BENTHIC FUNCTION AND STRUCTURE IN THE NORTHERN GULF OF MEXICO HYPOXIC ZONE: SEDIMENT BIOGEOCHEMISTRY AND MACROBENTHIC COMMUNITY DYNAMICS IN THE DEAD ZONE

A Dissertation

by

CLIFTON CHARLES NUNNALLY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2012

Major Subject: Oceanography

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Approved by:

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ABSTRACT

Benthic Function and Structure in the Northern Gulf of Mexico Hypoxic Zone: Sediment Biogeochemistry and Macrobenthic Community Dynamics in the Dead Zone.

(May 2012)

Clifton Charles Nunnally, B.S., Abilene Christian University;

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Chair of Advisory Committee: Dr. Gilbert T. Rowe

Coastal low oxygen areas are expanding globally and are predicted to increase in size and duration due to climatic changes associated with a warming ocean. The Gulf of Mexico Hypoxic Zone (GoMHZ) is the second largest regularly occurring hypoxic habitat in the world and has increased in size since it was first mapped in the 1980s. The Mississippi Atchafalaya River System (MARS) floods the Louisiana continental shelf with fresh water high in nitrogenous compounds enhancing primary production which sinks to the sea floor. Stratification that occurs as a result of density differences and coastal currents creates a strong pycnocline that prevents bottom waters from being aerated causing seasonally hypoxic bottom waters (< 2.0 mg L^{-1}). The Mechanisms Controlling Hypoxia (MCH) project (hypoxia.tamu.edu) made regular cruises during 2004-2005 and 2007-2009 to the GoMHZ performing shelf wide hydrographic surveys and occupying central mooring sites within theoretical zones of differing hypoxic potential. Sediment cores were collected for incubation experiments using Batch

Microincubation Chambers (BMICs) to measure rates of sediment community oxygen consumption and nutrient regeneration. Results of incubation experiments characterized sediments as net sources of dissolved inorganic nitrogen, mostly ammonium, and silicate and a net sink of phosphate. Modeling simulations of benthic-pelagic coupling focused in the western study zones related field measurements of benthic nutrient regeneration and primary production to important processes that maintain summertime hypoxia when surface waters are nitrogen limited. After incubations were completed macrofaunal individuals were removed from the cores enumerated and identified to the lowest possible taxon. Macrofauna communities in 2004-2005 were dominated by a hypoxia tolerant community dominated by polychaetes. Hurricanes Katrina and Rita in August and September of 2005 drastically reorganized macrobenthic communities decreasing abundances and negatively impacting diversity. These new communities collapsed under hypoxic stresses potentially impacting the ability of demersal foragers to utilize an important food resource. Large variations in biogeochemical fluxes and patchy distribution of fauna impeded the delineation of significant zones in benthic function and structure.

DEDICATION

This dissertation is dedicated in part to my advisor and friend Gil Rowe. During my decade plus of graduate school he has been my academic father and role model. We should all hope to be as smart and as humble as he. Thanks.

As important as my advisor has been to my intellectual success, Allison Parnell has keyed my will to finish and at the same time kept me sane. Allison is my sheltered shore, my safe harbor and guiding light. Drowning in my work and inner demons, she saved me from the tempest and guided me safely home. The rest of my life is well spent if it is done by her side.

ACKNOWLEDGEMENTS

It is prudent to first recognize the various members of the Deep-Sea Biology Lab at Texas A&M, Galveston: Fain Hubbard, Yousria Soliman, Chih-Lin Wei, Kim Larsen, Courtney Horne, William Greenwood, Ligita Kuklyte and Fangyuan Qu. Several undergraduate workers and sample sorters also assisted in compiling faunal data during this study and should also be mentioned: Michelle Puig, Celine Jarron, and Justin Collier. I would also like to thank the graduate student population of the Oceanography Department in College Station and all of the various graduate students who contribute to our group dynamic in Galveston.

Logistically this dissertation could not have been completed without the captains and crews of the R/V Gyre (TAMU) and the R/V Pelican (LUMCON). Also important are the impeccable group of men at GERG including but not limited to: Eddie Webb, Paul Clark, Chris Schmidt, Andy Dancer, John Walpert and Marty Bohn. The Mechanisms Controlling Hypoxia (MCH) project provided summer support for this research and opportunity to sample the Gulf of Mexico Hypoxic Zone on numerous occasions. The lead scientists Steve DiMarco and Piers Chapman deserve credit for their logistical planning and foresight. Equally important was the monitoring and distribution of data by Matt Howard. During MCH cruises valuable assistance was provided by Federico Alvarez during daylight hours. This work was funded by two grants from the NOAA Center for Sponsored Coastal Research (NA03N0S4780039 and NA06N0S4780198).

NOMENCLATURE

ANOVA	Analysis of Variance
BMICs	Batch Micro Incubation Chambers
CTD	Conductivity, Temperature, Depth
DIC	Dissolved Inorganic Carbon
DIN	Dissolved Inorganic Nitrogen
DMSO	Dimethyl Sulfoxide
DNRA	Dissimilatory Nitrate Reduction to Ammonia
DOC	Dissolved Organic Carbon
DON	Dissolved Organic Nitrogen
GERG	Geochemical and Environmental Research Group
GoMHZ	Gulf of Mexico Hypoxic Zone
HCL	Hydrochloric Acid
IPP	Integrated Primary Productivity
KW	Kruskall-Wallis
MW	Mann-Whitney
MARS	Mississippi-Atchafalaya River System
MCH	Mechanisms Controlling Hypoxia
N	Nitrogen
NGOM	Northern Gulf of Mexico
nMDS	Non-metric Multidimensional Scaling

NOAA	National Oceanic Atmospheric Administration
OM	Organic Matter
P	Phosphorus
PAR	Photosynthetically Active Radiation
PCA	Principal Component Analysis
PO	“Peak of Opportunists”
POC	Particulate Organic Carbon
POM	Particulate Organic Matter
PON	Particulate Organic Nitrogen
PP	Particulate Phosphorus
SAB	Species-Abundance-Biomass
SCOC	Sediment Community Oxygen Consumption
Si	Silicate
SOD	Sediment Oxygen Demand
TAMU	Texas A&M University

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CHAPTER I

INTRODUCTION

In the region under the Mississippi River Plume and extending West along the Louisiana continental shelf low oxygen areas form and cannot be aerated during summer months due to strong thermohaline stratification (Bianchi et al., 2010; Rabalais et al., 1999; Turner and Rabalais, 1994; Turner et al., 2005; Wiseman et al., 1997). Enhanced biological productivity in surface waters caused by elevated nutrients in river discharge provides ample substrates for heterotrophic respiration in waters (Dortch et al., 1994; Lehrter et al., 2009) and sediments (Rowe et al., 2002, Rowe, 2001) beneath the pycnocline. Over time and under strong seasonal stratification this leads to large zones of hypoxia in bottom waters that persist until oxygen can by physically mixed from the surface. These processes of eutrophication, stratification and respiration combine to create the Texas-Louisiana "Dead Zone." The northern Gulf of Mexico Hypoxic Zone (GoMHZ) can form in March and last until September reaching sizes in excess of 22,000 km^2 (Turner et al., 2008). This has potentially disastrous effects on non-motile, benthic animals that are important to sediment functioning and as prey for demersal fisheries.

Processes that create and maintain hypoxia are unequal in time and space, thus variations in biogeochemical processes (Morse and Rowe, 1999) need to be identified and quantified to better predict consequences of river runoff (Dagg and Breed, 2003;

This dissertation follows the style of Continental Shelf Research.

Rabalais et al., 1999), wetland particulate organic carbon (POC) contributions (Bianchi et al., 2009), and physical forcing (Cochrane and Kelly, 1986; DiMarco et al., 2009; Wiseman et al., 1997). The scope of the research presented here seeks to define benthic processes that operate under different temporal and spatial scales relative to the water column. By defining these processes I will attempt to answer one central question, "What role does the benthos play in creating, fueling and maintaining bottom water hypoxia on the Louisiana continental shelf?" Sediments regulate nitrogen cycling that impacts primary production on local scales or can impact global nitrogen cycling by removing or returning fixed N compounds from coastal systems (Burdige, 2006; Codispoti et al., 2001). Sedimentary processes that consume oxygen and remineralize nutrients can create positive feedbacks capable of exacerbating hypoxic conditions (Lehrter et al., 2011).

Buoyant river plumes and coastal boundary currents create a sequence of zones of differing hypoxic potential (Rowe and Chapman, 2002). Near the Mississippi River mouth a 'brown' zone of heavy sediment loading impedes light penetration and limits primary productivity within the plume. Further away from the river plume a 'green' zone is defined by elevated nutrients and high primary productivity which ostensibly deposits large loads of marine derived organics to the benthos (Turner and Rabalais, 1994). West of Terrebonne Bay a 'blue' zone is dominated by intense seasonal stratification and a strong pycnocline, nutrients are limiting at this distance from river input and most primary production is fueled by recycled nutrients (Dortch and Whitledge, 1992). Transition areas between the green and blue zone inputs of dissolved

organic matter from the Atchafalaya River and Terrebonne Bay provide additional POC independent of the main Mississippi River outflow (Bianchi et al., 2010).

Localized benthic respiration is dependent on the quantity and quality of carbon sources available. Stratified water bodies decrease the amount of particulate organic matter (POM) exported from the surface because sinking particles are suspended in the pycnocline (Hargrave and Phillips, 1986; Redalje et al., 1994); the quality of sinking particles also decreases if they are subject to long residence times and bacterial degradation within the pycnocline (Tribovillard et al., 2009). Intense or long-term physical stratification of the water column can lead to nutrient limitation in the surface mixed layer once the local nutrient sources are depleted by phytoplankton (Quigg et al., 2011; Sylvan et al., 2006; Weston et al., 2008). Consequently nutrient concentrations and chlorophyll *a* levels at the thermocline and in the bottom mixed layer become elevated (Weston et al., 2008). Physical and biogeochemical processes in each of the conceptual zones are different and thus the products of primary production and the export of particulate organic matter to the bottom are unequal (Redalje et al., 1994). Hypoxia impacts redox conditions in bottom waters and sediments that control the functioning of sediment communities. Low oxygen conditions are also deleterious to the macrobenthic invertebrate community structure which influences sediment biogeochemical processes through the processes of bioirrigation and bioturbation (Aller, 1982).

Microbes dominate the cycling of carbon, nitrogen, phosphorous and metals in sediments, but the greatest facilitators of benthic biogeochemistry are the macrofauna

because of their active reworking of sediments (Aller, 1982). Animal death under low oxygen conditions in the northern Gulf of Mexico hypoxic zone (GoMHZ) provides a natural laboratory for studying the effects of the macrobenthos on sediment reactions. Hypoxia in bottom waters can be seen as early as late February and may continue into October (Rabalais et al., 1999). This long term exposure to little or no oxygen will slowly deplete the sediments of metazoan fauna, but some macrofauna survive regardless of the duration or intensity of hypoxia (Gaston, 1985; Gaston et al., 1985; Harper et al., 1991; Harper et al., 1981; Rabalais et al., 2001). These 'survivors' act as the brood stock for recolonization of the sediments once bottom waters are reoxygenated in part becuase their larvae may remain in the zooplankton during low oxygen conditions (Powers et al., 2001).

Sediments communities consume oxygen and remineralize carbon to CO_2; however the ultimate fate of nitrogen within sediments can be equivocal. Depending on the amount of active denitrification sediment can serve as sink or a source of nitrogen within the system (Seitzinger et al., 1984). Regeneration of nutrients within the sediments can provide nitrogen and phosphorous substrates for primary productivity in the water column or for microphytobenthos. In the GoMHZ this release of N and P is only available for phytoplankton beneath the strong pycnocline that forms during the summer, but the stratification limits its availability to the surface mixed layer. Mixing events such as storms and internal waves however can introduce bottom derived nutrients into the euphotic zone where it can then be incorporated into the pelagic food web (DiMarco et al., 2009). Sediment-released nutrients could be important to primary

production in the western ‘blue’ zones that tend to be nitrogen limited in late summer because light penetrates below the pycnocline (Dortch et al., 1994; Lehrter et al., 2009; Rowe, 2001).

Interactions between water column processes and benthic ecosystem response are widely studied and the benthic dependence upon carbon fixed within the euphotic zone accepted. Direct impacts of benthic processes affecting pelagic systems are harder to quantify especially since benthic supplied nutrients are in dissolved form and easily assimilated by both microbes and phytoplankton. Sediments release appreciable amounts of nitrogen, phosphorous and silica all known to limit primary production in coastal systems (Redfield, 1958; Rowe et al., 1975), with sediments “tending to promote” nitrogen limitation (Redfield, 1934). This tendency of unequal nitrogen returns is attributed to sediment denitrification which removes biologically available nitrogen returning it as N_2 gas (Burdige, 2006; Seitzinger, 1990; Seitzinger et al., 1983). Since we are not yet able to systematically follow every regenerated nutrient molecule from sediment to phytoplankton, the contribution of benthic nutrients contributing to pelagic productivity is an estimate based on Redfield stoichiometry (Redfield, 1958).

Nixon (1981) found that 25-50% of the organic matter consumed by sediments was associated with the movement of inorganic nutrients from sediment to water. Benthic coupling to pelagic primary production can be considered an extended line of the biological pump, in which nitrogen and carbon are continuously remineralized for biological use until exported from the system. The returns from this line have been estimated by measuring benthic nutrient regeneration and applying the fluxes of N, P

and Si out of sediments to the requirements of measured overhead primary production (Hargrave and Phillips, 1986; Hopkinson, 1987; Hopkinson et al., 2001; Rowe et al., 1977; Rowe et al., 1975). Rowe et al. (1975) estimated that an excess amount of nitrogen needed for photosynthesis could be provided by benthic regeneration of ammonium. Further studies by Rowe et al. (1977) off the coast of Saharan Africa determined that sediments could only provide 30-39% of nitrogen for local primary production. The relative intracellular requirements for nitrogen and phosphorous by phytoplankton are different. The release of these nutrients from sediments does not follow any known stoichiometry thus while one element may be present at worthwhile concentrations the other element may limit growth. This is shown in a study by Hopkinson (1987) where sediment regeneration could supply 40% of the phosphorous needed but only 11% of nitrogen needed for pelagic productivity.

The complex nature of sediment function and spatial heterogeneity of macrofauna within the hypoxic zone require integrated approaches to understand the response of the sediment community to sustained low oxygen events. Hypoxia/anoxia causes reduced macrofauna abundance (Baustian and Rabalais, 2009; Gaston, 1985; Gaston et al., 1985; Gray et al., 2002; Harper et al., 1991; Harper et al., 1981); decreased abundance reduces the amount and extent of bioirrigation and bioturbation (Aller, 1978, 1982; Karlson et al., 2007; Rosenberg et al., 1991); and depletion of burrow habitats decreases the amount of surface areas that contain microhabitats of redox potential available for microbial colonization (Aller, 1982). During large hypoxic seasons these

harmful effects can have consequences for the following summer if excess organic material and nitrogen are retained on the shelf (Turner et al., 2008).

Substantial increases in summertime hypoxic area on the Louisiana-Texas continental shelf noticed in the 1990s (Rabalais et al., 1999) foreshadow regional scale changes within the continental shelf ecosystem. Detailed studies that began in the 1980s do not have enough historical perspective for us to answer simple questions about the nature of what constitutes a healthy ecosystem for the region. This makes predicting ecosystem collapse especially difficult. The benthic communities of infauna are the most severely affected by the hypoxic phenomenon and thus serve as critical indicators of ecosystem health. Sediment functioning is heavily influenced by the macrofauna structure (abundance, biomass and diversity) but also responds to environmental conditions where it has the potential to control certain aspects of nitrogen cycling. For these reasons seasonal studies of benthic biogeochemistry within the Northern Gulf of Mexico Hypoxic Zone are important in determining what role sediments play within an altered continental shelf ecosystem.

The design of the Mechanisms Controlling Hypoxia project and my station locations for benthic incubation experiments focus on conceptual zones of hypoxic potential outlined by Rowe and Chapman (2001). These stations will be used to determine if POC input is accurately predicted based on conditions of the surface mixed layer. The amount of biogeochemical cycling of POM within the pycnocline prior to deposition on the sea floor is unknown. Thus the quantity and quality of organic material reaching the sea floor can only be inferred from the rates of carbon and nitrogen

sediment fluxes. Knowing the sediment oxygen demand allows us to model the benthic contribution to oxygen depletion below the mixed layer. Net fluxes of dissolved inorganic nitrogen (DIN) can determine the fate of nitrogen during oxic and hypoxic conditions and determine under what conditions sediment acts as a sink for this element.

The seasonal nature of hypoxia on the Texas-Louisiana coast makes it a natural laboratory to study the interplay of benthic function and structure. Hypoxia creates areas of low oxygen and accumulation of sulfides and ammonium in the sediments which cause macrofauna death, reducing spatial homogeneity of sediments that impact benthic fluxes. The process of habitat degradation from oxic to hypoxic, and in some cases anoxic conditions, is followed during normoxic periods by recolonization of the defaunated sediments. The recovery of macrobenthic populations following the hypoxic season is a slow process and the benthos may not fully recover from year to year depending on severity of the event. If this gradual deterioration of the basal food web continues it could lead to regime changes (any impact that changes dominant food-web pathways) that may precede overall community collapse.

The ultimate goal of this study is to combine studies of shelf-wide ecosystem processes that occur in the benthos, specifically oxygen consumption and nutrient regeneration, with the seasonal structuring of the macrobenthos. Combining structure and function was pursued to answer two questions that cannot be answered by other studies investigating benthic processes. Are sediment biogeochemistry and macrofauna structure inherently tied to one another? What are the feedbacks created by each and how do they impact the relative flux rates and faunal changes observed? Not only will

this work seek to combine structure and function on the sea floor but also to accurately model the fate of nutrients remineralized in sediments to processes in the overlying water column. The study of inherently patchy biogeochemical cycles and variable faunal effects was possible because a natural removal of organisms occurs each summer as dissolved oxygen concentration drops.

The following chapter (Chapter II) will characterize the rates of these sedimentary biogeochemical processes based on the temporal, spatial and environmental framework of the Mechanisms Controlling Hypoxia project. Mass recycling of nutrients by sediments impacts the overall cycle of limiting nutrients on the continental shelf relative to river inputs. System feedbacks that influence eutrophic processes may counteract managed controls of nutrient loading in the Mississippi-Atchafalaya River System (MARS).

Chapter III will present a steady state STELLA model of benthic-pelagic coupling based on the measured rates of benthic nutrient regeneration and primary production below the pycnocline. Model simulations deviating from the steady state (perturbations) will seek to answer key questions about hypoxia within the western regions of the GoMHZ. How do large areas of the sea floor become and stay hypoxic in a region of the continental shelf that experiences minute physical impacts of the Mississippi River and is nutrient limited? Can the lower water column and sediments act as a nutrient reservoir?

Chapter IV will move the focus from the biogeochemistry of the sediments to the biology of the macrofauna community. The rise and fall of the infaunal macrobenthos

population begins with the seasonal creation of hypoxia and ends in late summer as stratification weakens and hypoxia breaks up. Hypoxic intensity on the continental shelf during hypoxia will be tracked through the abundance, diversity and biomass of the benthic macrofauna community. Five major groups of invertebrates (Polychaetea, Bivalvia, Gastropoda, Amphipoda and Cumacea) have been identified to species and will illustrate ecological processes that determine community diversity. Comparisons with historical studies of the macrobenthos on the Louisiana continental shelf will address the long term resiliency of infaunal communities subject to intense, regular hypoxic events. Hypoxia is a dominate feature of the continental shelf during an annual cycle and benthic macroinfaunal communities potentially have transitioned to a stressed faunal assemblage.

