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The University of Southern Mississippi

MACROBENTHIC COMMUNITIES IN THE NORTHERN

GULF OF MEXICO HYPOXIC ZONE: TESTING

THE PEARSON-ROSENBERG MODEL

by

Shivakumar Shivarudrappa

Abstract of a Dissertation
Submitted to the Graduate School
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

December 2015

ABSTRACT

MACROBENTHIC COMMUNITIES IN THE NORTHERN

GULF OF MEXICO HYPOXIC ZONE: TESTING

THE PEARSON-ROSENBERG MODEL

by Shivakumar Shivarudrappa

December 2015

The Pearson and Rosenberg (P-R) conceptual model of macrobenthic succession

was used to assess the impact of hypoxia (dissolved oxygen [DO] ≤ 2 mg/L) on the

macrobenthic community on the continental shelf of northern Gulf of Mexico for the first

time. The model uses a stress-response relationship between environmental parameters

and the macrobenthic community to determine the ecological condition of the benthic

habitat. The ecological significance of dissolved oxygen in a benthic habitat is well

understood. In addition, the annual recurrence of bottom-water hypoxia on the

Louisiana/Texas shelf during summer months is well documented.

The P-R model illustrates the decreasing impact of organic enrichment on the

macrobenthic community distally from the source. To test the underlying principles of

the P-R model using bottom-water concentration of dissolved oxygen as a proxy for

distance from the source of organic enrichment, four sites were chosen based on the

frequency of hypoxia occurrence in the hypoxic zone of the northern Gulf of Mexico.

The chosen sites were arrayed from west to east on the Louisiana continental shelf, where

site A was farthest from the Mississippi River and least impacted by seasonal hypoxia

with <25% annual exposure time, and site D was closest to the Mississippi River and

most impacted by seasonal hypoxia with >75% annual exposure time. Site C was

impacted by seasonal hypoxia between 25% and 50% of the time. Site B was impacted by

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seasonal hypoxia between 50% and 75% of the time. Sites B and C were situated near the vicinity of the Atchafalaya River between sites A and D.

To measure the spatio-temporal effect of hypoxia on the macrobenthic community, samples were collected during early spring (April 2009), late summer (September 2009), and mid-summer (August 2010). Results indicated that the macrobenthos collected during mid-summer were the most stressed community, with the exception of site C. The cumulative effect of annual hypoxia on the macrobenthos at each site was apparent from the species diversity, abundance, and biomass.

High values of species diversity, richness and evenness at site A and low values at site D indicated the existence of a westward-diminishing hypoxic gradient on the Louisiana/Texas shelf interrupted by the Atchafalaya River discharge. Assessment of successional stages of the benthic communities of the four sites with the multivariate analyses of nonmetric multi-dimensional scaling and principal component analysis identified the spatial gradient of hypoxia. Examination of the macrobenthos and available environmental data with canonical correspondence analysis indicated that sedimentary organic carbon, as well as bottom-water dissolved oxygen, had a strong impact on the benthic community structure. The study successfully demonstrated the applicability of the Pearson-Rosenberg model on the Louisiana/Texas continental shelf, and the results were consistent with the predictions of the model. Site A was in the advanced phase of stage II succession; whereas sites B and C were in the intermediate phase of stage II succession, and site D was in the intermediate phase of stage I succession in the Pearson-Rosenberg successional continuum.

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A Dissertation
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I would like to thank my parents, friends and family for their continued support and

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CHAPTER I

INTRODUCTION

Oxygen and Hypoxia

Oxygen is an essential element for most marine organisms for respiration and

metabolism. The bioavailability of dissolved oxygen for marine organisms depends on

various physicochemical and biological factors that determine the concentration of

oxygen in seawater (Canadian Council of Ministers of the Environment, 1999). Those

factors that determine the concentration of oxygen in seawater are atmospheric exchange,

temperature, barometric pressure, salinity, tides, currents, upwelling, vertical mixing, and

biological processes like photosynthesis and respiration. Oxygen enters the system

through atmospheric exchange, and is, also, produced *in situ* by photosynthesis. Usually,

oxygen levels are high in surface waters due to exchange with the atmosphere and

photosynthesis in the euphotic zone where photosynthesis exceeds respiration, and results

in a net production of oxygen (Glud, 2008; Canadian Council of Ministers of the

Environment, 1999). Below the euphotic zone, respiration of oxygen exceeds its

production, resulting in a net consumption (Canadian Council of Ministers of the

Environment, 1999). In neritic environments, bottom waters that have limited light,

restricted circulation and abundant organic matter supply will have a higher biological

oxygen demand than surface waters. Failure of oxygen renewal to the deeper waters due

to lack in photosynthesis, breakdown in vertical mixing, and increase in oxygen

consumption by bacteria during aerobic decomposition of organic matter will contribute

to the reduction of oxygen concentrations in bottom waters (Canadian Council of

Ministers of the Environment, 1999). Dissolved oxygen plays a critical role in marine

environment because its concentration can change drastically in a short span of time (Diaz and Rosenberg, 1995).

An aquatic system is considered hypoxic by definition when the dissolved oxygen concentration drops below 2 mg/L. Hypoxia changes behavioral and/or physiological responses in various organisms as a feedback mechanism. These responses can range from avoidance of hypoxic waters to mass mortality, depending on the mobility and tolerance of the organism (Diaz and Rosenberg, 1995; Rabalais and Turner, 2001; Diaz and Rosenberg, 2008).

Mobile organisms can avoid the hypoxic area by moving horizontally or vertically to an area with higher dissolved oxygen concentrations within the water column (Counsell, 2013). This would increase the densities of conspecific species in the surrounding waters with normal dissolved oxygen concentration. This could lead to heightened inter- and intra-species competition that potentially leads to indirect ecological effects such as stunted growth, reduced fecundity, altered reproduction and altered behaviors. Some demersal fish exhibit enhanced foraging behavior to take advantage of stressed benthic prey by briefly entering hypoxic bottom waters to feed (Counsell, 2013).

Hypoxia is most harmful to sessile benthic organisms because of their inability to retreat from hypoxic waters. Low dissolved oxygen concentration induces behavioral changes in sessile benthic organisms before eventual mortality. Benthic organisms would stop feeding, leave their burrows and tubes, and migrate upwards to the surface of sediment (Diaz and Rosenberg, 1995; Nilsson and Rosenberg, 2000). Hence, dissolved

oxygen plays a critical role in structuring marine benthic communities (Diaz and Rosenberg, 1995).

Evidence suggests that hypoxia has been a growing problem in coastal marine environments around the world and is attributed to the increasing use and manufacturing of fertilizers (Stachowitsch et al., 2007; Rabalais and Turner, 2001; Diaz and Rosenberg, 2008). Many of the major coastal systems throughout the world are experiencing increased fluxes of nutrients to coastal waters (Rabalais and Turner, 2001; Diaz and Rosenberg, 2008). These nutrients along with other organic substances enter the coastal system from a wide variety of point and non-point sources (e.g., fertilizer from agricultural lands, discharge from sewage treatment plants, discharge of industrial effluents, improper disposal of animal manure, deposition of nitrogen from the atmosphere, and erosion of nutrient-rich marsh soils). This excess influx of nutrients typically results in phytoplankton blooms.

Phytoplankton multiply in binary fashion, hence the population expansion is geometric. Every phytoplankton cell produces another daughter cell; hence, their population growth is exponential when uninhibited. This uninhibited growth can only occur in the absence of predators for a few cohorts in time (Sommer, 2002). However, the shortage of resources such as minerals, nutrients, and light will eventually cause the rate of phytoplankton multiplication to decline due to loss of factors like grazing, sinking of cells, parasitism, viral lysis, and physiological mortality (Sommer, 2002). Over the course of population growth, phytoplankton exhaust one or several essential nutrients and limit population growth. If the exhaustion of resources does not occur, the over-growth of

phytoplankton results in self-shading and reduced light penetration through the water column due to high density (Sommer, 2002).

Phytoplankton produce oxygen under sunlight by photosynthesis, and consume oxygen in darkness during respiration contributing to heterotrophy. Normally, phytoplankton produce more oxygen during the day than they consume at night. However, weather conditions like cloudiness and extremely calm conditions during the day may cause a reduction in the amount of oxygen produced by a bloom without changing its nightly oxygen consumption (LSU AgCenter, 2010). During the summer, the decrease in oxygen dissolving capacity of water under higher temperatures may cause the surplus oxygen produced by photosynthesis to escape into the atmosphere faster, leaving less dissolved oxygen for inflated phytoplankton population to draw from at night. The most common cause of increased mortality in phytoplankton blooms under heavy competition for light and nutrients is the depletion of essential trace minerals (LSU AgCenter, 2010). When there is a sudden increased mortality, bacterial decomposition and loss of oxygen producing cells can lead to hypoxia due to oxygen depletion (Sommer, 2002; LSU AgCenter, 2010).

Apart from phytoplankton mortality, fecal pellets from herbivorous zooplankton can also contribute to hypoxia. Typically, following phytoplankton bloom, the zooplankton population will increase due to increased food supply. These primary consumers cannot graze all the cells in the phytoplankton bloom, and eventually, the unconsumed phytoplankton cells may sink to the bottom−either on their own or by adhering to settling fecal pellets from primary consumers (Rabalais and Turner, 2001). The dead phytoplankton cells and fecal pellets reaching the sediment serve as a source of

carbon and energy for bacteria as well as multicellular benthic organisms (Glud, 2008). Consumption of dissolved oxygen by benthic fauna and bacteria leads to decreased dissolved oxygen concentration near the water-sediment interface, with the potential to create hypoxia in neritic bottom waters.

Dissolved oxygen is an essential element in marine sediments for benthic faunal respiration, aerobic heterotrophic activity of bacteria, and for the oxidization of anaerobically reduced inorganic products during heterotrophic bacterial degradation (Glud, 2008). Normally marine sediments, especially coastal sediments are reducing environments, where oxygen penetrates only the top few millimeters (Glud, 2008; Kristensen, 2000). This oxygen penetration depth is determined by the balance between downward transportation of oxygen from overlying water and consumption of organic matter by benthic organisms (Kristensen, 2000). Organic matter mineralization by many aerobic and anaerobic bacteria also affects depth of oxygen penetration. The rate of organic matter mineralization depends on factors like quality and age of organic matter as well as water temperature (Kristensen, 2000).

Hence, systems enriched with organic matter undergo a series of events before becoming hypoxic. Initially, systems experience occasional (lasting from days to weeks) oxygen depletion (O_2 concentration < 2 mg/L) and continued eutrophication increases the frequency of oxygen depletion episodes in space and time. Under continued enrichment, the system can experience episodic hypoxia (less than one event per year) or seasonal hypoxia (recurring every year), as occurs in the northern Gulf of Mexico (Diaz and Rosenberg, 2008). Once the system experiences hypoxia, it loses its resilience due to an imbalance in stabilizing feedback processes like sediment bio-irrigation activities

(burrowing and tube construction) and oxygen as an electron acceptor. The imbalance in internal buffers makes the system prone to future hypoxia by lowering the threshold limits of nutrient input at which future hypoxia could occur (Conley et al., 2009). This accelerates the frequency and duration of hypoxia, eventually making the system persistently hypoxic and bringing forth the shift in macrobenthic regime from equilibrium to a pioneering community (Diaz and Rosenberg, 2008).

Different bodies of water with different settings experience varying degrees of hypoxia on highly varying temporal and spatial scales. The processes controlling hypoxia on the inner shelf (< 100 m water depth), and those on the outer shelf (100 to 500 m water depth) are very different (Levin et al., 2009). The inner shelves of Southern California, Oregon, and Chile are influenced by ENSO, and the Arabian Sea off the coast of Pakistan and the west coast of India are influenced by the West African monsoon. These climatic factors regulate the upwelling cycles and control seasonal oxygen depletion patterns and the shoaling of the oxygen minimum zone (Naqvi et al., 2000; Levin et al., 2009; McClatchie et al., 2010). Outer hypoxic shelves are influenced by a different set of phenomena like the inter-annual climate cycles and seasonal wind cycles that regulate the up-/downwelling and advection patterns, which in turn dictate the seasonal oxygen minimum zone (Levin et al., 2009). Coastal waters and estuaries often experience seasonal or episodic hypoxia in proximity to specific tributaries or shallow reaches due to organic enrichment and water column stratification (Diaz and Rosenberg, 2001). Enclosed seas may experience permanent or long-term hypoxia over large spatial scales as opposed to shallow, well-mixed settings where hypoxia may occur over diel cycles (Verity et al., 2006).

Hypoxia around the World

At present, more than 550 separate aquatic systems around the world have reported hypoxic conditions (Hypoxia in the northern Gulf of Mexico, n. d.). With the increased use of agricultural fertilizers, hypoxia is growing in magnitude and approximately 245,000 km^2 of seafloor have been affected by hypoxia globally (Diaz and Rosenberg, 2008). A majority of these hypoxic systems are proximal to large human populations and their agricultural needs. One of the adverse consequences of hypoxia that directly affects humans is the loss of valuable biomass because of an altered energy pathway. Hypoxia increases the energy supply to the microbial pathway and reduces the secondary production of benthic fauna. The recent available data indicate that the loss of secondary production in the form of benthic biomass ranges from 343,000 to 734,000 metric tons (MT) of carbon per year (Diaz and Rosenberg, 2008). On an average, every hypoxic system around the world is losing ~1400 to 2996 kg/C/y/km^2 in terms of benthic biomass. Reducing freshwater runoff, stratification strength, nutrients and organic carbon loadings could reverse the loss of biomass (Diaz and Rosenberg, 2008).

Many biological systems at the turn of the 20th century showed higher yields and production than systems at the turn of the 21st century. The first reported incident of hypoxia was in Chesapeake Bay in the 1930s (Diaz and Rosenberg, 2008). The northwestern continental shelf of the Black Sea became hypoxic in the 1940s, the northern Adriatic Sea became hypoxic in the 1950s, and the Baltic Sea became hypoxic in the 1960s (Diaz and Rosenberg, 2008). Many systems around the world, including the northern Gulf of Mexico, started reporting hypoxia for the first time in the 1970s. Usually, hypoxia went unrecognized until higher tropic levels manifested its undesirable

impacts on the socioeconomic conditions of the region. For example, in the Kattegat off Denmark, hypoxia was not a major environmental concern when it was first reported in the 1980s. It gained attention only after mass fish mortalities and the collapse of the Norway lobster fishery (Diaz and Rosenberg, 2008).

Hypoxia in the Gulf of Mexico

From a regional perspective, hypoxia in the Gulf of Mexico has expanded in severity and magnitude ever since the first reporting in the 1970s. Because of hypoxia, the Gulf of Mexico is losing an estimated 17,000 MT C/y in benthic faunal biomass that could have been potential food for many commercially important fishes (Diaz and Rosenberg, 2008). Although hypoxia-induced, mass, fish mortalities have been reported in the Gulf of Mexico, there are no deleterious signs of hypoxia reported in fish landings (Rabalais and Turner, 2001). Instead, fish landings have shown stable, sustained production, and the ecosystem response to hypoxia has been gradual over the past few decades (Diaz, 2001).

The cause of hypoxia in the northern Gulf of Mexico is a much debated and controversial topic in the scientific community, but the nutrient-centric view model is the most widely accepted concept. According to the nutrient-centric model, hypoxia in the northern Gulf of Mexico is primarily attributed to the confluence of two major phenomena. One is the water column stratification induced by the Mississippi River discharge, and the other is the microbial decomposition of organic matter in the bottom waters. Hypoxia strongly correlates to nutrient-rich, freshwater discharge from the Mississippi River (Rabalais and Turner, 2001). The warm, low-salinity water mass from the Mississippi River tends to float on top of the cooler, more saline water mass near the

bottom, thus creating density-stratified layers. Nutrient-rich water from the Mississippi River along with an ample supply of sunlight promotes an increase in primary production in the stratified surface waters of the northern Gulf of Mexico during the summer months, which ultimately results in increased flux of fecal material and other organic detritus to lower depths in the water column (Bianchi et al., 2010). The strong pycnocline inhibits downward mixing of oxygen to lower depths of the water column where oxygen consumption exceeds its production by photosynthesis or other source processes, and leads to depletion of oxygen concentration in the bottom water, thus triggering hypoxia (Bianchi et al., 2010).

The variability in development, maintenance, and expansion of hypoxia in the northern Gulf of Mexico is linked to the dynamics of freshwater discharge from the Mississippi River system (Rabalais and Turner, 2001). The Mississippi River system is among the ten lengthiest rivers of the world and drains 41% of the total watershed of the continental United States. Discharge from the Mississippi River system to the Gulf of Mexico is split between the Mississippi and Atchafalaya Rivers, which deliver 70% and 30% (respectively) of this freshwater to the northern Gulf of Mexico. The general trend in regulated discharge of the Mississippi River system indicates a seasonal pattern, with high discharges during March-May and low discharges during September-November. Of these waters, about 67% of the total discharged freshwater flows west along the Louisiana shelf towards the Texas coast (Rabalais and Turner, 2001). These seasonal patterns of high and low discharges of the Mississippi River system typically mark the onset and the degradation of water column stratification (Baustian et al., 2009).

The first reported hypoxia event in the northern Gulf of Mexico was measured off Barataria and Terrebonne Bays in 1972 (Turner et al., 2005). Analysis of organic and inorganic geochemical tracers and benthic foraminiferal analysis of a gravity cores and box cores showed the episodic low-oxygen bottom-water conditions in the northern Gulf of Mexico for the past 1000 ^{14}C-dated years (Swarzenski et al., 2008). The systematic, shelf-wide measurement of hypoxia did not begin until 1985, and such surveys are usually conducted in late July to early August of every year (Rabalais and Turner, 2001). Initially (1985-1992), the occurrence of hypoxia was discontinuous and separated into discrete patches west of the Mississippi and Atchafalaya River deltas, and covering approximately 7,000 to 9,000 km^2. However, from 1993 to 1997, the patches merged into a continuous hypoxic zone that had doubled in areal extent, reaching 16,000 to 18,000 km^2. The maximum area of hypoxia recorded since 1985 was 22,000 km^2 (Figure 1), which occurred in 2002 (Rabalais et al., 2008).

Bottom water hypoxia on the Louisiana/Texas (LaTex) inner shelf can extend from 4 to 5 m water depth near the shore to as deep as 60 m on the continental shelf, but it most frequently ranges between 5 and 30 m (Rabalais and Turner, 2001). The vertical extent of hypoxia in the water column was recorded as close as 2 m from the surface at the 10-m isobath (Rabalais and Turner, 2001).
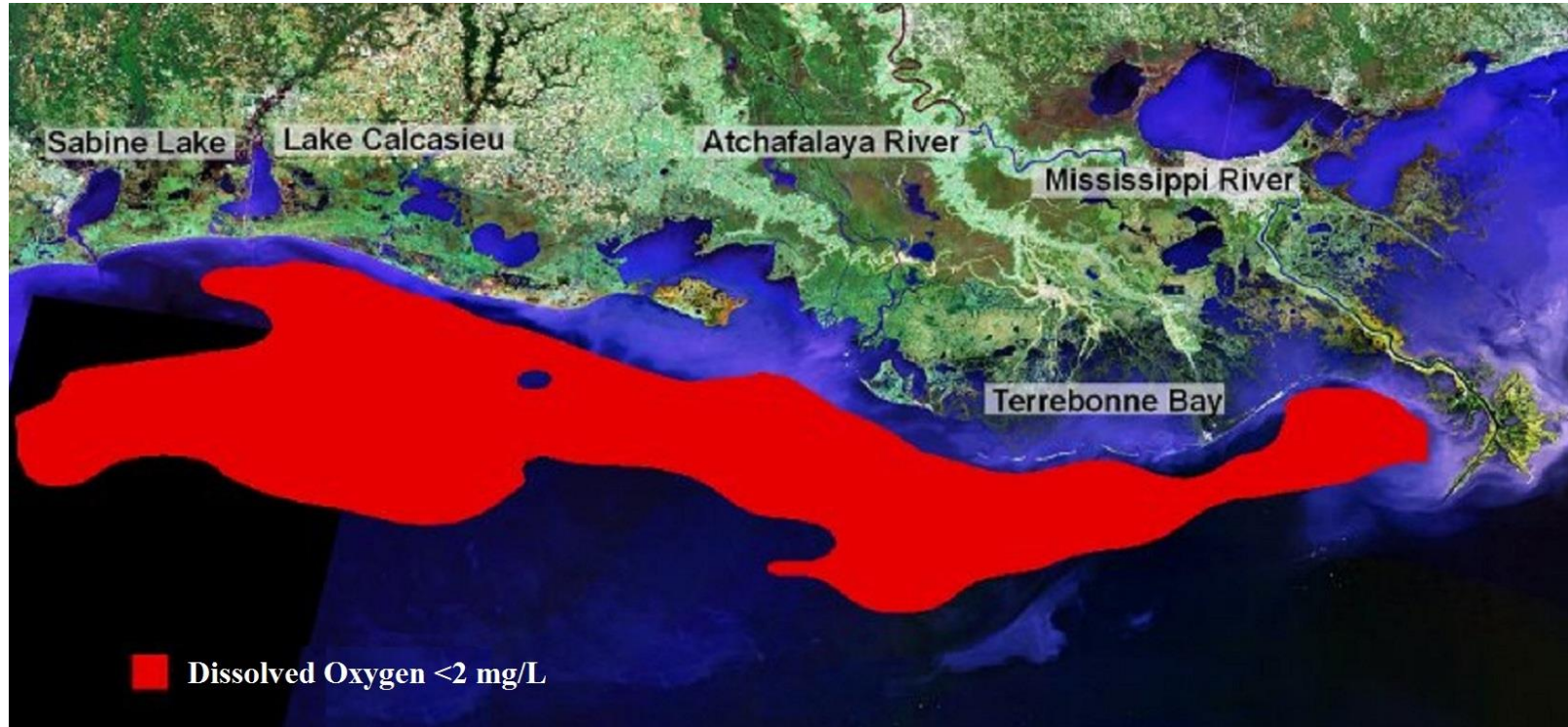
Figure 1. Areal extent of hypoxia in northern Gulf of Mexico continental shelf during 2002. Source: www.gulfhypoxia.net/Research/.

The duration of seasonal hypoxia varies annually. It has been recorded as early as late February and can last as late as early October—until the collapse of water column stratification by the strong winds of tropical storms or by cold fronts. During early spring months, hypoxia is usually inconsistent and transient from late February through May, but it is most extensive, persistent, and most depleted in oxygen during the summer months of June, July and August (Rabalais and Turner, 2001). Extension of hypoxia into September and October is rare and is generally dependent on wind patterns. Other factors that contribute to the development, extent, and maintenance of bottom water hypoxia are water clarity, current patterns, wind speed and direction, nutrient concentration in the water column, quality of organic matter reaching the seafloor, and oxygen consumption rates in the sediments (Rabalais et al., 1991).

Second School of Thought

The nutrient-centric view of freshwater discharge and nutrient loading from the Mississippi River system being the cause for hypoxia in the Gulf of Mexico is widely accepted. However, a part of the scientific community believes that it is an oversimplification of many complex processes. The reasoning of critics is that hypoxia in the Gulf of Mexico is river-dominated; hence, it is not comparable with the traditional model devised for semi-enclosed estuarine systems (Hetland and DiMarco, 2008). Unlike in semi-enclosed estuaries, hypoxia in the Gulf of Mexico is a vertical process rather than the product of horizontal advection. Hence, hypoxia in the Gulf of Mexico is created, maintained and destroyed by the balance or imbalance between respiration and vertical mixing (Hetland and DiMarco, 2008). Occurrence of hypoxia in the Gulf of Mexico is ascribed to water column respiration from the east of Terrebonne Bay to the Mississippi

River plume. The cause for hypoxia from the west of Terrebonne Bay towards the Texas shelf is ascribed to bottom respiration. This difference in respiration is credited to different sources of organic matter and topographical variation in the Louisiana continental shelf. River borne nutrients are the main source of organic matter to the east of Terrebonne Bay and coastal wetland loss and upwelling are responsible for the hypoxic events to the west of Terrebonne Bay. This difference is due to the variation in the geometry of the shelf; east of Terrebonne Bay the shelf is steep and narrow, whereas west of Terrebonne Bay the shelf is broad and gently-sloping (Hetland and DiMarco, 2008).

In this alternative view, the hypoxic area in the northern Gulf of Mexico is separated into three zones based on the factors exerting control on development, maintenance and the severity of hypoxia. These three zones are located around the Mississippi and Atchafalaya River mouths. The hypoxia in each zone is regulated by different variables. The size of each zone changes depending on river discharge strength, currents and wind with unclear boundaries that change through time (Rowe and Chapman, 2002; Bianchi et al., 2010; Environmental Protection Agency, 2007).

Zone one is adjacent to the river mouth, where the sediment deposition is highest, and hypoxia is controlled by the respiration of organic carbon from the river and nutrient-induced eutrophication. Here the water column is highly turbid due to sedimentary material coming from the river. The high sedimentation of particulate organic carbon coming from the river induces light limitation; thus, low light penetration inhibits phytoplankton production in this zone. These high rates of sediment accumulation increase the high biological oxygen demand. An anaerobic metabolism of allochthonous

material and strong stratification will induce hypoxia (Rowe and Chapman, 2002; Bianchi et al., 2010; Environmental Protection Agency, 2007).

Zone two is an intermediate zone farther away from the river mouths where the phytoplankton production is high because of improved light levels due to decreased turbidity and high nutrient levels. High rates of primary production, strong stratification, and fast rates of water column respiration will induce bottom water hypoxia. Here, the nutrient-centric model applies and decomposition of deposited organic matter on the sediment is aerobic in the initial stages. Sustained phytoplankton production in the euphotic zone, would encourage the anaerobic decomposition in the sediments, and will intensify the hypoxia (Rowe and Chapman, 2002; Bianchi et al., 2010; Environmental Protection Agency, 2007).

Zone three occurs where water column stratification plays a significant role in the development and maintenance of hypoxia. It is the largest zone where the freshwater discharged by the river regulates hypoxia. Nutrient load in the surface waters is nearly zero hence, the local phytoplankton production is low. Labile organic matter introduced from the adjacent zone two deposited on the bottom sediment might drive aerobic respiration in this zone. Hence, the sediment respiration is more important than the water column respiration. In this zone, though the aerobic sediment respiration is important, hypoxia is largely controlled by the persistent strong stratification, which acts as an essential barrier to water column mixing preventing the ventilation of bottom water. However, pre-existing low oxygen concentration in the bottom layer is prompted by the predominant westward flow of river discharge, and the continuing metabolic demand of

oxygen in the bottom waters likely to induce hypoxia in this zone (Rowe and Chapman, 2002; Bianchi et al., 2010; Environmental Protection Agency, 2007).

Though this alternative model provides new and sophisticated conceptual ideas, it is not free from criticism. Other studies have suggested that this alternative model ignores the westward flowing Louisiana coastal current, which is presumed to carry bottom waters with high nutrient concentration along the coast to fuel the phytoplankton production in the northern Gulf of Mexico (Bianchi et al., 2010). Apart from that, there are uncertainties around the relative importance of allochthonous organic carbon as the chief cause of hypoxia in zone one. Other studies have showed dominant *in-situ* phytoplankton production immediate to the Mississippi River plume, which is presumed to be a low phytoplankton production zone by this model (Environmental Protection Agency, 2007). Though there are certain degrees of ambiguity in both the hypotheses, this study was designed based on the widely accepted nutrient-centric model with an anticipation that this research would either affirm or differ from either of the two models.

Effects of Hypoxia on Macrobenthos

Elevated input of nutrients and organic materials to any aquatic system leads to eutrophication, which in turn brings changes in the abiotic and biotic factors regulating the shape and structure of the faunal and floral community within that system. The fauna living in marine sediments are typically grouped into three size categories based on the shortest dimension of their body size (Levinton, 2001): microfauna (< 0.1 mm), meiofauna (from 0.1 mm to 0.5 mm) and macrofauna (> 0.5 mm). Benthic macrofauna, or macrobenthos, are an important link in the food web; they convert the sediment organic content to body mass and serve as food for higher trophic-level organisms

(Herman et al., 1999). Their limited mobility and relatively longer lifespan (years to decades) compared to the micro- and meiofauna, make them good indicator species for environmental monitoring and assessment. Macrobenthos more accurately reflect the changes in environmental quality at a particular location over a long period (Herman et al., 1999). Macrobenthos respond to their surrounding environment by altering the character and size of their community. In fact, the variation in organic matter is one of the prime reasons for variations in the structure of benthic communities in coastal marine environment (Pearson and Rosenberg, 1978; Herman et al., 1999).

Any changes in the benthic invertebrate community structure can be assessed by identifying and enumerating the taxonomic groups or feeding guilds (or a combination of both), depending on the objective of the study. The taxonomic-group approach is warranted, if the objective of the study is to measure the biodiversity or the community response to a given stress (such as hypoxia). If the objective of the study is to measure the ecosystem condition, the feeding guild approach will likely provide the best information in that regard (Cummins et al., 2005). To assess the ecosystem response, as well as the community response to a given stressor, a combination of taxonomic groups and feeding guild analysis should be employed.

Typically, the taxonomic groups approach is implemented by measuring species diversity, abundance and biomass (SAB). These measures are the basic and central theme for the greater part of benthic community investigations (Pearson and Rosenberg, 1978). Any variations in the physical environment often result in spatial and temporal changes to the SAB parameters of a macrobenthic community. Hence, SAB parameters of the macrobenthic community will fluctuate as a response to hypoxia (Rumohr et al.,

1996) on the Louisiana shelf, and are useful indicators of hypoxia history.

Equilibrium and Pioneering Species

In a marine benthic ecosystem, the sediment and the animals living within that sediment influence each other to create a unique benthic community structure (Rhoads and Boyer, 1982). Properties such as current speed, grain size, organic matter concentration, dissolved oxygen concentration of pore-water, and depth of the redox-potential discontinuity (RPD) can determine the benthic community structure. Conversely, the animals living in the sediment can change the physicochemical properties of sediment such as permeability, porosity, erodibility, shear strength, and RPD depth by biological activities such as feeding, movement, and burrowing (Snelgrove and Butman, 1994). The response of a benthic community to any environmental variable defines its structure, and the reaction of each species to these variables is a function of their genetic and evolutionary makeup (Pearson and Rosenberg, 1978). Each species has its upper and lower limits that are defined by its genetic traits and evolutionary history. Hence, the concept of "niche limits" plays a major role in the inclusion or elimination of a particular species from a community experiencing a particular environmental stress (Pearson and Rosenberg, 1978). Therefore, if the environmental stress is within an animal's niche limits, then the species will survive and adapt to that particular environmental stressor. If an environmental stressor exceeds the niche limits of a particular species, it will be replaced by another species that is more capable of responding to that particular environmental stressor (Pearson and Rosenberg, 1978). This paradigm is well suited for macrobenthos living in a hypoxic environment, where dissolved oxygen is a niche-limiting environmental stress factor. In a hypoxic

environment, macrobenthos sensitive to low dissolved oxygen concentration will be replaced by the macrobenthos that are less sensitive to hypoxic conditions.

According to Pearson and Rosenberg (1978), macrobenthos living in a stable environment and macrobenthos living in oxygen-limited environments have very different genetic and evolutionary traits, in accordance with the *r*/*K* (growth rate/carrying capacity) selection theory of ecology. This theory states that organisms living in a stable environment typically produce fewer offspring (with low mortality) compared to the organisms living in an unstable environment, which produce many offspring as an evolutionary strategy for species persistence despite high mortality rates (Heylighen and Bernheim, 2004).

Organisms classified as *r*-selected have evolved strategies to persist in unstable, frequently perturbed environments. The *r*-selected organisms are generally small, mature early, and survive to reproduce only once (but produce numerous offspring). Hence, the energy expended to produce a single offspring is low and consequently their offspring are metabolically "inexpensive." The offspring experience high mortality rates, and only a few individuals survive into adulthood.

In contrast, the *K*-selected organisms have evolved different strategies to persist in stable, less disturbed environments. The *K*-selected organisms are generally large, produce only few offspring, and often provide prolonged parental care. They reach maturity late, and an individual will usually survive to reproduce more than once in their lifetime. Their life expectancy is long because the energy used to produce a single offspring is high and, hence, more individuals are expected to survive into adulthood when compared to *r*-selected species (Heylighen and Bernheim, 2004).

Pearson and Rosenberg (1978) were able to demonstrate this theory's applicability to the macrobenthos community. In an unstable benthic ecosystem, initial colonizers arrive after the denudation of benthic fauna due to a significant environmental disturbance (such as bottom water anoxia/hypoxia), to utilize the unexploited space and excess supply of food. These opportunist species have all the traits of r-strategists. When the hypoxia is annulled, the environment recovers and eventually becomes a stable ecosystem where the K-selected equilibrium species ultimately replace the r-selected opportunist species, thereby reflecting a more mature macrobenthic community.

The opportunist species thrive in unstable conditions because of their reproductive and growth patterns that allow them to capitalize on sudden environmental change that provides them with a new and unexploited niche. Opportunist species thrive in hypoxic environments due to increased food supply, altered physical and chemical conditions of sediments (Figure 2, panel A), and reduced pressure from biological interactions, such as competition and predation, the lack of which allows the development of large populations (Pearson and Rosenberg, 1978).

Pearson and Rosenberg's SAB model describes the transition of the benthic community from K-selected to r-selected over space and time along the increasing organic matter gradient, according to a predictable stressor-response relationship (Figure 2). They concluded that genetically flexible (can withstand wide fluctuation in environmental variables) organisms have a higher survival rate in an unstable environment than genetically rigid (can only sustain small range of fluctuations in environmental variables) organisms, because genetically flexible organisms can withstand and adapt to unstable conditions better than genetically rigid organisms. Hence,

genetically more flexible opportunist organisms are found in unstable low oxic or

hypoxic environments. Thus, opportunist macrobenthos species are considered good

indicators of environmental disturbance related to hypoxia.
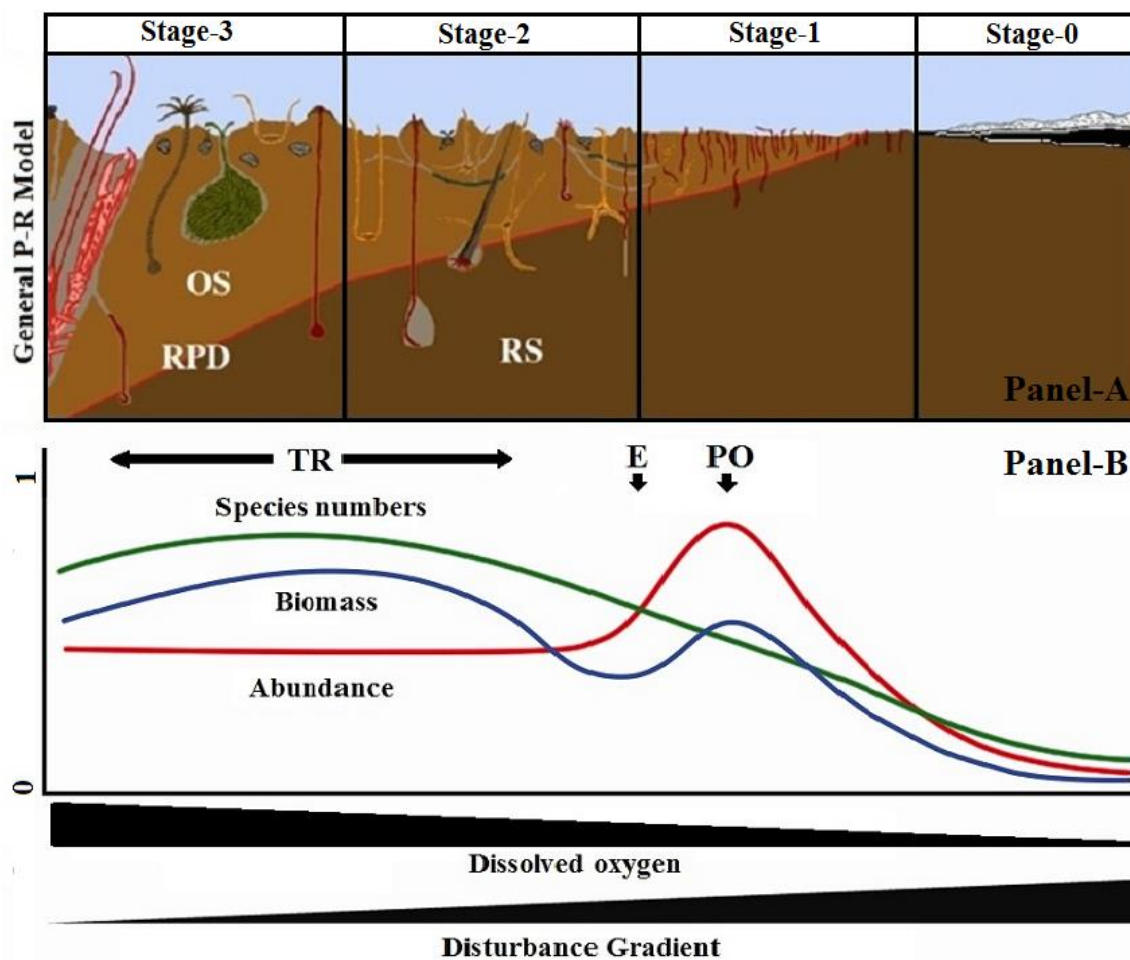
Figure 2. A graphical representation of the Pearson and Rosenberg (1978) SAB model, illustrating the changes in species richness, total abundance, and total biomass along a gradient of organic enrichment and decreasing dissolved oxygen concentration. PO, peak of opportunists; E, ecotone point; TR, transition zone; OS, oxidized sediment; RS, reducing sediment; RPD, redox potential discontinuity layer; General P-R Model, generalized Pearson and Rosenberg model. Source: Pearson and Rosenberg (1978).

The use of "indicator species" to evaluate the status of ecosystems is one of the

earliest and most reliable approaches used in ecological investigations (Pearson and

Rosenberg, 1978). Indeed, the macrobenthos community structure is a good indicator of the condition of the ecosystem because groups of species are better indicators of ecosystem perturbation than just a single species or total abundance. Additionally, using groups of endemic benthic organisms is useful in forming comparable and informative inferences of community degradation and recovery in diverse ecosystems (Magni et al., 2009). A particularly important characteristic of a good ecological indicator is the presence of a strong stressor-response relationship for variables, like macrobenthos species richness, based on faunal abundance or biomass (Magni et al., 2009). The Pearson-Rosenberg model of macrobenthic succession, as it relates to eutrophication and hypoxia, uses a classic and well-tested stressor-response relationship.

<div align="center">Pearson-Rosenberg Model</div>

Pearson and Rosenberg developed the model using the data from semi-enclosed, low-energy water bodies like fjords and sea lochs, which are characteristically high deposition environments with a long residence time. In the model, Pearson and Rosenberg explained the stress-response relationship between the macrobenthic community and the organic enrichment in those environmental settings. In this investigation, underlying principles of Pearson-Rosenberg model will be tested in the dynamic, open-water continental shelf environment of northern Gulf of Mexico. This model will be used to understand the stress-response relationship between the macrobenthic community and seasonal hypoxia. On the LaTex shelf, hypoxia is a seasonal phenomenon during summer months, where the bottom water oxygen concentration decreases as the water column stratification and organic enrichment increases. In this study, bottom water dissolved oxygen concentration will be used as

proxy for organic enrichment. Because dissolved oxygen concentration functions in an opposing fashion to organic enrichment, as the organic enrichment increases the dissolved oxygen concentration decreases.

Pearson and Rosenberg (1978) describes the general pattern of benthic community response to eutrophication that leads to hypoxia, and then to anoxia (Figure 2). In this model, Pearson and Rosenberg looked at changes in the benthic community structure along a gradient of organic enrichment and used these changes in the benthic community structure as a bioindicator to classify the condition of the ecosystem. They used the group of endemic species as bioindicators, whose distribution was charted over the gradient of organic enrichment using the species richness, abundance, and biomass (SAB) of the community. This SAB model is centered on alterations occurring in the species richness, abundance, and biomass parameters on a decreasing organic input away from a point source. These parameters define change not only on a spatial gradient but also on a temporal scale in organic enrichment-induced, low-oxygen or hypoxic systems. The SAB model is applicable to any system experiencing eutrophication and the consequential effects of eutrophication, such as hypoxia and anoxia (Pearson and Rosenberg, 1978).

The SAB model categorizes the sediments of a eutrophic system into five different zones, defined in terms of spatial and/or temporal proximity to the point source of pollution: grossly polluted, polluted, ecotone point, transitory, and normal. The sediment at the point source, where the organic input is highest and oxygen is lowest, is devoid of macrobenthos and only few meiobenthos can be found in this zone. Farther away from the point source, opportunist species are projected to increase in abundance

slowly to reach a peak in response to eutrophication, with a corresponding small and initial peak in the biomass because of high abundances of *r*-selected opportunist species. This increase is attributed to the increased abundance of one or two opportunist species that are capable of colonizing the empty niche with nonexistent competition and abundant food supply from eutrophication. The next point along the organic enrichment gradient is the ecotone zone that Odum and Odum (1959, p. 25) defined as "a transition between two or more diverse communities, the ecotone community contains many of the organisms of each of the overlapping communities and organisms characteristic or restricted to the ecotone." In the ecotone zone, the macrobenthos assemblage is comprised of organisms from both polluted and transitory zones. The sediments in this zone have high abundances of certain opportunist species but with the decreasing biomass compared to adjacent zones. Beyond the ecotone zone is a transition zone (Figure 2) where the biomass reaches its secondary peak and subsequently its highest values. The meaningful explanation for this peak in benthic biomass is that organic matter in the sediment is high enough to provide a rich food source for large *K*-selected species but not high enough to seriously decrease the oxygen level. Beyond this point, species richness and abundance reach stable values on the SAB curve against a decreasing organic input and the benthic faunal assemblage gradually approaches the characteristics of a normoxic environment. Temporal changes in the basic parameters (SAB) of a benthic community are expected to occur in the same way as spatial changes, but along the gradient of time.

RPD and Vertical Disequilibrium

Macrobenthos community structure changes not only horizontally, but also vertically in the sediments. The vertical changes in macrobenthic community structure

with increasing organic loading are a response to changing dissolved oxygen concentration in the overlying water and changing redox potential discontinuity (RPD) depth (RPD marks the transition from chemically oxidative to reducing processes). Given that dissolved oxygen plays a prominent role in controlling the SAB of benthic communities, it also affects biogeochemical cycling of phosphorus, nitrogen, manganese, iron, hydrogen sulfide and methane (Santschi et al., 1990). Because macrobenthos rely on dissolved oxygen for their respiration, the amount of dissolved oxygen affects mobility, and it is this activity (related to feeding) that mixes and irrigates the sediments (Glud, 2008). This activity builds a thin layer of oxidized sediments near the water-sediment interface. Normally, dissolved oxygen enters only the top few millimeters of the sediment by molecular diffusion at the water-sediment interface (Glud, 2008; Kristensen, 2000). However, dissolved oxygen penetrates deeper through bio-irrigation accomplished by burrowing of macrobenthos (Tyson and Pearson, 1991; Diaz and Rosenberg, 1995; Nilsson and Rosenberg, 1994). Oxygenated water enters the burrows either by advection/diffusion or by animals actively pumping oxygenated water into the burrow. Once oxygenated water enters the burrow, it diffuses into the pore spaces within the surrounding sediment of the burrow walls. Therefore, bioturbation, bio-irrigation and burrow-building activities of infauna are critical to sustaining oxidized conditions deeper in the sediment (Rosenberg et al., 2001).

This animal-sediment interaction changes during hypoxic conditions, altering the structure and behavior of the benthic community. The reduction of bioturbation (due to the lack of dissolved oxygen supply to macrofauna) is reversible if the hypoxia event is not intense or prolonged. When hypoxia leads to mass mortality, the change in

bioturbation rate is irreversible unless the benthic community is completely re-established (Rosenberg et al., 2001).

As evidence of this phenomenon, Aller (1982) observed the vertical distribution of benthos to be limited to the uppermost layer of the sediment because of a shallow RPD depth in an organically enriched region where dissolved oxygen was low. He observed that the area was dominated by a few colonizing, small-bodied, opportunist (*r*-selected) species. He also observed the deepening of the RPD depth as the distance from the source of pollution increased. Outside the area of organic enrichment, the benthic faunal community was diverse, contained large-bodied organisms creating large, deep burrows, and consisted of many feeding guilds, indicating a mature community with equilibrium (*K*-selected) species (Nilsson and Rosenberg, 2000; Aller, 1982; Pearson and Rosenberg, 1978).

The changes in animal-sediment interactions also alter geochemical processes, thereby changing chemical gradients in the sediment. Not only is oxygen used for respiration by benthic organisms, it is also used as an electron acceptor in oxidizing the reduced compounds produced by bacterial metabolism in anoxic sediments. However, in the absence of oxygen, microbes can exploit other compounds as electron acceptors such as NO_3^-, MnO_4, $FeOH$, SO_4^{2-}, and $(CH_2O)_n$ which are reduced to N_2, Mn^{2+}, Fe^{2+}, HS^- and CH_4, respectively (Glud, 2008).

Hydrogen sulfide (H_2S), widely present in marine sediments, is a result of bacteria using sulfate as an electron acceptor while utilizing organic material within anoxic sediments and is highly toxic to benthic fauna (Glud, 2008). Because hydrogen sulfide is prevalent in hypoxic marine sediments, it is one of the most important environmental

factors controlling benthic community structure in highly polluted and/or organically enriched areas. The presence of hydrogen sulfide is usually restricted to the deeper anoxic sediment layers below the RPD in normoxic conditions. However, during hypoxic conditions the influx of organic material increases the sulfate reduction rate, which, in turn, shallows the RPD depth and increases H_2S concentration in marine sediments (Wlodarska-Kowalczuk and Ianas, 1996), exposing macrobenthos species to an increased concentration of toxic H_2S.

Role of Feeding Guilds in Ecological Succession

In addition to species richness, abundance, and biomass, environmental stress also affects the trophic structure of the macrobenthos community, which ultimately leads to a reworking of the feeding guild composition. A feeding guild is defined as a group of different species with similar, co-occurring functional traits that affect ecosystem processes in the same way. Feeding guilds are possibly the most evident features that can explain the flow of energy, in the form of carbon and other biologically mediated materials, through feeding interactions within a particular community. The transfer of energy (and feeding interactions) within an ecosystem are functional rather than structural traits of the community (Pearson and Rosenberg, 1978). When the structure of the benthic community changes, those changes also affect the functional traits of the community. Therefore, feeding guilds analysis of the macrobenthos community is useful in examining the ecosystem responses to stress along the eutrophication-induced hypoxia gradient (Pla et al., 2012).

Feeding guilds are one of the fundamental parameters of benthic community analysis. However, lack of knowledge on feeding habits of many benthic species and the

complexity in accurately assigning the single feeding habits to a feeding guild have made it a less popular parameter for benthic community analysis. Apart from that, many of the benthic species can swap between feeding habits as a stress-response adaptation (Pearson and Rosenberg, 1978; Fauchald and Jumars, 1979). Nonetheless, a firm understanding of the feeding habits and mobility limitations of benthic fauna could explain several aspects of the community structure. For instance, assigning a trophic level to an organism (Leibold et al., 1997) can allow generalizations to be made about community succession and the stress-response of an ecosystem (Pearson and Rosenberg, 1978).

The feeding guilds of benthic fauna can be divided into five broad groups to include 1) suspension feeders (SF); 2) surface deposit feeders (SDF); 3) sub-surface deposit feeders (SSDF); 4) herbivores (Herb); and 5) carnivores (Carn). The feeding guilds of benthic fauna can be sub-divided into as many as 22 groups (Fauchald and Jumars, 1979) based on feeding habits, feeding apparatus, food type, and motility. These sub-divisions can increase the descriptive accuracy of benthic communities and help in the understanding of the elasticity (the rate at which an ecosystem can returns to its each original conditions) of the ecosystem (Pearson and Rosenberg, 1978; Fauchald and Jumars, 1979; Nilsson and Rosenberg, 2000). Generally, the number of functional groups decreases as the dissolved oxygen concentration decreases (Pearson and Rosenberg, 1978). A diverse community with intricate food-web interactions will generally be reduced to a simplified community containing only deposit feeders as the stress level increases. Despite the broad groupings of feeding behavior, the broadly defined guilds are still useful in giving an overall description of some prominent ecosystem processes (Pearson and Rosenberg, 1978).

The dominance of deposit feeders in the population is a response to the increasing organic influx, which leads to the exclusion of suspension feeders in the population, via a process known as "trophic group amensalism" (Rhoads and Young, 1970). The increased number of deposit feeders results in increased feeding and burrowing activity at the sediment surface, which renders the sediment unsuitable as a substratum for the attachment or survival of suspension feeders by decreasing the sediment stability. Other factors that contribute to the elimination of suspension feeders are high deposition rates of particulate organic matter resulting in ciliary clogging, burying of limited motility species within the sediment, and the alteration of critical physico-chemical conditions related to the changing RPD (Pearson and Rosenberg, 1978).

Understanding the composition of benthic feeding guilds along a stress gradient offers a useful and interpretable insight to changing ecological conditions and successional stages as a response to variation in that environmental stressor. For example, the abundance of deposit feeders typically reaches its maximum at high organic influx, whereas suspension feeders reach their maximum at somewhere around the center of the gradient, and carnivores are found in areas of both high and low organic influxes along the gradient (Pearson and Rosenberg, 1978). High organic fluxes usually result in benthic communities that are mostly composed of deposit feeders restricted to only the top few millimeters of the sediment, thus making them vulnerable to the predators that are capable of surviving harsh hypoxic conditions (Pearson and Rosenberg, 1978).

Ecological Succession

Ecological succession is a process that leads the communities to maturity or stability. According to Odum (1969, p. 262), the ecological succession follows three

basic principles. (I) Succession of community is an orderly process, fairly directional, and hence predictable. (II) Succession is a biological process controlled by the physical environment, which determines the pattern, rate, and extent of community development. (III) Succession end is marked by the stabilization of an ecosystem where biomass attains a maximum and biological interactions of organisms are fueled by available biomass.

Successional stages are shaped by the interaction between environmental stresses, faunal adaptability, and species/guild representation within the ecosystem. In the case of environmental disturbance, the succession of a benthic community is a continuous process, where faunal assemblages change along a stress gradient, where species-rich, stable communities are transformed into species-poor, (opportunist dominated) transient communities and then on to denuded afaunal regions, through specific, successional stages. Conversely, if environmental conditions are favorable, the disturbed benthic community can reverse the succession from any stage and return to the stable, mature community (Rumohr et al., 1996).

Pearson and Rosenberg (1978) identified and labeled successional stages based on measured variables, where the scale of transformation was large, and they used reference points to evaluate the outcome of certain ecological changes. The objective of this investigation necessitates a detailed description of the different successional stages of the macrobenthos, specifically in relation to hypoxia. The basis for the characterization of the successional stages is the Pearson and Rosenberg model (1978). The stages of succession are defined below in terms of the SAB parameters and the associated feeding guilds.

Stage 0: Grossly Polluted

The environment around the discharge point or source of organic enrichment is considered as stage 0. Here, the sediment is grossly polluted and species found in this successional stage are few in number and small in size. At this stage, species diversity, abundance, and biomass are at their lowest (Table 1).

Stage 1: Polluted

At the polluted stage, the community is composed of a few pollution-tolerant, *r*-selected, opportunist species, with only a few species in high abundance. This stage is the peak of opportunists (PO) (Figure 2). The species diversity is more than that of Stage 0 but less than or equal to that of Stage 3 (Table 1). The abundance is highest of all the stages and the biomass is more than or equal to Stage 1 or 3. The populations within the study area typically comprise high numbers of the sub-surface-deposit-feeding, polychaete-opportunist *Capitella* and the surface-deposit-feeding, polychaete-opportunist *Scolelepis*.

Table 1

Summary of defining characteristics of four successional stages in the Pearson and Rosenberg model (Pearson and Rosenberg, 1978; Nilsson and Rosenberg, 2000; Rosenberg et al., 2001).

Stages	0	1	2	3
Terminology	Grossly polluted	Polluted	Transitory	Normal
Diversity	Lowest	>0, >3	Highest	>0, > 1, and < 2
Abundance	Lowest	Highest	<1, > 0 and 3	<1, > 0 and 2
Biomass	Lowest	≥ 0 and 3	Highest	<2, = 1 and >0
Life strategy	Few animals	*r*-selected	Both *r-K* selected	*K*- selected

The Ecotone Point (boundary between Stages 1 and 2)

Ecotone communities are generally composed of members from differing, but adjacent, communities. In a successional continuum, changes in the ecotone point (E) (Figure 2) occur within a community rather than between communities; that is, *r*-selectees that dominate in initial pioneering communities co-exist with *K*-selectees that dominate in mature communities. In the successional continuum, two extreme communities (mature and pioneering) are very predictable (Pearson and Rosenberg, 1978), whereas intermediate stages between these two stages are unpredictable. The unpredictability is due to the mixing of adult mobile species from these communities with the settling larvae from the overlying water column, which act as the basis for the subsequent intermediate stages in the successional continuum. The ecotone point is situated between stages 1 and 2 and acts as a boundary marking two intermediate communities.

Pearson and Rosenberg (1978) identified the ecotone point as the stage occurring after the highest abundances of opportunist species occur in a polluted zone, but before the highest species richness occurs in a transitory zone. This region is poorly populated with many niches unoccupied. The biomass is low, and the abundance and number of certain species are high compared to adjacent zones. The community encountered on the polluted (Stage 1) side of an ecotone point is less diverse with fewer functional groups than are the communities growing on the transitory (Stage 2) side.

Stage 2: Transitory

Stage 2 is considered a transitory zone, in this successional stage. Oscillating, transitory, macrobenthos assemblages gradually progress towards a more stable mature

community, closely resembling the unpolluted environment assemblages. Species

diversity and biomass are highest in this stage, whereas abundance is less than in Stages 0

and 1, but more than or equal to that of Stage 3 (Table 1). Typical species populating this

stage are the polychaetes *Goniada* (Carn), *Chaetozone* (SDF)*, Pectinaria* (SSDF),

Myriochele (SSDF)*,* and *Pholoe* (Carn)*;* the bivalves include *Corbula* (SF); and the

holothurians (SDF).

Stage 3: Normal

In a normal stage, macrobenthos assemblages resemble a mature community

and are dominated by *K*-selected, deep-burrowing species with long life cycles. At this

stage as a community propagates from transitory to mature, the species diversity will

decrease slightly, and the first order opportunists will be absent at this stage. Abundance

will remain the same as that in the transitory stage due to improved species richness.

Biomass will decrease slightly due to increased competition under decreasing food

supply (Figure 2; Table 1). The population consists of a mature community with *K*-

selected species of echinoderms, bivalves, large polychaetes, and epifaunal crustaceans.

Hypotheses and Objectives

According to the nutrient-centric model, hypoxia in the northern Gulf of Mexico is tightly coupled with nutrient-rich, freshwater discharge from the Mississippi and Atchafalaya Rivers (Rabalais et al., 2007: Hetland and DiMarco, 2008: Bianchi et al., 2008). According to model, though these rivers discharge on to open continental shelf, the magnitude of flow, annual current pattern, and residence time of freshwater on the shelf suggest that the discharges are largely carried westward along the inner and mid LaTex shelf, particularly during the peak discharge time (spring) (Rabalais et al., 2007). The model also suggest that the shelf acts as an unbounded estuary stratified for the most part of the year. The stratification is primarily due to salinity differences in two water masses, which strengthens during summer due to increase in the sea surface temperature (Rabalais et al., 2007).

The model also hypothesizes that the hypoxia in the northern Gulf of Mexico develops due to westward horizontal advection of nutrient-rich freshwater discharged from the rivers (Hypoxia in the northern Gulf of Mexico, n. d.). The Pearson and Rosenberg model uses a stress-response relationship to evaluate the ecological condition, where the effect of a stressor on the benthic community decreases from the event source along a geographic and/or temporal gradient remote from that event. In the present investigation, four sites labelled A through D were chosen based on the frequency of hypoxia occurrence on the LaTex shelf in the northern Gulf of Mexico over a period of three decades from 1985 to 2005 (Baustian and Rabalais, 2009). The sites chosen for investigation are arrayed on the Louisiana continental shelf from east (proximal to the Mississippi River Southwest Pass outlet) to west (remote from the Mississippi River

outfall), thereby establishing a geographic hypoxic gradient from the Mississippi River that diminishes to the west.

Hypothesis 1 (H1): SAB Response

If there is a westward-diminishing gradient of hypoxia impact along the LaTex shelf, then the westernmost site (A) should contain the least stressed community, whereas the easternmost site (D) nearest the Mississippi River should contain the most stressed community.

Objectives for Hypothesis 1

To assess the spatio-temporal variability of the response to stress induced by seasonal hypoxia on the macrobenthos community structure at sites A, B, C and D using the SAB parameters species diversity, abundance, and biomass.

Hypothesis 2 (H2): Feeding Guild Response

If there is a westward-diminishing gradient, then the westernmost site A should exhibit a diverse community with diverse feeding guilds, whereas the easternmost site D should contain a less diverse community dominated by only a few feeding guilds.

Objectives for Hypothesis 2

To test/reaffirm the interpretation of stress using SAB parameters with those based on feeding behaviors of the macrobenthos at sites A, B, C and D during spring and late-summer of one year and summer of the following year.

Dominance of opportunist species indicates deteriorated environmental conditions. Since hypoxia in the northern Gulf of Mexico is a recurring event, the affected sites would not have enough time to recover from their previous hypoxic incident. Thus, recurrence of hypoxia at the same site would lead to further deterioration of the recovery. This would promote the dominance of opportunist species. Therefore, the dominance of the opportunist species is a cumulative effect of hypoxia recurrence at a given site.

Hypothesis 3 (H3): Opportunist Species Response

If the above statement is true then site A should have a smaller percentage of opportunist species, whereas site D should have a greater percentage of opportunist species.

Objectives for Hypothesis 3

To explain the observed SAB parameters and feeding guild diversity by examining the relationship between low-oxygen conditions and the dominance of opportunist species. Also, explain the observed successional stages at all four sites.

Overview of Studies Objectives

1. To categorize the macrobenthic community at sites A, B, C and D as to their respective successional stages using SAB and feeding guild parameters.

2. To explain the response of the macrobenthic community structure to hypoxia in relation to the environmental variables of grain size distribution, bottom water dissolved oxygen concentration, sediment organic carbon content and the sediment C/N ratio.

3. To evaluate the ecological standing (successional stage) of the macrobenthic community on the northern Gulf of Mexico continental shelf along the 30-m isobath using the Pearson and Rosenberg model.

4. To establish the effect of hypoxia in structuring observed macrobenthic community successional stages in relation to percentages of opportunist species at all four sites.

CHAPTER II

METHODS

Study Area

Samples for the study were collected in the northern Gulf of Mexico, on the Louisiana continental shelf from west of the Mississippi River bird foot delta to just west of Atchafalaya Bay at 30 to 39 m water depth (Figure 3; Table 2). Four sites were chosen based on their history of hypoxia exposure, determined using the pre-existing bottom-water oxygen data collected during the annual, mid-summer, shelf-wide cruise conducted since 1985 by Nancy Rabalais (Rabalais et al., 2002; Baustian and Rabalais, 2009; Rabotyagov et al., 2014). Shallow water stations were avoided for their susceptibility to intense, episodic sediment reworking during seasonal storms and hurricanes, and all sites were chosen along the 30 to 39 m water depth contour to reduce the influence of physical disturbance induced anomalies on benthic communities (Figure 3).

Table 2

Latitude, longitude and water column depth (in meters) of sampling sites.

Site	Latitude	Longitude	Depth (m)
A	28º 39.2977'N	92º 22.8130'W	37.1
B	28º 36.4785'N	91º 14.4120'W	30.0
C	28º 30.1620'N	90º 50.0145'W	31.9
D	29º 00.7180'N	89º 44.9290'W	39.1
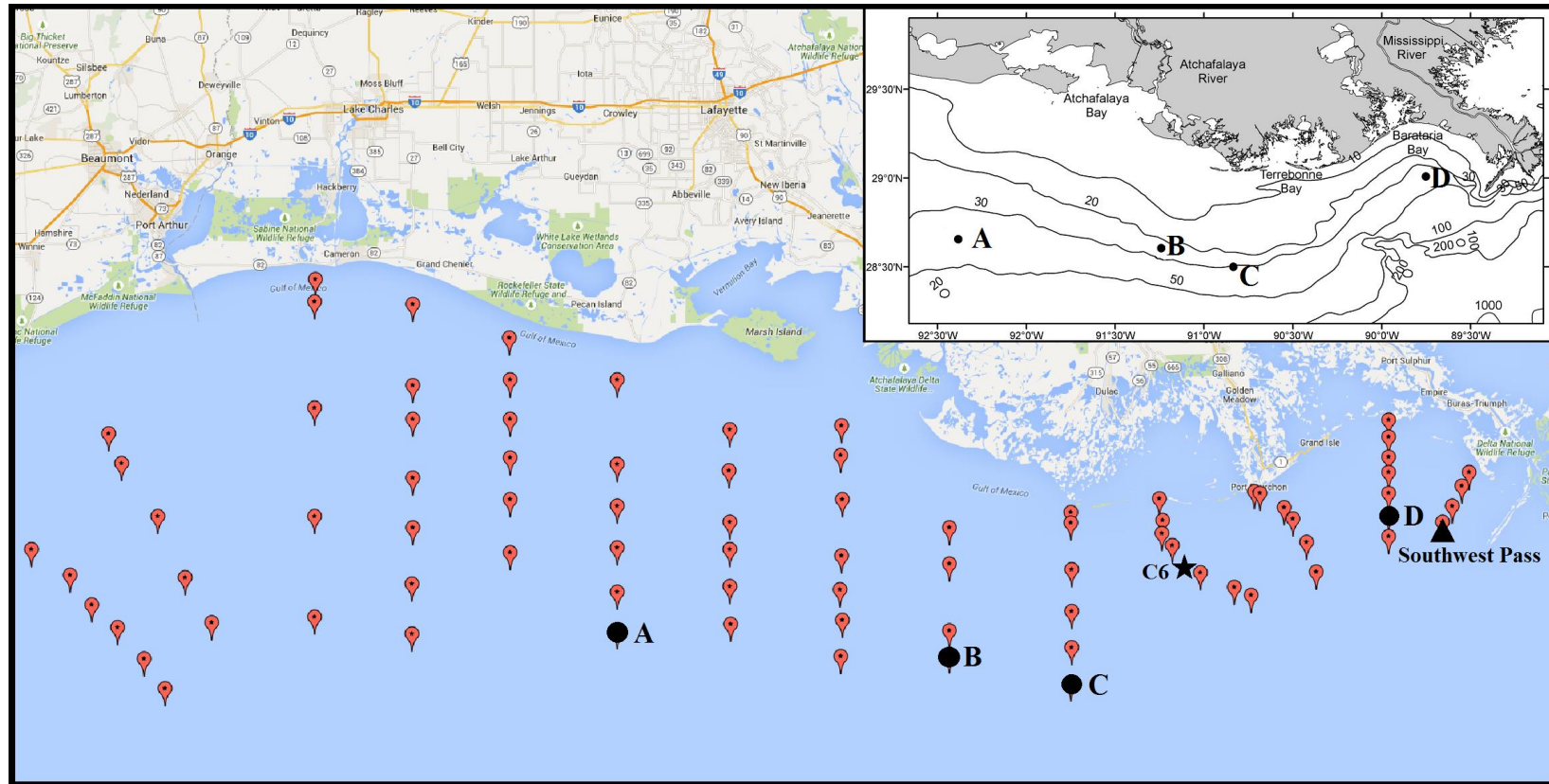
Figure 3. Map of the eastern LaTex shelf showing the locations of the four sites, the LUMCON shelf-wide stations, and N. Rabalais' C6 station. Water depth contours in the map inset are in meters.

LUMCON survey stations H7, E4, D5 and A6 were chosen and renamed as A, B, C and D respectively (Figure 3) for sample collection. Site A was located southwest of Atchafalaya Bay and was exposed to hypoxia $< 25\%$ of the times surveyed by Rabalais (Figure 4). Site B was located south of the Atchafalaya River and was exposed to hypoxia between 50% and 75% of the time (Figure 4). Site C was located southwest of Terrebonne Bay and was exposed to hypoxia between 25% and 50% of the time (Figure 4), and Site D was located west of the Southwest Pass of the Mississippi River bird foot delta and was exposed to hypoxia $\geq 75\%$ of the time (Figure 4).

Sites with similar sediment type were selected on the Louisiana shelf based on archived sediment data from the littoral database of the Naval Oceanographic Office, Stennis Space Center, Mississippi (pers. comm., Kevin Briggs, 2015). The objective was to sample the same benthic communities at each site and to avoid any sediment grain-size-related anomalies in the samples.
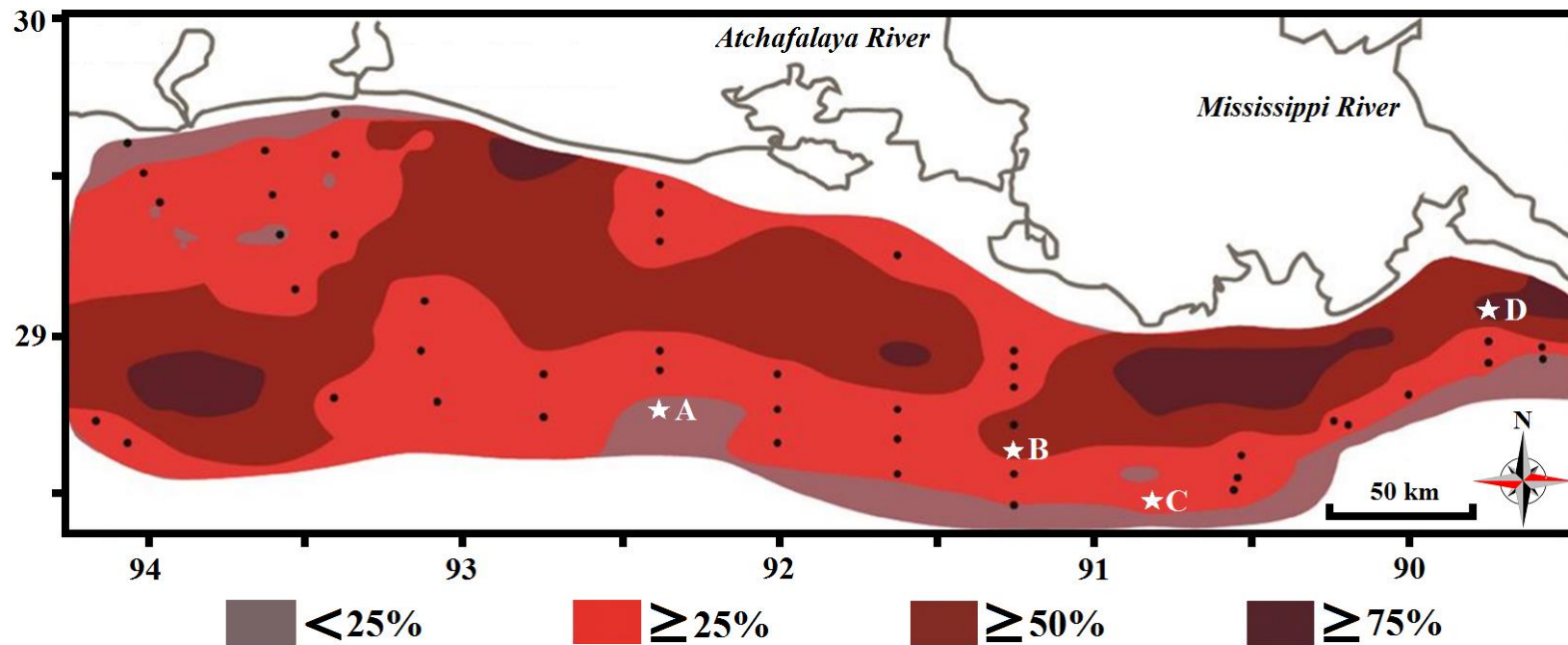
Figure 4. Frequency of hypoxia on the LaTex shelf for the past 23 years from 1985 to 2008. Percentage (%) in legend indicates the number of times and/or years that station recorded hypoxia (≤ 2 mg/L O_2) during the annual shelfwide mid-summer cruise conducted by N. N. Rabalais. Black dots are 60 to 80 stations sampled during the mid-summer cruise. White stars indicate the sites A, B, C and D chosen for this study based on their frequency of hypoxia. Longitudes are represented in degrees West on the horizontal axis. Latitudes are represented in degrees North on the vertical axis. *Source:* Rabotyagov et al., (2014).
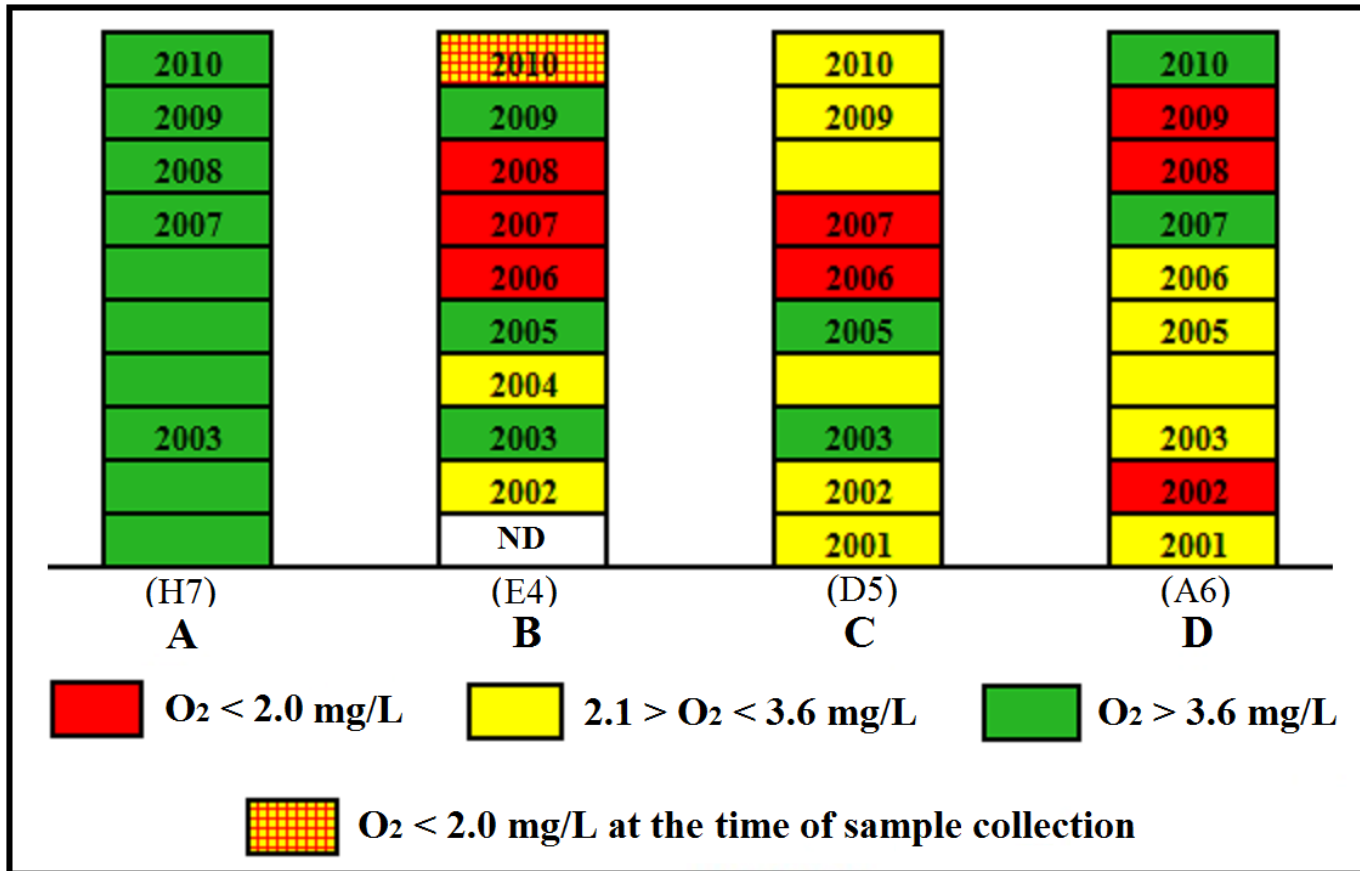
Figure 5. Recent frequency of hypoxia near the seafloor determined by LUMCON cruises at sites A, B, C and D for years 2001-10. The designations in parentheses correspond to station designations used by N. N. Rabalais' annual shelfwide mid-summer cruise. Blank year occurrences of oxygen concentration are inferred from mid-summer shelf-wide cruise protocol that terminated bottom water sampling of deeper stations along the shore-normal transect after consecutive unchanged measurements. ND = no data.

Experimental Design

Each site has a different character based on its pattern of exposure to hypoxia and the recovery time since the most recent occurrence of seasonal hypoxia. Based on historical hypoxia data collected from the four chosen sites (Figure 4), site A experienced hypoxia less than 25% of the measured times since 1985 and had no exposure to hypoxic bottom-water in the previous ten years (Figure 5). In contrast, sites B, C, and D experienced hypoxia more than 25% of the time since 1985, but varied in terms of their annual exposure in recent years (Figures 4 and 5).

