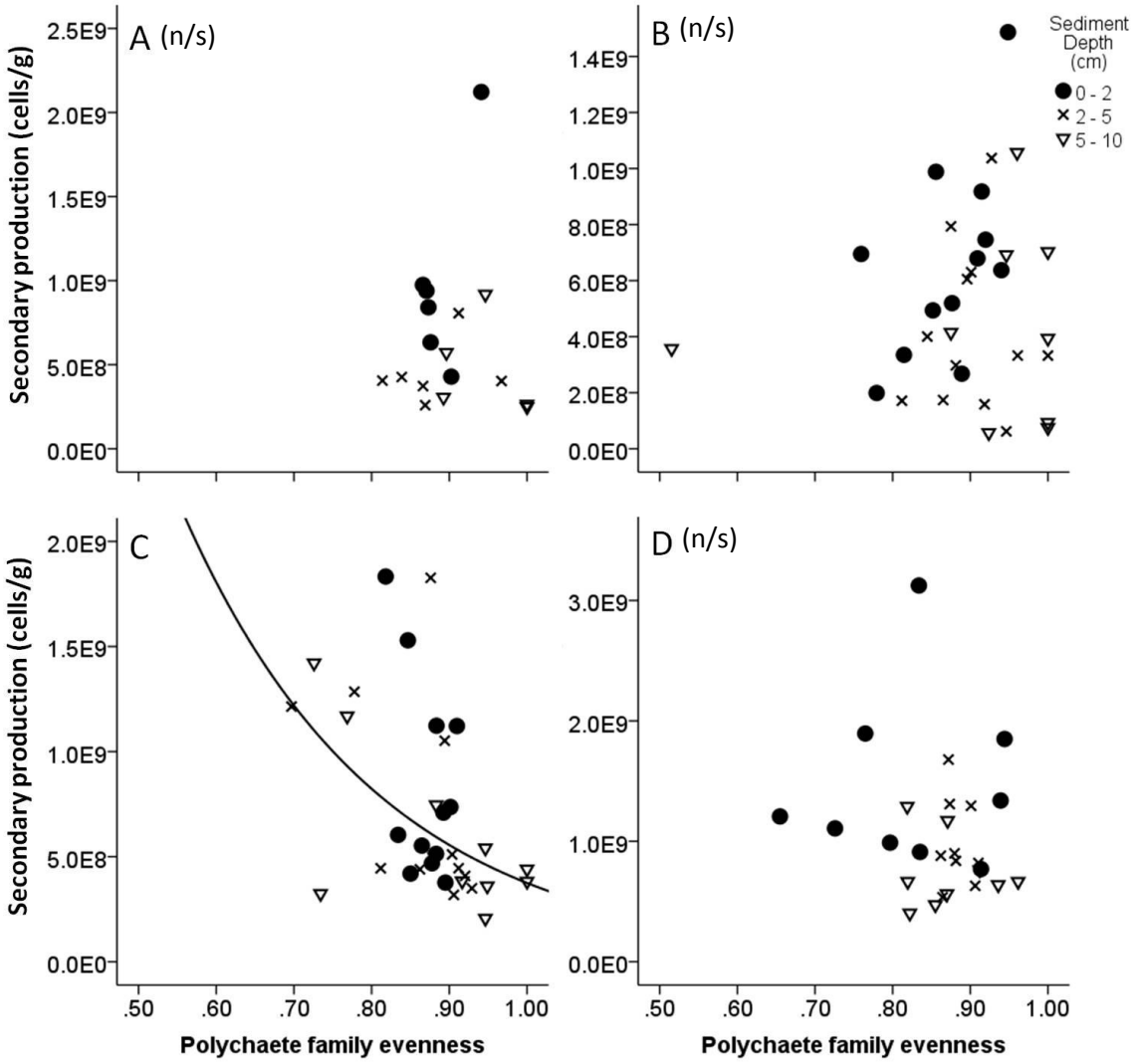

Figure G4. Relationships between secondary production and polychaete **family** evenness (A, B, C; [y = 1 / (0 + 5.2e-011 * 50.9**x)], R^2 = 0.238, p = 0.003, D) within Crowell (A; n = 6), Georges (B; n = 12), Jordan (C; n = 12), and Roseway (D; n = 9). Measurements from all three sediment depth layers included. (n/s) indicates non-significance.