In the summary I will focus on biogeochemical and faunal community knowledge gained from this study with the ultimate aim of creating predictions that govern interactions of chemistry, biology in the face of a stressed, eutrophic ecosystem. The results of this synthesis will be discussed and relationships between metazoan contributions to benthic fluxes considered. Hopefully pointing towards what information would be needed for a manuscript that synthesizes benthic function and structure together.

CHAPTER II

OXYGEN CONSUMPTION AND NUTRIENT REGENERATION BY SEDIMENTS IN THE NORTHERN GULF OF MEXICO HYPOXIC ZONE

2.1 Overview

Seasonal summer stratification and enhanced nutrient loading of the Louisiana continental shelf (USA) west of the Mississippi River create hypoxic regions that affect large areas of the benthos. Total sediment oxygen uptake and nutrient recycling were measured during different, pre-, early, late and post hypoxic regimes using shipboard Batch Micro-Incubation Chambers (BMICs) in 2004 to 2005 and again in 2007 to 2009. Sediment community oxygen consumption during oxic regimes (dissolved oxygen > 63 µmol L^{-1}) was -9.5 ± 0.7 mmol O_2 m^{-2} d^{-1} (mean ± SE), almost twice that measured (-5.8 ± 0.6 mmol O_2 m^{-2} d^{-1}) during suboxic conditions. During the summer when hypoxia occurred, the benthos consumed nitrate and nitrite (-0.14 ± 0.04 and -0.10 ± 0.02 mmol N m^{-2} d^{-1} respectively) and produced ammonium (1.6 ± 0.39 mmol N m^{-2} d^{-1}). Released ammonium from the benthos is a source of nutrients for primary production in the euphotic zone, but it also provides reduced nitrogen for nitrification and microbial respiration, both of which reinforce the intensity and duration of hypoxia. Sediments actively scavenged phosphate from the bottom waters (-98.4 ± 21.3 µmol P m^{-2} d^{-1}) and released silicate (2.62 ± 0.31 mmol Si m^{-2} d^{-1}). The addition of reactive nitrogen and removal phosphorous due to benthic community metabolism could potentially be accentuating phosphorous limitation on the continental shelf.

2.2 Introduction

In the region under the Mississippi-Atchafalaya River Plume along the Louisiana continental shelf low oxygen areas form during summer months due to strong thermohaline stratification (Bianchi et al., 2010; (Hetland and DiMarco, 2008); Rabalais, Turner, and Wiseman, 1999; Turner et al., 2005; Wiseman et al., 1997). Enhanced biological productivity in surface waters caused by elevated nutrients in river discharge provides ample substrate for respiration in the water column (Dortch et al., 1994; Lehrter et al., 2009; Quigg et al., 2011) and sediments (Rowe et al. 2002; Rowe, 2001) beneath the pycnocline. Over time and under strong seasonal stratification, this leads to large zones of hypoxia in bottom waters that persist until oxygen can be physically mixed from the surface or offshore. These processes of eutrophication, stratification and respiration combine to create the northern Gulf of Mexico Hypoxic Zone (GoMHZ). All of these processes vary in time and space and thus variations in sedimentary biogeochemical processes (Morse and Rowe, 1999; Rowe et al., 2002) need to be understood to better predict consequences of river runoff (Dagg and Breed, 2003; Rabalais et al., 1999; Quigg et al., 2011), wetland particulate and dissolved organic carbon (POC and DOC) contributions (Bianchi et al., 2011; Bianchi et al., 2010; Bianchi et al., 2009), and physical forcing (Cochrane and Kelly, 1986; DiMarco et al., 2009; Wiseman et al., 1997).

River plume dynamics and coastal boundary currents create unique zones with differing hypoxic potential within the GoMHZ (Rowe and Chapman, 2002). Near the river mouth, a ‘brown’ zone of heavy sediment loading impedes light penetration and

limits primary productivity within the plume. Further away from the river plume, a 'green' zone is defined by elevated nutrients and high primary productivity which ostensibly deposits large loads of marine derived organics to the benthos (Turner and Rabalais, 1994). West of Terrebonne Bay a 'blue' zone is dominated by intense seasonal stratification and a strong pycnocline; nutrients are limiting at this distance from river input and most primary production is fueled by recycled nutrients (Dortch and Whitledge, 1992; Quigg et al., 2011). Transition areas associated with coastal bays (Timbalier, Terrebonne and Atchafalaya Bays) between these zones provide inputs of dissolved organic matter independent of the main Mississippi River outflow (Bianchi et al., 2010).

Sediments consume oxygen and remineralize organic carbon to CO_2; however the ultimate fate of nitrogen within sediments can be equivocal. Depending on the amount of active denitrification, sediments can serve as sink or a source of nitrogen (Seitzinger et al., 1984). Regeneration of nutrients within the sediments can provide nitrogen and phosphorous needed for primary productivity in the water column or for microphytobenthos. In the GoMHZ, this release of N and P is likely only available for phytoplankton beneath the strong pycnocline that forms during the summer. Storms and internal waves can introduce bottom-derived nutrients into the euphotic zone where they can then be incorporated into the pelagic food web (DiMarco et al., 2009). Sediment derived nutrients could be important to primary production in the western 'blue' zones that tend to be nitrogen limited in late summer because increased light penetration would allow deeper waters to become photosynthetically active (Dortch et al., 1994; Lehrter et

al., 2009, Quigg et al., 2011). Sediment release of ammonium can further eutrophicate waters beneath the pycnocline by stimulating primary producers (Rowe et al., 1975) and fueling further respiration (Nixon, 1981).

Substantial increases in summertime hypoxic area on the Louisiana-Texas continental shelf observed in the 1990s (Rabalais et al., 1999) predict regional scale changes within the continental shelf ecosystem. Detailed studies that began in the 1980s do not have enough historical perspective for us to answer simple questions about the nature of what constitutes a healthy ecosystem for the region. This makes predicting ecosystem collapse especially difficult. As ecosystems deteriorate to a less desirable state, feedbacks tend to enhance processes, ultimately accelerating the shift to an alternate state. For these reasons benthic biogeochemical studies during prolonged hypoxic episodes within the GoMHZ are important in determining the role sediments play within an altered continental shelf ecosystem. Determining benthic respiration rates allows sediment oxygen demand (SOD) to be incorporated into oxygen budgets of dynamic hypoxic water masses (Hetland and DiMarco, 2008). Likewise the quantification of nutrient remineralization within the sediments are important components of coupled physical-biogeochemical models (Fennel et al., 2011). Benthic nitrogen dynamics within a eutrophic, hypoxic system play an important role in determining the ultimate fate of anthropogenic nutrient input from the Mississippi-Atchafalaya River System (MARS).

During the hypoxic seasons of 2004 to 2005 and 2007 to 2009 regular hydrographic cruises visited the Louisiana continental shelf as part of the Mechanisms

Controlling Hypoxia (MCH) project (www.hypoxia.tamu.edu). Different zones of hypoxic potential were characterized based on physical, chemical and biological properties. Within the center of each theoretical zone, at respiration stations, sediments were collected for incubation experiments to determine the rates of seafloor biogeochemical processes. Shipboard incubation experiments focused on the utilization of oxygen by sediments and the exchange of nutrients between sediment and overlying water. MCH cruises were dynamic, constantly searching for the edges of hypoxic areas, which did not allow for regular visits to all respiration stations. Therefore three experimental hypotheses were developed to test the importance of space, time and dissolved oxygen concentrations on benthic functioning. First (H_{01}), spatial proximity to riverine and marsh sources of organic carbon (OC) affects rates of oxygen consumption and nutrient regeneration. River input to the shelf provides large amounts of sediment POC and marshes add reactive DOC for respiration and remineralization (Bianchi et al., 2011; Rowe and Chapman, 2002). Second (H_{02}), temporal duration of hypoxia impacts sedimentary biogeochemistry causing hysteresis of the system. Since hypoxia in the GoMHZ is a dominant feature of the ecosystem present for most of the year, organic matter storage in sediments from previous seasons can amount to higher nitrogen loading as it is recycled in the sediments. Thus environmental conditions from the previous year on the Louisiana continental shelf can have deterministic impacts on current biogeochemical cycling (Turner et al., 2008). Third (H_{03}), biogeochemical rates are dependent on the dissolved oxygen concentration of the overlying water. Oxic and anoxic niches are important for microbial processes such as nitrification-denitrification

coupling; hypoxic conditions (< 63 μmol L^{-1}) will obliterate important microhabitats and decrease oxygen gradients at the sediment-water interface thus influencing the rates of Sediment Community Oxygen Consumption (SCOC) and organic matter (OM) remineralization (Middleburg and Levin, 2009).

2.3 Materials and Methods

2.3.1 Study Area

Respiration measurements were made at 4 designated incubation stations within the MCH framework for each of the study zones A, B and C initially, with D added in July of 2005 (Fig. 2.1). Each study zone was created to examine the paradigm suggested for the creation and control of bottom water hypoxia by Rowe and Chapman (2002). The "brown" zone or Zone A, is closest to the Mississippi River and controlled by light limitation and heavy deposition of organic material bound to clay sediments. The "green" zone or Zone B (located South of Terrebonne and Timbalier Bays), is within the region of greatest primary productivity where light is no longer limiting due to the deposition of particulate organic matter and sediments but there are ample nutrients. The "blue" zone or Zones C & D is the largest of the study areas and is heavily stratified due to the volume of freshwater delivered by the rivers (Wiseman et al., 1997). Zones A and C are both situated within the outflow of the two large rivers that define this coastal system, but the type of river output is dramatically different between the two (Pakulski et al., 2000). The Zone A incubation station sits directly off Southwest Pass where the channelized Mississippi River empties onto the continental shelf and waters contain large amounts of total nitrogen and phosphorous (Pakulski et al., 2000) (Fig. 2.1). River

nutrients and carbon experience little degradation prior to the entry of these river waters into the ocean. Zone C sits south of Atchafalaya Bay and receives river water from the Atchafalaya River after extensive nutrient filtering by marshes that change the nature of particulate organics (greater relative amounts of dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) (Pakulski et al., 2000) while removing river sediment loadings.

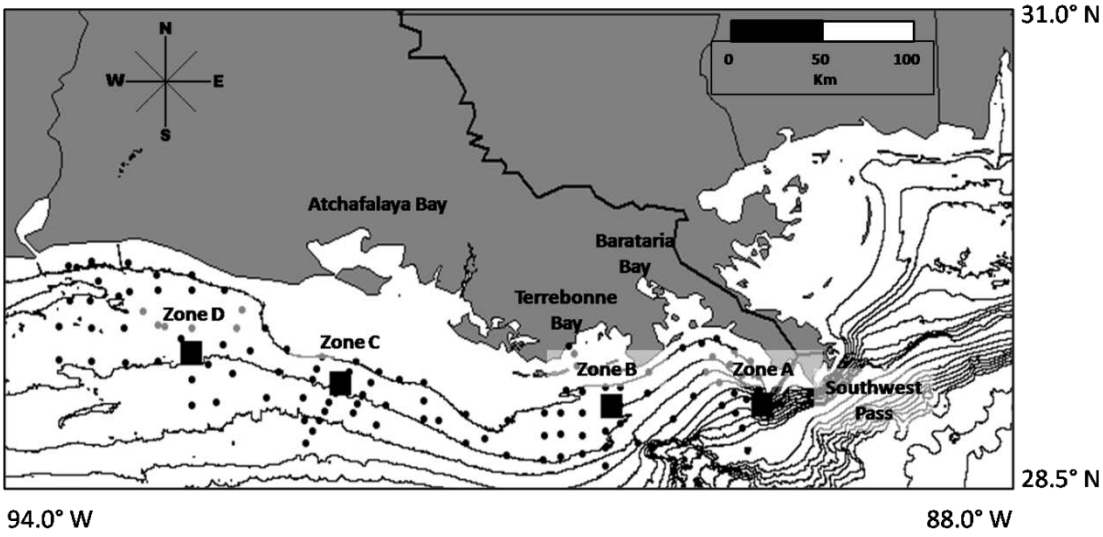


Fig. 2.1. Map of the Mechanisms Controlling Hypoxia BMIC incubation stations within the Northern Gulf of Mexico Hypoxic Zone on the Louisiana continental shelf. The Mississippi River enters the Gulf at Southwest Pass. The Atchafalaya River flows through Atchafalaya Bay before entering the Gulf. The small dots represent grid of CTD and oxygen profiles (DiMarco et al., 2009).

2.3.2 Determination of Hypoxic Season

Hypoxic seasons of this study roughly resemble cruise schedules for the MCH program which normally allowed for three to four cruises each year during March through September. Pre-Hypoxia refers to cruises in March and April in which incubation stations had bottom water oxygen concentrations greater than 2.0 mg L^{-1}. Early Hypoxia was determined as cruises prior to July in which bottom water at incubation stations was less than 2.0 mg L^{-1}. The Late Hypoxia season was defined by hypoxic bottom waters during July through September. The Post Hypoxia season occurred only on two occasions in September when bottom water had returned to dissolved oxygen concentrations greater than 2.0 mg L^{-1}.

2.3.3 Batch Micro Incubation Chambers

Shipboard incubations of recovered sediments were made using Batch Micro Incubation Chambers (BMICs) which consist of a hollow Plexiglas tube with a beveled bottom edge for easier penetration into sediments. Top and bottom caps are firmly clamped to the core by 3 metal straps; this ensures no leakage of mud or water once the core has been extracted. Top caps are lined with a rubber o-ring to prevent leakage. Top caps have a threaded port that allows a Model 57 YSI oxygen electrode (YSI Inc., Yellow Springs, Ohio) to be screwed into the chamber above a small stirring bar that prevents stagnation near the electrodes. Top caps contain multiple syringe ports for extraction of overlying water. Experiments were made in triplicate using BMIC chambers with an area of 0.125 m^2 that would incorporate ~1 liter of water when filled halfway with sediment. Actual depth of sediments in cores was recorded and the

remaining overlying water volume calculated. Respiration contributed by the overlying core water alone was determined by incubating the bottom water without sediment.

2.3.4 Core Collection

Sediments were collected from mooring sites using a GOMEX box core with a sample area of 0.2 m^2 (Boland and Rowe, 1991). Box cores were inspected for leaking mud or water and an intact sediment water interface before they were considered appropriate for collection of sediments to use in BMIC experiments. Preservation of the mud-water interface is of key importance in incubation experiments using recovered cores (Pamatmat, 1971). Overlying core water was collected and stored to be used in the water bath and to replace extracted sample water from the BMICs. BMICs were placed into the sediments and capped before core water had been completely drained to capture overlying water inside the chambers. Immediate capping of BMICs was made to prevent re-oxygenation of overlying water volumes.

2.3.5 Core Incubation

Recovered BMICs were placed in a water bath of local bottom water kept in the dark at room temperature (ca. 20°C). Oxygen electrodes were screwed into the lids and any air space inside cores was replaced with ambient bottom water. BMICs were allowed to sit for 1-2 hours until flocculent material settled and overlying water was clear. An overhead rotating magnet caused interior stirring magnets to spin inside each BMIC. Dissolved oxygen concentrations and temperature were recorded at 1 hour intervals. Regeneration of nutrients (NH_4^+, NO_3^-, NO_2^-, $HSiO_3$, HPO_4 and urea) was measured by removing overlying water through syringe ports at the beginning, middle

and end of the incubation. Removal of overlying core water for nutrient analysis was replaced with bottom water collected from the box core. Replacement water was kept in 60 cc syringes inside the experimental water bath. Cores were allowed to incubate for a period of 6-14 hours or until changes in dissolved oxygen were no longer measurable.

2.3.6 Calculation of Sediment Community Oxygen Consumption (SCOC) and Nutrient Regeneration

The uptake of dissolved oxygen by the sediments was calculated as the change in dissolved oxygen in overlying water normalized for the volume of water, the area of the sediments and the time of the incubation (Equation 2.1). The flux of nutrients between sediment and overlying water was also calculated using Equation 2.1. Movement of dissolved nutrients into sediments from the overlying water is considered a loss and has a negative value. Release of dissolved nutrients by the sediments into overlying water is considered a gain and as such has a positive value. The net movement of dissolved inorganic nitrogen species (net DIN) was determined by summing ammonium, nitrate and nitrite fluxes.

$$\frac{(\text{change in dissolved molecule x volume of overlying water})}{(\text{sediment area x time of incubation})} \qquad (2.1)$$

Potential artifacts of temperature differences between the laboratory and *in-situ* bottom conditions were accounted for by using a Q_{10} of 2. Experimental rates of oxygen consumption were corrected to *in-situ* temperatures using Equation 2.2 (Valiela, 1995). Respiration measured in BMICs (r_1) at experimental temperatures ($t_{1)}$ were converted to

a new temperature corrected oxygen consumption rates (r2) for the bottom temperature (t_2) measured during core collection using the derived Equation 2.3.

$$Q_{10} = [r_1/r_2]^{[10/(t_1 - t_2)]} \quad (2.2)$$

$$r_2 = r_1 * Q_{10}^{[(t_2 - t_1)/10]} \quad (2.3)$$

2.3.7 Nutrient Analysis

Nutrient samples drawn from the BMICs were filtered through a 0.2 µm syringe filter and frozen for analysis. Filtered nutrient samples were processed by the Geochemical and Environmental Research Group (GERG) at Texas A&M University. Analytes of interest were determined using a Technicon II Autoanalyzer and a refined method of that commonly used for seawater analyses (Strickland and Parsons, 1972). Nitrogenous nutrients measured were nitrate, nitrite, total nitrate + nitrite, ammonium and urea. Silicate and phosphate were also determined using the autoanalyzer. Nitrate and nitrite analyses utilized a ground Cd column for reduction of NO_3^- to NO_2^- (Armstrong et al., 1967). Orthophosphate was measured using chemistry gained from the investigations of Bernhardt and Wilhelms (1967) with the modification of hydrazine as reductant. Silicate concentration was determined incorporating stannous chloride and was based on the methods of Armstrong et al. (1967). Ammonium analysis is based on the method of (Harwood and Kühn, 1970). Urea determination was measured using diacetyl monoximine and micarbozide.

Table 2.1 Mean ± standard error of benthic fluxes measured during MCH project for season, zone and oxygen concentration. Negative values indicate nutrient consumption by sediments and positive values indicate nutrient release by sediments.