Using these criteria, variations in exposure among the sites were established. Three cruises, in spring, late summer and mid-summer, were undertaken to collect the samples using the research vessel R/V *Pelican*: two cruises in 2009 and one cruise in 2010 (Table 3). The first set of samples was collected between March 30 and April 6, 2009; the second set of samples was collected during September 5-11, 2009; and the third set of samples was collected during August 3-9, 2010.

Site A was not hypoxic from 2001 until the first sample collection in 2009 (Figure 5); hence, this site was used as the reference site. Site B experienced seasonal hypoxia from 2006 to 2008 prior to the cruises in 2009, and it was experiencing hypoxia at the time of the cruise in 2010. Site C had not experienced seasonal hypoxia since 2007, after a previous exposure in 2006. Site D experienced seasonal hypoxia in 2008 and during sampling in September 2009 but not in 2010 (Figure 5).

Table 3

Cumulative number of months during which recovery could occur from the previously documented hypoxic events at sites B, C, and D before first, second, and third sample collections. Note that Site A did not experience hypoxia for an extended period prior to sampling and therefore served as the reference site.* implies that the site was hypoxic during sample collection.

Cruise	Spring 2009	Late-Summer 2009	Summer 2010
Sampling Dates	31 March-4 April	6-9 September	4-8 August
Site A	60	65	77
Site B	6	11	22*
Site C	18	26	34
Site D	6	1	9

All of the sites that experienced seasonal hypoxia were assumed to be in different phases of recovery because the time available to rebuild the community since the previous hypoxic event was different for each site. Therefore, community recovery from hypoxia begins at the conclusion of hypoxia, which typically occurs in early October of every year. Because there is no clear demarcation for the initiation of hypoxia, the time period between early October and the sample collection date was used to calculate the recovery period for each site (Table 3).

Based on these criteria, samples from Site B (spring 2009) should be representative of a macrobenthic community with a maximum of six months to recover from the previously documented hypoxic event (summer 2008). Because site B was not experiencing hypoxia during the sample collection in the late-summer 2009 cruise, the macrobenthos could have had 11 months of recovery time. Although this site was experiencing hypoxia during the summer 2010 cruise, the hypoxia had just developed

since the previous bottom-water sampling less than a week before and the collected

samples should be considered representative of a macrobenthic community with 22

months to recover from the previously documented hypoxic event in 2008.

The macrobenthic community at site C had a maximum of 18 months to recover

from the 2007-documented hypoxic event, before the samples were collected in the

spring 2009 cruise. Because there was no documented hypoxia at site C during 2009, the

macrobenthic community sampled during the late-summer 2009 cruise had 26 months of

recovery time. Because it is likely that this site did not experience hypoxia after the late

summer 2009 cruise, and there was no documented hypoxia at this site during 2010, the

samples collected in mid-summer 2010 should be representative of a macrobenthic

community with 34 months to recover from the 2007 hypoxic event.

The macrobenthic community from site D had only six months to recover from

the documented hypoxia event in 2008 by the time of the spring 2009 cruise. It was

documented as hypoxic immediately before the late summer cruise. The macrobenthic

community sampled at this site during the summer 2010 cruise was representative of one

that had nine months to recover from the hypoxia in 2009 (Table 3).

<div align="center">Sampling Procedure</div>

Sediment samples were collected at each of the four sites using Ocean

Instruments Bx-650 Box Corer (0.25 m^2-area) for each of the three cruises (spring 2009,

late-summer 2009, and mid-summer 2010). From each site, six box cores were collected

and from each box core, three sample subcores, each of area 53.4 cm^2, were collected for

macrobenthos sampling. Additional sample subcores were collected from box cores for

the measurement of sediment organic matter, sediment organic carbon and nitrogen ratio and sediment grain-size distribution.

Samples were processed immediately after coring. From each site, 9 out of 18 macrobenthos sample cores were randomly selected, extruded and sliced sequentially into seven sections at intervals of 0-1, 1-2, 2-4, 4-6, 6-8, 8-10 and 10-15 cm sediment depth (Figure 6). These samples were sieved through 0.3-mm Nitex mesh to collect organisms smaller than the macrofauna usually retained on a 0.5-mm mesh sieve. The smaller mesh was used because it was anticipated that the macrobenthos found in the hypoxia-affected area could be smaller as a result of oxygen stress and because it was important to capture newly recruited individuals due to recovery from hypoxia. After sieving samples through the 0.3-mm sieve, the benthic fauna retained on the mesh were immediately fixed in a 5% buffered rose Bengal-formalin solution to stain and preserve organisms while at sea. Later, all the collected fauna were transferred to 70% isopropanol solution in the laboratory for preservation. Because of smaller (0.3-mm) mesh size usage, some of the bigger meiofauna were also collected along with the macrofauna.
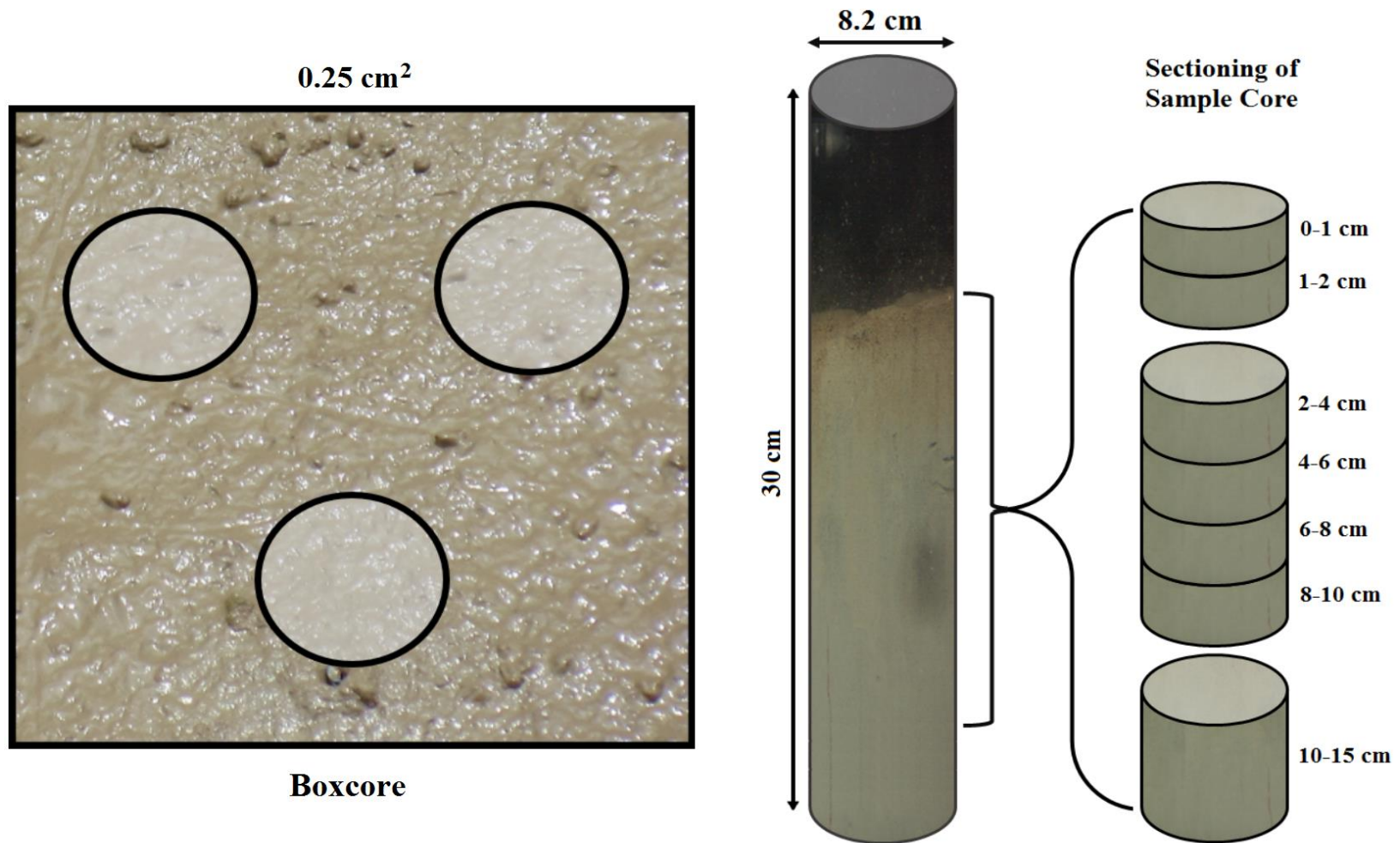
Figure 6. Schematic representation of the sampling and the sectioning procedure employed in the study to collect and analyze the macrobenthos samples.

Laboratory Procedure for Benthic Invertebrate Analysis

The preserved macrofauna were microscopically sorted from the debris, identified to the most specific taxonomic level (Appendix A) possible. Identified organisms were enumerated for abundance, weighed for biomass, and assessed as to vertical distribution within the sediment cores. Abundance found in a subcore of 53.4 cm^2 area was extrapolated to 100 cm^2 area and was expressed as number of individuals per 100 cm^2 (Appendix B). Biomass found in a subcore of 53.4 cm^2 area was extrapolated to 100 cm^2 area and was expressed as ash-free dry weight per 100 cm^2 (AFDW/100 cm^2) (Appendix C). Meiofauna larger than 0.3-mm mesh size collected along with the macrofauna were sorted, and identified to the lowest taxonomic level possible (Appendix D; table D1). The identified meiofauna were counted separately for total abundance and expressed as number per 100 cm^2 (Appendix D; table D2) and weighed separately for total biomass and expressed as AFDW biomass/100 cm^2 (Appendix D; table D3).

Since the sample cores were sectioned at 1, 2, and 5 cm intervals, some of the larger organisms were separated into two or more fragments during sectioning. These fragments were reunited with the head of that particular specimen and the specimen was assigned to the sediment depth at which the head was found. Biomass was measured as wet weight using a Mettler Toledo UMX2 ultramicrobalance. This instrument measures up to 2.1 g with readability of 0.0001 mg (0.1 μg) and repeatability (accuracy) of 0.00025 mg (0.25μg). The preserved specimens in 70% isopropanol were removed and transferred to a sheet of absorbent paper for 30 seconds to wick away excess moisture. Specimens were then transferred to a tared piece of tin foil and then to the ultramicrobalance. The specimens were weighed in a confined compartment of the balance, and weights were

recorded as soon as the reading was stable. Biomass was measured as wet weight (WW) then converted into ash-free dry weight (AFDW) for the enumerated individuals using conversion factors given in Ricciardi and Bourget (1998) and Greenstreet et al., (2007) as presented in Table 4. During the biomass measurement, the shells of molluscs were cracked before the weighing protocol described above was implemented.

Table 4

Multiplication factors used to convert WW to AFDW for individual taxa, according to Ricciardi and Bourget (1998).

Taxon	AFDW/WW	Notes
Polychaeta	0.156	
Gastropoda	0.063	
Scaphopoda	0.063	used Gastropoda
Bivalvia	0.055	
Amphipoda	0.165	
Isopoda	0.142	
Decapoda	0.165	
Mysidacea	0.155	
Cumacea	0.075	
Tanaidacea	0.140	average of all Crustacea
Brachiopoda	0.098	average of Bivalvia + Crustacea
Ophiuroidea	0.065	
Echinoidea	0.027	
Holothuroidea	0.082	
Porifera	0.105	
Actiniaria	0.133	
Nemertea	0.200	
Turbellaria	0.252	
Pripulida	0.065	
Sipunculida	0.110	
Echiurida	0.110	used Sipunculida
Ectoprocta	0.073	
Hemichordata	0.178	used Polychaeta/Nemertea
Phoronida	0.178	used Polychaeta/Nemertea
Pycnogonida	0.075	used Cumacea

Feeding Guild Diversity

All identified macrobenthos were assigned a feeding guild (Appendix E) from information obtained from Fauchald and Jumars (1979) for polychaetes and from the taxonomic sources listed in the Taxonomic References (reference section) for other taxa. Macrobenthos were grouped into five different feeding guilds: 1) suspension feeders (SF), 2) surface deposit feeders (SDF), 3) sub-surface deposit feeders (SSDF), 4) herbivores (Herb), and 5) carnivores (Carn). Most of the feeding guild information available in the literature was appropriate to family level. Feeding guild information for many taxa was found on the WoRMS (World Register of Marine Species) website (www.marinespecies.org). Information on feeding guilds for molluscs was obtained from the NMITA (Neogene Marine Biota of Tropical America) website (porites.geology.uiowa.edu/nmita.htm). If the information about feeding guild was not available for the particular species, the information available for genus or, failing that, the information for family was used.

Opportunist Species

All identified macrobenthos were examined for their opportunist lifestyle using information available in literature (Pearson-Rosenberg, 1978; Diaz and Rosenberg, 1995; Rakocinski et al., 1999; Borja et al., 2000; and Salen-Picard et al., 2003). Opportunist species were categorized into three different groups: V, IV, and III (Appendix F). Group V organisms are first-order of opportunist species to appear in a highly stressed environment. Group IV organisms are second-order of opportunist species to appear after Group V opportunists species. Group III organisms occur under normal conditions but

are tolerant to high organic loading, and their population increases under organic enrichment (Borja et al., 2000).

Statistical Data Analysis

The distribution of macrobenthos abundance, biomass and estimated average individual biomass data collected at each site during the three cruises were examined for normality using the Shapiro-Wilk normality test (Appendix G; Tables G2, G3 and G4) as well as Quantile-Quantile plot (Appendix G; Figures G1, G2 and G3). The data were not normally distributed hence the range, minimum, maximum, median, lower quartile, upper quartile, and outliers were reported. The median values of macrobenthos abundance, biomass and estimated average individual biomass from nine replicate sample cores from each site were tested for differences using the Mann-Whitney U-test (Appendix H) (H_0: there is no significant differences in medians between sites).

Nine replicates sample cores for each site during the three cruises were assessed for species diversity using both the Shannon diversity index (H') and the inverse Simpson's index ($1/D$). The inverse Simpson index ($1/D$) was preferred over the Shannon index to explain the variation in diversity between sites and samplings because of its robustness, insensitivity to sample size and consistency in ranking assemblages. The distribution of values for the Shannon diversity index (H'), Pielou's evenness (J), Margalef's index of species richness (SR), and inverse Simpson's index ($1/D$) were examined for normality using the Shapiro-Wilk normality test (Appendix G; Tables G5, G6, G7 and G8) as well as Quantile-Quantile plot (Appendix G; Figures G4, G5, G6 and G7). The Shannon diversity index (H'), and Pielou's evenness (J) values were not normally distributed hence the range, minimum, maximum, median, lower quartile, upper

quartile, and outliers were reported. The median values from nine replicate sample cores from each site were tested for differences using the Mann-Whitney U-test (Appendix H). The Margalef's index of species richness (SR) and inverse Simpson's index ($1/D$) values were normally distributed hence the mean and standard deviation were reported. The values from nine replicate sample cores from each site were tested for differences using the parametric Welch's t-test (Appendix H). Welch's t-test compares two independent samples from different locations and tests unequal variances (H_0: there is no significant difference in variance between sites).

Sanders-Hurlbert's rarefaction was used to compare species diversity between sites and between sample collections. Species richness exhibits a linear relationship with sample size and sampling effort. Rarefaction is a method used to correct uneven sample size of assemblages when comparing their taxonomic diversity (Magurran, 2004; Gotelli and Colwell, 2010). It is considered an ecologically meaningful substitute for other less satisfactory diversity indices (Oksanen et al., 2015). The rarefaction curve technique is also a widely used technique to study benthic community changes induced by organic enrichment (Pearson and Rosenberg, 1978).

Because the sample cores collected for macrobenthos analysis were sorted and processed for abundance and biomass at seven discrete depth intervals (Figure 6), total abundance and biomass for each site, and sampling were represented as a function of sediment depth with spindle diagrams that distributed the seven sections among 15 one-cm intervals. Notations were used for identification of sample cores: the first number specifies the cruise number, 1, 2 or 3; the second letter specifies sites A, B, C or D; and the third number specifies the subcore number 1 to 9.

To understand and evaluate commonly occurring species associations, the Bray-Curtis dissimilarity coefficient was used to measure the ecological distance between and within sample collections among sites and also used to identify species associations within and between sites. The influence of rare species is reduced and the influence of dominant species is increased in the calculation of the Bray-Curtis distance measurement. If the dataset is strongly dominated by a few species, then proper data transformation should be employed to get the correct outcome. Because the dataset had a sparsely populated station-species matrix, a $\log_{10}(n+1)$ transformation was applied prior to the Bray-Curtis analysis. If two assemblages share many of the same species, then the ecological distance between them is small and the Bray-Curtis distance (which ranges from $0.0 - 1.00$) is small; if the assemblages share only a few species then the ecological distance is large.

The Bray-Curtis analysis was performed on the transformed species abundance data to estimate the dissimilarity between different species assemblages. The unweighted pair-cluster method using arithmetic averages (UPGMA) was used to amalgamate clusters into dendrograms. UPGMA allows a subcore or a species to join a cluster at the mean of the distances between a subcore or a species and all the subcores or species of that cluster. When two clusters of subcores or species join together, they join at the mean of the distances between all the subcores or species of one cluster and all the subcores or species of the other cluster.

All observed species were used to generate the Q-mode Bray-Curtis dendrograms that measure the dissimilarities in association between sample cores for both sites, as well as sample collections. Species that occurred only four or more times were used to

generate the R-mode dendrograms that measure the dissimilarities in association between species at individual sites, as well as each sample collections. The rare species that occurred less than four times were removed to reduce the noise in the data as well as to maximize robustness of the comparisons.

Several multivariate methods were used to explore community structure: non-metric multi-dimensional scaling (nMDS), canonical correspondence analysis (CCA), and principal component analysis (PCA). To extract the strongest patterns in community structure, the algorithms for nMDS, CCA (vegan package by Oksanen, et al., 2015) and PCA (FactoMineR package by Husson et al., 2015) were obtained from the R-project statistical software (R Core Team, 2012). Because these methods operate under a multivariate normal distribution assumption, the data distributions were tested for normality using the Shapiro-Wilk normality test. The species abundance data was log transformed ($\log_{10}(n+1)$) to correct the imbalance between significance of abundant and rare species before performing nMDS and CCA.

The nMDS was performed on $\log_{10}(n+1)$-transformed species abundance data for each individual sample collection to determine and graphically depict the ecological inter-distance among sites. The nMDS fits the points on numbered axes and displays ordination of those points in for a predetermined number of dimensional (in this case two-dimension) space. Two sites that are the closest in the distance matrix would be placed immediately next to each other in the ordination plot; two sites that are far apart from one another in the distance matrix would be separated far from each other in the ordination plot. The final result in nMDS is obtained through an iterative search for global minima among the rank-order of distances in the original distance matrix

(Oksanen, 2015). The quality of the representation is indicated by a "stress" value—the smaller the stress value, the better the ordination and the representation of the data. To represent the species abundance data accurately, stress values smaller than 0.1, or 10%, are preferred, but any value smaller than 0.3, or 30%, is acceptable (Oksanen, 2015).

Canonical correspondence analysis (CCA) was performed on the $\log_{10}(n+1)$-transformed abundance data and the environmental variables—percentage sediment organic carbon, sediment organic carbon-nitrogen ratio, bottom water oxygen concentration, and percentage mud (silt + clay). Dr. Kevin Yeager's laboratory analyzed the percentage sediment organic carbon and sediment organic carbon-nitrogen ratio using Costech 4010 CHN/SO analyzer (Briggs et al., 2015). The Naval Research Laboratory, Stennis Space Center, MS. performed the sediment grain size analysis using Quantachrome Ultrapycnometer (Briggs et al., 2015). Bottom water dissolved oxygen concentration was measured onboard the R/V Pelican during sample collection using the dissolved oxygen sensor, SBE 43, on a CTD package. These environmental parameters data was used to understand the influence of environmental variables on species distribution during the first and second samplings during April and September 2009. During the August 2010 cruise sedimentary organic carbon and the sediment C/N ratio were not measured, hence, CCA was performed with the only two measured environmental variables—bottom water oxygen concentration and percentage mud.

The CCA is used to understand the relationships among the community constituents and the environment in which they live in. CCA compares two different multivariate datasets against each other, and the main goal of CCA is to allow the use of environmental data in the final ordination plot (ter Braak, 1986; ter Braak and

Verdonschot, 1995). CCA is a linear model requiring a dependent matrix (species abundance data) and an independent matrix (environmental variables data) (ter Braak, 1986; Clarke and Ainsworth, 1993). In community ecology, a dependent matrix consists of species at specific sites, and an independent matrix consists of environmental factors. These data must be collected simultaneously at the same location (ter Braak, 1986; ter Braak, 2011). CCA facilitates the entire expression of the gradient in a community matrix and independently evaluates the significance of the measured environmental variables. Consequentially, it disregards any community structure that is not related to the environmental variables (McCune, 2002; ter Braak, 2011).

Principal component analysis (PCA) is a basic ordination method that uses eigenvectors. Pearson (McCune, 2002; Clarke and Ainsworth, 1993) first designed it, and he showed that the best-fitting linear relationship in a given sample exists in a centroid. In other words, knowledge of the means, standard deviations, variance, and covariance are the basis for the best possible solution, which means the best-fitting line represents the first principal components, and second-best-fitting plane is represented by the first and second principal components (McCune, 2002). The general objectives of PCA are data reduction and interpretation, which occurs by explaining the variance-covariance structure in the dataset or population (McCune, 2002; Johnson and Wichern, 2007).

The PCA illustrates the relationships that were previously unknown, allowing better interpretations of the data (McCune, 2002; Johnson and Wichern, 2007). PCA is the best technique to use when data have linear relationships among its variables (McCune, 2002). If the sample does not have linear relationships among the variables, then the ordination is poor. PCA is used to visualize the arrangements of sites on an axis

using the species diversity values of abundance, biomass, number of species, and

Simpson's diversity; the trophic diversity values of percentage of carnivores, herbivores,

surface deposit feeders, sub-surface deposit feeders and percentage suspension feeders;

and the environmental variable of bottom water oxygen concentration.

Linear regression fit was performed on the annual, mid-summer, shelfwide cruise

average bottom water oxygen values obtained from N. N. Rabalais (Appendix I) for 2000

to 2010 against the percentage of opportunist species. Average bottom-water oxygen

values from 2000 to 2008 were regressed against April 2009 percentage of opportunist

species. Average bottom-water oxygen values from 2000 to 2009 were regressed against

September 2009 percentage of opportunist species. Average bottom-water oxygen values

from 2000 to 2010 were regressed against August 2010 percentage of opportunist

species. Two regression fits were performed, one with all sites included and another by

excluding the reference site A.

CHAPTER III

RESULTS

General data description

A total of 6,715 individual specimens belonging to 394 different species
(Appendix A) of macrobenthos were indentifed from 108 sample cores taken from 72
different box cores collected from four different sites during the three sampling cruises
conducted during April 2009, September 2009 and August 2010. These 394
macrobenthos species were grouped into eight major taxonomic groups: Annelida,
Bivalvia, Other Molluscs, Crustacea, Echinodermata, Nemertea, Sipuncula, and Other
Minor Phyla. Annelida had 208 species belonging to 43 families and two classes
(Polychaeta and Oligochaeta). Only two species of oligochaetes were found. Bivalvia had
45 species belonging to 20 families. The Other Molluscs group was comprised of
Gastropoda and Scaphopoda, where gastropods were represented by 39 species belonging
to 17 families, and scaphopods were represented by three species belonging to two
families. Crustacea, represented by Mysida, Amphipoda, Cumacea, Isopoda, Tanaidacea
and Decapoda, consisted of three species of mysids belonging to one family, ten species
of amphipods belonging to five families, seven species of cumaceans belonging to three
families, nine species of isopods belonging to eight families, four species of tanaidaceans
belonging to three families, and 15 species of decapods belonging to nine families.
Nemertea was represented by eight species belonging to three families. Sipuncula was
represented by nine species belonging to five families. Minor phyla grouped Cnidaria,
Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda, and Hemichordata
together. This group was represented by 15 species belonging to 13 families.

Polychaete annelids dominated the overall abundance, followed by bivalves, during all three cruises at all four sites. There were some spatial and temporal differences in the less abundant groups. Echinoderms contributed more to site B assemblages than to site A (Figures 7, 8 and 9), and crustaceans decreased from spring 2009 to the summer months of 2009 and 2010 at site B. Polychaete annelids also dominated the overall biomass (Figures 10, 11 and12) during all three cruises at all four sites.
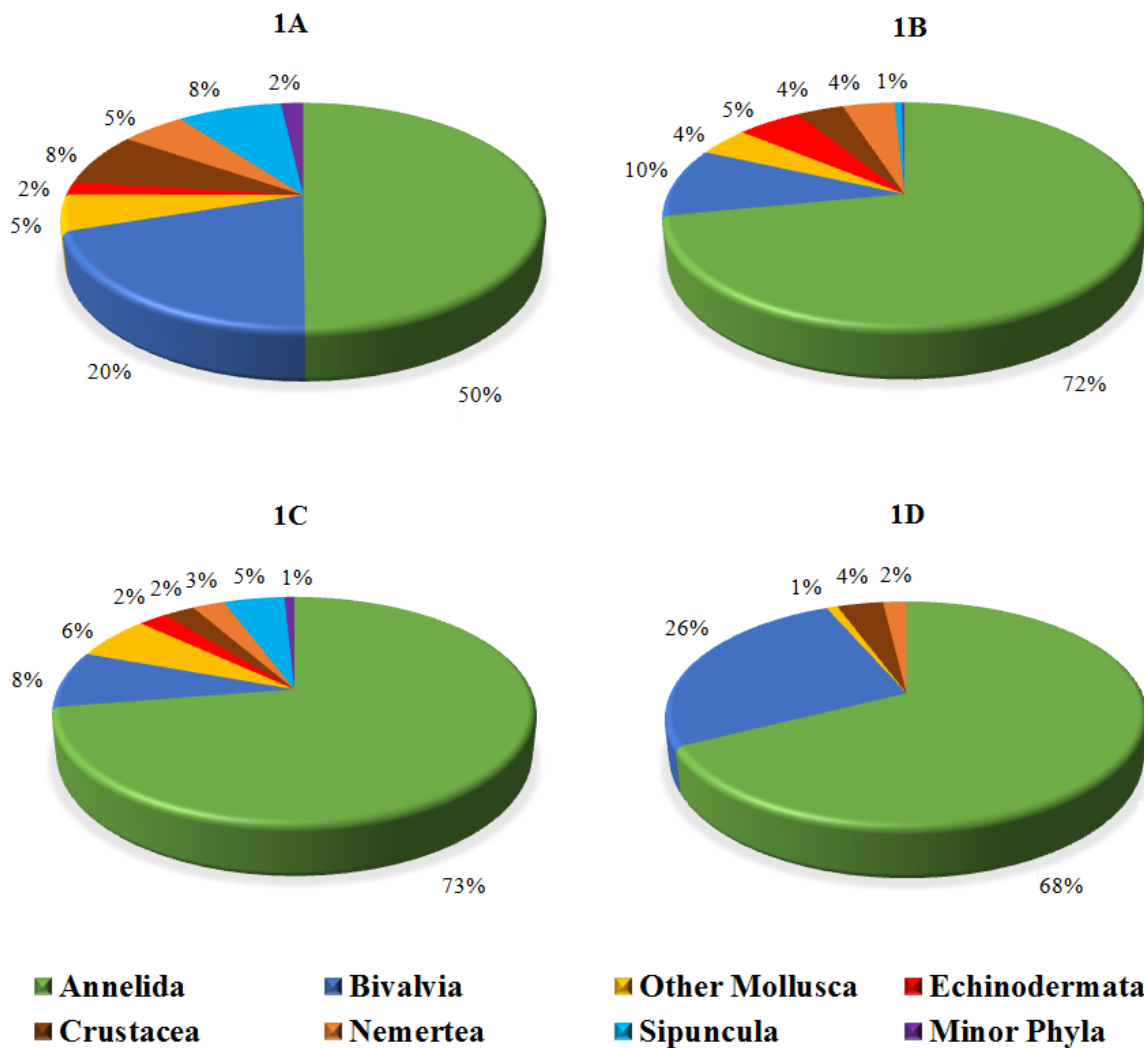
Figure 7. Percentage contribution of different taxa to total abundance at sites A, B, C and D during April 2009. Annelida consists of Polychaeta and Oligochaeta. Other Mollusca consists of Gastropoda and Scaphopoda. Minor Phyla consists of Cnidaria, Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda and Hemichordata.

2A

2B

2C

2D

- ■ Annelida
- ■ Bivalvia
- ■ Other Mollusca
- ■ Echinodermata
- ■ Crustacea
- ■ Nemertea
- ■ Sipuncula
- ■ Minor Phyla
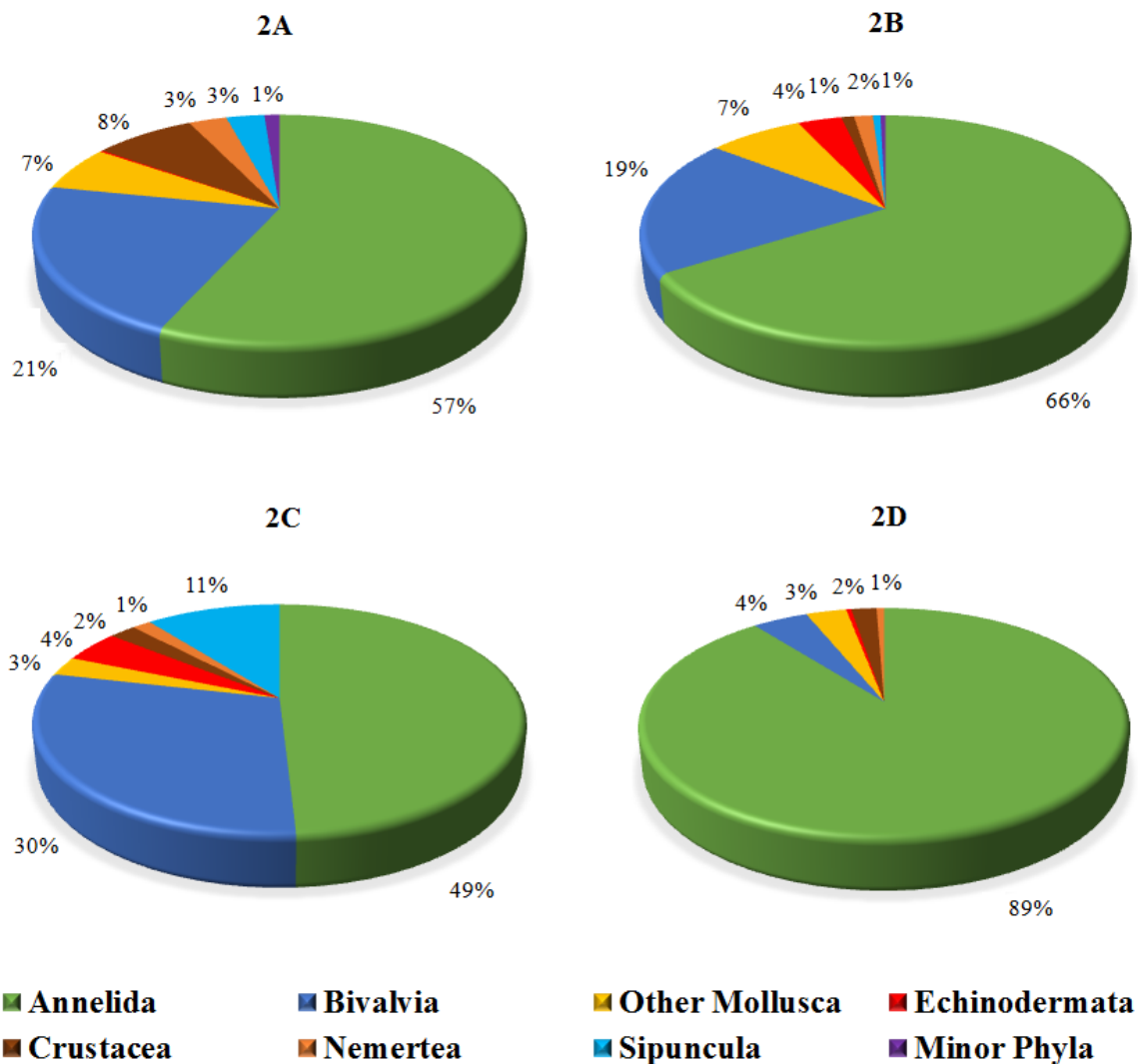
Figure 8. Percentage contribution of different taxa to total abundance at sites A, B, C and D during September 2009. Annelida consists of Polychaeta and Oligochaeta. Other Mollusca consists of Gastropoda and Scaphopoda. Minor Phyla consists of Cnidaria, Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda and Hemichordata.

3A

3B

3C

3D

- Annelida
- Bivalvia
- Other Mollusca
- Echinodermata
- Crustacea
- Nemertea
- Sipuncula
- Minor Phyla
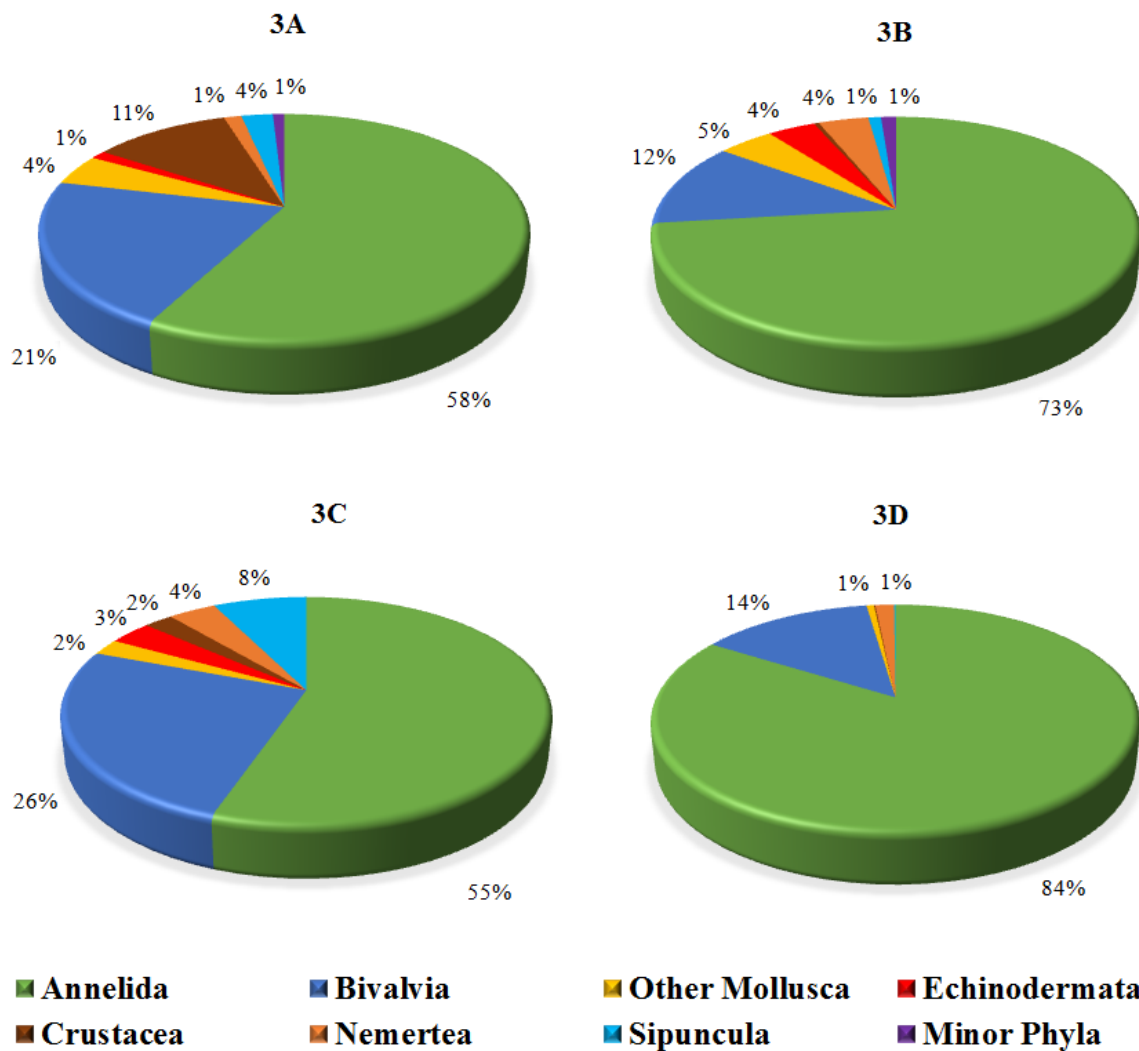
Figure 9. Percentage contribution of different taxa to total abundance at sites A, B, C and D during August 2010. Annelida consists of Polychaeta and Oligochaeta. Other Mollusca consists of Gastropoda and Scaphopoda. Minor Phyla consists of Cnidaria, Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda and Hemichordata.
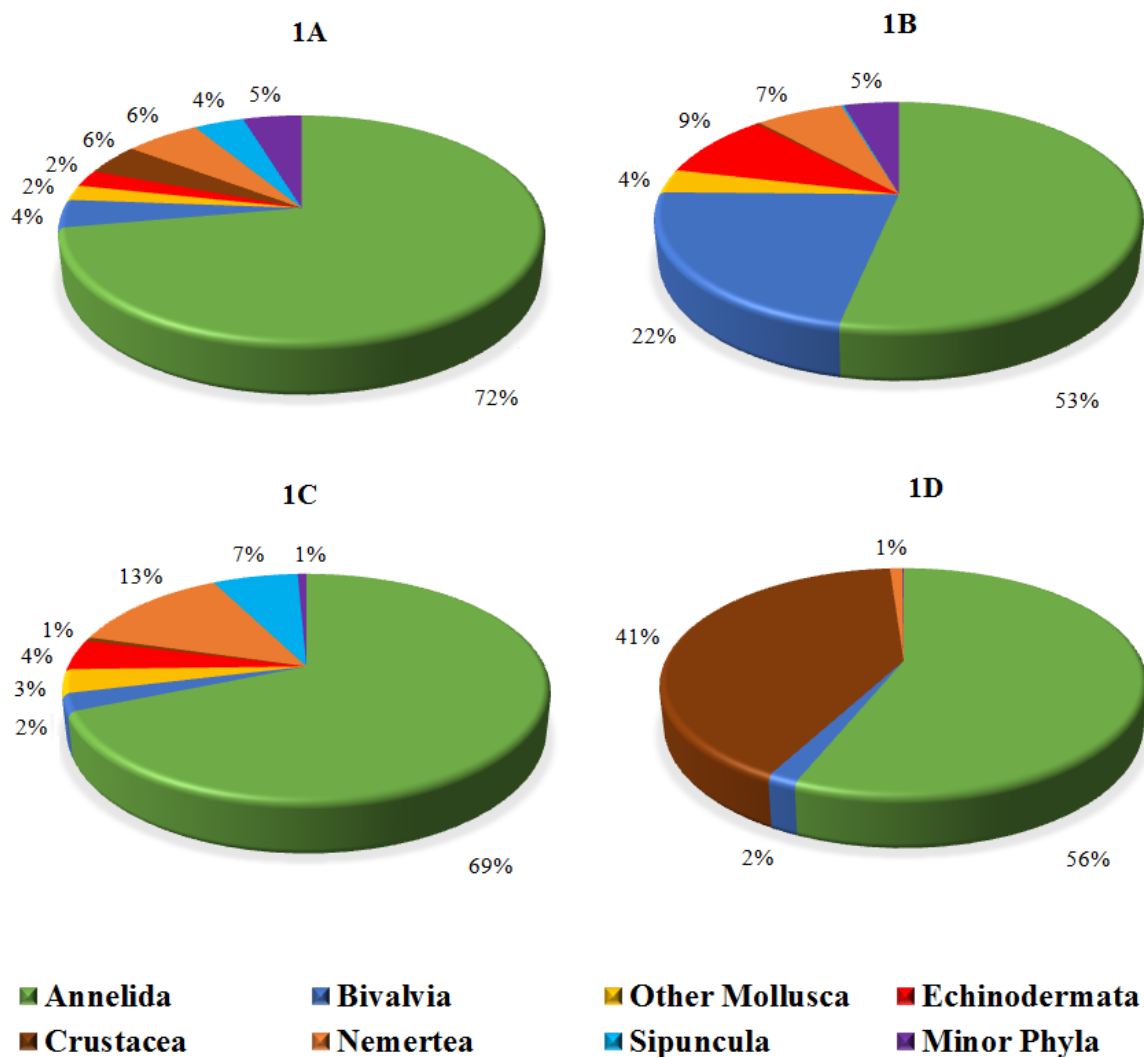
Figure 10. Percentage contribution of different taxa to total biomass at sites A, B, C and D during April 2009. Annelida consists of Polychaeta and Oligochaeta. Other Mollusca consists of Gastropoda and Scaphopoda. Minor Phyla consists of Cnidaria, Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda and Hemichordata.
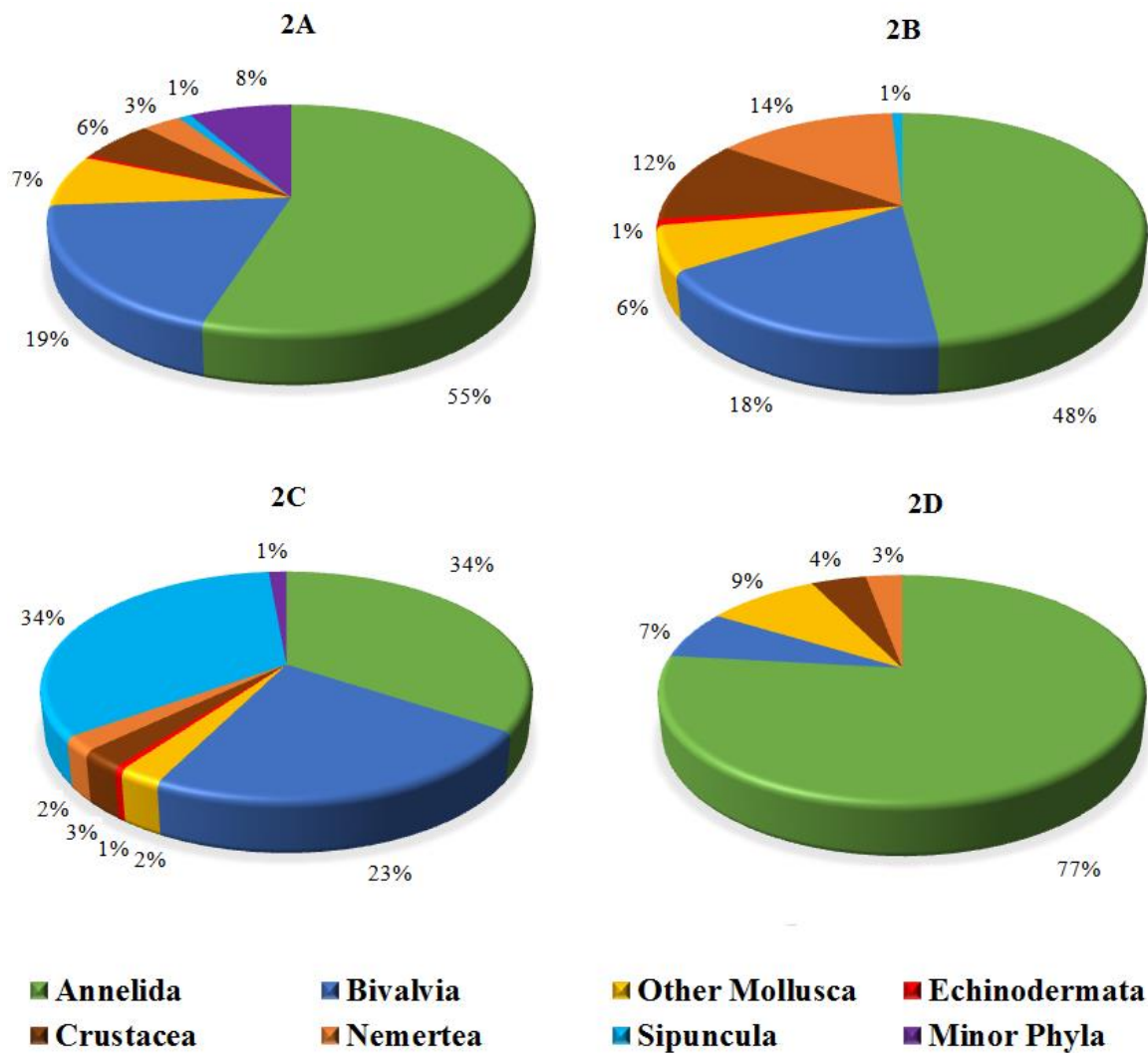
Figure 11. Percentage contribution of different taxa to total biomass at sites A, B, C and D during September 2009. Annelida consists of Polychaeta and Oligochaeta. Other Mollusca consists of Gastropoda and Scaphopoda. Minor Phyla consists of Cnidaria, Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda and Hemichordata.
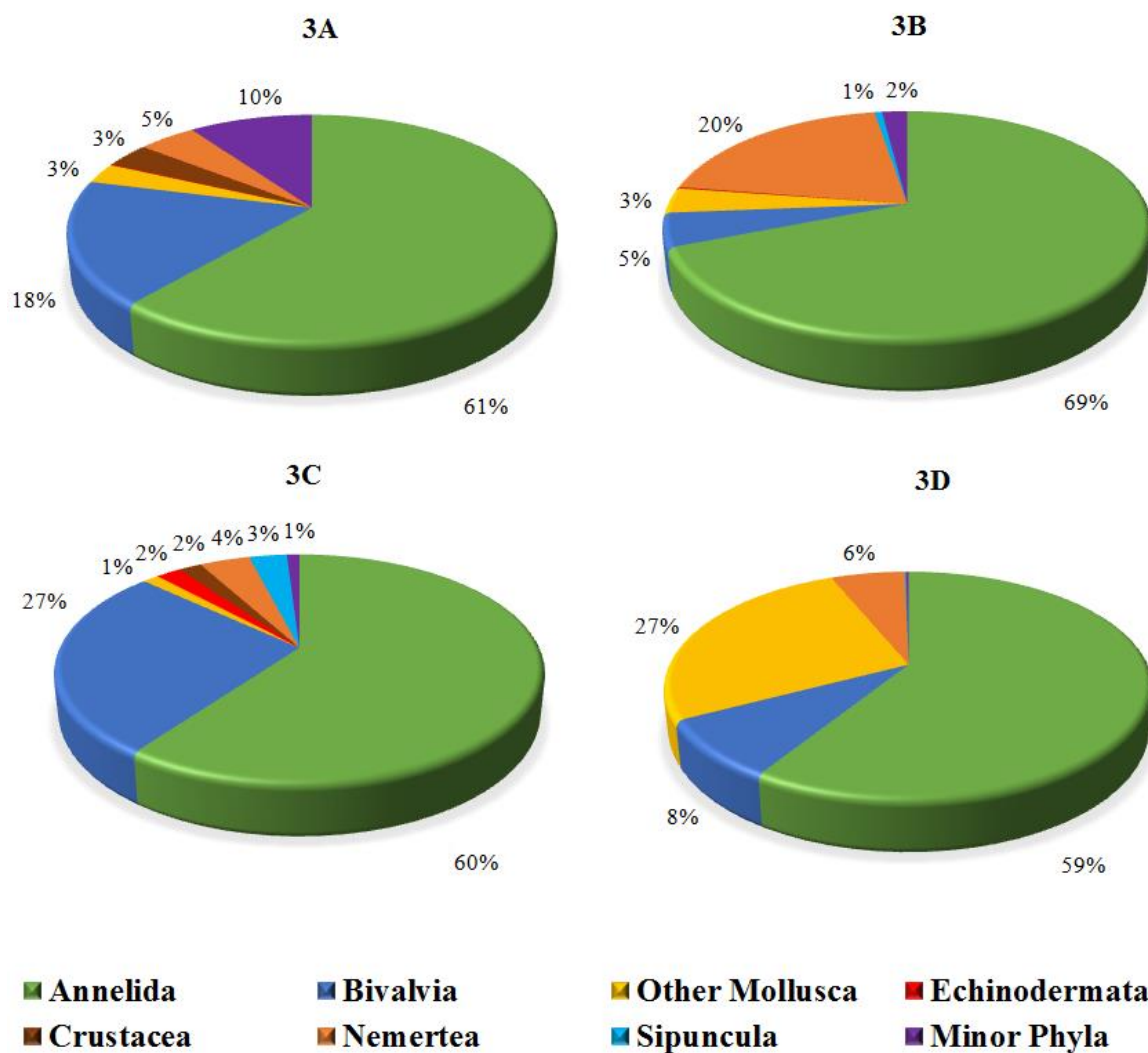
Figure 12. Percentage contribution of different taxa to total biomass at sites A, B, C and D during August 2010. Annelida consists of Polychaeta and Oligochaeta. Other Mollusca consists of Gastropoda and Scaphopoda. Minor Phyla consists of Cnidaria, Turbellaria, Priapulida, Echiura, Bryozoa, Entoprocta, Brachiopoda and Hemichordata

Data Distribution

Abundance and biomass data at each site and sampling were examined for possible effects of hypoxic stress on the macrobenthos communities. Two large specimens of *Speocarcinu*s sp. and *Solenosteira cancellaria* were removed from subcore 2B5 and 3D2, respectively, to correct skewness observed in the biomass data. Macrobenthos abundance, biomass, estimated average individual biomass, Shannon diversity index and Pielou's evenness index data were also tested for normal distribution using the Shapiro-Wilk test (Appendix G; Tables G2, G3, G4, G5 and G6) as well as Quantile-Quantile plot (Appendix G; Figure G1, G2, G3, G4 and G5) for sites A, B, C and D for April 2009, September 2009 and August 2010. These data were not normally distributed; hence, the nonparametric Mann-Whitney *U*-test was used to assess the significance of the differences between the sites. The distributions of diversity metrics of the inverse Simpson index and Margalef's species richness index were also tested for normality using the Shapiro-Wilk test (Appendix G; Tables G7 and G8) as well as Quantile-Quantile plot (Appendix G; Figures G6 and G7) for sites A, B, C and D for April 2009, September 2009 and August 2010. The distributions of these values were normally distributed; hence, the parametric Welch's *t*-test was used to assess the significance of the differences between the means of diversity indices at the sites. Species data had numerous zero values; thus, the $\log_{10}(n+1)$ transformation was performed before calculation of the Bray-Curtis dissimilarity coefficient and the ordination techniques, such as non-metric multidimensional scaling (nMDS) and canonical correspondence analysis (CCA).

Abundance

Comparisons of macrobenthos abundance among the three samplings indicated that the median specimen abundance per 100 cm^2 was the highest at site A during August 2010 and the lowest was recorded during April 2009 at site D (Figure 13).

Comparisons between sites with the Mann-Whitney *U*-test using median abundance values from April 2009 sample cores revealed significant differences between the reference site (A) and sites C and D; between site B and sites C and D; and between site C and site D (Table 5). The September 2009 sample cores comparison showed significant differences between site A and sites B and C; and between site B and C (Figure 13). In August 2010, comparisons of abundance from subcores exhibited significant differences among sites A, B and C. The remaining comparisons of abundance values did not show any significant differences (Table 5).

Comparisons between samplings for site A using the Mann-Whitney *U*-test for median abundance values for April 2009, September 2009, and August 2010 subcores showed a significant difference only between April 2009 and August 2010 at site A (Table 6). Comparisons between samplings for site C subcores for median abundance values showed significant differences between April and September 2009 and between April 2009 and August 2010. The comparisons between April 2009 and August 2010 and between September 2009 and August 2010 showed significant differences in macrobenthos abundance (Table 6).
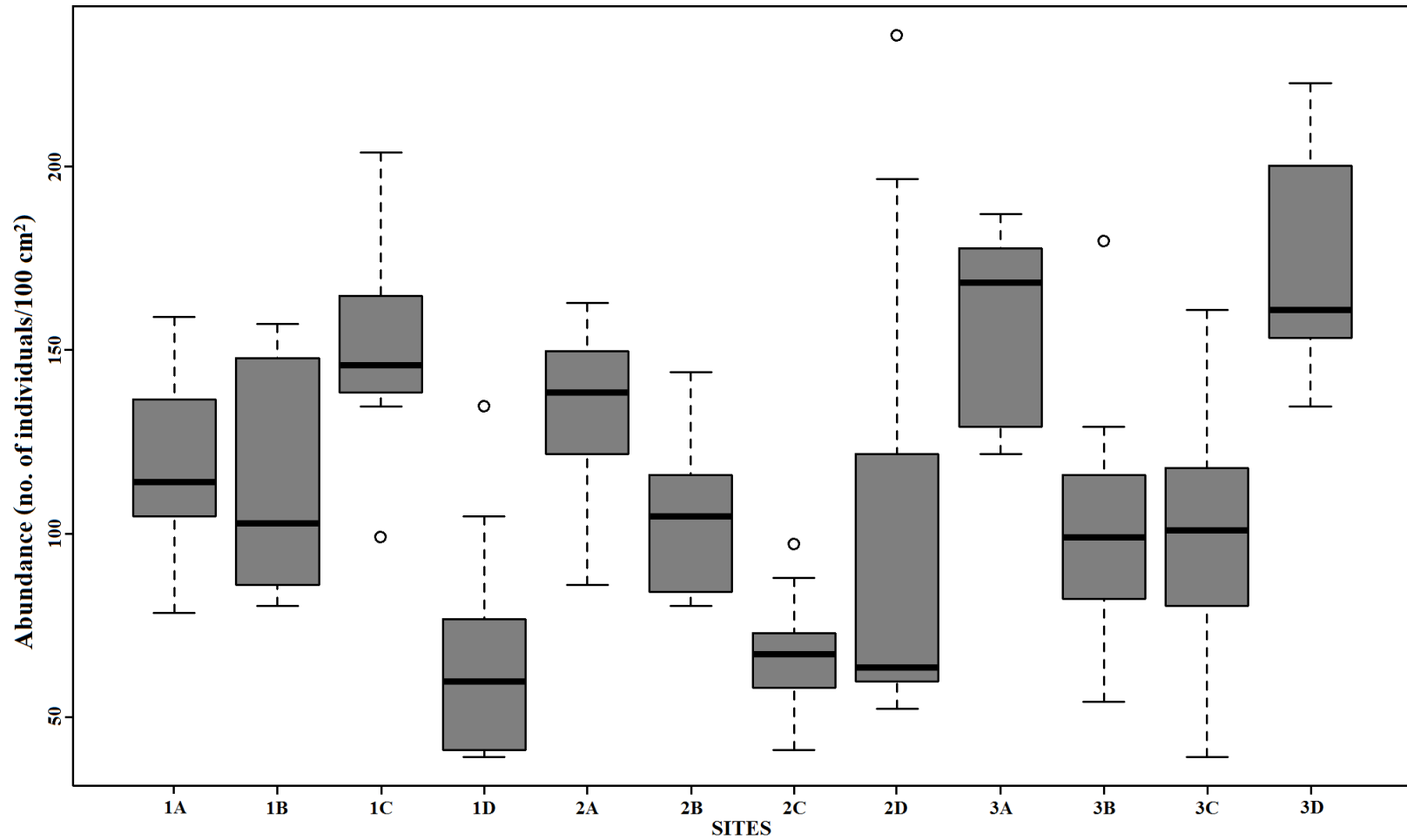
Figure 13. The range, minimum, maximum, median, lower quartile, upper quartile, and outliers (hollow circles) for macrobenthos abundance (n = 9) at sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Table 5

Statistical comparisons of median abundance values between sites using the Mann-Whitney U-test (Appendix H; Table H1) for samplings in April 2009, September 2009 and August 2010 sample collections. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	n.s.	*	**	2A	*	***	n.s.	3A	**	**	n.s.
1B		*	**	2B		**	n.s.	3B		n.s.	**
1C			***	2C			n.s.	3C			***

*P<0.05   **P<0.01   ***P<0.001

Table 6

Statistical comparisons of median abundance values between sample collections using the Mann-Whitney U-test (Appendix H; Table H2) for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	*	1	n.s.	n.s.	1	***	**	1	n.s.	***
2		n.s.	2		n.s.	2		n.s.	2		*

*P<0.05   **P<0.01   ***P<0.001

Biomass

Comparisons of macrobenthos AFDW biomass among the three samplings indicated that the median biomass per 100 cm^2 was the highest at site C during August 2010 and the lowest was recorded during September 2009 at site D (Figure 14).

Comparisons of median AFDW biomass values for April 2009 subcores using the Mann-Whitney *U*-test did not show any significant differences between sites (Table 7). September 2009 subcores comparisons showed significant differences between all sites except between sites A and B. The comparisons of the August 2010 subcores showed significant differences in median biomass values between all sites except between sites A and B and between sites B and D.

Site-wise comparison of the three sample collections indicated the median AFDW biomass did not significantly fluctuate temporally at sites A and B, whereas site C biomass significantly varied temporally (Table 8). At site D, September 2009 biomass varied significantly from August 2010.
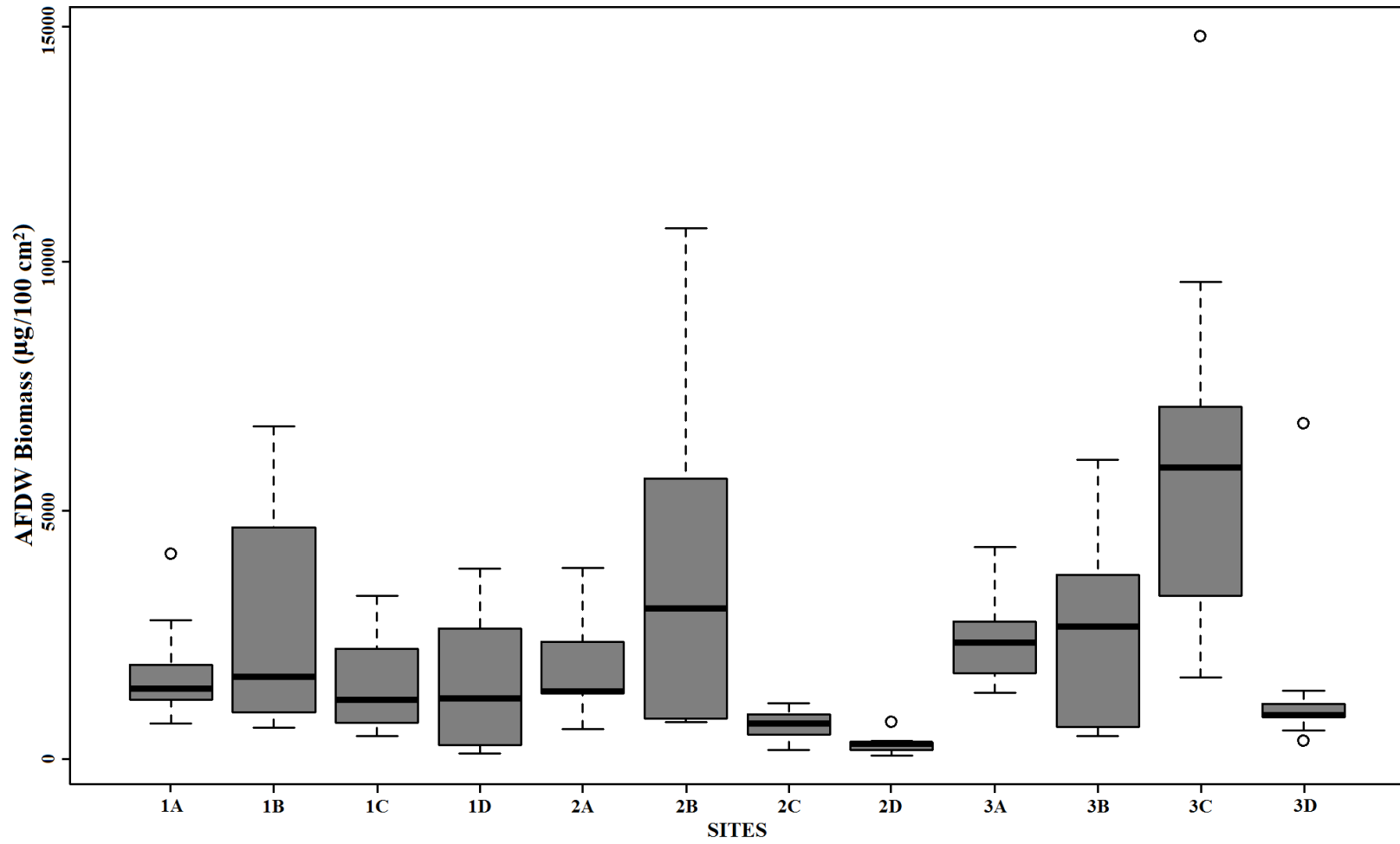
Figure 14. The range, minimum, maximum, median, lower quartile, upper quartile, and outliers (hollow circles) for macrobenthos AFDW biomass (n = 9) at sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Table 7

Statistical comparisons of median AFDW biomass values between sites using the Mann-Whitney U-test (Appendix H; Table H3)for samplings in April 2009, September 2009 and August 2010. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	n.s.	n.s.	n.s.	2A	n.s.	**	***	3A	n.s.	**	**
1B		n.s.	n.s.	2B		**	***	3B		*	n.s.
1C			n.s.	2C			**	3C			***

*P<0.05   **P<0.01   ***P<0.001

Table 8

Statistical comparisons of median AFDW biomass values between sample collections using the Mann-Whitney U-test (Appendix H; Table H4)for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	n.s.	1	n.s.	n.s.	1	*	***	1	n.s.	n.s.
2		n.s.	2		n.s.	2		***	2		***

*P<0.05   **P<0.01   ***P<0.001

Estimated Average Individual Biomass

The size of individual macrobenthos was estimated for each site and sampling to determine if hypoxic stress could affect the growth and longevity of the communities. Average individual biomass was estimated by dividing total AFDW biomass value of a particular species by its total abundance value in each subcore within each sectioning. Analysis of the estimated average individual biomass of macrobenthos indicated that site 3C had the largest average size (73 µg) during August 2010 and site 2D had the smallest average size (4 µg) during September 2009 (Figure 15). In September 2009, average size fluctuated between 4 and 34 µg, with the largest macrobenthos found at site B and the smallest macrobenthos found at site D. In August 2010, site C had the largest macrobenthos (73 µg) and site D had the smallest individuals (9 µg) (Figure 15).

Site-wise analysis of individual macrobenthos size from the three sample collections indicated that site A values varied from a low value of 14 µg AFDW during April 2009 to a high value of 17 µg AFDW in August 2010. At site B the smaller macrobenthos were found during April 2009 and August 2010 (25 µg AFDW), but larger macrobenthos were found during September 2009 (34 µg AFDW) (Figure 15). Site C showed considerable variation, and the estimated average individual biomass of macrobenthos varied from a low value of 10 µg AFDW in April 2009 and September 2009 to a high value of 73 µg AFDW in August 2010. Site D had the lowest collective values among all four sites in all three sample collections and the values ranged between 4 µg AFDW in September 2009 and 27 µg AFDW in April 2009 (Figure 15).

Comparison of the median values for estimated average individual biomass between sites for April 2009 subcores using the Mann-Whitney U-test did not show any

significant differences between sites (Table 8). In September 2009, macrobenthos showed significant differences in size among all sites except, sites A and B. In August 2010, the macrobenthos from the reference site A were significantly smaller in size than those from sites C and significantly bigger than site D. Site C had significantly bigger organisms than site D. Among rest of the sites, there were no significant differences in size.

Comparison of subcores between the sample collections using the Mann-Whitney *U*-test (Table 10) showed that the differences among the sizes of macrobenthos at site A and site B were not significant. Comparison of site C subcores showed that the size of macrobenthos significantly different in August 2010 than the macrobenthos collected in April and September 2009, but not significantly different between April and September 2009. Macrobenthos size did not significantly change at site D, between April and September 2009, but macrobenthos size in August 2010 was significantly larger than in September 2009.
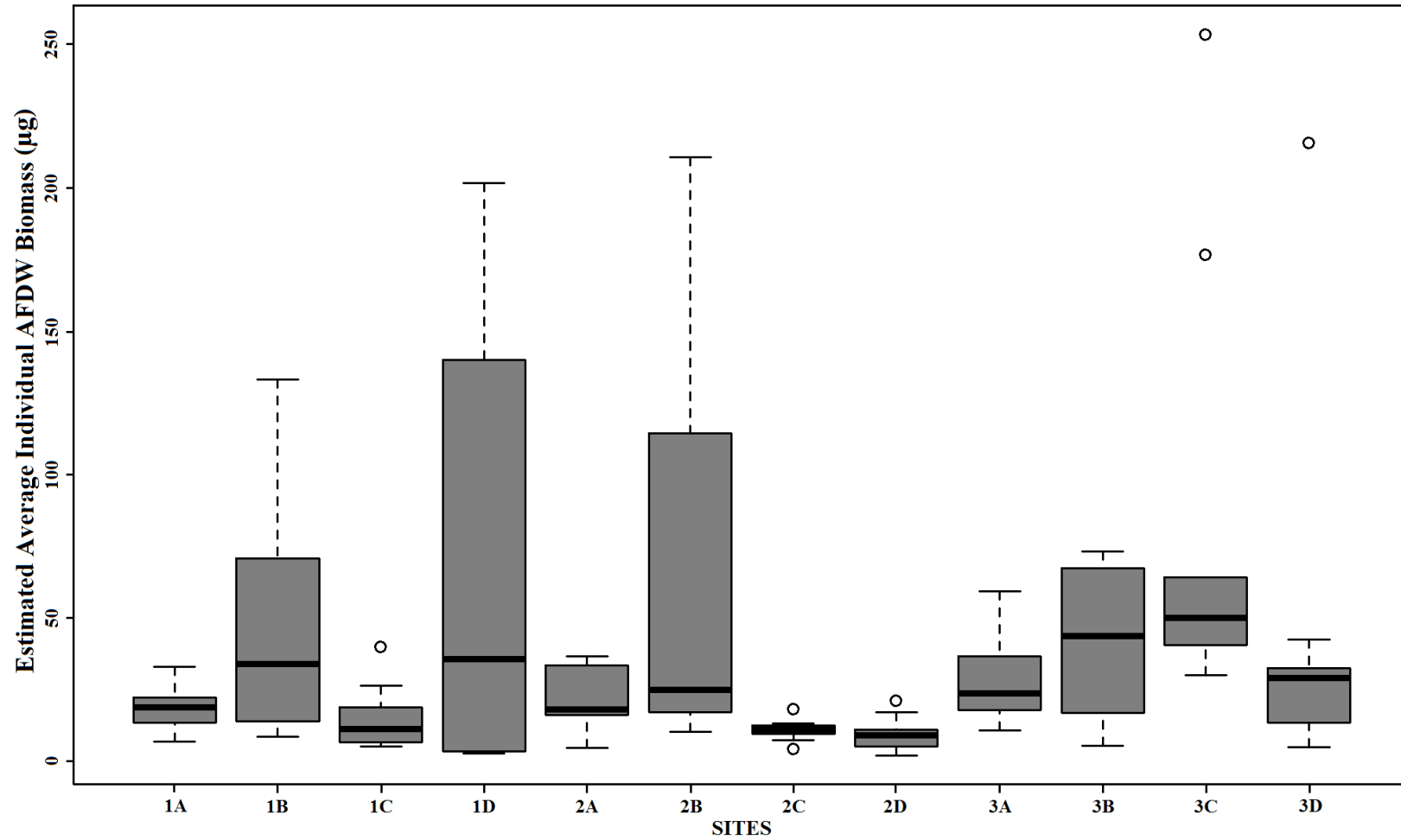
Figure 15. The range, minimum, maximum, median, lower quartile, upper quartile, and outliers (hollow circles) for macrobenthos estimated average individual biomass (n = 9) during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections at sites A, B, C and D.

Table 9

Statistical comparisons of medians of the estimated average individual AFDW biomass values between sites using the Mann-Whitney U-test (Appendix H; Table H5) for samplings in April 2009, September 2009 and August 2010. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	n.s.	n.s.	n.s.	2A	n.s.	**	***	3A	n.s.	*	**
1B		n.s.	n.s.	2B		**	***	3B		n.s.	n.s.
1C			n.s.	2C			*	3C			**

　　　　*P<0.05　　　　　　　　　　　**P<0.01　　　　　　　　　　***P<0.001

Table 10

Statistical comparisons of medians of estimated average individual biomass between sample collections using the Mann-Whitney U-test (Appendix H; Table H6) for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	n.s.	1	n.s.	n.s.	1	n.s.	**	1	n.s.	n.s.
2		n.s.	2		n.s.	2		***	2		*

*P<0.05　　　　　　　　　　**P<0.01　　　　　　　　　***P<0.001

Vertical Distribution of Abundance

The distribution of the macrobenthos in the top 15 cm of the sediment was examined to determine if hypoxic stress affected the location of the infauna within the sediment. The vertical distributions of macrobenthos abundance within the sediment are presented as percentages of total abundance occurring within each depth interval for sites A, B, C and D during the April 2009, September 2009 and August 2010 samplings. The total abundance for each site, and sample collection is displayed in Table 11. In every case, the largest abundance of macrobenthos was found in the 0-1 cm interval followed by the 1-2 cm interval. During April 2009, the highest percentage of macrobenthos found in the top 2 cm occurred at site C (94%), and the lowest percentage of macrobenthos found in the top 2 cm occurred at site D (82%). During September 2009, the highest percentage of macrobenthos found in the top 2 cm occurred at site A (86%) and the lowest percentage of macrobenthos found in the top 2 cm occurred at site D (84%) (Figure 16). During August 2010, the highest percentage of macrobenthos found in the top 2 cm occurred at site A (91%) and the lowest percentage of macrobenthos found in the top 2 cm occurred at site D (70%) (Figure 16).

Table 11

Total specimen abundance (in nine subcores) at sites A, B, C and D during the April 2009, September 2009 and August 2010 sample collections.

Sites	April 2009	September 2009	August 2010
A	564	648	753
B	537	518	506
C	733	330	474
D	323	502	827
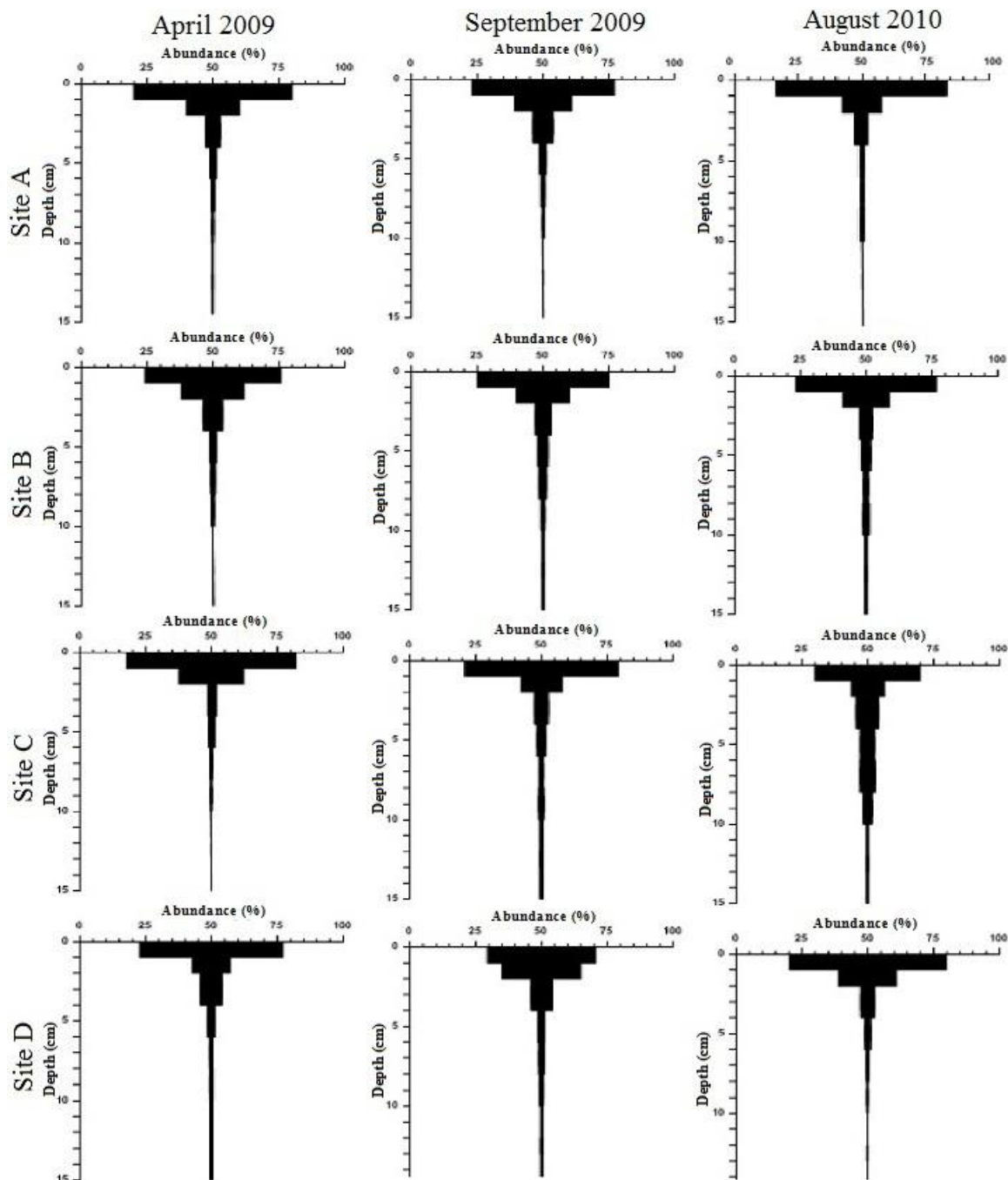
Figure 16. Within sediment vertical distributions of average percentage specimen abundance (normalized to 1-cm intervals) at sites A, B, C and D during April 2009, September 2009 and August 2010.