APPENDIX H – Results from feeding guild biodiversity analyses

Table H1. Summary of two-way ANOVAs (generalized linear model) showing the effect of whole core polychaete **feeding guild** biodiversity measures and Basin on ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4.

		Diversity (H')			**Richness (d)**			**Evenness (J')**		
EF	**Source of Variation**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**	χ^2	**df**	**Sig.**
SB	Basin x Biodiversity	2.7	3	0.441	1.6	3	0.657	7.1	3	0.069
	Biodiversity	0.2	1	0.677	0.8	1	0.386	3.5	1	0.062
	Basin	2.4	3	0.490	1.3	3	0.726	6.9	3	0.077
DB	Basin x Biodiversity	3.8	3	0.283	6.5	3	0.091	0.7	3	0.874
	Biodiversity	0.6	1	0.431	2.8	1	0.096	5.1	1	0.024
	Basin	5.1	3	0.167	8.7	3	0.033	1.1	3	0.767
SO	Basin x Biodiversity	2.1	3	0.552	5.5	3	0.141	1.9	3	0.586
	Biodiversity	0.5	1	0.471	0.5	1	0.479	0.7	1	0.406
	Basin	3.6	3	0.307	7.2	3	0.066	3.2	3	0.360

Table H2. Summary of two-way [*three-way] ANOVAs (generalized linear model) showing the effect of polychaete **feeding guild** biodiversity measures and Basin [*and Sediment Depth] on ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38), Basin n = 4, Sediment Depth n = 3.

			Diversity (H')			**Richness (d)**			**Evenness (J')**		
EF	**Sediment Depth (cm)**	**Source of Variation**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**	**χ^2**	**df**	**Sig.**
SB	0 - 2	Biodiversity x Basin	3.3	3	0.354	0.9	3	0.818	3.8	3	0.281
		Biodiversity	1.7	1	0.190	1.1	1	0.289	0.3	1	0.555
		Basin	3.1	3	0.381	1.0	3	0.797	3.4	3	0.330
	2 - 5	Biodiversity x Basin	2.5	3	0.482	0.8	3	0.852	1.9	3	0.585
		Biodiversity	8.2	1	0.004	1.4	1	0.230	1.6	1	0.207
		Basin	1.6	3	0.658	0.3	3	0.953	1.3	3	0.726
	5 - 10	Biodiversity x Basin	4.1	3	0.249	0.1	3	0.988	2.9	3	0.402
		Biodiversity	3.0	1	0.081	1.0	1	0.329	3.0	1	0.083
		Basin	6.9	3	0.076	0.3	3	0.965	3.8	3	0.287
DB	0 - 2	Biodiversity x Basin	2.0	3	0.569	2.4	3	0.493	0.8	3	0.843
		Biodiversity	0.2	1	0.640	0.0	1	0.893	1.8	1	0.180
		Basin	3.3	3	0.346	4.9	3	0.178	0.5	3	0.921
	2 - 5	Biodiversity x Basin	4.3	3	0.228	4.7	3	0.198	1.6	3	0.651
		Biodiversity	0.7	1	0.416	0.7	1	0.406	0.9	1	0.343
		Basin	3.5	3	0.326	5.0	3	0.171	2.3	3	0.513

Table H2. cont.