		SCOC	NH_4	NO_3	NO_2	Net DIN	PO_4	Si	Urea
		(mmol m^{-2} d^{-1})							
SEASON									
	Pre-Hypoxia	12.7 ± 1.3	0.64 ± 0.12	-0.14 ± 0.05	-0.10 ± 0.06	0.42 ± 0.13	-0.10 ± 0.04	1.9 ± 0.4	-0.10 ±0.06
	Early Hypoxia	7.5 ± 0.9	1.0 ± 0.2	-0.03 ± 0.05	-0.07 ± 0.02	0.92 ± 0.17	-0.05 ± 0.02	2.8 ± 0.2	0.02 ± 0.04
	Late Hypoxia	9.1 ± 1.1	1.8 ± 0.5	-0.26 ± 0.05	-0.13 ± 0.03	1.4 ± 0.5	-0.13 ± 0.04	2.8 ± 0.6	0.02 ± 0.07
	Post Hypoxia	9.9 ± 2.0	1.3 ± 0.6	-0.18 ± 0.09	-0.04 ± 0.01	1.1 ± 0.5	-0.03 ± 0.02	4.4 ± 2.1	-0.03 ± 0.12
ZONE									
	Zone A	14.1 ± 1.9	3.4 ± 1.2	-0.35 ± 0.07	-0.12 ± 0.04	3.1 ± 1.3	-0.15 ± 0.07	2.5 ± 0.4	-0.05 ± 0.11
	Zone B	8.1 ± 1.6	0.87 ± 0.13	-0.16 ± 0.07	-0.05 ± 0.02	0.66 ± 0.11	-0.06 ± 0.04	2.1 ± 0.3	0.07 ± 0.07
	Zone C	10.4 ± 0.9	0.91 ± 0.13	-0.13 ± 0.04	-0.14 ± 0.05	0.60 ± 0.12	-0.11 ± 0.04	3.5 ± 0.7	0.03 ± 0.05
	Zone D	6.5 ± 0.6	0.70 ± 0.14	-0.09 ± 0.04	-0.06 ± 0.01	0.55 ± 0.16	-0.08 ± 0.01	1.7 ± 0.3	-0.20 ± 0.07
OXYGEN CONCENTRATION									
	Oxic	11.1 ± 0.9	0.90 ± 0.14	-0.19 ± 0.04	-0.10 ± 0.04	0.63 ± 0.13	-0.12 ± 0.04	3.1 ± 0.6	-0.05 ± 0.04
	Suboxic	8.4 ± 0.9	1.6 ± 0.4	-0.14 ± 0.04	-0.10 ± 0.02	1.3 ± 0.4	-0.08 ± 0.02	2.2 ± 0.2	0.01 ± 0.06
TOTAL		**9.6 ± 0.6**	**1.3 ± 0.2**	**-0.16 ± 0.03**	**-0.10 ± 0.02**	**1.0 ± 0.2**	**-0.10 ± 0.02**	**2.6 ± 0.3**	**-0.02 ± 0.03**
n		**97**	**98**	**94**	**98**	**94**	**96**	**98**	**95**

2.3.8 Statistical Analysis

Kolomogorov-Smirnov and Levene's Equality of Variances tests revealed that benthic flux data were neither normally distributed nor possessed homogenous variances thus precluding the use of parametric tests to determine differences in spatial, temporal and environmental factors. Determination of statistically significant differences in benthic fluxes was assessed using Kruskal-Wallis tests to compare spatial (zone) and temporal (season) scales. The Kruskal-Wallis H test is a non-parametric alternative to a one-way between-groups analysis of variance. Post-hoc testing of significant Kruskal-Wallis results was made using a Mann-Whitney U test that determined significant differences between two independent groups. A Mann-Whitney U test was performed to determine statistical significance oxic and suboxic conditions on benthic fluxes. For all tests the critical p-value was 0.05 using SPSS (version 16.0) statistical software.

2.4 Results

Oxygen and nutrient flux mean values are a result of 107 total replicate incubations, spanning five years, within a seven month time frame of a typical hypoxia season. This includes four seasons encompassing the four defined zones within the Mississippi-Atchafalaya River Plumes along the Louisiana continental shelf. Oxygen was consumed by sediments at a mean rate of -9.6 ± 0.6 (mean ± SE) mmol O_2 m^{-2} d^{-1} (Fig. 2.2 and Table 2.1). Ammonium and silicate efflux were greatest in magnitude, releasing these nutrients at rates of 1.26 ± 0.22 and 2.62 ± 0.31 mmol m^{-2} d^{-1} respectively (Table 2.1). Mean uptake of reduced DIN (nitrate and nitrite) accounted for -0.163 ± 0.029 and -0.100 ± 0.021 mmol N m^{-2} d^{-1} respectively (Fig. 2.3). The net sum of all DIN

fluxes was a positive release of 1.0 mmol N m^{-2} d^{-1} (Fig. 2.4). Dissolved organic nitrogen measured as urea, was consumed by sediments at a rate of -0.018 ± 0.034 mmol N m^{-2} d^{-1} (Table 2.1).

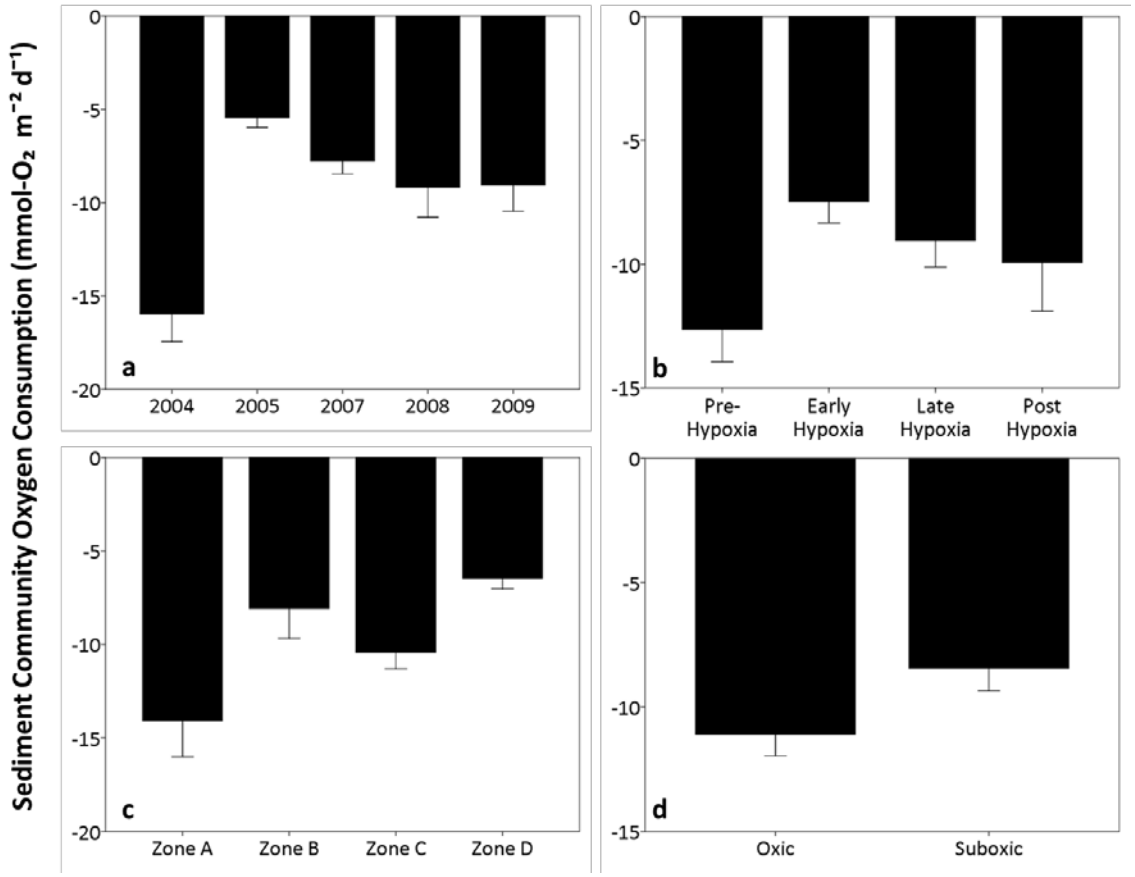


Fig. 2.2. Sediment Community Oxygen Consumption (SCOC) within the Northern Gulf of Mexico Hypoxic Zone (GoMHZ): (a) SCOC at all sites for each MCH study years, (b) Temporal mean SCOC of each defined hypoxia season, (c) Spatial mean SCOC of MCH Zones, and (d) Mean SCOC of oxic and suboxic incubations. Error bars represent 1 standard error of the mean (SE).

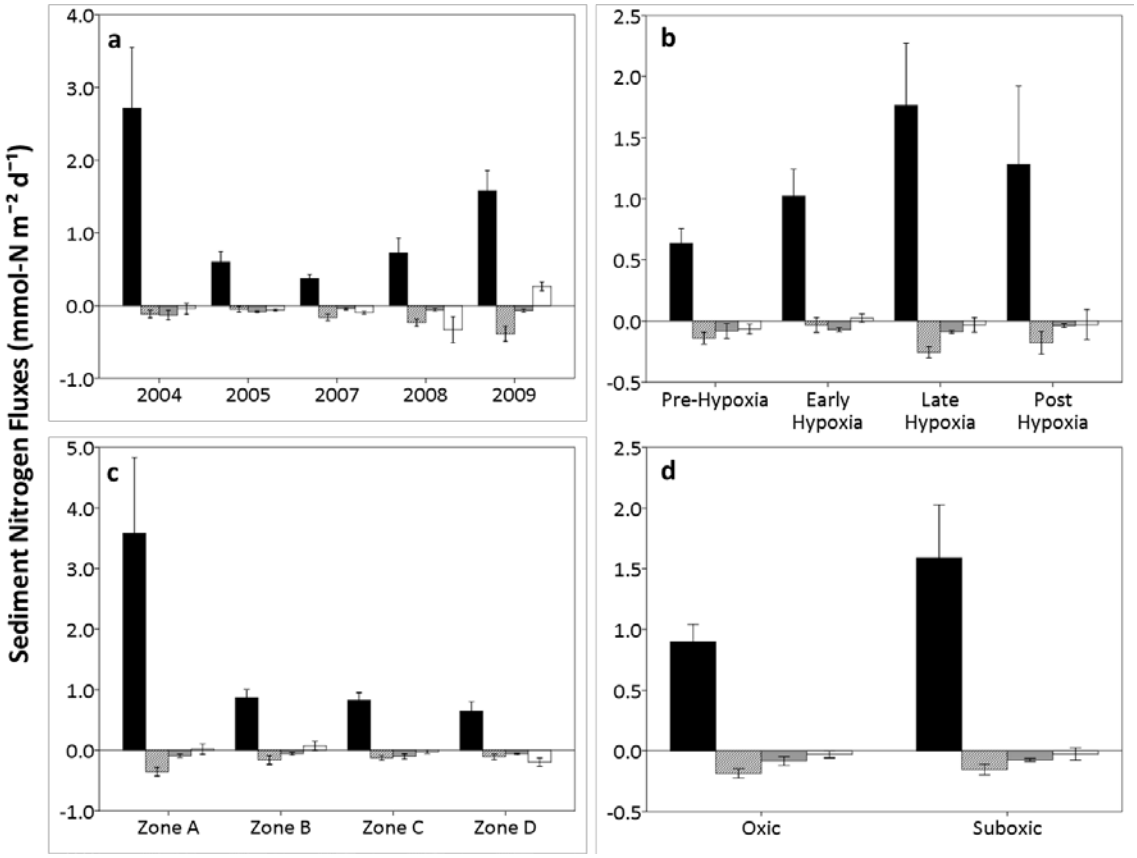


Fig. 2.3. Fluxes of ammonium, nitrate, nitrite and urea of sediments within the Northern Gulf of Mexico Hypoxic Zone (GoMHZ): (a) Mean nitrogen fluxes displayed for MCH study years, (b) Temporal mean nitrogen fluxes of hypoxia seasons, (c) Spatial mean nitrogen fluxes of MCH Zones, (d) Mean nitrogen fluxes of oxic and suboxic incubations. Black bars = ammonium. Hatched bars = nitrate. Grey bars = nitrite. White bars = urea. Error bars represent 1 standard error of the mean (SE).

Mean phosphate uptake by sediments occurred at a rate of -0.098 ± 0.021 mmol P m^{-2} d^{-1} (Fig. 2.5 and Table 2.1).

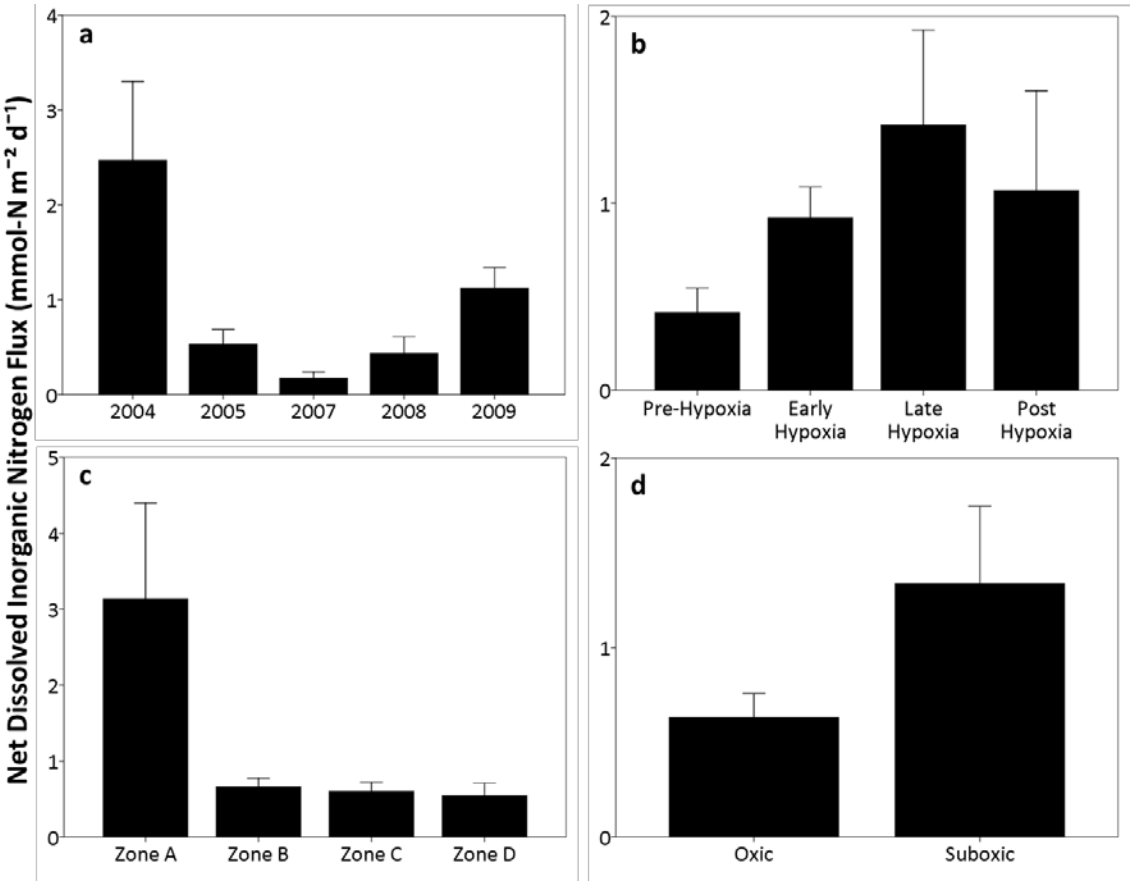


Fig. 2.4. The net Dissolved Inorganic Nitrogen (DIN) flux by sediments within the Northern Gulf of Mexico Hypoxic Zone (GoMHZ): (a) Mean net DIN displayed for MCH study years, (b) Temporal mean net DIN of hypoxia seasons, (c) Spatial mean net DIN of MCH Zones, (d) Mean net DIN of oxic and suboxic incubations. Error bars represent 1 standard error of the mean (SE).

Trends in the direction of fluxes for most nutrients were not statistically significant over the course of the study regardless of temporal, spatial or environmental factors. However, a Kruskal-Wallis test revealed statistically significant differences between study years for all measured fluxes, except for phosphate.

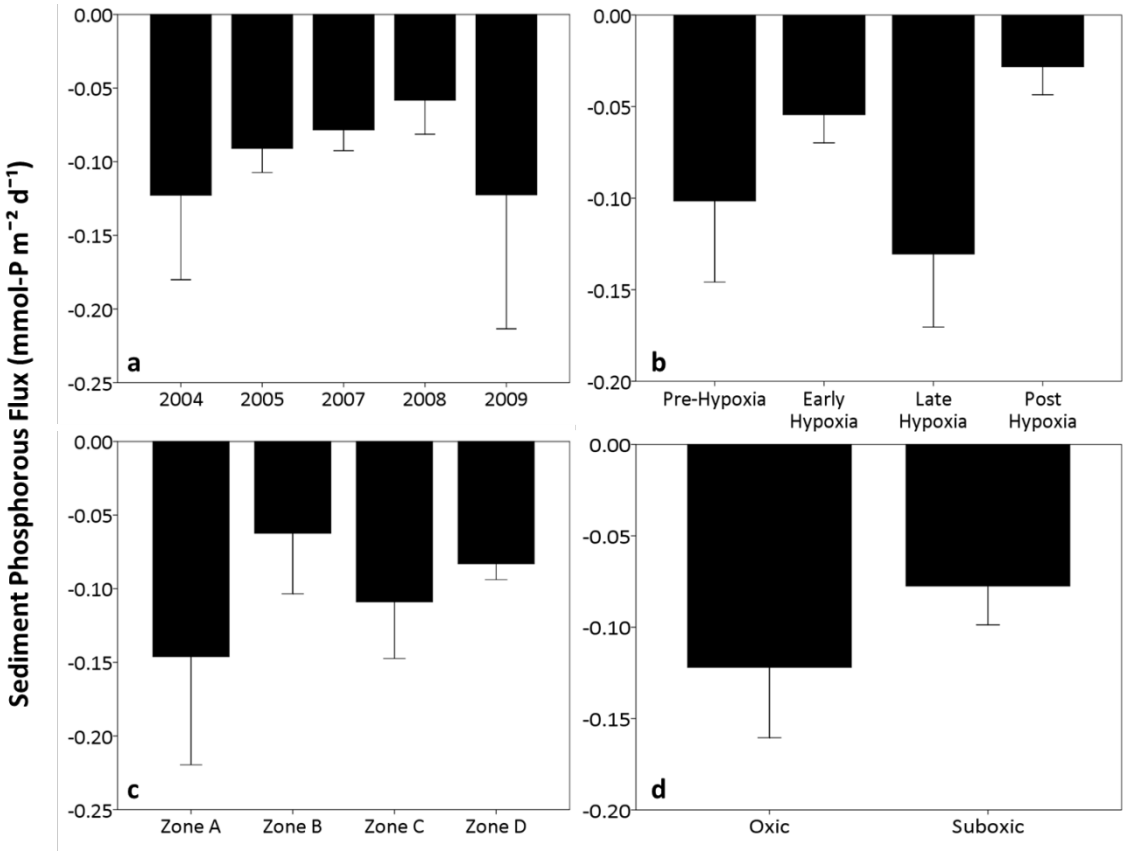


Fig. 2.5. The mean retention of phosphate by sediments within the Northern Gulf of Mexico Hypoxic Zone (GoMHZ): (a) Mean phosphate flux displayed for MCH study years, (b) Temporal mean phosphate flux of hypoxia seasons, (c) Spatial mean phosphate flux of MCH Zones, (d) Mean phosphate flux of oxic and suboxic incubations. Error bars represent 1 standard error of the mean (SE).

2.4.1 Temporal Patterns (Hypoxia Seasons)

Sediment community oxygen consumption was greatest during Pre- and Post Hypoxia consuming -12.7 ± 1.3 and -8.4 mmol O_2 m^{-2} d^{-1}, respectively (Table 2.2). Pre and Post Hypoxia SCOC were statistically the same. Early and Late Hypoxia SCOC

were significantly lower with rates of -7.5 ± 0.9 and -9.1 ± 1.1 mmol O_2 m^{-2} d^{-1} respectively (Fig. 2.2). A Kruskal-Wallis test indicated a statistically significant difference in SCOC rates across the four hypoxia seasons (Table 2.3). A post-hoc Mann-Whitney U test revealed that Pre-Hypoxia SCOC was significantly greater than

Table 2.2 Mean ± standard error of dissolved oxygen and nutrient concentrations from bottom water during MCH project.