Vertical Distribution of Biomass

The vertical distributions of macrobenthos AFDW biomass within the sediment are presented as percentages of total biomass occurring within each depth interval for sites A, B, C and D during the April 2009, September 2009 and August 2010 samplings (Figure 17). The total biomass for each site and sample collection is displayed in Table 12. In most samplings (10 of the 12 site-sampling combinations), the highest biomass of macrobenthos was found in the top 2 cm (Figure 17). During April 2009, the highest percentage of macrobenthos biomass was found in the top 2 cm at site D (85%), and the lowest percentage of macrobenthos biomass was found in the top 2 cm occurred at site C (47%). Site C had a large percentage of macrobenthos biomass (50%) distributed from 2 to 8 cm depth in the sediment (Figure 17).

During September 2009, the highest percentage of macrobenthos biomass was found in the top 2 cm at site A (64%) and the lowest percentage of macrobenthos biomass found in the top 2 cm occurred at site B (23%) (Figure 17). Those sites that had a recent and more frequent history of hypoxia exposure (B, C and D) had high percentages of macrobenthic biomass occurring deeper than the top 2 cm. At site B, 52% of the macrobenthic biomass was found at the depth interval of 2-8 cm and an additional 25% of the biomass was found in the depth interval of 8-15 cm. At site C, 47% of the macrobenthic biomass was found in the depth interval of 2-10 cm. At site D, 50% of the macrobenthic biomass was found in the 2-10 cm depth interval (Figure 17).

During August 2010, the highest percentage of macrobenthos biomass was found in the top 2 cm at site A (59%) and the lowest percentage of macrobenthos biomass found in the top 2 cm occurred at site C (21%) (Figure 17). As found in the other summer

sampling in the previous year, sites that had a recent history of hypoxia exposure (B, C and D) had higher percentages of macrobenthic biomass occurring deeper in the sediment than found below the surface at the reference site A. At site B, 32% of the macrobenthic biomass was found in the 2-8 cm depth interval and an additional 37% of the biomass was found in the 8-15 cm depth interval. At site C, 68% of the macrobenthic biomass was found at the depth interval of 2-8 cm. At site D, 32% of the macrobenthic biomass was found in the 2-8 cm depth interval and an additional 18% was found in the 8-15 cm depth interval (Figure 17).

Table 12

Total AFDW biomass (μg in nine subcores) at sites A, B, C and D during April 2009, September 2009 and August 2010 sample collection.

Sites	April 2009	September 2009	August 2010
A	15,666	16,902	22,169
B	25,295	31,618	23,370
C	13,720	6,403	54,751
D	10,393	2,792	10,169
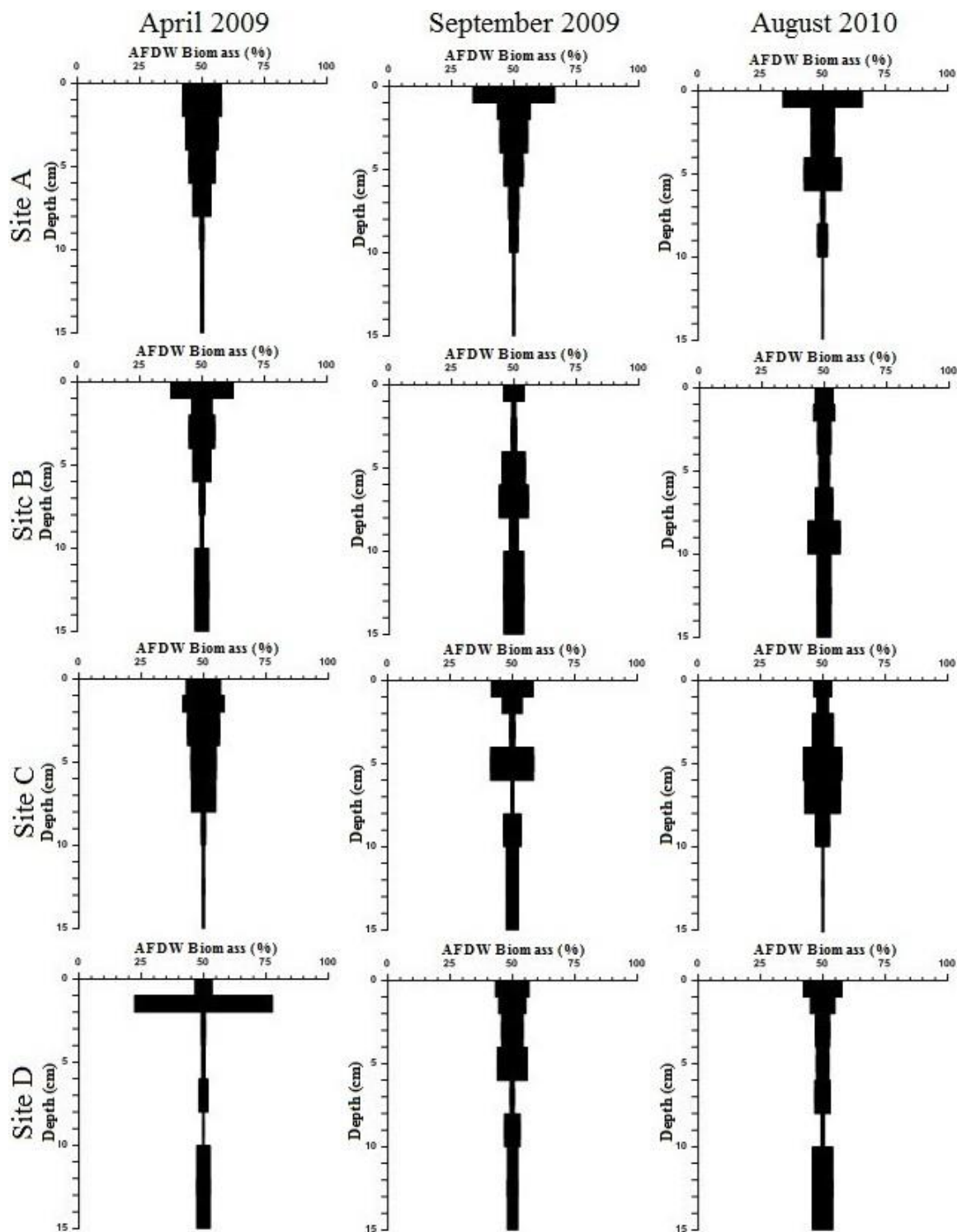
Figure 17. Within sediment vertical distributions of average percentage AFDW biomass (normalized to 1-cm intervals) at sites A, B, C and D during April 2009, September 2009 and August 2010.

Vertical Distribution of Estimated Average Individual Biomass

The vertical distributions of the estimated average individual biomass of macrobenthos within the sediment was determined from the values of abundance and AFDW biomass for each depth interval, site, and sampling (Figure 18). Estimated average individual biomass was calculated by dividing the macrobenthos AFDW biomass in each depth interval by the total abundance in each depth interval. At sites A and C, during the April 2009 sampling, the smallest macrobenthos specimens were found in the top 2 cm, and the largest macrobenthos specimens were found at the 6-8 cm depth interval. The average size of the macrobenthos from site C found in the 6-8 cm depth was twice the average size of the macrobenthos from site A found at the same depth. Site B had large macrobenthos specimens at depth intervals of 10-15 cm (224 µg) and 4-6 cm (60 µg). Site D had large macrobenthos specimens at depth intervals of 1-2 cm (106 µg) and 6-8 cm (51 µg) (Figure 18).

During the September 2009 sampling, the macrobenthos specimens found in the top 2 cm were generally smaller than those found deeper in the sediment (Figure 18). At site A, the largest macrobenthos were found at a depth of 8-10 cm. At sites B and D, the largest macrobenthos were found at the 6-8 cm depth interval. At site C, the largest macrobenthos were found at the 4-6 cm depth interval. The macrobenthos specimens at site D were generally smaller in estimated average individual biomass than the macrobenthos specimens at the other three sites.

During the August 2010 sampling, as in the September 2009 sampling, the macrobenthos specimens found in the top 2 cm were generally smaller than those found deeper in the sediment (Figure 18). At site A the largest macrobenthos were found at a

depth of 4-6 cm. At site B the largest macrobenthos were found in the 8-10 cm depth interval. At site C the large macrobenthos were found at the 4-6 and 6-8 cm depth intervals. At site D the macrobenthos were generally smaller than those found at the other sites, and the largest specimens were found in the 10-15 cm depth interval (Figure 18).
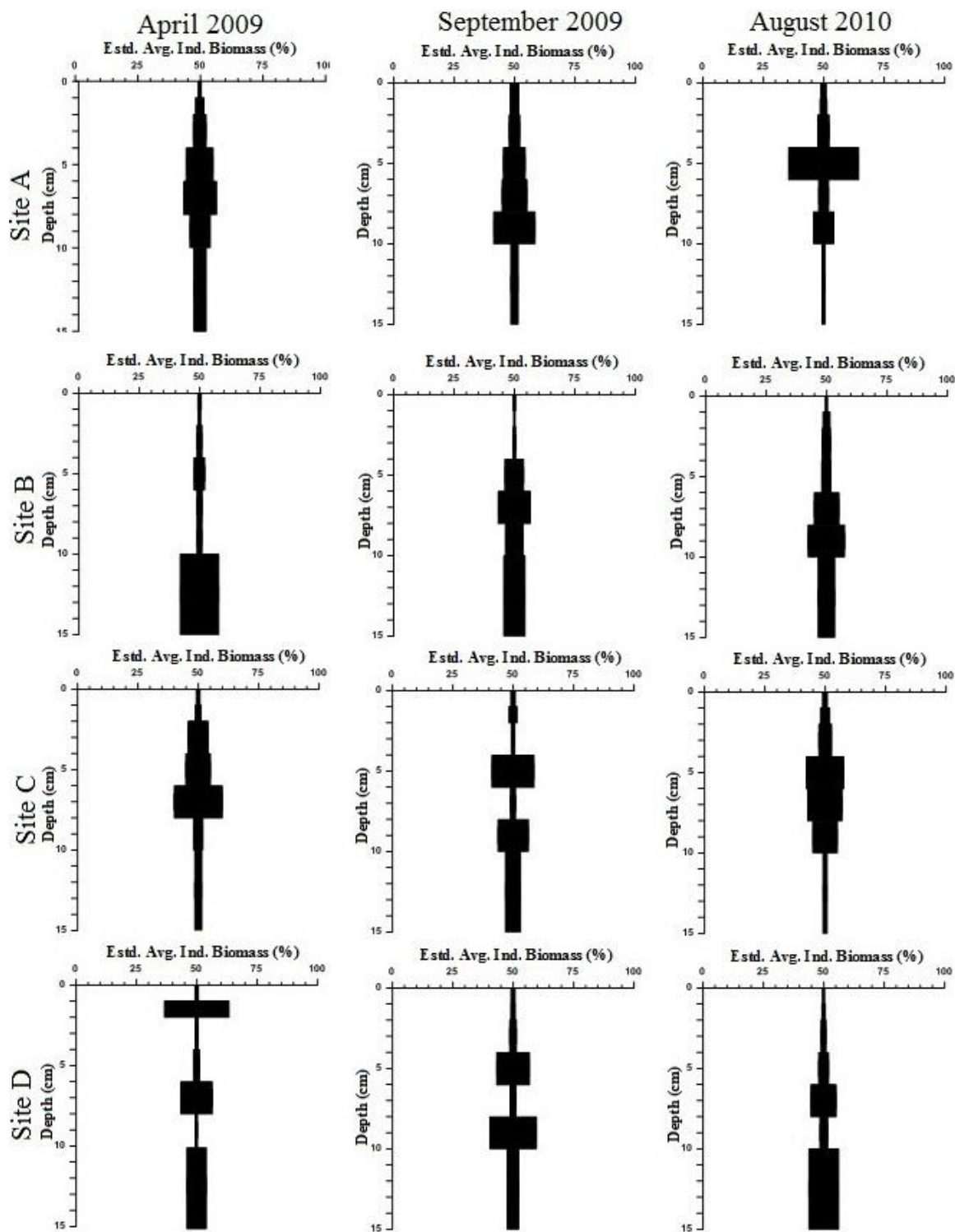
Figure 18. Within sediment vertical distributions of estimated average individual biomass (normalized to 1-cm intervals) at sites A, B, C and D during April 2009, September 2009 and August 2010.

Shannon Diversity Index (H')

The distribution of the various species at each site and sampling was examined as an indicator of the effects of hypoxic stress on the communities. The first sampling in April 2009 revealed that site A had the highest diversity (H') of 3.3 followed by site C at 3.2, site B at 2.7 and site D with the lowest diversity at 1.7. In the late-summer sampling (September 2009), site A had the highest diversity of 3.4 and site D had the lowest diversity of 1.9. During the sampling in August 2010, sites A and C had the highest diversity at 3.0 followed by site B at 2.7 and site D had the lowest diversity at 1.6 (Figure 19).

Comparison of Shannon diversity index (H') values between sites using the Mann-Whitney *U*-test (Table 13) for April 2009 subcores revealed that H' was significantly greater at sites A than at sites B and D. H' was significantly greater at site C than at site B. H' was significantly greater at site B than at site D, and H' was significantly greater at site C than at site D. Diversity at site A was not significantly different from that at site C. In September 2009, site A had significantly greater H' values than sites B, C and D; site B had significantly greater H' values than site D; and site C had significantly greater H' values than site D. The diversity at site B was not significantly greater than that of site C. In August 2010, site A had significantly greater H' values than sites B and D; site B had significantly greater H' values than site D; and site C had significantly greater H' values than sites B and D. The diversity at site A was not significantly different than that of site C.

Site-wise analysis of species diversity using the Shannon diversity index indicated that site A had consistently greater diversity during all three sample collections. Site C

was the second-most consistently diverse site during the sample collections. Site B was the third-most diverse site during the collections. Site D was consistently the least diverse site among all four stations during all three sample collections (Figure 19).

Comparisons between samplings of site A using the Mann-Whitney U-test for Shannon diversity index values showed significant differences in diversity, except between April and September 2009 samplings (Table 14). There were no significant differences in H' values between samplings at site B. Comparisons of H' values between samplings for site C indicated that H' values were significantly different between April 2009 and September 2009, and also between September 2009 and August 2010 (Table 14). Comparisons of H' values between samplings for site D did not show significant differences, except between September 2009 and August 2010 samplings.
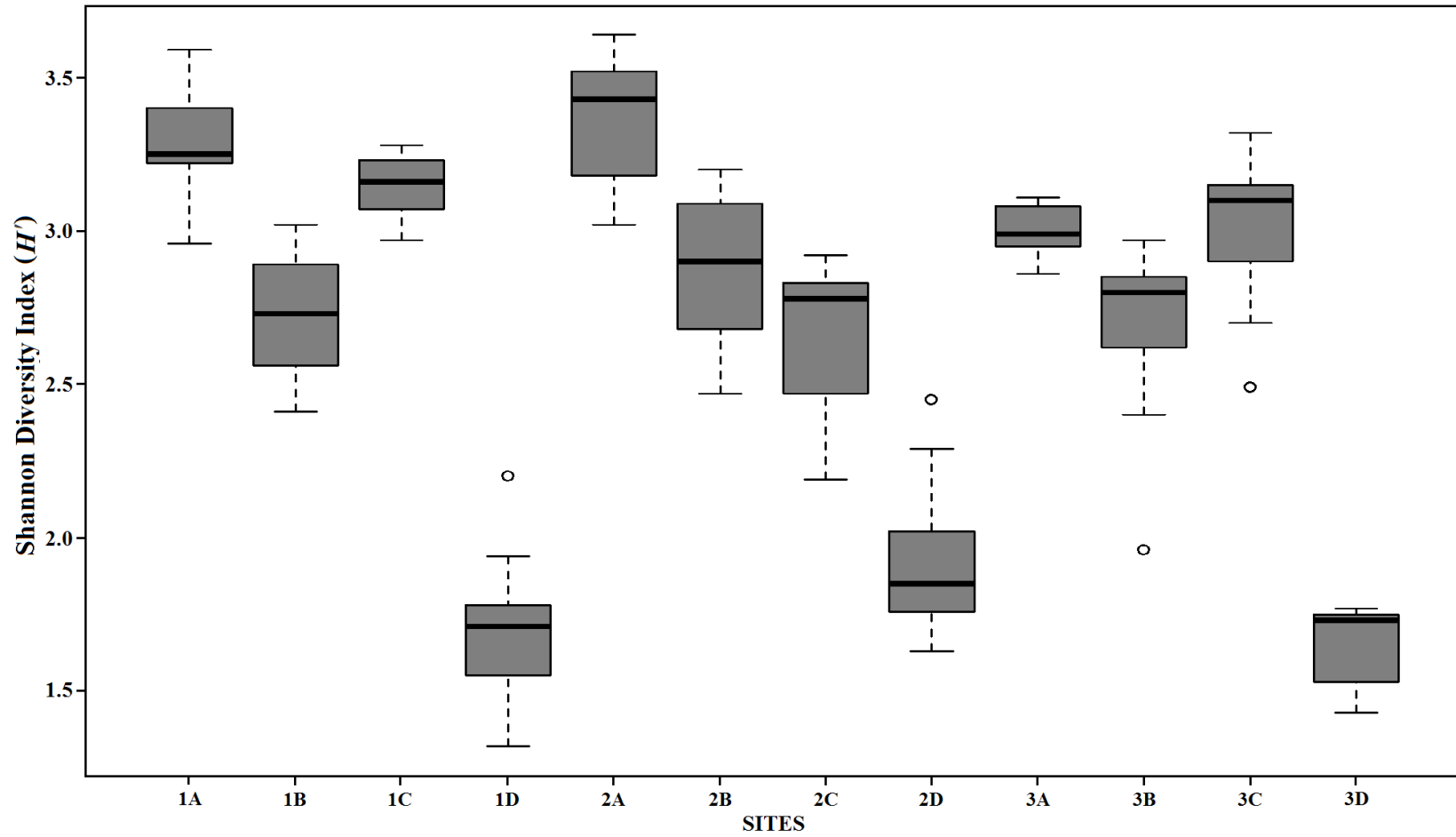
Figure 19. The range, minimum, maximum, median, lower quartile, upper quartile, and outliers (hollow circles) for Shannon diversity index (*H'*) (n = 9) at sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Table 13

Statistical comparisons of medians of the Shannon's diversity index (H') between sites using the Mann-Whitney U-test (Appendix H; Table H7) for April 2009, September 2009 and August 2010 sample collections. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	***	n.s.	***	2A	***	***	***	3A	**	n.s.	***
1B		***	***	2B		n.s.	***	3B		*	***
1C			***	2C			***	3C			***

*P<0.05   **P<0.01   ***P<0.001

Table 14

Statistical comparisons of Shannon diversity index (H') median values between sample collections using the Mann-Whitney U-test (Appendix H; Table H8) for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	**	1	n.s.	n.s.	1	***	n.s.	1	n.s.	n.s.
2		**	2		n.s.	2		**	2		*

*P<0.05   **P<0.01   ***P<0.001

Pielou's Evenness (*J*)

Analysis of species evenness using Pielou's evenness (*J*) index indicated that sites A, B, and C had consistently high evenness, and site D had consistently the lowest evenness (Figure 20).

Comparisons of medians of Pielou's evenness (*J*) index between sites using the Mann-Whitney *U*-test for April 2009 revealed significant differences between all sites (Table 15). In September 2009, macrobenthos from site D showed significant differences in evenness values with sites A, B, and C. However, evenness values were not significantly different between sites A, B, and C. In August 2010, all sites showed significant differences in *J* values, except between sites A and B (Table 15).

Comparisons between samplings of site A using the Mann-Whitney *U*-test for medians of Pielou's evenness (*J*) index showed significant differences in evenness between all samplings except between April 2009 and September 2009 (Table 16). Site B had smaller evenness values in April 2009 sampling than those in September 2009 and August 2010. Comparisons of site B showed there was no significant difference between all samplings except between April 2009 and August 2010. Comparisons between samplings for site C showed no significant differences in evenness between samplings except between April 2009 and August 2010. Comparisons of evenness between samplings for site D showed significant differences between samplings except during April 2009 and September 2009 (Table 16).
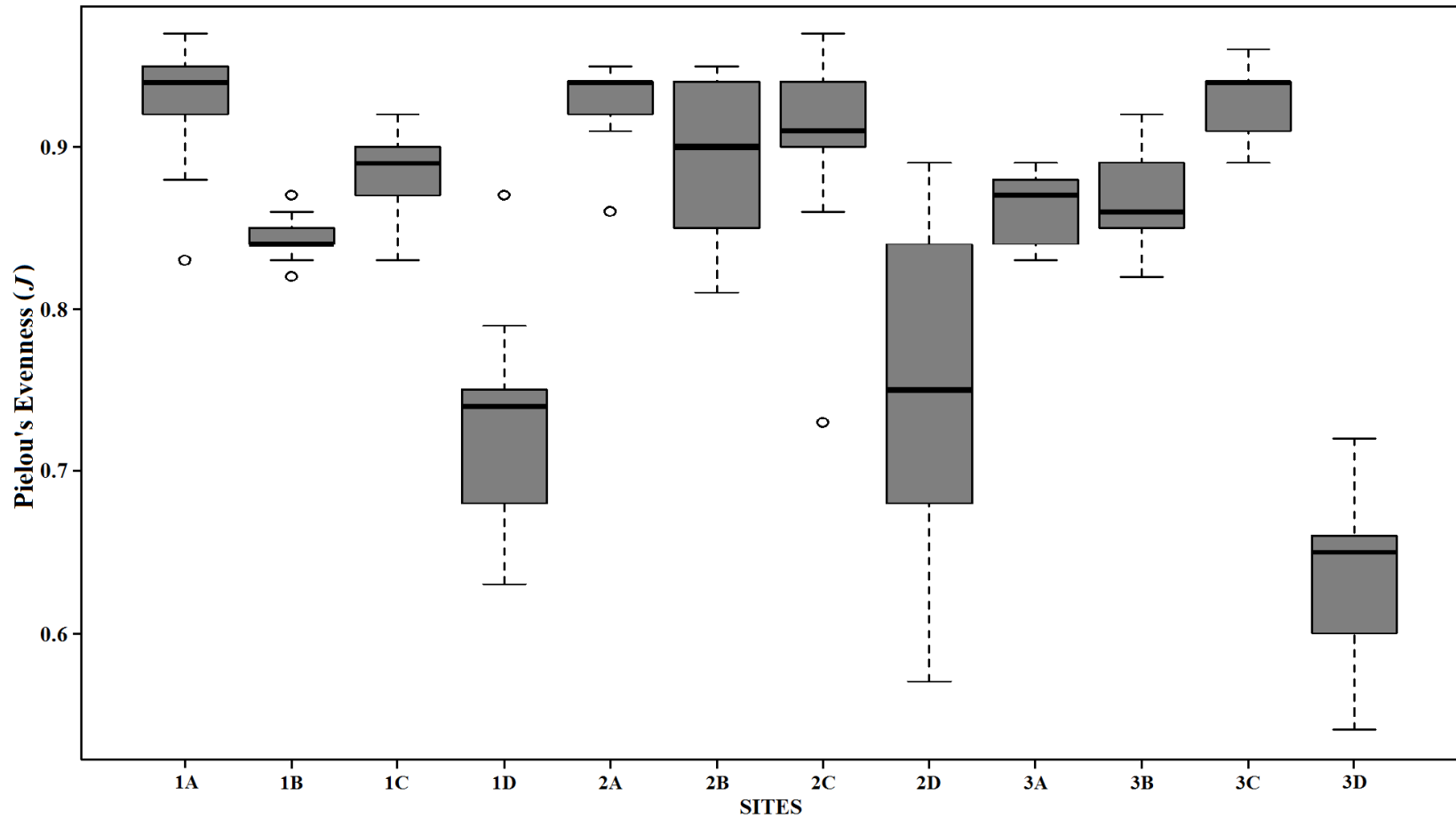
Figure 20. The range, minimum, maximum, median, lower quartile, upper quartile, and outliers (hollow circles) for Pielou's evenness (*J*) index (n = 9) at sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Table 15

Statistical comparisons of medians of Pielou's Evenness Indices (J) between sites using the Mann-Whitney U-test (Appendix H; Table H9) for April 2009, September 2009 and August 2010 sample collections. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	**	*	***	2A	n.s.	n.s.	***	3A	n.s.	***	***
1B		**	**	2B		n.s.	**	3B		**	***
1C			***	2C			**	3C			***

*P<0.05   **P<0.01   ***P<0.001

Table 16

Statistical comparisons of medians of Pielou's Evenness Indices (J) between sample collections using the Mann-Whitney U-test (Appendix H; Table H10) for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	**	1	n.s.	*	1	n.s.	**	1	n.s.	**
2		**	2		n.s.	2		n.s.	2		**

*P<0.05   **P<0.01   ***P<0.001

Margalef's Species Richness Index (SR)

Analysis of species richness using Margalef's richness index (SR) indicated that site A had consistently higher species richness, and site D had consistently lower species richness (Figure 21).

Comparisons of means of Margalef's richness index (SR) between sites using Welch's unequal variances *t*-test for April 2009 revealed that the macrobenthos from all sites exhibited significant differences in richness, except for sites A and C (Table 17). Comparisons of September 2009 richness values revealed that the macrobenthos from all sites exhibited significant differences (Table 17). In August 2010, the species richness values of the macrobenthos from all sites showed significant differences, except between sites A and C and between sites B and C (Table 17).

Comparisons between samplings for site A using Welch's unequal variances *t*-test for means of Margalef's richness index (SR) showed that there was no significant difference between samplings, except between April 2009 and September 2009 (Table 18). SR values for the macrobenthos from sites B and D did not show any significant differences among the three sample collections. SR values for site C were significantly greater in April 2009 than in August 2010, and significantly greater in August 2010 than in September 2009.
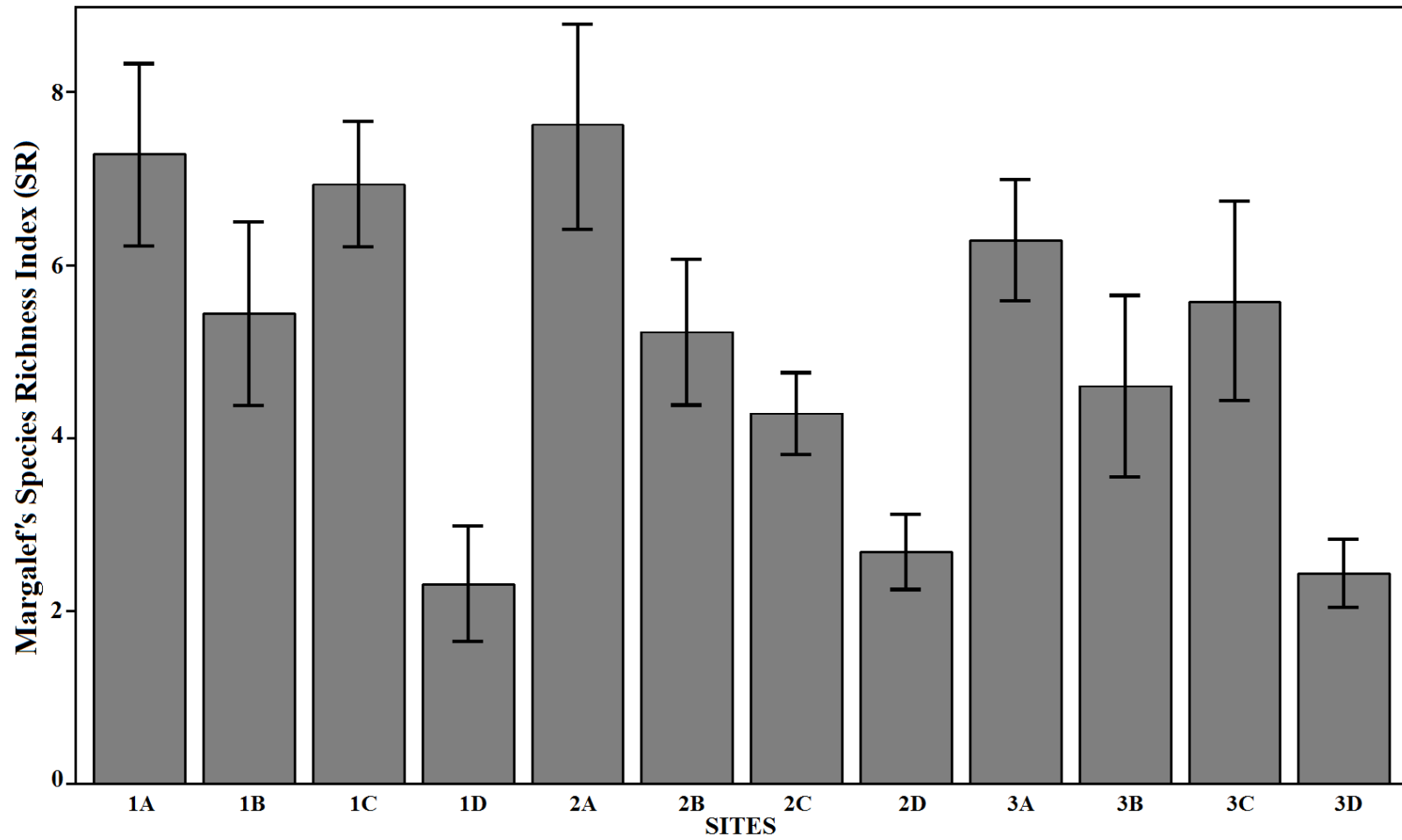
Figure 21. Mean values (bars) ± one standard deviation (capped lines) of Margalef's species richness index (*SR*) during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections at sites A, B, C and D.

Table 17

Statistical comparisons of means of Margalef's species richness indices (SR) between sites using Welch's unequal variances t-test (Appendix H; Table H11) for the April 2009 (1), September 2009 (2), and August 2010 (3) sample collections. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	**	n.s.	**	2A	***	***	***	3A	***	n.s.	***
1B		**	***	2B		**	***	3B		n.s.	***
1C			***	2C			***	3C			***

*P<0.05   **P<0.01   ***P<0.001

Table 18

Statistical comparisons of means of Margalef's species richness indices (SR) between sample collections using Welch's unequal variances t-test (Appendix H; Table H12) for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	*	1	n.s.	n.s.	1	***	**	1	n.s.	n.s.
2		**	2		n.s.	2		**	2		n.s.

*P<0.05   **P<0.01   ***P<0.001

Inverse Simpson Diversity Index (1/D)

Analysis of species diversity using the inverse Simpson diversity index indicated that site A had higher diversity in April and September 2009 than in August 2010, and that site D consistently had the lowest diversity (Figure 22). During the sampling in August 2010, site C had the highest diversity (Figure 22).

Comparisons of means of the inverse Simpson diversity index between sites using Welch's unequal variances *t*-test for April 2009 revealed that sites were significantly different (Table 19). In September 2009, sites had a significant difference in diversity except between B and C (Table 19). In August 2010, sites had a significant difference in diversity except between site A and B (Table 19).

Comparisons of the means of the inverse Simpson diversity index between samplings for site A using Welch's unequal variances *t*-test showed significant differences in diversity, except between April 2009 and September 2009 samplings (Table 20). Comparisons between samplings for site B showed no significant difference in diversity between samplings, except between April 2009 and September 2009 samplings. Comparisons between samplings for site C showed significant differences in diversity between samplings, except between September 2009 and August 2010 samplings (Table 20). Comparisons between samplings for site D showed significant differences in diversity between samplings, except between April 2009 and September 2009 samplings (Table 20).
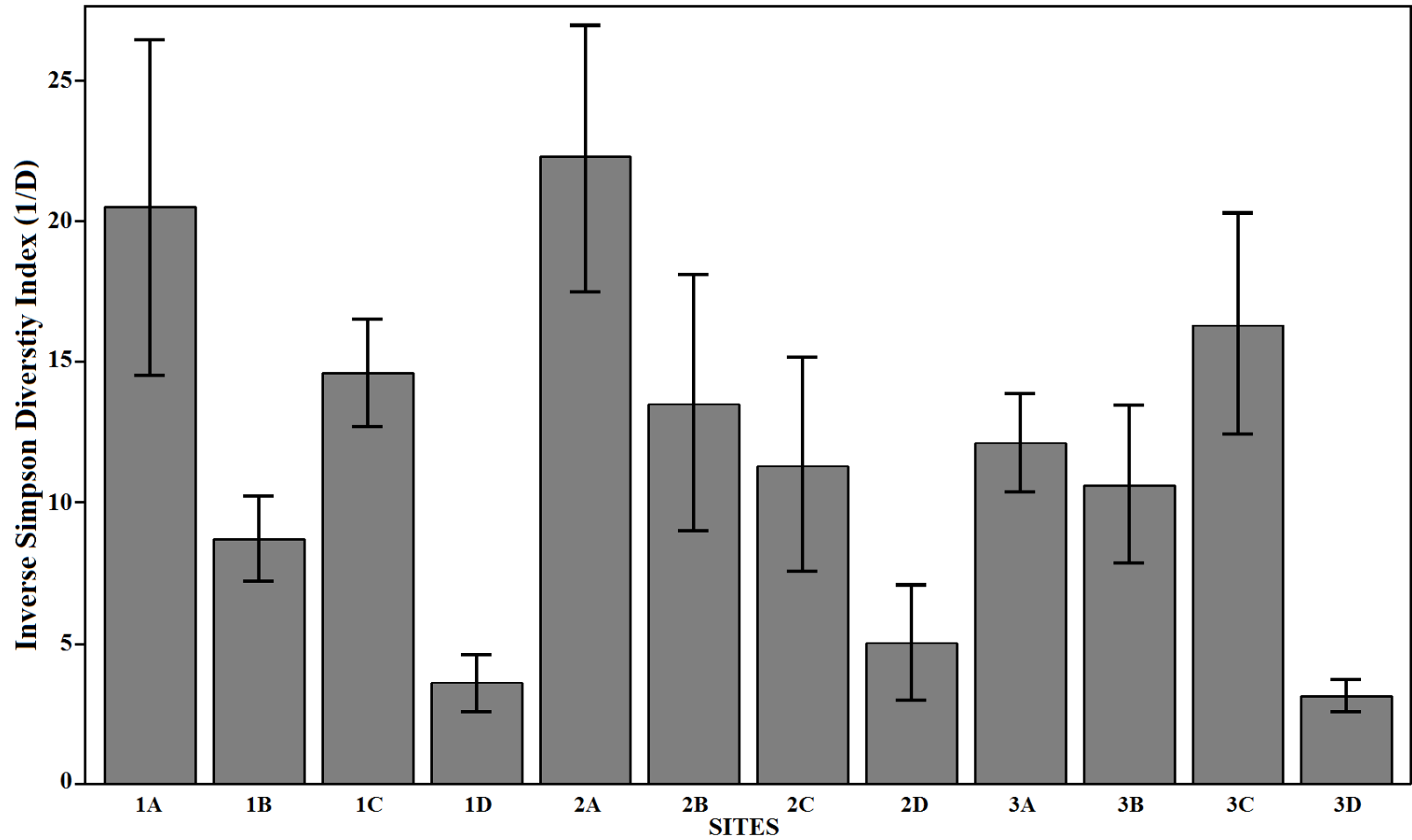
Figure 22. Means (bars) ± one standard deviation (capped lines) of the inverse Simpson diversity index (1/D) during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections at sites A, B, C and D.

Table 19

Statistical comparisons of means of Simpson's diversity indices (1/D) between sites using Welch's unequal variances t-test (Appendix H; Table H13) for April 2009, September 2009 and August 2010 sample collections. n.s. signifies there is no significant difference between sites.

	1B	1C	1D		2B	2C	2D		3B	3C	3D
1A	***	**	***	2A	***	***	***	3A	n.s.	**	***
1B		***	***	2B		n.s.	***	3B		**	***
1C			***	2C			***	3C			***

*P<0.05   **P<0.01   ***P<0.001

Table 20

Statistical comparisons of Simpson's Inverse diversity indices (1/D) between sample collections using Welch's unequal variances t-test (Appendix H; Table H14) for sites A, B, C and D. n.s. signifies there is no significant difference between sites.

	Site A			Site B			Site C			Site D	
	2	3		2	3		2	3		2	3
1	n.s.	**	1	**	n.s.	1	*	**	1	n.s.	*
2		***	2		n.s.	2		n.s.	2		*

*P<0.05   **P<0.01   ***P<0.001

Rarefaction Curves

The initial slope of the rarefaction curve represents species evenness of the macrobenthos assemblage, and the endpoints of the curve indicate the species richness of the macrobenthos assemblage. Rarefaction analysis of macrobenthos abundance data for sites A, B, C and D during the three sample collections in April 2009, September 2009, and August 2010 indicated that site D consistently had the lowest richness, whereas site A consistently had the highest richness (Figure 23). At site A, the August 2010 assemblage (3A) showed a decrease in richness and evenness. At site B, the macrobenthos assemblages exhibited values of richness and evenness intermediate between those of sites A and D, with a slight decrease in richness and evenness occurring in the August 2010 assemblage (3B). At site C, the April 2009 macrobenthos assemblage (1C) exhibited values of richness and evenness intermediate between those of sites A and B, but the September 2009 and August 2010 assemblages (2C, 3C) exhibited decreases in richness and evenness that were similar to those at site B (Figure 23). Rarefaction analysis of macrobenthos AFDW biomass data for sites A, B, C and D during the three sample collections in April 2009, September 2009 and August 2010 reaffirmed the trends shown in the analysis of the abundance data (Figure 24).
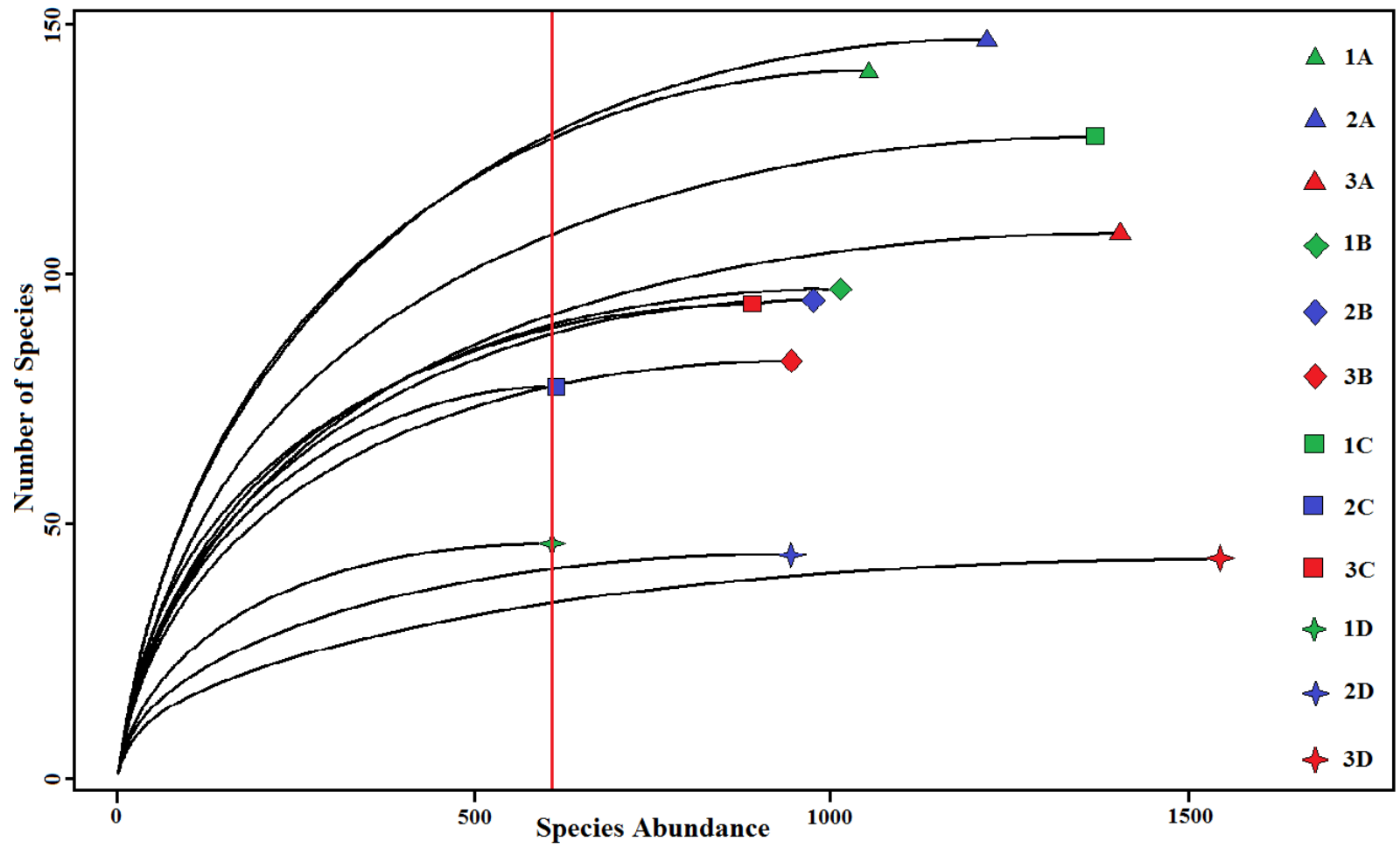
Figure 23. The Sanders-Hurlbert rarefaction curves for macrobenthos abundance at sites A, B, C and D during the April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The red vertical line intersects the endpoint of the site with lowest diversity and abundance to which other sites could be compared.
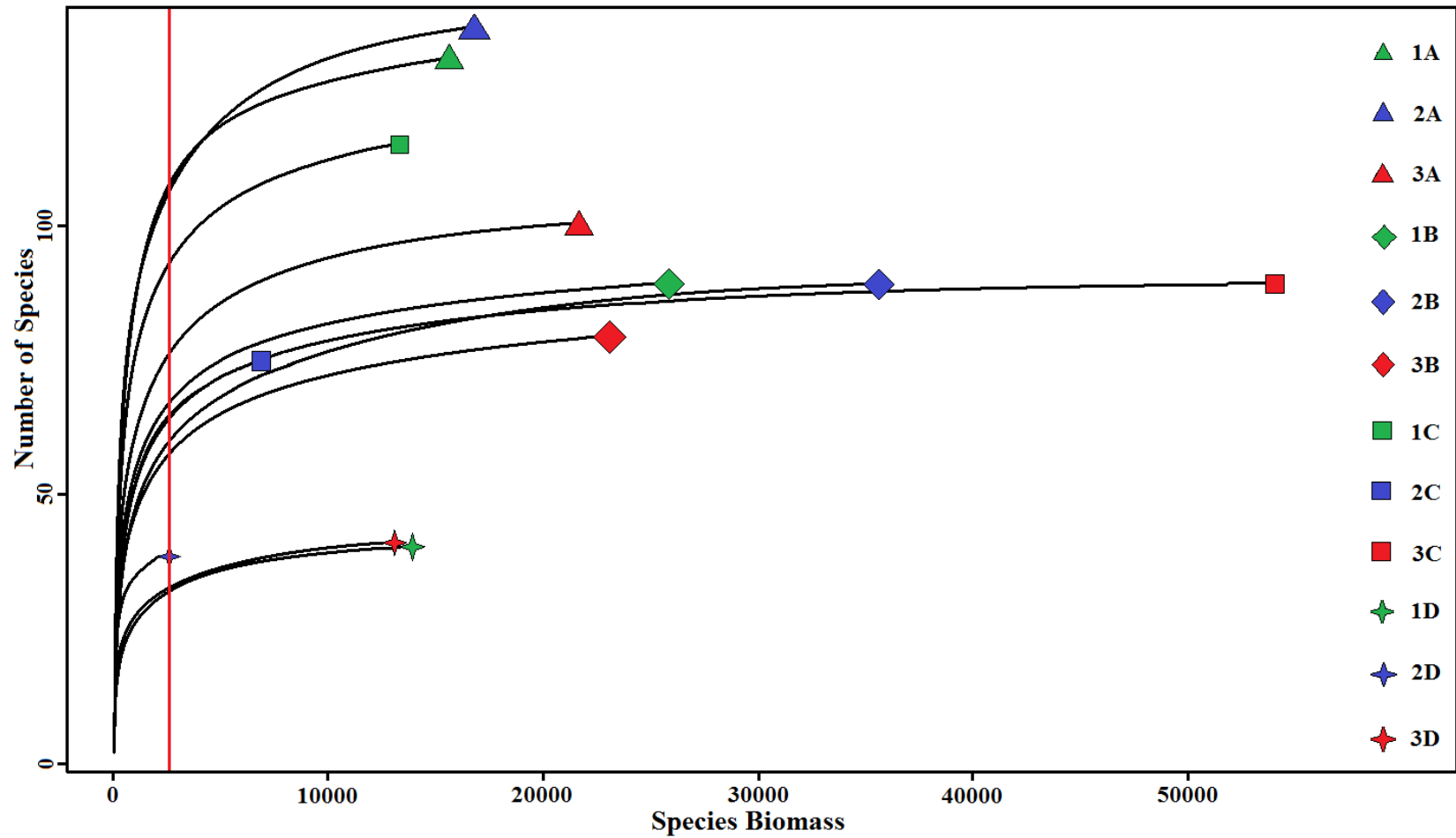
Figure 24. The Sanders-Hurlbert rarefaction curve for macrobenthos AFDW biomass at sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The red vertical line intersects the endpoint of the site with the lowest diversity and biomass to which other sites could be compared.

Feeding Guilds: Abundance

The identified macrobenthos species were classified according to their mode of feeding to identify possible differences in functional diversity among sites that could be due to the effects of hypoxic stress on communities. Macrobenthos collected at sites A, B, C, and D from April 2009, September 2009 and August 2010 samplings were split into five different feeding guilds: carnivores (Carn), herbivores (Herb), surface deposit feeders (SDF), sub-surface deposit feeders (SSDF), and suspension feeders (SF). Sub-surface deposit feeders were the dominant feeding guild, and herbivores were the least abundant feeding guild in terms of abundance of all sample collections. In fact, herbivores were notably absent from site D during the summer samplings of September 2009 and August 2010.

In April 2009 surface deposit feeders were the dominant feeding guild at site A, followed in order of abundance by sub-surface deposit feeders, carnivores, suspension feeders and herbivores. Sub-surface deposit feeders were the dominant feeding guild at site B, followed in order of abundance by surface deposit feeders, carnivores, herbivores and suspension feeders. Sub-surface deposit feeders were the dominant feeding guild at sites C and D, followed in order of abundance by surface deposit feeders, suspension feeders, carnivores and herbivores (Figure 25).

During the September 2009 sample collections, surface deposit feeders dominated the macrobenthos assemblages at sites A, B, and C, but sub-surface deposit feeders dominated at site D. Sub-surface deposit feeders were the second-most abundant feeding guild at sites A and B, but carnivores were the second-most abundant feeding guild at sites C and D. Carnivores represented the third-most abundant feeding guild at sites A

and B, but, at site C, sub-surface deposit feeders represented the third-most abundant

feeding guild. At site D surface deposit feeders represented the third-most abundant

feeding guild (Figure 25).

Figure 25. Percentage contribution of different feeding guilds by abundance during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections at sites A, B, C and D. Numbers on the bars are percentages.

During August 2010, surface deposit feeders and sub-surface deposit feeders were the first- and second-most abundant feeding guilds at sites A, B and C, followed by carnivores. At site D, sub-surface deposit feeders dominated the assemblage followed by surface deposit feeders and carnivores (Figure 25).

The temporal variability in feeding guilds at different sites from spring 2009 to late summer 2009 and summer 2010 indicated that surface deposit feeders are the dominant group at site A regardless of sampling time. Surface deposit feeders also dominate the assemblages at sites B and C, but only in the summer samplings. Carnivores increased at sites B, C and D from spring 2009 to late summer 2009, but only increased at site B during summer 2010. Sub-surface deposit feeders dominated sites B and C during spring 2009, but surface deposit feeders replaced them in terms of dominance in late summer 2009 and summer 2010 samplings. Suspension feeders were most numerous on average at site C during all three sample collections. At site D, sub-surface deposit feeders dominated the assemblages during all three samplings. Their proportion increased from April 2009 to September 2009, but their proportion decreased from September 2009 to August 2010 (Figure 25). At this site, the proportion of surface deposit feeders decreased as the proportion of carnivores increased.

Feeding Guilds: Biomass

Carnivores were the most dominant feeding guild followed by Sub-surface deposit feeders, and herbivores were the least dominant feeding guild in terms of AFDW biomass during all sample collections (Figure 26).

During April 2009, the reference site (A) had a much higher proportion of macrobenthos biomass represented by surface deposit feeders and a much lower proportion of macrobenthos biomass represented by carnivores than that at site (D) with more recent oxygen stress (Figure 26). When the proportion of biomass of the feeding guilds was compared with the proportion of abundance of the feeding guilds, carnivore biomass was dominated by larger individuals and sub-surface-deposit-feeder biomass was dominated by smaller individuals. Carnivores found at sites B, C and D in April 2009 were generally large in size. At site C, suspension feeders contributed only 7% of the biomass, but 20% of the abundance. Carnivores contributed almost half of the macrobenthos biomass of site C, but only 16% of the abundance (Figures 25 and 26). At site D, large carnivores constituted the 60% of the biomass. Sub-surface deposit feeders, surface deposit feeders and suspension feeders at site D were all small individuals.
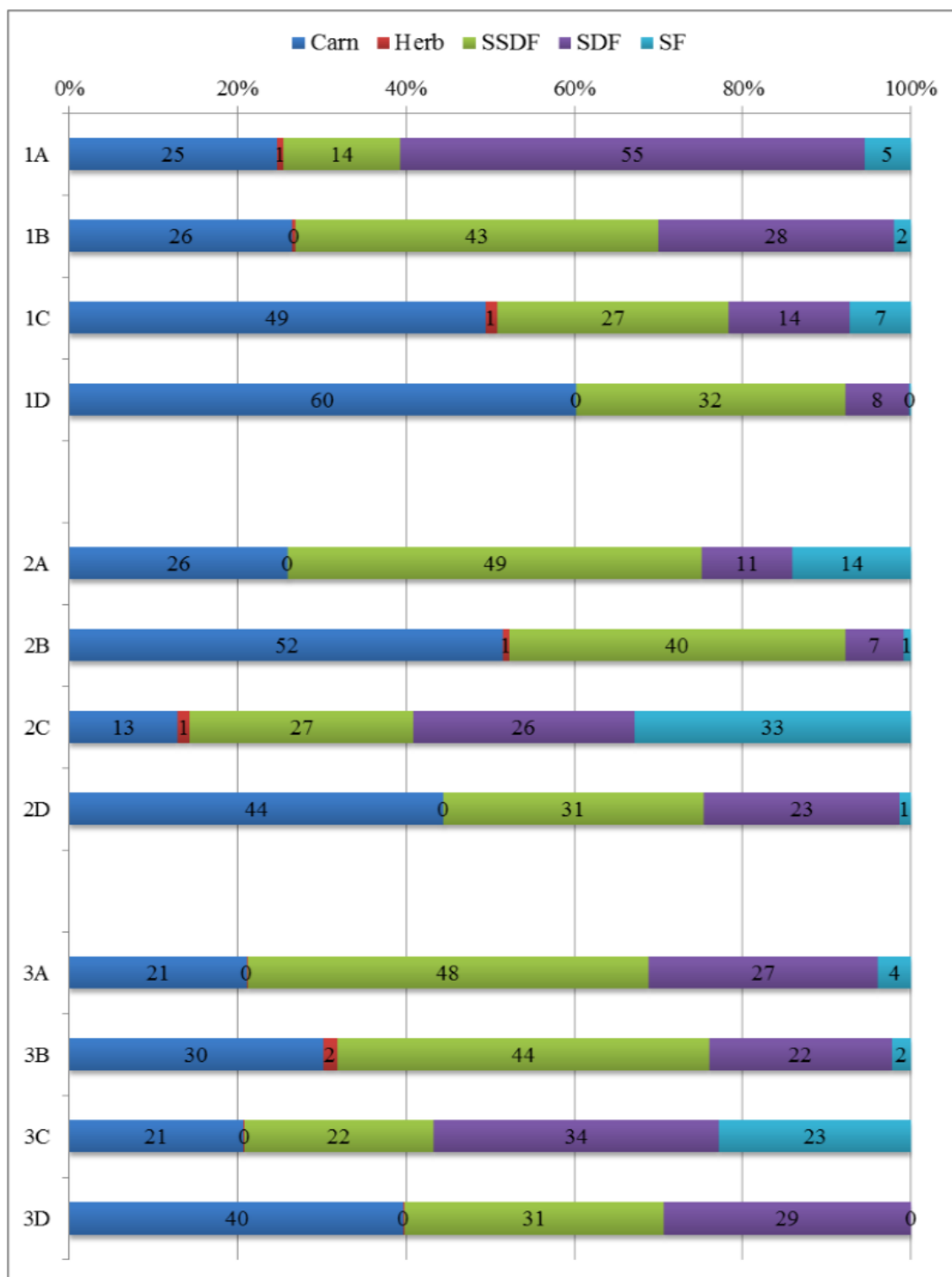
Figure 26. Percentage AFDW biomass contribution of different feeding guilds during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections at sites A, B, C and D. Numbers on the bars are percentages.

During September 2009, the macrobenthos at site A was comprised chiefly of large carnivores and sub-surface deposit feeders but small surface deposit feeders (Figures 25 and 26). The macrobenthos at site B was comprised chiefly of large carnivores and small surface deposit feeders. The macrobenthos at site C was comprised chiefly of small carnivores and surface deposit feeders and large suspension feeders. The macrobenthos at site D was comprised chiefly of large carnivores and surface deposit feeders and small subsurface deposit feeders (78% in terms of abundance, but only 31% in terms of biomass).

During August 2010, the macrobenthos assemblages at sites A and B were comprised chiefly of large carnivores and subsurface deposit feeders, but small surface deposit feeders (Figures 25 and 26). The macrobenthos at site C was comprised of large carnivores, sub-surface deposit feeders and suspension feeders, but small surface deposit feeders (34% of biomass, 55% of abundance). The macrobenthos at site D was comprised of very large carnivores (40% of the biomass, 8% of the abundance) and large surface deposit feeders (29% of the biomass, 19% of the abundance), but small sub-surface deposit feeders (31% of the biomass, 73% of the abundance).

Percentage of Opportunist Species

The percentages of opportunist species identified at sites A, B, C and D were analyzed for April 2009, September 2009 and August 2010 sample collections to identify the contribution of the opportunist species to the total abundance (Figure 27). Site D consistently had the highest percentage of opportunist species over all three sample collections. Site C had the lowest percentage of opportunist species among the sites sampled during the summer collections in September 2009 and August 2010, whereas the reference site (A) had the lowest average number of opportunist species during the April 2009 sample collection. After site D, site B had the next-highest proportion of opportunists over all three sample collections, but exhibited decreasing percentages of opportunist species in September 2009 and again in August 2010 (Figure 27). The percentages of macrobenthos opportunists fluctuated but stayed nearly the same from spring to summer samplings at site C. Sites A and D were the only sites to show increases in the proportions of opportunists from spring to late-summer and to the following summer; in both assemblages, these increases were due to increases in the abundances of the capitellid polychaete *Mediomastus californiensis*.
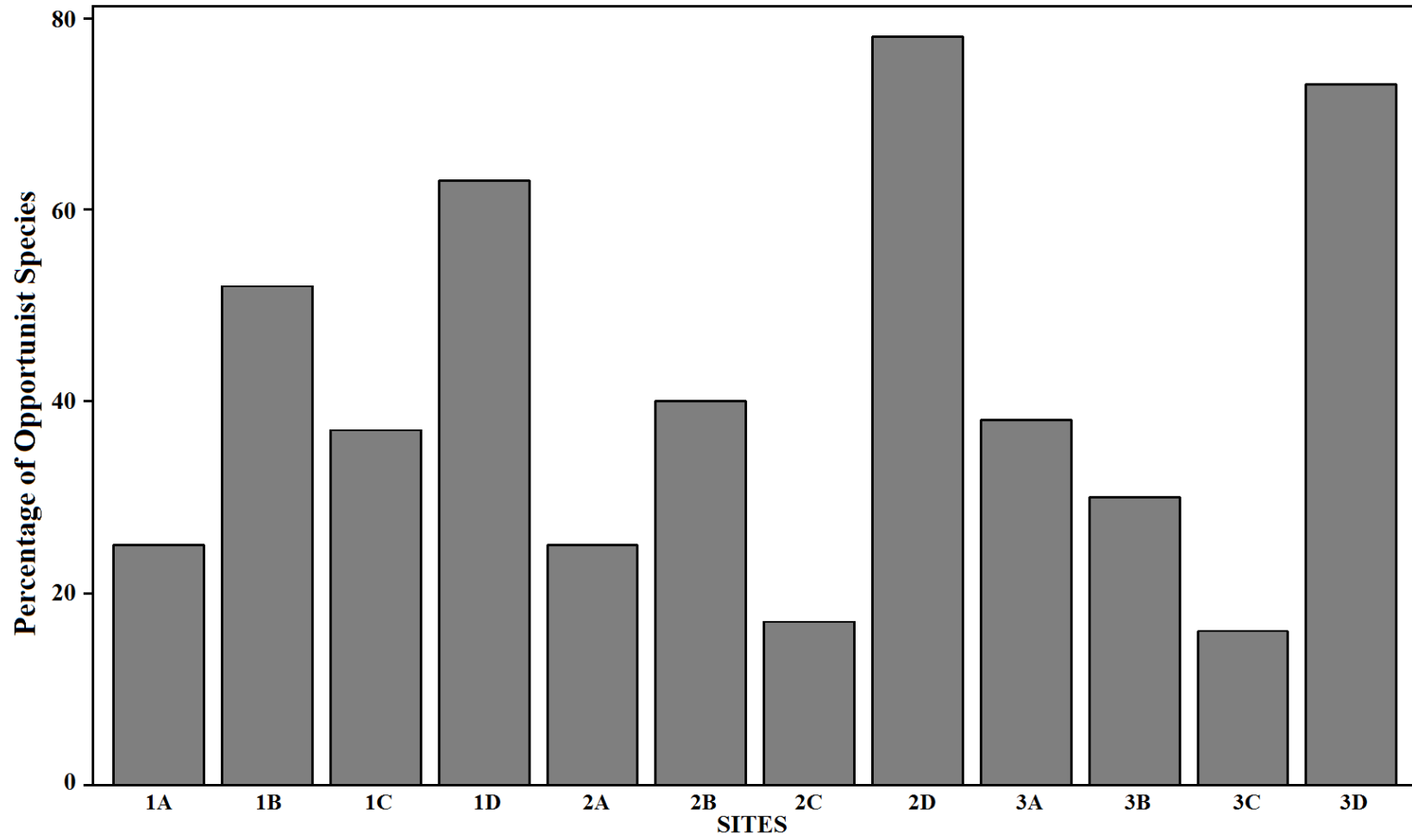
Figure 27. Percentages of opportunist species at sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Assessment of Species Associations

Analysis of macrobenthos specimen abundance for the three individual sample

collections during 2009 and 2010 used the Bray-Curtis dissimilarity distance to assess

natural faunal associations among the subcores (Figures 28, 29 and 30). Dendrogram

clusters were identified by visual inspection. Instead of choosing a cut-off significance

value for Q-mode dendrogram, the natural grouping of subcores as sites were analyzed.

Subcores from April 2009 at sites A, B, C and D grouped within the respective sites

except for subcore 1C3, which joined the clusters of site B subcores (Figure 28). In April

2009 site C had the lowest dissimilarity (highest similarity): eight out of nine subcores

belonging to site C joined at 0.60 dissimilarity. The subcores belonging to site B joined

with site C at 0.80 dissimilarity. Subcores belonging to site D joined the cluster of sites C

and B at 0.90 dissimilarity and site A joined these clusters at 0.97 dissimilarity. This

indicates that the site C assemblage had more similar macrobenthos species than the other

three sites and it shared the most common species with site B. Among all four sites, the

assemblage at site A was the most dissimilar to those from the other three sites in April

2009 (Figure 28).

In September 2009, subcores from the four sites grouped with their respective

sites (Figure 29). Site D subcores grouped at the lowest dissimilarity (0.65) among the

four sites and these subcores joined the subcores from site B at 0.85 dissimilarity.

Subcores from site C joined the cluster of sites B and D at 0.92 dissimilarity. Subcores

from site A joined the cluster of sites B, C and D at 0.96 dissimilarity, making the

assemblage at site A the most dissimilar assemblage. Although the least dissimilar

macrobenthos assemblage changed from the one at site C in the spring to the one at site D

in late summer, site A had the most dissimilar community among all four sites in 2009 (Figure 29).

In the third sample collection during August 2010 all subcores grouped with their respective sites except 3C5, which had the lowest abundance among all 36 subcores (Figure 30). Site D shared the most species among all three samplings, the subcores joining as a cluster at 0.55 dissimilarity. Subcores from site B formed a cluster at 0.70 dissimilarity and joined site D at 0.75 dissimilarity. Subcores from site A formed a cluster at 0.65 dissimilarity and joined site C at 0.80 dissimilarity. The clusters composed of assemblages from sites B and D joined the clusters composed of assemblages from sites A and C at 0.85 dissimilarity. In terms of outliers, one of the subcores of site B (3B2) was included in the cluster of site C and subcore 3C5 joined the clusters of sites A, B, C and D as a simplicifolious leaf (Drout and Smith, 2012) (Figure 30).
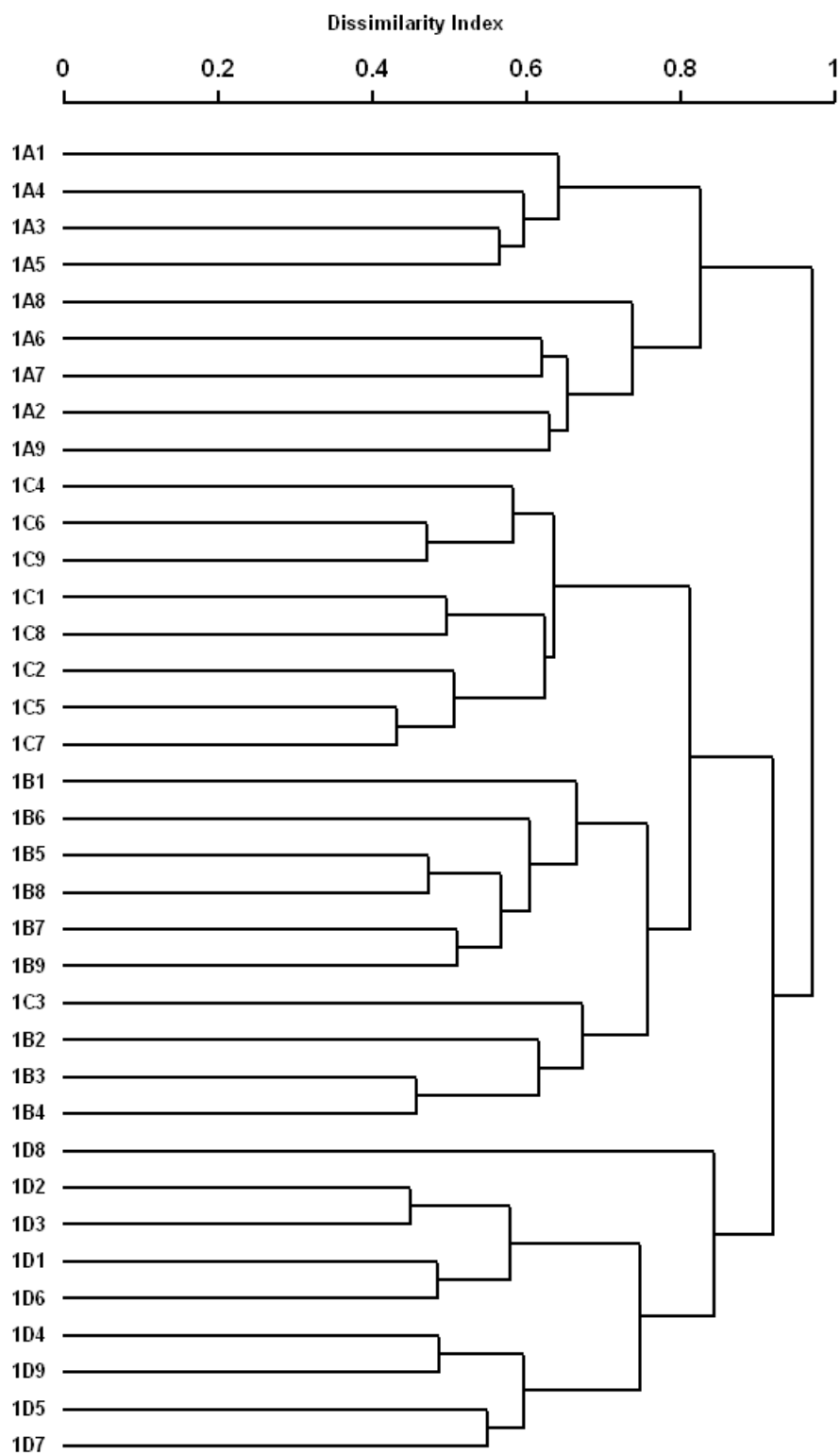
Figure 28. Q-mode Bray-Curtis dissimilarity index dendrogram calculated from specimen abundance for sites A, B, C and D during the April 2009 (1) sample collection.
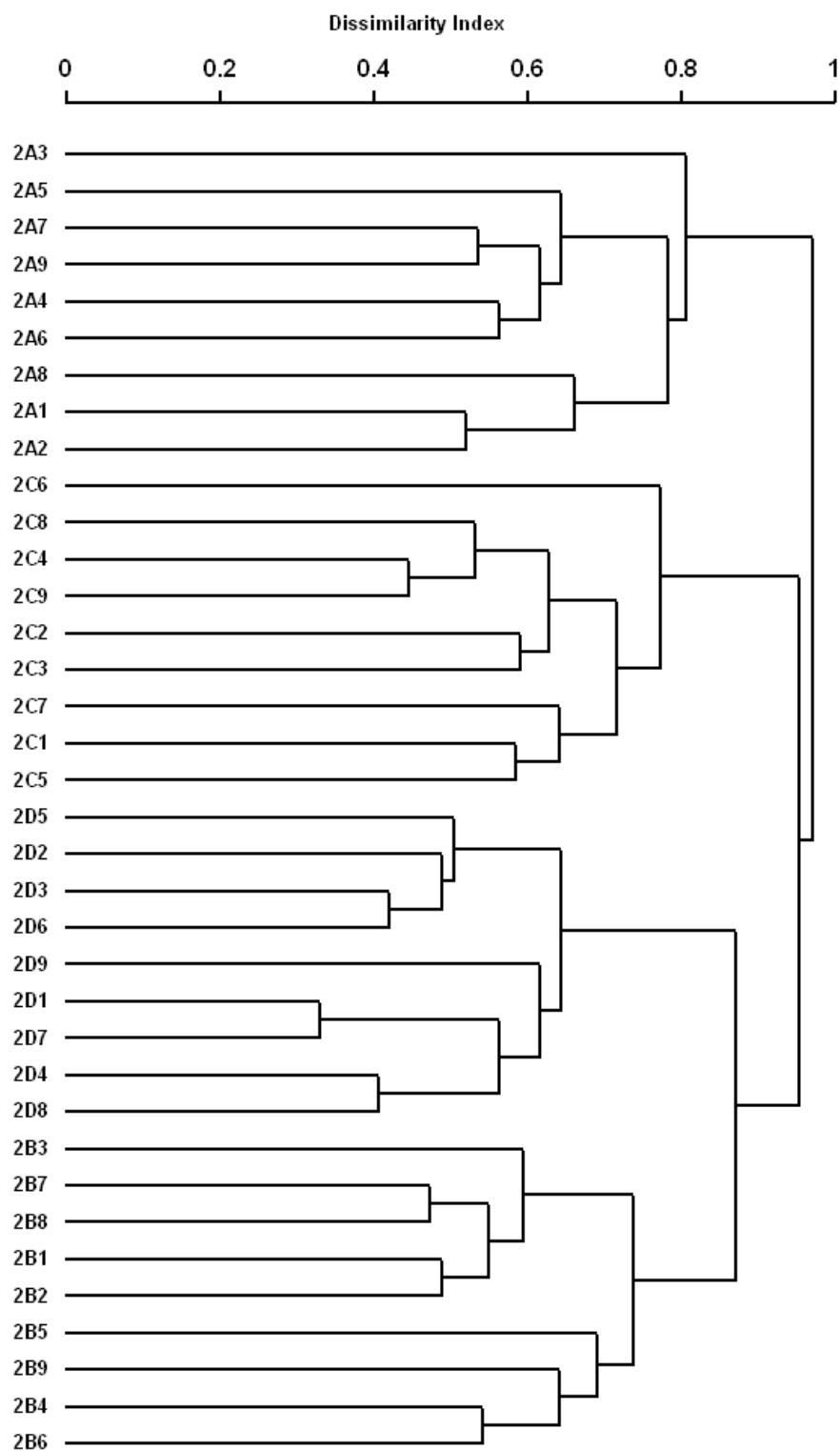
Figure 29. Q-mode Bray-Curtis dissimilarity index dendrogram calculated from specimen abundance for sites A, B, C and D during the September 2009 (2) sample collection.
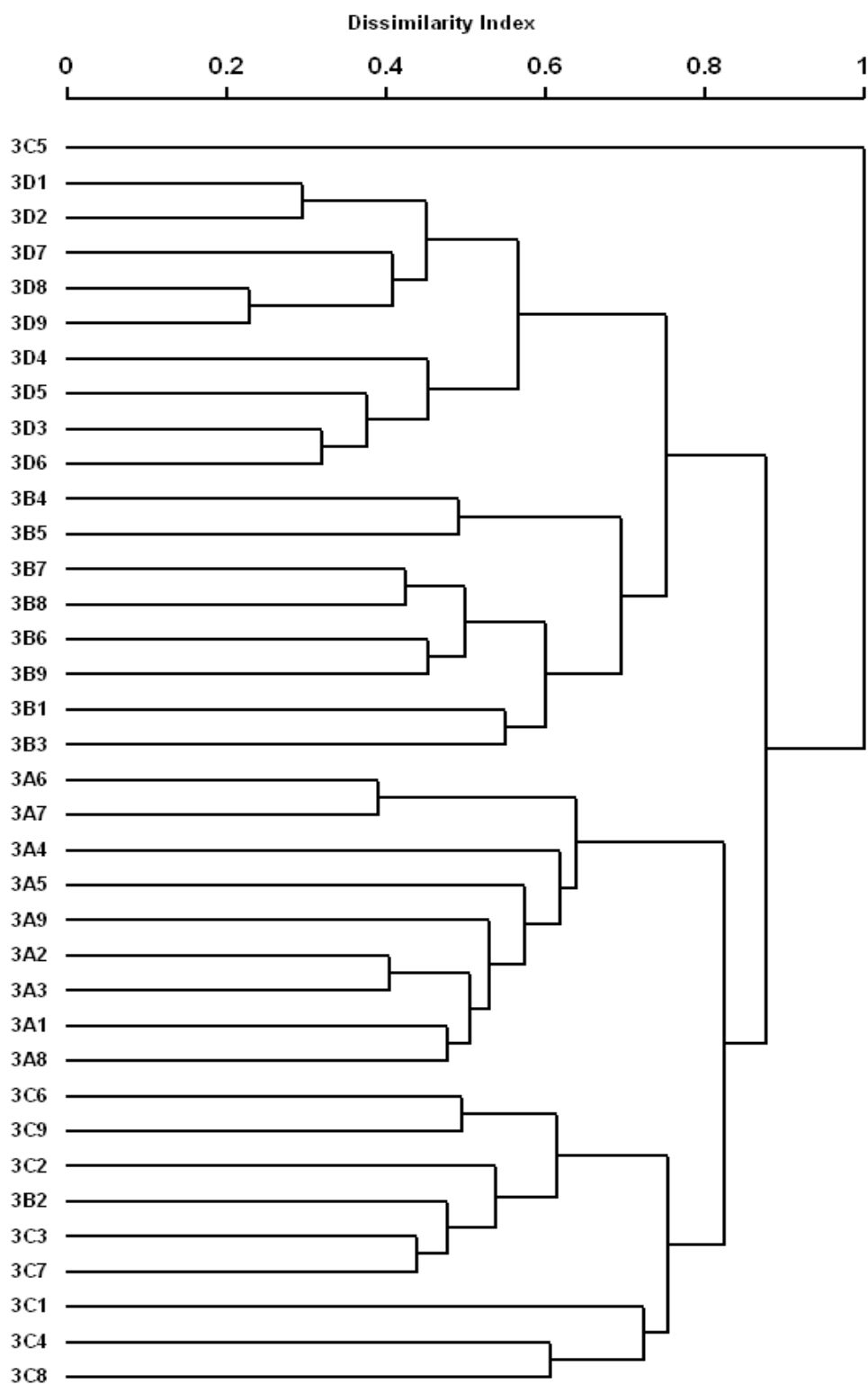
Figure 30. Q-mode Bray-Curtis dissimilarity index dendrogram calculated from specimen abundance for sites A, B, C and D during the August 2010 (3) sample collection.