EF	Sediment Depth (cm)	Source of Variation	Diversity (H') χ^2	df	Sig.	Richness (d) χ^2	df	Sig.	Evenness (J') χ^2	df	Sig.
DB	5 - 10	Biodiversity x Basin	3.5	3	0.324	0.1	3	0.986	3.1	3	0.382
		Biodiversity	0.3	1	0.608	0.8	1	0.360	4.6	1	0.032
		Basin	7.8	3	0.051	1.4	3	0.715	5.4	3	0.145
SO	0 - 2	Biodiversity x Basin	1.2	3	0.753	4.3	3	0.229	1.5	3	0.689
		Biodiversity	1.4	1	0.238	0.0	1	0.844	1.0	1	0.313
		Basin	2.2	3	0.535	6.4	3	0.094	2.5	3	0.473
	2 - 5	Biodiversity x Basin	2.2	3	0.535	0.4	3	0.945	5.8	3	0.123
		Biodiversity	4.6	1	0.032	2.2	1	0.141	4.8	1	0.028
		Basin	6.4	3	0.092	3.5	3	0.323	7.1	3	0.068
	5 - 10	Biodiversity x Basin	6.7	3	0.083	6.2	3	0.101	1.0	3	0.808
		Biodiversity	0.1	1	0.713	0.1	1	0.764	0.0	1	0.836
		Basin	16.8	3	0.001	12.8	3	0.005	1.3	3	0.725
*SP	n/a	Biodiversity x Basin x Sediment Depth	7.8	6	0.256	4.7	6	0.577	7.8	6	0.250
		Biodiversity x Basin	0.9	3	0.832	2.2	3	0.529	2.2	3	0.539
		Biodiversity x Sediment Depth	0.6	2	0.760	2.7	2	0.257	1.8	2	0.403
		Basin x Sediment Depth	6.6	6	0.363	5.3	6	0.506	7.3	6	0.292
		Biodiversity	2.0	1	0.161	0.0	1	0.831	0.1	1	0.817
		Basin	1.9	3	0.593	5.2	3	0.157	2.3	3	0.522
		Sediment Depth	0.3	2	0.863	2.8	2	0.245	1.2	2	0.559

Table H3. Summary of regression analyses for whole core polychaete **feeding guild** biodiversity measures and ecosystem functions. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

EF	Biodiversity Measure	Regression	R^2	Sig.
SB	Diversity	Quadratic	0.033	0.555
	Richness	Quadratic	0.110	0.130
	Evenness	Quadratic	0.108	0.135
DB	Diversity	Linear	0.023	0.358
	Richness	**Inverse**	**0.124**	**0.028**
	Evenness	Exponential	0.038	0.236
SO	**Diversity**	**Quadratic**	**0.189**	**0.023**
	Richness	**Exponential**	**0.100**	**0.049**
	Evenness	Quadratic	0.017	0.736