		$[O_2]$ (mmol/L)	**$[NH_4]$**	**$[NO_3]$**	**$[NO_2]$**	**$[PO_4]$**	**[Si]**	**[Urea]**
					(µmol/L)			
SEASON								
	Pre-Hypoxia	0.14 ± 0.01	1.2 ± 0.2	4.1 ± 0.7	0.58 ± 0.08	0.50 ± 0.05	11.2 ± 1.3	0.94 ± 0.13
	Early Hypoxia	0.05 ± 0.01	1.2 ± 0.3	4.2 ± 0.5	3.5 ± 0.7	0.81 ± 0.07	25.2 ± 2.5	0.71 ± 0.11
	Late Hypoxia	0.04 ± 0.004	1.9 ± 0.4	6.1 ± 0.4	2.0 ± 0.2	1.4 ± 0.2	32.4 ± 2.5	0.79 ± 0.13
	Post Hypoxia	0.10 ± 0.01	0.54 ± 0.09	1.2 ± 0.5	0.33 ± 0.06	0.35 ± 0.12	25.1 ± 0.0	0.66 ± 0.00
ZONE								
	Zone A	0.09 ± 0.01	2.8 ± 0.5	7.5 ± 0.6	1.4 ± 0.2	1.2 ± 0.1	14.0 ± 1.3	0.67 ± 0.07
	Zone B	0.05 ± 0.01	0.65 ± 0.12	4.7 ± 0.6	1.1 ± 0.3	0.70 ± 0.08	17.8 ± 2.0	0.44 ± 0.06
	Zone C	0.09 ± 0.01	1.4 ± 0.4	3.5 ± 0.5	1.6 ± 0.2	1.0 ± 0.2	26.4 ± 2.7	0.89 ± 0.12
	Zone D	0.05 ± 0.01	1.2 ± 0.2	4.8 ± 0.6	3.7 ± 0.8	0.89 ± 0.08	31.0 ± 3.1	1.3 ± 0.2
OXYGEN CONCENTRATION								
	Oxic	0.12 ±0.01	1.4 ± 0.3	3.7 ± 0.5	0.99 ± 0.16	0.82 ± 0.17	16.4 ± 2.1	0.91 ± 0.09
	Suboxic	0.03 ± 0.002	1.5 ± 0.3	5.8 ± 0.4	2.6 ± 0.4	1.0 ± 0.06	30.2 ± 1.8	0.72 ± 0.10
TOTAL		**0.07 ± 0.01**	**1.4 ± 0.19**	**4.8 ± 0.3**	**1.8 ± 0.2**	**0.94 ± 0.09**	**23.4 ± 1.5**	**0.82 ± 0.07**
n		**107**	**107**	**107**	**107**	**107**	**99**	**96**

Early and Late Hypoxia SCOC, but was not different from Post Hypoxia SCOC rates (Table 2.4). Bottom water oxygen concentrations ranged from a high of 0.21 mmol L^{-1} during Pre-Hypoxia and a low of 0.001 mmol L^{-1} in Late Hypoxia (Table 2.2).

Nitrate and nitrite fluxes were always into sediments with ammonium almost exclusively occurring as a product of sediment remineralization (Table 2.2). DIN (ammonium, nitrate and nitrate) and phosphate fluxes were during Late Hypoxia (Table 2.2). Mean ammonium efflux ranged from 0.64 ± 0.12 mmol NH_4 m^{-2} d^{-1} to of 1.77 ± 0.47 mmol NH_4 m^{-2} d^{-1} (Table 2.2). Ammonium concentrations of bottom waters were relatively constant during Pre, Early and Late Hypoxia (1.2 ± 0.2, 1.2 ± 0.3 and 1.9 ± 0.4 µmol L^{-1} respectively) but dropped to a low of 0.54 ± 0.09 µmol L^{-1} during Post Hypoxia (Table 2.2). Nitrate fluxes ranged from uptake of -0.99 mmol N m^{-2} d^{-1} to release of 0.25 mmol N m^{-2} d^{-1}. Nitrite fluxes ranged from uptake of -1.42 mmol N m^{-2} d^{-1} to release of 0.29 mmol N m^{-2} d^{-1}. A Kruskal-Wallis test showed statistically significant differences in nitrate and nitrite fluxes across four different hypoxia seasons (Table 2.3). A post hoc Mann-Whitney U test showed a significant difference in nitrate uptake by sediments between Early and Late Hypoxia, with greater uptake of nitrate occurring during Late Hypoxia (Tables 2.5 and 2.2). Nitrate fluxes were lowest during Early Hypoxia measuring only -0.028 ± 0.053 mmol N m^{-2} d^{-1} (Fig. 2.3). Nitrite flux was appreciably less Post Hypoxia, being consumed at only -0.037 ± 0.032 mmol N m^{-2} d^{-1} (Fig. 2.3). A post-hoc Mann-Whitney U test revealed that Pre-Hypoxia sediment nitrite fluxes were statistically lower than Early and Late Hypoxia rates and were statistically similar to Post Hypoxia rates. Nitrate concentrations in bottom waters ranged from a

low of 0.12 µmol L^{-1} in Early Hypoxia and a high of 12.1 µmol L^{-1} in Late Hypoxia (Table 2.2).

Table 2.3 Between groups Kruskal-Wallis test statistic (Chi Square) of benthic fluxes for study year, hypoxic season and MCH zone. Between groups Mann-Whitney U test statistic of benthic fluxes for oxygen concentration. Statistically significant values are shown in bold.

	SCOC	NH_4	NO_3	NO_2	Net DIN	PO_4	Si	Urea
YEAR	**35.51**	**36.68**	**11.34**	**14.08**	**33.78**	1.81	**34.26**	**22.38**
SEASON	**11.74**	6.79	**13.93**	**11.86**	6.87	5.66	7.07	3.27
ZONE	**18.50**	7.68	**8.59**	3.97	7.70	1.34	4.04	5.95
OXYGEN CONCENTRATION	**745**	958	961	974	896	1103	1172	1076

2.4.2 Spatial Patterns (MCH Zones)

Sediment community oxygen consumption differed spatially among the four zones with the highest rates of consumption occurring closest to the mouth of the Mississippi River, Zone A and the lowest rates furthest from the river's outflow, Zone D (Table 2.3). Average Zone A SCOC was -14.1 ± 1.9 mmol O_2 m^{-2} d^{-1}, Zone B SCOC was -8.1 ± 1.6 mmol O_2 m^{-2} d^{-1}, Zone C SCOC was -10.4 ± 0.9 mmol O_2 m^{-2} d^{-1} and Zone D SCOC was -6.5 ± 0.6 mmol O_2 m^{-2} d^{-1} (Fig. 2.2). A Kruskal-Wallis test revealed statistically significant differences in SCOC rates between the four MCH zones (Table 2.3). Post hoc Mann-Whitney U tests revealed that all four zones had statistically significant differences in SCOC rates (Table 2.6). Zones A and C had identical mean bottom water dissolved oxygen concentrations of 0.9 ± 0.01 mmol L^{-1};

mean dissolved oxygen concentrations in Zones B and D were also identical at 0.05 ± 0.01 mmol L^{-1} (Table 2.2).

Table 2.4 Between groups Mann-Whitney U test statistic for SCOC between hypoxic seasons. Statistically significant values are shown in bold.

SCOC	**PRE-HYPOXIA**	**EARLY HYPOXIA**	**LATE HYPOXIA**	**POST HYPOXIA**
PRE-HYPOXIA	X			
EARLY HYPOXIA	**143**	X		
LATE HYPOXIA	**315**	480	X	
POST HYPOXIA	56	37	82	X

Table 2.5 Between groups Mann-Whitney U test statistic for nitrate flux between hypoxic seasons. Statistically significant values are shown in bold.

NO_3	**PRE-HYPOXIA**	**EARLY HYPOXIA**	**LATE HYPOXIA**	**POST HYPOXIA**
PRE-HYPOXIA	X			
EARLY HYPOXIA	202	X		
LATE HYPOXIA	298	**206**	X	
POST HYPOXIA	56	37	85	X

The greatest single measured ammonium efflux, 18.8 mmol NH_4 m^{-2} d^{-1} was in Zone A closest to the Mississippi River Mouth; likewise this location had the highest mean ammonium efflux: 3.4 ± 1.2 mmol NH_4 m^{-2} d^{-1} (Table 2.1). Ammonium efflux ranged from highs in Zone A to lows in Zone D (-0.17 mmol N m^{-2} d^{-1}) which had a mean efflux of 0.70 ± 0.14 mmol NH_4 m^{-2} d^{-1} (Table 2.3). A Kruskal-Wallis test

revealed no statistically significant difference in ammonium fluxes between the four MCH zones (Table 2.3 and Fig. 2.3). Ammonium concentrations in bottom waters ranged from a low of 0.05 µmol L^{-1} to a high of 8.7 µmol L^{-1}, both measured in Zone C (Table 2.2).

Mean nitrate consumption ranged from -0.35 ± 0.07 mmol NO_3 m^{-2} d^{-1} in Zone A to -0.09 ± 0.04 mmol N m^{-2} d^{-1} in Zone D (Fig. 2.3). Mean nitrite consumption ranged from -1.42 to 0.29 within Zone C alone (Table 2.3). A Kruskal-Wallis test revealed

Table 2.6 Between groups Mann-Whitney U test statistic for SCOC between MCH zones. Statistically significant values are shown in bold.

SCOC	**ZONE A**	**ZONE B**	**ZONE C**	**ZONE D**
ZONE A	X			
ZONE B	**80**	X		
ZONE C	216	**272**	X	
ZONE D	**47**	217	**208**	X

significant differences in nitrate flux rates but not for nitrite fluxes between the four MCH zones (Table 2.3). Post hoc Mann-Whitney U tests determined that Zone A had statistically greater nitrate fluxes when compared to Zones B, C and D (Table 2.7).

Highest mean nitrate concentrations in bottom waters occurred in Zone A at 7.5 ± 0.6 µmol L^{-1} (Table 2.2). Highest mean nitrite concentrations in bottom waters occurred in Zone D at 3.7 ± 0.9 µmol L^{-1} (Table 2.2).

2.4.3 Oxic versus Suboxic Fluxes

Removal of oxygen from bottom water by sediment respiration occurred nearly twice as fast in oxic waters, -11.1 ± 0.9 mmol O_2 m^{-2} d^{-1} compared to a suboxic SCOC of -8.4 ± 0.9 mmol O_2 m^{-2} d^{-1} (Fig. 2.2 and Table 2.4). SCOC ranged from a low of -0.79 mmol O_2 m^{-2} d^{-1} under suboxic conditions compared to a high of -34.2 mmol O_2 m^{-2} d^{-1} under oxic conditions. A Mann-Whitney U test supported these differences in SCOC rates (Table 2.3) as a function of oxygen concentration. Mean bottom water dissolved oxygen was 0.12 ± 0.01 mmol L^{-1} during oxic conditions and 0.03 ± 0.002 mmol L^{-1} at suboxic conditions (Table 2.2).

Table 2.7 Between groups Mann-Whitney U test statistic for nitrate between MCH zones. Statistically significant values are shown in bold.

NO_3	**ZONE A**	**ZONE B**	**ZONE C**	**ZONE D**
ZONE A	X			
ZONE B	**97**	X		
ZONE C	**144**	388	X	
ZONE D	**69**	228	355	X

Nutrient exchanges between sediments and overlying water showed no substantial differences as a function of oxygen concentration of overlying water (Table 2.4). A Mann-Whitney U test confirmed that the differences in nutrient recycling rates were statistically similar regardless of oxic or suboxic conditions of experiments (Table 2.3). Ammonium generated by sediments influenced by suboxic waters was 1.6 ± 0.39 mmol N_4 m^{-2} d^{-1}, compared to ammonium release under oxic conditions of 0.80 ± 0.14

mmol N_4 m^{-2} d^{-1} (Table 2.4). Nitrate was consumed at a rate of -0.185 ± 0.039 mmol NO_3 m^{-2} d^{-1} during oxic periods and at a rate of -0.144 ± 0.042 mmol NO_3 m^{-2} d^{-1} during suboxic conditions (Fig. 2.3). Suboxic net exchange of DIN was of 1.3 ± 0.41 mmol N m^{-2} d^{-1}, compared to 0.63 ± 0.13 mmol N m^{-2} d^{-1} under oxic conditions (Table 2.4).

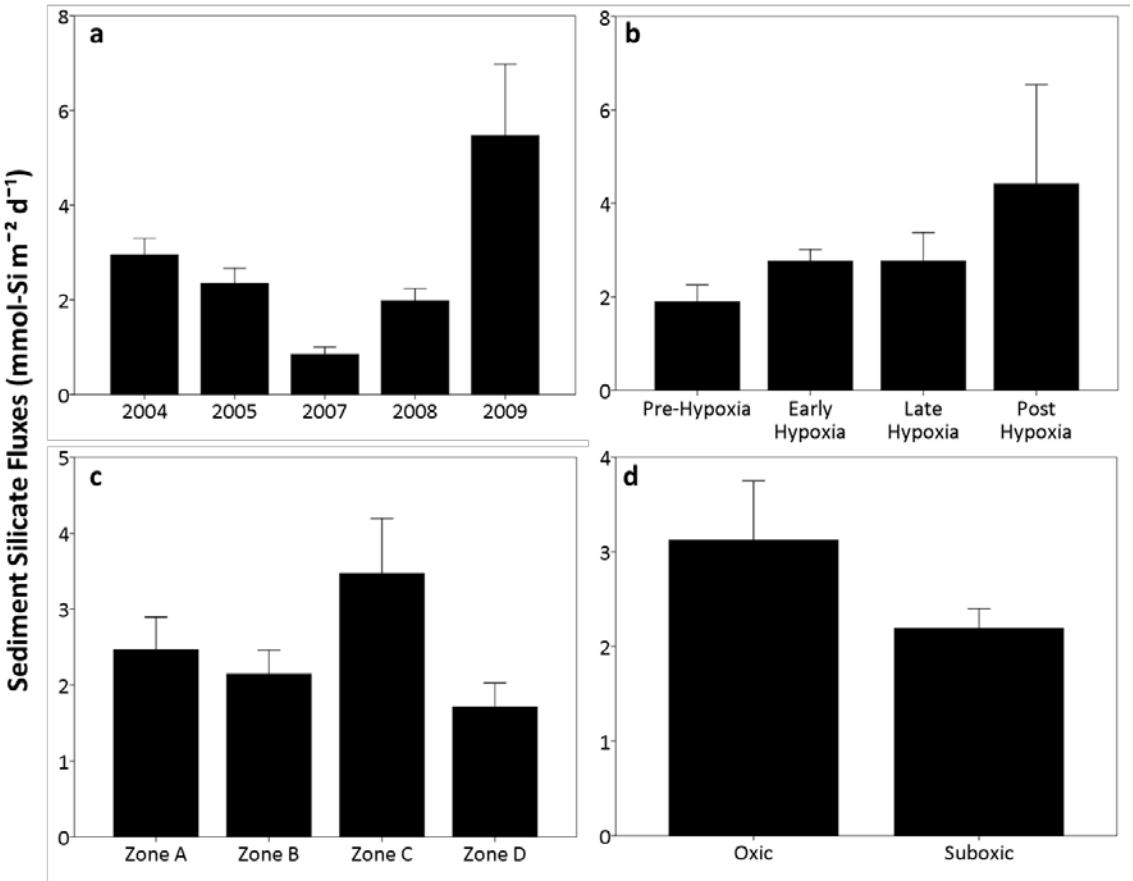


Fig. 2.6. The mean flux of silicate by sediments within the Northern Gulf of Mexico Hypoxic Zone (GoMHZ): (a) Mean silicate flux displayed for MCH study years, (b) Temporal mean silicate flux of hypoxia seasons, (c) Spatial mean silicate flux of MCH Zones, (d) Mean silicate flux of oxic and suboxic incubations. Error bars represent 1 standard error of the mean (SE).

Suboxic conditions did not change the direction of phosphate fluxes (Fig. 2.5). Oxic efflux of silicate by was 3.1 ± 0.63 mmol m^{-2} d^{-1} versus 2.2 ± 0.21mmol Si m^{-2} d^{-1} when suboxic (Fig. 2.6). The net direction of urea fluxes shifted from mean urea uptake during oxic conditions of -0.052 ± 0.037 mmol N m^{-2} d^{-1} to a mean efflux of 0.01 ±0.06 mmol N m^{-2} d^{-1} under suboxic conditions (Table 2.4).

2.5 Discussion

Biogeochemical cycling within GoMHZ sediments was incredibly variable; even the scope of this long term study that includes over 100 replicate incubation experiments over 6 years was unable to establish a set of rules to describe sediment functioning based on our experimental hypotheses. Many of the temporal and spatial patterns of oxygen and nutrient cycling that may seem intuitive were not supported statistically due to the wide range of flux rates. Nutrient fluxes were especially unpredictable regardless of the concentration of nutrient present in bottom water (Table 2.2). SCOC was significantly greater in Zones A and C, areas of enhanced carbon delivery from the Mississippi and Atchafalaya Rivers. Spatial heterogeneity of benthic sediments in terms of organic content, grain size (data not shown), micro and macrofauna, and redox states has been shown to be incredibly patchy affecting the system in a stochastic manner (Morse and Rowe, 1999). Sediment fluxes within GoMHZ did not correspond to the amount of freshwater or dissolved nutrients delivered to the continental shelf by the MARS system, factors important to pelagic productivity (Dagg et al., 2007; Lohrenz et al., 1997; Quigg et al., 2011; Turner et al., 1998). This is likely due to decoupling of water column processes above the pycnocline and the flux of material to the sea floor and indicates the

need for a better understanding of how pycnocline properties affect export of surface POC.

SCOC was sensitive to the spatial, temporal and environmental scales detailed within this study. Rates of SCOC decreased with distance from Southwest Pass indicating a decrease in POC flux to the seafloor. The common assumption that sedimentation is related to nitrogen loading is neither supported by model results (Breed et al., 2004) or measurements of POC export on the continental shelf (Redalje et al., 1994). However rates of sedimentation do decrease with distance from the Mississippi River mouth (Bianchi et al., 2002). Suppressed SCOC during suboxic conditions is similar to findings by Rowe et al. (2002) and Lehrter et al., (2011). The mean SCOC of -9.6 ± 0.6 mmol O_2 m^{-2} d^{-1} reported from this study is lower than those published by Rowe et al. (1992) (-19.0 mmol O_2 m^{-2} d^{-1}), Miller-Way et al. (1994) (-46.5 mmol O_2 m^{-2} $d^{-1)}$, Morse and Rowe (1999) (-24.8 mmol O_2 m^{-2} d^{-1}), and Rowe et al. (2002) (-19.2 mmol O_2 m^{-2} d^{-1}); our values are closer in magnitude to the studies of Gardner et al. (1993) (-7.9 mmol O_2 m^{-2} d^{-1}), Murrell and Lehrter (2010) (-12.3 mmol O_2 m^{-2} d^{-1}) and Lehrter et al. (2011) (-8.7 mmol O_2 m^{-2} d^{-1}). The values in our study may be lower due to the fact that over half of sediment incubations were made during periods of hypoxia with mean bottom water dissolved oxygen concentration of 0.07 ± 0.01 mmol L^{-1}.

Net dissolved inorganic nitrogen (DIN) fluxes are the sum of nitrate, nitrite and ammonium. The net movement of dissolved inorganic nitrogen that occurred seasonally represents the change in the relative portions of nitrate and nitrite consumed by sediments in contrast to ammonium released by sediments (Fig. 2.4). Net DIN fluxes

from this study are positive indicating return of nitrogen to the system as ammonium. Although not all nitrogen transformations were measured, this metric of major biogeochemical nitrogen reservoirs indicates that little nitrogen was being removed from the system; most was returned to the water column to further enhance the nitrogen pool of sub-pycnocline waters. Peak net flux of DIN from the sediments occurred closest to the Mississippi River outflow at Southwest Pass (Zone A) during Late Hypoxia after months of prolonged benthic exposure to low oxygen. Ammonium fluxes in Zone A during Late Hypoxia were 7.0 ± 2.6 mmol N m^{-2} d^{-1}, 40 times greater than the Pre-Hypoxia efflux in Zone D of 0.16 ± 0.10 mmol N m^{-2} d^{-1}. Similar ranges in net ammonium regeneration in the northern Gulf of Mexico were found by Lin et al. (2011) who reported high ammonium regeneration of 7.7 mmol N m^{-2} d^{-1} at a seasonally hypoxic site and low ammonium regeneration of 0.36 mmol N m^{-2} d^{-1} at a normoxic site.