The Bray-Curtis dissimilarity index among subcores was analyzed at each site for the three different sample collections during April 2009, September 2009 and August 2010 to assess temporal variations in abundance within sites (Figures 31, 32, 33 and 34). Log-transformed macrobenthos abundance data was used in the analysis. Analysis of site A subcores indicated that the subcores from sample collections 1 and 2 intermingled with each other, whereas the subcores from sampling 3 grouped into separate cluster, indicating that the benthic assemblage at site A changed from 2009 to 2010 (Figure 31). Subcores from August 2010 had the most similar macrobenthic assemblage composition, forming a cluster at 0.65 dissimilarity, and this cluster eventually joined the cluster composed of subcores collected from April and September 2009 at 0.90 dissimilarity. Subcores of macrobenthos collected during April and September 2009 were more disparate than the subcores collected in August 2010, not forming a cluster until 0.84 dissimilarity and sharing only 10% of the species with the August 2010 subcores (Figure 31).

Analysis of site B subcores in April 2009, September 2009 and August 2010 showed a separated cluster pattern seen in the analysis of site A (Figure 32). At this site, however, three subcores from the September 2009 (2) sampling intermingled with the subcores from the August 2010 (3) sampling and formed a cluster at 0.80 dissimilarity, and one subcore was grouped with the subcores from the April 2009 (1) sampling that clustered at 0.72 dissimilarity. Because the two summer samplings (September 2009 and August 2010) joined separately from the (mostly) April 2009 sampling, which showed more affinity at 0.72 dissimilarity, there is a seasonal aspect to the groupings. Among all

sites, site B had the most similar assemblages, with the maximum dissimilarity among macrobenthos found at this site at 0.85 (Figure 32).

Bray-Curtis analysis of site C subcores showed that most of the April 2009 subcores joined together at 0.65 dissimilarity, except for 1C3, which joined with subcores from the August 2010 sampling (Figure 33). The subcores from the April 2009 and the August 2010 samplings clustered together at 0.81 dissimilarity and this cluster was ultimately joined by the September 2009 subcores at 0.95 dissimilarity. Subcores from site C grouped with their respective three samplings except subcores 1C3 and 3C5. Subcore 1C3 from the April 2009 sampling joined the August 2010 cluster, whereas subcore 3C5 from the August 2010 sampling joined the September 2009 cluster at 0.83 dissimilarity as a simplicifolious leaf. These groupings signify that although the three samplings constituted distinct assemblages, there were similarities between the assemblages of August 2010 and September 2009 and between the assemblages of April 2009 and September 2009 (Figure 33).

Analysis of site D subcores for April 2009, September 2009 and August 2010 samplings revealed three major clusters (Figure 34). Six subcores from the September 2009 sampling grouped at 0.64 dissimilarity; all the subcores from August 2010, some of the subcores from April 2009 sampling and the remaining subcores from the September 2009 sampling grouped at 0.70 dissimilarity; and five subcores from the April 2009 sampling grouped at 0.78 dissimilarity. These groupings signify that the assemblages at site D shared many of the same macrobenthos species during the three sample collections (Figure 34).
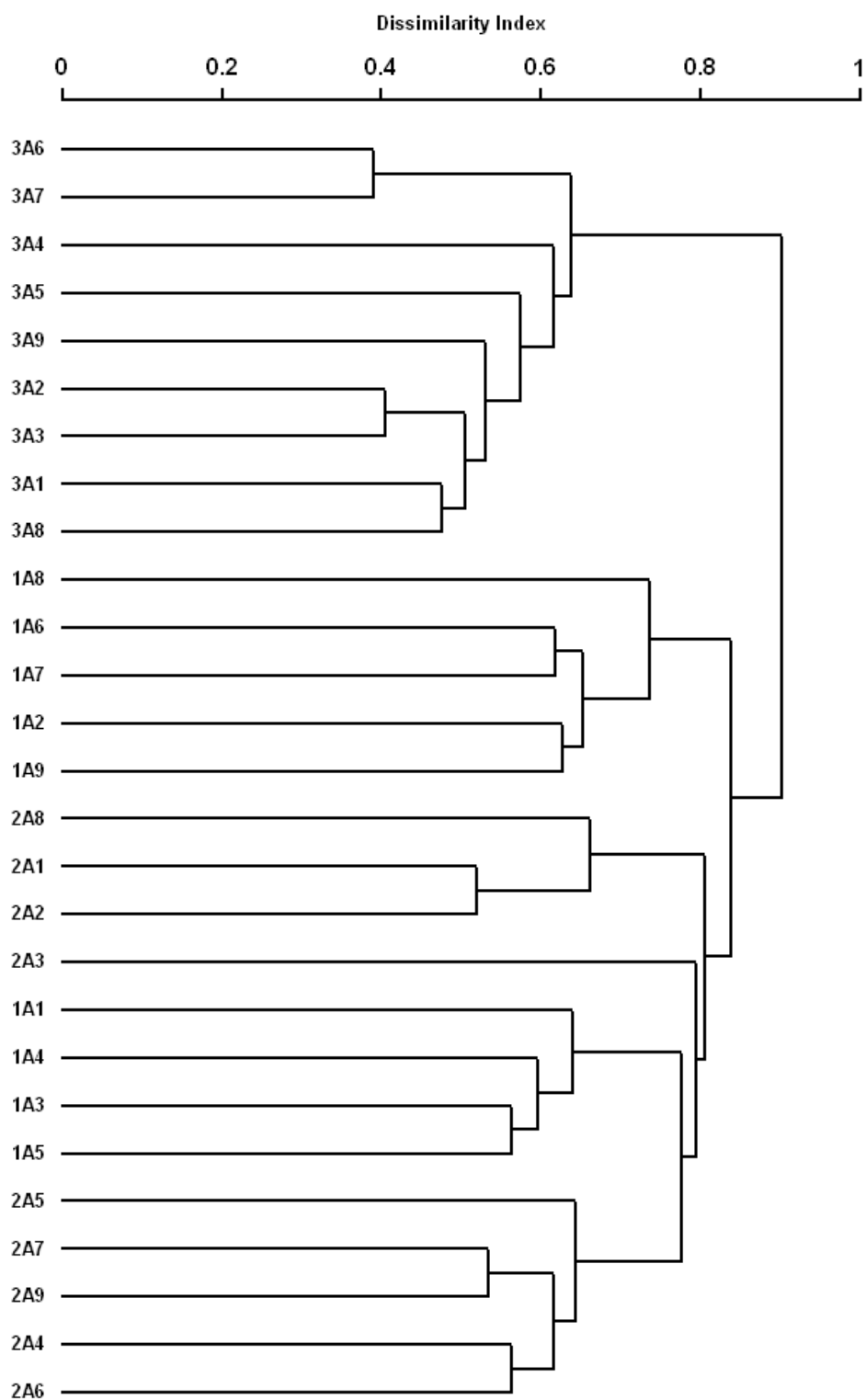
Figure 31. Q-mode Bray-Curtis dissimilarity index dendrogram for specimen abundance for site A during the April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.
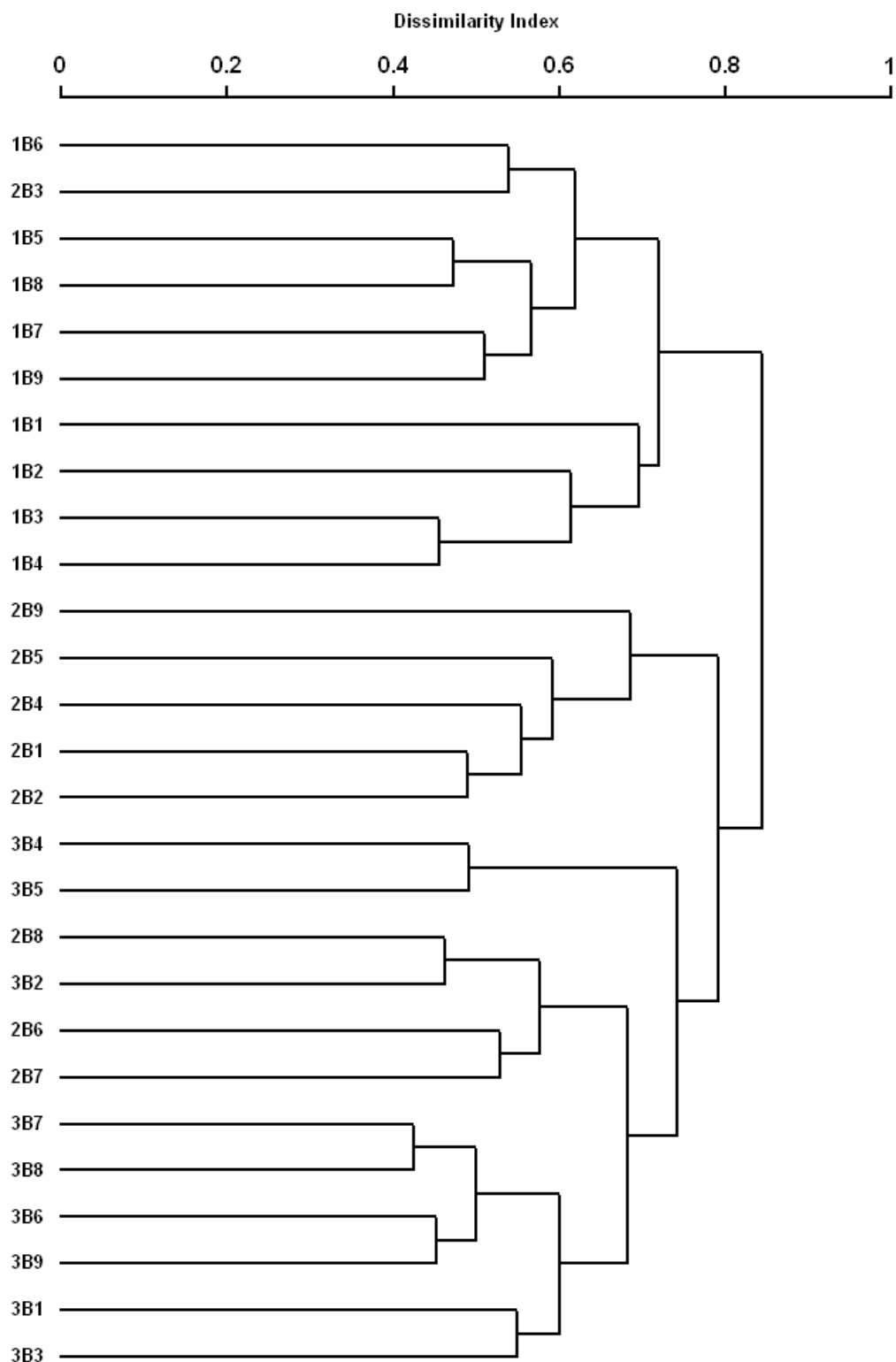
Figure 32. Q-mode Bray-Curtis dissimilarity index dendrogram for specimen abundance for site B during the April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.
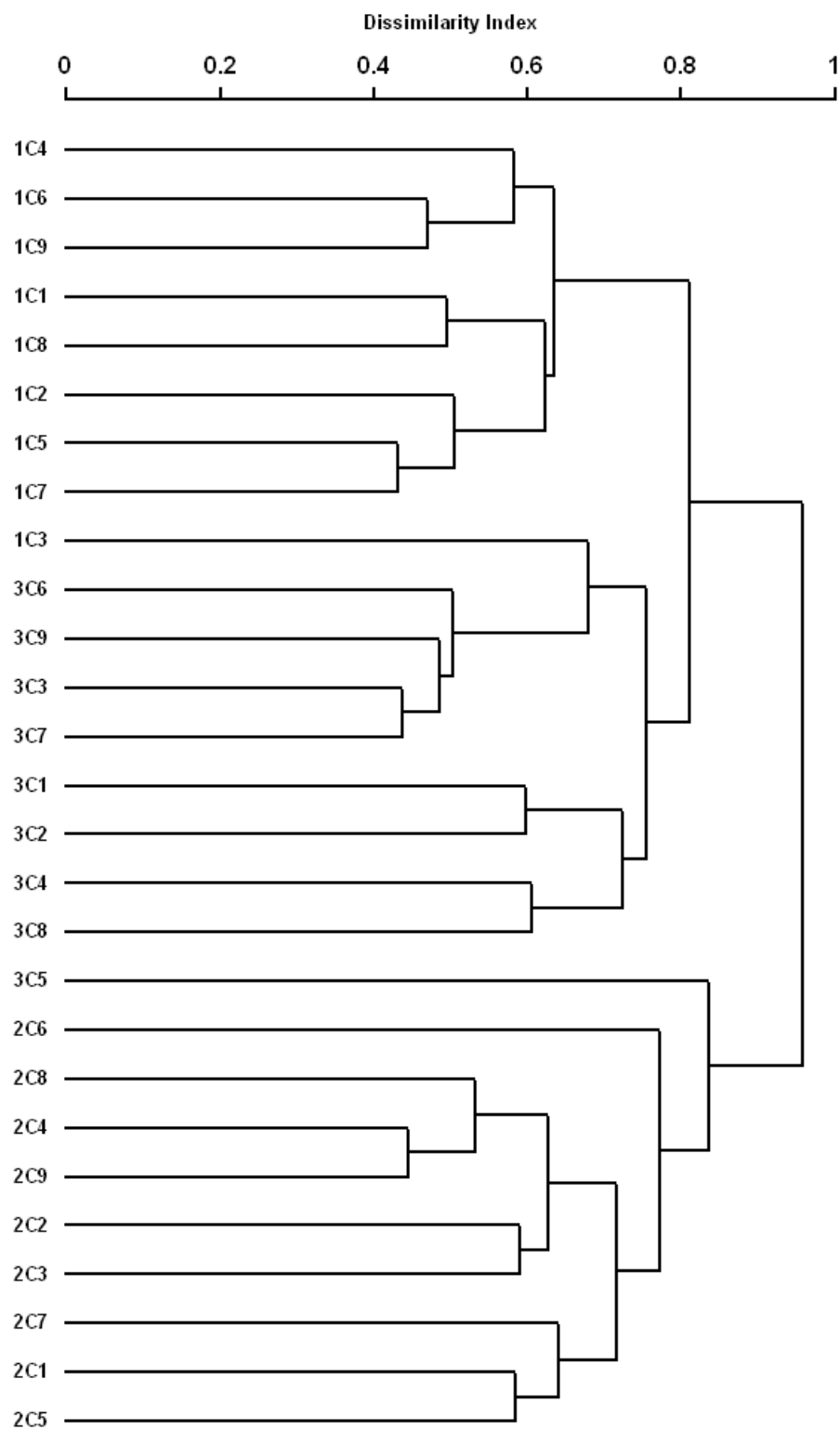
Figure 33. Q-mode Bray-Curtis dissimilarity index dendrogram for specimen abundance for site C during the April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.
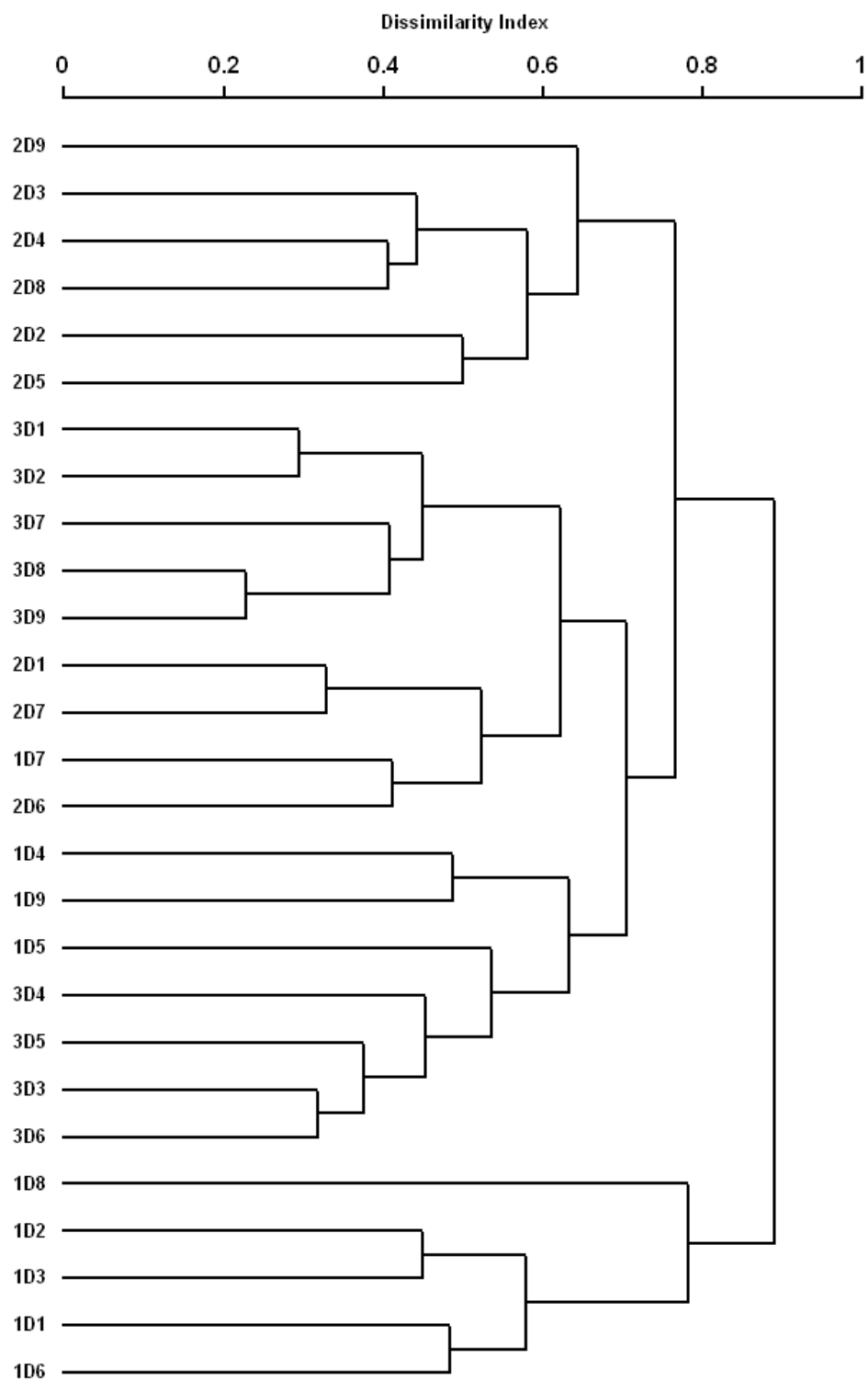
Figure 34. Q-mode Bray-Curtis dissimilarity index dendrogram for specimen abundance for site D during the April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Macrobenthos Species Associations

Macrobenthos species associations within April 2009, September 2009, and August 2010 sample collections were analyzed using the Bray-Curtis dissimilarity index at sites A, B, C and D to identify distinct assemblages (Figures 35). Dendrogram clusters were identified by visual inspection, and clusters with ≤ 0.5 dissimilarity were considered significant in R-mode dendrograms. During the April 2009 sampling, there were close associations between the species *P. pinnata* and Lineidae sp. 2; *A. aequalis* and *N. acuta*; *C. soyeri* and *M. californiensis*; *Golfingia* sp. 3 and *A. agilis*; *P. margaritaceum* and *E. sowerbyi*; *Chaetozone* sp. D and *T. deichmannae*; *Diastylis* sp. and *Brisaster* sp; *Photis* sp. and *Maldane* sp.; *Axiothella* sp. A and *P. fallax*; Amphiuridae sp. 2, *S. iris*, and *A. wassi*; *Nothria* sp. A and *Chaetozone* sp. A; *F. gibbosa* and *Oxyurostylis* sp.; *L. carinata* and *D. quadrisulcata*; *C. martinicensis* and *P. melanica*; *T. stroemii* and *Golfingia* sp. 1; Echiura sp. 1 and *Phascolion* sp.; *A. trilobata* and *T. ornata*; *X. brevitelson* and *S. missionensis*; and *E.* cf. *southerni* and *Euchone* sp. A (Figure 35). These associations were derived from the presence of these species at certain sites and samplings: *P. pinnata*, Lineidae sp. 2, A. *aequalis*, and *N. acuta* are moderately dominant species and were present at all four sites. *C. soyeri*, and *M. californiensis* were also found at all sites, but they dominated the assemblages at site D. *Golfingia* sp. 3, *A. agilis*, *P. margaritaceum*, and *E. sowerbyi* were found only at sites A and C. *Chaetozone* sp. D, *T. deichmannae*, *Diastylis* sp., and *Brisaster* sp. were found only at sites B and C. *Photis* sp., *Maldane* sp., *Axiothella* sp. A, *P. fallax*, Amphiuridae sp. 2, *S. iris*, and *A. wassi* were found at sites A, B and C. *Nothria* sp. A, *Chaetozone* sp. A, *F. gibbosa*, and *Oxyurostylis* sp. were found only at site C. *L. carinata,* and *D. quadrisulcata* were found only at site

D. *C. martinicensis*, *P. melanica*, *T. stroemii, Golfingia* sp. 1, Echiura sp. 1, *Phascolion* sp., *A. trilobata*, *T. ornata*, *X. brevitelson*, *S. missionensis*, *E.* cf. *southerni*, and *Euchone* sp. A were found only at site A.

During the September 2009 sample collection there were close associations between the macrobenthos species *C. soyeri* and *M. californiensis*; *C. capitata* and *N. acuta*; *N. proxima* and *P. squamifera*; *Euclymene* sp. A and *A. philbinae*; *M. pulleyi*, and *H. incisa*; *P. melanica*, and *D. soror*; *N. micromma*, and *E. lourei; A. nana* and *Crepidula* sp.; *Pseudotanais* sp. A and *A. suecica*; *Amphictene* sp. A and *G. cerina*; *Cerapus* sp. and *B. spiratus* (Figure 36). These associations were derived from the presence of these species at certain sites and samplings: *C. soyeri* and *M. californiensis*; and *C. capitata* and *N.* acuta were present at all 4 sites and accounted for a major portion of the abundance at site D. *N. proxima* and *P. squamifera* were present only at sites A, B and C. *Euclymene* sp. A and *A. philbinae* were present only at sites A and B. *M. pulleyi* and *H. incisa* were found only at site B. *P. melanica*, *D. soror*, *N. micromma*, *E. lourei*, *A. nana*, *Crepidula* sp., *Pseudotanais* sp. A, *A. suecica*, *Amphictene* sp. A, *G. cerina*, *Cerapus* sp., and *B. spiratus* were found only at site A (Figure 36).

During August 2010 sample collection, there were close associations between the macrobenthos species *P. pinnata* and *M. californiensis*; *S. tentaculata* and *A. wassi*; *Photis* sp. and *E. dispar*; *Cerapus* sp. and *P. melanica*; *Phascolion* sp. and *P. gouldii*; and Lineidae sp. 1 and *S. cancellaria* (Figure 37). These associations were derived from the presence of these species at certain sites and samplings: *P. pinnata* and *M. californiensis* are dominant species found at all four sites. *S. tentaculata* and *A. wassi* are found at all four sites, but in greatest abundance at site B. *Photis* sp., *E. dispar, Cerapus* sp., *P.*

melanica, *Phascolion* sp., and *P. gouldii* are found only at site A. Lineidae sp. 1 and *S. cancellaria* are found only at sites A and D (Figure 37).

Dissimilarity Index
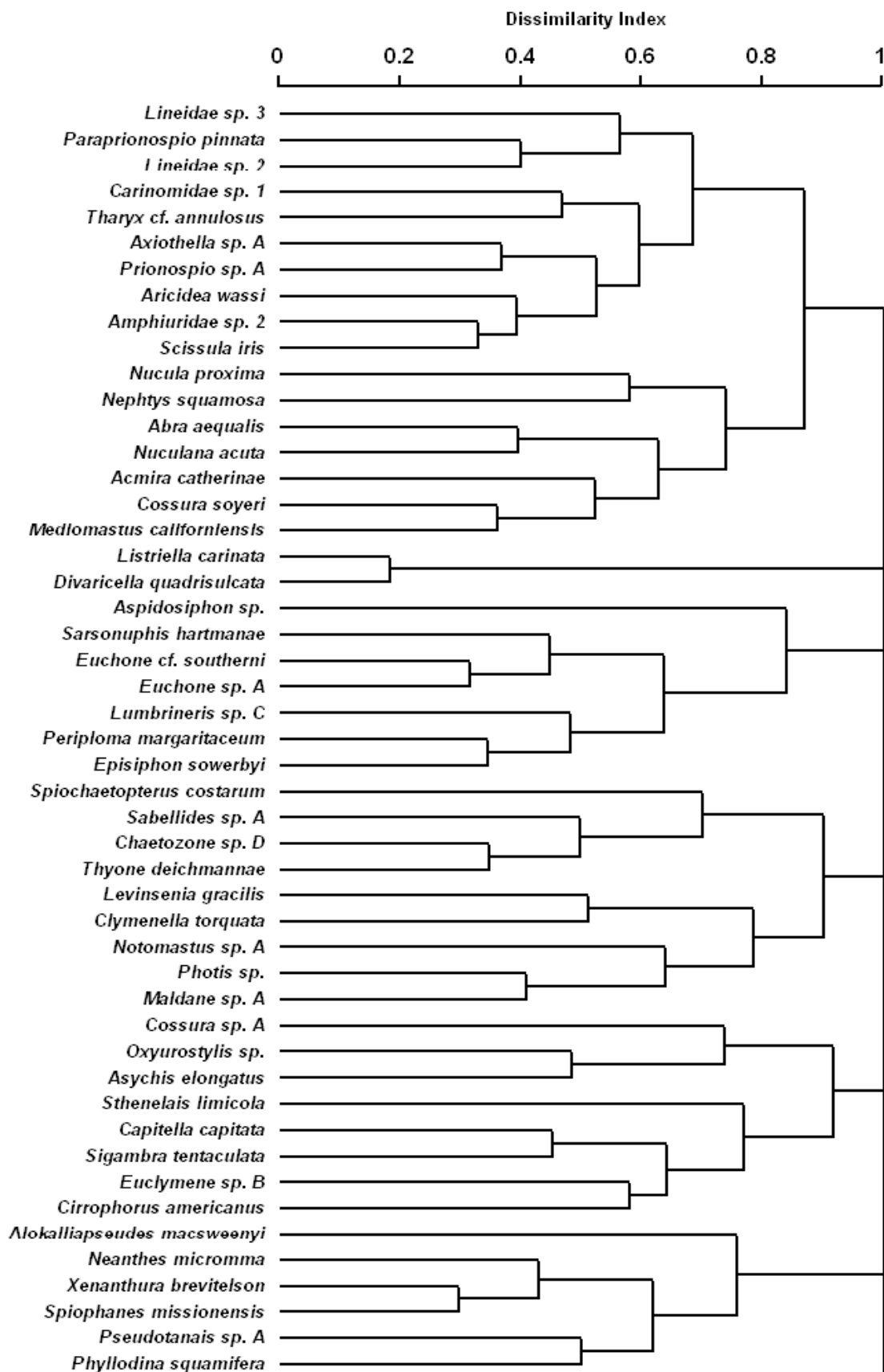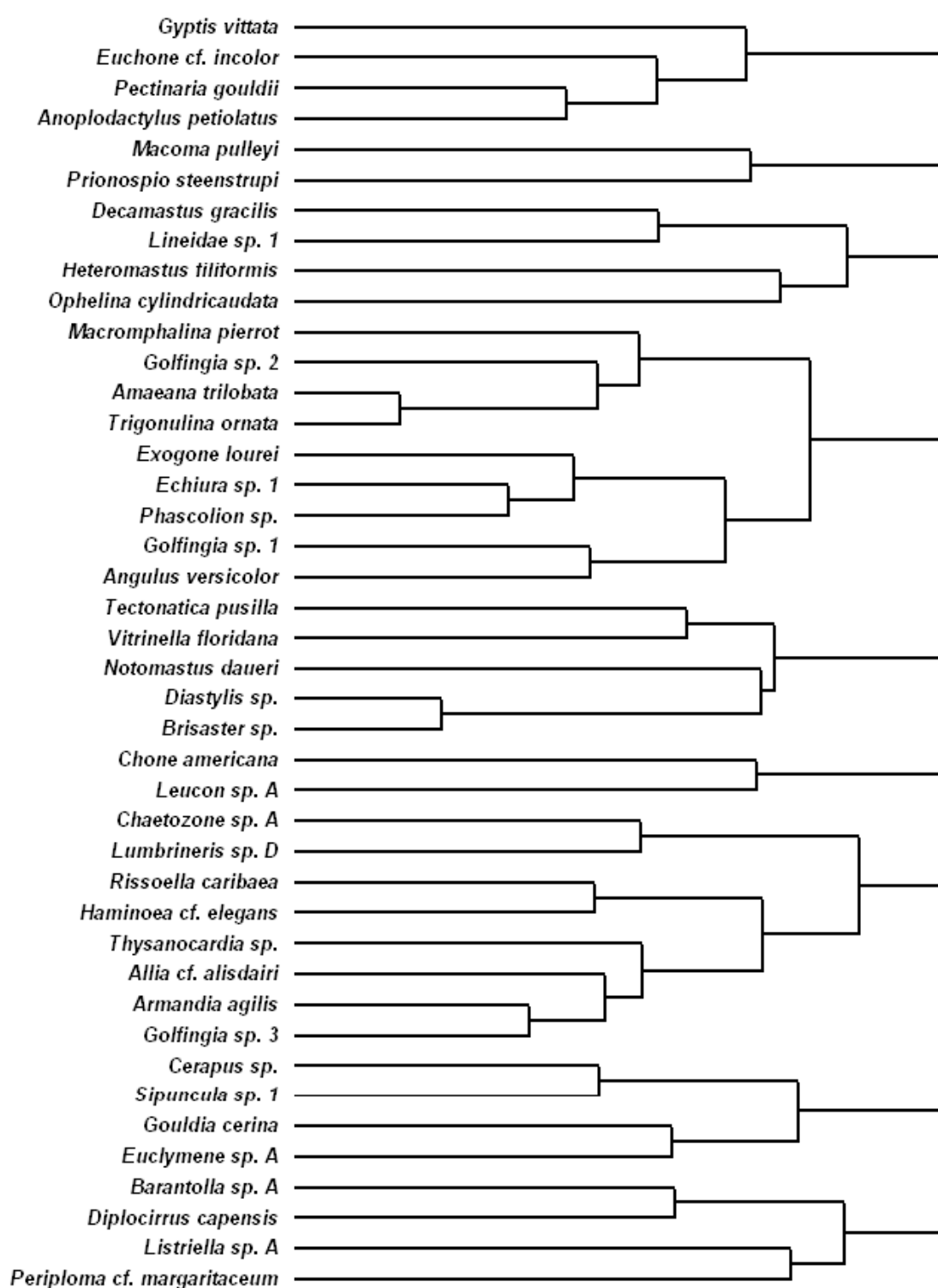
Figure 35. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at sites A, B, C and D during the April 2009 sample collection.

Dissimilarity Index

| 0 | 0.2 | 0.4 | 0.6 | 0.8 | 1 |

Nephtys squamosa
Gyptis vittata
Levinsenia gracilis
Abra aequalis
Thysanocardia sp.
Nucula proxima
Phyllodina squamifera
Amphiuridae sp. 2
Scissula iris
Aricidea (Allia) sp. A
Cirrophorus americanus
Fimbriosthenelais minor
Acmira catherinae
Cossura sp. A
Sigambra tentaculata
Armandia agilis
Mediomastus californiensis
Cossura soyeri
Episiphon sowerbyi
Tharyx cf. annulosus
Prionospio sp. A
Capitella capitata
Nuculana acuta
Prionospio fallax
Paraprionospio pinnata
Aricidea wassi
Amphiuridae sp. 3
Cirrophorus cf. forticirratus
Volvulella texasiana
Nevertia duplicata
Trigonulina ornata
Apoprionospio pygmaea
Xenanthura brevitelson
Prionospio steenstrupi

Figure 36. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at sites A, B, C and D during the September 2009 sample collection.

Dissimilarity Index

| 0 | 0.2 | 0.4 | 0.6 | 0.8 | 1 |

Cossura soyeri
Prionospio sp. A
Paraprionospio pinnata
Mediomastus californiensis
Nuculana acuta
Sigambra tentaculata
Aricidea wassi
Abra aequalis
Gyptis vittata
Angulus versicolor
Lineidae sp. 3
Armandia agilis
Lineidae sp. 2
Listriella sp. A
Cirrophorus americanus
Amphiuridae sp. 2
Acmira catherinae
Levinsenia gracilis
Phyllodina squamifera
Scissula iris
Prionospio steenstrupi
Caryocorbula contracta
Tharyx sp.
Golfingia sp. 3
Tectonatica pusilla
Chaetozone sp. D
Clymenella torquata
Tharyx cf. annulosus
Volvulella texasiana
Neanthes micromma
Euchone sp. A
Amaeana trilobata
Brada villosa
Cirrophorus cf. forticirratus
Thysanocardia sp.

Figure 37. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at sites A, B, C and D during the August 2010 sample collection.

Macrobenthos species associations within each individual site were analyzed using the Bray-Curtis dissimilarity index for the April 2009, September 2009 and August 2010 sample collections to characterize the assemblage specific to each site (Figures 38 - 49). Site A had a consistent association among the polychaetes *M. californiensis*, *N. micromma*, *P. fallax*, *T*. cf. *annulosus*, and *P. pinnata* and the bivalve *N. acuta* during the sample collections in April 2009 (0.86 dissimilarity; Figure 38), September 2009 (0.70 dissimilarity; Figure 42), and August 2010 (0.82 dissimilarity; Figure 46). Within the two sampling collections in 2009, there were two clusters of consistent associations. The first clusters of consistent association comprised of the isopod *X. brevitelson*, the nemertean worm *Lineidae* sp. 3, and the sipunculan worm *Golfingia* sp. 3 (0.71 and 0.73 dissimilarity in April and September, respectively). The second clusters of consistent association was comprised of the polychaetes *A*. wassi and *E. lourei*, the bivalve *T. ornata*, the scaphopod *E. sowerbyi*, and the sipunculan worm *Phascolion* sp. (0.76 and 0.90 dissimilarity in April and September, respectively; Figures 38 and 42). Within the two summer samplings in September 2009 and August 2010, there were four clusters of consistent associations. The first cluster was comprised of the polychaetes *A. wassi*, *A. agilis*, and *L. gracilis* (0.70 and 0.82 dissimilarity in 2009 and 2010, respectively). The second cluster was comprised of *Phascolion* sp., the bivalves *C. martinicensis* and *E. sowerbyi*, and the polychaete *S. limicola* (0.90 and 0.99 dissimilarity in 2009 and 2010, respectively). The third cluster was comprised of the polychaete *P. gouldii* and the amphipod *P. melanica* (0.60 and 0.65 dissimilarity in 2009 and 2010, respectively). The fourth cluster was comprised of the bivalves, *P. squamifera*, *A. versicolor*, and *P*.cf. *margaritaceum* (0.82 dissimilarity in both 2009 and 2010; Figures 42 and 46).

Site B had a consistent association among *N. acuta*, *S. tentaculata*, *P. fallax*, *C. soyeri*, *A. wassi*, the nemertean worm Lineidae sp. 3, and the brittle star Amphiuridae sp. 2, during the sample collections in April 2009 (0.99 dissimilarity; Figure 39), September 2009 (0.86 dissimilarity; Figure 43), and August 2010 (0.99 dissimilarity; Figure 47). Within the two sample collections in 2009, there was a cluster of consistent associations comprised of the polychaetes *N. squamosa*, *M. californiensis*, and *C. capitata*, and the bivalves *S. iris* and *A. aequalis*, (0.99 and 0.86 dissimilarity in April and September, respectively; Figures 39 and 43). Within the two summer samplings in September 2009 and August 2010, there was a cluster of consistent associations comprised of *P. squamifera*, *P. pinnata*, *A. agilis* and *L. gracilis* (0.86 and 0.69 dissimilarity in 2009 and 2010, respectively; Figures 43 and 47).

Site C had a consistent association between the polychaetes *P. pinnata*, *S. tentaculata*, *L. gracilis*, *A. wassi*, *C. americanus*, *G. vittata*, and *P. fallax*; the bivalves *A. aequalis* and *S. iris*; the brittle star Amphiuridae sp. 2; and the sipunculan worm *Thysanocardia* sp. Those associations were clustered at 0.99, 0.79, and 0.99 dissimilarities during April 2009, September 2009, and August 2010 sample collections, respectively (Figures 40, 44 and 48). Within the two sample collections in 2009, there was a cluster of consistent associations comprised of *N. proxima* and *N. acuta* (0.89 and 0.79 dissimilarity in April and September, respectively; Figure 40 and 44). Within the two summer sample collections, there was only one species shared between September 2009 and August 2010: the bivalve *P. squamifera* (Figures 44 and 48).

Site D had consistent associations between the polychaetes *C. soyeri*, *A. catherinae*, and *M. californiensis* and the bivalve *N. acuta* during all three, sample

collections (0.99 dissimilarity for each sampling; Figures 41, 45 and 49). No other

associations were observed only in April 2009 and September 2009; whereas, during

September 2009 and August 2010 there were consistent associations at 0.99 dissimilarity

among *A. agilis*, *P. pinnata*, *S. tentaculata*, *P. fallax*, and *A. catherinae* (Figures 45 and

49).
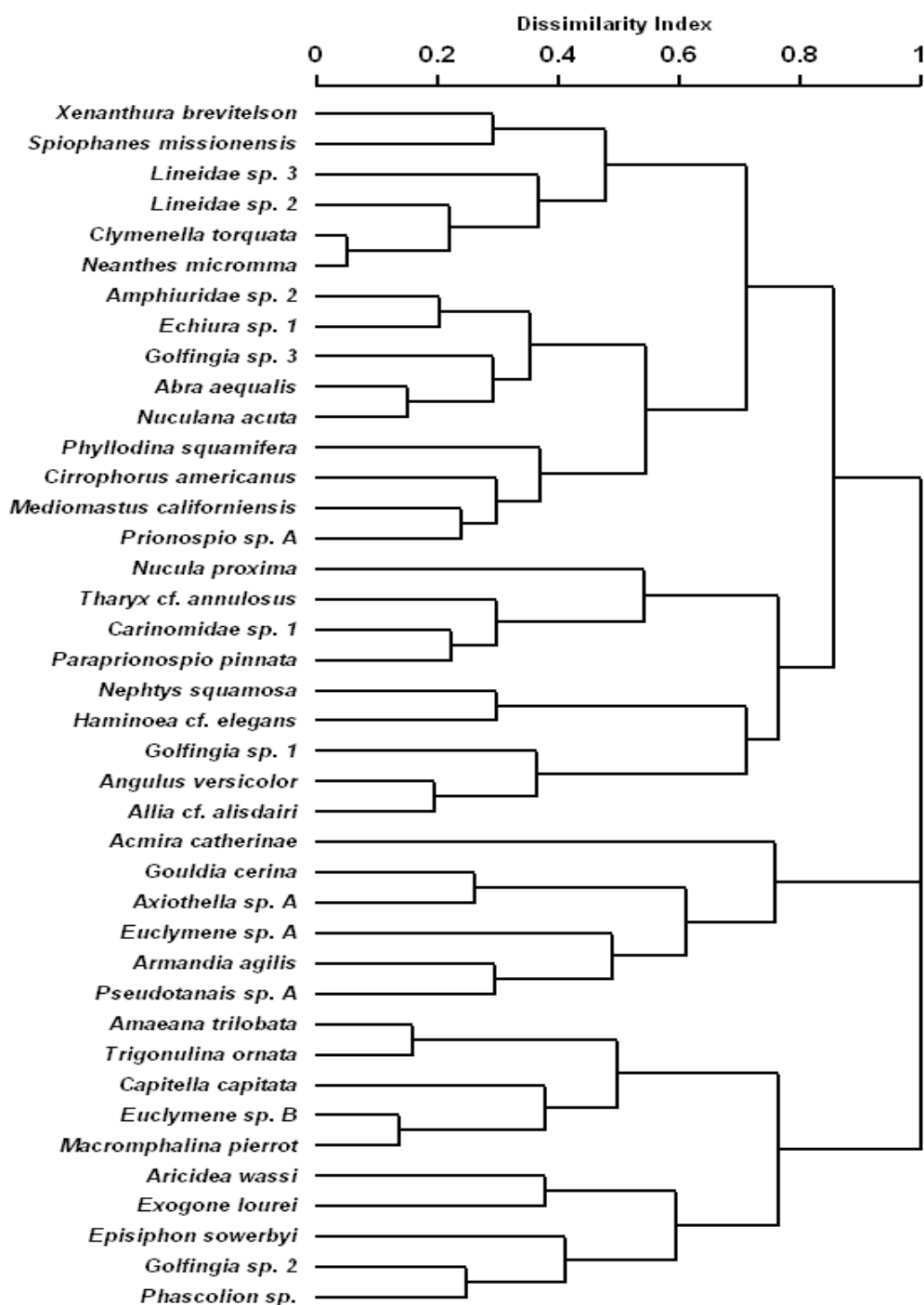
Figure 38. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site A during the April 2009 sample collection.
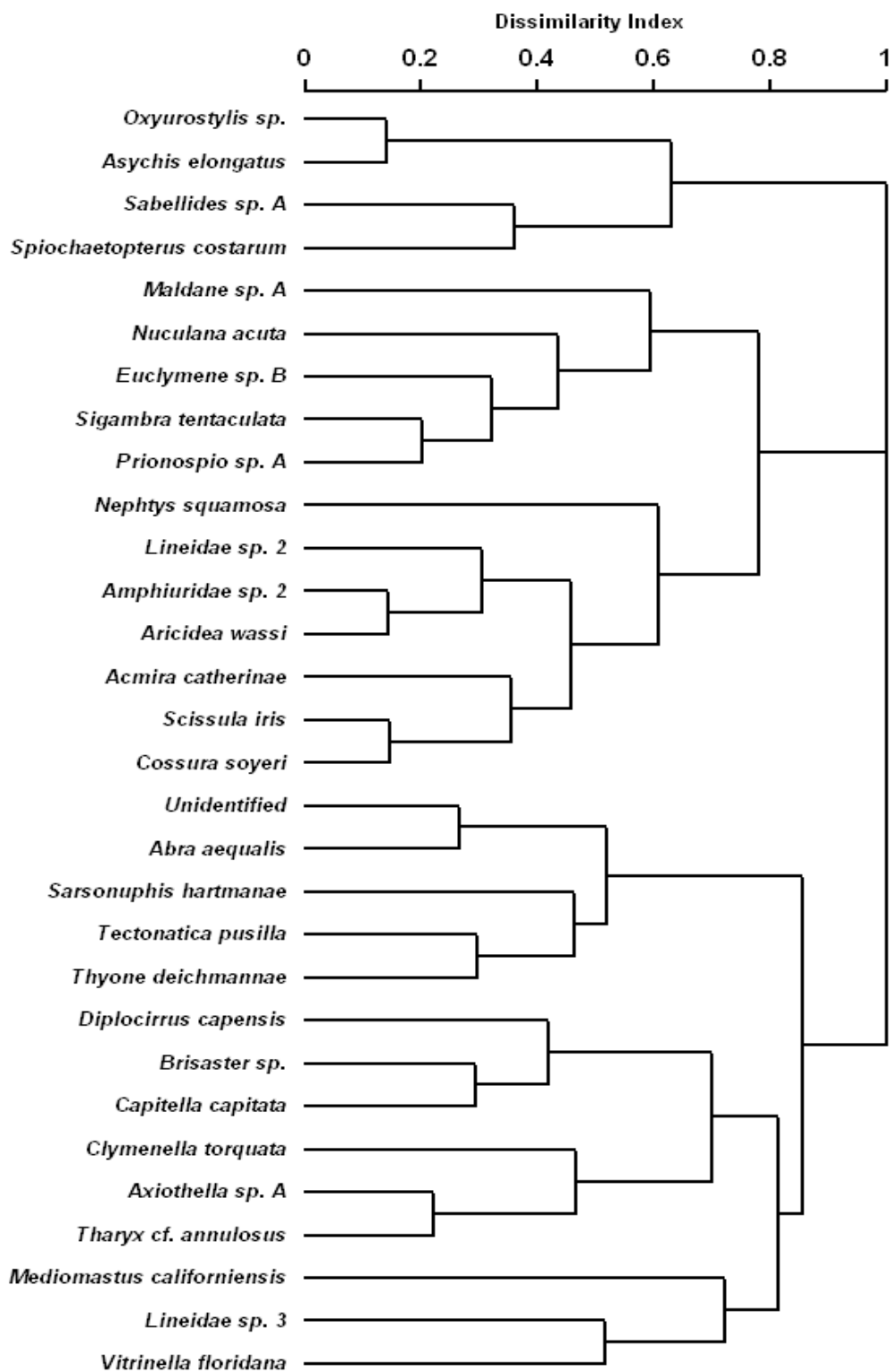
Figure 39. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site B during the April 2009 sample collection.
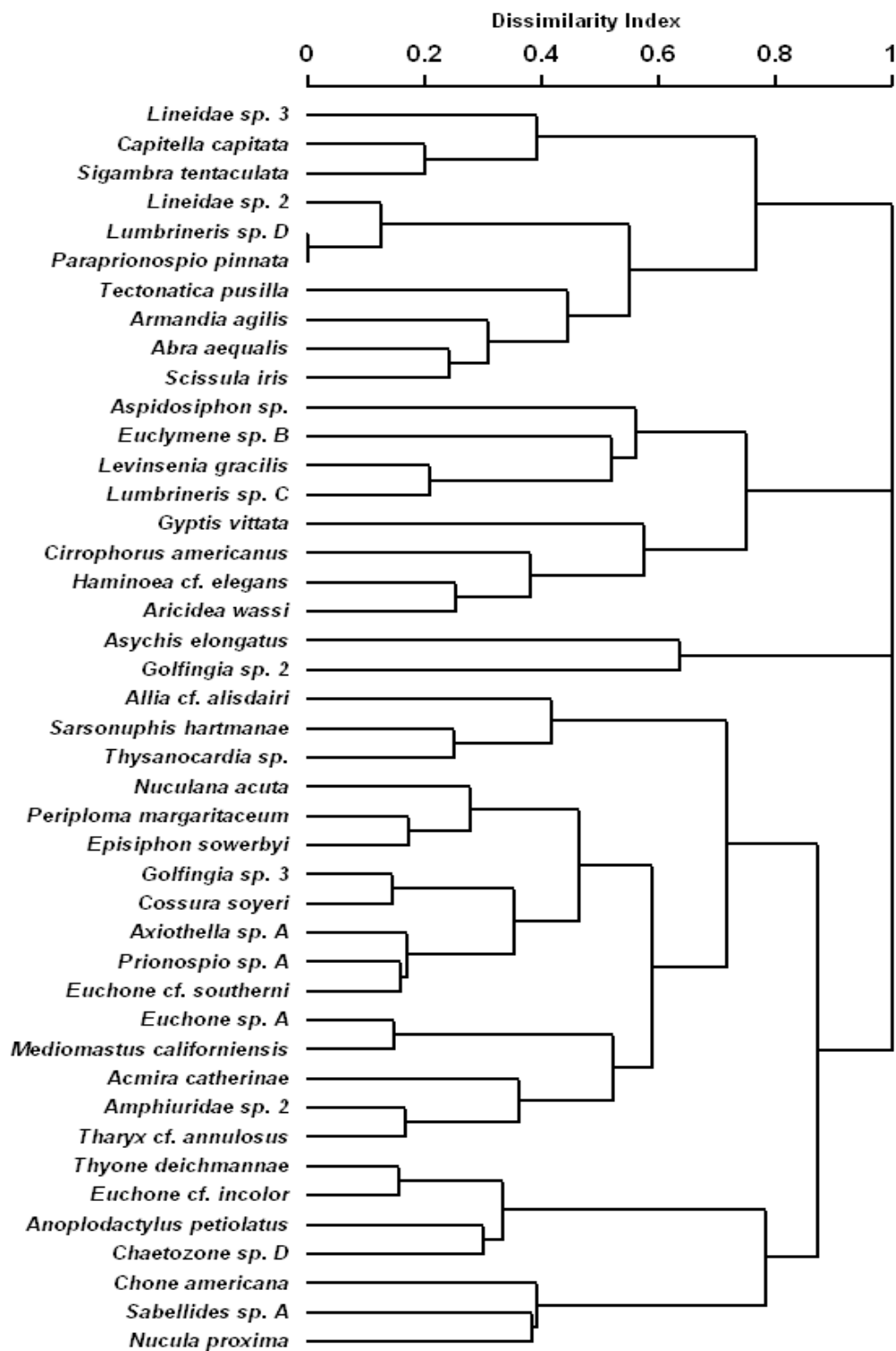
Figure 40. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site C during the April 2009 sample collection.
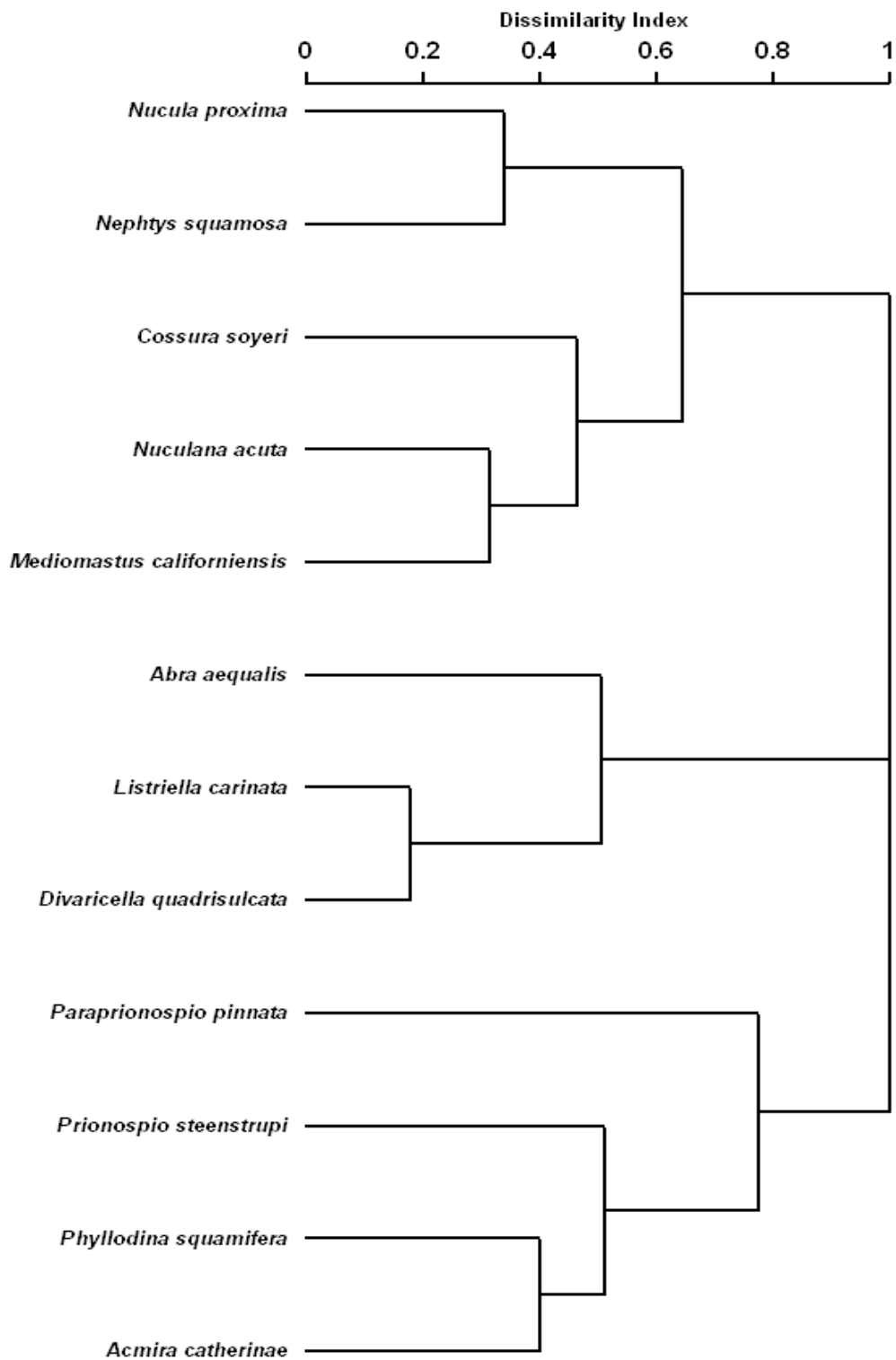
Figure 41. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site D during the April 2009 sample collection.
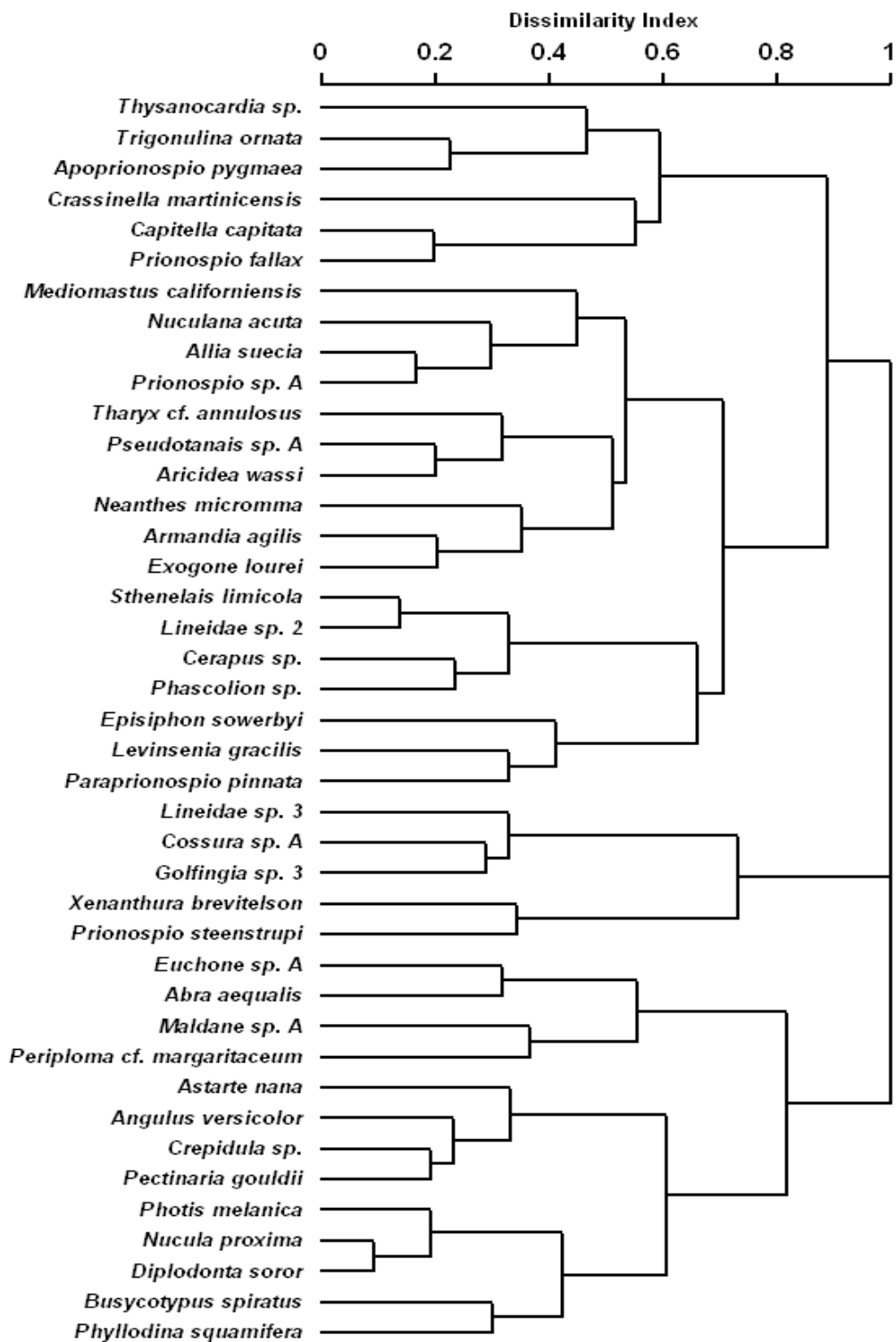
Figure 42. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site A during the September 2009 sample collection.
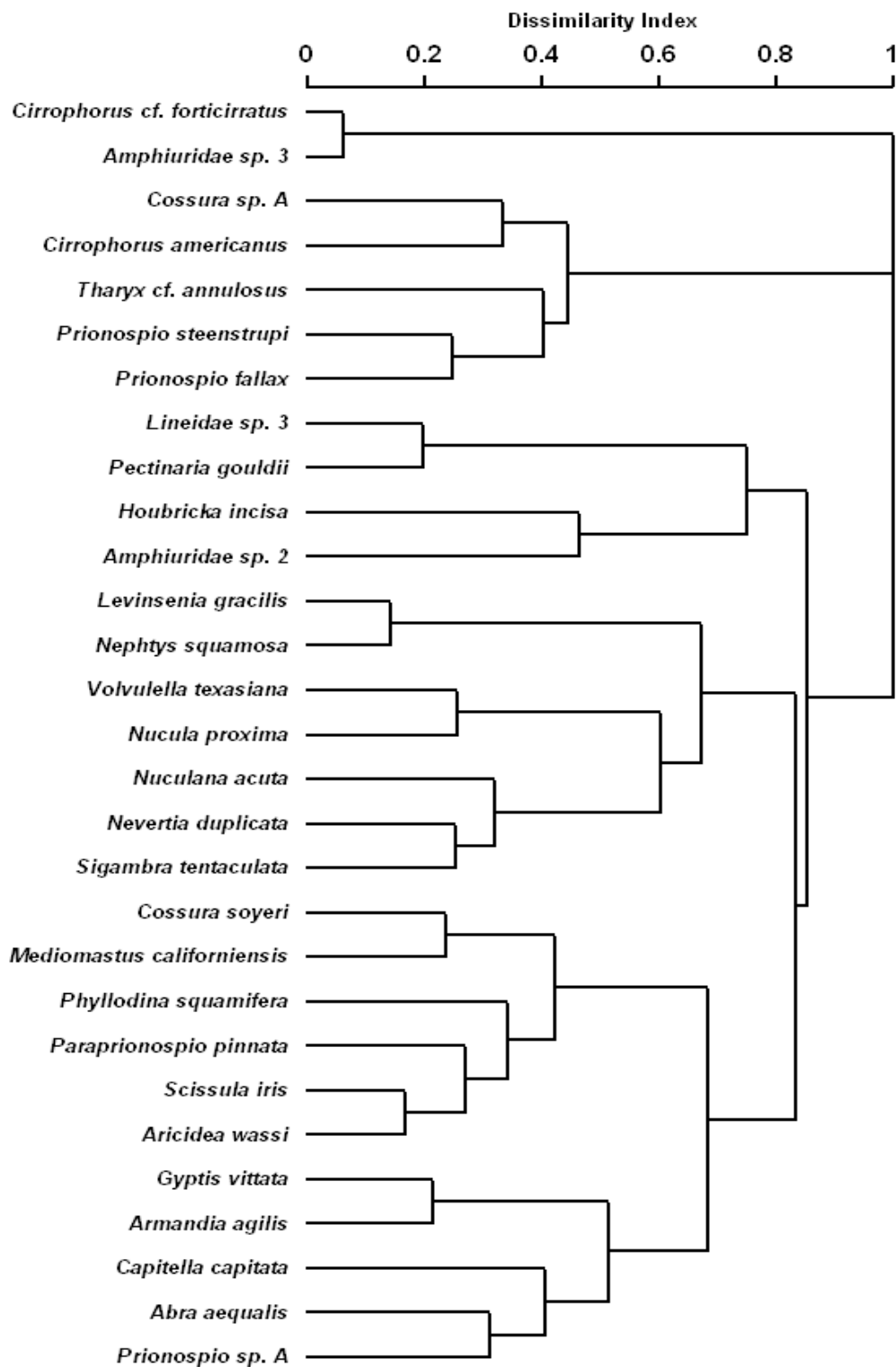
Figure 43. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site B during the September 2009 sample collection.
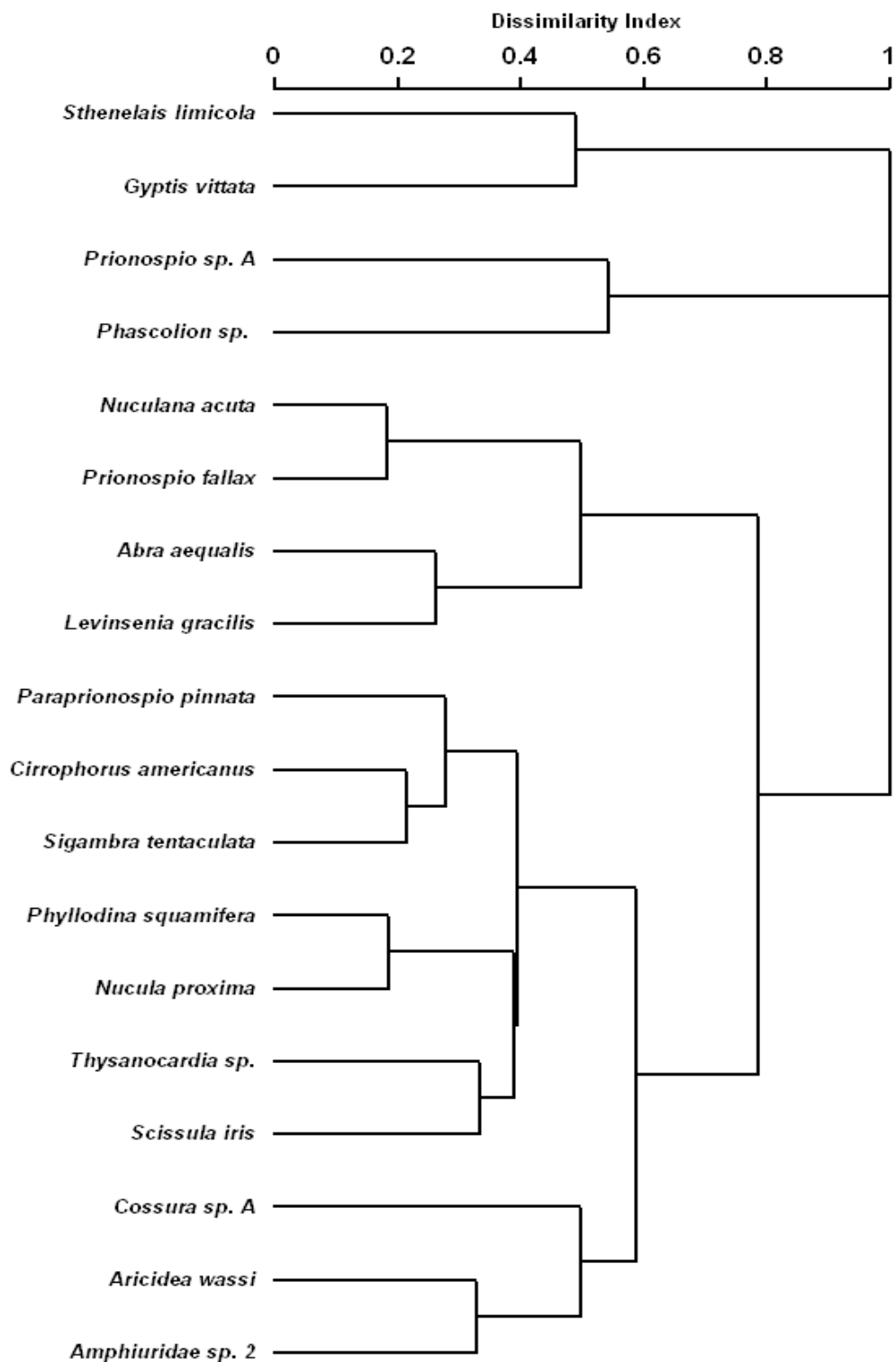
Figure 44. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site C during the September 2009 sample collection.
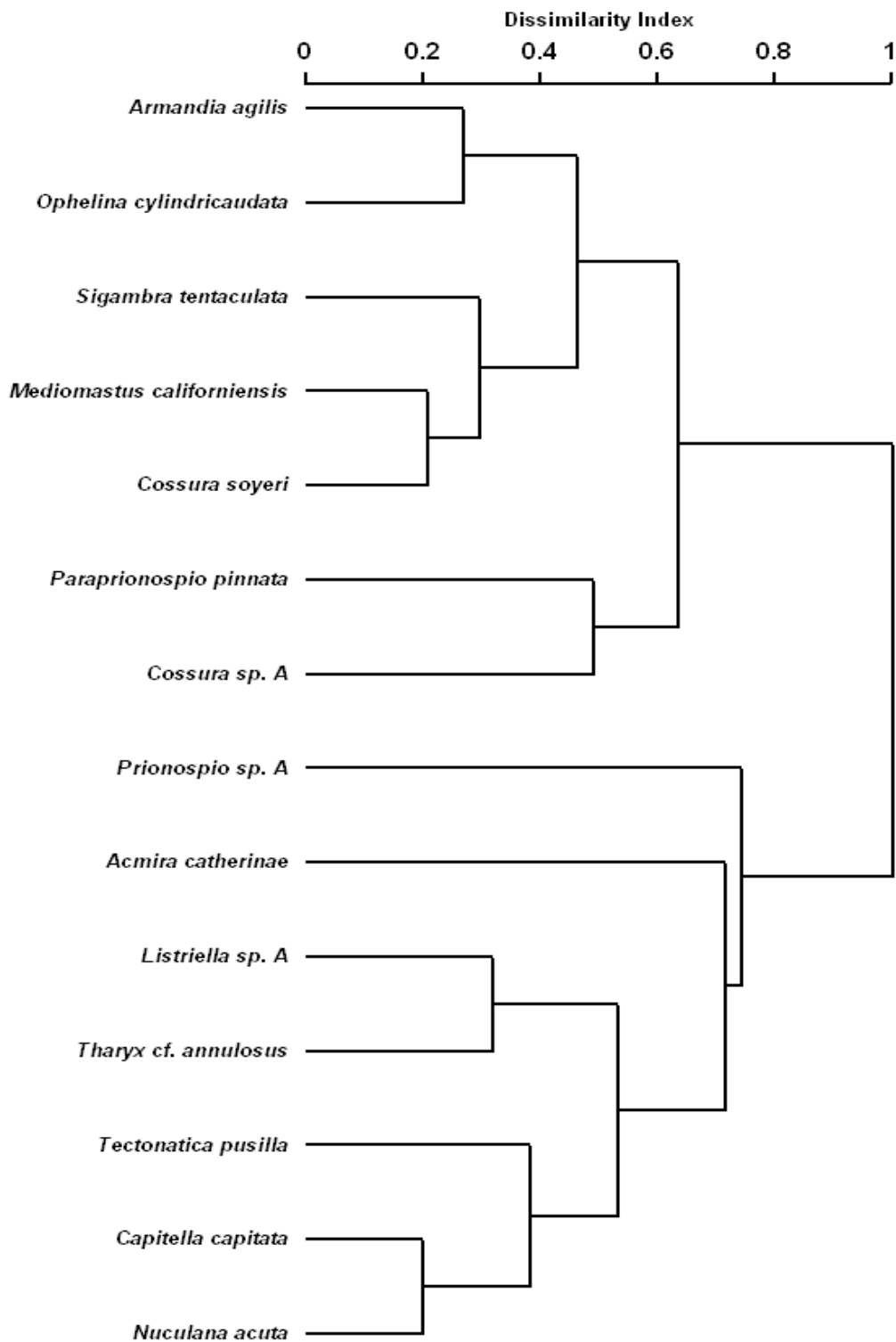
Figure 45. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site D during the September 2009 sample collection.
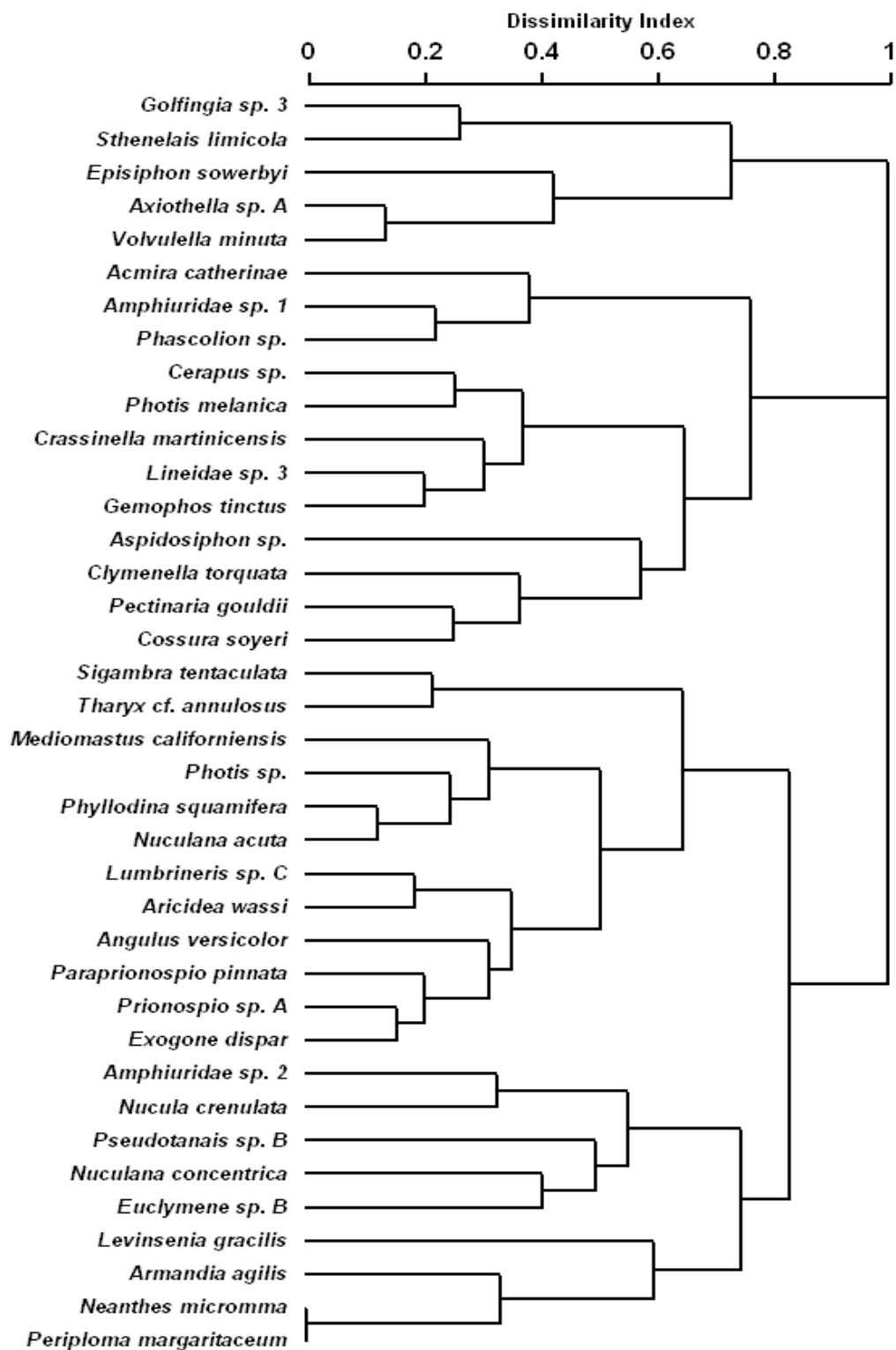
Figure 46. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site A during the August 2010 sample collection.
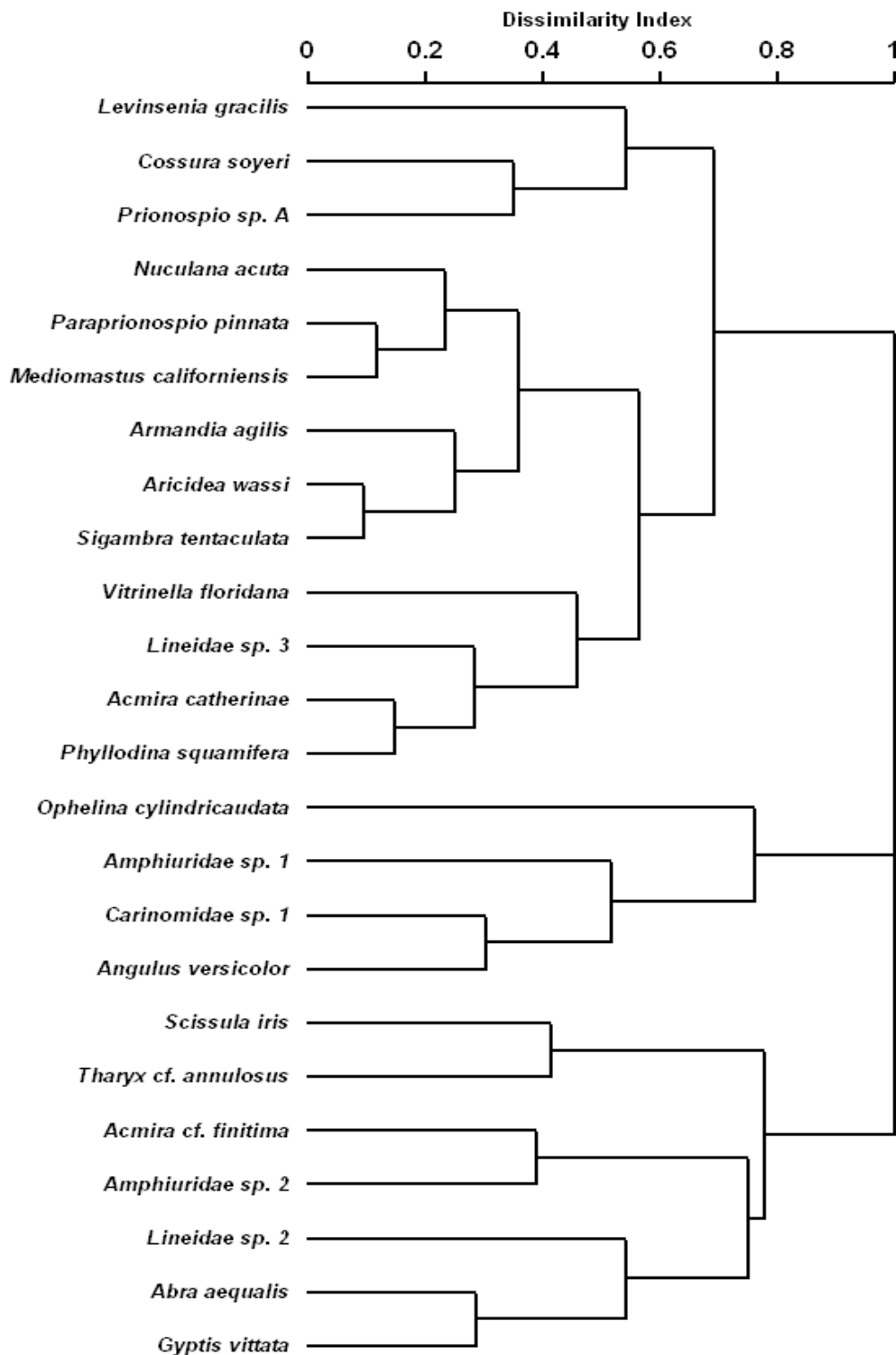
Figure 47. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site B during the August 2010 sample collection.
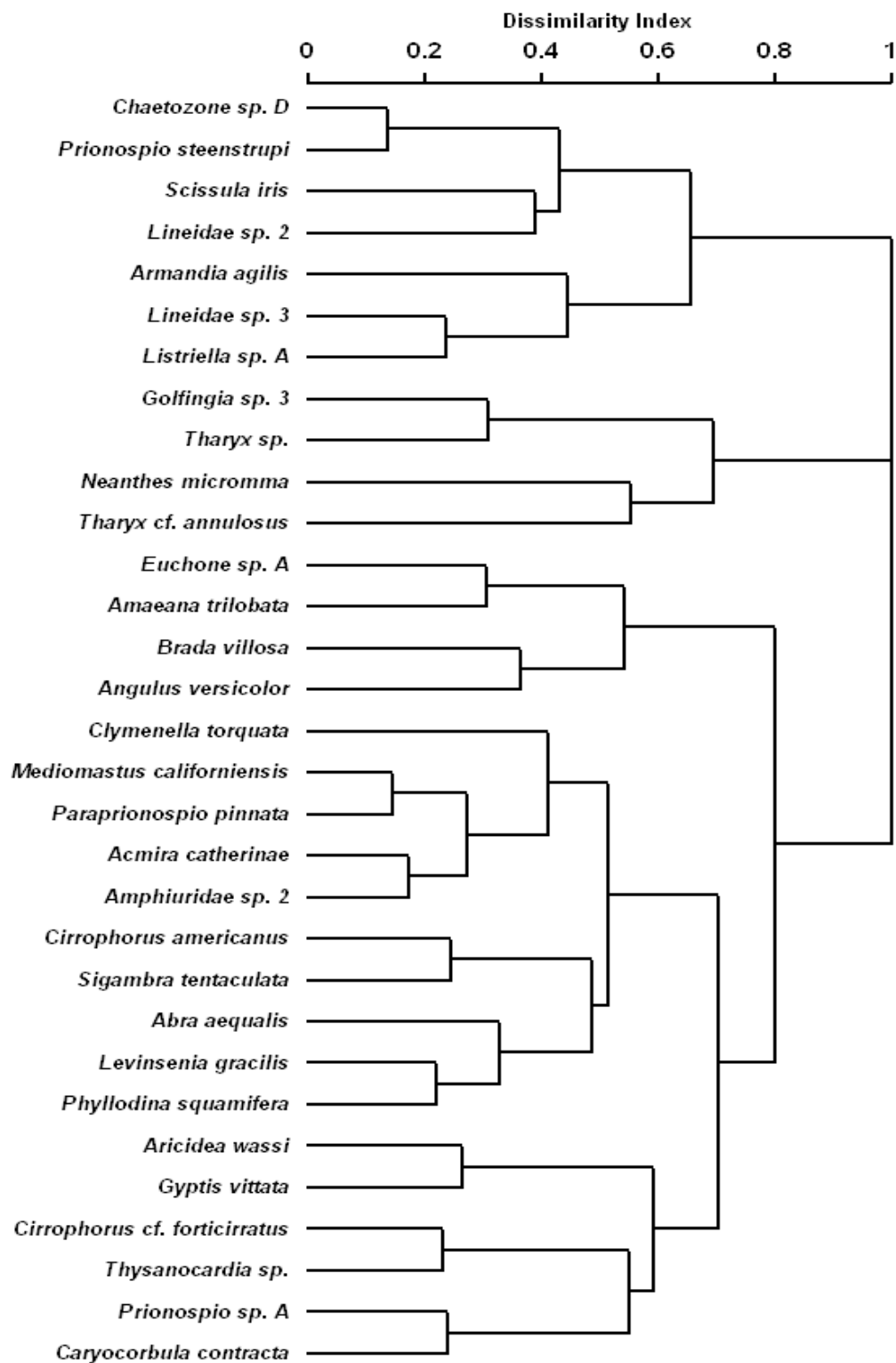
Figure 48. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site C during the August 2010 sample collection.
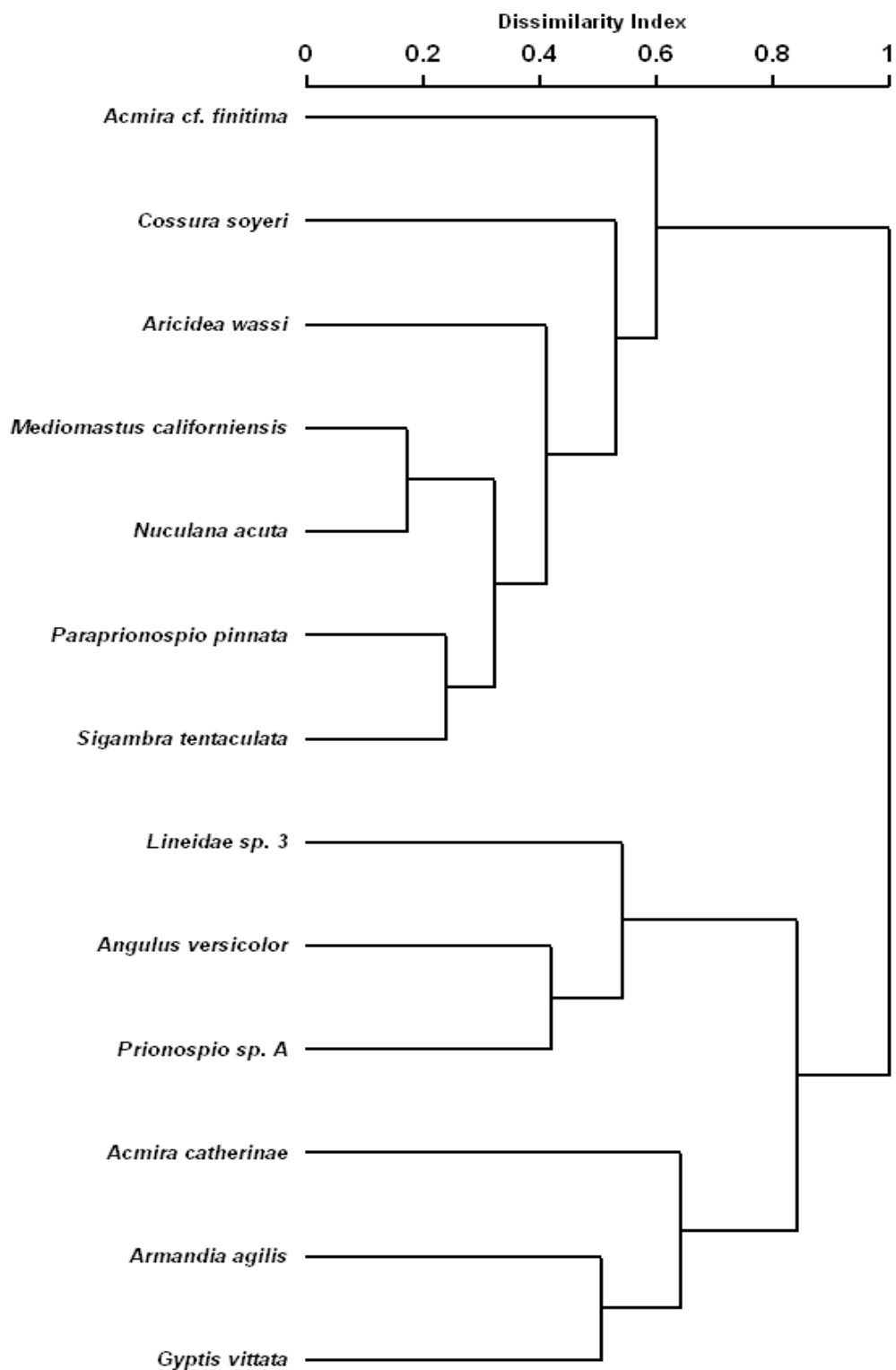
Figure 49. R-mode Bray-Curtis dissimilarity index dendrogram showing species associations at site D during the August 2010 sample collection.