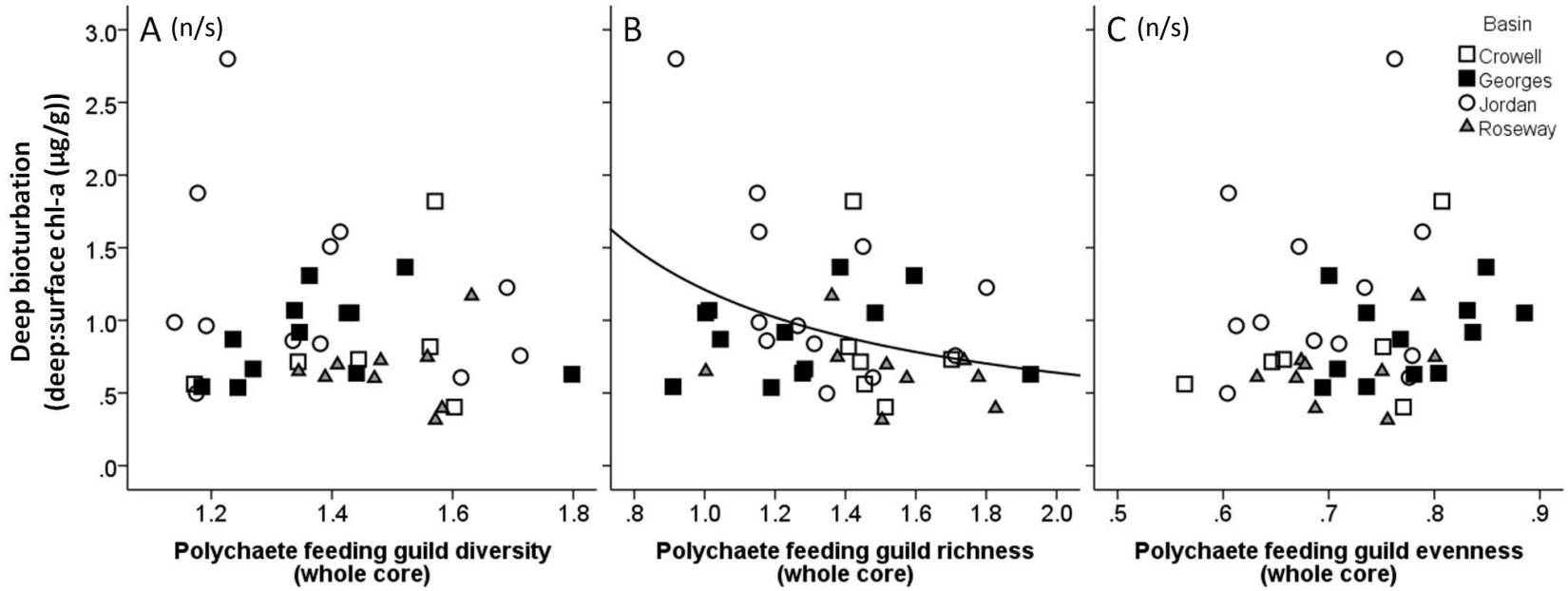

Figure H1. Relationship between deep bioturbation and whole core polychaete feeding guild biodiversity measures: diversity (A), richness (B; [y = 0.1 + 1.1 / x], R^2 = 0.124, p = 0.028), and evenness (C). n = 39. (n/s) indicates non-significance.