It is evident that massive amounts of ammonium are being released by sediments in the course of organic matter remineralization. Yet the easily assimilated nature of ammonium by nitrifying bacteria (Pakulski et al., 1995)and phytoplankton (Falkowski and Raven, 2007) predicates that it will not persist. Ammonium production will also benefit the microphytobenthos during late summer when reduced sediment loads allow deeper light penetration (Dortch et al., 1994). Remineralized ammonium fueled anammox within the Peruvian oxygen minimum zone was the principal nitrogen removal pathway over denitrification The final fate of recycled DIN (in the form of ammonium) is equivocal and more studies are needed to determine the relative importance of all N pathways (Seitzinger et al., 2006).

Depletion of nitrate from bottom waters makes it likely that denitrification rates will also decrease as aerobic nitrification is effectively stopped with remineralized nitrogen escaping sediments in the form of ammonium via the dissimilatory nitrate reduction to ammonium (DNRA) pathway (Middleburg and Levin, 2009). The almost continual sedimentary consumption of NO_3^-, presumably taken up by denitrifying and DNRA bacteria, accompanied by a release of NH_4^+, suggests there was minimal coupling between nitrification and denitrification. This may be due to toxic effects of sulphide (Morse and Rowe, 1999) on nitrifying bacteria (Joye and Hollibaugh, 1995). Most other studies of benthic nutrient remineralization within the GoMHZ reported uptake of oxidized DIN (NO_3^- and NO_2^-) similar to our values (Gardner et al., 1993; Miller-Way et al., 1994; Rowe et al., 2002). Nitrate production only occurred in Zones B, C and D during Early Hypoxia under suboxic conditions.

Phosphate uptake by sediments was common during this study (83% of incubations) although smaller in magnitude compared to other studies from the area (Miller-Way et al., 1994). The common paradigm however calls for P release by sediments experiencing anoxia (Ingall and Jahnke, 1994; Twilley et al., 1999); such is the case for other studies of benthic nutrient fluxes from the GoMHZ (Lehrter et al., 2011; Morse and Rowe, 1999). Surprisingly, little P was released over the entire course of this study, suggesting that the sediment never became entirely anoxic. Recent evidence of bacterially mediated phosphorous sequestration by sulfide-oxidizing bacteria of the genus *Thiomargarita* and *Beggiatoa* (Goldhammer et al., 2010) under anoxic conditions may explain the mean uptake of phosphate by sediments. Within this study

small patches of white filamentous bacteria, *Beggiatoa*, would form from time to time on the top of sediments during incubation similar to previous reports from other studies from the Louisiana continental shelf (Rowe et al., 2002). Phosphorous cycling within sediments is tightly coupled to the cycling of iron oxides and as such dependent on the oxygen concentration of bottom waters (Middleburg and Levin, 2009; Rozan et al., 2002). Increased benthic infaunal mortality due to low oxygen severely reduces bioturbation activities that move iron oxides towards the surface, consequently limiting the amount phosphate release by sediments.

As silicate is not utilized by any sediment heterotrophs, the constant efflux of silicate demonstrates that the BMICs were working as designed and not subject to experimental artifacts. Silicate efflux can be used to determine experimental integrity because sediment concentrations of silicate are always greater than in the overlying water. The large, constant efflux of silicate was similar to total net efflux in other measurements made on the Louisiana shelf (Lehrter et al., 2011; Miller-Way et al., 1994). Our values fall in between the high rates of Miller-Way et al. (1994) and lower values of Lehrter et al. (2011), 6.6 and 1.7 mmol m^{-2} d^{-1}, respectively.

Urea fluxes showed the greatest variability between sediment uptake and efflux primarily because dissolved organic nitrogen is heavily influenced by environmental factors that determine biological release and utilization by the sediment community. Urea is the only dissolved nutrient that reversed the direction of exchange between oxic and suboxic bottom water conditions. High rates of urea efflux (0.7 mmol m^{-2} d^{-1}) in oxygenated sediments on the Bering Shelf accounted for 47-70 % of total nitrogen flux

and may contribute up to 80% of gross NH_4 production (Lomstein et al., 1989). It is likely that the relatively low urea flux (1.2% of total N fluxes) in this study is a result of the conversion of urea to NH_4 or the uptake of urea as a N source by primary producers and bacteria (Solomon et al., 2010).

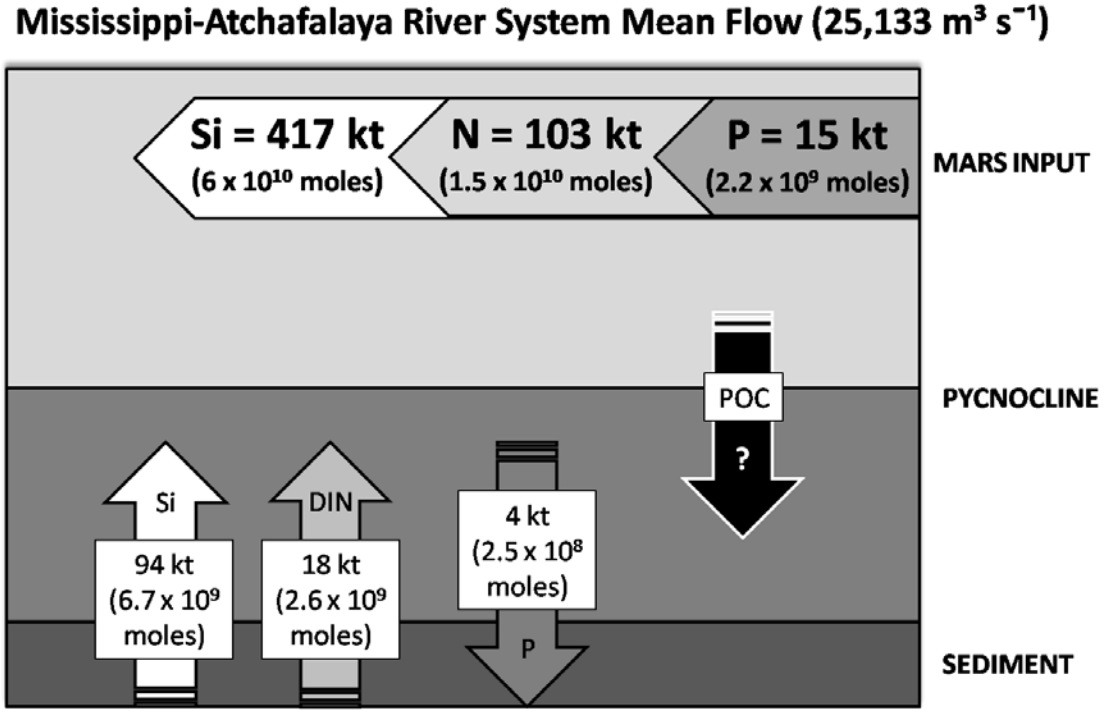


Fig. 2.7. River loading of silicate, nitrogen (NOx) and phosphorous (TP) delivered to the Louisiana continental shelf during the hypoxic season (March-August) in relation to remineralization processes in sediments. Values in arrow are kilotons of the specified element. Values within parentheses are moles.

The earliest works measuring nutrient fluxes in marine sediments display the considerable patchiness associated with benthic flux measurements (Rowe et al., 1977,

Rowe et al., 1975). Our fluxes agree well with those of Rowe et al. (1975) that measured ammonium efflux of 1.28 mmol m^{-2} d^{-1}, but not those measured by Rowe et al. (1977) that measured it as 5.64 mmol m^{-2} d^{-1}. The measurements of sediment nutrient remineralization from Buzzards Bay, Massachusetts (Rowe et al., 1975) are much more similar in magnitude to our fluxes compared with those off of Cap Blanc, Western Sahara (Rowe et al., 1977). Phosphate consumption measured from Buzzards Bay of -0.04 mmol m^{-2} d^{-1} was similar to our measured consumption and radically different from the massive release measured in Cap Blanc of 1.2 mmol m^{-2} d^{-1}. Similarly net DIN measured off Cap Blanc was 9.8 mmol m^{-2} d^{-1} compared to 1.4 mmol m^{-2} d^{-1} in Buzzards Bay, which agrees closely with our net DIN of 1.0 mmol m^{-2} d^{-1}.

2.6 Conclusions

Complex interactions of river inputs, POC export, and the duration and severity of hypoxia in the Northern Gulf of Mexico Hypoxic Zone control the overall rates of benthic biogeochemical cycling. After months of suboxic conditions, from April to August, on the Louisiana continental shelf rates of ammonium, nitrate, nitrite and phosphate remineralization reach a peak intensity. Rates then decrease Post Hypoxia when nutrient concentrations in bottom waters are low and sedimentary processes are no longer stressed by low oxygen. Benthic functioning within hypoxic zones does not exhibit a clear pattern, but spatio-temporal patterns appear in nutrient recycling independent of surface processes. Murrell and Lehrter (2010) reported limitation of sediment community oxygen consumption at low dissolved oxygen concentrations but this was not observed in bottom water plankton community respiration. Under hypoxic

conditions SCOC may contribute less to oxygen utilization; however sediments may impact bottom water respiration by releasing reduced chemical species (e.g. iron, ammonium, sulfide). Sediment metabolism generates large amounts of nutrients that can fuel autochthonous primary production beneath the pycnocline extending the length of the hypoxia season. By scaling nutrient remineralization rates to an average hypoxia area (16,700 km^2 from 2000-2007 (Turner et al., 2008)) and hypoxia season (153 days) specific rates of nutrient fluxes can be related to river inputs as kilotons of nutrient input. The MARS system delivered 417, 103 and 15 kilotons of silicate, nitrogen and phosphorous respectively during an average hypoxia season for the study years (Alexander et al., 2008) (Fig. 2.7). Remineralization of nitrogen, phosphate and silicate by sediment during the hypoxia season accounted for 17, 27 and 23% of the total river input, respectively (Fig. 2.7). If river loads of nitrogen are reduced as currently suggested (Rabalais et al., 2002), then benthic remineralization in hypoxic areas will become an even more important source of nutrients that cannot be overlooked in management considerations. Nutrients in river effluent are utilized by primary producers in the surface and are transferred to sediments as sinking organic matter. While sediments are a sink for P, they return large amounts of N because severe hypoxia tends to decouple nitrification-denitrification, thus limiting the sediment's ability to remove nitrogen as N_2 gas. Yet this positive feedback mechanism of eutrophic conditions is equivocal because ammonium and silicate are returned to the system and phosphate is removed and likely enhances productivity near river inputs that are not P-limited (Sylvan et al., 2006). Eutrophic processes responsible for bottom water hypoxia

are inhibited by nutrient limitation in surface waters (Dagg et al., 2007; Quigg et al., 2011; Sylvan et al., 2006) towards the end of the hypoxic season yet hypoxia is quickly reformed after physical mixing (Wiseman et al., 1997). Disruption of stratified water would not only mix oxygen into bottom waters but inject regenerated nutrients into the euphotic zone. Consequently benthic-pelagic coupling within the GoMHZ depends not only on benthic nutrient remineralization but the physical mechanisms needed to transfer nutrients to areas where they are available to primary producers. Resolving the quantity and quality of the "black arrow" (Fig. 2.7) of POC flux to the benthos will help close the stoichiometric gap between surface and benthic processes.

Rowe and Chapman (2002) have previously stressed the need to better understand the flux of particles from the upper mixed layer to the benthos. They proposed that the Mississippi River plume could be partitioned into along-shelf regions of brown, green and blue water subsystems each with differing hypoxia-causing mechanisms. Recent work has shown that Atchafalaya River water (Hetland and DiMarco, 2008; Quigg et al., 2011) and export from adjacent marshes (Bianchi et al., 2011) also need to be considered as drivers of hypoxic potential on the Louisiana shelf. Lerhter et al. (2011) has partitioned the continental shelf into a cross-shelf set of zones with emphasis on the Mississippi River outflow at Southwest Pass and the Atchafalaya River as it flows through Atchafalaya Bay. This agrees well with our results that show Zones A and C as similar areas of intense benthic remineralization. These recent developments are poignant reminders that even as our knowledge of this complicated system increases the depth of the uncertainties remain.

Eutrophication of sub-pycnocline water masses not governed by riverine nutrients have the potential to stimulate the fixation of carbon that will be deposited to the benthos without undergoing extensive degradation as it sinks to the sea floor. This secondary mechanism of POC input may increase the amount of organics available for burial during periods of low oxygen and this potentially translates into greater carbon sequestered within the sediments. Coastal ecosystems that experience prolonged seasonal hypoxia or oxygen minimum zones are important areas of organic matter storage on geological time scales and as such will require further research to delineate the impacts of anaerobic sedimentary processes.

CHAPTER III

BENTHIC-PELAGIC COUPLING IN THE GULF OF MEXICO HYPOXIC ZONE: SEDIMENTARY ENHANCEMENT OF EUTROPHIC CONDITIONS AND NEAR BOTTOM PRIMARY PRODUCTION

3.1 Overview

Seasonal bottom water hypoxia covers large portions of the Louisiana continental shelf despite nitrogen and phosphorous limitation of surface waters that occurs on the continental shelf West of Atchafalaya Bay. During summer hypoxia sediments become a net source of fixed nitrogen providing an important limiting nutrient to the system when river input of nutrients has diminished. Presumably the stage is set for the utilization of benthic nutrients to fuel photosynthesis creating a positive feedback on particulate organic matter production that when respired controls bottom water oxygen concentrations. Coupled measurements of benthic nutrient regeneration, water column productivity, and carbon and nitrogen analysis of phytoplankton were used to validate a simple steady state model. The objective of this simulation powered by field measurements was to determine the importance of sub-pycnocline processes that contribute to bottom water hypoxia. During summertime sub-pycnocline productivity was greater than that in the surface mixed layers. The dynamic nature of the pycnocline can control nutrient availability moving benthic regenerated nutrients up in the water column. These findings illustrate the importance of subsurface processes in maintaining bottom water hypoxia for the western Gulf of Mexico Hypoxic Zone.

3.2 Introduction

In the northern Gulf of Mexico the Mississippi and Atchafalaya Rivers deposit nutrient rich freshwater laden with anthropogenic nitrogen and phosphorous derived from agriculture in the Midwestern United States of America. As a consequence of increased nutrient loading (Rabalais et al., 2002) and strongly stratified water column (DiMarco et al., 2009; Wiseman et al., 1997) large areas of the sea floor are overlain by hypoxic waters; seasonal summertime hypoxia impacts biological food-webs, cycling of carbon, and the stoichiometric relationship between nutrients on the continental shelf (Dodds, 2006; Turner and Rabalais, 1994). The northern Gulf of Mexico Hypoxic Zone (GoMHZ) has increased in size since regular measurements began in 1985 (Rabalais et al., 1999; Turner et al., 2008) with western regions of the Louisiana continental shelf exhibiting prolonged summer hypoxia. Bottom water hypoxia west of the Atchafalaya Bay and Mississippi River occurs in areas where surface primary production is nitrogen limited (Quigg et al., 2011) and thus do not produce large amounts of sinking particulate organic matter (POM). Current paradigms of nutrient enhanced coastal eutrophication resulting in hypoxia thus cannot explain these large regions of low bottom water oxygen concentrations. Lacking enhanced primary production at the surface, these areas must have other means of producing organic matter (OM) that fuels hypoxia. What then are the biogeochemical processes that maintain hypoxia throughout the summer months?

Pelagic recycling of nutrients is rapid compared to benthic biogeochemical cycling (Billen, 1978). The lag time associated with benthic remineralization allows spring and early summer particulate organic carbon (POC) input to be available as

recycled nutrients later in the year. In the case of the northern GoMHZ, benthic nutrient release can fuel phytoplankton growth at the end of the summer when river and surface waters become nitrogen limited (Quigg et al., 2011; Sylvan et al., 2006) and the euphotic zone deepens (Lehrter et al., 2009). And while the connection between these two processes has been estimated in numerous studies, they are rarely measured simultaneously, so that few direct comparisons have been made.

Nitrogen limitation of primary productivity is evident in the western region of the GoMHZ (Quigg et al., 2011). Suspended particulates associated with river input are negligible in this region which increases the penetration of photosynthetically active radiation (PAR) creating chlorophyll maxima near the bottom. In this far west region surface waters are depleted of nitrogen but show enhanced phytoplankton growth in deep waters that are ostensibly supported by nutrient regenerated by sediments (Lehrter et al., 2009; Murrell and Lehrter, 2011; Nunnally et al., In Review). Sediments in this area are a source of ammonium that is preferentially scavenged by autotrophs and heterotrophs alike, creating competitive interactions among nitrifiers and phototrophs. As a consequence between 25 and 50% of the total primary production on the shelf can be found beneath the pycnocline layer (Lehrter et al., 2009).

Nitrification ($NH_4^- \rightarrow NO_2^- \rightarrow NO_3^-$) that occurs below the pycnocline consumes oxygen and may play a role in prolonging hypoxia in far west regions of the northern GoMHZ (Pakulski et al., 2000). Nitrification contribution to ammonium removal increases near the bottom of the photic zone (Ward et al., 1984). Thus competition for ammonium resources plays out between heterotrophic bacteria and autotrophic

phytoplankton both consuming the resource based on Monod kinetics (Monod, 1942; Monod, 1949) (See methods for a further review of mathematical models of uptake kinetics). Nitrifiers should have a competitive advantage for ammonium uptake near the bottom where phototrophs are light limited. Partitioning of ammonium in the lower water column near the sediments enhances oxygen depletion though nitrification and heterotrophic microbial respiration. This production adds to the available POM pool in the near-bottom water through the microbial loop (Azam et al., 1983). All of these processes contribute to the systemic causes of hypoxia in the western regions of the Louisiana continental shelf. Sub-pycnocline photosynthesis adds dissolved oxygen to the depleted bottom layer however previous studies examining oxygen budgets in GoMHZ provide little support that this is a significant deterrent to bottom water hypoxia (Dortch et al., 1994; Rowe, 2001).

Research cruises during 2004-2005 sought to cooperatively assess the impact of benthic nutrient regeneration on water column processes in the western region of the northern Gulf of Mexico Hypoxic Zone (GoMHZ). Seven cruises during the two years were made as part of the National Oceanic and Atmospheric Administration (NOAA) funded Mechanisms Controlling Hypoxia (MCH) project (hypoxia.tamu.edu). In the study areas west of Atchafalaya Bay nutrients were concentrated in the lower water column from May through August. Measurements of nutrient cycling within the sediments, phytoplankton productivity, and water column nutrient concentrations at several depths were made concurrently at the same locations. During summer when river input to the shelf decreases and surface waters become nitrogen limited, we

hypothesized that regeneration of nutrients in sediments fuel sub-pycnocline primary production and enhance water column nitrification. These two processes then act to sustain hypoxic bottom water through the production of new substrates for respiration and utilization of oxygen during nitrification. These processes can now be incorporated into a steady state model following limiting nutrients (N and P) from remineralization in the sediment through the sub-pycnocline water column until they are utilized by primary producers. At steady state the proportion of near bottom primary production fueled by sediment remineralization can be estimated with precision. Ultimately the goal of this modeling exercise is to describe the biological processes that prolong seasonal bottom water hypoxia when the surface layer is nutrient limited and does not export large amounts of organic matter. Our second hypothesis is that in the western regions of GoMHZ benthic-pelagic coupling acts to prolong and maintain bottom water hypoxia.