Non-metric Multidimensional Scaling (nMDS)

Non-metric multidimensional scaling ordination of macrobenthos abundance data during the April 2009 sampling showed the ecological inter-site distance between sites B and C to be the shortest and suggested the species compositions of these two sites were the most similar (Figure 50). The inter-site distance between sites A and D was the longest, indicating that the species compositions of these two sites were the least similar. Sites A, B and C were separated from site D in terms of bottom water oxygen concentration. The nMDS ordination of macrobenthos species abundance had acceptable stress values of 0.18, 0.17 and 0.18 for April 2009, September 2009 and August 2010 samplings, respectively.

During the September 2009 sampling, sites A, C and D surround site B (Figure 51). This indicated that site B shared species with sites A, C and D, but that sites A, C and D shared few species among each other. In contrast with the spring sampling, site D is more aligned with low oxygen concentration than the other sites (Figure 51).

During the August 2010 sampling, the ecological inter-site distance between sites B and A was the longest, but site B was closer to sites C and D, indicating that site B had more species in common with sites C and D than it had with site A (Figure 52). As in the summer sampling in 2009, site D was associated more closely with low oxygen concentration than sites A, B and C (Figure 52).
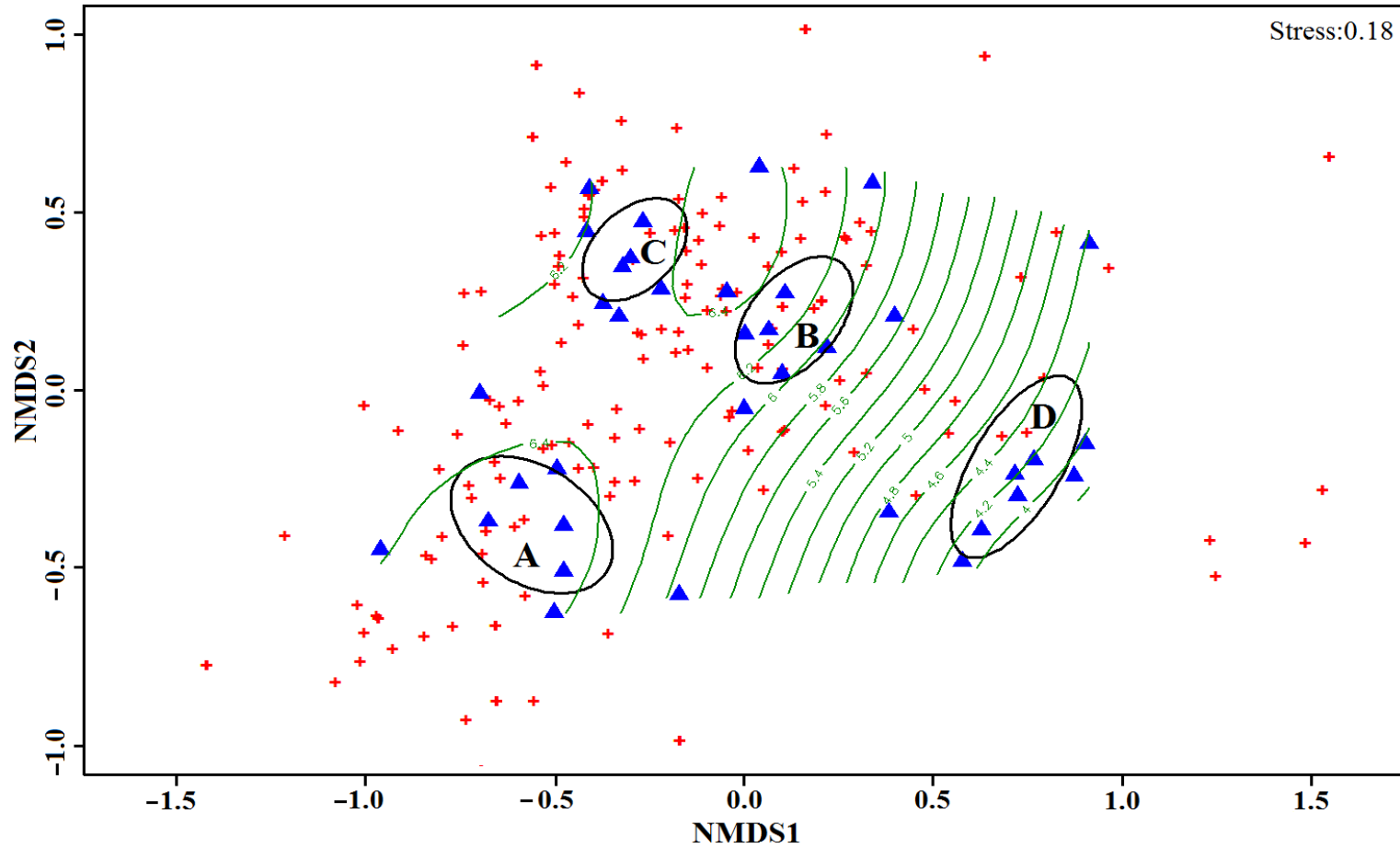
Figure 50. Non-metric multidimensional scaling (nMDS) ordination of macrobenthos abundance collected at sites A, B, C and D during April 2009. Species are marked in red crosses (+), sample cores are designated in blue triangles and bottom water oxygen concentration is shown in green contours. Black ellipses are drawn around 0.95 confidence limit dispersion of site subcores.
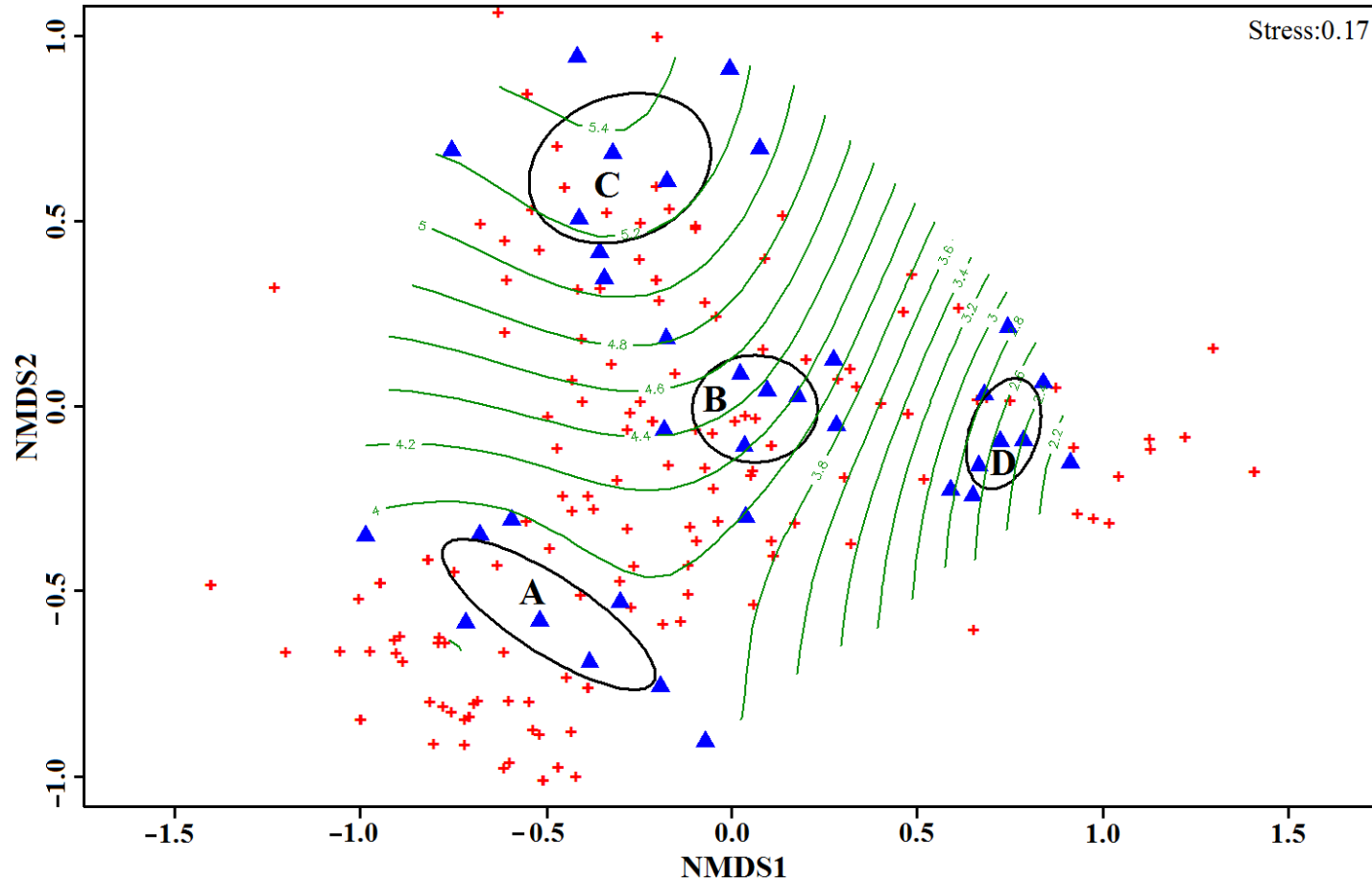
Figure 51. Non-metric multidimensional scaling (nMDS) ordination of macrobenthos abundance collected at sites A, B, C and D during September 2009. Species are marked in red crosses (+), subcores are designated in blue triangles and bottom water oxygen is concentration shown in green contours. Black ellipses are drawn around 0.95 confidence limit dispersion of site subcores.
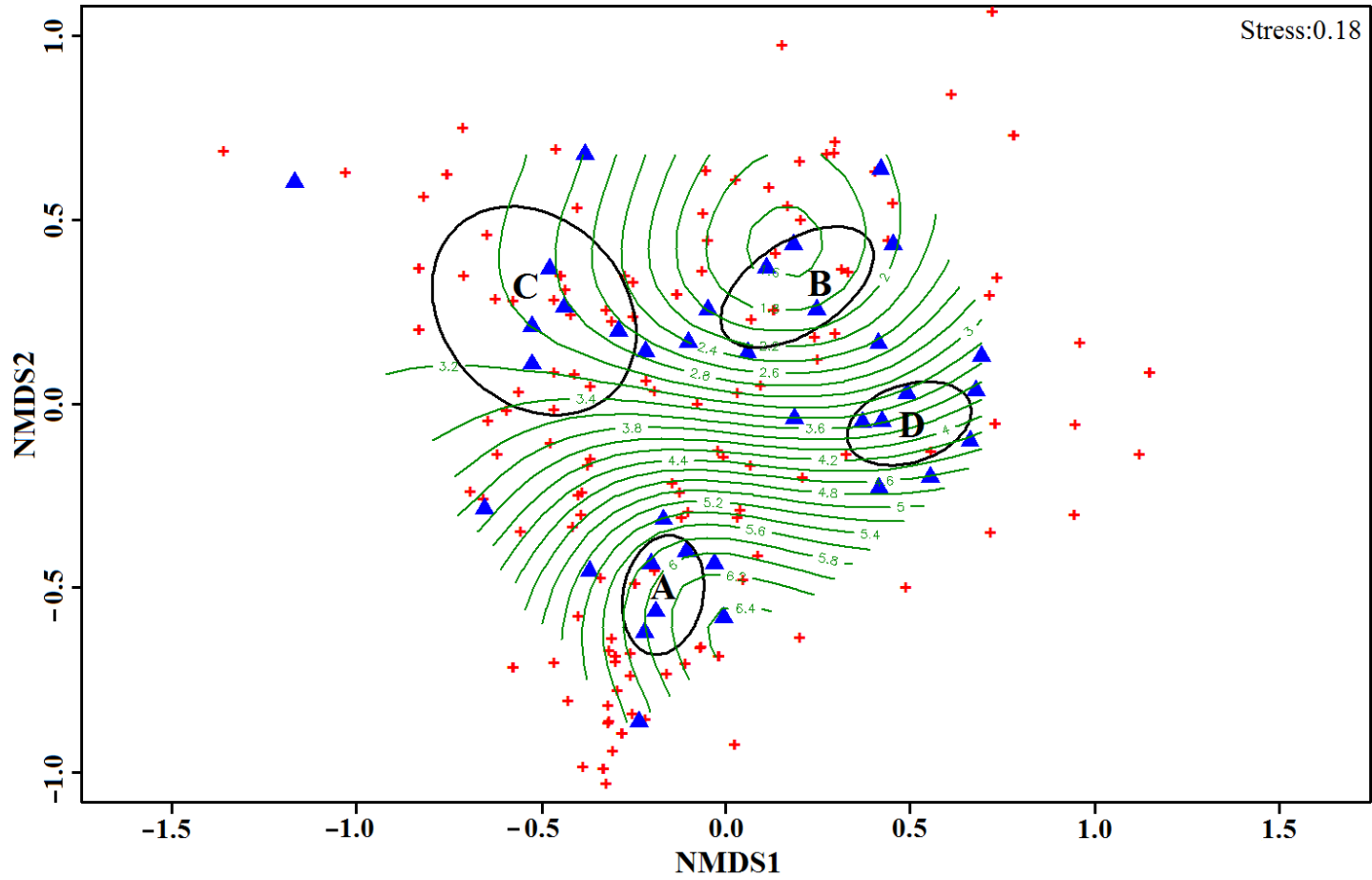
Figure 52. Non-metric multidimensional scaling (nMDS) ordination of macrobenthos abundance collected at sites A, B, C and D during August 2010. Species are marked in red crosses (+), subcores are designated in blue triangles and bottom water oxygen concentration is shown in green contours. Black ellipses are drawn around 0.95 confidence limit dispersion of site subcores.

Environmental Variables Used in CCA

Table 21

Values of environmental variables with n = number of observations per sampling used in canonical correspondence analysis of sites A, B, C and D during April 2009 (1), September 2009 (2) and August 2010 (3) samplings: sediment carbon-nitrogen ratio (C/N ratio), sedimentary organic carbon percentage (orgC), bottom water oxygen concentration in mg/L (DO), percentage silt + clay (Mud). -ND- is No Data.

Sampling	DO	orgC	C/N ratio	Mud
1A	6.40	0.04	11.95	30.32
1B	6.20	0.06	10.00	58.67
1C	6.30	0.05	10.51	65.17
1D	4.10	0.15	9.99	99.74
2A	3.90	0.04	15.43	22.90
2B	4.30	0.06	9.25	66.53
2C	5.30	0.15	10.90	78.41
2D	2.50	0.06	9.03	99.17
3A	6.00	-ND-	-ND-	24.66
3B	1.70	-ND-	-ND-	56.06
3C	3.00	-ND-	-ND-	66.13
3D	4.00	-ND-	-ND-	99.94
Obs/Sampling	n =1	n = 18	n = 18	n = 9

Bottom water dissolved oxygen concentration was measured on board during all three samplings; values varied between 1.7 and 6.4 mg/L (Table 21). Values of dissolved oxygen concentration exceeded the concentration below which defines hypoxia (2 mg/L) at all sites among all three sample collections, except site B duing the August 2010 sampling.

Sediment organic carbon content (Appendix J; Table J1) varied between 0.04 and 0.15 % during April and September 2009. Site A had the lowest sediment organic carbon content during both sampling in 2009, whereas site D highest sediment organic carbon content in spring of 2009 and site C in late summer of 2009 (Table 21). Sediment organic carbon content was not measured during the August 2010 sampling.

Sediment organic carbon-nitrogen ratio (Appendix J; Table J2) varied between 9.99 and 11.95 during April 2009 and between 9.03 and 15.43 during September 2009. Site D had the lowest and site A had highest sediment organic carbon-nitrogen ratio during April 2009 as well as in September 2009 (Table 21). Sediment organic carbon and nitrogen ratio was not measured during August 2010 sampling.

Though the effort was made to sample sites with similar sedimentological characteristics, sediment grain size varied significantly (Appendix K; Tables K1 to K12). Percentage of mud (silt and clay) varied greatly, ranging from 22.90 to 99.97% among all the four sites (Table 21). Site D had the highest percentage of mud, and site A had the lowest percentage of mud among all four sites.

Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis was performed on subcores collected during April 2009, September 2009 and August 2010 samplings to determine the influence of the environmental variables sediment carbon-nitrogen ratio (C/N ratio), sedimentary organic carbon percentage (orgC), bottom water oxygen concentration (DO), and silt + clay percentage (Mud) (Table 21) (independent axis) on the macrobenthos species abundance (dependent axis). Macrobenthos samples collected in April 2009 exhibited a total inertia value in CCA of 6.3, with approximately 15% of the inertia determined by the environmental variables sediment C/N ratio, sediment organic carbon and bottom water oxygen. The remaining 85% of the inertia was determined by the variation in 32 of the 36 subcores (Table 22). Most of the differences in species distribution between sites A and B were explained by the horizontal axis (CCA1), whereas most of the differences in species distribution between sites C and D were explained by the vertical axis (CCA2). Site A had a highly positive influence from sediment C/N ratio, whereas site D had a highly positive influence from sediment organic carbon and a highly negative influence from bottom water oxygen. None of the four sites were influenced to a measureable extent by the sediment mud content (Figure 53).

Table 22

Canonical correspondence analysis (CCA) ordination results for macrobenthos species abundance during April 2009.

	Inertia	Proportion	Rank
Total	6.296	1	
Constrained	0.941	0.1494	3
Unconstrained	5.355	0.8506	32
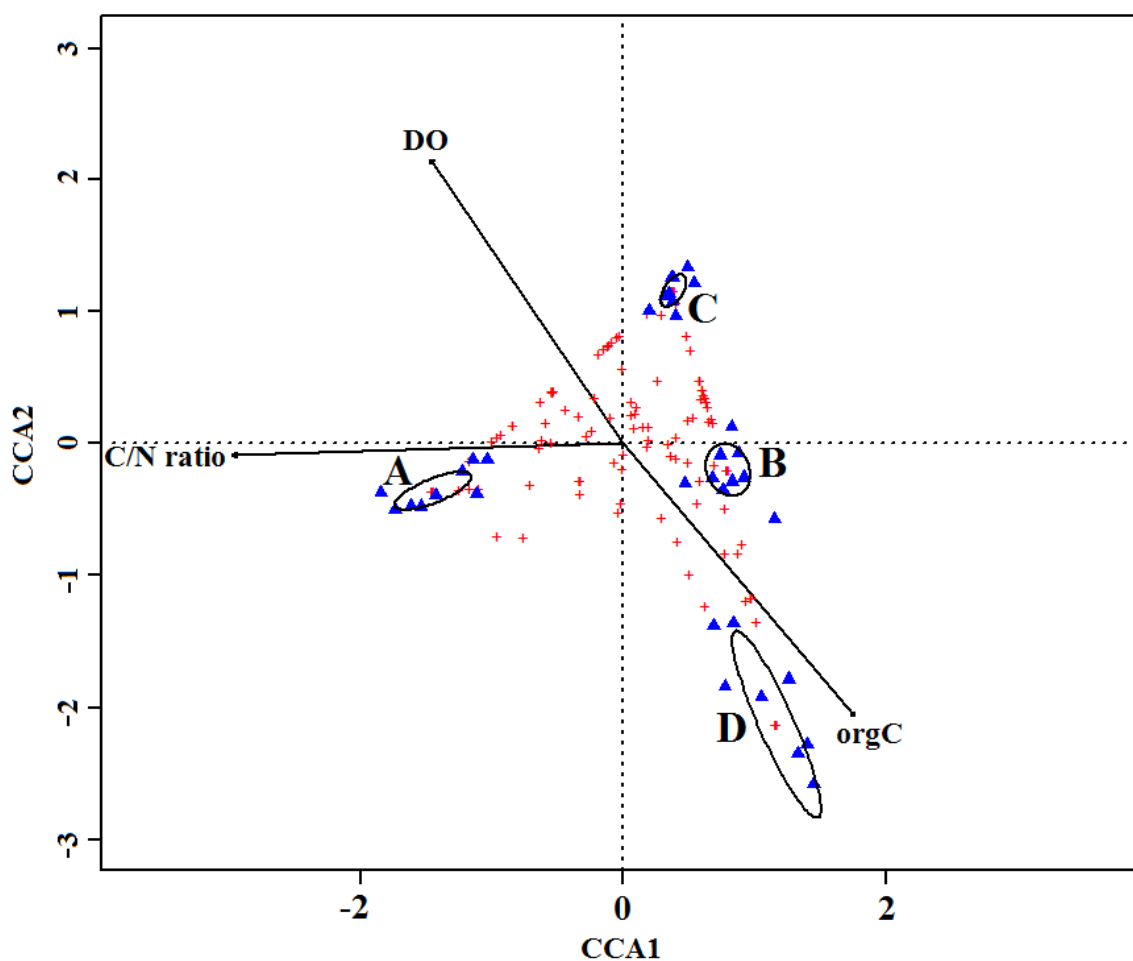
Figure 53. Canonical correspondence analysis (CCA) ordination of macrobenthos species abundance collected at sites A, B, C and D during April 2009. Species are marked in red crosses (+), subcores are marked in blue triangles and environmental variables are shown as black vectors. Black ellipses are drawn around the 0.95 confidence limit dispersion of site subcores.

Macrobenthos samples collected in September 2009 exhibited a total inertia value in CCA of 6.7, with approximately 16.5% of the inertia determined by the environmental variables sediment C/N ratio, sediment organic carbon and bottom water oxygen. The remaining 83.5% of the inertia was determined by 32 of the 36 subcores (Table 23). Most of the differences in species distribution between sites A and B were explained by the horizontal axis (CCA1), whereas the differences in species distribution at sites C and D were explained by the vertical axis (CCA2). Site A had a highly positive influence from sediment C/N ratio, whereas site D had a highly negative influence from bottom water oxygen. Site C had highly positive influences from sediment organic carbon and bottom water oxygen. None of the four sites was influenced to a measureable extent by the sediment mud content (Figure 54).

Table 23

Canonical correspondence analysis (CCA) ordination results for macrobenthos species abundance during September 2009.

	Inertia	Proportion	Rank
Total	6.696	1	
Constrained	1.103	0.1648	3
Unconstrained	5.593	0.8352	32
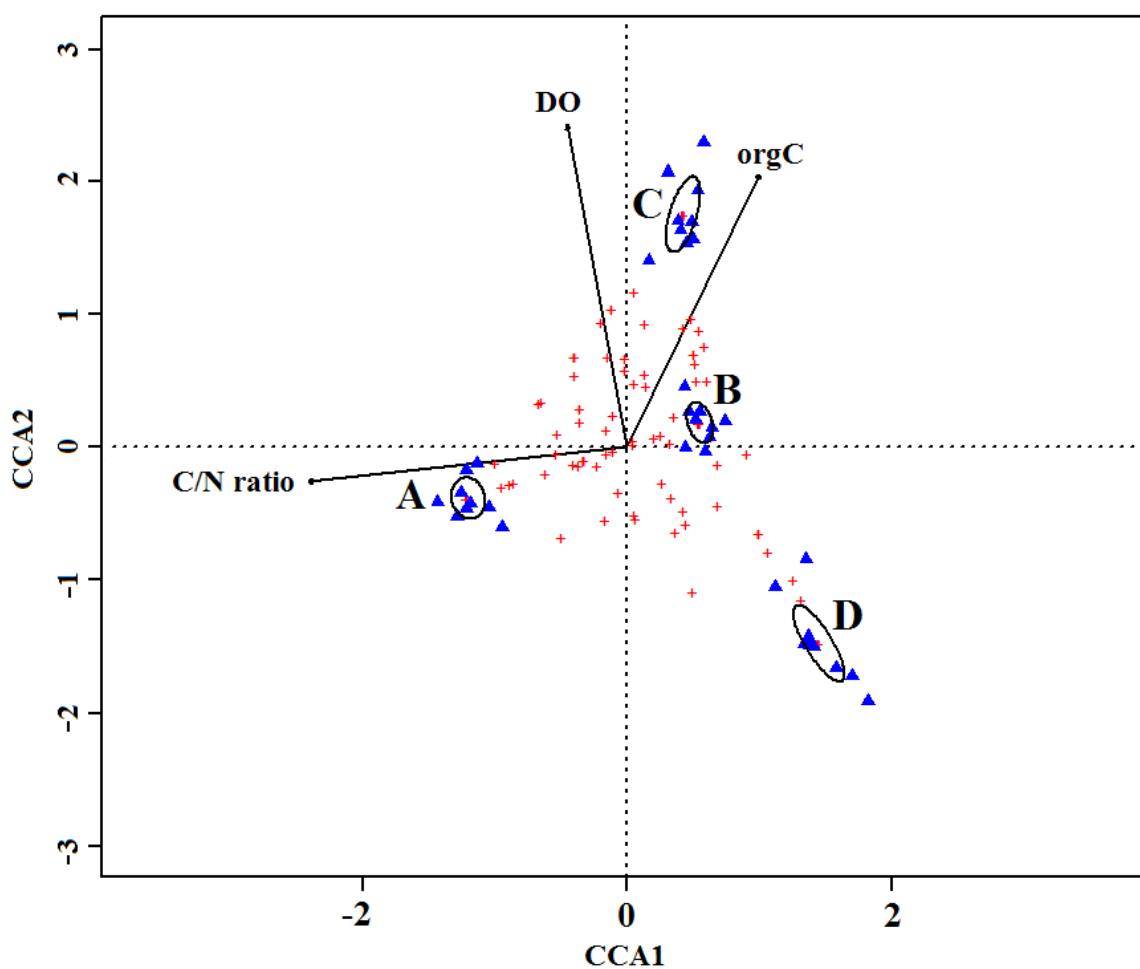
Figure 54. Canonical correspondence analysis (CCA) ordination of macrobenthos species abundance collected at sites A, B, C and D during September 2009. Species are marked in red crosses (+), subcores are marked in blue triangles and environmental variables are shown as black vectors. Black ellipses are drawn around the 0.95 confidence limit dispersion of site subcores.

During the August 2010 sample collection, sedimentary organic carbon and sediment C/N ratio samples were not collected: hence, CCA was performed with the only two measured environmental variables—bottom water oxygen concentration and percentage mud. Macrobenthos samples exhibited a total inertia value in CCA of 5.3, with approximately 11.9 % of the inertia determined by the environmental variables bottom water oxygen and mud content. The remaining 88.1% of the inertia was determined by 33 of the 36 subcores (Table 24). Most of the differences in species distribution between site A and the other three sites were explained by the horizontal axis (CCA1), whereas the differences in species distribution among sites B, C and D were explained by the vertical axis (CCA2). The reference site (A) had a highly positive influence from bottom water oxygen, whereas sites B and C had highly negative influences from bottom water oxygen. Sites B, C, and especially D had positive influences from sediment mud content. Neither sediment organic carbon nor sediment C/N ratio were measured in August 2010 so they were not included in this CCA (Figure 55).

Table 24

Canonical correspondence analysis (CCA) ordination results for macrobenthos species abundance during August 2010.

	Inertia	Proportion	Rank
Total	5.322	1	
Constrained	0.633	0.1188	2
Unconstrained	4.69	0.8812	33
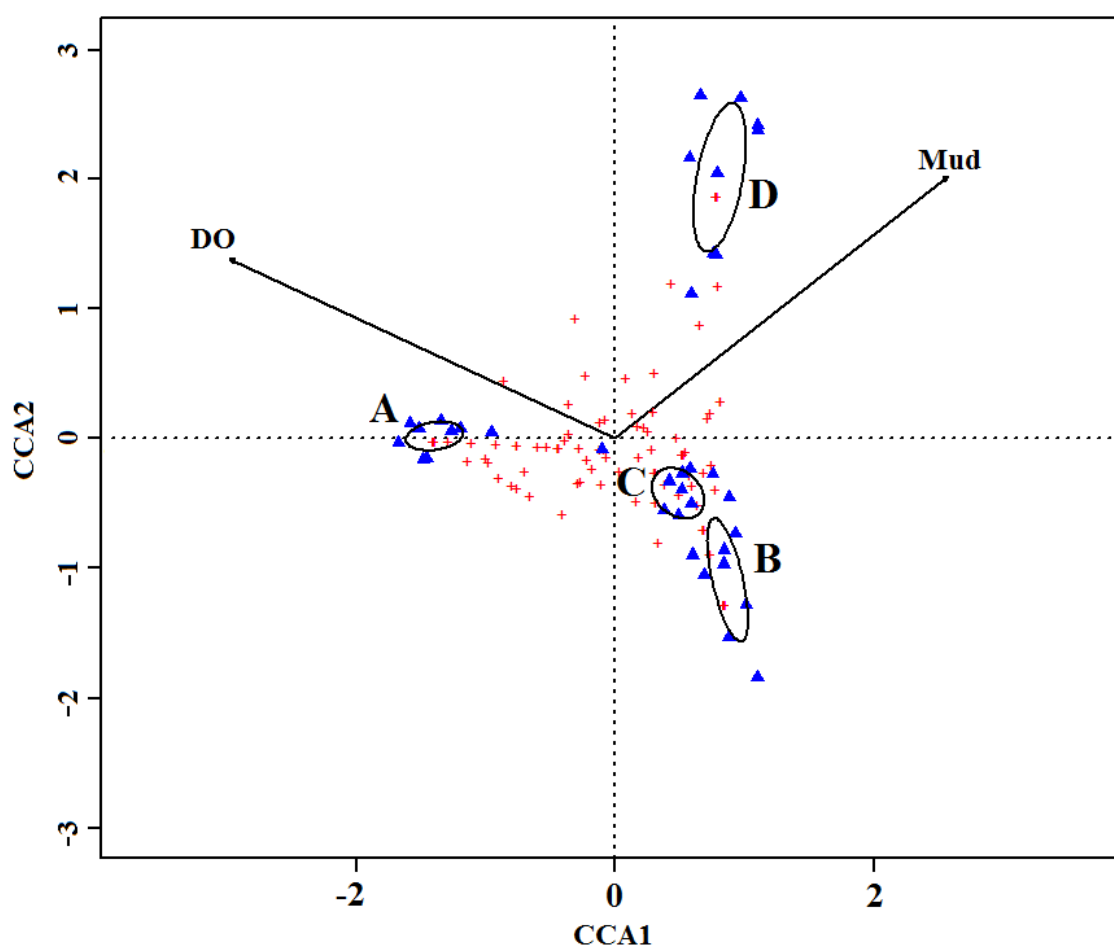
Figure 55. Canonical correspondence analysis (CCA) ordination of macrobenthos species abundance collected at sites A, B, C and D during August 2010. Species are marked in red (+), subcores are marked in blue triangles and environmental variables are marked as black vectors. Black ellipses are drawn around the 0.95 confidence limit dispersion of site subcores.

Principal Component Analysis (PCA)

Principal component analysis was performed to examine the relationships among the variables abundance, biomass, diversity, number of species, percentage of carnivores, percentage of herbivores, percentage of sub-surface deposit feeders, percentage of surface deposit feeders, percentage of suspension feeders, and bottom water oxygen concentration at all four sites from all three sample collections. When visualizing the first two axes, 70% of the total variance among the variables is accounted for, 49.45% in the horizontal axis and 20.65% in the vertical axis (Figure 56).

A comparison of Figures 56 and 57 allows insights into which sites show strong covariance with the various environmental variables. Sites A and C during April 2009, and site A during August 2010, covaried with values for bottom water oxygen concentration, percentage of herbivores, and number of species. In September 2009, site A covaried with percentage of suspension feeders and species diversity, whereas the samplings from site D lacked any covariance with these two variables. Samplings of site D covaried with percentage of sub-surface deposit feeders. Sites B and C during April 2009 and September 2009 covaried with percentage of surface deposit feeders, percentage of carnivores, and macrobenthos biomass (Figures 56 and 57).
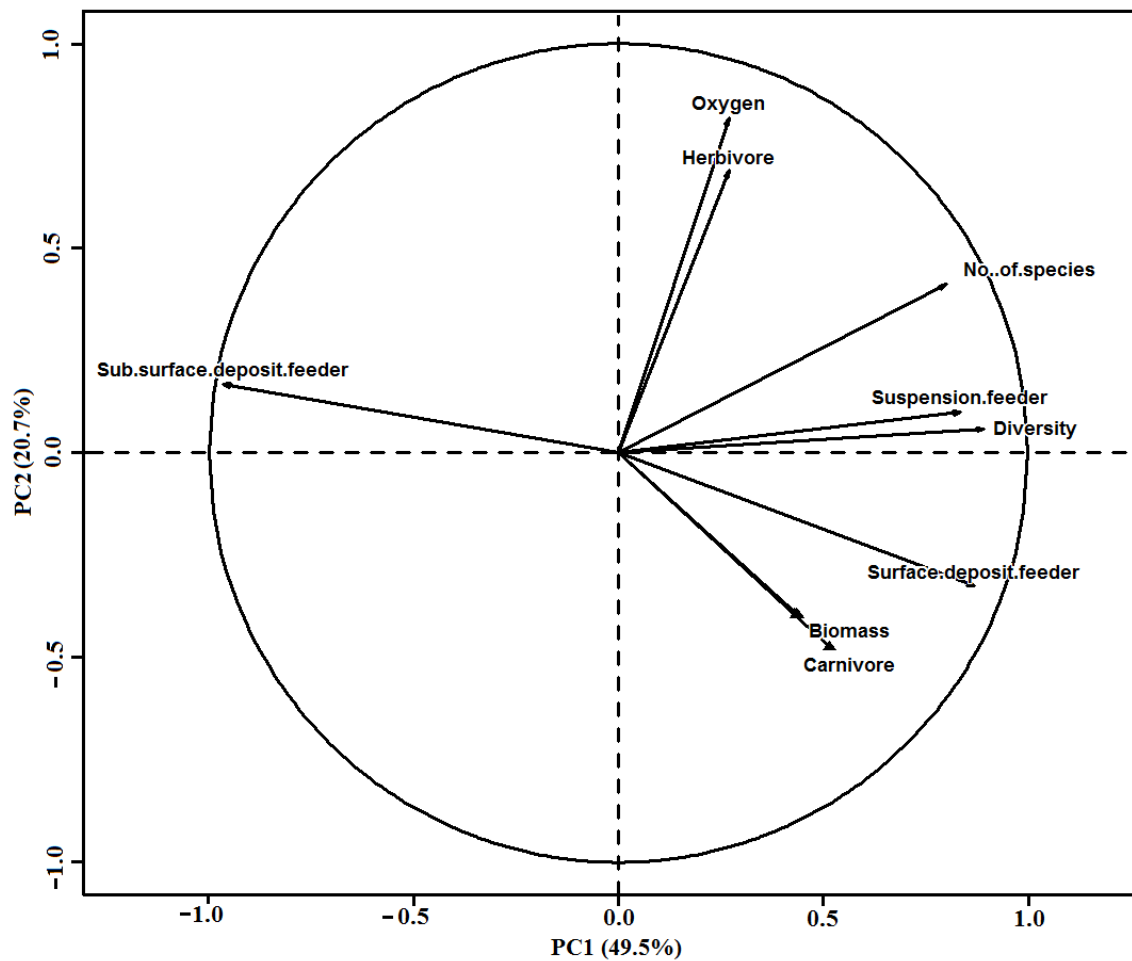
Figure 56. Principal component analysis (PCA) variables factor map for sites A, B, C and D during April 2009, September 2009 and August 2010. The circle is a correlation circle with maximum value of 1. Arrow lengths indicate the correlation coefficient value for the particular environmental variable.
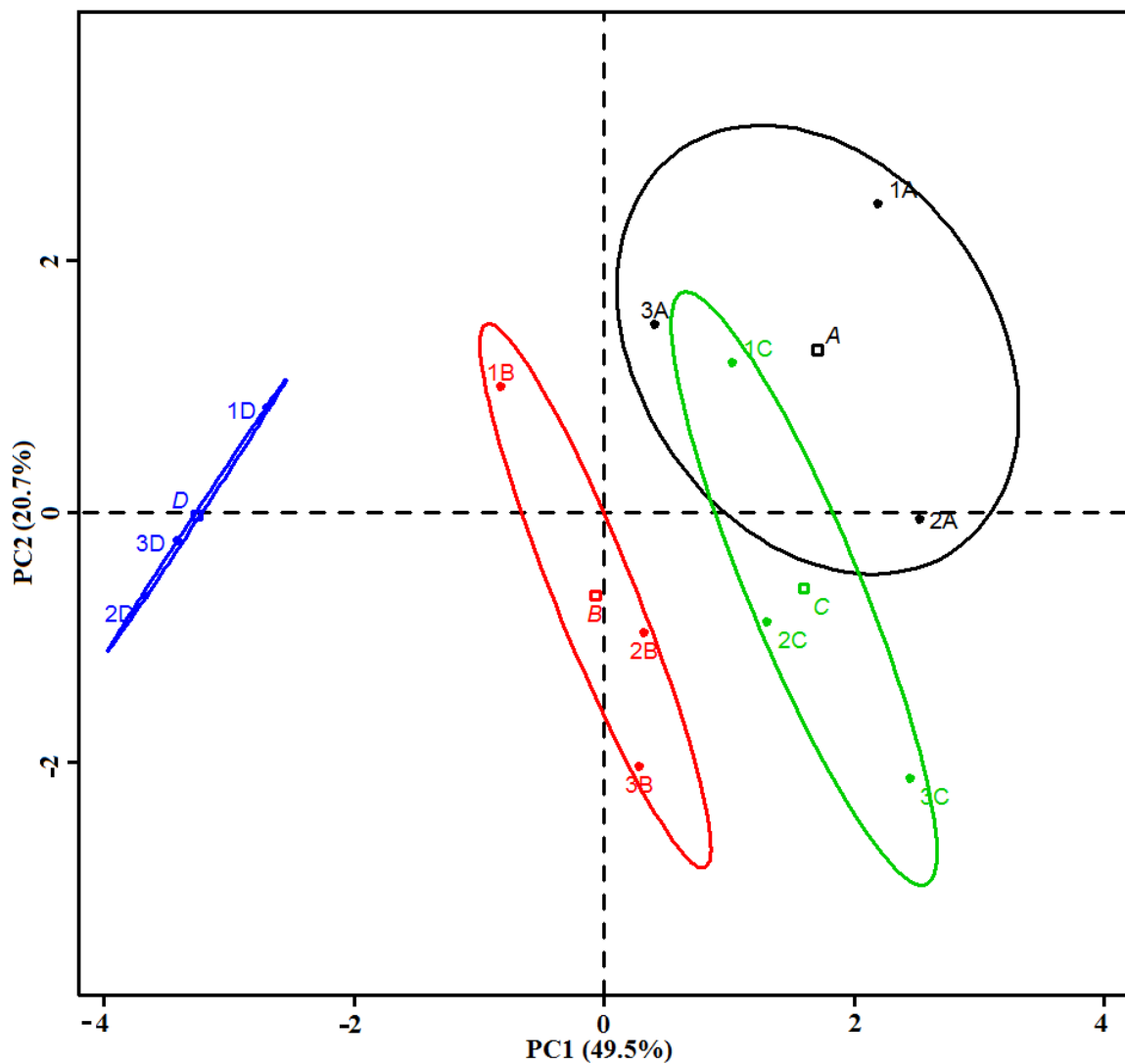
Figure 57. Principal component analysis (PCA) ordination of sites A, B, C and D during April 2009, September 2009 and August 2010. Size and shape of ellipses are drawn around the 0.95 confidence limit dispersion of sites. The square at the center of each ellipse represents the centroid of that site's data.

Cumulative Hypoxia Effect

The percentage of opportunist species found at sites A, B, C and D during April 2009, September 2009 and August 2010 were regressed on the average bottom-water oxygen values collected from 2000 to 2010 during annual shelfwide, mid-summer cruise. The linear regression fitted for sites A, B, C and D during April 2009, September 2009 and August 2010 had an R^2 value of 0.72 (Figure 58, Panel A). The linear regression fitted for only sites B, C and D, excluding reference site A, during April 2009, September 2009 and August 2010 had an increased R^2 value of 0.92 (Figure 58, Panel B).
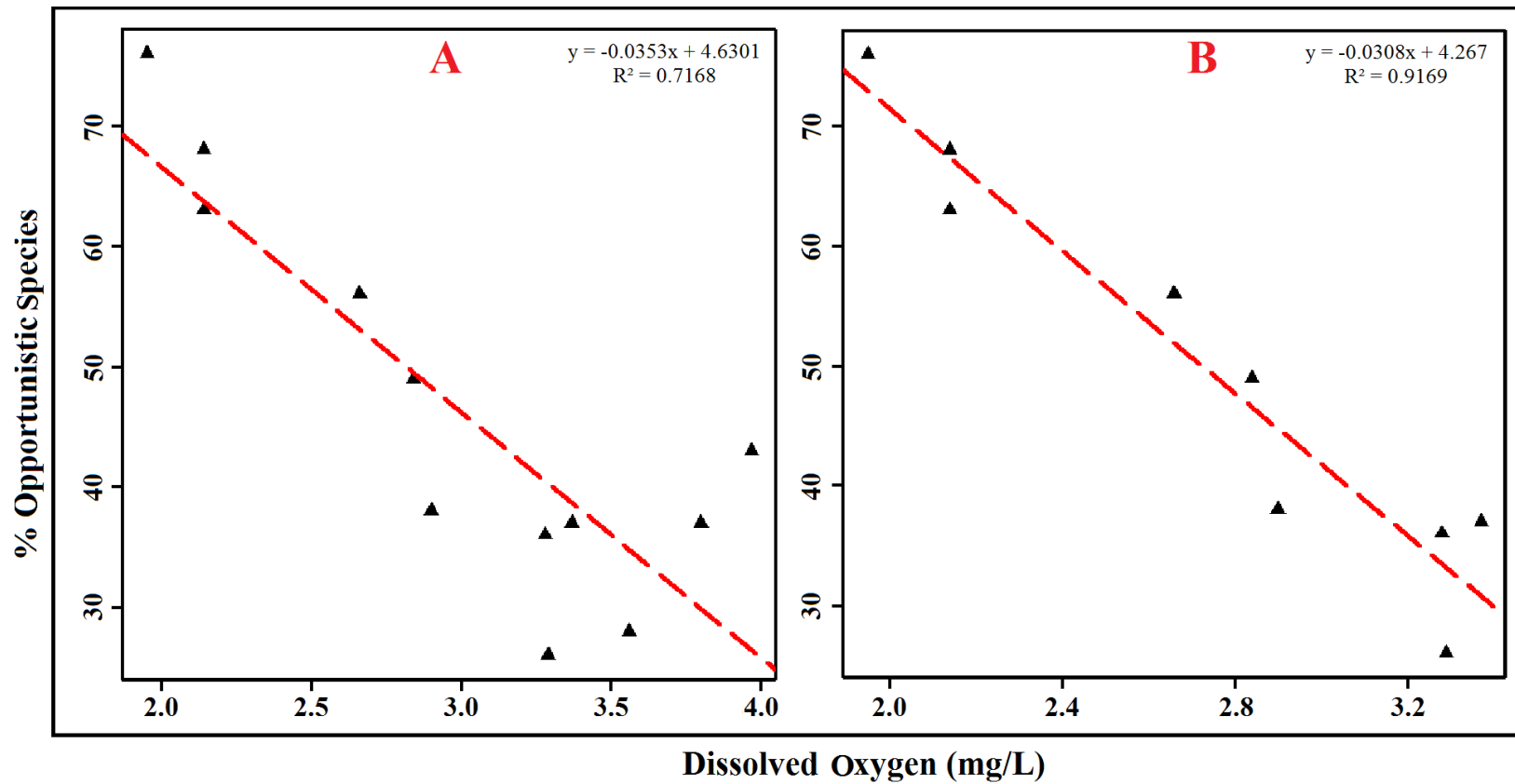
Figure 58. Linear regression of percentage of opportunist species (dependent variable) during the April 2009, September 2009 and August 2010 sample collections on the mean dissolved oxygen concentration (independent variable). The panel A includes all the sites and panel B excludes reference site A.

CHAPTER IV

DISCUSSION

Gulf of Mexico Hypoxia in 2009 and 2010

Hypoxia is an annually recurring phenomenon in the northern Gulf of Mexico.

Hypoxia is most persistent, widespread and severe during the summer months: June, July

and August. Hypoxia may persist to September or early October if the water column is

left unperturbed by tropical storms, hurricanes or cold fronts (Rabalais and Turner, 2001).

Because the hypoxia in the northern Gulf of Mexico is seasonal, stress induced by the

hypoxia is also seasonal. Once the stress of hypoxia has subsided, the seasonally

disturbed benthic community may take a few years to recover completely and become a

mature community (Janssen et al., 2010). If hypoxia is seasonally recurring, the benthic

community has little time to recover between hypoxic periods, and the community may

endure a significant loss in diversity because of stress induced by hypoxia on a

recovering community (Janssen et al., 2010). The benthic community structure reflects its

recent encounter with hypoxia as well as the cumulative response of repeated hypoxic

events.

For this investigation, it was critical to discern the impact of seasonal hypoxia on

the community structure of the macrobenthos. To achieve a stable oxic condition for

assessing hypoxia impacts in the 2009 analyses (and to maximize the recovery time since

the last likely hypoxia event), it was critical to collect the first set of samples in early

April. Around April, hypoxia is rare, water column stratification is incipient, and the

macrobenthos community is just emerging from the winter "resting stage," and about to

enter the growing season. To capture the potential impacts of a 2009 hypoxia event, the

second set of samples were collected in early September, when the hypoxia season is ending, water column stratification is entering the fall transition, and the macrobenthos community is concluding its growing season. To capture the effects of hypoxia at the height of the summer hypoxia season, the third and final set of samples were collected in early August of 2010. In August, water column stratification is strongest, and hypoxia is typically well developed and widespread. The macrobenthos community bears the full and immediate impacts of the present hypoxic stress and stress from the hypoxic events of previous years.

How hypoxia affects the variability in structure and distribution of the macrobenthos community in this investigation is linked to the source of hypoxia in the northern Gulf of Mexico. Hypoxia in the northern Gulf of Mexico is tightly coupled with the Mississippi River system discharge. The Mississippi River system discharge is controlled and divided between the Mississippi and Atchafalaya Rivers, which fuel the development of hypoxia (Rabalais and Turner, 2001).

Site D was situated close to the Mississippi bird foot delta and is heavily influenced by the Mississippi River discharge. By contrast, sites B and C were close to the Atchafalaya River, (Figure 3). Although the influence of the Atchafalaya River on the perennial hypoxic zone is unclear (Krug, 2007), it could explain the variations in macrobenthos community structure observed at sites B and C. The sediment and water discharged by the Atchafalaya River is more efficient in depleting oxygen than sediment discharged by the Mississippi River because the Mississippi River extends onto the continental shelf, whereas the Atchafalaya River opens at the innermost edge of the continental shelf, where the hypoxic zone is centered (Krug, 2007; Krug and Merrifield,

2007). The nutrient-rich freshwater and sediment discharged from the Atchafalaya River that fuels the localized hypoxia settles east, west and south of the river mouth, throughout the hypoxic zone, depending on the prevailing winds, currents and river discharge (Krug, 2007; Krug and Merrifield, 2007; Hetland and DiMarco, 2008; Bianchi et al., 2008; Bianchi et al., 2010). The Atchafalaya discharge could be the chief driver of documented hypoxia at site B during July 2008 and August 2010 (Table 25; Figure 59). Site C, though geographically close to site B, might have benefited from organic enrichment as a fringe effect of nearby hypoxia, where primary production is high enough to act as a food source for the benthos but not high enough to prompt hypoxia (Figure 59). Site A, situated far west from the bird foot delta and reasonably far from the Atchafalaya discharge is used as a reference site based on the recent hypoxia history (Figure 59).

Table 25

Bottom water oxygen concentration (mg/L) at sites A, B, C and D during the three NRL sample collections (shaded rows) and the LUMCON annual mid-summer shelfwide cruise in July 2008, 2009 and 2010. Hypoxic concentrations are marked in red.

Sample Dates	Site A	Site B	Site C	Site D
July 2008	5.64	0.54	2.30	0.07
April 2009	6.40	6.20	6.30	4.10
July 2009	6.00	4.50	2.60	0.20
September 2009	3.90	4.30	5.30	2.50
July 2010	5.70	3.49	3.13	3.39
August 2010	6.00	1.70	3.00	4.00
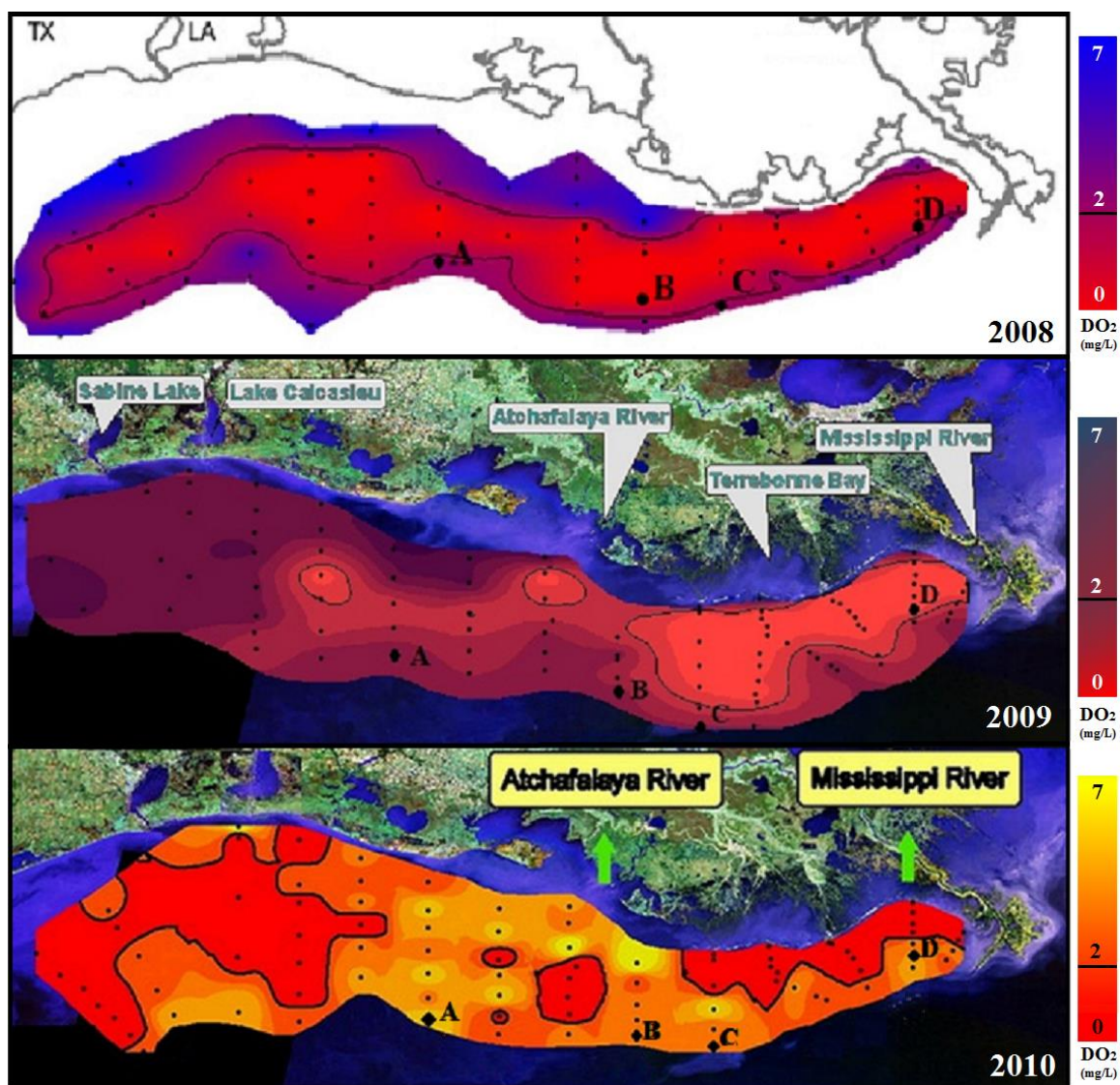
Figure 59. Areal extent of hypoxia in northern Gulf of Mexico continental shelf during (from top) 2008, 2009 and 2010. Source: http://www.gulfhypoxia.net/Research/.
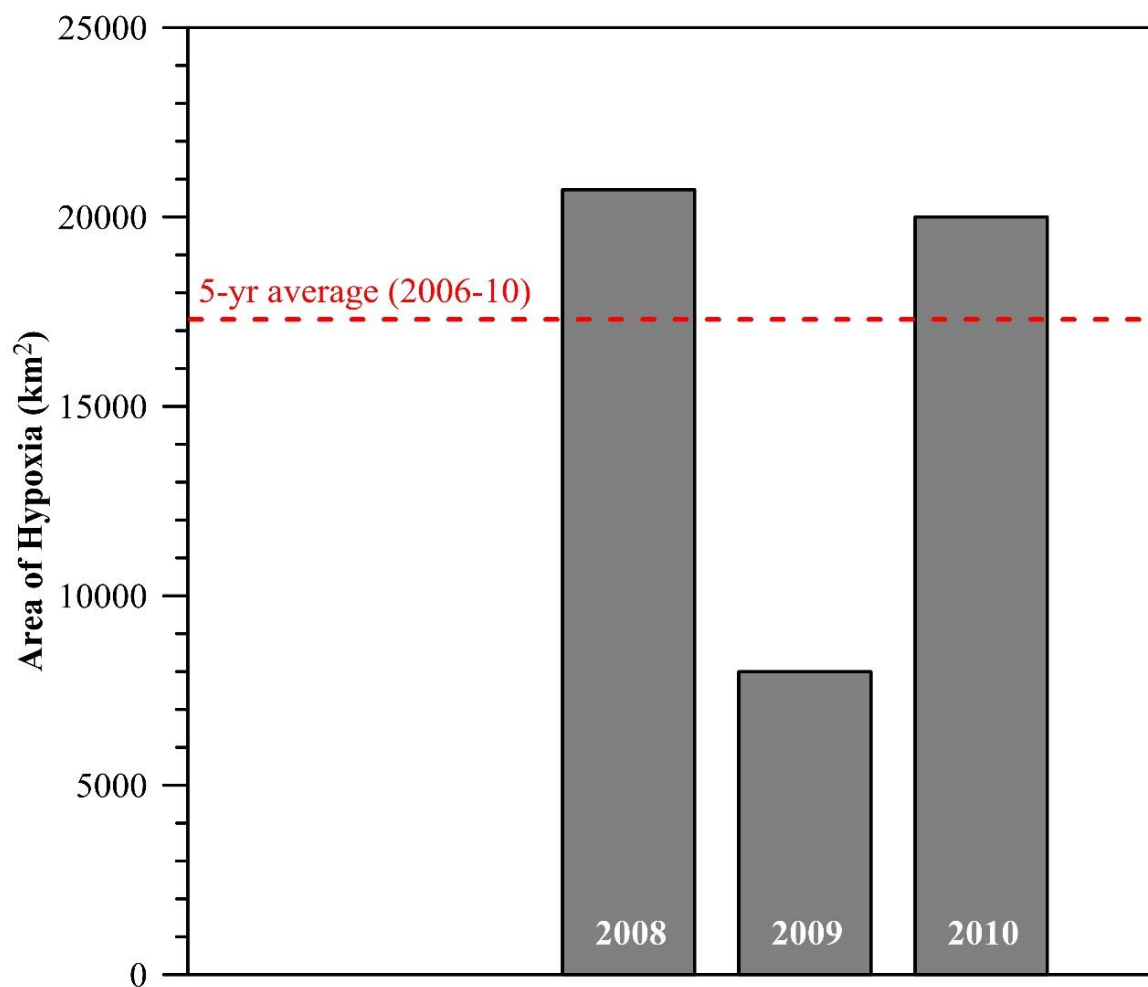
Figure 60. Areal extent of hypoxia in the northern Gulf of Mexico continental shelf during 2008, 2009 and 2010. The red dotted line is a five- year average from 2006-10. Data source; http://www.gulfhypoxia.net/Research/.

Benthic Community Response

Benthic communities in transition or recovery are highly unpredictable. In the successional continuum, only the pioneering and final stages are predictable and only the final stage is habitat-dependent (Pearson and Rosenberg, 1978). Nevertheless, scrupulous interpretations of the macrobenthos censuses can provide insight into the dynamics of community structure. Hence, to test the SAB response hypothesis and assess the stress-response induced by seasonal hypoxia on the macrobenthic communities, the parameters of abundance, biomass, estimated average individual biomass, species diversity, richness, evenness, and percentage of opportunist species were interpreted at sites A, B, C and D.

Site A

Site A generally showed the characteristics of a stable community with high values for macrobenthos abundance, biomass, evenness and diversity during spring and late summer of 2009. In the summer of 2010, although the abundance values were higher, the diversity values were lower than in 2009. Furthermore, the percentage of opportunist species also increased due to the dominance of the capitellid polychaete *M. californiensis* during summer 2010. This might be because the areal extent of hypoxia measured during annual, mid-summer, shelfwide cruise in July 2010 was one of the largest off the upper LaTex shelf since the beginning of hypoxia monitoring in 1985 (Figures 59 and 60). The total area reported was smaller than the actual size of the hypoxic water mass because time constraints precluded the measurement of the full extent of the hypoxic area (Rabalais and Turner, 2010). Moreover, *M. californiensis* is a second-degree opportunist and a good indicator of unpredictable environment (Borja et al., 2000). This polychaete is usually present in unpredictable environments. When favorable conditions are present,

their population size increases, and once the recovery process starts, they tend to disappear due to increased competition (Grassle and Grassle, 1974). Capitellid polychaetes generally produce planktonic larvae during the summer months and their population attains a large size when the populations of other species are reduced. The capitellid population increase is due to elimination of competition from highly sensitive species and a consequent increased food supply due to their absence. Gaston (1985) observed hypoxia-induced elimination of macrobenthos that contribute rarely and moderately to the abundance. He also observed a noticeable decrease in species richness during hypoxia and a regime shift in the macrobenthos community towards juveniles and opportunist species off the western inner shelf of Louisiana. However, an increase in abundance of *M. californiensis*, a typical opportunist, at site A during August 2010 might be due to a degradation of normally favorable conditions as a result of an unusually large nearby hypoxic zone in the year 2010 or it might have been due to random variation in its population.

Based on the three observations made at site A, the community can be termed as stable, progressing towards the normal stage on the successional continuum, which supports the SAB response hypothesis. Site A appears to be in the last phase of stage II in the Pearson-Rosenberg model (Figure 2).

<div align="center">Site B</div>

Site B experienced hypoxia in 2006-2008, three consecutive years before the first sample collection (Figure 5) and historically experienced hypoxia between 50% and 75% of the time, but hypoxia was not present in April, July or September of 2009 (Table 25; Figure 5). The areal extent of hypoxia in 2009 was one of the smallest (Figures 59 and

60), covering only 8000 km^2 (Rabalais and Turner, 2009). The macrobenthos abundance at this site remained approximately the same in spring and in late summer of 2009. An increase in biomass and estimated mean individual biomass of macrobenthos from spring to late summer showed the growth of the community as a response to conditions more favorable than those of the previous three summers (Figures 14 and 15). An increase in diversity and evenness of the macrobenthos assemblage from spring to late summer indicated the improved health of the assemblage (Figures 19, 20 and 22). The decrease in percentage of opportunist species from spring to late summer probably indicated the increased competition for food and the filling of previously unoccupied niches (Figure 27). Briefly, the macrobenthos community at site B was recovering from a hypoxia event from the previous year during spring 2009, and the community was progressing forward with the continued recovery in late summer 2009.

Site B was surveyed on 30 July 2010 during the annual mid-summer shelfwide cruise and reported as not hypoxic (gulfhypoxia.net-2010 cruise log). However, when the macrobenthos were sampled on 5 August 2010, 7 days later, the bottom water at the site was found to be hypoxic (Table 25). This is an example of the transience and unpredictability of hypoxia development. Because the critical oxygen level for survival of the macrobenthos is 0.7 mg/L (Nilsson and Rosenberg, 2000), only the highly sensitive species would have been eliminated at the 1.7 mg/L value recorded during the August 2010 macrobenthos sampling (Table 25). During August 2010, macrobenthos abundance, biomass and estimated average individual biomass decreased, as did the diversity, richness and percentage of opportunist species. The decrease in biomass and estimated average individual biomass might be due to the elimination of highly sensitive, large-

bodied, *K*-selected species. Elimination of these equilibrium species would explain the decrease in the indices of species diversity. Because the hypoxia at site B had just developed or shifted into the area (≤ 7 days) before the macrobenthos sampling in August 2010, the community was likely unaffected by the incipient hypoxia and instead exhibited signs of recovery from the 2008 hypoxia. The duration of exposure of site B to hypoxia at the time of sampling was not long enough for opportunists to have colonized the location, which would explain the low percentage of opportunist species found there. The lack of the effect of the incipient hypoxia was also observed in the meager populations of opportunists like the sub-surface deposit-feeding polychaetes *M. californiensis* and *C. soyeri*, which dominated site B during spring and late summer of 2009. The former was only the fourth-most dominant species and the latter was insignificant in abundance in 2010 (Appendix B). The relatively high evenness value (0.87) was another indication of low dominance of opportunist species at site B in August 2010.

The benthic community at site B was recovering from 2008 hypoxia in 2009, the community began to deteriorate from exposure to oxygen stress again in summer 2010. Based on the three observations made at site B, the community can be termed as a recovering community exposed to recent stress by recurring hypoxia. Site B lagged behind both sites A and C in the successional continuum and appears to be in the initial phase of stage II in the Pearson-Rosenberg model (Figure 2). This supports the SAB response hypothesis.

Site C

Site C experienced hypoxia during 2006 and 2007, but not in 2008 and 2009. The

break in hypoxia could have allowed the community sampled during April 2009 three

consecutive, hypoxia-free summers to grow and recover from documented hypoxic event

in 2007. The samples collected in spring at this site had a high abundance, moderate

biomass, high diversity, high species richness (126 species), high evenness and a low

percentage of opportunist species, all of which indicated a healthy community. The

macrobenthos abundance and biomass, but not the average individual biomass, drastically

decreased in September 2009. In addition, both the percentage of opportunist species and

the number of all species (77 species) decreased by late summer. Similarly, Rabalais et

al., (2001) observed high species richness of macrobenthos in spring and low species

richness in summer and late summer months in 1990 and 1991 in <20 m water depth on

the Louisiana continental shelf. Furthermore, Baustian and Rabalais (2009) found the

macrobenthic communities to be three times less-abundant and diverse in September and

October of 2004 compared to those in March and April of 2004 communities at stations

shallower (~20 m water depth) than those of this study (30-40 m water depth).

It is important to note that during September 2009, site C was on the periphery of

the hypoxic zone, according to the annual mid-summer shelfwide cruise in July (Figure

59). Baustian (2005) studied macrobenthos and benthic megafauna near this site during

2003 and determined that demersal fish were moving away from hypoxia-affected areas

to surrounding non-hypoxic areas to escape or avoid the low-oxygen conditions. She also

observed increased predation on the benthic invertebrates by Atlantic croakers in the

adjacent non-hypoxic areas. This phenomenon might have been occurring at site C during

the late summer of 2009. The nearby hypoxia might have increased the predation by demersal fish on the macrobenthos community, and resulted in the reduced abundance, biomass, diversity and species richness. The decreased percentage of opportunist species, larger estimated average individual biomass, and higher evenness were indications that the site did not experience hypoxia and that site C was in a better state of health despite the reduced population size.