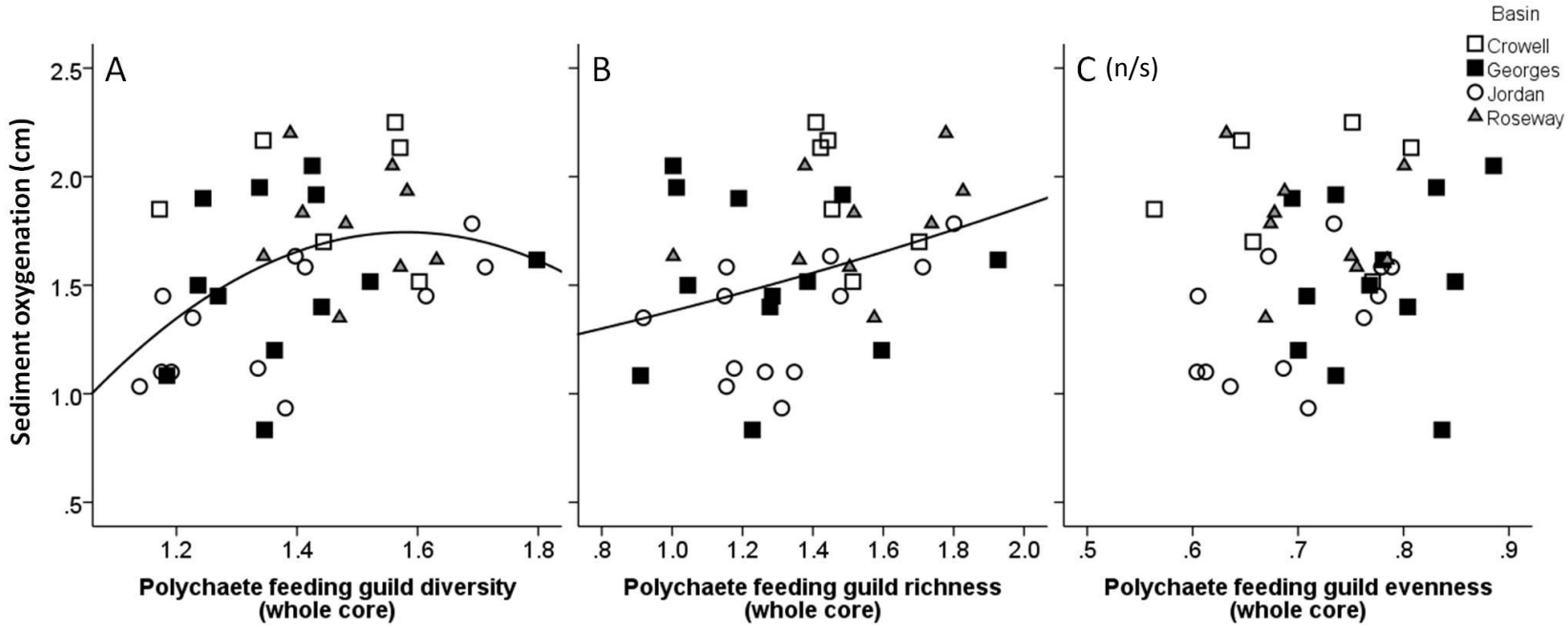

Figure H2. Relationship between sediment oxygenation and whole core polychaete feeding guild biodiversity measures: diversity (A; [y = -5.1 + 8.6 * x + -2.7 * x*x], R^2 = 0.189, p = 0.023), richness (B; [y = 1.0 * exp(0.3 * x)], R^2 = 0.100, p = 0.049), and evenness (C). n = 39. (n/s) indicates non-significance.

Table H4. Summary of regression analyses for polychaete **feeding guild** biodiversity measures and ecosystem functions separated by sediment depths [*not applicable]. Bolded results indicate significant results. Core replicate n = 39 (except for SB n = 38).

EF	Biodiversity Measure	Sediment Depth (cm)	Regression	R^2	Sig.
SB	**Diversity**	0 - 2	Quadratic	0.012	0.817
		2 - 5	**Quadratic**	**0.220**	**0.013**
		5 - 10	Quadratic	0.006	0.908
	Richness	0 - 2	Quadratic	0.112	0.125
		2 - 5	Quadratic	0.088	0.199
		5 - 10	Linear	0.015	0.488
	Evenness	**0 - 2**	**Inverse**	**0.121**	**0.032**
		2 - 5	Quadratic	0.049	0.427
		5 - 10	Quadratic	0.102	0.210
DB	Diversity	0 - 2	Inverse	0.005	0.669
		2 - 5	Exponential	0.080	0.082
		5 - 10	Quadratic	0.056	0.355
	Richness	0 - 2	Inverse	0.060	0.134
		2 - 5	Exponential	0.061	0.129
		5 - 10	Quadratic	0.021	0.710
	Evenness	0 - 2	Linear	0.057	0.144
		2 - 5	Quadratic	0.016	0.749
		5 - 10	Exponential	0.036	0.289
SO	**Diversity**	**0 - 2**	**Quadratic**	**0.172**	**0.033**
		2 - 5	Exponential	0.002	0.780
		5 - 10	Quadratic	0.082	0.213
	Richness	0 - 2	Quadratic	0.073	0.256
		2 - 5	Quadratic	0.008	0.861
		5 - 10	Quadratic	0.094	0.207

Table H4. cont.

EF	Biodiversity Measure	Sediment Depth (cm)	Regression	R^2	Sig.
SO	Evenness	0 - 2	Exponential	0.029	0.298
		2 - 5	Quadratic	0.052	0.394
		5 - 10	Quadratic	0.023	0.706
***SP**	**Diversity**	Whole Core	**Exponential**	**0.202**	**< 0.01**
	Richness	Whole Core	**Quadratic**	**0.059**	**0.036**
	Evenness	Whole Core	**Quadratic**	**0.107**	**0.002**