3.3 Materials and Methods

3.3.1 Site and Season Selection

MCH project design called for a series of research cruises within the plume and shelf regions that are affected by seasonal summer hypoxia along the Louisiana continental shelf (Fig. 3.1). Cruises were scheduled in the spring and throughout the summer months to characterize the processes that play a role in the formation, and breakup of water column stratification and associated hypoxia (hypoxia.tamu.edu). Eutrophic processes that lead to hypoxic bottom waters below the Atchafalaya and Mississippi River plumes have well characterized. In the far western areas of the GoMHZ a stratified water column prevents mixing which eventually leads to hypoxia

despite nitrogen limitation during the summer. These areas with little shading by suspended fluvial sediments are ideal to study the coupling of benthic nutrient regeneration and deep photosynthesis. More importantly they may shed light onto how these far field hypoxic areas remain hypoxic beyond anthropogenic nutrient influence.

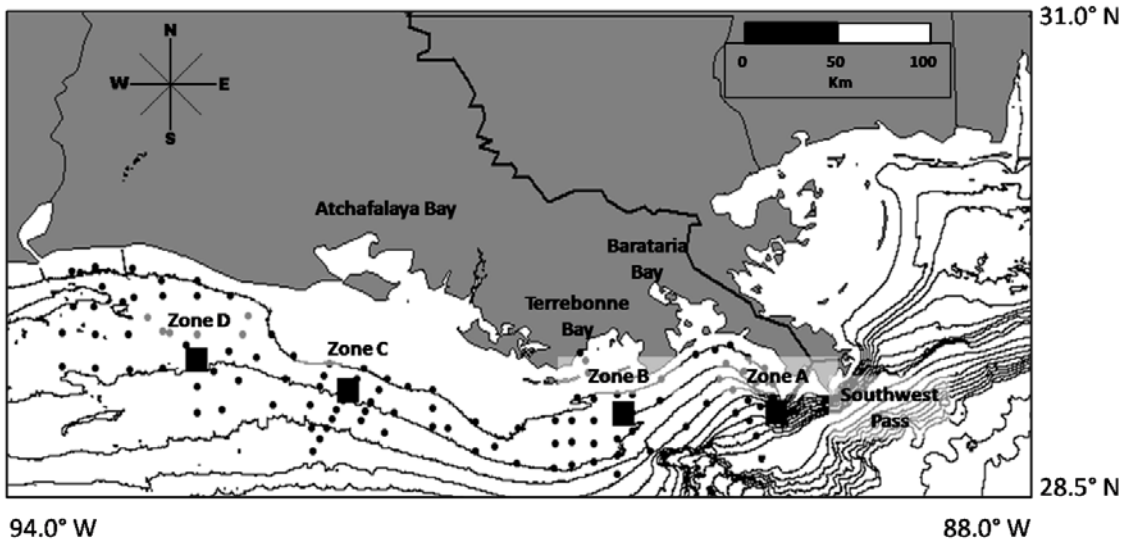


Fig. 3.1. Map of Mechanisms Controlling Hypoxia study stations on the Louisiana continental shelf. Hydrographic survey stations are denoted as small circles and process oriented mooring station are represented by large squares. Study stations for Zone C and Zone D are represented by the black squares.

Seven cruises during 2004 and 2005 were conducted as part of the NOAA funded MCH project; in all but two (April 2004 and March 2005) the shelf areas West of Atchafalaya Bay were characterized by strong nutraclines with nutrients concentrated near the bottom. Zones C (08C) and D (29 and 33 D) within the MCH dsign during

summer cruises 2, 3, 5, 6 and 7 (June and August 2004; May, July and August 2005) were selected as the best combination of temporal and spatial parameters that provide a clear picture of the interaction between the water column and benthos. Summer MCH cruises occurred when surface waters were experiencing nitrogen and phosphorous limitation accompanied by a significant increase in photic zone depth (Table 3.1). Late summer periods in the western regions of the MCH study area also displayed the most occurrences of the chlorophyll maxima on or associated with the sea floor.

3.3.2 CTD Profiles

Hydrographic data and nutrient concentrations were obtained using a Seabird 911 CTD system deployed with a twelve bottle rosette for discrete water sampling at different depths. Instrumentation included a Seabird SBE- 43 oxygen probe, Chelsea CStar transmissometer, Chelsea Aqua 3 fluorometer, Seatech LS6000 Optical Backscatter unit, and Biospherical/ Licor irradiance sensor. Discrete measurements (surface, bottom and 5-m increments) of nutrients and dissolved oxygen concentration were made using Winkler titration and 6 channel autoanalyzer (NO_3^-/NO_2^-, H_2SiO_3, PO_4^-, NH_4^+, and Urea) using standard protocols (GERG-TAMU).

3.3.3 Primary Production and Elemental Ratios of Phytoplankton

3.3.3.1 ^{14}C Primary Production

The relationship between photosynthesis and irradiance (P-I) was determined using the small volume ^{14}C incubation method of (Lewis and Smith, 1983)Temperature was kept constant during incubations with a circulating water bath set to the ambient water

Table 3.1. Station details of MCH Zones C and D. Mean values and standard error shown.

	Zone C	Zone D
MCH Cruises	2, 3, 5, 6 & 7	6 & 7
Lat. and Long.	29.0003°N, 92.0004°W	29.2039°N, 92.706°W
Station Depth	20.4 ± 2.5 m	19.5 ± 0.2 m
Mean Salinity	34.2 ± 1.0 PSU	34.5 ± 1.5 PSU
Mean Temperature	23.9 ± 1.6 °C	26.8 ± 0.4 °C
Mean Pycnocline z	8.2 ± 2.5 m	13.0 ± 3.0 m
Mean Below Pycnocline [O_2]	3.16 ± 0.63 mg L^{-1}	2.33 ± 0.61 mg L^{-1}
Mean Below Pycnocline [chl-a]	0.47 ± 0.09 µg L^{-1}	0.74 ± 0.18 µg L^{-1}
Mean Bottom Water [NH_4]	37.9 ± 4.4 umol L^{-1}	43.6 ± 1.1 umol L^{-1}
Mean Bottom Water [NO_3]	8.8 ± 0.8 umol L^{-1}	7.8 ± 2.2 umol L^{-1}
Mean Bottom Water [$HSiO_3$]	1.1 ± 0.2 umol L^{-1}	1.2 ± 0.1 umol L^{-1}
Mean Bottom Water [HPO_4]	5.9 ± 0.7 umol L^{-1}	3.9 ± 0.9 umol L^{-1}
Mean Bottom Water DIN:P	8.7 ± 0.9	15.2 ± 3.2

temperature at the time of collection. Sample water was removed from the ship's Niskin bottles into acid-washed brown bottles and immediately assayed. An aliquot (25 ml) of seawater was spiked with ^{14}C-sodium bicarbonate (Amersham, Inc.) to a final concentration of 1 µCi ml^{-1} and incubated in a photosynthetron for 30 minutes in July and August and 45 minutes in March and in May at a range of irradiances from 5 to 1500 µmol quanta photons m^{-2} s^{-1}. Quantum irradiance (µmol quanta m^{-2} s^{-1}) in each

position in the photosynthetron was measured using a calibrated Biospherical Instruments Model QSL-100 irradiance meter with a QSL-101 4π sensor. Incubations were terminated with buffered formalin (100 μL) and samples placed on a shaker table overnight with 50% HCl (1 mL) to purge off unincorporated label. After no less than 12 hours, Ecolume scintillation cocktail (5 mL) was added to each vial. Disintegrations per minute were counted on a calibrated counter (Beckman LS8100 Scintillation Counter). Triplicate (1 mL) samples for background (T_o) counts (with 100 μL of buffered formalin) and total (T_c) counts (with 250 μL of phenethylamine and 5 ml of Ecolume scintillation cocktail) were prepared at the start of each incubation and kept at the same temperature as the samples in the photosynthetron. P-I curves were constructed by fitting the Chl *a* normalized data to the equation of (Platt et al., 1980).

Dissolved inorganic carbon (DIC) in seawater was determined from representative sites using a LiCor model LI6252 CO_2 analyzer according to the method of (DOE, 1994). Water samples were collected and stored with mercuric chloride (50 μmol L^{-1}; the average DIC at these stations was 1.975 (±0.102 std dev; n >18) mmol C l^{-1}.

Integrated primary production (g C m^{-2} day^{-1}) was estimated by assuming a 12 hr photoperiod in March and a 14 hr photoperiod in May, July and August. Due to technical difficulties, we did not always have simultaneous access to a surface and underwater photosynthetic photon flux meters to collect surface and vertical profiles of irradiance at all stations on all of the research cruises. In the majority of cases, we were able to collect in situ water profiles of irradiance. Hence, when we used the vertical attenuation

coefficients calculated by Lohrenz et al. (1990; 1997) for waters in NGOM, as well as their recommendations to estimate integrated productivity. Despite combining Lohrenz et al. (1997; 1990) data with our own, calculated values of integrated primary productivity were similar to those previously published.

3.3.3.2 Chlorophyll a Determination

Seawater was filtered onto GF/F filters which were frozen immediately. After returning to the lab, filters were placed in DMSO/90% acetone solution (40:60) in the dark at –20°C for at least 24 hours. Concentrations of Chl *a* (corrected for phaeopigments) were determined according to Lohrenz et al. (1990). Calibration was performed using a Sigma Chl *a* standard.

3.3.3.3 Organic Carbon and Nitrogen Composition of Phytoplankton

Samples were collected on precombusted (600ºC for 4 hrs) 13mm Gelman filters for organic C and N, folded and stored frozen prior to analysis on a Perkin-Elmer 2400 CHNS analyzer. Organic C and N samples were dried for 24 hrs, then acidified by placing samples in a humidifier with 8N HCl for 24 hrs, and subsequently drying samples for another 24 hrs. These samples were then packed and analyzed using the same procedures. After every 10th sample, a standard was run to account for machine drift, if any. Calibration curves were prepared prior to starting a batch of samples, and re-run if the column was changed prior to a set of samples being completed.

Additional particulate organic carbon (POC) and nitrogen (PON) and particulate phosphorous (PP) data were taken from (Sylvan, 2008) to complete C:N:P ratios for phytoplankton west of Atchafalaya Bay.

3.3.4 Model Development

The biogeochemical models were designed to examine the benthic regeneration of nutrients and the incorporation of benthic nutrients by phytoplankton and bacteria. The focus of this study is to tie together the processes that fuel regenerated primary production beneath the pycnocline and as such the model ignores processes that occur in the surface layer. Nitrogen (Fig. 3.2) and phosphorous (Fig. 3.3) models are solved for steady state using STELLA Modeling Software (Version 9), but can then be used to address the relative impact of processes by perturbing the system. The two key components of each model generated by field measurements and incubation experiments are the primary production estimates integrated through the water column and the flux of nutrients from sediment to overlying water. Also measured in the field are the concentrations of limiting nutrients (N and P) at discrete depths. Benthic sediment fluxes were not mathematically linked to the concentration of nutrients in the bottom water, but were instead used to supply the standing stock of N and P available for uptake. The other measured stock, primary production, was integrated for selected depth intervals from surface to the bottom, and from pycnocline to bottom. Stocks of the limiting nutrients, nitrogen (as DIN = Σ NH_4^+ + NO_3^- + NO_2^-) and phosphate, are based in units of mg-(N, Pi) m^{-3}. Stocks are related to each other through flows of nutrients expressed in units of mg-(N, P) m^{-3} d^{-1}. Model components, values and literature sources are summarized in Table 3.2.

Our model incorporates kinetic uptake of nutrient by the phytoplankton stock using literature values and measured nutrient concentrations necessary to solve the

Monod equation (Equation 3.1) (Monod, 1942). V the uptake rate of the limiting nutrient is a function of Vmax, which is the maximum uptake rate of the nutrient, as it relates to the concentration of the limiting nutrient, S and the half-saturation constant, K_T.

Monod Equation: $V = V_{max} [S / (K_t + S)]$ (3.1)

The Monod equation (Monod, 1942) modifies simple empirical laws common to the initial Michaelis equation as modified by Dugdale (1967) from observed Michaelis-Menton kinetics for steady state conditions. Comparatively, Droop (1973) uses a similar kinetic relationship to adjust uptake (or growth) as dependent on a limiting nutrient based on the cellular quota of the nutrient. This in turn has been less successful in describing kinetic uptake of silicate and nitrogen (McCarthy, 1982). However both the Monod expression and the Droop equation perform well for studies at steady state.

It must be kept in mind that solutions to the Michaelis-Menton, Monod and the adapted Monod equation of Dugdale (1967) are instantaneous uptake rates (Goldman and Glibert, 1983). Using Michaelis-Menton kinetics to describe uptake by phytoplankton within the model allows competition for resources with the microbial sinks of nitrogen and phosphorous based on the concentration of the limiting nutrient.

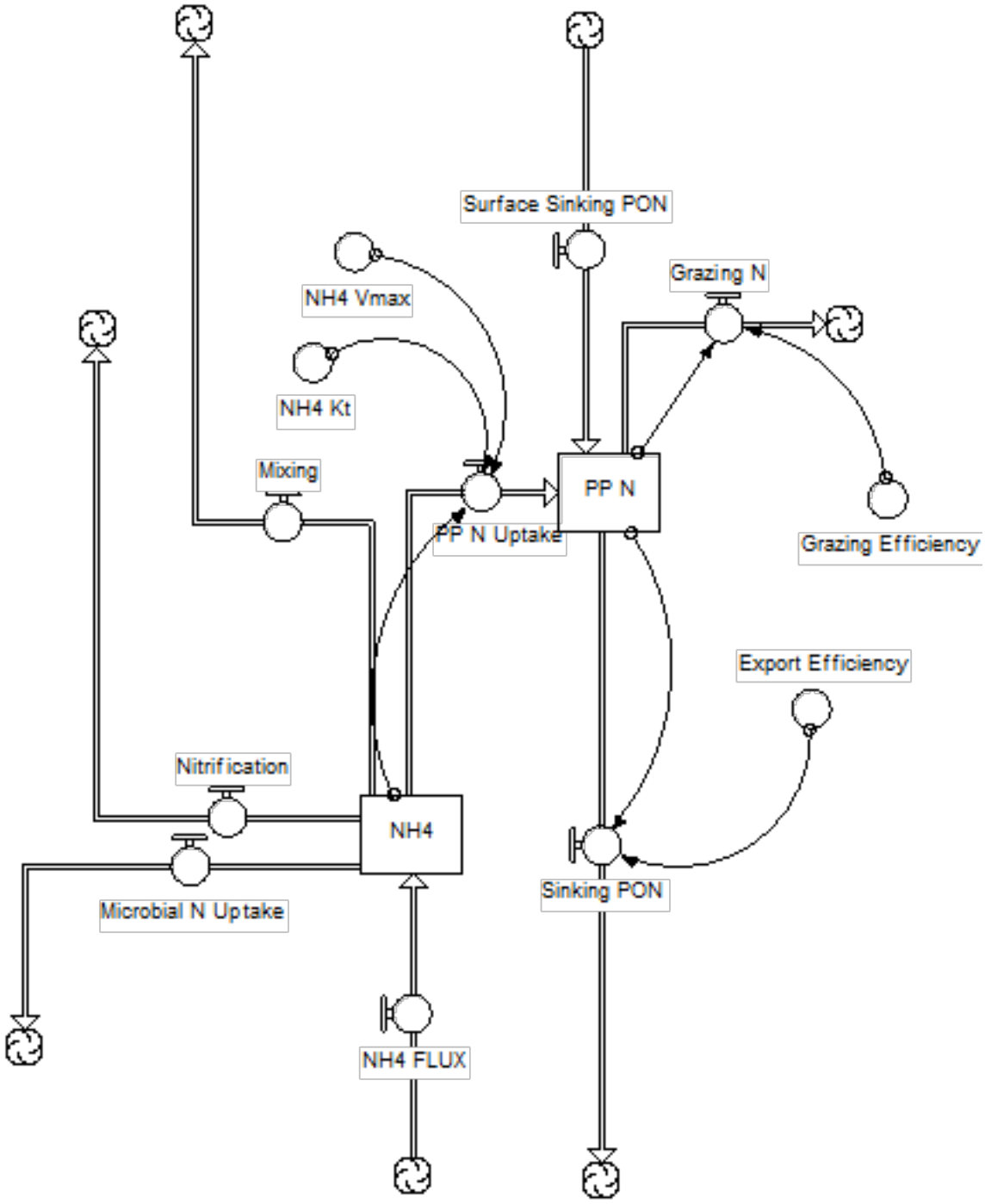


Fig. 3.2. Benthic-pelagic coupling model for nitrogen created in STELLA. Boxes are the stock variable, arrows represent flows and circles are converters or model constants.

A characteristic of coupled sediment geochemical models is the deposition of particulate organic matter (POM) that in turn drives organic matter turnover and thus the release of nutrient at the boundary layer (Soetaert et al., 2000). In the northern GoMHZ estimating this flux of OM to sediments is problematic due to several complicating factors. Resuspension of particles near the bottom that overestimates POM flux rates

Table 3.2 Flow values and literature sources used for N and P STELLA models.

Model Parameter	Value	Source
Nitrification	0.112 mg-N L^{-1} d^{-1}	Pakulski et al. (2000)
PP N V_{MAX}	0.45 h^{-1}	Goldman and Glibert (1983)
PP N K_T	0.0112 mg-N L^{-1}	Eppley et al. (1969)
PP P V_{MAX}	0.93 d^{-1}	Goldman et al. (1979)
PP P K_T	15.8 µg-P L^{-1}	Burmaster (1979)
PP Si V_{MAX}	0.0176 h^{-1}	Derived from Paasche (1973)
PP Si K_T	0.0224 mg-Si L^{-1}	Paasche (1973)
Microbial N Uptake	2.52 µg-N L^{-1} h^{-1}	Wheeler and Kirchman (1986)
Microbial P Uptake	0.62 µg-P L^{-1} h^{-1}	Derived from Rhee (1972)
Grazing N	14 mg-N m^{-2} d^{-1}	Dagg (1995)
Grazing P	0.875 mg-P m^{-2} d^{-1}	Derived from Dagg (1995)
Grazing Si	14 mg-Si m^{-2} d^{-1}	Derived from Dagg (1995)
Sinking PON	30 mg-N m^{-2} d^{-1}	Redalje et al. (1994)
Sinking POP	1.875 mg-P m^{-2} d^{-1}	Derived from Redalje et al. (1994)
Sinking POS	30 mg-Si m^{-2} d^{-1}	Derived from Redalje et al. (1994)
K_d	0.0038 m^{-2} h^{-1}	Gargett (1984)

when using sediment traps. This severely limits the calculation of POM input through a model/equation based on surface productivity because most equations are only applicable to depths greater than 50 m (Suess, 1980). A stratified water column with a

strong pycnocline increases the residence time of sinking particles subject to microbial degradation (Tribovillard et al., 2009) and can limit the amount of primary production sinking to the bottom (Redalje et al., 1994). This unknown imbalance of organic matter lability above and below the pycnocline is physically hard to sample. Sediment community oxygen consumption (SCOC) traditionally used as a proxy of POM input is not trustworthy because it does not measure anaerobic OM degradation which occurs at low oxygen concentrations (Murrell and Lehrter, 2011; Nunnally et al., In Review; Rowe, 2001). For the purposes of balancing the model we incorporated sinking particulates as the lone input directly across the pycnocline from the surface mixed layer.