In summer 2010, however, site C was far away from the hypoxia-affected area and presumably did not experience hypoxia in 2010 (Figure 59; Table 25). During summer 2010, the macrobenthos assemblage at site C increased in abundance, biomass, diversity, evenness and richness, with biomass increasing approximately tenfold. This profusion could be a result of site C being subject to organic enrichment, reduced predation pressure and sufficient oxygen for growth. The presence of the large-bodied, *K*-selected macrobenthos—like the bivalves *Angulus versicolor* and *Caryocorbula contracta* and the polychaetes *Ameana trilobata*, *Clymenella torquata*, *Diopatra neotridens*, and *Euclymene* sp. A—provided the large increase in biomass. Hence, the presence of large-bodied, equilibrium species with increased abundance, diversity and richness indicated that the community at site C had progressed toward recovery from previous hypoxic events in 2010.

The macrobenthos community at site C was the only community to progress in recovery during the investigation. Based on the three observations made at site C, the community can be termed as recovering and progressing towards the normal stage and lagging behind site A in the successional continuum. Site C appears to be in the

intermediate phase of stage II in the Pearson-Rosenberg model (Figure 2). This supports the SAB response hypothesis.

<center>Site D</center>

During April 2009, the bottom water at site D was depleted in oxygen, but not hypoxic (Table 25). Site D had low macrobenthos abundance, but high biomass and large estimated mean individual biomass. High values for biomass and estimated mean individual biomass were due to the presence of the large epibenthic shrimp *Alpheus* cf. *macrocheles* and *Alpheus* nov. sp. These epibenthic fauna were absent from late summer samples because motile organisms can move away from low-oxygen areas to avoid hypoxic stress (Craig, 2012). For example, crabs, shrimps, and eels were observed swimming upwards to avoid the hypoxia on the Louisiana shelf during the 2009 annual mid-summer shelfwide cruise (Rabalais and Turner, 2009).

During September of 2009, the macrobenthos abundance and the percentage of opportunist species showed an increase, but macrobenthos biomass and estimated average individual biomass showed a drastic reduction at site D. Although the bottom water oxygen concentration (2.5 mg/L) was above the hypoxic threshold when the macrobenthos were sampled (Table 25), the annual mid-summer shelfwide cruise conducted during 18-23 July found it to be hypoxic (Figure 59; Table 25). The July hypoxic event may have killed the large-bodied macrobenthos previously found during the spring and small opportunist species occupied the empty niche. The macrobenthos at site D were collected on 6 September, giving a two- to three-week growing period for the newly settled opportunists that could account for the low values for average specimen size (average individual biomass).

Chief among the opportunist polychaetes at site D was the cossurid *C. soyeri*. Cossurid polychaetes are small-bodied, grow up to 15 mm and breed multiple times in a growing season. Bachelet and Laubier (1994) found ovigerous females from February to April of every year, and Uebelacker and Johnson (1984) found gravid individuals of *C. soyeri* and *C. delta* in the northern Gulf of Mexico during mid-fall. Zhadan et al., (2012) found a bimodal distribution of cossurid species, indicating the presence of two different cohorts of juveniles and adults in their study in the central basin of the White Sea of the Russian Arctic. In this investigation, two different populations of cossurids were observed at site D during 2009. In spring samples before the hypoxic event in July 2009, cossurids made up to 42% of the population, and their average individual body size was 1.4 µg AFDW. After the hypoxic event in late summer, their contribution to the abundance remained the same (42%), but the cossurids were smaller, with an estimated average individual biomass of 0.36 µg AFDW. The recorded value for the bottom water oxygen concentration in July 2009 was 0.2 mg/L (Table 25), well below the critical oxygen level of macrobenthos survival of 0.7 mg/L (Nilsson and Rosenberg, 2008). This near-anoxic condition might have killed the spring cossurid cohort. Cossurids are known to have a semi-planktonic, juvenile, dispersal phase, and the cohort found in late summer might have been newly settled recruits. This could explain the stable macrobenthos abundance, yet reduced biomass found in the late-summer sampling.

During August 2010, the macrobenthos abundance drastically increased due to heavy contributions from the opportunist *C. soyeri* (53%, or 827 individuals per site) and other opportunist polychaetes like *M. californiensis*, *Sigambra tentaculata* and *Paraprionospio pinnata.* Besides the opportunist species, the bivalve *Nuculana acuta* and

the paraonid polychaetes *Acmira finitima* and *Aricidea wassi* were also found in large numbers, thus contributing to the increased biomass. The high abundance of these non-opportunists and the reduction in the percentage of opportunist species raised the species evenness at this site in summer 2010.

After late summer 2009, cossurid contribution to the abundance increased by 11% (to 53%) and their estimated average individual biomass increased from 36 µg to 47µg AFDW. This might be due to a co-existence of adult and juvenile cohorts in the cossurid population because site D did not experience hypoxia in summer 2010, allowing the juvenile cohort from spring 2009 (2010 adults) to co-exist with the new juvenile recruitment from summer 2010.

High abundance, high opportunist species percentage and low values of biomass, small estimated average individual biomass, low species diversity, low richness, and low evenness during the three sample collections at site D is in accordance with the community being comprised of few dominate, opportunist species. These characteristics are a clear indication of a stressed community, which supports the first (SAB response) and third (opportunist species response) hypotheses.

The macrobenthos assemblages at this site exhibited the greatest effects of stress of all the sites and displayed the effects in all three sample collections. Based on the three observations made at site A, the community can be termed as most stressed among all four communities, which supports the SAB response hypothesis. Site D appears to be in the intermediate phase of stage I in the Pearson-Rosenberg model and lagging behind sites A, C and B on the successional continuum (Figure 2).

Feeding Guild Response

Macrobenthic community structure can not only evaluated by taxonomic

diversity, but also by feeding guild diversity. To test the feeding guild response

hypothesis and understand feeding guild structure, this novel effort for the Louisiana

continental shelf was made. The feeding guild compositions and relationships among

guilds examine a functional, rather than a structural, organization of a community in that

they infer exploitation of available food resources, escape from predation, and

propagation of the species through reproduction (Pearson and Rosenberg, 1978; Pearson,

2001). The macrobenthos community, vis-a-vis the feeding guilds distribution pattern,

seems to be structured above all else by food availability. Putro (2009) saw a decrease in

abundance of carnivores, filter feeders and surface deposit feeders as sub-surface deposit

feeders increased at sites with high organic matter accumulation. If food availability at

the surface decreases, sub-surface deposit feeding could become more important to the

macrobenthos community, and the abundance of suspension feeders and surface deposit

feeders may wane. Reference site A, which had experienced hypoxia less than 25% of the

time, had the lowest percentage of opportunist species, whereas site D, which had

experienced hypoxia more than 75% of the time, had the highest percentage of

opportunist species. The opportunist species that dominated the samples belong to the

sub-surface deposit feeding polychaete families Capitellidae and Cossuridae (Fauchald

and Jumars, 1979), in support of the feeding guild response and opportunist species

response hypotheses.

Hypoxia is a secondary effect of organic enrichment in water isolated from

oxygen replenishment. Organic enrichment generates one of two responses from the

benthic community: one is increased benthic biomass due to the increased food supply,

and the other is mortality due to hypoxia generated by continued eutrophication

(Rosenberg, 2004). In an organic enrichment gradient, the complicated and diverse

trophic assemblages found at the oligotrophic end grade into a simplified and less

diverse, trophic community, consisting entirely of deposit feeders at the eutrophic end

(Pearson and Rosenberg, 1978). This decrease in species diversity over time was

observed at sites A, C and D but not at site B, and was likely a response to the water

column stratification. During April 2009, when water column stratification was weak and

the macrobenthos community was less oxygen-stressed, the sites A, C and D had a

relatively low percentage of deposit feeders (Table 26). During September 2009 when

water column stratification was strong, but vulnerable to destruction by weather events,

communities that had been exposed to summer-long stratification experienced an increase

in the percentage of deposit feeders at sites A, C and D. This increase in deposit feeders

was also fueled by a seasonal increase in the food supply. During August 2010 when the

water column stratification was strong and communities were severely stressed, sites A,

C and D had the highest percentage of deposit feeders among all three sample collections.

This increase in deposit feeders coinciding with deceasing species diversity, richness, and

evenness (Figures 19, 20, 21 and 22) was likely due to increased food supply and

decreased competition from other species. This decrease in species diversity and richness

parallels the decrease in trophic diversity that result in the loss of functional groups,

which negatively affects the ecosystem functioning (Putro, 2009).

All sites showed progressive increase in deposit-feeder percentage from one

sample collection to another except site B. At site B, the percentage of deposit feeders

remained approximately the same from spring to late summer of 2009 (Table 26).

However, in summer 2010 the percentage of deposit feeders decreased. This might be

because the macrobenthos community at site B in July 2010 was exposed to low oxygen

(3.5 mg/L) (Table 25), which might have killed highly sensitive, non-opportunist deposit

feeders. At site A, surface deposit feeders are marginally dominant over sub-surface

deposit feeders during all three sample collections (Figure 25). Site A had the most

diverse community, in terms of both species diversity and trophic diversity, because it

had more proportional representation from all feeding groups except herbivores.

Herbivores contributed very little to the abundance or biomass at all sites (Figures 25 and

26). This might be due to the scarceness of marine algae that support the herbivore

populations. The 30-m isobaths of the northern Gulf of Mexico shelf might receive little

sunlight that supports the growth of benthic diatoms and other algae, especially in the

turbid water continuously supplied by the Mississippi and Atchafalaya Rivers.

Table 26

Percentage of deposit (surface and subsurface) feeders at sites A, B, C and D during the April 2009, September 2009 and August 2010 sample collections.

Sampling	A	B	C	D
April 2009	67	82	57	80
September 2009	69	81	65	86
August 2010	77	70	71	92

According to Pearson and Rosenberg (1978), suspension feeders are abundant at

the middle of the organic enrichment gradient. Site C was located both ecologically and

geographically between site A, which is the most stable community, and site D, which is

the least stable community (Figure 57). Site C had a high percentage of suspension

feeders during spring 2009 and summer 2010; hence, the assemblage at site C could be

deemed as an intermediate community on the hypoxic gradient in the northern Gulf of

Mexico. These results agree well with the Pearson and Rosenberg model and tend to

support the second feeding guild response hypothesis. The percentage of suspension

feeders decreased from spring to late summer 2009 at site C. Furthermore, the percentage

of suspension feeders at site C fluctuated inversely with the percentage of carnivores

during 2009, but stabilized in summer 2010 (Figure 25). The decrease in suspension

feeders also coincides with a 50% decrease in the overall macrobenthos abundance in late

summer of 2009. These decreases could be due to increased predation by fish and

carnivorous invertebrates.

During spring 2009, the macrobenthos community at site D was represented by

five different feeding guilds, whereas, during late summer 2009 herbivores were

completely absent and the percentage of suspension feeders decreased tenfold. In summer

2010, both herbivores and suspension feeders were completely absent from site D. The

decreases in trophic diversity (and species diversity) suggest that this site was the most

stressed among the four study sites. These findings support the SAB response and feeding

guild response hypotheses. Both abundance and biomass of surface deposit feeders

increased as the abundance of carnivores decreased at site D from 2009 to 2010, and the

inverse patterns of this were also observed (Figures 25 and 26). Putro (2009), studying

the effect of fish farm waste discharge in South Australia has also observed this inverse

relationship between carnivores and surface deposit feeders. The cyclical dominance of

surface deposit feeders—an effect of organic enrichment—followed by the dominance of

carnivores, fueled by abundant food resources that include surface deposit feeders, possibly explains the inverse relationship between these two feeding guilds.

<div align="center">Opportunist Species Response</div>

Dominance of opportunist species indicates deteriorated environmental conditions. The reestablishment of sensitive species that are tolerant to low stress requires complete abatement of hypoxia-induced stress (Sanz-Lázaro and Marín, 2011). Because hypoxia in the northern Gulf of Mexico is an annually recurring event, the affected sites would not have enough time to recover from their previous incident and such sequential exposure would promote the proliferation of opportunist species. To examine this general principle and to test the opportunist species response hypothesis for the continental shelf of Louisiana the percentages of opportunist species were regressed on the bottom water oxygen values. This analysis is the first of its kind on the continetal shelf of Louisiana. The linear regression was performed using the average, bottom water oxygen concentration values from 2000 to 2010 from the annual, mid-summer, shelfwide cruises. The empirical relationship indicated that the lower O_2 concentrations correlated with higher percentages of opportunist species that can thrive in the stressed environment. Environments with higher O_2 concentrations (above 2 mg/L) had fewer opportunist species as the sites were not stressed thus meeting the objective associated with the opportunist species response hypothesis.

The lower R^2 value (0.72) for the linear regression fitted for the data from all sites (Figure 58) is due to the increase in species abundance and percentage opportunist species at site A during late summer 2009 and summer 2010. The increase in species abundance and percentage of opportunist species at all sites during late summer of 2009

is exemplified by the increased abundance of *P. cristata, P. fallax, C. capitata* and *M. californiensis* (Appendix B). Increase in species abundance and percentage of opportunist species in the site A assemblage during summer of 2010 is due to sheer dominance of *M. californiensis* (Appendix B).

Site A, despite being a reference site with the highest oxygen concentration among all sites, showed an increase in percentage of opportunist species during late summer 2009 and summer 2010. However, when oxygen concentration becomes a non-limiting factor, other variables, like C, N, pollutants, or temporally varying parameters (spring blooms, storms or flood events) can become the controlling factors. In this way, annual factors promoting summer growth might have prompted the proliferation of both *r*- and *K*-selected species. Additionally, the samples collected at site A during late-summer 2009 and summer 2010 were at the end of the hypoxic season, which might have allowed more sensitive *K*-selected species to be eliminated and prompted the growth of opportunists such as spionid and capitellid polychaetes to thrive under unstable environments (Borja et al., 2000).

Exclusion of site A values from the linear regression model improved the R^2 value to 0.92 (Figure 58), which emphasizes the effect of hypoxia on the benthic communities experiencing the greatest stress in the northern Gulf of Mexico. At the same time, employing this regression requires the caveat of depending on only a single measurement of bottom water oxygen concentration to represent the entire hypoxic season. However, a single measurement of bottom water oxygen on the LaTex shelf may be necessary to expose long-term and interannual trends in macrobenthic community structure, but it is not sufficent to explain short-term and intraannual variations.

Vertical Distribution

The vertical distribution of macrobenthos abundance showed essentially the same pattern at all sites during all three sample collections. More than 80% of the animals were distributed in the top 2 cm and the abundance decreased as the depth in the sediment increased. The vertical distribution of biomass did not show any regular pattern; whereas, vertical distribution of the estimated average individual biomass indicated that larger animals lived deeper in the sediment. Macrobenthos found in the top 2 cm are generally small-bodied animals.

Community Dissimilarity

The measure of dissimilarity among the four sites using species abundance showed the presence of four different communities during sample collections in April 2009, September 2009 and August 2010. However, all sites shared some common species and seemed to group them into clusters at 97%, 96% and 87% dissimilarity for sample collections in April 2009, September 2009 and August 2010, respectively. Community dissimilarity was higher during the 2009 samplings than during the 2010 sampling. The lower dissimilarity in summer 2010 might be due to the decrease in the number of species combined with an increase in overall abundance of specimens (Tables 27 and 11).

Table 27

Total number of species at sites A, B, C and D during the April 2009, September 2009 and August 2010 sample collections.

Sampling	A	B	C	D
April 2009	139	96	126	46
September 2009	145	94	77	44
August 2010	107	82	93	43

The similarity between the sites increased as macrobenthos assemblages changed from diverse groups to more opportunist groups. An approximate 3% similarity between all sites during spring 2009 could be attributed to the presence of the nemertean Lineidae sp. 2; the bivalves *A. aequalis* and *N. acuta*; and the polychaetes *P. pinnata*, *C. soyeri,* and *M. californiensis* at all four sites in April 2009. The similarity between sites appeared to increase as the bottom water became more isolated due to water column stratification. In spring 2009, water column stratification was weak, bottom water oxygen was yet to be notably depleted by community respiration and the macrobenthos community was more diverse. Although the number of associations found was high, the similarity among sites was low. This might have occurred because the assemblages in April 2009 were speciose (Table 27). During late summer 2009, the 4% similarity among sites could be attributed to the presence of the opportunist polychaetes *C. soyeri*, *M. californiensis* and *C. capitata* and the bivalve *N. acuta* occurring at all sites. The meager (1%) similarity increase might be due to decreases in community diversity and species associations in opposition to an increase in the percentage of opportunist species, resulting from the exposure of the

communities to low oxygen stress during the summer. During summer 2010, the similarity between sites increased to 13%, but the only common species at all sites were the opportunist polychaetes *P. pinnata* and *M. californiensis*. During summer, the macrobenthos communities were exposed to oxygen stress due to strong and persistent water column stratification, which could deleteriously affect the sensitive species populations and promote the opportunist species populations. From late summer 2009 to summer 2010 the abundance of macrobenthos increased, whereas the numbers of species representing the assemblages decreased at sites A and D (Tables 11 and 27). The increase in abundance predominantly consisted of a few opportunist species.

All four sites had a group of common macrobenthos species that were present during all three sample collections. Hence, these species are regarded as core species of that particular site's macrobenthos community, and the majority of these core species were opportunist species (Appendix F). *M. californiensis*, *N. micromma*, *N. acuta*, *P. fallax*, *Tharyx* cf. *annulosus,* and *P. pinnata* were common to site A. *N. acuta*, *S. tentaculata*, *P. fallax*, Amphiuridae spp. and *A. wassi* were common to site B. *P. pinnata*, *S. tentaculata*, *L. gracilis*, *A. wassi* and *C. americanus* were common to site C. *C. soyeri* and *M. californiensis* were common to site D.

<center>Community Succession</center>

Community succession was assessed with the nMDS, CCA and PCA multivariate analyses. In the April 2009 sampling, 235 species were collected but 55% of those species were found only at any one site and the 45% were shared by more than one site. The nMDS ordination technique performed on abundance data grouped all sites separately. The ecological inter-site distance between sites A and D was the largest,

followed by the distance between sites A and C (Figure 50). The ecological distance between sites B and C was the shortest. Though site C is close to site D geographically, site B was closer to site D ecologically, meaning site D had more common species with site B than with sites C or A. The disparity between the spatial and ecological distances might be due to the similar influences of the Mississippi River discharge on site D and the Achafalaya River discharge on site B (Krug, 2007; Krug and Merrifield, 2007; Hetland and DiMarco, 2008; Bianchi et al., 2010). The CCA was performed with abundance data to determine the effect of the environmental variables sedimentary organic carbon, sediment C/N ratio, bottom water oxygen concentration and percentage mud on the macrobenthos community structure. The sediment C/N ratio had high influence on the macrobenthos at site A and sedimentary organic carbon heavily influenced the macrobenthos at site D, factors reasonably attributable to river discharge.

During the late summer 2009 sampling, there were 230 different species and 6% were found at all four sites, and the rest were shared by a few sites. The nMDS analysis revealed that the arrangement of site assemblages did not see any remarkable changes from spring to late summer in 2009, suggesting that the community composition remained similar. For instance, site D was scaled in the low-oxygen contours, as depicted for the spring sampling. In the late summer sampling CCA revealed a high influence of the sediment C/N ratio on the assemblage at site A, as depicted for the spring sampling. Site C was more heavily influenced than site D by sedimentary organic carbon as depicted by CCA in the late summer sampling. The percentage mud was not a factor in the distribution of the macrobenthic community in spring or late summer samples (Figure 53 and 54). The bottom water dissolved oxygen did not have a consistent impact on any

site because the time duration required for the benthic community to respond to hypoxia is different for different animals. This species-specific response to hypoxic conditions was demonstrated by a laboratory experiment conducted by Nilsson and Rosenberg (1994), which showed the brittle star *Amphiura filiformis* leaving the sediment and coming to the surface after five days in severe hypoxic conditions. By contrast, the bivalve *Mysella bidentata*, the polychaete *Pectinaria koreni*, and the polychaete *Nephtys hornbergii* took 7, 8 and 11 days, respectively, to rise to the surface of the sediment under the same conditions. This suggests that measuring hypoxia on a regular basis is necessary to unequivocally distinguish the impact of bottom water oxygen on the benthic community. However, most of the hypoxic zone in the northern Gulf of Mexico lacks data collected on a continuous basis.

During the summer 2010 sampling there were 188 different species and 9% were found at all four sites. The nMDS revealed that site B was farthest in ecological inter-site distance from site A, although site B was geographically closer to sites C and D. Site B was ecologically close to sites C and D, indicating that site B had more species in common with sites C and D. However, site B had fewer species in common with site A. During the August 2010 cruise sedimentary organic carbon and the sediment C/N ratio were not measured, which unfortunately inflated the meager influence of percentage mud to appear as an important determinant of the macrobenthos community structure according to CCA. Without the ecologically important variables of sedimentary organic matter and the sediment C/N ratio, the ordination of the four sites with the vectors of bottom water oxygen and percentage mud is trivial and possibly misleading (Figure 55).

The Principal Component Analysis (PCA) was used to determine the order of community succession. The analysis relied on parameters of abundance, biomass, species diversity, number of species, percentage of carnivores, percentage of herbivores, percentage of sub-surface deposit feeders, percentage of surface deposit feeders, percentage of suspension feeders and bottom water oxygen concentration for each site during all three sample collections to understand the distribution of sites along various axes. The output indicated that site D was the site most affected by hypoxic stress as expected from the preponderance of data, and that site A was in an advanced stage of succession as compared to the other sites. The expectation for site B to be more affected by hypoxia than sites A and C due to its history of exposure to low oxygen was supported by PCA. Site C was in a more advanced stage of succession than site B. This might be due to an organic enrichment effect from the Atchafalaya River discharge on site B, because of the proximity of site B to the Atchafalaya River (Figure 57). These ecological rankings of sites are consistent with the hypoxia exposure frequency of sites during the times surveyed by Rabalais (Figure 4).

The Pearson-Rosenberg model developed using organic enrichment as a stressor for the semi-enclosed water bodies was applied and tested in the open neritic waters of the Gulf of Mexico with hypoxia as a stressor and the results show agreement with the model predictions. The values of species diversity, richness, and evenness decreased, and the percentage of opportunist species increased as the frequency of hypoxia exposure increased. Magni et al., (2009) studied the applicability of the Pearson-Rosenberg model in three coastal lagoons of Mediterranean Sea and found the response patterns of the benthic communities matched the model predictions. Their study documented an increase

in opportunist species abundance in benthic communities as a response to increasing total organic carbon. In this northern Gulf of Mexico study, all sites were in the intermediate stages (I and II) of succession according to the Pearson-Rosenberg model (Figure 2). In this study, none of the sites have shown any sign of a climax stage (III) or an afaunal stage (0). These results prove all three hypotheses of the investigation and suggest the existence of spatial environmental gradient within the seasonally recurring hypoxic zone in the northern Gulf of Mexico.

CHAPTER V

CONCLUSIONS

Variability in macrobenthos distribution is impossible to explain with any one factor because the fauna live within a dynamic water-sediment interface. Traditionally, studies have attributed the distribution of macrobenthos to the grain size distribution, but there is very little evidence to support this paradigm (Newell et al., 1998). According to Snelgrove and Butman (1994) in their review of animal-sediment relationships, the observed variability cannot be explained by grain size distribution alone; there is no demonstrated evidence that the sediment grain size limits the distribution of an organism. They argue that the same organism can be found in many sedimentary habitats and is not confined to just one sedimentary type. Furthermore, an organism encounters many different kinds of sediments vertically, depending on the length of the burrow. Besides, determination of sediment grain size is based entirely on the disaggregation of sediment samples, which may have little significance to what an organism encounters in the natural habitat. Hence, the focus has switched to other important factors such as availability of food, larval settlement, trophic interaction, organic microbial content, sediment dynamics and prevailing physicochemical conditions that play a significant role in controlling the distribution of an organism (Snelgrove and Butman, 1994; Newell et al., 1998).

Pearson and Rosenberg (1978) emphasized the importance of behavior and genetic flexibility of the species to withstand the unstable environment. They concluded that genetically flexible organisms have a higher survival rate in an unstable environment compared with genetically rigid organisms. They demonstrated the concept by considering reproductive strategies and related resource availability using the *r*-selected

to *K*-selected continuum on an environmental gradient. Although it is necessary to explain patterns of macrobenthos using a multivariate approach, a meaningful and predictive relationship can be obtained by systematically examining the factor of interest (Snelgrove and Butman, 1994). Therefore, to study the effect of seasonal hypoxia on macrobenthos community structure, samples were examined from four sites with different hypoxia occurrence histories. Heeding the assertions of Snelgrove and Butman (1994) and Newell et al., (1998) that water depth is a major influence in structuring macrobenthos communities, the sites were chosen along the 30-m isobaths. Because of the rich database from the Gulf of Mexico supported, generated and compiled by NOAA, four sites arrayed across 284 km of the Louisiana continental shelf between the Atchafalaya and Mississippi Rivers were available to study a naturally occurring hypoxic gradient.

The results of this study have suggested the existence of a spatial environmental gradient within the seasonally recurring hypoxic zone in the northern Gulf of Mexico, where hypoxia is controlled in part by water column stratification due to the discharge of nutrient-rich freshwater from the Mississippi River and Atchafalaya River. The nutrient-rich freshwater from the rivers and organic carbon leaching from deltaic marshes of active and abandoned river channels promotes eutrophication, which increases the dissolved oxygen utilization by heterotrophic activity. Consequently, the neritic seafloor environment shifts from an oxic to an anoxic condition, in which the macrobenthos response can vary from stressed to mortality, depending on the degree of oxygen depletion in the bottom water. A benthic community will go through various successional stages according to the duration of the exposure to the oxygen-depleted condition. These

various successional stages have been identified and defined by Pearson and Rosenberg (1978) in their ecological model based on an organic enrichment gradient.

The Pearson-Rosenberg paradigm was developed using data from semi-enclosed, low-energy water bodies like fjords and sea lochs, which are characteristically high-deposition habitats with bottom water that has a long residence time. In this study, this model was adopted to a high-energy, open-water, marine enviroment, specifically the LaTex shelf, where oxygen concentration of bottom water was used as a proxy for organic enrichment to test three hypotheses.

The objective of the first hypothesis was to categorize the spatio-temporal variability in the macrobenthos community response to stress induced by seasonal hypoxia at sites A, B, C and D using species diversity, abundance, and biomass (SAB) parameters. Ranking the macrobenthic communities at sites A, B, C and D using species diversity, richness, and evenness indicated that site A had the highest values, site C had the second highest values, site B had the third highest values, and site D had the lowest values. These rankings were consistent with the sites' history of hypoxia exposure and fit the SAB response hypothesis that site A should have the least stressed community and that site D, nearest the Mississippi River, should have the most stressed community.

The objective of the second hypothesis was to determine the effects of hypoxia—induced stress on feeding guild diversity of the macrobenthos at sites A, B, C and D and to compare the effects with those from the SAB parameters. The feeding guild analyses indicated that the site A had the highest number of species contributing to all five feeding guilds. Site C had a high representation from suspension feeders and carnivores and agrees with the Pearson and Rosenberg model in terms of recovery from stress by the

macrobenthos. Finally, site D had the least number of species, contributing to only three feeding guilds. These findings are consistent with the sites' history of hypoxia exposure and fit the feeding guild response hypothesis that site A should exhibit a diverse community in terms of feeding guilds and that site D should contain a community dominated by only a few feeding guilds.

The objective of the third hypothesis was to explain the observed SAB parameters and feeding guild diversity by examining the relationships between low-oxygen conditions and the dominance of opportunist species, and by extension, the successional stages found at sites A, B, C and D. Results indicated that site A had the lowest percentage of opportunists, site C had approximately the same percentage of opportunists as site A, site B had the second highest percentage of opportunists, and site D had the highest percentage of opportunists. These findings are consistent with the sites' history of hypoxia exposure and fit the opportunist species response hypothesis that site A should have least opportunist species and that site D should have the most opportunist species.

An analysis of opportunist species revealed that the macrobenthos population was dominated by typical opportunist polychaetes like *Cossura soyeri*, *Mediomastus californiensis* and *Prionospio fallax*. It would be useful to understand the life histories of the species *Nuculana acuta*, *Phyllodina squamifera*, *Aricidea wassi*, *Nucula proxima*, *Abra aequalis*, and *Scissula iris,* which contributed heavily to the assemblages, but little is known. Knowledge of the life cycles of these species would improve the interpretations of the impact of hypoxia on the macrobenthic community in the northern Gulf of Mexico.

The results of this study indicated that all the sites are in the intermediate stages (I and II) of the Pearson-Rosenberg model, and none of the sites are in climax stage (III) or an afaunal stage (0). These results supported all three hypotheses of the investigation and confirmed the existence of a spatial environmental gradient within the seasonally recurring hypoxic zone in the northern Gulf of Mexico. The general westward-diminishing gradient of hypoxia on the northern Gulf of Mexico continental shelf is influenced by the Atchafalaya River discharge, as evidenced by the macrobenthos communities nearest the river's outflow (sites B and C). As Krug (2007), suggested the knowledge on the impact of Atchafalaya River discharge on the Gulf hypoxia development and maintenance is incomplete. Therefore, much more significance should be given to the Atchafalaya River discharge to improve predictive models of hypoxia on the continental shelf of the northern Gulf of Mexico.

The hypoxia in the Gulf of Mexico is tightly coupled with the freshwater discharge and nutrient loading from the Mississippi River system (Rabalais and Turner, 2001). Owing to global climate change, various models have predicted a 30% decrease to a 40% increase in the Mississippi River water discharge by the year 2057 (Justić et al., 2007). Despite the uncertainties in quantifying Mississippi River discharge, the nutrient loading from the river is likely to increase despite legal efforts to regulate loading. The global trends in riverine nitrogen flux have shown increasing nitrogen loading due to the growing human population and associated agricultural fertilizer usage (Justić et al., 2007). Besides, hypoxia in the Gulf of Mexico responds to phenomena like the Pacific Decadal Oscillation, El Niño–Southern Oscillation (ENSO), and global wind cycles (Justić et al., 2007; Hetland and DiMarco, 2008). Various models have predicted a 67 to

90% chance of more frequent El Niño events and a 33 to 66% chance of intensified

tropical storms by the end of the 21st century (Easterling et al., 2000). It is expected that

these climate changes would intensify hurricanes, storms, and consequently floods in the

Mississippi River system catchment area, which would result in an increased flux of

nutrients and freshwater to the Gulf of Mexico (Hetland and DiMarco, 2008). The areal

extent of the hypoxic zone is considerably larger in wet years than dry years (Justić et al.,

2007; Rabalais and Turner, 2001), and this study reveals the imprints of recurring

seasonal hypoxic events on the macrobenthos community integrated over ten years

(Figure 58). If the severity of hypoxia increases, the benthic community structure will

deteriorate. One of the major consequences of benthic community deterioration is the loss

of benthic biomass that could have been a valuable food source for demersal fishes of

commercial importance. The loss of valuable benthic biomass would likely affect the

regional fisheries and, ultimately, the national economy.

Although the sample collections were made at different periods during the

growing seasons, the structure of the macrobenthos assemblages showed a clear impact

of hypoxia on the macrobenthic communities in the northern Gulf of Mexico.

Additionally, the results indicated the possible presence of a spatial gradient induced by

hypoxia. Despite the observations of the assemblages' response to hypoxic events, the

recovery could not be quantified as a function of hypoxia because three sample

collections over two years were too few to generate temporal trends of a dynamic

macrobenthic community. Furthermore, seasonally recurring hypoxia might have erased

any recovery made during non-hypoxic seasons. These fluctuations were recorded in the

samples, but the individual series of events that led the community to an observed

successional stage could not be captured. Ideally, these macrobenthic communities should be monitored throughout the year to develop a spatio-temporal pattern of benthic community structure in the Gulf of Mexico over an entire season of hypoxia. This would provide valuable information about the impact of hypoxia on the macrobenthic community and these patterns could be useful to incorporate into conceptual models for use in predicting habitat vulnerability and response of various fisheries in the Gulf of Mexico.

Higher R^2 values from regression between to the percentages of opportunist species and bottom water oxygen concentration values indicate the long-term effect of hypoxia on the macrobenthos. This study sucessfully demonstarted the applicability of Pearson-Rosenberg model for restricted marine environments on the LaTex shelf which is a more open shelf environment affected by an hypoxia gradient. These findings set the precedent for more robust benthic community indices like the AZTI marine biotic index (AMBI) and the benthic quality index (BQI) that would give an advanced understanding of the benthic habitat health to help monitor mitigation of hypoxia. These robust benthic community indices would be helpful to examine and establish the benthic habitat health status in the three zones proposed by Rowe and Chapman (2002).

Hypoxia causes both short-term as well as long-term effects on the macrobenthos community on the LaTex shelf. More rigorous monitoring of hypoxia is required to better understand and explain the macrobenthic community variation. Establishing a year-round, intense sampling would capture spatial and temporal variability that would allow detection of impacts and recovery from seasonal hypoxia and would also illuminate how the short term and inter-annual variations in the macrobenthic community interact.

Investigation of the effects of environmental variables, like sediment grain size, bottom water dissolved oxygen, sediment organic carbon, and the sediment C/N ratio, on the benthic community indicated that the influence of sediment organic carbon, and the sediment C/N ratio is strong at three of the four sites. Hence, these environmental variables are important for future studies. The study has provided a valuable taxonomic description of macrobenthos species with their respective feeding guilds on the northern Gulf of Mexico shelf, as well as an evaluation of opportunist behavior associated with hypoxic conditions.

MACROBENTHOS SPECIES LIST

Table A1

Macrobenthos taxonomic classification from phylum to species performed using the literature in the appendix L.

Phylum	Class	Order	Family	Species
Cnidaria	Anthozoa	Actiniaria	Edwardsiidae	*Edwardsia* sp.
			Haloclavidae	*Haloclava* sp.
Platyhelminthes	Turbellaria	Polycladida	Polycladida	Polycladida sp. 1
				Polycladida sp. 2
Nemertea	Enopla	Monostilifera	Amphiporidae	*Amphiporus bioculatus*
				Amphiporus sp.
	Anopla	Paleonemertea	Carinomidae	Carinomidae sp. 1
				Carinomidae sp. 2
		Heteronemertea	Lineidae	Lineidae sp. 1
				Lineidae sp. 2
				Lineidae sp. 3
				Micrura sp.
Mollusca	Gastropoda	Vetigastropoda	Skeneidae	*Parviturbo rehderi*
		Caenogastropoda	Scaliolidae	*Finella dubia*
		Littorinimorpha	Barleeiidae	*Amphithalamus vallei*
			Caecidae	*Caecum floridanum*
			Tornidae	*Cyclostremiscus jeannae*
				Solariorbis infracarinatus
				Teinostoma parvicallum
				Vitrinella floridana

Table A1 (continued).

Phylum	Class	Order	Family	Species
			Calyptraeidae	*Crepidula convexa*
				Crepidula sp.
			Vanikoridae	*Macromphalina pierrot*
			Naticidae	*Nevertia duplicata*
				Polinices lacteus
				Tectonatica pusilla
		Caenogastropoda	Eulimidae	*Umbilibalcis lata*
				Umbilibalcis sp.
				Hemiliostraca auricincta
		Littorinimorpha	Ficidae	*Ficus communis*
		Neogastropoda	Muricidae	*Urosalpinx* sp.
			Buccinidae	*Busycotypus spiratus*
				Gemophos tinctus
				Solenosteira cancellaria
		Heterobranchia	Rissoellidae	*Rissoella caribaea*
			Pyramidellidae	*Careliopsis styliformis*
				Eulimastoma canaliculatum
				Evalea emeryi
				Fargoa gibbosa
				Fargoa sp.
				Houbricka incisa
				Odostomia cf. *hendersoni*
				Odostomia laevigata
				Petitilla crosseana
				Turbonilla heilprini

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Turbonilla levis
		Cephalaspidea	Acteonidae	*Acteon candens*
			Cylichnidae	*Acteocina recta*
			Haminoeidae	*Haminoea* cf. *elegans*
				Haminoea succinea
			Retusidae	*Volvulella minuta*
				Volvulella texasiana
	Bivalvia	Nuculida	Nuculidae	*Nucula calcicola*
				Nucula crenulata
				Nucula proxima
				Ennucula aegeensis
		Nuculanoida	Nuculanidae	*Nuculana acuta*
				Nuculana concentrica
				Nuculana unca
		Mytiloida	Mytilidae	*Musculus lateralis*
		Arcoida	Glycymerididae	*Glycymeris decussata*
		Pectinoida	Dimyidae	*Dimya tigrina*
		Lucinoida	Lucinidae	*Divaricella quadrisulcata*
				Radiolucina amianta
		Veneroida	Ungulinidae	*Diplodonta punctata*
				Diplodonta soror
				Phlyctiderma semiaspera
				Sphaerella verrilli
		Carditoida	Astartidae	*Astarte nana*
			Crassatellidae	*Crassinella martinicensis*
		Veneroida	Cardiidae	*Laevicardium mortoni*

Table A1 (continued).

Phylum	Class	Order	Family	Species
			Tellinidae	*Angulus versicolor*
				Eurytellina lineata
				Macoma constricta
				Macoma pseudomera
				Macoma pulleyi
				Phyllodina squamifera
				Scissula iris
				Tellidora cristata
			Semelidae	*Abra aequalis*
			Corbiculidae	*Polymesoda caroliniana*
			Veneridae	*Chioneryx grus*
				Gemma gemma
				Gouldia cerina
				Pitar fulminatus
				Puberella intapurpurea
		Myoida	Corbulidae	*Caryocorbula contracta*
			Pholadidae	*Martesia striata*
		Anomalodesmata	Pandoridae	*Pandora arenosa*
				Pandora bushiana
				Pandora sp.
				Pandora trilineata
			Periplomatidae	*Periploma* cf. *margaritaceum*
				Periploma margaritaceum
			Verticordiidae	*Trigonulina ornata*
			Cuspidariidae	*Cardiomya costellata*
	Scaphopoda	Dentaliida	Dentaliidae	*Paradentalium americanum*
		Gadilida	Gadilidae	*Episiphon sowerbyi*

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Gadila mayori
Annelida	Polychaeta	Capitellida	Capitellidae	*Barantolla* sp. A
				Capitella capitata
				Decamastus gracilis
				Decamastus sp. A
				Heteromastus filiformis
				Mediomastus californiensis
				Notomastus americanus
				Notomastus daueri
				Notomastus hemipodus
				Notomastus latericeus
				Notomastus lineatus
				Notomastus lobatus
				Notomastus sp. A
				Notomastus tenuis
				Paraheteromastus sp.
				Peresiella sp. A
				Scyphoproctus platyproctus
				Scyphoproctus sp.
		Scolecida	Cossuridae	*Cossura soyeri*
				Cossura sp. A
			Maldanidae	*Asychis elongatus*
				Axiothella sp. A
				Boguea enigmatica
				Boguea sp. A
				Boguella sp. A
				Clymenella torquata

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Euclymene sp. A
				Euclymene sp. B
				Macroclymene sp. A
				Maldane sp. A
				Petaloproctus sp.
			Opheliidae	*Armandia agilis*
				Armandia maculata
				Ophelina cf. *acuminata*
				Ophelina cylindricaudata
				Travisia hobsonae
			Orbiniidae	*Phylo felix*
				Scoloplos sp. A
			Paraonidae	*Acmira catherinae*
				Acmira cerrutii
				Acmira cf. *finitima*
				Acmira lopezi
				Acmira philbinae
				Acmira simplex
				Acmira taylori
				Allia cf. *alisdairi*
				Allia cf. *trilobata*
				Allia suecia
				Aricidea (*Aedicira*) sp. A
				Aricidea (*Allia*) sp. A
				Aricidea cf. *pseudoarticulata*
				Aricidea fragilis

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Aricidea quadrilobata
				Aricidea wassi
				Cirrophorus americanus
				Cirrophorus branchiatus
				Cirrophorus cf. *forticirratus*
				Levinsenia gracilis
				Levinsenia reducta
				Paraonis fulgens
				Paraonis pygoenigmatica
		Phyllodocida	Nephtyidae	*Aglaophamus verrilli*
				Inermonephtys inermis
				Nephtys cf. *hombergii*
				Nephtys incisa
				Nephtys simoni
				Nephtys squamosa
			Phyllodocidae	*Eulalia bilineata*
				Hypereteone heteropoda
				Paranaitis polynoides
				Phyllodoce longipes
				Pterocirrus macroceros
				Mystides borealis
			Sphaerodoridae	*Clavodorum* sp. A
				Sphaerephesia sp. A
			Aphroditidae	*Aphrogenia* sp. A
			Eulepethidae	*Grubeulepis augeneri*
			Sigalionidae	*Fimbriosthenelais hobbsi*

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Fimbriosthenelais minor
				Pholoe sp. C
				Sigalion sp. A
				Sthenelais limicola
				Sthenelanella sp. A
				Sthenolepis cf. *grubei*
				Sthenolepis sp. A
			Hesionidae	*Gyptis brevipalpa*
				Gyptis vittata
			Nereidae	*Neanthes micromma*
				Neanthes succinea
			Pilargidae	*Ancistrosyllis hartmanae*
				Ancistrosyllis papillosa
				Ancistrosyllis sp. A
				Ancistrosyllis sp. B
				Ancistrosyllis sp. C
				Ancistrosyllis jonesi
				Glyphohesione klatti
				Sigambra tentaculata
			Syllidae	*Exogone dispar*
				Exogone lourei
				Exogone sp. B
				Syllis (*Ehlersia*) sp. A
			Glyceridae	*Glycera americana*
				Glycera dibranchiata
				Glycera sp. A

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Glycera sp. D
				Glycera sp. E
			Goniadidae	*Glycinde solitaria*
				Goniada littorea
		Amphinomida	Amphinomidae	*Eurythoe* sp. A
				Paramphinome sp. B
		Eunicida	Dorvilleidae	*Dorvillea* sp. A
				Dorvillidae genus B
				Meiodorvillea sp. B
				Pettiboneia sp. A
				Schistomeringos pectinata
				Schistomeringos sp. A
			Eunicidae	*Eunice vittata*
				Marphysa sanguinea
			Lumbrineridae	*Lumbrineris* sp. A
				Lumbrineris sp. C
				Lumbrineris sp. D
				Lumbrineris sp. E
				Lumbrineris tenuis
				Ninoe sp. A
				Ninoe sp. B
			Onuphidae	*Kinbergonuphis* sp. A
				Kinbergonuphis sp. B
				Mooreonuphis pallidula
				Nothria sp. A
				Onuphis sp. A

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Sarsonuphis hartmanae
				Diopatra cf. *papillata*
				Diopatra cuprea
				Diopatra neotridens
		Sabellida	Oweniidae	*Myriochele oculata*
				Myriochele sp. A
				Owenia sp. A
			Sabellidae	*Chone americana*
				Chone cf. *americana*
				Euchone cf. incolor
				Euchone cf. southerni
				Euchone sp. A
				Fabricia sp. A
				Jasmineira cf. *pacifica*
				Megalomma bioculatum
				Megalomma sp. A
				Sabella microphthalma
				Sabella sp. A
				Parasabella microphthalma
				Sabella melanochlora
		Terebellida	Cirratulidae	*Caulleriella* cf. *zetlandica*
				Caulleriella sp. B
				Chaetozone sp. A
				Chaetozone sp. B
				Chaetozone sp. C
				Chaetozone sp. D

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Cirriformia sp. B
				Cirriformia sp. C
				Tharyx cf. *annulosus*
				Tharyx sp.
			Flabelligeridae	*Brada villosa*
				Diplocirrus capensis
				Diplocirrus sp. A
				Pherusa inflata
				Pherusa sp.
				Piromis roberti
			Sternaspidae	*Sternaspis scutata*
			Ampharetidae	*Amphicteis gunneri*
				Ampharete sp. A
				Ampharete sp. B
				Isolda pulchella
				Melinna cristata
				Sabellides sp. A
			Pectinariidae	*Amphictene* sp. A
				Pectinaria gouldii
			Terebellidae	*Amaeana trilobata*
				Eupolymnia nebulosa
				Loimia viridis
				Pista sp.
				Pista sp. B
				Polycirrus plumosus
			Trichobranchidae	*Terebellides stroemii*
		Spionida	Chaetopteridae	*Spiochaetopterus costarum*

Table A1 (continued).

Phylum	Class	Order	Family	Species
			Magelonidae	*Magelona* sp. G
				Magelona sp. H
				Magelona sp. I
				Magelona sp. J
				Magelona sp. L
			Heterospionidae	*Heterospio longissima*
			Poecilochaetidae	*Poecilochaetus johnsoni*
			Spionidae	*Aonidella dayi*
				Aonides mayaguezensis
				Apoprionospio pygmaea
				Boccardiella sp. A
				Laonice cirrata
				Minuspio cirrifera
				Paraprionospio pinnata
				Prionospio cristata
				Prionospio fallax
				Prionospio sp. A
				Prionospio steenstrupi
				Scolelepis texana
				Spiophanes missionensis
			Trochochaetidae	*Trochochaeta* sp.
	Clitellata	Haplotaxida	Tubificidae	*Tubificoides amplivasatus*
			unidentified	unidentified Oligochaeta
	unidentified	unidentified	unidentified	unidentified Pogonophora
Arthropoda	Malacostraca	Mysida	Mysidae	*Americamysis stucki*
				Promysis atlantica

Table A1 (continued).

Phylum	Class	Order	Family	Species
				Taphromysis bowmani
		Amphipoda	Ampeliscidae	*Ampelisca agassizi*
				Ampelisca sp. A
				Ampelisca sp. C
			Argissidae	*Argissa hamatipes*
			Iphimedidae	Iphimedidae sp. 1
			Liljeborgiidae	*Listriella barnardi*
				Listriella carinata
				Listriella sp. A
			Oedicerotidae	*Americhelidium* sp.
				Hartmanodes sp.
				Oedocerotidae sp. 1
				Oedocerotidae sp. 2
				Oedocerotidae sp. 3
			Sebidae	Sebidae sp. 1
			Caprellidae	*Caprella* sp.
			Ischyroceridae	*Cerapus* sp.
				Cerapus sp. C
			Photidae	*Photis melanica*
				Photis sp.
		Isopoda	Anthuridae	*Amakusanthura magnifica*
				Cyathura sp.
			Hyssuridae	*Xenanthura brevitelson*
				Hyssura sp.
			Munnidae	*Uromunna* cf. *hayesi*

Table A1 (continued).

Phylum	Class	Order	Family	Species
			Serolidae	*Serolis mgrayi*
			Gnathiidae	*Gnathia* sp.
			Holognathidae	*Cleantioides planicauda*
			Idoteidae	*Edotea montosa*
		Tanaidacea	Apseudidae	*Apseudes* sp. A
			Kalliapseudidae	*Alokalliapseudes macsweenyi*
			Pseudotanaidae	*Pseudotanais* sp. A
				Pseudotanais sp. B
		Cumacea	Bodotriidae	*Cyclaspis platymerus*
				Cyclaspis pustulata
			Diastylidae	*Diastylis* sp.
				Oxyurostylis smithi
				Oxyurostylis sp.
			Leuconidae	*Eudorella* sp.
				Leucon sp. A
		Decapoda	Luciferidae	*Lucifer faxoni*
			Palaemonidae	Pontoninae sp.
			Alpheidae	*Alpheus* cf. *macrocheles*
				Alpheus nov. sp.
				Automate sp.
			Processidae	*Processa* sp.
			Porcellanidae	*Pachycheles* sp.
			Paguridae	*Pagurus longicarpus*
				Pagurus maclaughlinae
				Pagurus sp.
			Menippidae	*Pseudocarcinus* sp.

Table A1 (continued).

Phylum	Class	Order	Family	Species
			Xanthidae	Xanthidae sp.
				Speocarcinus sp.
			Pinnotheridae	*Pinnixa retinens*
				Pinnixa sp.
	Pycnogonida	Pantopoda	Phoxichilidiidae	*Anoplodactylus petiolatus*
Echiura	Echiuroidea	Echiurida	Echiuroidae	Echiura sp. 1
Sipuncula	Sipunculidea	Golfingiida	Sipunculidae	Sipuncula sp. 1
				Sipunculus nudus
			Golfingiidae	*Golfingia* sp. 1
				Golfingia sp. 2
				Golfingia sp. 3
				Thysanocardia sp.
			Phascolionidae	*Phascolion* sp.
	Phascolosomatidea	Phascolosomatida	Phascolosomatidae	*Apianosoma trichocephalus*
		Aspidosiphonida	Aspidosiphonidae	*Aspidosiphon sp.*
Bryozoa	Gymnolaemata	Cheilostomatida	Cupuladriidae	*Cupuladria* sp.
			Microporellidae	*Microporella* sp.
			Smittinidae	*Parasmittina* sp.
		Ctenostomatida	Vesiculariidae	*Vesicularia* sp.
Brachiopoda	Lingulata	Lingulida	Lingulidae	*Glottidia pyramidata*
Echinodermata	Ophiuroidea	Ophiurida	Amphiuridae	Amphiuridae sp. 1
				Amphiuridae sp. 2
				Amphiuridae sp. 3
				Amphiuridae sp. 4

Table A1 (continued).

Phylum	Class	Order	Family	Species
			Ophiactidae	*Ophiactis* sp. 1
			Ophiolepididae	Ophiolepididae sp.
	Echinoidea	Spatangoida	Brissidae	*Brisaster* sp.
				Brissopsis alta
	Echinoidea	Holasteroida	Pourtalesiidae	Pourtalesiidae sp. A
	Holothuroidea	Dendrochirotida	Phyllophoridae	*Thyone deichmannae*
Hemichordata	Enteropneusta		Ptychoderidae	*Balanoglossus* sp. 1
				Balanoglossus sp. 2

APPENDIX B

SPECIES ABUNDANCE

Table B1

Abundance (no. /100 cm^2) of different macrobenthos species at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Abra aequalis	37.4	28.1	13.1	29.9	18.7	26.2	7.5	5.6	1.9	11.2	35.5	5.6
Acmira catherinae	7.5	24.3	29.9	11.2	1.9	1.9	5.6	7.5	15.0	16.8	20.6	43.0
Acmira cerrutii	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Acmira cf. *finitima*	0.0	0.0	1.9	0.0	1.9	0.0	0.0	5.6	0.0	9.4	0.0	78.5
Acmira lopezi	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Acmira philbinae	0.0	0.0	0.0	0.0	1.9	3.7	0.0	3.7	0.0	0.0	0.0	0.0
Acmira simplex	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0
Acmira taylori	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Acteocina recta	1.9	0.0	0.0	0.0	0.0	0.0	1.9	0.0	3.7	0.0	0.0	0.0
Acteon candens	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Aglaophamus verrilli	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Allia cf. *alisdairi*	24.3	3.7	16.8	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9	1.9
Allia cf. *trilobata*	0.0	0.0	1.9	0.0	3.7	1.9	1.9	0.0	0.0	1.9	3.7	0.0
Allia suecia	1.9	0.0	1.9	0.0	31.8	3.7	0.0	0.0	3.7	1.9	3.7	0.0
Alokalliapseudes macsweenyi	9.4	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alpheus cf. *macrocheles*	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alpheus nov. sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amaeana trilobata	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.1	0.0
Amakusanthura magnifica	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Americamysis stucki	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Americhelidium sp.	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Ampelisca agassizi	1.9	0.0	0.0	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0
Ampelisca sp. A	1.9	0.0	1.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Ampelisca sp. C	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Ampharete sp. A	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ampharete sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Amphicteis gunneri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Amphictene sp. A	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphiporus bioculatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Amphiporus sp.	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Amphithalamus vallei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Amphiuridae sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	7.5	0.0	0.0
Amphiuridae sp. 2	15.0	22.4	20.6	0.0	0.0	20.6	26.2	3.7	9.4	24.3	24.3	0.0
Amphiuridae sp. 3	0.0	0.0	0.0	0.0	0.0	13.1	1.9	0.0	0.0	1.9	0.0	0.0
Amphiuridae sp. 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Ancistrosyllis hartmanae	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Ancistrosyllis jonesi	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ancistrosyllis papillosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Ancistrosyllis sp. A	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Ancistrosyllis sp. B	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	1.9	0.0	0.0
Ancistrosyllis sp. C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0
Angulus versicolor	18.7	0.0	5.6	0.0	18.7	0.0	1.9	0.0	65.5	13.1	13.1	7.5
Anoplodactylus petiolatus	5.6	0.0	11.2	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0
Aonidella dayi	0.0	0.0	0.0	0.0	3.7	0.0	3.7	0.0	0.0	0.0	0.0	0.0
Aonides mayaguezensis	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aphrogenia sp. A	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Apianosoma trichocephalus	0.0	0.0	0.0	0.0	1.9	0.0	3.7	0.0	5.6	0.0	0.0	0.0
Apoprionospio pygmaea	0.0	0.0	0.0	0.0	15.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0
Apseudes sp. A	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argissa hamatipes	0.0	3.7	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aricidea (*Aedicira*) sp. A	0.0	0.0	0.0	0.0	1.9	0.0	3.7	0.0	0.0	0.0	0.0	0.0
Aricidea (*Allia*) sp. A	0.0	1.9	1.9	0.0	5.6	0.0	5.6	0.0	0.0	0.0	0.0	0.0
Aricidea cf. *pseudoarticulata*	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Aricidea fragilis	0.0	0.0	0.0	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Aricidea quadrilobata	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aricidea wassi	11.2	22.4	18.7	1.9	46.8	56.1	15.0	0.0	28.1	102.9	13.1	56.1

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Armandia agilis	11.2	0.0	13.1	0.0	22.4	28.1	0.0	41.1	7.5	112.2	16.8	11.2
Armandia maculata	0.0	3.7	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0
Aspidosiphon sp.	1.9	0.0	9.4	0.0	0.0	0.0	0.0	0.0	7.5	0.0	5.6	0.0
Astarte nana	0.0	0.0	0.0	0.0	7.5	0.0	0.0	0.0	3.7	0.0	0.0	0.0
Asychis elongatus	5.6	11.2	7.5	0.0	0.0	0.0	0.0	0.0	1.9	0.0	3.7	0.0
Automate sp.	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Axiothella sp. A	15.0	7.5	78.5	0.0	3.7	1.9	0.0	1.9	7.5	1.9	0.0	0.0
Balanoglossus sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0
Balanoglossus sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0
Barantolla sp. A	0.0	5.6	0.0	1.9	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Boccardiella sp. A	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Boguea enigmatica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Boguea sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Boguella sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Brada villosa	0.0	0.0	1.9	0.0	0.0	1.9	0.0	0.0	1.9	0.0	7.5	3.7
Brisaster sp.	0.0	7.5	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brissopsis alta	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Busycotypus spiratus	0.0	0.0	0.0	0.0	16.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caecum floridanum	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Capitella capitata	7.5	9.4	16.8	3.7	50.5	18.7	1.9	24.3	1.9	1.9	3.7	1.9
Caprella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Cardiomya costellata	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Careliopsis styliformis	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Carinomidae sp. 1	15.0	5.6	5.6	0.0	1.9	3.7	1.9	1.9	0.0	11.2	3.7	3.7
Carinomidae sp. 2	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	3.7	0.0	0.0
Caryocorbula contracta	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	59.8	0.0
Caulleriella cf. *zetlandica*	0.0	0.0	0.0	0.0	1.9	0.0	1.9	0.0	1.9	0.0	0.0	0.0
Caulleriella sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Cerapus sp.	5.6	0.0	1.9	0.0	11.2	0.0	0.0	0.0	22.4	1.9	0.0	0.0
Cerapus sp. C	1.9	0.0	0.0	0.0	1.9	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Chaetozone sp. A	0.0	1.9	5.6	0.0	3.7	1.9	1.9	0.0	5.6	0.0	1.9	0.0
Chaetozone sp. B	1.9	0.0	1.9	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Chaetozone sp. C	0.0	0.0	1.9	0.0	3.7	0.0	0.0	0.0	3.7	0.0	1.9	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Chaetozone sp. D	0.0	5.6	13.1	3.7	0.0	3.7	1.9	0.0	5.6	1.9	9.4	0.0
Chioneryx grus	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chone americana	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9	0.0
Chone cf. *americana*	3.7	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cirriformia sp. B	0.0	0.0	1.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Cirriformia sp. C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Cirrophorus americanus	29.9	3.7	13.1	0.0	5.6	9.4	18.7	0.0	1.9	3.7	15.0	0.0
Cirrophorus branchiatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	1.9	0.0
Cirrophorus cf. *forticirratus*	5.6	0.0	0.0	0.0	1.9	9.4	3.7	0.0	0.0	1.9	16.8	0.0
Clavodorum sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cleantioides planicauda	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clymenella torquata	9.4	7.5	5.6	0.0	0.0	1.9	0.0	0.0	11.2	1.9	16.8	0.0
Cossura soyeri	5.6	76.7	31.8	256.2	1.9	56.1	3.7	398.3	24.3	9.4	5.6	826.5
Cossura sp. A	1.9	1.9	1.9	3.7	7.5	7.5	9.4	61.7	1.9	0.0	1.9	0.0
Crassinella martinicensis	5.6	0.0	0.0	0.0	9.4	0.0	0.0	0.0	16.8	0.0	0.0	0.0
Crepidula convexa	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crepidula sp.	0.0	0.0	0.0	0.0	16.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cupuladria sp.	1.9	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyathura sp.	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclaspis platymerus	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclaspis pustulata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Cyclostremiscus jeannae	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Decamastus gracilis	0.0	5.6	5.6	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Decamastus sp. A	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9	0.0
Diastylis sp.	0.0	3.7	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dimya tigrina	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diopatra cf. *papillata*	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diopatra cuprea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0
Diopatra neotridens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0
Diplocirrus capensis	1.9	20.6	0.0	1.9	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0
Diplocirrus sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Diplodonta punctata	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplodonta soror	0.0	0.0	0.0	0.0	39.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Divaricella quadrisulcata	0.0	0.0	0.0	35.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorvillea sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Dorvillidae genus B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0
Echiura sp. 1	15.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Edotea montosa	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Edwardsia sp.	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	5.6	0.0	0.0
Ennucula aegeensis	0.0	0.0	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Episiphon sowerbyi	7.5	0.0	28.1	0.0	13.1	3.7	0.0	5.6	7.5	0.0	0.0	0.0
Euchone cf. *incolor*	0.0	0.0	11.2	0.0	0.0	1.9	0.0	0.0	1.9	0.0	0.0	0.0
Euchone cf. *southerni*	1.9	1.9	50.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euchone sp. A	0.0	3.7	132.8	0.0	7.5	1.9	0.0	0.0	3.7	0.0	7.5	0.0
Euclymene sp. A	13.1	1.9	0.0	0.0	1.9	3.7	0.0	0.0	1.9	3.7	5.6	0.0
Euclymene sp. B	7.5	9.4	13.1	0.0	3.7	1.9	0.0	0.0	9.4	3.7	0.0	0.0
Eudorella sp.	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eulalia bilineata	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eulimastoma canaliculatum	1.9	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eunice vittata	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eupolymnia nebulosa	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurytellina lineata	0.0	0.0	1.9	1.9	1.9	0.0	0.0	0.0	5.6	0.0	0.0	0.0
Eurythoe sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Evalea emeryi	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Exogone dispar	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	80.4	0.0	0.0	0.0
Exogone lourei	69.2	0.0	0.0	0.0	31.8	0.0	0.0	0.0	5.6	0.0	0.0	0.0
Exogone sp. B	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fabricia sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fargoa gibbosa	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fargoa sp.	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Ficus communis	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fimbriosthenelais hobbsi	1.9	0.0	0.0	0.0	3.7	5.6	0.0	0.0	0.0	0.0	0.0	0.0
Fimbriosthenelais minor	0.0	0.0	0.0	0.0	3.7	1.9	5.6	0.0	0.0	0.0	0.0	0.0
Finella dubia	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gadila mayori	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Gemma gemma	0.0	1.9	0.0	3.7	3.7	0.0	5.6	1.9	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Gemophos tinctus	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	22.4	1.9	1.9	0.0
Glottidia pyramidata	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycera americana	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Glycera dibranchiata	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Glycera sp. A	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycera sp. D	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0
Glycera sp. E	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycinde solitaria	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Glycymeris decussata	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glyphohesione klatti	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Gnathia sp.	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Golfingia sp. 1	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	1.9	0.0
Golfingia sp. 2	11.2	3.7	7.5	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Golfingia sp. 3	20.6	0.0	18.7	0.0	7.5	0.0	5.6	0.0	7.5	0.0	16.8	0.0
Goniada littorea	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Gouldia cerina	11.2	0.0	0.0	1.9	5.6	0.0	0.0	0.0	0.0	5.6	0.0	0.0
Grubeulepis augeneri	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gyptis brevipalpa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Gyptis vittata	1.9	1.9	7.5	3.7	0.0	15.0	52.4	1.9	0.0	24.3	16.8	29.9
Haloclava sp.	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	1.9	0.0	0.0	0.0
Haminoea cf. *elegans*	15.0	5.6	13.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Haminoea succinea	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Harmathoe sp.	0.0	1.9	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	1.9	0.0
Hemiliostraca auricincta	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteromastus filiformis	0.0	5.6	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heterospio longissima	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Houbricka incisa	0.0	0.0	0.0	0.0	1.9	11.2	0.0	0.0	1.9	5.6	1.9	0.0
Hypereteone heteropoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	1.9	0.0
Hyssura sp.	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inermonephtys inermis	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Iphimedidae sp. 1	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isolda pulchella	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jasmineira cf. *pacifica*	1.9	1.9	1.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Kinbergonuphis sp. A	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0
Kinbergonuphis sp. B	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laevicardium mortoni	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laonice cirrata	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Leucon sp. A	3.7	0.0	3.7	0.0	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0
Levinsenia gracilis	1.9	5.6	9.4	0.0	11.2	11.2	13.1	1.9	11.2	11.2	29.9	3.7
Levinsenia reducta	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Lineidae sp. 1	1.9	5.6	5.6	1.9	0.0	0.0	0.0	0.0	3.7	0.0	0.0	3.7
Lineidae sp. 2	22.4	15.0	9.4	5.6	13.1	3.7	3.7	0.0	5.6	9.4	20.6	1.9
Lineidae sp. 3	15.0	15.0	15.0	3.7	16.8	7.5	1.9	1.9	11.2	11.2	9.4	13.1
Listriella barnardi	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Listriella carinata	0.0	0.0	0.0	11.2	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0
Listriella sp. A	0.0	1.9	1.9	3.7	0.0	0.0	0.0	7.5	1.9	1.9	11.2	0.0
Loimia viridis	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Lucifer faxoni	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris sp. A	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris sp. C	3.7	0.0	13.1	0.0	0.0	0.0	0.0	0.0	22.4	3.7	1.9	0.0
Lumbrineris sp. D	1.9	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0
Lumbrineris sp. E	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Lumbrineris tenuis	0.0	0.0	1.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Macoma constricta	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macoma pseudomera	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macoma pulleyi	0.0	0.0	1.9	5.6	1.9	5.6	0.0	0.0	0.0	0.0	1.9	0.0
Macroclymene sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macromphalina pierrot	7.5	0.0	5.6	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona sp. G	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona sp. H	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9	0.0
Magelona sp. I	0.0	1.9	1.9	0.0	0.0	1.9	0.0	0.0	3.7	1.9	0.0	0.0
Magelona sp. J	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona sp. L	1.9	0.0	0.0	0.0	1.9	0.0	0.0	0.0	3.7	0.0	0.0	0.0
Maldane sp. A	3.7	7.5	3.7	0.0	9.4	1.9	0.0	0.0	0.0	1.9	0.0	0.0
Marphysa sanguinea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Martesia striata	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Mediomastus californiensis	44.9	288.0	243.1	44.9	72.9	175.8	1.9	114.1	308.6	74.8	39.3	87.9
Megalomma bioculatum	0.0	1.9	1.9	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Megalomma sp. A	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meiodorvillea sp. B	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melinna cristata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Microporella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0
Micrura sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Minuspio cirrifera	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mooreonuphis pallidula	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Musculus lateralis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Myriochele oculata	0.0	0.0	0.0	0.0	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0
Myriochele sp. A	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	3.7	0.0	1.9	0.0
Mystides borealis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Neanthes micromma	11.2	0.0	1.9	0.0	16.8	0.0	0.0	0.0	9.4	5.6	7.5	0.0
Neanthes succinea	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	1.9	0.0	3.7	0.0
Nephtys cf. *hombergii*	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Nephtys incisa	0.0	0.0	0.0	1.9	0.0	3.7	0.0	3.7	0.0	5.6	0.0	0.0
Nephtys squamosa	7.5	13.1	3.7	24.3	0.0	11.2	5.6	1.9	0.0	5.6	0.0	5.6
Nephtys simoni	0.0	0.0	0.0	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0
Nevertia duplicata	1.9	0.0	0.0	0.0	3.7	20.6	0.0	0.0	0.0	0.0	0.0	0.0
Ninoe sp. A	0.0	1.9	1.9	0.0	0.0	0.0	0.0	1.9	0.0	0.0	1.9	1.9
Ninoe sp. B	0.0	1.9	0.0	0.0	0.0	3.7	0.0	0.0	0.0	3.7	1.9	1.9
Nothria sp. A	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Notomastus americanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Notomastus daueri	0.0	5.6	1.9	0.0	1.9	3.7	0.0	1.9	1.9	0.0	1.9	0.0
Notomastus hemipodus	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomastus latericeus	1.9	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomastus lineatus	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Notomastus lobatus	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Notomastus sp. A	5.6	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Notomastus tenuis	0.0	0.0	0.0	0.0	3.7	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Nucula calcicola	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Nucula crenulata	0.0	1.9	0.0	0.0	0.0	0.0	3.7	0.0	9.4	1.9	1.9	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Nucula proxima	9.4	1.9	13.1	22.4	28.1	16.8	56.1	1.9	1.9	0.0	1.9	0.0
Nuculana acuta	52.4	15.0	20.6	43.0	31.8	37.4	9.4	31.8	95.4	43.0	5.6	192.6
Nuculana concentrica	0.0	1.9	0.0	1.9	1.9	0.0	0.0	0.0	7.5	0.0	3.7	1.9
Nuculana unca	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odostomia cf. *hendersoni*	0.0	0.0	1.9	0.0	3.7	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Odostomia laevigata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Oedocerotidae sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Oedocerotidae sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Oedocerotidae sp. 3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Onuphis sp. A	0.0	0.0	1.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	3.7
Ophelina cf. *acuminata*	0.0	1.9	0.0	0.0	3.7	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Ophelina cylindricaudata	0.0	0.0	5.6	3.7	0.0	1.9	1.9	56.1	0.0	20.6	0.0	0.0
Ophiactis sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9	0.0
Ophiolepididae sp.	1.9	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Owenia sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0
Oxyurostylis smithi	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxyurostylis sp.	0.0	9.4	5.6	0.0	0.0	0.0	3.7	0.0	1.9	0.0	0.0	0.0
Pachycheles sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Pagurus longicarpus	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagurus maclaughlinae	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Pandora arenosa	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pandora bushiana	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pandora sp.	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pandora trilineata	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paradentalium americanum	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Paraheteromastus sp.	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramphinome sp. B	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	3.7	1.9	0.0
Paranaitis polynoides	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraonis fulgens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Paraonis pygoenigmatica	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraprionospio pinnata	24.3	5.6	7.5	13.1	20.6	28.1	31.8	15.0	41.1	59.8	46.8	43.0
Parasabella microphthalma	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Parasmittina sp.	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parviturbo rehderi	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Pectinaria gouldii	1.9	0.0	5.6	0.0	20.6	7.5	1.9	0.0	22.4	0.0	0.0	0.0
Peresiella sp. A	0.0	0.0	0.0	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Periploma cf. *margaritaceum*	3.7	0.0	5.6	1.9	9.4	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Periploma margaritaceum	1.9	0.0	26.2	0.0	0.0	0.0	0.0	0.0	9.4	0.0	0.0	0.0
Petaloproctus sp.	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Petitilla crosseana	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Pettiboneia sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	1.9
Phascolion sp.	20.6	0.0	3.7	0.0	16.8	1.9	11.2	0.0	11.2	0.0	1.9	0.0
Pherusa sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Pherusa inflata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Phlyctiderma semiaspera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Pholoe sp. C	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Phoronida sp. 1	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Photis melanica	3.7	0.0	1.9	0.0	24.3	0.0	0.0	0.0	33.7	0.0	0.0	0.0
Photis sp.	3.7	3.7	5.6	0.0	0.0	0.0	0.0	0.0	69.2	0.0	1.9	0.0
Phyllodina squamifera	28.1	1.9	0.0	7.5	48.6	56.1	46.8	0.0	69.2	28.1	84.2	0.0
Phyllodoce longipes	3.7	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Phylo felix	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pinnixa retinens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Pinnixa sp.	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Piromis roberti	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pista sp.	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pista sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Pitar fulminatus	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poecilochaetus johnsoni	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Polinices lacteus	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Polycirrus plumosus	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polycladida sp. 1	1.9	1.9	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polycladida sp. 2	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polymesoda caroliniana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Pontonidae sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Pourtalesidae sp. A	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prionospio cristata	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	1.9	0.0
Prionospio fallax	0.0	0.0	3.7	0.0	50.5	18.7	11.2	0.0	5.6	1.9	0.0	0.0
Prionospio sp. A	87.9	22.4	44.9	3.7	76.7	29.9	9.4	9.4	71.1	24.3	52.4	22.4
Prionospio steenstrupi	1.9	3.7	0.0	9.4	11.2	16.8	1.9	0.0	3.7	1.9	11.2	0.0
Processa sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Promysis atlantica	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudocarcinus sp.	0.0	0.0	0.0	1.9	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotanais sp. A	28.1	1.9	0.0	0.0	18.7	0.0	0.0	0.0	5.6	0.0	0.0	0.0
Pseudotanais sp. B	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	7.5	0.0	0.0	0.0
Pterocirrus macroceros	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Puberella intapurpurea	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Radiolucina amianta	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rissoella caribaea	5.6	0.0	5.6	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0
Sabella melanochlora	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sabella microphthalma	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sabella sp. A	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sabellides sp. A	0.0	9.4	9.4	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sarsonuphis hartmanae	0.0	11.2	24.3	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Schistomeringos pectinata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9	0.0
Schistomeringos sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Scissula iris	3.7	41.1	20.6	1.9	1.9	44.9	48.6	0.0	0.0	9.4	18.7	3.7
Scolelepis texana	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scoloplos sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Scyphoproctus platyproctus	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Scyphoproctus sp.	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Sebidae sp. 1	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Serolis mgrayi	0.0	1.9	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sigalion sp. A	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Sigambra tentaculata	1.9	20.6	26.2	3.7	0.0	28.1	35.5	61.7	13.1	102.9	24.3	54.2
Sipuncula sp. 1	5.6	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Sipunculus nudus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Solariorbis infracarinatus	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Solenosteira cancellaria	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	5.6	0.0	0.0	1.9
Speocarcinus sp.	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Sphaerella verrilli	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphaerephesia sp. A	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spiochaetopterus costarum	1.9	9.4	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spiophanes missionensis	9.4	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Sternaspis scutata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Sthenelais limicola	3.7	1.9	5.6	0.0	7.5	0.0	16.8	0.0	9.4	1.9	3.7	1.9
Sthenelanella sp. A	0.0	0.0	0.0	1.9	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0
Sthenolepis cf. *grubei*	0.0	0.0	1.9	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sthenolepis sp. A	0.0	0.0	0.0	0.0	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Syllis (*Ehlersia*) sp. A	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Taphromysis bowmani	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Tectonatica pusilla	0.0	9.4	7.5	0.0	0.0	1.9	1.9	24.3	5.6	0.0	3.7	3.7
Teinostoma parvicallum	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0
Tellidora cristata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Terebellides stroemii	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tharyx cf. *annulosus*	11.2	15.0	20.6	3.7	26.2	11.2	1.9	9.4	20.6	13.1	11.2	5.6
Tharyx sp.	0.0	0.0	0.0	1.9	3.7	0.0	0.0	0.0	3.7	0.0	16.8	1.9
Thyone deichmannae	0.0	18.7	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanocardia sp.	5.6	0.0	26.2	0.0	7.5	1.9	44.9	0.0	0.0	5.6	39.3	0.0
Travisia hobsonae	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trigonulina ornata	9.4	0.0	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trochochaeta sp.	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tubificoides amplivasatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Tubiluchus corallicola	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Turbonilla heilprini	0.0	0.0	3.7	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Turbonilla levis	0.0	0.0	0.0	0.0	0.0	3.7	1.9	0.0	1.9	0.0	0.0	0.0
Umbilibalcis lata	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Umbilibalcis sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0
unidentified	5.6	24.3	3.7	0.0	3.7	0.0	0.0	0.0	1.9	0.0	0.0	0.0
unidentified Entoprocta	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
unidentified Oligochaeta	0.0	0.0	0.0	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0

Table B1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
unidentified Pogonophora	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Uromunna cf. *hayesi*	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Urosalpinx sp.	0.0	0.0	0.0	0.0	5.6	5.6	0.0	0.0	0.0	0.0	0.0	0.0
Vesicularia sp.	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vitrinella floridana	1.9	24.3	3.7	5.6	0.0	0.0	0.0	0.0	0.0	31.8	0.0	0.0
Volvulella minuta	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	7.5	0.0	5.6	0.0
Volvulella texasiana	3.7	1.9	0.0	0.0	0.0	7.5	1.9	0.0	1.9	3.7	5.6	0.0
Xanthidae sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
Xenanthura brevitelson	7.5	0.0	0.0	0.0	9.4	0.0	0.0	0.0	1.9	0.0	0.0	0.0