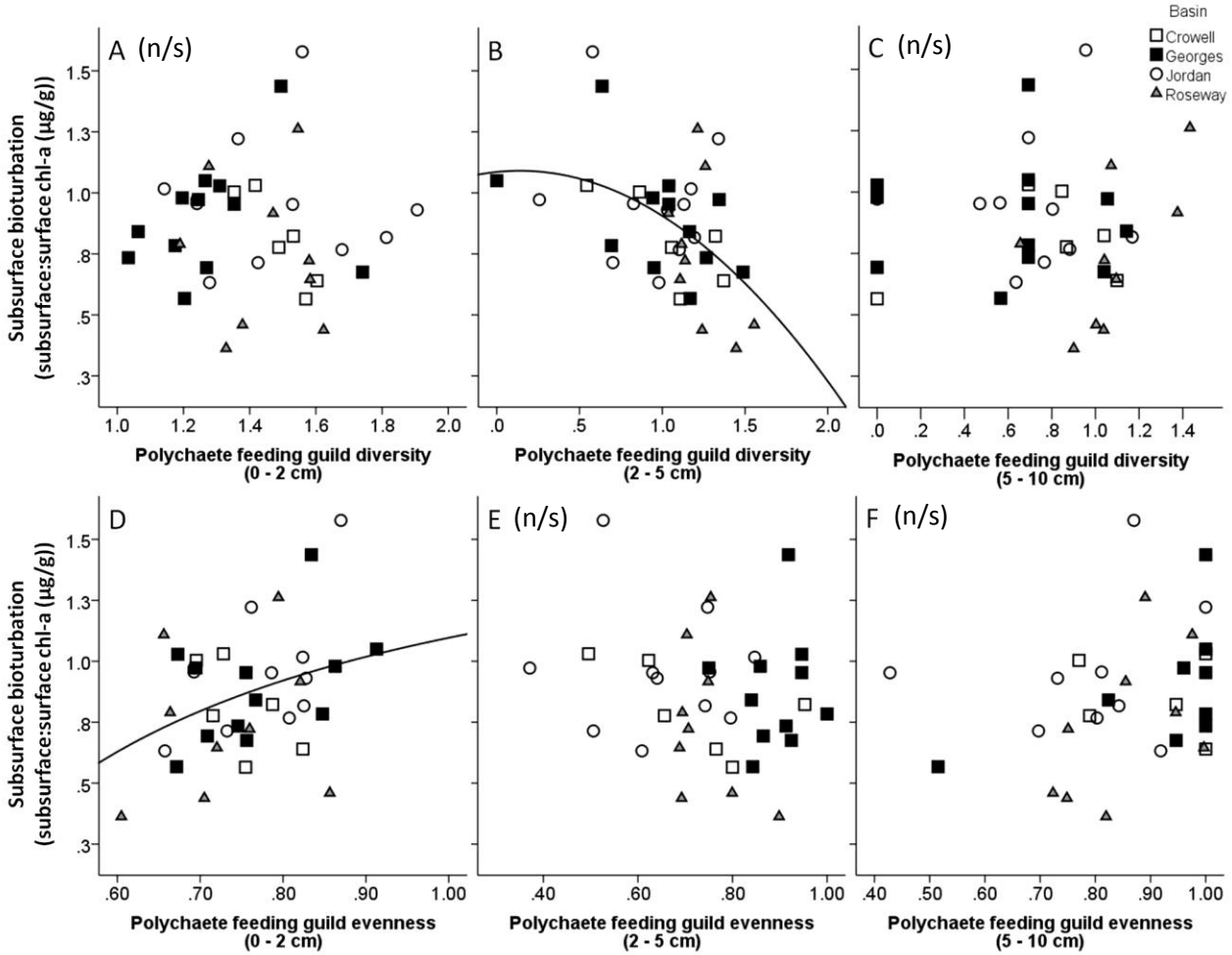

Figure H3. Relationship between subsurface bioturbation and **feeding guild** diversity (A, B, C) and evenness (D, E, F) at surface (A, D; [y = 1.8 + -0.7 / x], R^2 = 0.121, p = 0.032), subsurface (B; [y = 1.1 + 0.1 * x + -0.2 * x*x], R^2 = 0.220, p = 0.013, E), and deep (C, F) sediment depths. n = 38. (n/s) indicates non-significance.