Redalje et al. (1994) reported large variations in the proportion of primary production exported from the surface based dependent on the strength of stratification. Using these estimates, particulate organic fractions leaving the pycnocline were assessed differently for the two zones studied. Zone C which typically has a much more dramatic density stratification had an export efficiency of 2-9%; Zone D which does not experience the same degree of stratification had an export efficiency of 64% (Lohrenz et al., 1997).

While this is a biologically driven model of nutrient transfer certain physical parameters could not be ignored even though we chose to describe the system as it exists below the pycnocline. The relationship of decreasing nutrients with increasing distance from the sea floor (source) is logarithmic and indicates the disappearing nature of the nutrients is not due to mixing alone which would be linear, but has a biological component as well (Fig. 3.2). Regardless of how small eddy diffusive mixing may be

when the system is at steady state, it is an important model variable indicative of physical controls on biological activity that can be used to test hypotheses. As such we chose to base the model flow as Fickian diffusion using the following equation (Equation 3.2) where K_d is a mixing coefficient from Gargett (1984).

$$\text{Mixing (flow)} = K_d ([\text{nut}]_{\text{BOTTOM}} - [\text{nut}]_{\text{PYCNOCLINE}})/\text{depth interval} \quad (3.2)$$

3.3.5 Model Equations

The nitrogen model is centered on the two stock variables of bottom water ammonium (NH_4) and phytoplankton nitrogen (PP N) (Fig. 3.2). The steady state equations for each are shown below in Equations 3.3 and 3.4.

$$\text{NH4}(t) = \text{NH4}(t - dt) + (\text{NH4\_FLUX} - \text{PP\_N\_Uptake} - \text{Nitrification} - \text{Microbial\_N\_Uptake} - \text{Mixing}) * dt \quad (3.3)$$

$$\text{PP\_N}(t) = \text{PP\_N}(t - dt) + (\text{PP\_N\_Uptake} + \text{Surface\_Sinking\_PON} - \text{Grazing\_N} - \text{Sinking\_PON}) * dt \quad (3.4)$$

The phosphorus model is centered on the two stock variables of bottom water phosphate (PO_4) and phytoplankton phosphorus (PP P) (Fig. 3.3). The steady state equations for each are shown below in Equations 3.5 and 3.6. The phosphorous model and related equations differs from the nitrogen and silica models because the sediments exhibit net uptake of P unlike N and Si.

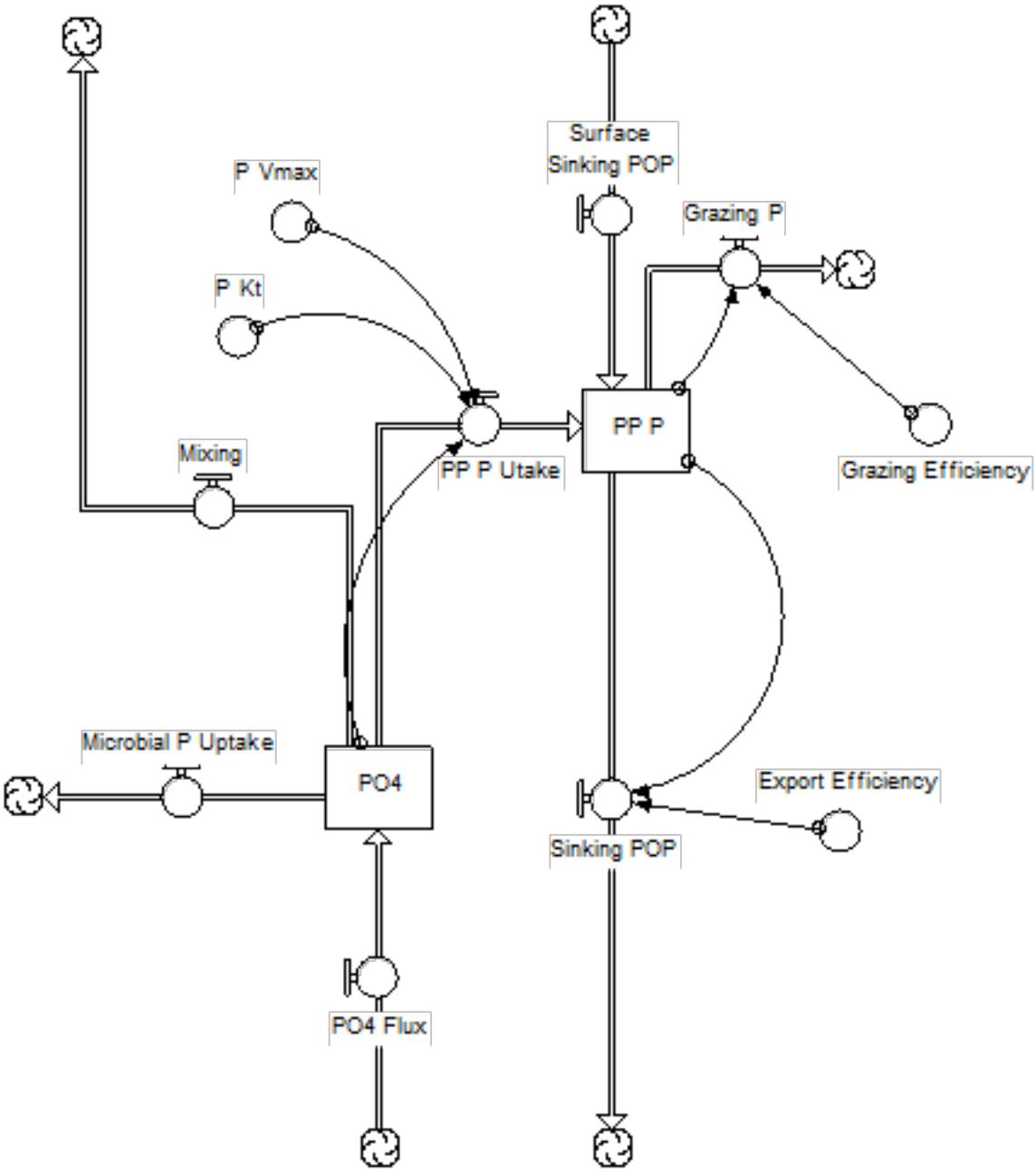


Fig. 3.3 Benthic-pelagic coupling model for phosphorus created in STELLA. Boxes are the stock variable, arrows represent flows and circles are converters or model constants.

PO4(t) = PO4 (t - dt) + (- PP_P_Utake - PO4_Flux - Microbial_P_Uptake - Mixing) * dt (3.5)

PP_P(t) = PP_P(t - dt) + (PP_P_Utake + Surface_Sinking_POP - Grazing_P - Sinking_POP) * dt (3.6)

3.4 Results

3.4.1 Profiles of Nutrient Concentrations

The vertical distribution of dissolved nutrients on the western Louisiana continental shelf in MCH Zones C and D (shown in Fig. 3.1), highest concentrations appear near the bottom but become depleted before reaching the pycnocline (Fig. 3.4). The disappearance of nitrate from the water column was linear with depth; a logarithmic curve describing the profiles of ammonium suggest a biological sink below they pycnocline. The logarithmic curve explains 70 and 55% of the variations with depth in Zone C for ammonium and nitrate, respectively (Fig. 3.5). The profile plot of nutrients and depth for Zone D is more striking because the logarithmic relationship of 3 nutrients (ammonium, nitrate and phosphate) and the linear decrease of silicate are shown (Fig. 3.6). The logarithmic curve explains 97, 76 and 67% of the variation with depth for ammonium, nitrate and phosphate, respectively. The linear relationship of silicate explains 75% of variation in this nutrient with depth; possible indicating that there is not a biological sink for this nutrient.

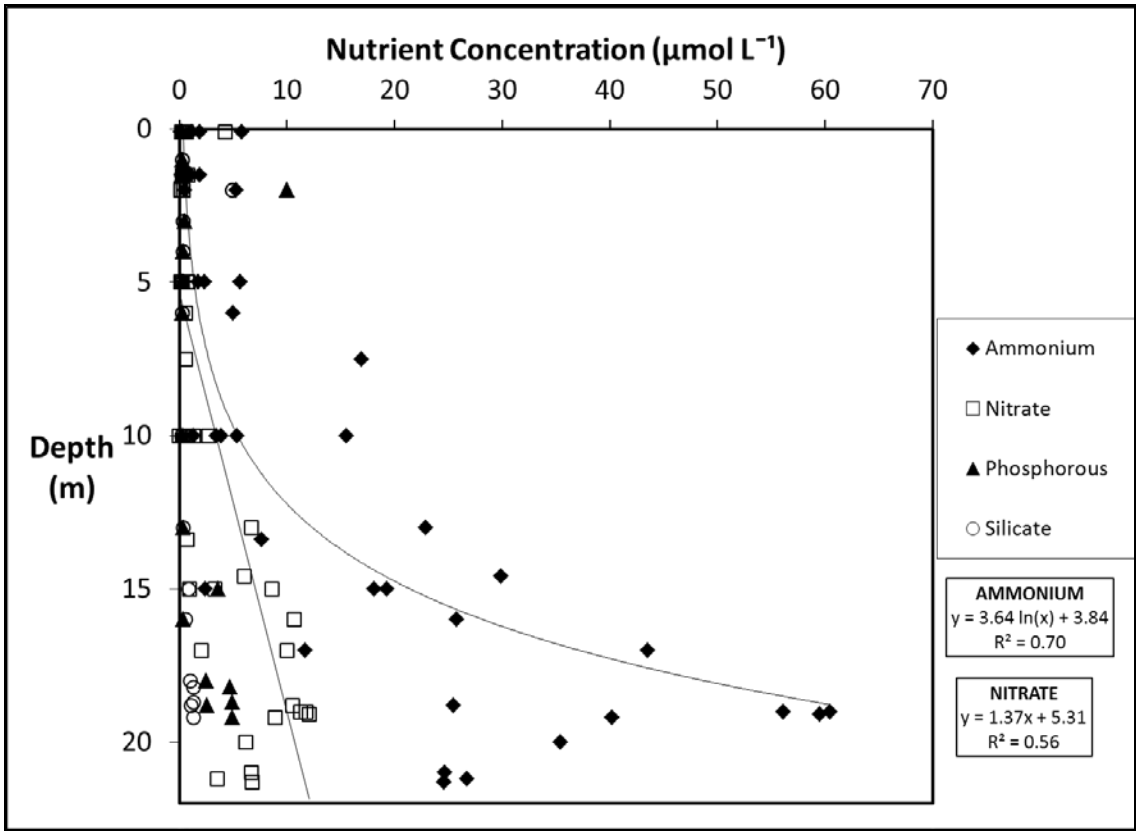


Fig. 3.4. Combined profiles of dissolved nutrients with depth in the western MCH Zones C and D during summer (May-August). Regression lines are plotted for nitrate (linear) and ammonium (logarithmic).

3.4.2 Phytoplankton Primary Production and Biomass

Primary production was calculated from discrete Niskin bottle samples from the surface and the deep chlorophyll maxima. Summertime primary production at the surface and at the deep chlorophyll maximum in Zone C were nearly equal (0.59 ± 0.22 (mean ± standard error) and 0.64 ± 0.38 g-C m^{-3} d^{-1}, respectively) (Fig. 3.7). At the furthest West station (Zone D) primary production at the deep chlorophyll maxima (0.6 ± 0.2 g-C m^{-3} d^{-1}) exceeded that of nitrogen limited surface waters (0.4 ± 0.1 g-c m^{-3} d^{-1})

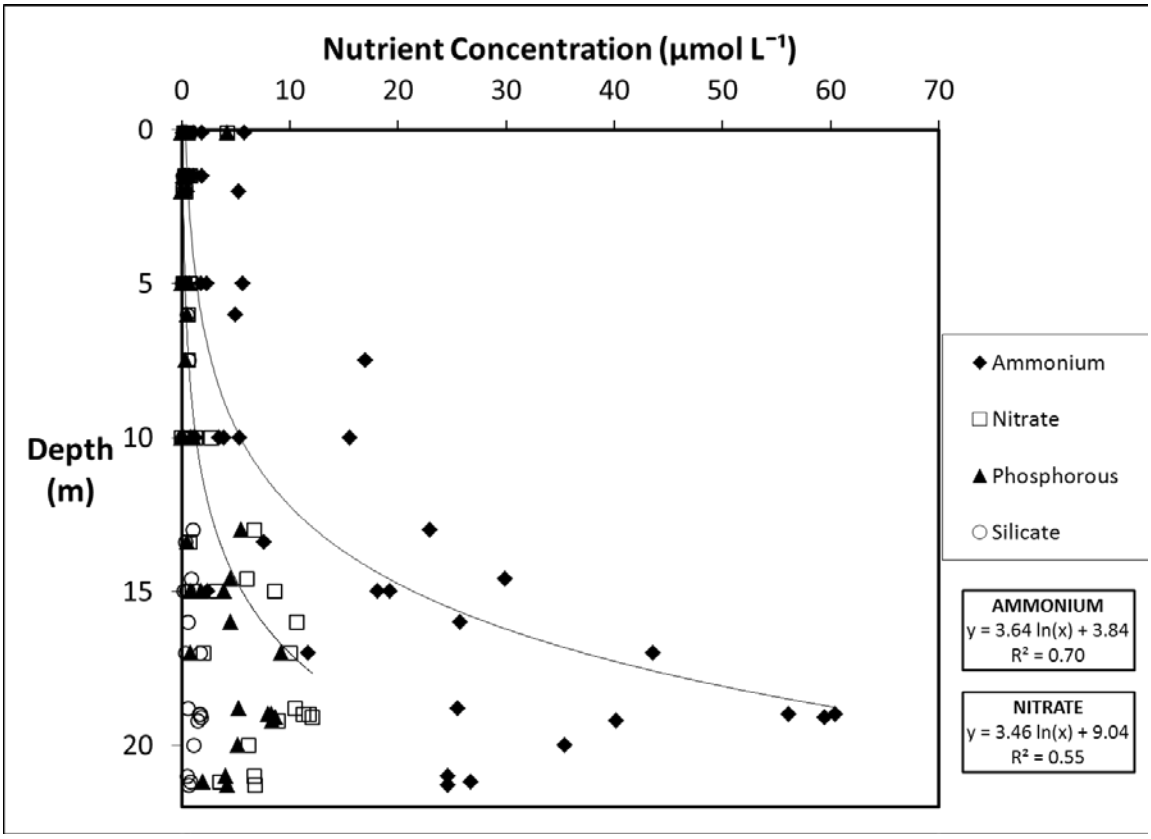


Fig. 3.5. Profiles of dissolved nutrients with depth in the western MCH Zones C during summer (May-August). Regression lines are plotted for nitrate (logarithmic) and ammonium (logarithmic).

during summer months. Nitrogen and extreme phosphorous limitation of surface waters in these western regions is further evidenced by higher bottom water concentrations of chlorophyll *a* (Fig. 3.7). Zone C mean bottom water phytoplankton biomass (4.1 ± 1.5 mg-chl-a m^{-3}) was twice as high as that measured at the surface (2.1 ± 0.4 mg-chl-a m^{-3}).

The same trend was seen in Zone D where bottom water phytoplankton biomass (5.6 ± 1.1 mg-chl-a m^{-3}) far exceeded that in the surface (1.7 ± 0.3 mg-chl-a m^{-3}). The greatest

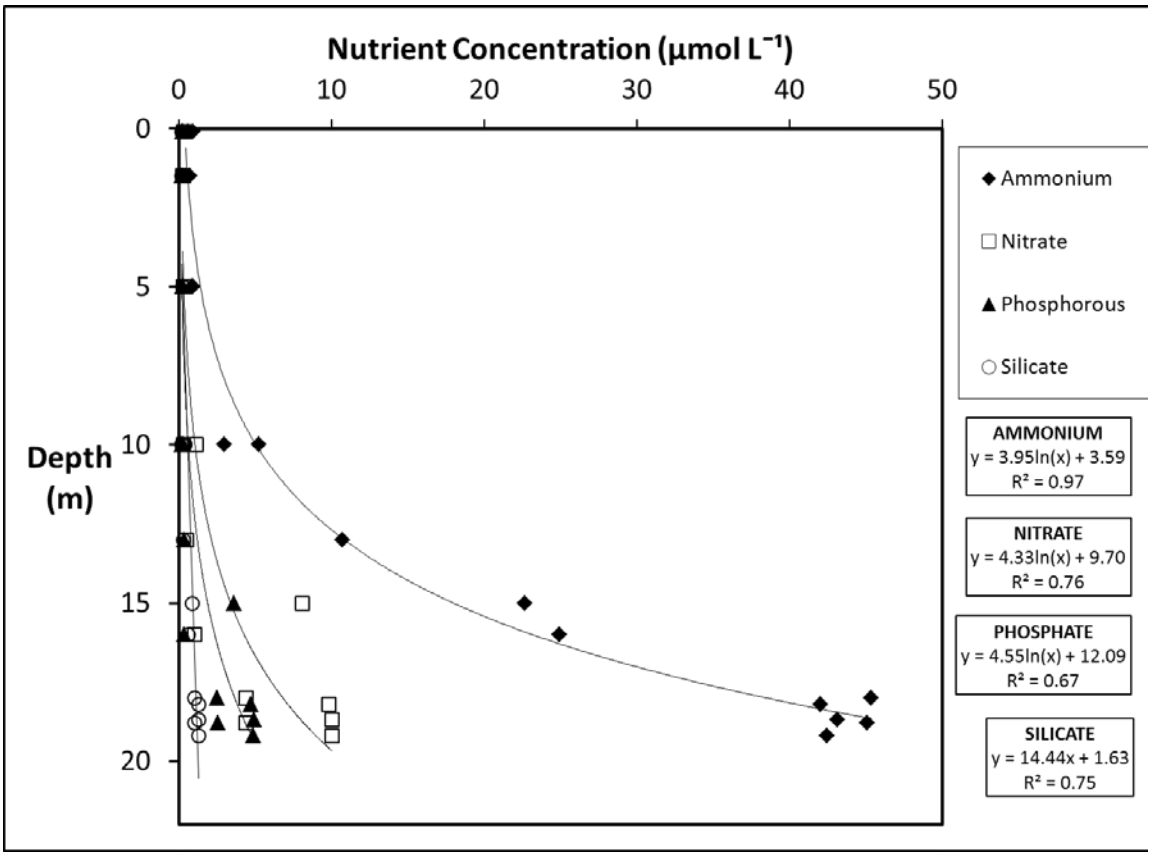


Fig. 3.6. Profiles of dissolved nutrients with depth in the western MCH Zones D during summer (July-August). Regression lines are plotted for nitrate (logarithmic), ammonium (logarithmic), phosphate (logarithmic) and silicate (linear).

primary production in these western stations was measured from surface Niskin sample at 4.8 g-C m^{-2} d^{-1} (not shown). Not surprisingly it also accounted for the greatest phytoplankton biomass of 24.3 mg-chl-a m^{-3} (not shown).