APPENDIX C

SPECIES BIOMASS

Table C1

Biomass (µg AFDW/100 cm^2) of different macrobenthos species at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Abra aequalis	10.1	13.0	5.1	6.0	10.6	21.6	7.9	1.1	1.4	33.4	114.9	2.1
Acmira catherinae	25.4	353.4	47.0	28.4	1.5	4.3	8.0	17.0	54.8	43.7	61.5	102.6
Acmira cerrutii	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Acmira cf. *finitima*	0.0	0.0	0.9	0.0	64.5	0.0	0.0	17.7	8.8	85.5	0.0	195.0
Acmira lopezi	0.0	0.0	0.0	0.0	0.0	20.7	0.0	0.0	0.0	0.0	0.0	0.0
Acmira philbinae	0.0	0.0	0.0	0.0	1.8	3.2	0.0	7.5	0.0	0.0	0.0	0.0
Acmira simplex	0.0	0.0	0.0	0.0	0.0	0.0	10.5	0.0	0.0	0.0	0.0	0.0
Acmira taylori	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0
Acteocina recta	11.7	0.0	0.0	0.0	0.0	0.0	1.7	0.0	3.9	0.0	0.0	0.0
Acteon candens	0.0	0.0	0.0	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0
Aglaophamus verrilli	0.0	20.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Allia cf. *alisdairi*	77.9	9.8	20.0	0.0	0.0	0.0	0.0	0.0	0.0	15.1	2.9	1.9
Allia cf. *trilobata*	0.0	0.0	0.8	0.0	5.7	2.7	11.8	0.0	0.0	1.5	8.8	0.0
Allia suecia	135.2	0.0	75.9	0.0	37.1	5.2	0.0	0.0	13.0	2.9	4.1	0.0
Alokalliapseudes macsweenyi	12.4	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alpheus cf. *macrocheles*	0.0	0.0	0.0	613.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alpheus nov. sp.	0.0	0.0	0.0	3181.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amaeana trilobata	4829.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11321	0.0
Amakusanthura magnifica	0.0	0.0	0.0	0.0	0.0	0.0	78.1	0.0	0.0	0.0	0.0	0.0
Americamysis stucki	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0
Americhelidium sp.	0.0	0.0	15.9	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Ampelisca agassizi	10.3	0.0	0.0	0.0	0.0	1.5	0.0	71.9	0.0	0.0	0.0	0.0
Ampelisca sp. A	7.9	0.0	0.8	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Ampelisca sp. C	0.0	0.0	0.0	0.0	58.6	0.0	0.0	0.0	15.5	0.0	0.0	0.0
Ampharete sp. A	0.0	2.9	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ampharete sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Amphicteis gunneri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.3	0.0
Amphictene sp. A	0.0	0.0	0.0	0.0	17.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphiporus bioculatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Amphiporus sp.	0.0	0.0	0.0	0.0	76.9	0.0	0.0	0.0	0.0	1533.4	0.0	0.0
Amphithalamus vallei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2
Amphiuridae sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	3.0	0.0	0.0
Amphiuridae sp. 2	28.8	128.3	66.3	0.0	0.0	162.5	17.1	0.4	6.6	19.8	17.2	0.0
Amphiuridae sp. 3	0.0	0.0	0.0	0.0	0.0	8.0	0.5	0.0	0.0	0.8	0.0	0.0
Amphiuridae sp. 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	987.4	0.0
Ancistrosyllis hartmanae	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0
Ancistrosyllis jonesi	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ancistrosyllis papillosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.2	0.0	0.0
Ancistrosyllis sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
Ancistrosyllis sp. B	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.9	0.0	0.0
Ancistrosyllis sp. C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	461.0	0.0	0.0
Angulus versicolor	21.6	0.0	81.5	0.0	28.8	0.0	5.9	0.0	1570.2	926.4	2390.7	23.7
Anoplodactylus petiolatus	3.8	0.0	17.8	0.0	0.0	0.0	0.0	0.0	9.8	0.0	0.0	0.0
Aonidella dayi	0.0	0.0	0.0	0.0	8.3	0.0	9.3	0.0	0.0	0.0	0.0	0.0
Aonides mayaguezensis	0.0	0.0	0.0	0.0	19.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aphrogenia sp. A	0.0	0.0	0.0	0.0	108.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Apianosoma trichocephalus	0.0	0.0	0.0	0.0	3.6	0.0	10.0	0.0	12.1	0.0	0.0	0.0
Apoprionospio pygmaea	0.0	0.0	0.0	0.0	41.4	0.0	0.0	6.3	0.0	0.0	0.0	0.0
Apseudes sp. A	0.0	0.0	0.0	0.0	46.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argissa hamatipes	0.0	21.7	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aricidea (*Aedicira*) sp. A	0.0	0.0	0.0	0.0	0.9	0.0	9.8	0.0	0.0	0.0	0.0	0.0
Aricidea (*Allia*) sp. A	0.0	11.7	1.1	0.0	2.7	0.0	5.2	0.0	0.0	0.0	0.0	0.0
Aricidea cf. *pseudoarticulata*	0.0	0.0	0.0	0.0	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0
Aricidea fragilis	0.0	0.0	0.0	0.0	0.9	25.2	0.0	0.0	0.0	0.0	0.0	0.0
Aricidea quadrilobata	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aricidea wassi	82.4	107.5	41.0	6.3	77.8	97.4	46.7	0.0	239.3	175.1	44.1	202.2

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Armandia agilis	46.1	0.0	16.7	0.0	53.6	46.0	0.0	87.0	6.8	153.7	27.0	71.6
Armandia maculata	0.0	51.3	0.0	0.0	0.0	6.2	0.0	0.0	0.0	0.0	0.0	0.0
Aspidosiphon sp.	5.5	0.0	66.7	0.0	0.0	0.0	0.0	0.0	34.4	0.0	166.7	0.0
Astarte nana	0.0	0.0	0.0	0.0	448.8	0.0	0.0	0.0	21.6	0.0	0.0	0.0
Asychis elongatus	6.1	354.0	276.4	0.0	0.0	0.0	0.0	0.0	1.2	0.0	116.2	0.0
Automate sp.	0.0	0.0	0.0	0.0	263.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Axiothella sp. A	140.2	35.4	1395.3	0.0	5.1	0.6	0.0	8.3	8.3	0.5	0.0	0.0
Balanoglossus sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	432.6	0.0	0.0
Balanoglossus sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.8	0.0	0.0	0.0
Barantolla sp. A	0.0	32.4	0.0	0.7	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Boccardiella sp. A	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Boguea enigmatica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.3	0.0
Boguea sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	35.3	0.0
Boguella sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0
Brada villosa	0.0	0.0	19.1	0.0	0.0	2.3	0.0	0.0	2.9	0.0	120.8	4.1
Brisaster sp.	0.0	2193.9	415.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brissopsis alta	261.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Busycotypus spiratus	0.0	0.0	0.0	0.0	54.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caecum floridanum	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0
Capitella capitata	36.7	24.1	55.0	7.5	160.7	38.0	4.5	52.7	3.5	4.4	1.3	0.6
Caprella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.7	0.0	0.0	0.0
Cardiomya costellata	0.0	0.0	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Careliopsis styliformis	0.0	0.0	0.0	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0
Carinomidae sp. 1	286.9	1456.1	81.9	0.0	20.0	249.7	3.8	78.7	0.0	1992.7	35.9	155.4
Carinomidae sp. 2	0.0	0.0	0.0	0.0	102.6	0.0	0.0	0.0	0.0	38.5	0.0	0.0
Caryocorbula contracta	0.0	473.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10951	0.0
Caulleriella cf. *zetlandica*	0.0	0.0	0.0	0.0	8.0	0.0	14.5	0.0	3.5	0.0	0.0	0.0
Caulleriella sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0
Cerapus sp.	16.7	0.0	3.4	0.0	48.3	0.0	0.0	0.0	30.5	8.0	0.0	0.0
Cerapus sp. C	7.7	0.0	0.0	0.0	2.6	0.0	0.0	0.0	167.0	0.0	0.0	0.0
Chaetozone sp. A	0.0	1.0	3.0	0.0	13.4	3.2	5.8	0.0	202.3	0.0	6.4	0.0
Chaetozone sp. B	1.1	0.0	64.2	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Chaetozone sp. C	0.0	0.0	2.6	0.0	7.6	0.0	0.0	0.0	35.8	0.0	17.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Chaetozone sp. D	0.0	105.6	89.9	3.0	0.0	3.2	5.8	0.0	19.5	0.4	24.9	0.0
Chioneryx grus	0.0	0.0	0.0	0.0	72.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chone americana	0.0	0.0	34.3	0.0	0.0	0.0	0.0	0.0	0.0	0.9	18.8	0.0
Chone cf. *americana*	39.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cirriformia sp. B	0.0	0.0	4.8	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0
Cirriformia sp. C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0
Cirrophorus americanus	81.0	3.5	21.5	0.0	7.3	38.7	188.8	0.0	20.2	14.2	83.2	0.0
Cirrophorus branchiatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.1	0.0	9.3	0.0
Cirrophorus cf. *forticirratus*	39.2	0.0	0.0	0.0	1.9	30.5	29.9	0.0	0.0	4.3	80.0	0.0
Clavodorum sp. A	7.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cleantioides planicauda	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clymenella torquata	146.3	328.6	384.7	0.0	0.0	3276.6	0.0	0.0	5301.6	2461.6	7410.9	0.0
Cossura soyeri	24.6	184.6	29.3	355.1	6.1	75.1	2.3	143.8	272.4	6.3	24.2	386.5
Cossura sp. A	14.6	3.0	43.8	1.0	39.0	26.9	35.6	16.5	4.0	0.0	36.4	0.0
Crassinella martinicensis	22.5	0.0	0.0	0.0	117.6	0.0	0.0	0.0	185.0	0.0	0.0	0.0
Crepidula convexa	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crepidula sp.	0.0	0.0	0.0	0.0	128.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cupuladria sp.	478.8	0.0	0.0	0.0	1193.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyathura sp.	30.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclaspis platymerus	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclaspis pustulata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0
Cyclostremiscus jeannae	0.0	0.0	0.0	0.0	0.0	0.0	56.4	0.0	0.0	0.0	0.0	0.0
Decamastus gracilis	0.0	11.0	135.7	0.0	0.0	94.2	0.0	0.0	0.0	0.0	0.0	0.0
Decamastus sp. A	23.0	12.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	27.7	139.7	0.0
Diastylis sp.	0.0	4.0	12.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dimya tigrina	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diopatra cf. *papillata*	0.0	0.0	0.0	8.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diopatra cuprea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	41.2	0.0	0.0
Diopatra neotridens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4680.1	0.0
Diplocirrus capensis	9.5	413.9	0.0	3.8	0.0	0.0	0.0	0.0	0.0	4.6	0.0	0.0
Diplocirrus sp. A	12.1	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0
Diplodonta punctata	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplodonta soror	0.0	0.0	0.0	0.0	89.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Divaricella quadrisulcata	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorvillea sp. A	10.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0
Dorvillidae genus B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	179.1	0.0
Echiura sp. 1	197.7	1069.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Edotea montosa	0.0	0.0	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Edwardsia sp.	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	5.8	0.0	0.0
Ennucula aegeensis	0.0	0.0	0.0	0.0	9.1	0.0	1.4	0.0	0.0	0.0	0.0	0.0
Episiphon sowerbyi	15.7	0.0	79.8	0.0	85.3	21.1	0.0	85.3	13.2	0.0	0.0	0.0
Euchone cf. incolor	0.0	0.0	23.5	0.0	0.0	1.6	0.0	0.0	2.0	0.0	0.0	0.0
Euchone cf. southerni	0.7	0.3	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euchone sp. A	0.0	2.4	71.1	0.0	2.7	1.9	0.0	0.0	2.7	0.0	11.3	0.0
Euclymene sp. A	21.6	3.9	0.0	0.0	6.9	1833.7	0.0	0.0	0.4	3177.0	2092.3	0.0
Euclymene sp. B	96.1	1372.3	7.7	0.0	4.1	7840.7	0.0	0.0	526.7	3809.8	0.0	0.0
Eudorella sp.	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eulalia bilineata	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eulimastoma canaliculatum	9.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eunice vittata	4.5	0.0	0.0	0.0	16.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eupolymnia nebulosa	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurytellina lineata	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurythoe sp. A	0.0	0.0	4.7	3.0	1.5	0.0	0.0	0.0	5.2	0.0	0.0	0.0
Evalea emeryi	20.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Exogone dispar	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Exogone lourei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	96.5	0.0	0.0	0.0
Exogone sp. B	64.7	0.0	0.0	0.0	46.8	0.0	0.0	0.0	14.6	0.0	0.0	0.0
Fabricia sp. A	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fargoa gibbosa	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fargoa sp.	0.0	0.0	68.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ficus communis	0.0	0.0	0.0	0.0	0.0	11.9	0.0	0.0	0.0	0.0	0.0	0.0
Fimbriosthenelais hobbsi	6.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fimbriosthenelais minor	20.3	0.0	0.0	0.0	36.8	117.5	0.0	0.0	0.0	0.0	0.0	0.0
Finella dubia	0.0	0.0	0.0	0.0	39.9	2.2	1.3	0.0	0.0	0.0	0.0	0.0
Gadila mayori	0.0	0.0	0.0	0.0	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gemma gemma	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.6

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Gemophos tinctus	0.0	0.1	0.0	0.1	8.9	0.0	2.6	0.1	0.0	0.0	0.0	0.0
Glottidia pyramidata	0.0	0.0	69.2	0.0	169.1	0.0	0.0	0.0	1929.7	12.0	305.5	0.0
Glycera americana	0.0	0.0	0.0	0.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycera dibranchiata	0.0	3150.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.7	0.0	0.0
Glycera sp. A	0.0	338.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0.0	0.0
Glycera sp. D	0.0	0.0	186.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycera sp. E	0.0	0.0	50.8	0.0	0.0	0.0	0.0	0.0	0.0	311.7	0.0	0.0
Glycinde solitaria	411.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycymeris decussata	0.0	0.0	0.0	0.0	0.0	0.0	74.3	0.0	0.0	0.0	0.0	0.0
Glyphohesione klatti	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gnathia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	71.0	0.0
Golfingia sp. 1	4.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Golfingia sp. 2	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.1	4.2	0.0
Golfingia sp. 3	15.9	52.3	34.2	0.0	0.6	7.0	0.0	0.0	0.0	0.0	0.0	0.0
Goniada littorea	121.5	0.0	104.6	0.0	26.2	0.0	298.7	0.0	59.4	0.0	683.1	0.0
Gouldia cerina	0.0	0.0	0.0	0.0	0.0	5947.2	0.0	0.0	0.0	0.0	0.0	0.0
Grubeulepis augeneri	33.0	0.0	0.0	0.1	17.1	0.0	0.0	0.0	0.0	10.4	0.0	0.0
Gyptis brevipalpa	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gyptis vittata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.6	0.0	0.0
Haloclava sp.	1.7	1.7	6.4	12.7	0.0	8.1	81.1	0.9	0.0	22.0	267.6	31.8
Haminoea cf. *elegans*	0.0	0.0	0.0	0.0	0.0	16.1	0.0	0.0	188.6	0.0	0.0	0.0
Haminoea succinea	84.1	8.5	64.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Harmathoe sp.	1.1	0.0	9.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiliostraca auricincta	0.0	0.3	0.0	0.0	0.0	0.0	8.7	0.0	0.0	0.0	39.2	0.0
Heteromastus filiformis	0.0	8.8	11.3	0.0	385.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heterospio longissima	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.0	8.6	0.0
Houbricka incisa	0.0	0.0	0.0	0.0	4.1	680.4	0.0	0.0	3.4	429.6	356.6	0.0
Hypereteone heteropoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	3.2	0.0
Hyssura sp.	0.0	0.0	0.0	0.0	128.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inermonephtys inermis	0.0	0.0	0.0	0.0	957.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Iphimedidae sp. 1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isolda pulchella	0.0	0.0	0.2	0.0	30.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jasmineira cf. *pacifica*	1.8	1.8	1.4	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Kinbergonuphis sp. A	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	131.7	0.0	0.0	0.0
Kinbergonuphis sp. B	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laevicardium mortoni	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laonice cirrata	1026.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	84.3	0.0	0.0	0.0
Leucon sp. A	10.7	0.0	5.3	0.0	0.0	2.1	1.1	0.0	0.0	0.0	0.0	0.0
Levinsenia gracilis	15.3	58.6	39.4	0.0	22.6	29.6	7.7	6.2	22.6	17.3	144.7	3.4
Levinsenia reducta	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Lineidae sp. 1	117.8	82.8	71.4	26.3	0.0	0.0	0.0	0.0	351.2	0.0	0.0	22.2
Lineidae sp. 2	303.1	175.2	1278.8	71.6	190.8	4844.5	78.1	0.0	122.0	449.8	449.9	28.0
Lineidae sp. 3	224.5	68.0	345.1	35.3	126.2	9.4	42.4	1.1	549.5	635.9	1719.5	601.5
Listriella barnardi	3.4	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Listriella carinata	0.0	0.0	0.0	1.6	0.0	0.0	0.0	9.6	0.0	0.0	0.0	0.0
Listriella sp. A	0.0	5.5	2.8	8.5	0.0	0.0	0.0	27.8	13.3	8.7	21.2	0.0
Loimia viridis	0.0	73.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Lucifer faxoni	6.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris sp. A	0.0	0.0	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris sp. C	6.0	0.0	49.5	0.0	0.0	0.0	0.0	0.0	354.0	80.5	6.0	0.0
Lumbrineris sp. D	797.9	0.0	1293.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	132.3	0.0
Lumbrineris sp. E	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0
Lumbrineris tenuis	0.0	0.0	3.7	0.0	0.0	26.0	0.0	0.0	0.0	0.0	0.0	0.0
Macoma constricta	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macoma pseudomera	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macoma pulleyi	0.0	0.0	1.1	86.1	2.2	1.9	0.0	0.0	0.0	0.0	3.1	0.0
Macroclymene sp. A	38.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macromphalina pierrot	9.7	0.0	68.9	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona sp. G	0.0	0.0	20.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona sp. H	0.0	12.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	72.5	19.4	0.0
Magelona sp. I	0.0	75.9	20.8	0.0	0.0	463.1	0.0	0.0	657.4	1454.8	0.0	0.0
Magelona sp. J	0.0	0.0	427.3	0.0	54.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona sp. L	54.6	0.0	0.0	0.0	92.1	0.0	0.0	0.0	485.0	0.0	0.0	0.0
Maldane sp. A	16.4	128.2	34.7	0.0	1716.7	96.5	0.0	0.0	0.0	0.9	0.0	0.0
Marphysa sanguinea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0
Martesia striata	0.0	0.0	8.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Mediomastus californiensis	156.1	681.2	424.4	84.8	144.2	362.4	2.2	168.5	1882.0	174.4	98.1	374.0
Megalomma bioculatum	0.0	0.7	3.5	0.0	0.6	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Megalomma sp. A	0.0	0.0	0.0	0.0	11.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meiodorvillea sp. B	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melinna cristata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0
Microporella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	195.4	0.0	0.0	0.0
Micrura sp.	0.0	0.0	0.0	0.0	0.0	0.0	9.5	0.0	0.0	0.0	0.0	0.0
Minuspio cirrifera	0.0	0.0	0.0	0.0	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mooreonuphis pallidula	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Musculus lateralis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.0	0.0	0.0	0.0
Myriochele oculata	0.0	0.0	0.0	0.0	0.0	0.1	1.1	0.0	0.0	0.0	0.0	0.0
Myriochele sp. A	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	5.3	0.0	3.4	0.0
Mystides borealis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Neanthes micromma	467.1	0.0	291.7	0.0	85.3	0.0	0.0	0.0	47.4	12.9	1792.9	0.0
Neanthes succinea	0.0	0.0	6.2	0.0	0.0	0.0	0.0	0.0	1.7	0.0	30.9	0.0
Nephtys cf. *hombergii*	0.0	0.0	0.0	0.0	0.0	0.0	42.1	0.0	0.0	0.0	0.0	0.0
Nephtys incisa	0.0	0.0	0.0	2027.5	0.0	613.1	0.0	387.3	0.0	693.0	0.0	0.0
Nephtys squamosa	89.2	547.0	1494.6	1610.1	0.0	47.0	75.0	195.5	0.0	9.1	0.0	899.2
Nephtys simoni	0.0	0.0	0.0	0.0	0.0	270.3	0.0	238.9	0.0	0.0	0.0	0.0
Nevertia duplicata	152.3	0.0	0.0	0.0	108.3	430.1	0.0	0.0	0.0	0.0	0.0	0.0
Ninoe sp. A	0.0	128.4	311.2	0.0	0.0	0.0	0.0	0.5	0.0	0.0	349.0	398.4
Ninoe sp. B	0.0	731.4	0.0	0.0	0.0	633.2	0.0	0.0	0.0	418.9	177.0	582.0
Nothria sp. A	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
Notomastus americanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	122.5	0.0	0.0	0.0
Notomastus daueri	0.0	161.0	1.4	0.0	225.0	226.1	0.0	59.9	71.2	0.0	464.7	0.0
Notomastus hemipodus	0.0	0.0	0.0	0.0	1024.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomastus latericeus	109.0	0.0	0.0	0.0	1544.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomastus lineatus	257.4	136.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2280.5
Notomastus lobatus	0.0	26.1	0.0	1527.8	0.0	0.0	0.0	0.0	0.0	291.4	0.0	0.0
Notomastus sp. A	41.1	23.4	42.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2
Notomastus tenuis	0.0	0.0	0.0	0.0	293.6	0.0	113.3	0.0	0.0	0.0	0.0	0.0
Nucula calcicola	122.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0	0.0
Nucula crenulata	0.0	131.4	0.0	0.0	0.0	0.0	9.2	0.0	79.8	5.1	2.9	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Nucula proxima	32.6	35.2	194.3	39.2	108.7	54.1	218.4	21.8	11.8	0.0	26.9	0.0
Nuculana acuta	185.5	12.5	19.5	84.9	657.9	125.4	990.2	169.4	626.5	109.0	128.5	1111.8
Nuculana concentrica	0.0	4828.3	0.0	4.4	1373.5	0.0	0.0	0.0	1216.6	0.0	706.9	2.0
Nuculana unca	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odostomia cf. *hendersoni*	0.0	0.0	7.0	0.0	10.4	0.0	0.0	0.0	0.0	0.0	5.8	0.0
Odostomia laevigata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.4	0.0	0.0	0.0
Oedocerotidae sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Oedocerotidae sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0
Oedocerotidae sp. 3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Onuphis sp. A	0.0	0.0	6.7	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	4.0
Ophelina cf. *acuminata*	0.0	2.1	0.0	0.0	3.0	0.0	0.0	0.0	0.0	5.1	0.0	0.0
Ophelina cylindricaudata	0.0	0.0	8.9	1224.7	0.0	1.9	4.4	134.5	0.0	40.1	0.0	0.0
Ophiactis sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	7.3	0.0
Ophiolepididae sp.	79.4	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Owenia sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.0	0.0	0.0
Oxyurostylis smithi	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxyurostylis sp.	0.0	29.5	3.3	0.0	0.0	0.0	2.2	0.0	2.1	0.0	0.0	0.0
Pachycheles sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0
Pagurus longicarpus	0.0	0.0	0.0	0.0	301.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagurus maclaughlinae	507.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	163.4	0.0	0.0	0.0
Pandora arenosa	8.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pandora bushiana	0.0	0.0	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pandora sp.	16.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pandora trilineata	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paradentalium americanum	8.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Paraheteromastus sp.	0.0	0.0	0.0	0.0	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramphinome sp. B	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	163.3	17.9	0.0
Paranaitis polynoides	0.0	0.0	0.0	0.0	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraonis fulgens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.1	0.0	0.0	0.0	0.0
Paraonis pygoenigmatica	0.0	0.0	0.0	0.0	39.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraprionospio pinnata	456.9	14.5	125.5	188.2	277.7	447.6	1026.9	262.5	1215.8	864.5	1507.3	1324.5
Parasabella microphthalma	76.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Parasmittina sp.	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parviturbo rehderi	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0
Pectinaria gouldii	0.9	0.0	39.8	0.0	127.9	6.0	7.6	0.0	331.7	0.0	0.0	0.0
Peresiella sp. A	0.0	0.0	0.0	0.0	2.0	12.8	0.0	0.0	0.0	0.0	0.0	0.0
Periploma cf. *margaritaceum*	15.6	0.0	1.0	1.4	17.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Periploma margaritaceum	16.4	0.0	9.1	0.0	0.0	0.0	0.0	0.0	26.6	0.0	0.0	0.0
Petaloproctus sp.	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Petitilla crosseana	0.0	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0
Pettiboneia sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	3.8
Phascolion sp.	514.5	0.0	19.5	0.0	56.1	16.8	43.7	0.0	58.8	0.0	17.2	0.0
Pherusa sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
Pherusa inflata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	42.9	0.0	0.0	0.0	0.0
Phlyctiderma semiaspera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0
Pholoe sp. C	0.0	0.0	0.0	0.0	0.0	0.0	10.9	0.0	0.0	0.0	0.0	0.0
Phoronida sp. 1	16.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Photis melanica	23.5	0.0	18.6	0.0	48.0	0.0	0.0	0.0	111.5	0.0	0.0	0.0
Photis sp.	2.8	2.0	5.1	0.0	0.0	0.0	0.0	0.0	107.9	0.0	2.1	0.0
Phyllodina squamifera	43.6	2.9	0.0	7.7	74.5	49.3	140.9	0.0	148.1	11.8	306.7	0.0
Phyllodoce longipes	16.5	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
Phylo felix	0.0	0.0	0.0	0.0	366.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pinnixa retinens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	154.1	0.0
Pinnixa sp.	0.0	0.0	0.0	0.0	0.0	201.6	0.0	0.0	0.0	0.0	0.0	0.0
Piromis roberti	0.0	0.0	0.0	0.0	45.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pista sp.	0.9	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pista sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	35.4	0.0	0.0	0.0
Pitar fulminatus	0.0	0.0	0.0	0.0	10.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poecilochaetus johnsoni	0.0	930.6	0.0	0.0	0.0	0.0	0.0	0.0	155.3	0.0	0.0	0.0
Polinices lacteus	0.0	0.0	0.0	0.0	0.0	36.5	0.0	0.0	0.0	0.0	0.0	0.0
Polycirrus plumosus	117.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polycladida sp. 1	6.3	30.3	0.0	0.0	17.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polycladida sp. 2	40.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polymesoda caroliniana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Pontonidae sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Pourtalesidae sp. A	0.0	0.0	35.4	0.0	73.0	136.7	14.0	0.0	22.6	0.5	0.0	0.0
Prionospio cristata	266.6	249.7	214.0	28.0	185.1	26.2	12.8	22.3	264.3	153.9	140.1	477.5
Prionospio fallax	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prionospio sp. A	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	4.4	0.0
Prionospio steenstrupi	14.9	8.4	0.0	379.1	50.9	39.5	5.1	0.0	2.7	4.4	51.3	0.0
Processa sp.	0.0	0.0	0.0	0.0	0.0	0.0	75.8	0.0	0.0	0.0	0.0	0.0
Promysis atlantica	8.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudocarcinus sp.	0.0	0.0	0.0	1753.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotanais sp. A	24.7	0.5	0.0	0.0	22.7	0.0	0.0	0.0	3.3	0.0	0.0	0.0
Pseudotanais sp. B	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	169.1	0.0	0.0	0.0
Pterocirrus macroceros	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Puberella intapurpurea	0.0	0.0	0.0	0.0	0.0	16.5	0.0	0.0	0.0	0.0	0.0	0.0
Radiolucina amianta	32.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rissoella caribaea	20.8	0.0	51.1	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.0	0.0
Sabella melanochlora	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sabella microphthalma	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sabella sp. A	0.0	0.0	5.0	0.0	21.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sabellides sp. A	0.0	10.5	6.9	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sarsonuphis hartmanae	0.0	8.6	5.2	0.0	244.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Schistomeringos pectinata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	1.2	0.0
Schistomeringos sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	4.1	0.0
Scissula iris	8.0	60.5	17.7	0.1	11.4	177.9	32.3	0.0	0.0	25.4	95.8	7.6
Scolelepis texana	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scoloplos sp. A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	258.1	0.0
Scyphoproctus platyproctus	165.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.2
Scyphoproctus sp.	0.0	0.0	0.0	0.0	0.0	67.8	0.0	0.0	0.0	0.0	0.0	0.0
Sebidae sp. 1	0.0	0.0	0.0	8.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Serolis mgrayi	0.0	0.8	0.0	0.0	46.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sigalion sp. A	0.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0
Sigambra tentaculata	2.2	35.3	49.1	3.5	0.0	73.3	69.7	69.3	19.2	252.3	155.8	61.9
Sipuncula sp. 1	8.8	0.0	19.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.1
Sipunculus nudus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Solariorbis infracarinatus	0.0	0.0	0.0	0.0	0.0	18.5	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Solenosteira cancellaria	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	274.6	0.0	0.0	3619.5
Speocarcinus sp.	0.0	0.0	0.0	0.0	0.0	3961.3	0.0	0.0	0.0	0.0	0.0	0.0
Sphaerella verrilli	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphaerephesia sp. A	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spiochaetopterus costarum	3.8	63.2	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spiophanes missionensis	17.5	0.0	0.0	0.0	14.2	0.0	0.0	0.0	0.0	0.0	0.0	5.7
Sternaspis scutata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0
Sthenelais limicola	129.1	13.2	120.0	95.0	26.3	0.0	53.1	0.0	490.8	2.8	19.6	9.4
Sthenelanella sp. A	0.0	0.0	0.0	0.0	0.0	0.0	56.9	0.0	0.0	0.0	0.0	0.0
Sthenolepis cf. *grubei*	0.0	0.0	1063.9	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sthenolepis sp. A	0.0	0.0	0.0	0.0	60.3	2.6	0.0	0.0	0.0	0.0	0.0	0.0
Syllis (*Ehlersia*) sp. A	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Taphromysis bowmani	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	444.2	0.0
Tectonatica pusilla	0.0	763.3	105.7	0.0	0.0	9.9	35.9	164.8	14.6	0.0	245.8	27.4
Teinostoma parvicallum	0.0	0.0	0.0	0.0	0.0	106.3	0.0	0.0	0.0	0.0	0.0	0.0
Tellidora cristata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0
Terebellides stroemii	241.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tharyx cf. *annulosus*	89.4	125.7	44.9	37.4	83.2	23.4	1.3	181.2	205.3	529.7	62.9	3.4
Tharyx sp.	0.0	0.0	0.0	0.0	203.2	0.0	0.0	0.0	32.5	0.0	135.8	713.7
Thyone deichmannae	0.0	47.7	66.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanocardia sp.	50.1	0.0	791.8	1.8	115.9	250.8	2100.2	0.0	0.0	79.0	1461.3	0.0
Travisia hobsonae	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trigonulina ornata	54.5	0.0	0.0	0.0	134.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trochochaeta sp.	0.0	2274.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tubificoides amplivasatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.5	0.0	0.0
Tubiluchus corallicola	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Turbonilla heilprini	0.0	0.0	8.9	0.0	37.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Turbonilla levis	0.0	0.0	0.0	0.0	0.0	386.1	4.0	0.0	38.3	0.0	0.0	0.0
Umbilibalcis lata	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Umbilibalcis sp.	0.0	0.0	0.0	0.0	0.0	0.0	15.8	0.0	0.0	0.0	0.0	0.0
unidentified	79.4	10.1	3.0	0.0	5.4	0.0	0.0	0.0	0.7	0.0	0.0	0.0
unidentified Entoprocta	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
unidentified Oligochaeta	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0

Table C1 (continued).

Species list	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
unidentified Pogonophora	0.0	0.0	14.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Uromunna cf. *hayesi*	0.0	10.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Urosalpinx sp.	0.0	0.0	0.0	0.0	785.7	375.4	0.0	0.0	0.0	0.0	0.0	0.0
Vesicularia sp.	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vitrinella floridana	0.3	70.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	338.5	0.0	0.0
Volvulella minuta	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	5.9	0.0	42.6	0.0
Volvulella texasiana	3.3	16.3	0.0	0.0	0.0	124.8	30.3	0.0	9.7	50.8	25.9	0.0
Xanthidae sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	273.2	0.0
Xenanthura brevitelson	23.7	0.0	0.0	0.0	41.0	0.0	0.0	0.0	14.2	0.0	0.0	0.0

APPENDIX D

MEIOFAUNA SPECIES

Table D1

Meiofauna taxonomic classification from phylum to species with associated feeding guilds and referenced sources.

Phylum	Class	Order	Family	Species	Feeding	Source
Cnidaria	Hydrozoa	Leptothecata	Tubulariidae	*Tubularia* sp.	SF	Barnes (1980)
			Haleciidae	*Halecium* sp.	SF	Barnes (1980)
			Campanulariidae	*Calycella* sp.	SF	Barnes (1980)
			Campanulariidae	*Campanularia* sp. 1	SF	Barnes (1980)
			Campanulariidae	*Campanularia* sp. 2	SF	Barnes (1980)
			Campanulariidae	*Campanularia* sp. 3	SF	Barnes (1980)
			Campanulariidae	*Clytia* sp.	SF	Barnes (1980)
			Sertulariidae	*Sertularia* sp. 1	SF	Barnes (1980)
Gastrotricha	−	Macrodasyida	Macrodasyidae	Macrodasyid sp.	SDF	Barnes (1980)
Kinorhyncha	−	Cyclorhagia	Echinoderidae	*Echinoderes* cf. *coulli*	SDF	Barnes (1980)
Arthropoda	Ostracoda	Myodocopida	Cypridinidae	Myodocopid sp. 1	Carn	Vannier et al., (1998)
				Myodocopid sp. 1a	Carn	Vannier et al., (1998)
			Philomedidae	Myodocopid sp. 2	Carn	Vannier et al., (1998)
				Myodocopid sp. 3	Carn	Vannier et al., (1998)
		Halocyprida	Halocyprididae	Halocyprid sp. 3	Carn	Vannier et al., (1998)
				Halocyprid sp. 4	Carn	Vannier et al., (1998)
		Platycopida	Cytherellidae	Platycopid sp. 6	SF	Cannon (1933)

Table D1 (continued).

Phylum	Class	Order	Family	Species	Feeding	Source
		Podocopida	Darwinulidae	Podocopid sp. A	SDF	Maddocks (1992)
			Cyprididae	Podocopid sp. 2	SDF	Maddocks (1992)
				Podocopid sp. 11	SDF	Maddocks (1992)
			Cytheridae	Podocopid sp. 5	SDF	Maddocks (1992)
				Podocopid sp. 8	SDF	Maddocks (1992)
			Loxoconchidae	Podocopid sp. 1	SDF	Maddocks (1992)
			Paradoxostomatidae	Podocopid sp. 4	SDF	Maddocks (1992)
			Thaerocytheridae	Podocopid sp. 7	SDF	Maddocks (1992)
				Podocopid sp. 10	SDF	Maddocks (1992)
	Copepoda	Harpacticoida	Ameiridae	Ameirid sp. 1	SDF	Rieper (1982)
				Ameirid sp. 2	SDF	Rieper (1982)
			Canthocamptidae	Canthocamptid sp. 1	SDF	Rieper (1982)
				Canthocamptid sp. 2	SDF	Rieper (1982)
			Cletodidae	Cletodid sp. 1	SDF	Rieper (1982)
				Cletodid sp. 2	SDF	Rieper (1982)
				Cletodid sp. 3	SDF	Rieper (1982)
				Cletodid sp. 5	SDF	Rieper (1982)
				Cletodid sp. 6	SDF	Rieper (1982)
			Diosaccidae	Diosaccid sp. 1	SDF	Rieper (1982)
				Diosaccid sp. 3	SDF	Rieper (1982)
			Ectinosomatidae	Ectinosomatid sp. 1	SDF	Rieper (1982)
			Metidae	Metid sp. 1	SDF	Rieper (1982)
			Thalestridae	Thalestrid sp. 1	SDF	Rieper (1982)
				Thalestrid sp. 2	SDF	Rieper (1982)
Tardigrada	Heterotardigrada	Arthrotardigrada	Batillipedidae	Batillipedid sp. 1	SDF	Barnes (1980)

Table D2

Abundance (no. /100 cm²) of different meiofauna species at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Species	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Ameirid sp. 1	31.79	43.01	35.53	18.7	3.74	0	7.48	1.87	0	1.87	5.61	1.87
Ameirid sp. 2	0	0	0	0	1.87	0	0	0	0	0	0	0
Batilipedid sp. 1	0	0	1.87	0	0	0	0	0	0	0	0	0
Calycella sp.	11.22	9.35	16.83	0	16.83	0	0	0	24.31	0	3.74	0
Campanularia sp. 1	1.87	0	0	5.61	3.74	0	0	3.74	13.09	0	0	0
Campanularia sp. 2	7.48	9.35	3.74	0	11.22	1.87	3.74	0	35.53	11.22	37.4	0
Campanularia sp. 3	0	0	1.87	0	0	0	0	0	0	0	0	0
Camptocamptid sp. 1	0	0	5.61	9.35	0	0	0	0	0	0	0	0
Camptocamptid sp. 2	0	0	0	0	0	0	1.87	0	0	0	0	0
Cletodid sp. 1	5.61	0	0	9.35	0	1.87	0	3.74	0	0	0	5.61
Cletodid sp. 2	28.05	0	0	0	0	0	0	5.61	1.87	0	1.87	3.74
Cletodid sp. 3	0	1.87	3.74	0	0	0	1.87	0	0	0	0	0
Cletodid sp. 5	0	0	0	0	1.87	0	0	0	0	0	0	0
Cletodid sp. 6	11.22	0	0	0	0	0	0	0	0	0	0	0
Clytia sp.	11.22	0	5.61	1.87	0	0	0	0	3.74	0	1.87	0
Diosaccid sp. 1	0	0	0	0	1.87	0	0	0	0	0	0	7.48
Diosaccid sp. 3	0	7.48	0	0	0	1.87	0	5.61	0	0	0	0
Echinoderes cf. *coulli*	7.48	9.35	7.48	0	16.83	82.28	33.66	22.44	1.87	26.18	0	102.85
Ectinosomatid sp. 1	0	0	0	1.87	0	5.61	0	9.35	0	0	0	0
Halecium sp.	0	0	0	0	0	0	0	0	3.74	0	1.87	0
Halocyprid sp. 3	0	1.87	0	0	3.74	0	0	0	0	0	0	0
Halocyprid sp. 4	0	0	0	0	0	0	0	0	0	0	5.61	0
Macrodasyid sp.	0	0	0	1.87	0	0	0	0	0	0	0	0
Metid sp. 1	0	0	0	0	1.87	0	0	3.74	0	0	0	0
Myodocopid sp. 1	22.44	0	0	0	37.4	0	1.87	0	35.53	0	0	0

Table D2 (continued).

Species	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Myodocopid sp. 1a	0	0	0	0	5.61	0	0	0	9.35	0	1.87	0
Myodocopid sp. 2	7.48	0	0	0	0	0	0	0	7.48	0	0	0
Myodocopid sp. 3	0	0	0	0	7.48	0	1.87	24.31	0	0	0	0
Podocopid sp. 1	0	11.22	5.61	0	1.87	43.01	7.48	0	1.87	3.74	3.74	0
Podocopid sp. 2	5.61	0	9.35	0	11.22	1.87	26.18	0	13.09	3.74	1.87	0
Podocopid sp. A	1.87	1.87	0	0	0	0	11.22	0	0	1.87	1.87	0
Podocopid sp. 4	3.74	0	1.87	0	0	0	0	0	5.61	0	0	0
Podocopid sp. 5	0	7.48	5.61	0	0	3.74	3.74	0	11.22	0	1.87	0
Platycopid sp. 6	16.83	0	0	0	24.31	0	0	0	20.57	0	0	5.61
Podocopid sp. 7	0	13.09	5.61	13.09	0	0	0	3.74	3.74	3.74	5.61	7.48
Podocopid sp. 8	0	0	0	1.87	0	0	0	0	0	0	0	0
Podocopid sp. 10	0	0	0	0	1.87	3.74	1.87	0	0	0	0	0
Podocopid sp. 11	0	0	0	0	0	1.87	0	0	0	0	0	0
Sertularia sp. 1	0	0	0	1.87	0	0	0	0	0	0	0	0
Thalestrid sp. 1	0	0	0	1.87	0	0	0	0	0	0	0	1.87
Thalestrid sp. 2	0	0	0	0	1.87	0	0	0	0	0	0	0
Tubularia sp.	31.79	44.88	5.61	3.74	0	3.74	0	0	1.87	16.83	3.74	0

Table D3

Biomass (μg AFDW/100 cm²) of different meiofauna species at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Species	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Ameirid sp. 1	9.7	1.7	1.1	2.3	0.1	0.0	0.7	0.1	0.0	0.1	0.3	1.0
Ameirid sp. 2	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Batilipedid sp. 1	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calycella sp.	8.6	0.2	4.8	0.0	0.1	0.0	0.0	0.0	0.4	0.0	0.2	0.0
Campanularia sp. 1	0.7	0.0	0.0	2.2	0.4	0.0	0.0	0.4	0.3	0.0	0.0	0.0
Campanularia sp. 2	1.7	1.2	0.3	0.0	0.1	1.1	1.4	0.0	0.2	1.7	0.2	0.0
Campanularia sp. 3	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Camptocamptid sp. 1	0.0	0.0	0.6	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Camptocamptid sp. 2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Cletodid sp. 1	1.6	0.0	0.0	1.2	0.0	0.2	0.0	0.3	0.0	0.0	0.0	4.5
Cletodid sp. 2	9.8	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.7	0.0	0.8	0.1
Cletodid sp. 3	0.0	0.3	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Cletodid sp. 5	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cletodid sp. 6	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clytia sp.	3.1	0.0	3.1	0.8	0.0	0.0	0.0	0.0	0.2	0.0	1.2	0.0
Diosaccid sp. 1	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Diosaccid sp. 3	0.0	0.3	0.0	0.0	0.0	0.2	0.0	0.3	0.0	0.0	0.0	0.0
Echinoderes cf. *coulli*	3.0	0.7	2.7	0.0	0.1	0.6	0.5	0.3	0.2	1.6	0.0	2.7
Ectinosomatid sp. 1	0.0	0.0	0.0	0.3	0.0	1.8	0.0	0.2	0.0	0.0	0.0	0.0
Halecium sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	47.0	0.0	1.4	0.0
Halocyprid sp. 3	0.0	0.8	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halocyprid sp. 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.5	0.0
Macrodasyid sp.	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metid sp. 1	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Myodocopid sp. 1	16.6	0.0	0.0	0.0	1.1	0.0	0.3	0.0	1.6	0.0	0.0	0.0

Table D3 (continued).

Species	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D
Myodocopid sp. 1a	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	1.8	0.0	3.2	0.0
Myodocopid sp. 2	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.7	0.0	0.0	0.0
Myodocopid sp. 3	0.0	0.0	0.0	0.0	1.6	0.0	1.0	0.2	0.0	0.0	0.0	0.0
Podocopid sp. 1	0.0	0.7	4.2	0.0	1.6	26.6	4.7	0.0	7.5	0.3	2.2	0.0
Podocopid sp. 2	22.7	0.0	5.8	0.0	2.6	5.2	30.4	0.0	7.5	13.2	9.2	0.0
Podocopid sp. A	0.5	0.1	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.7	5.0	0.0
Podocopid sp. 4	7.3	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Podocopid sp. 5	0.0	7.5	6.7	0.0	0.0	5.9	1.9	0.0	8.7	0.0	6.1	0.0
Platycopid sp. 6	55.4	0.0	0.0	0.0	6.1	0.0	0.0	0.0	11.1	0.0	0.0	2.9
Podocopid sp. 7	0.0	3.1	2.8	0.3	0.0	0.0	0.0	2.1	1.3	30.0	1.9	2.5
Podocopid sp. 8	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Podocopid sp. 10	0.0	0.0	0.0	0.0	9.0	16.6	10.5	0.0	0.0	0.0	0.0	0.0
Podocopid sp. 11	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Sertularia sp. 1	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thalestrid sp. 1	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Thalestrid sp. 2	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tubularia sp.	10.2	1.2	0.1	2.6	0.0	0.4	0.0	0.0	0.9	0.1	2.6	0.0

APPENDIX E

FEEDING GUILDS BY SPECIES

Table E1

List of macrobenthos species with associated feeding guilds and referenced sources: carnivores (Carn), herbivores (Herb), surface deposit feeders (SDF), sub-surface deposit feeders (SSDF) and suspension feeders (SF).

Species list	Feeding	Reference
Abra aequalis	SDF	NMiTA
Acmira catherinae	SDF	Fauchald and Jumars (1979); WoRMS
Acmira cerrutii	SDF	Fauchald and Jumars (1979); WoRMS
Acmira cf. *finitima*	SDF	Fauchald and Jumars (1979); WoRMS
Acmira lopezi	SDF	Fauchald and Jumars (1979); WoRMS
Acmira philbinae	SDF	Fauchald and Jumars (1979); WoRMS
Acmira simplex	SDF	Fauchald and Jumars (1979); WoRMS
Acmira taylori	SDF	Fauchald and Jumars (1979); WoRMS
Acteocina recta	Carn	NMiTA
Acteon candens	Carn	NMiTA
Aglaophamus verrilli	Carn	Fauchald and Jumars (1979); WoRMS
Allia cf. *alisdairi*	SDF	Fauchald and Jumars (1979); WoRMS
Allia cf. *trilobata*	SDF	Fauchald and Jumars (1979); WoRMS
Allia suecia	SDF	Fauchald and Jumars (1979); WoRMS
Alokalliapseudes macsweenyi	SF	Drumm (2005)
Alpheus cf. *macrocheles*	Carn	Palomar et al., (2005)
Alpheus nov. sp.	Carn	Palomar et al., (2005)
Amaeana trilobata	SDF	Fauchald and Jumars (1979)
Amakusanthura magnifica	Carn	Wetzer et al., (1997)
Americamysis stucki	Carn	Hunt et al., (2002)
Americhelidium sp.	SDF	WoRMS
Ampelisca agassizi	SDF	Guerra-Garcia et al., (2014)
Ampelisca sp. A	SDF	Guerra-Garcia et al., (2014)
Ampelisca sp. C	SDF	Guerra-Garcia et al., (2014)
Ampharete sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Ampharete sp. B	SDF	Fauchald and Jumars (1979); WoRMS
Amphicteis gunneri	SDF	WoRMS
Amphictene sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Amphiporus bioculatus	Carn	Macdonald et al., (2010)
Amphiporus sp.	Carn	Macdonald et al., (2010)
Amphithalamus vallei	Herb	NMiTA
Amphiuridae sp. 1	SDF	Fratt and Dearborn (1984); Stöhr et al., (2012)
Amphiuridae sp. 2	SDF	Fratt and Dearborn (1984); Stöhr et al., (2012)
Amphiuridae sp. 3	SDF	Fratt and Dearborn (1984); Stöhr et al., (2012)
Amphiuridae sp. 4	SDF	Fratt and Dearborn (1984); Stöhr et al., (2012)
Ancistrosyllis hartmanae	Carn	Fauchald and Jumars (1979); WoRMS
Ancistrosyllis jonesi	Carn	Fauchald and Jumars (1979); WoRMS
Ancistrosyllis papillosa	Carn	Fauchald and Jumars (1979); WoRMS
Ancistrosyllis sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Ancistrosyllis sp. B	Carn	Fauchald and Jumars (1979); WoRMS
Ancistrosyllis sp. C	Carn	Fauchald and Jumars (1979); WoRMS

Table E1 (continued).

Species list	Feeding	Reference
Angulus versicolor	SDF	NMiTA
Anoplodactylus petiolatus	Carn	WoRMS
Aonidella dayi	SDF	Fauchald and Jumars (1979); WoRMS
Aonides mayaguezensis	SDF	Fauchald and Jumars (1979); WoRMS
Aphrogenia sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Apianosoma trichocephalus	SSDF	Murina (1984)
Apoprionospio pygmaea	SDF	Fauchald and Jumars (1979); WoRMS
Apseudes sp. A	SF	Drumm (2005)
Argissa hamatipes	SF	Carlton (2007)
Aricidea (*Aedicira*) sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Aricidea (*Allia*) sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Aricidea cf. *pseudoarticulata*	SDF	Fauchald and Jumars (1979); WoRMS
Aricidea fragilis	SDF	Fauchald and Jumars (1979); WoRMS
Aricidea quadrilobata	SDF	Fauchald and Jumars (1979); WoRMS
Aricidea wassi	SDF	Fauchald and Jumars (1979); WoRMS
Armandia agilis	SSDF	Fauchald and Jumars (1979); WoRMS
Armandia maculata	SSDF	Fauchald and Jumars (1979); WoRMS
Aspidosiphon sp.	SDF	Murina (1984)
Astarte nana	SF	NMiTA
Asychis elongatus	SSDF	Fauchald and Jumars (1979); WoRMS
Automate sp.	Carn	Palomar et al., (2005)
Axiothella sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Balanoglossus sp. 1	SF	Ruppert and Barnes (1994)
Balanoglossus sp. 2	SF	Ruppert and Barnes (1994)
Barantolla sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Boccardiella sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Boguea enigmatica	SSDF	Fauchald and Jumars (1979); WoRMS
Boguea sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Boguella sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Brada villosa	SDF	Fauchald and Jumars (1979); WoRMS
Brisaster sp.	SSDF	WoRMS
Brissopsis alta	SSDF	WoRMS
Busycotypus spiratus	Carn	NMiTA
Caecum floridanum	SDF	Tunnell, Jr. et al., (2010)
Capitella capitata	SSDF	Fauchald and Jumars (1979)
Caprella sp.	Carn	Keith (1969)
Cardiomya costellata	Carn	NMiTA
Careliopsis styliformis	Carn	NMiTA
Carinomidae sp. 1	Carn	Macdonald et al., (2010)
Carinomidae sp. 2	Carn	Macdonald et al., (2010)
Caryocorbula contracta	SF	NMiTA
Caulleriella cf. *zetlandica*	SDF	Fauchald and Jumars (1979); WoRMS
Caulleriella sp. B	SDF	Fauchald and Jumars (1979); WoRMS
Cerapus sp.	SF	Barnard et al., (1991)
Cerapus sp. C	SF	Barnard et al., (1991)
Chaetozone sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Chaetozone sp. B	SDF	Fauchald and Jumars (1979); WoRMS
Chaetozone sp. C	SDF	Fauchald and Jumars (1979); WoRMS
Chaetozone sp. D	SDF	Fauchald and Jumars (1979); WoRMS
Chioneryx grus	SF	NMiTA
Chone americana	SF	Fauchald and Jumars (1979); WoRMS
Chone cf. *americana*	SF	Fauchald and Jumars (1979); WoRMS

Table E1 (continued).

Species list	Feeding	Reference
Cirriformia sp. B	SDF	Fauchald and Jumars (1979); WoRMS
Cirriformia sp. C	SDF	Fauchald and Jumars (1979); WoRMS
Cirrophorus americanus	SDF	Fauchald and Jumars (1979); WoRMS
Cirrophorus branchiatus	SDF	Fauchald and Jumars (1979); WoRMS
Cirrophorus cf. *forticirratus*	SDF	Fauchald and Jumars (1979); WoRMS
Clavodorum sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Cleantioides planicauda	Carn	Brusca et al., (2001)
Clymenella torquata	SSDF	Fauchald and Jumars (1979); WoRMS
Cossura soyeri	SSDF	Fauchald and Jumars (1979); WoRMS
Cossura sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Crassinella martinicensis	SF	NMiTA
Crepidula convexa	SF	NMiTA
Crepidula sp.	SF	NMiTA
Cupuladria sp.	SF	Cook (1965a); Cook (1965b)
Cyathura sp.	Carn	Wägele et al., (1981)
Cyclaspis platymerus	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Cyclaspis pustulata	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Cyclostremiscus jeannae	Herb	NMiTA
Decamastus gracilis	SSDF	Fauchald and Jumars (1979); WoRMS
Decamastus sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Diastylis sp.	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Dimya tigrina	SF	NMiTA
Diopatra cf. *papillata*	Carn	Fauchald and Jumars (1979); WoRMS
Diopatra cuprea	Carn	Fauchald and Jumars (1979); WoRMS
Diopatra neotridens	Carn	Fauchald and Jumars (1979); WoRMS
Diplocirrus capensis	SDF	Fauchald and Jumars (1979); WoRMS
Diplocirrus sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Diplodonta punctata	SF	NMiTA
Diplodonta soror	SF	NMiTA
Divaricella quadrisulcata	SF	Dupleiss et al., (2004)
Dorvillea sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Dorvillidae genus B	Carn	Fauchald and Jumars (1979); WoRMS
Echiura sp. 1	SDF	Jaccarini and Schembri (1977)
Edotea montosa	Carn	WoRMS
Edwardsia sp.	SDF	WoRMS; Macdonald et al., (2010)
Ennucula aegeensis	SSDF	NMiTA
Episiphon sowerbyi	Carn	Tunnell, Jr. et al., (2010)
Euchone cf. *incolor*	SF	Fauchald and Jumars (1979); WoRMS
Euchone cf. *southerni*	SF	Fauchald and Jumars (1979); WoRMS
Euchone sp. A	SF	Fauchald and Jumars (1979); WoRMS
Euclymene sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Euclymene sp. B	SSDF	Fauchald and Jumars (1979); WoRMS
Eudorella sp.	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Eulalia bilineata	Carn	Fauchald and Jumars (1979); WoRMS
Eulimastoma canaliculatum	Carn	NMiTA
Eunice vittata	Carn	Fauchald and Jumars (1979); WoRMS
Eupolymnia nebulosa	SDF	Fauchald and Jumars (1979)
Eurytellina lineata	SDF	NMiTA
Eurythoe sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Evalea emeryi	Carn	NMiTA
Exogone dispar	Carn	Fauchald and Jumars (1979)
Exogone lourei	Carn	Fauchald and Jumars (1979)

Table E1 (continued).

Species list	Feeding	Reference
Exogone sp. B	Carn	Fauchald and Jumars (1979)
Fabricia sp. A	SF	Fauchald and Jumars (1979); WoRMS
Fargoa gibbosa	Carn	NMiTA
Fargoa sp.	Carn	NMiTA
Ficus communis	Carn	NMiTA
Fimbriosthenelais hobbsi	Carn	Fauchald and Jumars (1979); WoRMS
Fimbriosthenelais minor	Carn	Fauchald and Jumars (1979); WoRMS
Finella dubia	Herb	Fauchald and Jumars (1979); WoRMS
Gadila mayori	Carn	Tunnell, Jr. et al., (2010)
Gemma gemma	SF	NMiTA
Gemophos tinctus	Carn	NMiTA
Glottidia pyramidata	SF	Paine (1963)
Glycera americana	Carn	Fauchald and Jumars (1979); WoRMS
Glycera dibranchiata	Carn	Fauchald and Jumars (1979); WoRMS
Glycera sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Glycera sp. D	Carn	Fauchald and Jumars (1979); WoRMS
Glycera sp. E	Carn	Fauchald and Jumars (1979); WoRMS
Glycinde solitaria	Carn	Fauchald and Jumars (1979); WoRMS
Glycymeris decussata	SF	NMiTA
Glyphohesione klatti	Carn	Fauchald and Jumars (1979); WoRMS
Gnathia sp.	SDF	Manship et al., (2012)
Golfingia sp. 1	SSDF	Murina (1984)
Golfingia sp. 2	SSDF	Murina (1984)
Golfingia sp. 3	SSDF	Murina (1984)
Goniada littorea	Carn	Fauchald and Jumars (1979); WoRMS
Gouldia cerina	SF	NMiTA
Grubeulepis augeneri	Carn	Fauchald and Jumars (1979); WoRMS
Gyptis brevipalpa	Carn	Fauchald and Jumars (1979); WoRMS
Gyptis vittata	Carn	Fauchald and Jumars (1979); WoRMS
Haloclava sp.	SF	Fautin et al., (2009)
Haminoea cf. *elegans*	Herb	NMiTA
Haminoea succinea	Herb	NMiTA
Hartmanodes sp.	SDF	Sainte-Marie and Brunei (1985)
Hemiliostraca auricincta	Carn	NMiTA
Heteromastus filiformis	SSDF	Fauchald and Jumars (1979); WoRMS
Heterospio longissima	SDF	Fauchald and Jumars (1979); WoRMS
Houbricka incisa	Carn	NMiTA
Hypereteone heteropoda	Carn	Fauchald and Jumars (1979); WoRMS
Hyssura sp.	Carn	Wetzer et al., (1997)
Inermonephtys inermis	Carn	Fauchald and Jumars (1979); WoRMS
Iphimedidae sp. 1	SDF	Michel (2011)
Isolda pulchella	SDF	Fauchald and Jumars (1979); WoRMS
Jasmineira cf. *pacifica*	SF	Fauchald and Jumars (1979); WoRMS
Kinbergonuphis sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Kinbergonuphis sp. B	Carn	Fauchald and Jumars (1979); WoRMS
Laevicardium mortoni	SF	NMiTA
Laonice cirrata	SDF	Fauchald and Jumars (1979); WoRMS
Leucon sp. A	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Levinsenia gracilis	SDF	Fauchald and Jumars (1979); WoRMS
Levinsenia reducta	SDF	Fauchald and Jumars (1979); WoRMS
Lineidae sp. 1	Carn	Macdonald et al., (2010)
Lineidae sp. 2	Carn	Macdonald et al., (2010)

Table E1 (continued).

Species list	Feeding	Reference
Lineidae sp. 3	Carn	Macdonald et al., (2010)
Listriella barnardi	SF	Reish and Barnard (1979)
Listriella carinata	SF	Reish and Barnard (1979)
Listriella sp. A	SF	Reish and Barnard (1979)
Loimia viridis	SDF	Fauchald and Jumars (1979)
Lucifer faxoni	Carn	Lee et al., (1992)
Lumbrineris sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Lumbrineris sp. C	Carn	Fauchald and Jumars (1979); WoRMS
Lumbrineris sp. D	Carn	Fauchald and Jumars (1979); WoRMS
Lumbrineris sp. E	Carn	Fauchald and Jumars (1979); WoRMS
Lumbrineris tenuis	Carn	Fauchald and Jumars (1979); WoRMS
Macoma constricta	SDF	NMiTA
Macoma pseudomera	SDF	NMiTA
Macoma pulleyi	SDF	NMiTA
Macroclymene sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Macromphalina pierrot	Herb	NMiTA
Magelona sp. G	SDF	Fauchald and Jumars (1979); WoRMS
Magelona sp. H	SDF	Fauchald and Jumars (1979); WoRMS
Magelona sp. I	SDF	Fauchald and Jumars (1979); WoRMS
Magelona sp. J	SDF	Fauchald and Jumars (1979); WoRMS
Magelona sp. L	SDF	Fauchald and Jumars (1979); WoRMS
Maldane sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Marphysa sanguinea	Carn	Fauchald and Jumars (1979); WoRMS
Martesia striata	SF	NMiTA
Mediomastus californiensis	SSDF	Fauchald and Jumars (1979); WoRMS
Megalomma bioculatum	SF	Fauchald and Jumars (1979); WoRMS
Megalomma sp. A	SF	Fauchald and Jumars (1979); WoRMS
Meiodorvillea sp. B	Carn	Fauchald and Jumars (1979); WoRMS
Melinna cristata	SDF	Fauchald and Jumars (1979); WoRMS
Microporella sp.	SF	WoRMS
Micrura sp.	Carn	Macdonald et al., (2010)
Minuspio cirrifera	SDF	Fauchald and Jumars (1979); WoRMS
Mooreonuphis pallidula	Carn	Fauchald and Jumars (1979); WoRMS
Musculus lateralis	SF	NMiTA
Myriochele oculata	SSDF	Fauchald and Jumars (1979)
Myriochele sp. A	SSDF	Fauchald and Jumars (1979)
Mystides borealis	Carn	Fauchald and Jumars (1979); WoRMS
Neanthes micromma	Carn	Fauchald and Jumars (1979); WoRMS
Neanthes succinea	Carn	Fauchald and Jumars (1979); WoRMS
Nephtys cf. *hombergii*	Carn	Fauchald and Jumars (1979); WoRMS
Nephtys incisa	Carn	Fauchald and Jumars (1979); WoRMS
Nephtys simoni	Carn	Fauchald and Jumars (1979); WoRMS
Nephtys squamosa	Carn	Fauchald and Jumars (1979); WoRMS
Nevertia duplicata	Carn	NMiTA
Ninoe sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Ninoe sp. B	SDF	Fauchald and Jumars (1979); WoRMS
Nothria sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Notomastus americanus	SSDF	Fauchald and Jumars (1979); WoRMS
Notomastus daueri	SSDF	Fauchald and Jumars (1979); WoRMS
Notomastus hemipodus	SSDF	Fauchald and Jumars (1979); WoRMS
Notomastus latericeus	SSDF	Fauchald and Jumars (1979); WoRMS
Notomastus lineatus	SSDF	Fauchald and Jumars (1979); WoRMS

Table E1 (continued).

Species list	Feeding	Reference
Notomastus lobatus	SSDF	Fauchald and Jumars (1979); WoRMS
Notomastus sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Notomastus tenuis	SSDF	Fauchald and Jumars (1979); WoRMS
Nucula calcicola	SSDF	NMiTA
Nucula crenulata	SSDF	NMiTA
Nucula proxima	SSDF	NMiTA
Nuculana acuta	SSDF	NMiTA
Nuculana concentrica	SSDF	NMiTA
Nuculana unca	SSDF	NMiTA
Odostomia cf. *hendersoni*	Carn	NMiTA
Odostomia laevigata	Carn	NMiTA
Oedocerotidae sp. 1	Carn	Guerra-Garcia et al., (2014)
Oedocerotidae sp. 2	Carn	Guerra-Garcia et al., (2014)
Oedocerotidae sp. 3	Carn	Guerra-Garcia et al., (2014)
Onuphis sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Ophelina cf. *acuminata*	SSDF	Fauchald and Jumars (1979); WoRMS
Ophelina cylindricaudata	SSDF	Fauchald and Jumars (1979); WoRMS
Ophiactis sp. 1	SDF	Fratt and Dearborn (1984); Stöhr et al., (2012)
Ophiolepididae sp.	SDF	Fratt and Dearborn (1984); Stöhr et al., (2012)
Owenia sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Oxyurostylis smithi	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Oxyurostylis sp.	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Pachycheles sp.	Carn	Gonor and Gonor (1973)
Pagurus longicarpus	Carn	WoRMS
Pagurus maclaughlinae	Carn	WoRMS
Pagurus sp.	Carn	WoRMS
Pandora arenosa	SF	NMiTA
Pandora bushiana	SF	NMiTA
Pandora sp.	SF	NMiTA
Pandora trilineata	SF	NMiTA
Paradentalium americanum	Carn	WoRMS
Paraheteromastus sp.	SSDF	Fauchald and Jumars (1979); WoRMS
Paramphinome sp. B	SDF	Fauchald and Jumars (1979); WoRMS
Paranaitis polynoides	Carn	Fauchald and Jumars (1979); WoRMS
Paraonis fulgens	SDF	Fauchald and Jumars (1979); WoRMS
Paraonis pygoenigmatica	SDF	Fauchald and Jumars (1979); WoRMS
Paraprionospio pinnata	SDF	Fauchald and Jumars (1979); WoRMS
Parasabella microphthalma	SF	Fauchald and Jumars (1979); WoRMS
Parasmittina sp.	SF	WoRMS
Parviturbo rehderi	Herb	NMiTA
Pectinaria gouldii	SSDF	Fauchald and Jumars (1979); WoRMS
Peresiella sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Periploma cf. *margaritaceum*	SF	NMiTA
Periploma margaritaceum	SF	NMiTA
Petaloproctus sp.	SSDF	Fauchald and Jumars (1979); WoRMS
Petitilla crosseana	Carn	NMiTA
Pettiboneia sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Phascolion sp.	SDF	Murina (1984)
Pherusa inflata	SDF	Fauchald and Jumars (1979); WoRMS
Pherusa sp.	SDF	Fauchald and Jumars (1979); WoRMS
Phlyctiderma semiaspera	SF	NMiTA
Pholoe sp. C	Carn	Fauchald and Jumars (1979); WoRMS

Table E1 (continued).

Species list	Feeding	Reference
Phoronida sp. 1	SF	NMiTA
Photis melanica	SDF	WoRMS
Photis sp.	SDF	WoRMS
Phyllodina squamifera	SDF	NMiTA
Phyllodoce longipes	Carn	Fauchald and Jumars (1979); WoRMS
Phylo felix	SSDF	Fauchald and Jumars (1979); WoRMS
Pinnixa retinens	Carn	WoRMS
Pinnixa sp.	Carn	WoRMS
Piromis roberti	SDF	Fauchald and Jumars (1979); WoRMS
Pista sp.	SDF	Fauchald and Jumars (1979)
Pista sp. B	SDF	Fauchald and Jumars (1979)
Pitar fulminatus	SF	NMiTA
Poecilochaetus johnsoni	SDF	Fauchald and Jumars (1979)
Polinices lacteus	Carn	NMiTA
Polycirrus plumosus	SDF	Fauchald and Jumars (1979)
Polycladida sp. 1	Carn	Barnes (1980)
Polycladida sp. 2	Carn	Barnes (1980)
Polymesoda caroliniana	SDF	NMiTA
Pontonidae sp.	Carn	Bruce (1972)
Pourtalesidae sp. A	SSDF	WoRMS
Prionospio cristata	SDF	Fauchald and Jumars (1979); WoRMS
Prionospio fallax	SDF	Fauchald and Jumars (1979); WoRMS
Prionospio sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Prionospio steenstrupi	SDF	Fauchald and Jumars (1979); WoRMS
Processa sp.	Carn	WoRMS
Promysis atlantica	Carn	Clarke (1956)
Pseudocarcinus sp.	Carn	Currie and Ward (2009)
Pseudotanais sp. A	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Pseudotanais sp. B	SDF	Blazewicz-Paszkowycz and Ligowski (2002)
Pterocirrus macroceros	Carn	Fauchald and Jumars (1979); WoRMS
Puberella intapurpurea	SF	NMiTA
Radiolucina amianta	SSDF	NMiTA
Rissoella caribaea	Herb	NMiTA
Sabella melanochlora	SF	Fauchald and Jumars (1979); WoRMS
Sabella microphthalma	SF	Fauchald and Jumars (1979); WoRMS
Sabella sp. A	SF	Fauchald and Jumars (1979); WoRMS
Sabellides sp. A	SDF	Fauchald and Jumars (1979); WoRMS
Sarsonuphis hartmanae	Carn	Fauchald and Jumars (1979); WoRMS
Schistomeringos pectinata	Carn	Fauchald and Jumars (1979); WoRMS
Schistomeringos sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Scissula iris	SDF	NMiTA
Scolelepis texana	SDF	Fauchald and Jumars (1979); WoRMS
Scoloplos sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Scyphoproctus platyproctus	SSDF	Fauchald and Jumars (1979); WoRMS
Scyphoproctus sp.	SSDF	Fauchald and Jumars (1979); WoRMS
Sebidae sp. 1	SF	Reish and Barnard (1979)
Serolis mgrayi	Carn	Poore and Bruce (2012)
Sigalion sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Sigambra tentaculata	Carn	Fauchald and Jumars (1979); WoRMS
Sipuncula sp. 1	SSDF	Murina (1984)
Sipunculus nudus	SSDF	Murina (1984)
Solariorbis infracarinatus	Herb	NMiTA

Table E1 (continued).

Species list	Feeding	Reference
Solenosteira cancellaria	Carn	NMiTA
Speocarcinus sp.	Carn	Ng et al., (2008)
Sphaerella verrilli	SF	NMiTA
Sphaerephesia sp. A	SSDF	Fauchald and Jumars (1979); WoRMS
Spiochaetopterus costarum	SDF	Fauchald and Jumars (1979); WoRMS
Spiophanes missionensis	SDF	Fauchald and Jumars (1979); WoRMS
Sternaspis scutata	SSDF	Fauchald and Jumars (1979); WoRMS
Sthenelais limicola	Carn	Fauchald and Jumars (1979); WoRMS
Sthenelanella sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Sthenolepis cf. *grubei*	Carn	Fauchald and Jumars (1979); WoRMS
Sthenolepis sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Syllis (*Ehlersia*) sp. A	Carn	Fauchald and Jumars (1979); WoRMS
Taphromysis bowmani	Carn	Clarke (1956)
Tectonatica pusilla	Carn	NMiTA
Teinostoma parvicallum	Herb	NMiTA
Tellidora cristata	SDF	NMiTA
Terebellides stroemii	SDF	Fauchald and Jumars (1979)
Tharyx cf. *annulosus*	SDF	Fauchald and Jumars (1979); WoRMS
Tharyx sp.	SDF	Fauchald and Jumars (1979); WoRMS
Thyone deichmannae	SSDF	WoRMS
Thysanocardia sp.	SF	Murina (1984)
Travisia hobsonae	SSDF	Fauchald and Jumars (1979); WoRMS
Trigonulina ornata	Carn	NMiTA
Trochochaeta sp.	SDF	Fauchald and Jumars (1979)
Tubificoides amplivasatus	SSDF	Monokov (1972)
Tubiluchus corallicola	SSDF	Kirsteuer and Rützler (1973)
Turbonilla heilprini	Carn	NMiTA
Turbonilla levis	Carn	NMiTA
Umbilibalcis lata	Carn	Tunnell, Jr. et al., (2010); WoRMS
Umbilibalcis sp.	Carn	NMiTA
unidentified Entoprocta	SF	Atkins (1932)
unidentified Oligochaeta	SSDF	Monokov (1972)
unidentified Pogonophora	SDF	Nørrevang (1965)
Uromunna cf. *hayesi*	Herb	WoRMS
Urosalpinx sp.	Carn	NMiTA
Vesicularia sp.	SF	WoRMS
Vitrinella floridana	Herb	NMiTA
Volvulella minuta	Herb	NMiTA
Volvulella texasiana	Herb	NMiTA
Xanthidae sp.	Carn	Ng et al., (2008)
Xenanthura brevitelson	Carn	Wetzer et al., (1997)

APPENDIX F

LIST OF OPPORTUNIST SPECIESE

Table F1

List of opportunist macrobenthos species with associated ecological groups and referenced sources (ND = no data).

Species list	Feeding	Reference
Abra aequalis	IV	Diaz & Rosenberg 1995
Amphiuridae sp. 1	IV	Diaz & Rosenberg 1995
Amphiuridae sp. 2	IV	Diaz & Rosenberg 1995
Amphiuridae sp. 3	IV	Diaz & Rosenberg 1995
Amphiuridae sp. 4	IV	Diaz & Rosenberg 1995
Aonidella dayi	ND	Borja et al., 2000
Aonides mayaguezensis	III	Borja et al., 2000
Apoprionospio pygmaea	ND	Borja et al., 2000
Astarte nana	V	Diaz & Rosenberg 1995
Asychis elongatus	IV	Diaz & Rosenberg 1995
Barantolla sp. A	ND	Borja et al., 2000
Boccardiella sp. A	ND	Borja et al., 2000
Capitella capitata	V	Borja et al., 2000
Caulleriella cf. *zetlandica*	III	Borja et al., 2000
Caulleriella sp. B	III	Borja et al., 2000
Chaetozone sp. A	IV	Borja et al., 2000
Chaetozone sp. B	IV	Borja et al., 2000
Chaetozone sp. C	IV	Borja et al., 2000
Chaetozone sp. D	IV	Borja et al., 2000
Cirriformia sp. B	IV	Borja et al., 2000
Cirriformia sp. C	IV	Borja et al., 2000
Cossura soyeri	ND	Salen-Picard et al., 2003
Cossura sp. A	ND	Salen-Picard et al., 2003
Decamastus gracilis	ND	Borja et al., 2000
Decamastus sp. A	ND	Borja et al., 2000
Heteromastus filiformis	III	Borja et al., 2000
Laonice cirrata	III	Borja et al., 2000
Lumbrineris sp. A	IV	Diaz & Rosenberg 1995
Lumbrineris sp. C	IV	Diaz & Rosenberg 1995
Lumbrineris sp. D	IV	Diaz & Rosenberg 1995
Lumbrineris sp. E	IV	Diaz & Rosenberg 1995
Lumbrineris tenuis	IV	Diaz & Rosenberg 1995
Magelona sp. H	V	Diaz & Rosenberg 1995
Mediomastus californiensis	III	Borja et al., 2000
Minuspio cirrifera	ND	Borja et al., 2000
Neanthes micromma	IV	Diaz & Rosenberg 1995
Neanthes succinea	V	Pearson-Rosenberg 1978
Nephtys cf. *hombergii*	V	Diaz & Rosenberg 1995
Notomastus americanus	III	Borja et al., 2000
Notomastus daueri	III	Borja et al., 2000
Notomastus hemipodus	III	Borja et al., 2000
Notomastus latericeus	III	Borja et al., 2000
Notomastus lineatus	III	Borja et al., 2000

Table F1 (continued).