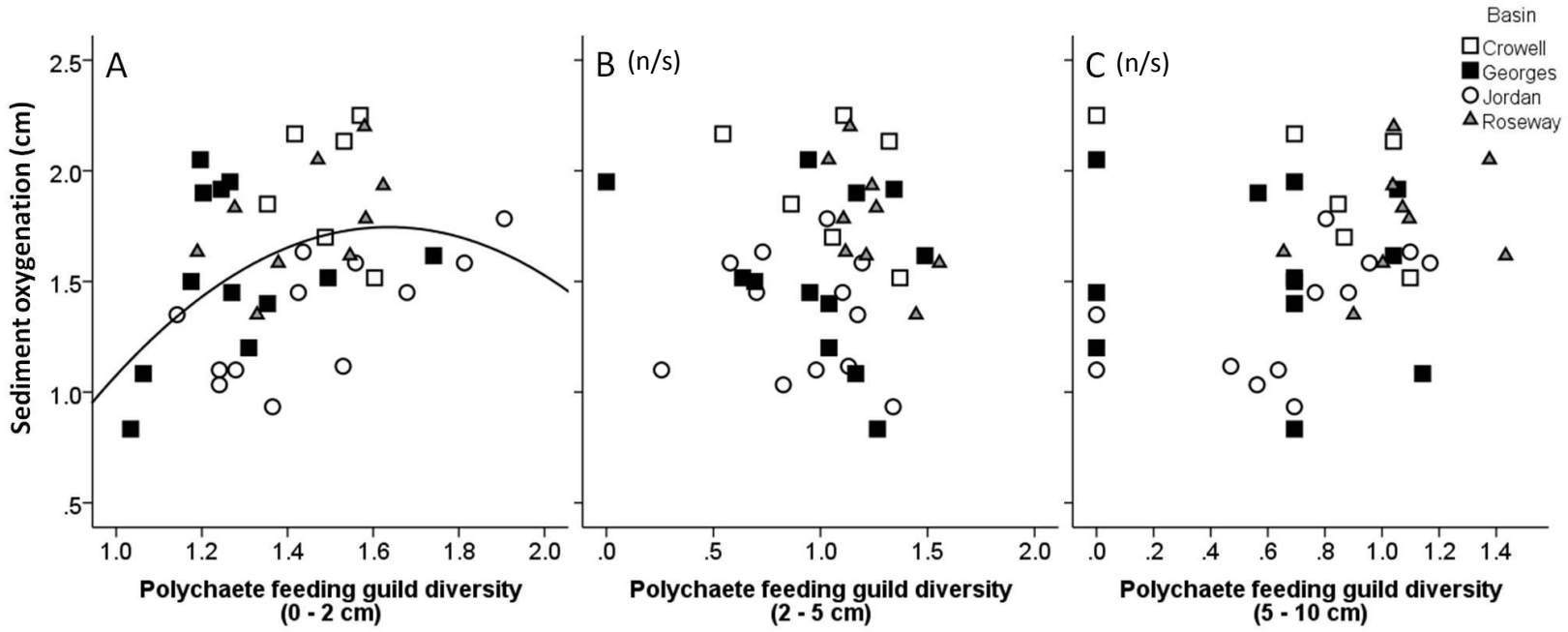

Figure H4. Relationship between sediment oxygenation and polychaete **feeding guild** diversity at surface (A; [y = -2.7 + 5.4 * x + -1.7 * x*x], $R^2 = 0.172$, p = 0.033), subsurface (B), and deep (C) sediment depths. n = 39. (n/s) indicates non-significance.