Species list	Feeding	Reference
Notomastus lobatus	III	Borja et al., 2000
Notomastus sp. A	III	Borja et al., 2000
Notomastus tenuis	III	Borja et al., 2000
Paraheteromastus sp.	ND	Borja et al., 2000
Paraprionospio pinnata	IV	Diaz & Rosenberg 1995
Pectinaria gouldii	IV	Diaz & Rosenberg 1995
Peresiella sp. A	ND	Borja et al., 2000
Phoronida sp. 1	V	Diaz & Rosenberg 1995
Prionospio cristata	IV	Borja et al., 2000
Prionospio fallax	IV	Borja et al., 2000
Prionospio sp. A	IV	Borja et al., 2000
Prionospio steenstrupi	IV	Borja et al., 2000
Scolelepis texana	III	Borja et al., 2000
Scoloplos sp. A	IV	Diaz & Rosenberg 1995
Scyphoproctus platyproctus	ND	Borja et al., 2000
Scyphoproctus sp.	ND	Borja et al., 2000
Sigambra tentaculata	ND	Rakocinski et al., 1999
Spiophanes missionensis	III	Borja et al., 2000
Tharyx cf. *annulosus*	ND	Borja et al., 2000
Tharyx sp.	ND	Borja et al., 2000
Tubificoides amplivasatus	V	Borja et al., 2000

APPENDIX G

BIOMETRICS DATA

Table G1

Total number of macrobenthos species found in each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections.

Subcore	1	2	3	4	5	6	7	8	9
1A	29	44	36	41	32	38	29	28	44
1B	21	32	32	28	37	25	18	26	21
1C	37	36	39	44	37	28	30	36	35
1D	10	7	11	10	17	10	6	16	9
2A	47	47	33	39	41	42	36	27	33
2B	22	21	23	35	26	26	24	22	29
2C	15	20	15	23	20	20	18	20	20
2D	10	9	16	17	13	13	14	15	11
3A	33	41	36	29	30	31	29	34	31
3B	19	25	11	28	27	26	21	17	28
3C	17	32	26	27	14	33	27	31	31
3D	13	15	15	16	14	14	11	13	10

Table G2

Total macrobenthos abundance (No. of individuals/100 cm²) found in each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	110	142	114	159	105	137	79	79	131	0.66
1B	86	112	148	148	157	82	88	103	80	0.06
1C	157	146	144	204	165	99	138	183	135	0.91
1D	39	39	43	65	135	77	41	105	60	0.06
2A	161	150	122	131	150	138	112	86	163	0.52
2B	80	116	103	144	140	84	84	112	105	0.34
2C	58	54	41	88	73	97	67	71	67	0.93
2D	60	60	88	196	62	64	122	236	52	0.01*
3A	168	174	187	178	122	151	122	129	178	0.08
3B	82	95	54	129	116	112	99	79	180	0.64
3C	49	80	101	94	39	118	127	161	118	0.86
3D	140	161	153	176	155	204	135	200	223	0.43
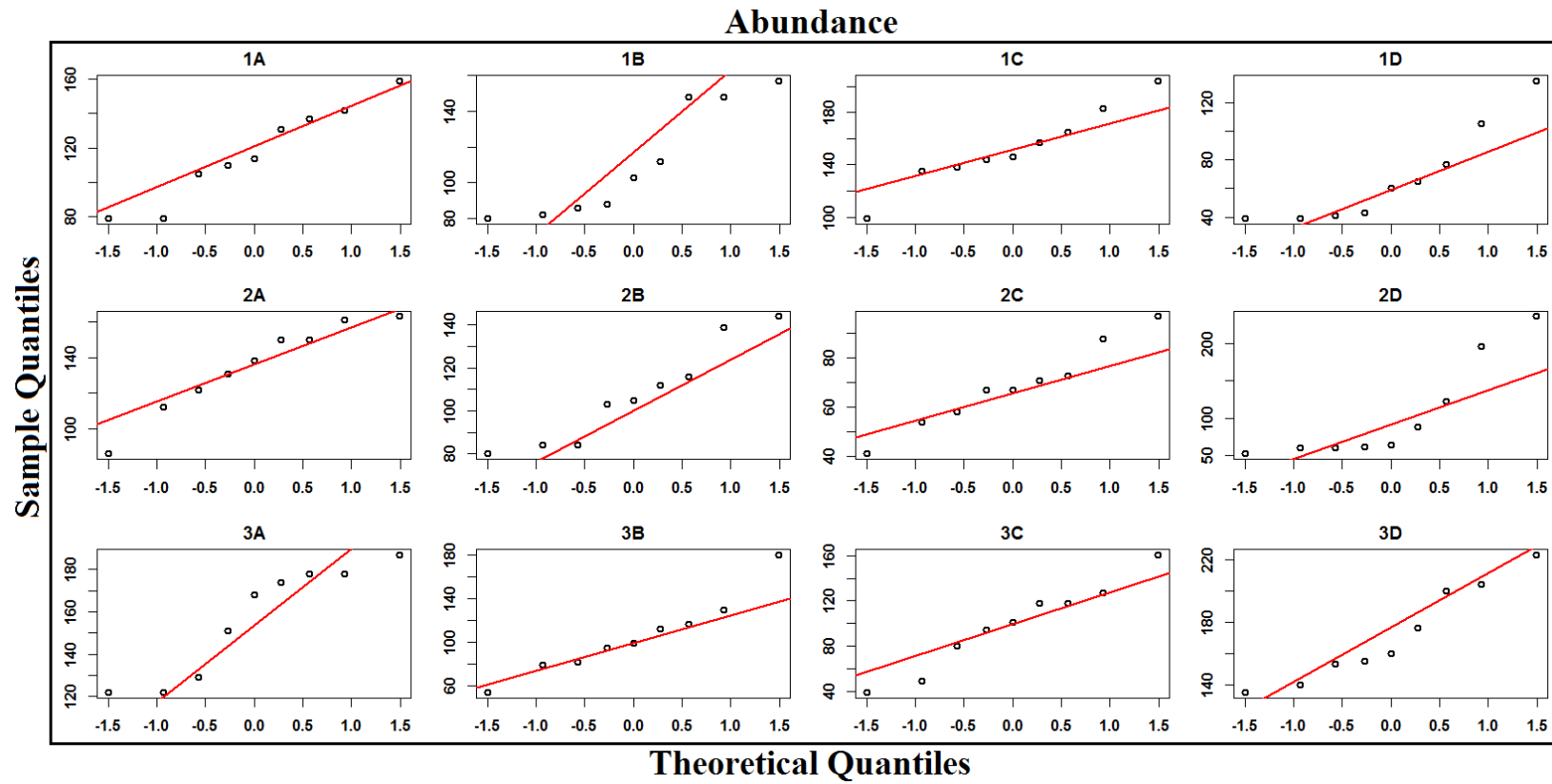
Figure G1. Quantile-Quantile (Q-Q) plots displaying the distribution of total macrobenthos abundance (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

Table G3

Total macrobenthos AFDW biomass (μg/subcore) from each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	1458	1897	1194	1412	715	2792	784	1288	4127	0.05
1B	630	4663	941	890	6345	1652	2069	6691	1415	0.02*
1C	1198	1003	2214	3279	679	735	464	1903	2245	0.37
1D	1217	2619	2893	2026	383	225	277	3823	111	0.07
2A	2350	605	2142	1324	2890	3843	1346	1042	1361	0.46
2B	1076	742	742	9183	10672	5636	806	3699	3023	0.12
2C	187	680	489	1120	439	718	885	987	897	0.88
2D	338	74	740	309	297	323	358	188	165	0.07
3A	2286	1329	2348	1391	3601	1720	2764	4267	2464	0.47
3B	642	3667	464	4333	6018	2664	3709	1261	612	0.28
3C	1639	3281	2884	3931	9601	7089	5923	5864	14539	0.26
3D	879	6744	361	577	1101	1371	847	860	1049	0.00*
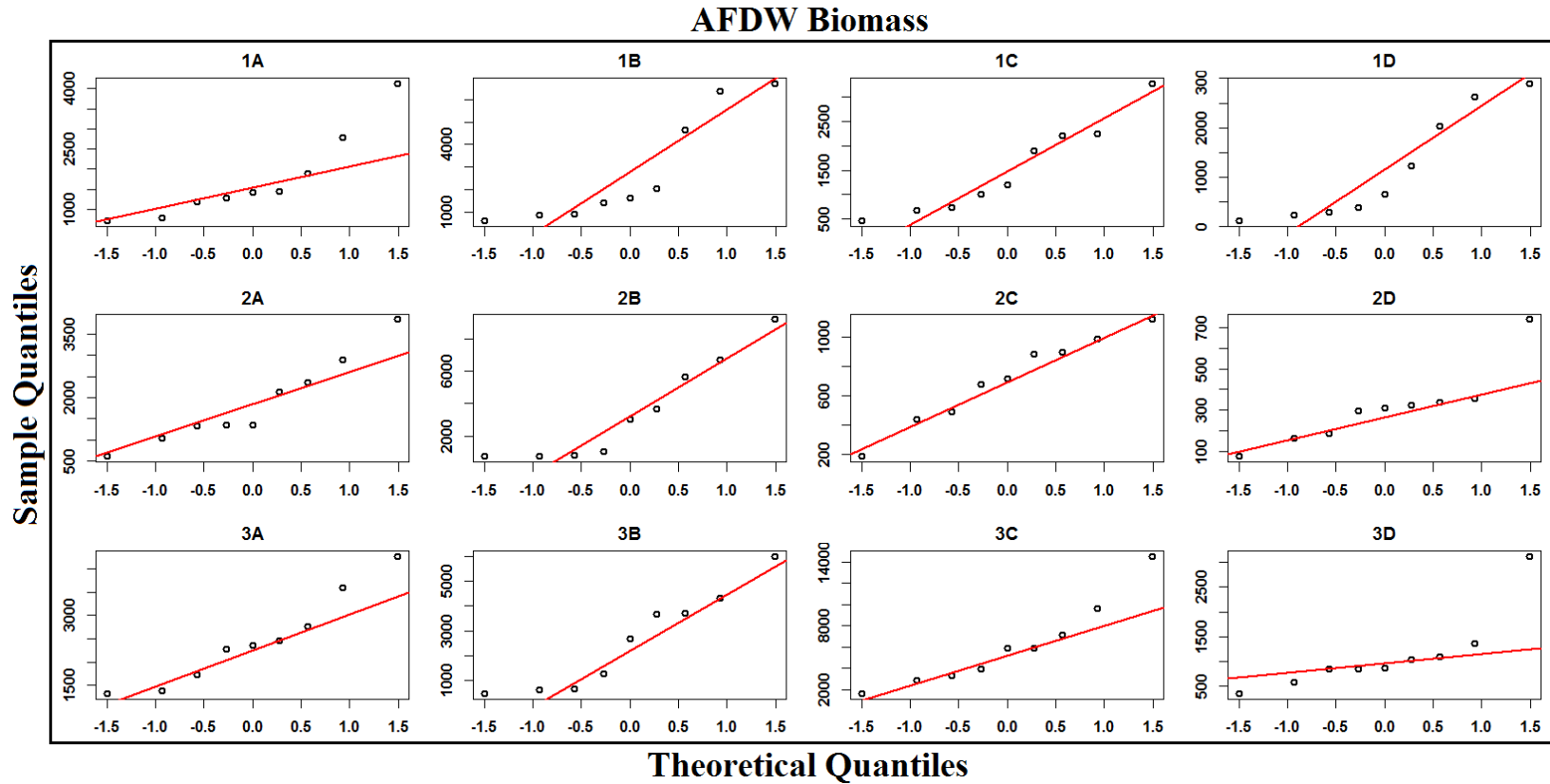
Figure G2. Quantile-Quantile (Q-Q) plots displaying the distribution of total macrobenthos AFDW biomass (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

Table G4

Estimated average individual AFDW biomass (μg) found in each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	642	893	442	674	222	1250	390	645	824	0.87
1B	290	2261	305	235	2977	847	988	3461	646	0.04*
1C	467	402	728	1672	188	179	189	257	918	0.02*
1D	321	1209	1540	989	146	34	14	2043	23	0.08
2A	1155	217	1065	637	1431	1536	576	487	369	0.43
2B	395	215	304	4843	5477	2972	410	1868	723	0.02*
2C	61	225	143	252	144	217	236	245	361	0.64
2D	171	25	336	86	143	116	131	30	62	0.12
3A	676	479	640	312	1658	734	1062	2010	894	0.19
3B	152	1640	184	2025	1977	1131	1411	454	151	0.10
3C	717	1722	777	1350	3295	2111	1008	1211	5471	0.02*
3D	406	3231	72	214	260	407	355	126	423	0.00*

Estimated Average Individual AFDW Biomass (µg)
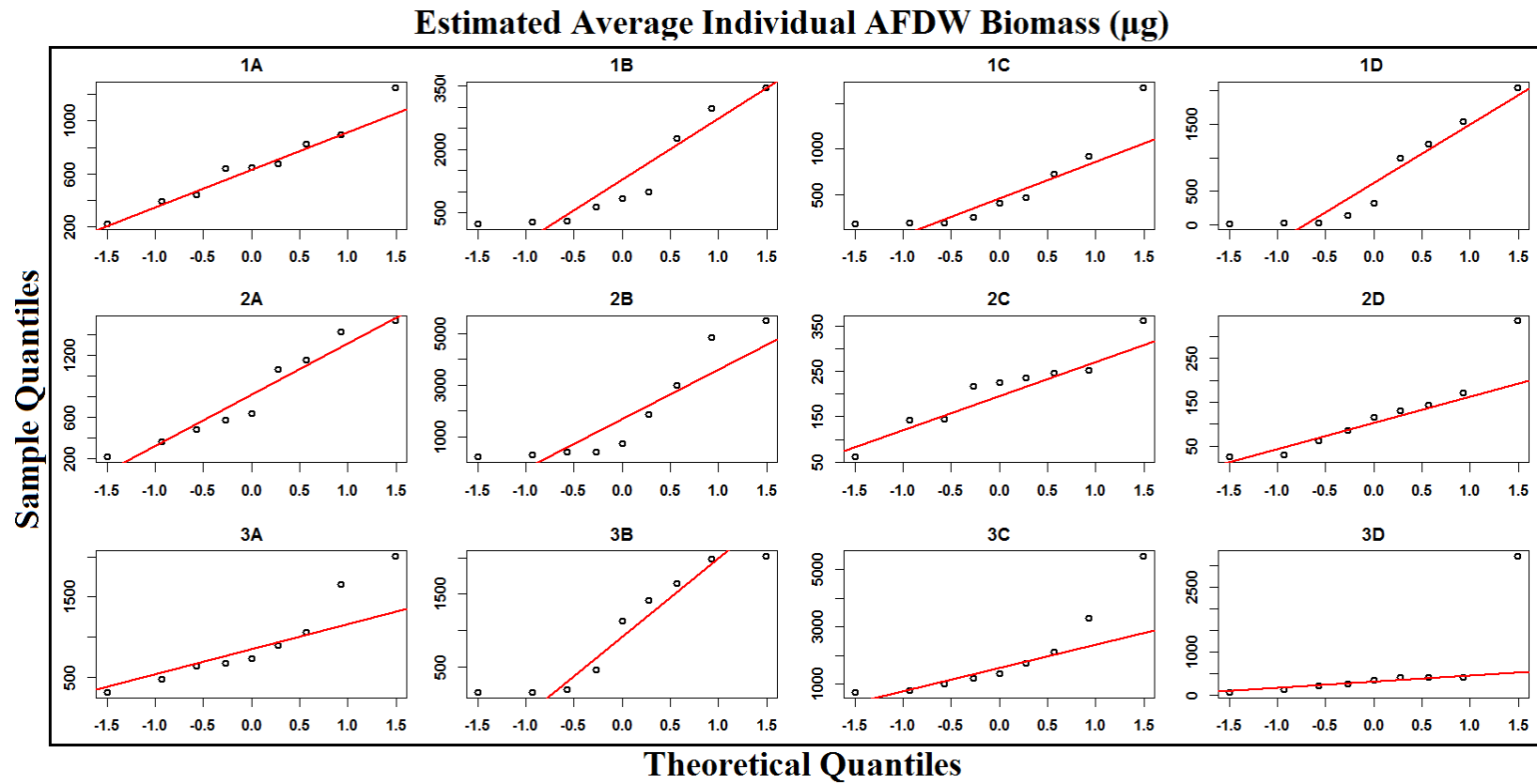
Figure G3. Quantile-Quantile (Q-Q) plots displaying the distribution of estimated average individual AFDW biomass (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

Table G5

Shannon diversity index (H') value for each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	2.96	3.54	3.40	3.09	3.25	3.36	3.24	3.22	3.59	0.91
1B	2.56	2.99	2.89	2.89	3.02	2.73	2.41	2.67	2.55	0.58
1C	3.23	3.19	3.28	3.16	3.15	3.07	2.97	3.07	3.24	0.72
1D	1.72	1.32	1.78	1.71	1.94	1.65	1.55	2.20	1.38	0.85
2A	3.55	3.64	3.18	3.43	3.44	3.52	3.40	3.09	3.02	0.36
2B	2.90	2.47	2.68	3.20	2.77	3.09	2.95	2.55	3.18	0.61
2C	2.43	2.92	2.47	2.85	2.83	2.19	2.49	2.81	2.78	0.17
2D	1.73	1.76	2.45	1.63	1.93	2.29	1.76	1.85	2.02	0.20
3A	3.10	3.11	3.02	2.95	2.96	2.86	2.99	3.08	2.86	0.37
3B	2.62	2.97	1.96	2.85	2.94	2.80	2.68	2.40	2.82	0.06
3C	2.70	3.32	2.90	3.10	2.49	3.30	2.96	3.15	3.13	0.48
3D	1.53	1.75	1.77	1.67	1.75	1.43	1.73	1.73	1.44	0.02*
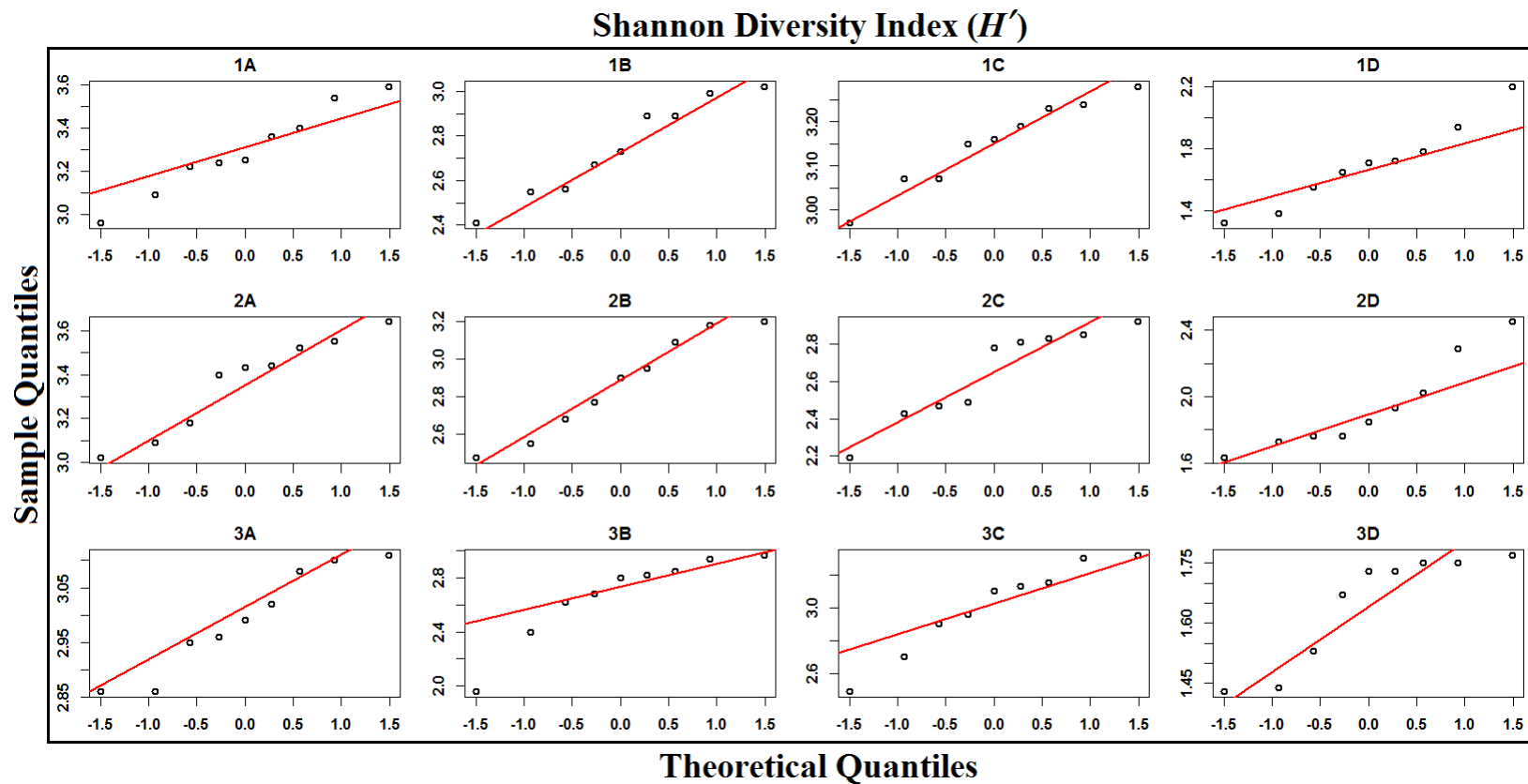
Figure G4. Quantile-Quantile (Q-Q) plots displaying the distribution of Shannon diversity index (*H'*) values (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

Table G6

Pielou's evenness (J) values for each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	0.88	0.94	0.95	0.83	0.94	0.92	0.96	0.97	0.95	0.04*
1B	0.84	0.86	0.83	0.87	0.84	0.85	0.84	0.82	0.84	0.59
1C	0.90	0.89	0.90	0.83	0.87	0.92	0.87	0.86	0.91	0.69
1D	0.75	0.68	0.74	0.74	0.68	0.72	0.87	0.79	0.63	0.77
2A	0.92	0.95	0.91	0.94	0.93	0.94	0.95	0.94	0.86	0.01*
2B	0.94	0.81	0.85	0.90	0.85	0.95	0.93	0.83	0.94	0.15
2C	0.90	0.97	0.91	0.91	0.94	0.73	0.86	0.94	0.93	0.02*
2D	0.75	0.80	0.88	0.57	0.75	0.89	0.67	0.68	0.84	0.72
3A	0.89	0.84	0.84	0.88	0.87	0.83	0.89	0.87	0.83	0.09
3B	0.89	0.92	0.82	0.86	0.89	0.86	0.88	0.85	0.85	0.88
3C	0.95	0.96	0.89	0.94	0.94	0.94	0.90	0.92	0.91	0.53
3D	0.60	0.65	0.65	0.60	0.66	0.54	0.72	0.67	0.63	0.85
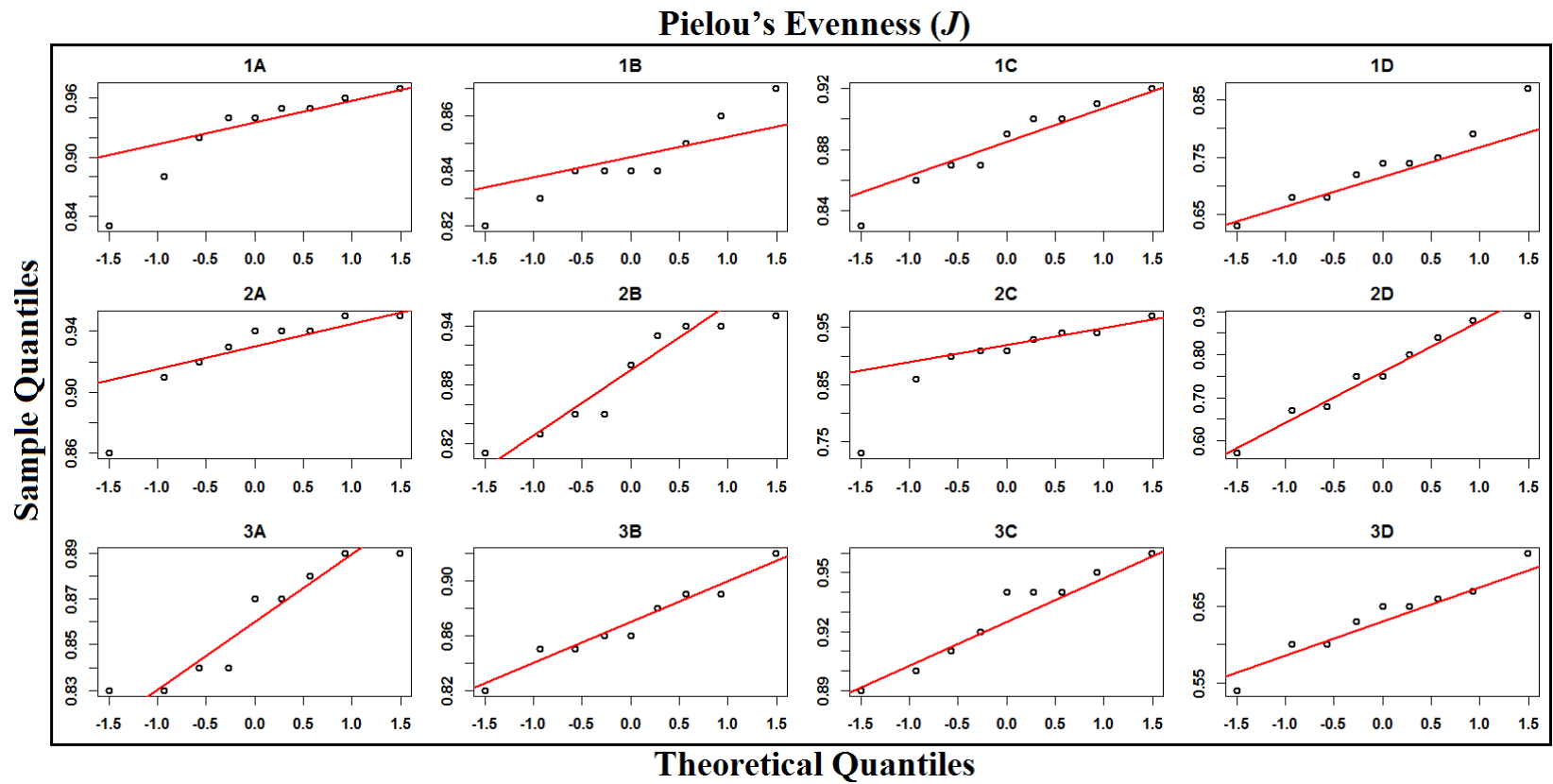
Figure G5. Quantile-Quantile (Q-Q) plots displaying the distribution of Pielou's evenness *(J)* values (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

Table G7

Margalef's species richness index (SR) values for each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	5.95	8.68	7.39	7.89	6.66	7.53	6.42	6.19	8.82	0.49
1B	4.49	6.57	6.21	5.40	7.12	5.44	3.80	5.40	4.56	0.86
1C	7.12	7.02	7.65	8.09	7.05	5.87	5.88	6.72	6.94	0.45
1D	2.45	1.63	2.66	2.15	3.26	2.07	1.35	3.22	1.96	0.70
2A	9.05	9.19	6.67	7.80	7.99	8.32	7.41	5.84	6.28	0.74
2B	4.79	4.21	4.75	6.84	5.06	5.64	5.19	4.45	6.02	0.59
2C	3.45	4.76	3.77	4.92	4.43	4.15	4.04	4.46	4.51	0.87
2D	2.20	1.96	3.35	3.03	2.91	2.89	2.71	2.56	2.53	0.96
3A	6.24	7.75	6.69	5.41	6.04	5.98	5.83	6.79	5.79	0.34
3B	4.08	5.27	2.50	5.56	5.47	5.30	4.35	3.67	5.20	0.09
3C	4.12	7.07	5.42	5.73	3.54	6.71	5.37	5.91	6.29	0.62
3D	2.43	2.76	2.78	2.90	2.58	2.44	2.04	2.26	1.67	0.59
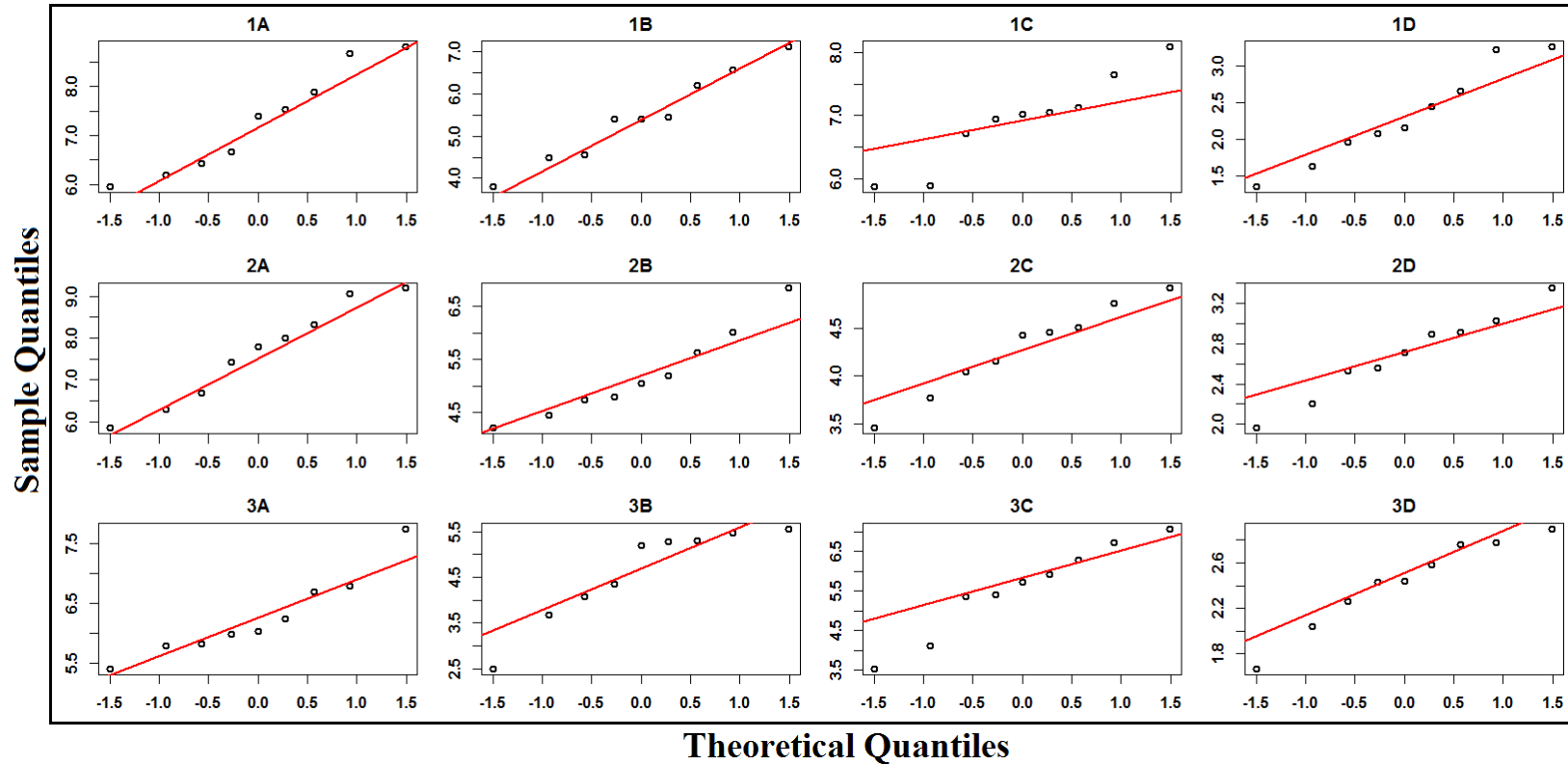
Figure G6. Quantile-Quantile (Q-Q) plots displaying the distribution of Margalef's species richness index (SR) values (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

Table G8

Inverse Simpson diversity index (1/D) value for each subcore at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. The p-value is from the Shapiro-Wilk normal distribution test: if the p-value is less than the chosen α value of 0.05(*), the data are not normally distributed.

Subcore	1	2	3	4	5	6	7	8	9	*p*-value
1A	12.13	26.50	24.64	9.13	18.89	21.23	22.05	22.05	27.84	0.30
1B	8.40	9.94	9.14	11.20	10.47	8.00	7.01	7.05	7.25	0.38
1C	16.33	15.60	15.98	12.63	13.78	15.18	12.39	11.83	17.40	0.51
1D	3.32	2.44	3.37	3.37	4.02	3.32	4.17	5.87	2.40	0.12
2A	24.33	29.36	17.98	24.02	23.53	26.08	24.66	17.63	12.68	0.41
2B	15.28	6.72	9.73	17.49	11.14	18.58	15.00	8.18	19.60	0.49
2C	8.98	17.16	8.96	13.07	14.49	4.25	7.62	14.16	12.71	0.79
2D	3.97	4.70	9.32	2.58	3.82	7.32	3.68	3.75	5.76	0.13
3A	15.34	10.99	11.04	13.57	11.21	9.90	13.24	13.04	10.71	0.37
3B	10.64	14.69	4.98	12.05	13.73	9.73	10.52	7.47	11.64	0.81
3C	13.00	21.75	12.57	18.12	10.26	22.17	14.27	18.31	16.61	0.69
3D	2.73	3.58	3.18	2.94	3.58	2.27	3.87	3.48	2.59	0.73

# Inverse Simpson Diversity Index (1/D)
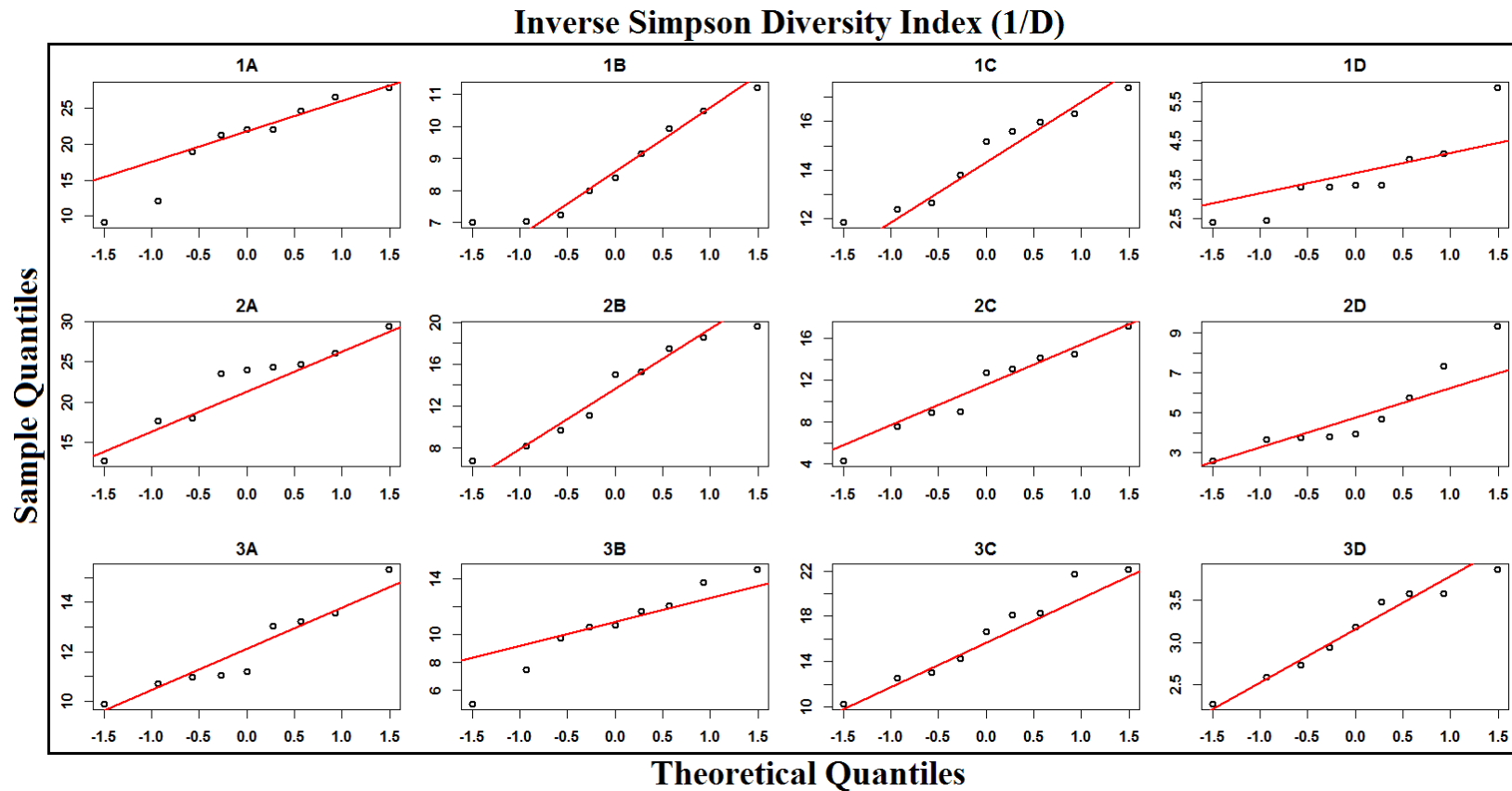
Figure G7. Quantile-Quantile (Q-Q) plots displaying the distribution of inverse Simpson diversity index (1/D) values (n = 9) at sites A, B, C and D for April 2009 (1), September 2009 (2) and August 2010 (3) sample collections. Red line is an estimated reference line indicating the normal distribution for the population of that sample collection.

APPENDIX H

STATISTICAL SIGNIFICANCE TEST RESULTS

Table H1

The Mann-Whitney U-test results for macrobenthos abundance between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	W	p-value	2.5% CI	97.5% CI	Estd. Difference
1A and 1B	43.000	0.860	-26.000	43.000	2.000
1A and 1C	15.000	0.027	-67.000	4.000	-33.000
1A and 1D	72.500	0.005	19.000	88.000	54.000
1B and 1C	17.500	0.047	-71.000	0.000	-47.000
1B and 1D	70.000	0.010	13.000	83.000	43.000
1C and 1D	78.500	0.001	56.000	118.000	94.000
2A and 2B	65.500	0.030	2.000	54.000	28.000
2A and 2C	79.000	0.001	45.000	92.000	68.000
2A and 2D	59.500	0.102	-35.000	88.000	52.000
2B and 2C	75.000	0.003	15.000	62.000	39.000
2B and 2D	53.000	0.289	-52.000	52.000	24.000
2C and 2D	33.500	0.565	-99.000	11.000	-8.000
3A and 3B	70.500	0.009	17.000	86.000	56.000
3A and 3C	75.000	0.003	21.000	90.000	60.000
3A and 3D	30.000	0.377	-45.000	21.000	-17.000
3B and 3C	42.000	0.930	-36.000	49.000	2.000
3B and 3D	6.000	0.003	-105.000	-36.000	-66.000
3C and 3D	4.500	0.002	-110.000	-35.000	-73.000

Table H2

The Mann-Whitney U-test results for macrobenthos abundance within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	W	p-value	2.5% CI	97.5% CI	Estd. Difference
1A and 2A	23.500	0.145	-47.000	9.000	-19.000
1A and 3A	13.000	0.017	-69.000	-12.000	-41.000
2A and 3A	21.000	0.092	-47.000	9.000	-24.000
1B and 2B	43.500	0.825	-27.000	36.000	2.000
1B and 3B	45.000	0.724	-28.000	45.000	4.000
2B and 3B	46.000	0.658	-28.000	32.000	4.000
1C and 2C	81.000	0.000	60.000	110.000	84.000
1C and 3C	71.000	0.008	19.000	95.000	50.000
2C and 3C	20.000	0.077	-60.000	5.000	-30.000
1D and 2D	25.000	0.184	-83.000	13.000	-21.000
1D and 3D	0.500	0.000	-139.000	-75.000	-101.000
2D and 3D	15.000	0.027	-116.000	-13.000	-88.000

Table H3

The Mann-Whitney U-test results for macrobenthos AFDW biomass between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	W	p-value	2.5% CI	97.5% CI	Estd. Difference
1A and 1B	32.000	0.480	-3553.000	658.000	-226.000
1A and 1C	46.000	0.659	-833.000	948.000	214.000
1A and 1D	48.000	0.537	-1311.000	1301.000	438.000
1B and 1C	50.000	0.427	-593.000	3984.000	454.000
1B and 1D	55.000	0.216	-1085.000	3798.000	830.000
1C and 1D	45.000	0.724	-1562.000	1253.000	239.000
2A and 2B	33.000	0.536	-5340.000	619.000	-809.000
2A and 2C	74.000	0.004	359.000	1955.000	907.000
2A and 2D	80.000	0.001	745.000	2276.000	1181.000
2B and 2C	68.000	0.017	88.000	8063.000	2305.000
2B and 2D	81.000	0.000	497.000	8443.000	2714.000
2C and 2D	70.000	0.010	131.000	690.000	409.000
3A and 3B	41.000	1.000	-1985.000	1706.000	68.000
3A and 3C	12.000	0.013	-5760.000	-517.000	-2822.000
3A and 3D	71.000	0.008	469.000	2187.000	1363.000
3B and 3C	17.000	0.042	-5934.000	-220.000	-2670.000
3B and 3D	52.000	0.331	-415.000	3132.000	900.000
3C and 3D	75.000	0.003	1835.000	6728.000	4493.000

Table H4

The Mann-Whitney U-test results for macrobenthos AFDW biomass within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	W	p-value	2.5% CI	97.5% CI	Estd. Difference
1A and 2A	37.000	0.791	-1156.000	683.000	-98.000
1A and 3A	22.000	0.112	-1680.000	129.000	-867.000
2A and 3A	25.000	0.185	-1459.000	426.000	-622.000
1B and 2B	38.000	0.860	-3984.000	1327.000	-112.000
1B and 3B	46.000	0.659	-2294.000	2636.000	299.000
2B and 3B	49.000	0.480	-2319.000	3235.000	278.000
1C and 2C	63.000	0.052	-1.000	1534.000	564.000
1C and 3C	5.000	0.002	-6625.000	-1378.000	-3678.000
2C and 3C	0.000	0.000	-8481.000	-2384.000	-4967.000
1D and 2D	59.000	0.112	-61.000	1952.000	333.000
1D and 3D	34.000	0.596	-768.000	1248.000	-232.000
2D and 3D	2.000	0.001	-1013.000	-287.000	-672.000

Table H5

The Mann-Whitney U-test results for estimated average individual AFDW biomass of macrobenthos between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	W	*p*-value	2.5% CI	97.5% CI	Estd. Difference
1A and 1B	31.000	0.427	-2039.000	352.000	-202.000
1A and 1C	52.000	0.331	-245.000	486.000	202.000
1A and 1D	46.000	0.659	-767.000	-767.000	199.000
1B and 1C	59.000	0.112	-112.000	2072.000	445.000
1B and 1D	54.000	0.251	-563.000	1940.000	325.000
1C and 1D	44.000	0.791	-952.000	444.000	81.000
2A and 2B	35.000	0.659	-3307.000	655.000	-178.000
2A and 2C	75.500	0.002	225.000	1094.000	433.000
2A and 2D	80.000	0.001	301.000	1130.000	551.000
2B and 2C	74.000	0.004	150.000	4482.000	498.000
2B and 2D	79.000	0.001	224.000	4507.000	607.000
2C and 2D	64.500	0.038	1.000	190.000	102.000
3A and 3B	42.000	0.930	-963.000	583.000	25.000
3A and 3C	17.000	0.042	-1637.000	-41.000	-571.000
3A and 3D	68.000	0.017	98.000	936.000	462.000
3B and 3C	25.000	0.185	-1884.000	403.000	-625.000
3B and 3D	54.000	0.251	-222.000	1514.000	382.000
3C and 3D	74.000	0.004	503.000	2039.000	995.000

Table H6

The Mann-Whitney U-test results for estimated average individual AFDW biomass of macrobenthos within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	W	*p*-value	2.5% CI	97.5% CI	Estd. Difference
1A and 2A	37.000	0.791	-675.000	273.000	-147.000
1A and 3A	28.000	0.289	-760.000	184.000	-198.000
2A and 3A	35.000	0.659	-575.000	479.000	-100.000
1B and 2B	38.000	0.860	-2500.000	773.000	-77.000
1B and 3B	48.000	0.537	-994.000	1484.000	153.000
2B and 3B	50.000	0.427	-1001.000	2821.000	243.000
1C and 2C	62.000	0.064	-29.000	666.000	177.000
1C and 3C	8.000	0.005	-1932.000	-432.000	-954.000
2C and 3C	0.000	0.000	-2934.000	-656.000	-1133.000
1D and 2D	53.000	0.289	-63.000	1204.000	205.000
1D and 3D	38.000	0.860	-372.000	1083.000	-49.000
2D and 3D	12.000	0.013	-344.000	-43.000	-224.000

Table H7

The Mann-Whitney U-test results for Shannon's diversity index (H') between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites Xi and Yi, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between Xi and Yi. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites Xi and Yi	W	p-value	2.5% CI	97.5% CI	Estd. Difference
1A and 1B	79.000	0.001	0.330	0.810	0.550
1A and 1C	60.500	0.085	-0.020	0.330	0.150
1A and 1D	81.000	0.000	1.340	1.870	1.600
1B and 1C	2.000	0.001	-0.610	-0.200	-0.400
1B and 1D	81.000	0.000	0.790	1.310	1.080
1C and 1D	81.000	0.000	1.260	1.690	1.470
2A and 2B	74.000	0.004	0.240	0.760	0.490
2A and 2C	81.000	0.000	0.520	0.990	0.690
2A and 2D	81.000	0.000	1.160	1.710	1.460
2B and 2C	58.500	0.122	-0.060	0.480	0.250
2B and 2D	81.000	0.000	0.660	1.250	0.920
2C and 2D	78.000	0.001	0.430	1.050	0.730
3A and 3B	75.000	0.003	0.080	0.480	0.240
3A and 3C	32.000	0.479	-0.240	0.200	-0.050
3A and 3D	81.000	0.000	1.210	1.490	1.330
3B and 3C	15.000	0.027	-0.560	-0.050	-0.310
3B and 3D	81.000	0.000	0.870	0.870	1.090
3C and 3D	81.000	0.000	0.000	1.590	1.400

Table H8

The Mann-Whitney U-test results for Shannon's diversity index (H') within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites Xi and Yi, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between Xi and Yi. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites Xi and Yi	W	p-value	2.5% CI	97.5% CI	Estd. Difference
A and 2A	32.000	0.480	-0.300	0.160	-0.080
A and 3A	73.500	0.004	0.130	0.490	0.290
2A and 3A	75.500	0.002	0.160	0.560	0.420
B and 2B	28.500	0.309	-0.390	0.120	-0.130
B and 3B	45.000	0.724	-0.240	0.310	0.050
2B and 3B	53.500	0.269	-0.140	0.500	0.150
C and 2C	81.000	0.000	0.290	0.750	0.450
C and 3C	53.500	0.269	-0.080	0.370	0.100
2C and 3C	11.500	0.012	-0.660	-0.090	-0.350
D and 2D	20.000	0.077	-0.530	0.020	-0.210
D and 3D	41.000	1.000	-0.180	0.270	0.010
2D and 3D	69.000	0.013	0.030	0.540	0.230

Table H9

The Mann-Whitney U-test results for Pielou's evenness (J) between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites Xi and Yi	W	p-value	2.5% CI	97.5% CI	Estd. Difference
1A and 1B	73.500	0.004	0.050	0.120	0.100
1A and 1C	67.000	0.021	0.010	0.080	0.050
1A and 1D	80.000	0.001	0.140	0.260	0.200
1B and 1C	10.000	0.008	-0.070	-0.020	-0.040
1B and 1D	72.500	0.005	0.070	0.160	0.110
1C and 1D	78.000	0.001	0.110	0.210	0.150
2A and 2B	57.500	0.140	-0.010	0.100	0.020
2A and 2C	53.000	0.283	-0.020	0.050	0.010
2A and 2D	79.000	0.001	0.060	0.260	0.170
2B and 2C	34.000	0.594	-0.080	0.040	-0.010
2B and 2D	71.000	0.008	0.050	0.230	0.130
2C and 2D	73.000	0.005	0.050	0.240	0.140
3A and 3B	33.500	0.563	-0.040	0.020	-0.010
3A and 3C	1.000	0.001	-0.100	-0.040	-0.070
3A and 3D	81.000	0.000	0.180	0.270	0.220
3B and 3C	4.500	0.002	-0.090	-0.030	-0.060
3B and 3D	81.000	0.000	0.190	0.280	0.230
3C and 3D	81.000	0.000	0.250	0.340	0.290

Table H10

The Mann-Whitney U-test results for Pielou's evenness (J) within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, test value (W), p-value, 2.5% confidence interval, 97.5% confidence interval, and estimated difference between X_i and Y_i. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites Xi and Yi	W	p-value	2.5% CI	97.5% CI	Estd. Difference
A and 2A	48.500	0.501	-0.030	0.030	0.010
A and 3A	70.500	0.009	0.040	0.110	0.070
2A and 3A	76.000	0.002	0.040	0.100	0.070
B and 2B	21.500	0.100	-0.100	0.010	-0.060
B and 3B	16.500	0.036	-0.050	0.000	-0.020
2B and 3B	49.000	0.477	-0.040	0.080	0.020
C and 2C	22.500	0.120	-0.070	0.010	-0.030
C and 3C	9.500	0.007	-0.070	-0.020	-0.040
2C and 3C	30.500	0.395	-0.050	0.020	-0.010
D and 2D	31.000	0.425	-0.130	0.070	-0.030
D and 3D	73.000	0.005	0.030	0.150	0.090
2D and 3D	70.500	0.009	0.030	0.220	0.130

Table H11

Welch's unequal variances t-test results for Margalef's Species Richness Index (SR) between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i =, t-test value (t), p-value, 2.5% confidence interval, 97.5% confidence interval, mean X_i ($\bar{X}$), mean Y_i ($\bar{Y}$) and difference between $\bar{X}$ and $\bar{Y}$. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	t	p-value	2.5% CI	97.5% CI	Mean X_i ($\bar{X}$)	Mean Y_i ($\bar{Y}$)	$\bar{X}$ - $\bar{Y}$
1A and 1B	3.684	0.002	0.780	2.895	7.281	5.443	1.838
1A and 1C	0.833	0.419	-0.558	1.267	7.281	6.927	0.354
1A and 1D	12.028	0.000	4.085	5.866	7.281	2.306	4.976
1B and 1C	-3.457	0.004	-2.403	-0.564	5.443	6.927	-1.483
1B and 1D	7.523	0.000	2.239	4.037	5.443	2.306	3.138
1C and 1D	14.172	0.000	3.929	5.313	6.927	2.306	4.621
2A and 2B	5.004	0.000	1.374	3.426	7.617	5.217	2.400
2A and 2C	7.906	0.000	2.405	4.275	7.617	4.277	3.340
2A and 2D	11.826	0.000	4.006	5.863	7.617	2.682	4.934
2B and 2C	2.961	0.011	0.252	1.628	5.217	4.277	0.940
2B and 2D	8.163	0.000	1.858	3.211	5.217	2.682	2.534
2C and 2D	7.532	0.000	1.145	2.044	4.277	2.682	1.594
3A and 3B	4.028	0.001	0.786	2.574	6.280	4.600	1.680
3A and 3C	1.578	0.138	-0.259	1.672	6.280	5.573	0.707
3A and 3D	14.370	0.000	3.270	4.432	6.280	2.429	3.851
3B and 3C	-1.891	0.077	-2.066	0.119	4.600	5.573	-0.973
3B and 3D	5.879	0.000	1.351	2.991	4.600	2.429	2.171
3C and 3D	7.791	0.000	2.243	4.046	5.573	2.429	3.144

Table H12

Welch's unequal variances t-test results for Margalef's Species Richness Index (SR) within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and $Y_i =$, t-test value (t), p-value, 2.5% confidence interval, 97.5% confidence interval, mean X_i ($\bar{X}$), mean Y_i ($\bar{Y}$) and difference between $\bar{X}$ and $\bar{Y}$. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	t	p-value	2.5% CI	97.5% CI	Mean X_i ($\bar{X}$)	Mean Y_i ($\bar{Y}$)	$\bar{X}$ - $\bar{Y}$
1A and 2A	-0.638	0.533	-1.452	0.781	7.281	7.617	-0.336
1A and 3A	2.375	0.032	0.097	1.906	7.281	6.280	1.001
2A and 3A	2.927	0.012	0.350	2.323	7.617	6.280	1.337
1B and 2B	0.504	0.621	-0.731	1.184	5.443	5.217	0.227
1B and 3B	1.704	0.108	-0.206	1.893	5.443	4.600	0.843
2B and 3B	1.395	0.183	-0.324	1.558	5.217	4.600	0.617
1C and 2C	9.208	0.000	2.032	3.268	6.927	4.277	2.650
1C and 3C	2.996	0.010	0.381	2.325	6.927	5.573	1.353
2C and 3C	-3.142	0.010	-2.209	-0.384	4.277	5.573	-1.297
1D and 2D	-1.441	0.172	-0.938	0.185	2.306	2.682	-0.377
1D and 3D	-0.483	0.637	-0.675	0.428	2.306	2.429	-0.123
2D and 3D	1.311	0.209	-0.157	0.663	2.682	2.429	0.253

Table H13

Welch's unequal variances t-test results for Inverse Simpson diversity index (1/D) between sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, t-test value (t), p-value, 2.5% confidence interval, 97.5% confidence interval, mean X_i ($\bar{X}$), mean Y_i ($\bar{Y}$) and difference between $\bar{X}$ and $\bar{Y}$. Subscript i = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	t	p-value	2.5% CI	97.5% CI	Mean X_i ($\bar{X}$)	Mean Y_i ($\bar{Y}$)	$\bar{X}$ - $\bar{Y}$
1A and 1B	5.471	0.000	6.907	-6.649	20.496	-8.718	29.213
1A and 1C	2.706	0.023	1.016	10.837	20.496	14.569	5.927
1A and 1D	7.984	0.000	12.069	21.749	20.496	3.587	16.909
1B and 1C	-6.983	0.000	-7.635	-4.067	8.718	14.569	-5.851
1B and 1D	8.217	0.000	3.792	6.471	8.718	3.587	5.131
1C and 1D	14.757	0.000	9.363	12.602	14.569	3.587	10.982
2A and 2B	3.752	0.002	3.793	13.662	22.252	13.524	8.728
2A and 2C	5.032	0.000	6.337	15.634	22.252	11.267	10.986
2A and 2D	9.309	0.000	13.166	21.360	22.252	4.989	17.263
2B and 2C	1.088	0.293	-2.151	6.667	13.524	11.267	2.258
2B and 2D	4.943	0.000	4.740	12.331	13.524	4.989	8.536
2C and 2D	4.107	0.001	2.950	9.605	11.267	4.989	6.278
3A and 3B	1.304	0.215	-0.994	4.014	12.116	10.606	1.510
3A and 3C	-2.818	0.017	-7.531	-0.918	12.116	16.340	-4.224
3A and 3D	14.647	0.000	7.604	10.356	12.116	3.136	8.980
3B and 3C	-3.367	0.004	-9.374	-2.095	10.606	16.340	-5.734
3B and 3D	7.360	0.000	5.154	9.786	10.606	3.136	7.470
3C and 3D	9.493	0.000	10.015	16.394	16.340	3.136	13.204

Table H14

Welch's unequal variances t-test results for Inverse Simpson diversity index (1/D) within sites A, B, C and D for April 2009, September 2009 and August 2010 sample collections. Comparisons between sites X_i and Y_i, t-test value (t), p-value, 2.5% confidence interval, 97.5% confidence interval, mean X_i ($\overline{X}$), mean Y_i ($\overline{Y}$) and difference between $\overline{X}$ and $\overline{Y}$ $_i$ = site A, B, C or D for April 2009, September 2009 or August 2010.

Sites X_i and Y_i	t	*p*-value	2.5% CI	97.5% CI	Mean X_i ($\overline{X}$)	Mean Y_i ($\overline{Y}$)	$\overline{X}$ - $\overline{Y}$
1A and 2A	-0.650	0.525	-7.502	3.989	20.496	22.252	-1.757
1A and 3A	3.862	0.004	3.492	13.268	20.496	12.116	8.380
2A and 3A	5.598	0.000	6.094	14.179	22.252	12.116	10.137
1B and 2B	-2.900	0.016	-8.514	-1.099	8.718	13.524	-4.807
1B and 3B	-1.677	0.119	-4.340	0.564	8.718	10.606	-1.888
2B and 3B	1.566	0.141	-1.092	6.930	13.524	10.606	2.919
1C and 2C	2.194	0.049	0.010	6.595	14.569	11.267	3.302
1C and 3C	-1.159	0.270	-5.118	1.576	14.569	16.340	-1.771
2C and 3C	-2.625	0.018	-9.170	-0.976	11.267	16.340	-5.073
1D and 2D	-1.773	0.102	-3.131	0.327	3.587	4.989	-1.402
1D and 3D	1.154	0.271	-0.401	1.303	3.587	3.136	0.451
2D and 3D	2.530	0.032	0.197	3.510	4.989	3.136	1.853

APPENDIX I

BOTTOM WATER OXYGEN CONCENTRATION

Table I1

Annual mid-summer shelfwide cruise average bottom-water oxygen concentration (mg/L) for sites A (H7), B (E4), C (D5) and D (A6) obtained from N. Rabalais for 2000 to 2010.

Years	A	B	C	D
2000	4.46	4.72	3.95	1.92
2001	2.10	3.23	3.22	2.71
2002	2.06	0.66	2.89	0.78
2003	6.36	3.85	5.52	2.76
2004	3.70	3.39	3.36	4.02
2005	3.26	4.36	4.69	2.51
2006	3.64	1.19	1.87	2.52
2007	4.00	2.50	2.50	2.00
2008	2.44	0.05	2.30	0.03
2009	6.00	4.50	2.60	0.20
2010	5.70	3.49	3.13	4.11

APPENDIX J

SEDIMENT ORGANIC CARBON AND CARBON/NITROGEN RATIO DATA

Table J1

Within sediment vertical distribution of C/N ratio at sites A, B, C and D for April and September 2009 sample collections. SD = within core standard deviation in C/N ratio vertically.

Depth (cm)	1A	1B	1C	1D	2A	2B	2C	2D
0.25	0.01	9.83	10.49	10.13	9.27	8.79	10.34	7.64
0.75	8.99	9.50	11.52	10.20	9.21	9.05	10.58	7.82
1.25	8.97	9.46	10.80	10.19	9.15	8.66	10.78	8.03
1.75	8.88	9.39	9.86	10.45	9.58	8.94	10.72	8.11
2.25	9.17	10.00	9.68	10.34	9.42	8.67	10.72	7.77
2.75	9.24	8.86	8.93	10.22	30.37	8.92	11.02	7.84
3.5	9.73	9.51	8.80	10.12	10.41	8.90	11.09	8.75
4.5	9.67	8.90	10.13	10.03	10.25	9.24	11.12	7.73
5.5	9.20	10.59	11.00	9.70	11.21	9.12	11.45	8.97
6.5	11.56	10.20	10.58	9.81	9.85	9.34	11.45	8.85
7.5	8.86	10.48	10.48	9.82	17.00	9.28	11.30	9.21
8.5	9.56	10.15	10.63	10.05	22.73	9.33	11.24	9.71

Table J1 (continued).

Depth (cm)	1A	1B	1C	1D	2A	2B	2C	2D
9.5	9.93	10.25	10.49	10.11	16.02	9.32	10.91	9.90
10.5	18.07	10.45	10.93	9.82	26.42	9.58	10.93	9.74
11.5	23.92	10.39	11.18	9.93	11.94	9.81	10.69	10.06
12.5	9.99	10.62	11.23	9.80	21.44	9.86	10.77	10.62
13.5	19.97	10.99	11.58	9.65	24.17	9.76	10.62	10.89
14.5	20.74	10.47	10.93	9.36	19.23	9.91	10.44	10.93
SD	4.94	0.61	0.79	0.27	6.97	0.41	0.33	1.15
Mean	11.47	10.00	10.51	9.98	15.43	9.25	10.90	9.03

Table J2

Within sediment vertical distribution of percent organic carbon at sites A, B, C and D for April and September 2009 sample collections. SD = within core standard deviation in percent organic carbon vertically.

Depth (cm)	1A	1B	1C	1D	2A	2B	2C	2D
0.25	0.06	0.07	0.06	0.16	0.03	0.07	0.16	0.06
0.75	0.05	0.07	0.07	0.16	0.03	0.07	0.19	0.05
1.25	0.03	0.06	0.03	0.15	0.03	0.06	0.11	0.09
1.75	0.02	0.04	0.02	0.15	0.03	0.06	0.12	0.05
2.25	0.02	0.02	0.02	0.15	0.03	0.05	0.14	0.03
2.75	0.03	0.01	0.01	0.15	0.08	0.05	0.13	0.05
3.5	0.03	0.02	0.02	0.15	0.03	0.05	0.15	0.05
4.5	0.03	0.06	0.05	0.14	0.03	0.05	0.14	0.07
5.5	0.03	0.06	0.06	0.14	0.03	0.05	0.16	0.06
6.5	0.04	0.05	0.06	0.14	0.03	0.04	0.15	0.06
7.5	0.03	0.07	0.06	0.14	0.05	0.05	0.16	0.06
8.5	0.03	0.06	0.06	0.14	0.05	0.06	0.20	0.05
9.5	0.03	0.06	0.06	0.14	0.04	0.07	0.15	0.07
10.5	0.05	0.07	0.06	0.14	0.07	0.08	0.17	0.06

Table J2 (continued).

Depth (cm)	1A	1B	1C	1D	2A	2B	2C	2D
11.5	0.06	0.07	0.06	0.14	0.03	0.08	0.15	0.06
12.5	0.03	0.07	0.05	0.15	0.05	0.08	0.15	0.06
13.5	0.05	0.07	0.05	0.15	0.06	0.08	0.16	0.06
14.5	0.05	0.07	0.05	0.15	0.05	0.08	0.12	0.09
SD	0.01	0.02	0.02	0.01	0.02	0.01	0.02	0.01
Mean	0.04	0.06	0.05	0.15	0.04	0.06	0.15	0.06

APPENDIX K

SEDIMENT GRAIN SIZE DATA

Table K1

Average (n = 3 subcores) sediment grain size (%) distribution at site A for April 2009.
SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.45	52.25	10.76	36.55	6.41	4.26	47.30
1	3.45	73.04	6.62	16.90	4.62	3.72	23.52
3	4.25	70.45	8.61	16.69	4.32	3.61	25.30
5	4.28	61.65	13.55	20.52	4.99	4.06	34.07
7	2.71	63.55	12.12	21.62	5.19	4.03	33.74
9	3.02	67.39	10.32	19.27	4.87	3.95	29.59
11	3.99	66.01	10.76	19.24	4.73	4.04	30.00
13	2.98	65.56	10.99	20.48	4.95	4.14	31.47
15	7.29	63.15	10.42	19.14	4.44	4.14	29.56
SD	1.81	5.92	1.97	5.99	0.61	0.21	6.83
MEAN	3.60	64.78	10.46	21.16	4.95	3.99	31.62

Table K2

Average (n = 3 subcores) sediment grain size (%) distribution at site A for September
2009. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	1.04	67.39	8.32	23.25	5.27	3.90	31.57
1	2.28	73.33	6.60	17.79	4.63	3.56	24.39
3	2.80	80.14	5.50	11.57	3.63	2.52	17.06
5	2.52	81.67	5.15	10.65	3.45	2.38	15.80
7	5.61	70.12	8.68	15.59	4.10	3.51	24.27
9	5.47	72.17	6.84	15.53	3.94	3.58	22.37
11	4.59	69.55	8.23	17.63	4.61	3.95	25.86
13	7.48	64.26	9.20	19.05	4.51	4.38	28.26
15	6.24	66.45	8.47	18.84	4.65	4.34	27.31
SD	2.15	5.94	1.47	3.88	0.58	0.71	5.10
MEAN	4.22	71.67	7.44	16.66	4.31	3.57	24.10

Table K3

Average (n = 2 subcores) sediment grain size (%) distribution in site A for August 2010. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.83	70.25	8.63	20.30	4.89	3.61	28.93
1	1.27	76.84	6.09	15.82	4.23	3.25	21.90
3	1.76	77.44	6.71	14.09	3.82	2.99	20.80
5	5.54	73.32	7.67	13.48	3.51	3.34	21.15
7	4.90	72.18	7.64	15.29	4.09	3.51	22.92
9	2.95	67.62	10.08	19.36	4.84	3.80	29.44
11	3.11	71.20	9.48	16.22	4.25	3.47	25.70
13	3.45	69.28	10.32	16.96	4.26	3.49	27.28
15	3.95	72.24	8.22	15.60	4.05	3.51	23.82
SD	1.60	3.25	1.46	2.25	0.44	0.23	3.31
MEAN	3.08	72.26	8.31	16.34	4.21	3.44	24.66

Table K4

Average (n = 4 subcores) sediment grain size (%) distribution at site B for April 2009. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.04	52.59	10.89	36.49	6.52	3.15	47.38
1	0.00	57.90	12.67	29.43	5.78	2.68	42.10
3	0.02	53.59	14.93	31.47	6.32	3.37	46.40
5	0.00	50.66	17.26	32.08	6.40	3.60	49.34
7	0.01	30.42	20.86	48.72	7.99	3.91	69.58
9	0.00	31.20	23.66	45.13	7.67	3.88	68.80
11	0.09	31.78	21.70	46.44	7.80	3.91	68.13
13	0.00	21.94	23.83	54.25	8.46	3.88	78.07
15	0.02	17.53	24.29	58.17	8.93	3.72	82.46
SD	0.03	15.12	5.11	10.50	1.09	0.43	15.12
MEAN	0.02	38.62	18.90	42.46	7.32	3.57	61.36

Table K5

Average (n = 2 subcores) sediment grain size (%) distribution at site B for September 2009. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	36.03	18.35	45.63	7.61	3.85	63.98
1	0.00	51.42	13.88	34.71	6.33	3.82	48.59
3	0.00	62.18	12.13	25.70	5.75	3.48	37.82
5	0.00	50.51	15.15	34.35	6.66	3.92	49.50
7	0.00	29.03	22.43	48.55	7.97	3.93	70.97
9	0.00	25.78	23.66	50.56	8.11	3.95	74.22
11	0.00	16.70	25.82	57.48	8.77	3.75	83.30
13	0.00	13.08	27.66	59.27	8.88	3.51	86.93
15	0.02	16.55	24.12	59.33	8.96	3.76	83.44
SD	0.01	17.70	5.63	12.19	1.18	0.17	17.70
MEAN	0.00	33.47	20.35	46.17	7.67	3.77	66.53

Table K6

Average (n = 4 subcores) sediment grain size (%) distribution at site B for August 2010. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	47.44	17.85	34.71	6.58	3.74	52.56
1	0.05	57.14	13.14	29.68	6.22	3.76	42.81
3	0.00	61.41	11.48	27.11	5.87	3.64	38.59
5	0.00	65.45	12.89	21.65	5.09	2.97	34.54
7	0.01	59.90	13.71	26.39	5.81	3.05	40.09
9	0.04	46.87	17.11	35.98	6.59	3.48	53.09
11	0.00	29.40	20.33	50.28	8.12	3.99	70.60
13	0.00	24.61	20.84	54.56	8.47	3.99	75.39
15	0.03	21.97	22.68	55.32	8.67	3.85	78.00
SD	0.02	16.76	4.04	12.87	1.29	0.38	16.76
MEAN	0.01	46.02	16.67	37.30	6.82	3.61	53.96

Table K7

Average (n = 3 subcores) sediment grain size (%) distribution at site C for April 2009.
SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	41.72	19.15	39.14	6.94	3.96	58.29
1	0.00	63.77	17.86	18.37	5.28	2.98	36.23
3	1.22	63.73	19.13	15.93	4.70	2.46	35.06
5	0.22	32.02	20.70	47.07	7.88	3.83	67.77
7	0.63	22.43	20.23	56.71	8.70	3.87	76.94
9	0.55	17.93	21.55	59.97	9.06	3.74	81.52
11	0.00	15.29	21.13	63.58	9.36	3.54	84.71
13	0.00	10.94	24.85	64.21	9.49	3.47	89.06
15	0.00	8.91	26.12	64.97	9.51	3.44	91.09
SD	0.43	21.33	2.70	19.36	1.85	0.48	21.50
MEAN	0.29	30.75	21.19	47.77	7.88	3.48	68.96

Table K8

Average (n = 2 subcores) sediment grain size (%) distribution at site C for September
2009. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	33.92	26.41	39.67	7.21	3.75	66.08
1	0.06	38.11	23.73	38.10	6.96	3.78	61.83
3	0.05	41.42	21.75	36.80	6.86	3.80	58.54
5	0.08	24.10	23.68	52.16	8.29	3.77	75.83
7	5.28	17.54	23.73	53.45	8.43	4.22	77.18
9	0.00	17.84	19.61	62.56	9.29	3.59	82.17
11	0.00	12.00	23.41	64.60	9.53	3.55	88.01
13	0.00	2.82	21.47	75.72	10.72	2.95	97.19
15	0.00	1.08	25.50	73.42	10.25	2.87	98.92
SD	1.75	14.65	2.08	14.92	1.43	0.43	14.62
MEAN	0.61	20.98	23.25	55.16	8.61	3.58	78.41

Table K9

*Average (n = 2 subcores) sediment grain size (%) distribution at site C for August 2010.
SD = within core standard deviation in sediment grain size vertically.*

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	38.36	23.70	37.94	7.01	3.85	61.64
1	0.00	44.64	20.72	34.64	6.75	3.84	55.36
3	0.00	51.15	15.54	33.32	6.54	3.86	48.86
5	0.01	47.19	16.69	36.11	6.87	3.84	52.80
7	1.07	40.70	16.38	41.87	7.24	3.94	58.24
9	0.04	30.97	16.83	52.17	8.24	4.03	69.00
11	0.13	29.08	17.77	53.04	8.21	4.02	70.80
13	0.22	12.43	20.52	66.83	9.63	3.59	87.35
15	0.00	16.67	17.10	66.23	9.42	3.75	83.33
SD	0.35	13.42	2.69	13.20	1.16	0.14	13.43
MEAN	0.16	34.57	18.36	46.90	7.77	3.85	65.26

Table K10

*Average (n = 3 subcores) sediment grain size (%) distribution at site D for April 2009.
SD = within core standard deviation in sediment grain size vertically.*

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	0.30	11.92	87.78	11.17	2.19	99.71
1	0.00	0.14	11.88	87.97	11.19	2.18	99.85
3	0.00	0.13	11.52	88.35	11.25	2.17	99.87
5	0.00	0.08	14.30	85.62	11.06	2.31	99.92
7	0.00	0.42	15.95	83.63	10.97	2.45	99.58
9	0.00	0.56	16.60	82.84	10.90	2.53	99.44
11	0.00	0.52	16.05	83.43	10.98	2.50	99.48
13	0.00	0.43	12.27	87.30	11.21	2.25	99.56
15	0.00	0.36	15.88	83.77	10.84	2.44	99.65
SD	0.00	0.18	2.13	2.25	0.15	0.14	0.18
MEAN	0.00	0.33	14.04	85.63	11.06	2.33	99.67

Table K11

Average (n = 2 subcores) sediment grain size (%) distribution at site D for September 2009. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	0.00	13.14	86.87	11.05	2.28	100.00
1	0.00	0.02	11.14	88.84	11.27	2.18	99.98
3	5.05	0.00	12.41	82.55	10.84	3.24	94.96
5	0.00	0.03	13.06	86.91	11.15	2.27	99.97
7	0.00	0.20	18.06	81.75	10.71	2.52	99.80
9	0.00	0.99	17.79	81.23	10.57	2.59	99.02
11	0.00	0.22	15.32	84.47	10.94	2.45	99.79
13	0.00	0.34	15.10	84.57	11.03	2.46	99.67
15	0.17	0.48	11.88	87.48	11.09	2.28	99.36
SD	1.68	0.32	2.50	2.72	0.22	0.32	1.61
MEAN	0.58	0.25	14.21	84.96	10.96	2.47	99.17

Table K12

Average (n = 2 subcores) sediment grain size (%) distribution at site D for August 2010. SD = within core standard deviation in sediment grain size vertically.

Depth (cm)	Gravel	Sand	Silt	Clay	Graphical mean	Sorting (σ)	Mud (silt+clay)
0.5	0.00	0.00	11.36	88.65	11.14	2.21	100.00
1	0.00	0.05	11.93	88.02	11.16	2.23	99.95
3	0.00	0.00	10.85	89.15	11.39	2.19	100.00
5	0.00	0.00	15.04	84.96	10.85	2.33	100.00
7	0.00	0.24	13.91	85.86	11.19	2.37	99.77
9	0.00	0.10	14.75	85.16	11.01	2.36	99.91
11	0.00	0.11	13.29	86.61	11.19	2.33	99.89
13	0.00	0.01	13.40	86.60	11.31	2.32	100.00
15	0.00	0.03	14.01	85.97	11.20	2.36	99.98
SD	0.00	0.08	1.48	1.51	0.16	0.07	0.08
MEAN	0.00	0.06	13.17	86.77	11.16	2.30	99.94

APPENDIX L

LIST OF TAXONOMY REFERENCES USED IN IDENTIFIACTION OF BENTHOS

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