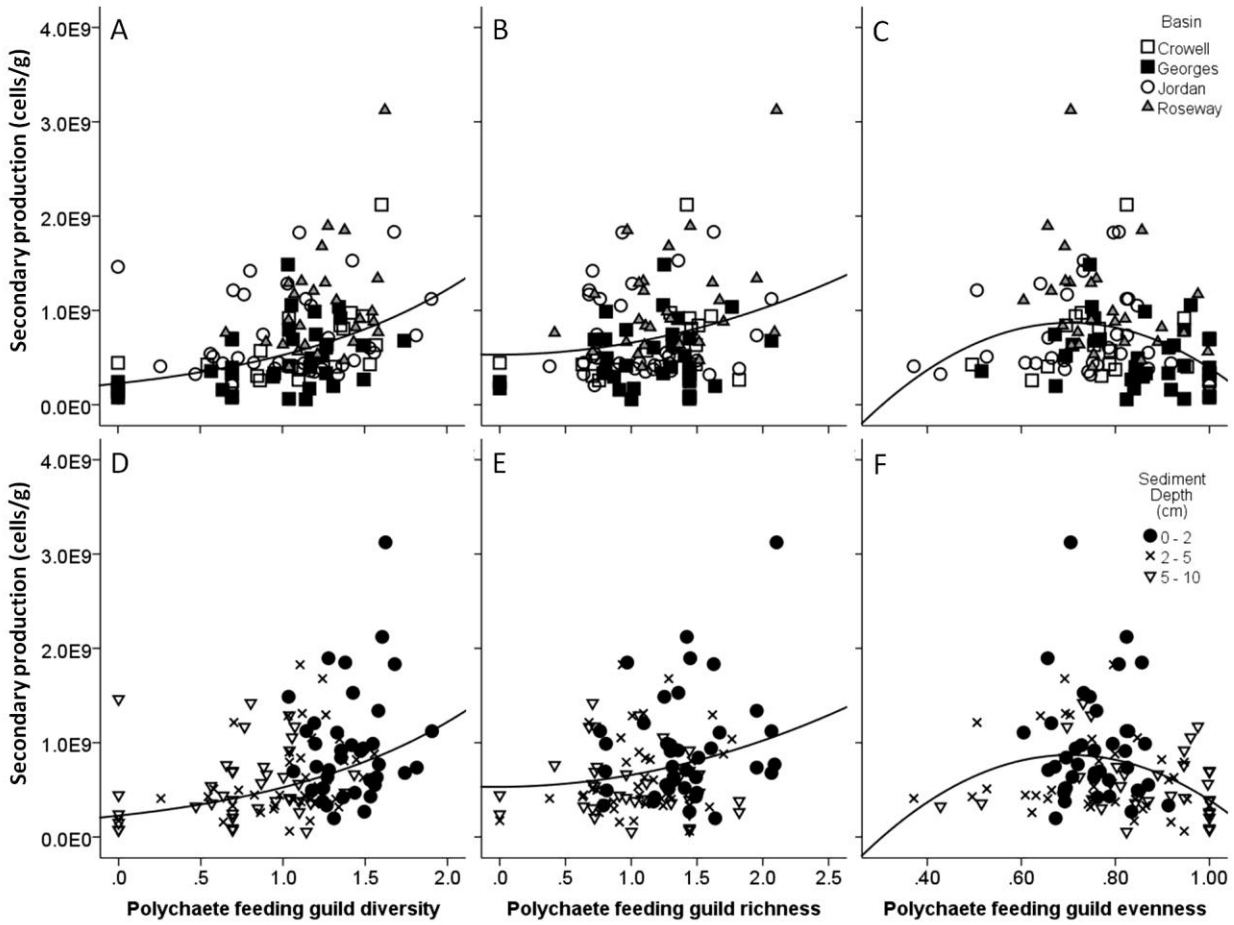

Figure H5. Relationship between secondary production and polychaete **feeding guild** diversity (A and D; [$y = 2.3 \times 10^8 * \exp(0.8 * x)$], $R^2 = 0.202$, $p = < 0.01$), richness (B and E; [$y = 5.3 \times 10^8 + 9.0 \times 10^6 * x + 1.2 \times 10^8 * x*x$], $R^2 = 0.059$, $p = 0.036$), and evenness (C and F; [$y = -1.8 \times 10^9 + 7.7 \times 10^9 * x + -5.4 \times 10^9 * x*x$], $R^2 = 0.107$, $p = 0.002$) across basins (A, B, C) and sediment depth layers (D, E, F); although neither impacts relationship. n = 39 for each basin and sediment depth.