Integrated primary productivity (IPP) for all stations and sampling dates was determined for water masses above and below the pycnocline. The relative proportions of total IPP both above and below the pycnocline varied during sampling time in relation to pycnocline depth and limiting nutrient (Fig. 3.8). Production beneath the pycnocline was greater during all sampling events in Zone C for both 2004 and 2005 with the

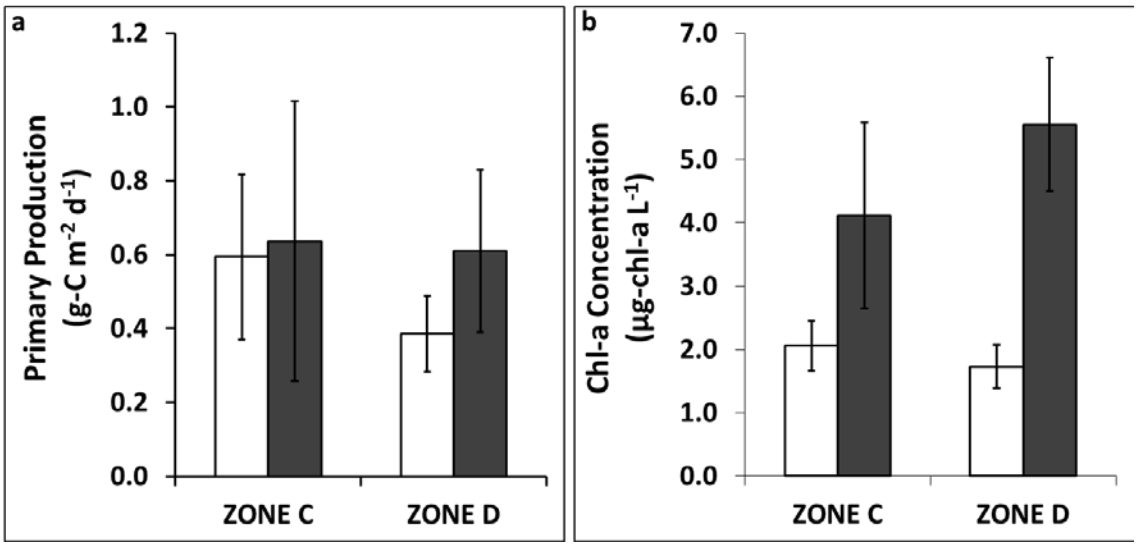


Fig. 3.7. Primary production and (a) chlorophyll-a concentration (b) from discrete Niskin samples collected during summer months in MCH Zones C and D. White bars are discrete samples from the surface. Gray bars are discrete samples taken from the chlorophyll maximum.

exception of July 2005. This sampling period saw a dramatic deepening of the pycnocline to 17.5 m compared to 8.5 m in May and 6.5 meters in August. During this time above pycnocline productivity (2.2 g-C m^{-2} d^{-1}) accounted for 70% of total IPP.

Zone C was revisited 4 days later at which time surface productivity accounted for an even greater proportion (85%) of total IPP. Disregarding July 2005, mean surface primary production at Zone C was only 18% of total water column primary production, with the remaining portion (1.6 ± 0.5 g-C m^{-2} d^{-1}) occurring below the pycnocline. The deep pycnocline (16 m) in July of 2005 also occurred at the furthest West site, Zone D, where above pycnocline productivity contributed 80% of IPP compared to only 6% the following month. August below pycnocline primary production in Zone C accounted for the highest production in a stratified water column (2.0 and 2.4 g-C m^{-2} d^{-1} for 2004 and 2005, respectively). June 2004 and May 2005 above pycnocline productivity represented the lowest contributions to IPP at 6 and 8%, respectively.

3.4.3 Photosynthetically Active Radiation

Photosynthetically Active Radiation (PAR) in the western region of the GoMHZ is an important environmental parameter necessary for deep photosynthesis and the 1% PAR level typically represents the bottom of the photic zone. In Zone C the 1% PAR level was deeper than 18 m for all cruises made in 2004 and 2005. The only instances when the 1% PAR level did extend to the bottom of Zone C were during April 2004 and March 2005. In Zone D during July and August of 2005 the PAR depth at the deepest sampled depth were 6% and 3% of surface PAR.

3.4.4 Stoichiometric Relationships

Carbon to nitrogen (C:N) ratios of phytoplankton from the surface waters west of Atchafalaya Bay during April and May of 2004 were less than the Redfield 6.625

indicating that nitrogen was not limiting during the earliest parts of the hypoxic season (Fig. 3.9). These C:N ratios eventually moved above the Redfield line reaching almost 9.5 in July. Carbon to nitrogen ratios decreased in August falling back below the Redfield line to similar May level. May and July C:N ratios were taken from (Sylvan, 2008). Carbon to phosphorous (C:P) and nitrogen to phosphorus (N:P) ratios indicated severe P limitation in May (1946 and 345, respectively). July C:P and N:P decreased by an order of magnitude (204 and 21, respectively) yet was still above the Redfield line for P limitation, similar to other studies that have already shown severe P limitation in the western regions of the GoMHZ (Quigg et al., 2011; Sylvan et al., 2006).

Carbon to nitrogen ratios of phytoplankton collected from surface and sub-pycnocline waters masses indicate a nutrient source that is more abundant in the surface mixed layer during spring months when river flow peaks. In late summer C:N in the surface layer indicates nitrogen limitation (greater than Redfield C:N of 6.6) (Fig. 3.8); beneath the pycnocline however, C:N ratios range between 0.2 and 6.1 in Zone C and 4.9 and 7.0 in Zone D. Mean C:N ratios of the phytoplankton were calculated for use in converting model parameters between carbon, nitrogen and phosphorous units. Carbon to nitrogen ratios of phytoplankton collected from surface waters was 5.07 for Zone C and 9.73 for Zone D. Carbon to nitrogen ratios for samples collected beneath the pycnocline were 5.13 and 5.88 for Zones C and D, respectively.

3.4.5 Model Simulations

Once the elemental models of benthic pelagic coupling have been solved for steady state they can then be perturbed by jolting a variable and re-run to assess its importance to

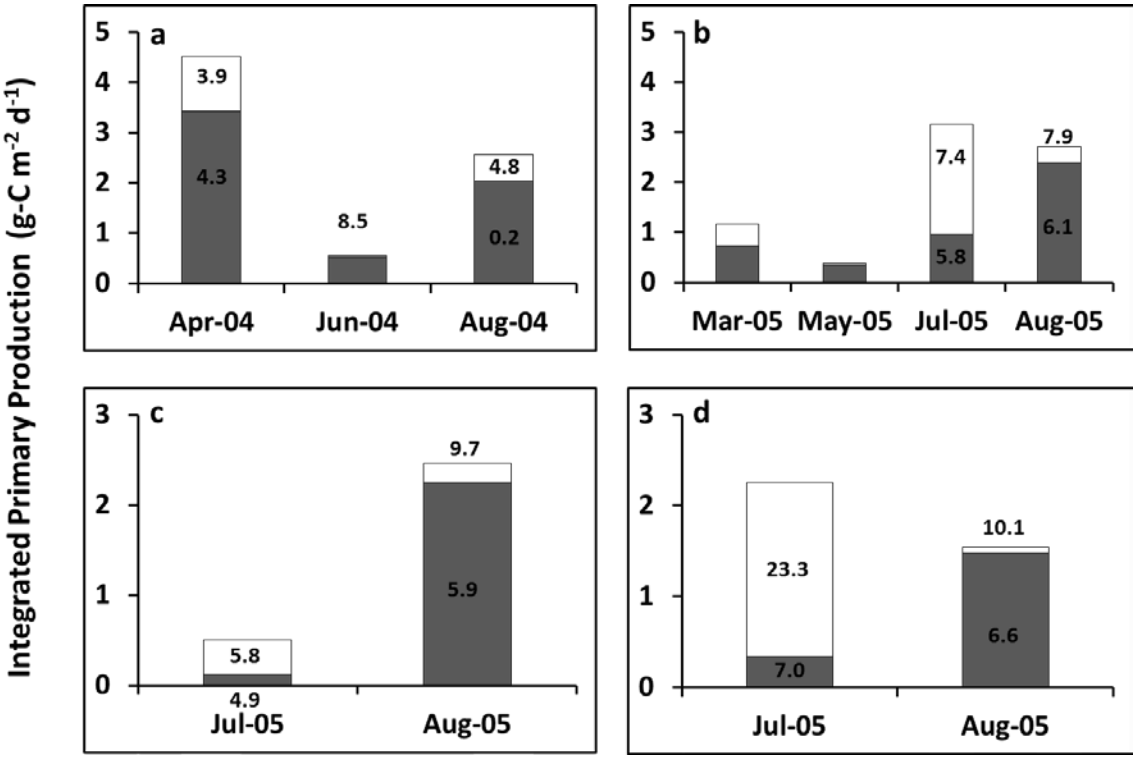


Fig. 3.8. Integrated primary production divided between waters above (white) and below (gray) the pycnocline. Numbers in black are the respective C:N ratios of the phytoplankton from each water mass. (a) Zone C (08C) 2004. (b) Zone C 2005. (c) Zone D (29D) 2005. (d) Zone D (33D) 2005.

ecosystem stability. For instance each model (N and P) could have the benthos decoupled by setting the benthic flux to zero. The resulting stock size and POM input for each element would react according to how important benthic nutrient input is to maintaining the phytoplankton population or the flow of particulates to the sea floor. In a similar manner diffusive mixing could be increased to simulate breakdown of stratified conditions in order to simulate of benthic-pelagic coupling in a thoroughly mixed water

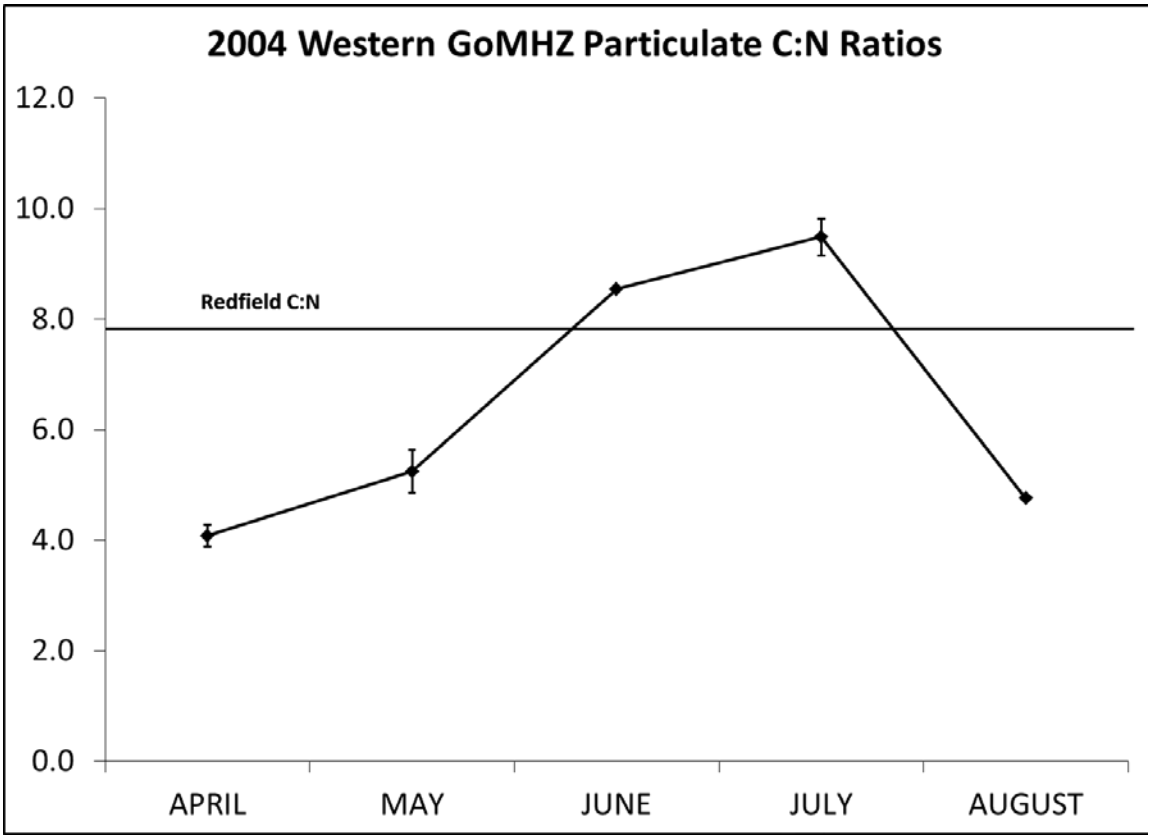


Fig. 3.9. Mean carbon to nitrogen molar ratios of suspended particulate matter in the surface mixed layer for regions west of 91.8° West longitude on the Louisiana continental shelf. May and July data are taken from (Sylvan, 2008). Error bars represent 1 standard error of the mean (SE).

column. A model solution must accurately represent the measured amount of sub-pycnocline primary production to be considered in steady state. At this point benthic fluxes already reported (Nunnally et al., In Review) can be inserted to the model; this new equilibrium state represents the amount of production that could be supported by nutrients recycled through the benthic pump.

3.4.6 Steady State

A nitrogen and phosphorus model was assembled for each MCH study zone using integrated below pycnocline productivity, *in-situ* bottom water nutrient concentrations and explicit physical, chemical and biological components unique to each study area. All models when solved for steady state are run for 120 days which correlates to the 4 months of summer in which increased 1% PAR depth makes sub-pycnocline benthic-pelagic coupling feasible. Models did not reach a steady phytoplankton population until after 20 days (not shown). Steady state conditions were considered achieved when phytoplankton populations were equivalent to the mean primary production measured beneath the pycnocline. Steady state conditions were primarily a function of benthic nutrient fluxes of ammonium and phosphate; bottom water nutrient stocks did not prove to be important regulators of phytoplankton populations but only determined the initial peak productivity.

3.4.7 Nitrogen Models

The steady state STELLA model solution of the Zone C nitrogen model was solved with a benthic ammonium flux equal to 0.21 g-N m^{-3} d^{-1} and sustained a steady phytoplankton population equivalent to 0.24 g-N m^{-3} d^{-1}. Primary production peaked at 0.36 g-N m^{-3} d^{-1}, declining to steady state production after 20 days. The model was then run using the benthic flux for this region of 0.20 g-N m^{-3} d^{-1}; the resulting phytoplankton population was equivalent to 0.11 g-N m^{-3} d^{-1}. The model solution predicts benthic ammonium efflux can support 47% of sub-pycnocline primary production in this region.

At steady state sinking PON was equal to 0.007 g-N m^{-3} d^{-1} and mixing loss to the surface was 0.00 g-N m^{-3} d^{-1}.

The Zone D nitrogen model was solved in a similar fashion. Benthic ammonium flux equal to 0.25 g-N m^{-3} d^{-1} sustained a steady phytoplankton population equivalent to 0.32 g-N m^{-3} d^{-1}. Peak production of 0.39 g-N m^{-3} d^{-1} occurred at 5 days and dropped to steady state at 20 days. The measured benthic flux for this region, 0.13 g-N m^{-3} d^{-1}, was able to support a steady phytoplankton population equivalent of 0.30 g-N m^{-3} d^{-1}. Despite the large gap between steady state and measured benthic fluxes, model results predicted that 94% of sub-pycnocline primary production was supported by benthic ammonium regeneration. At steady state sinking PON was equal to 0.01 g-N m^{-3} d^{-1} and mixing loss to the surface was 0.00 g-N m^{-3} d^{-1}.

3.4.8 Phosphorus Models

Phosphorous models of benthic-pelagic coupling for Zones C and D can only be solved for steady state as sediments are a sink for P incapable of supporting primary productivity (Nunnally et al., In Review). Steady state was achieved in Zone C with a benthic P release of 16.3 mg-P m^{-3} d^{-1} and steady state population equal to 6.1 mg-P m^{-3} d^{-1}. This initially supported a phytoplankton population equivalent to 100.7 mg-P m^{-3} d^{-1} at 12 days and delayed steady state conditions until after 30 days (the only model run that did not achieve steady state within 20 days. Zone D steady state was achieved with a benthic P release of 9.1 mg-P m^{-3} d^{-1} that supported a population equivalent to 6.2 mg P m^{-3} d^{-1}. Initial productivity peaked at 54.2 mg-P m^{-3} d^{-1} and reached steady state at 20

days. In both the Zone C and D phosphorus models productivity fell to zero using the measured P fluxes of -26.6 and -29.4 mg-P m^{-3} d^{-1}, respectively.

3.4.9 Model Perturbations

Each nitrogen model was perturbed to test model dynamics and predict the consequences of no benthic fluxes and a well-mixed water column. This involved changing two model parameters, the flux of ammonium and the mixing coefficient. In both Zone C and Zone D models zero benthic fluxes resulted in no sub-pycnocline primary production, demonstrating that as constructed the systems cannot support appreciable production without benthic inputs.

The second test of the system was designed to assess the fate of benthic regenerated nitrogen when the water column is mixed. This occurs at the end of summer when stratification is broken down by storms or changes in the shelf hydrography. It can also be a test why in some instances hypoxia can reform after the passage of tropical storms that destroy summertime stratification. In Zone C a well-mixed water column was achieved by changing the mixing constant to 4, this caused both sinking PON and primary production to cease and exported 0.06 g-N m^{-3} d^{-1} to the surface layer. In Zone D a similar result was achieved using a mixing constant of 5 and resulted in an export of 0.08 g-N m^{-3} d^{-1}.

3.5 Discussion

Continental shelves receive significant amounts of nutrients from terrestrial sources and rivers. Consequently the recycling of nutrients is presumed to have less influence on productivity compared to central ocean basins where nutrients limit primary

production (Eppley and Peterson, 1979). Regenerated production is fueled by the cycling of organic matter through the biological pump within the euphotic zone, whereas new production near shore is fueled by river input, upwelling, nitrogen fixation and atmospheric deposition. On shallow continental shelves nutrients are regenerated by sediments that fuel primary production in the water column (Billen, 1978; Hopkinson, 1987; Rowe et al., 1977; Rowe et al., 1975). However the quantification of this process is difficult in an energetic water column with multiple physical mechanisms that determine nutrient fate beyond biological and chemical reactions. In strongly stratified water columns the interplay of the benthic and pelagic can be discretely de-coupled by the pycnocline (Carpenter and McCarthy, 1975); it is also a more likely scenario of how benthic remineralization influence pelagic production on the Louisiana continental shelf.

Through this exercise it has been possible to generate three sets of estimates for benthic contribution to sub-pycnocline productivity. Classically, it has been calculated by estimating the amount of nitrogen or phosphorous that could support a phytoplankton community with Redfield proportions (Hopkinson, 1987; Rowe et al., 1977; Rowe et al., 1975). Based on this assumption benthic ammonium effluxes could support 102 and 22% of sub-pycnocline nitrogen needed for primary production in Zones C and D, respectively. Clearly the phytoplankton populations on the Louisiana continental shelf do not adhere to these strict proportions but the same calculation can be made based on the elemental proportions of the measured phytoplankton. These estimates suggest that 82 and 40% of sub-pycnocline nitrogen demand, in Zones C and D respectively, can be met by benthic ammonium efflux. Model simulations show that benthic ammonium

efflux could support 47% of the nitrogen demand by primary production in Zone C and 94% in Zone D. Previous model simulations in the GoMHZ predict ammonium efflux can support 25 to 60% of primary production on the shelf (Eldridge and Morse, 2008). More recent studies that measured benthic ammonium efflux estimate that that < 10% of water column primary production could be supported (Lehrter et al., 2011). If we expand our estimates based on actual phytoplankton stoichiometry to the entire water column, measured benthic ammonium efflux could support 59 and 39% of primary production in Zones C and D, respectively.

This wide range of estimates seem confounding but it is interesting to note that the model predictions differ greatly from the stoichiometric estimates; model results were about half of the stoichiometric estimates in Zone C but in Zone D predicted twice as much as the other estimates. The largest difference in model parameters between the two zones is the proportion of surface productivity that sinks below the pycnocline. In Zone D a greater fraction of sinking PON adds to the sub-pycnocline phytoplankton stock because stratification is weaker in this region. Results could also be affected by the inability to sufficiently model the competitive interactions surrounding ammonium between phytoplankton, nitrifying bacteria and heterotrophic bacteria. Unfortunately there have not been enough studies that have sought to elucidate the complicated biological interactions. Estimates of a similar nature for phosphorus contributions are futile since sediments are a net sink for P in these western regions and contribute to already severe phosphorus limitation (Quigg et al., 2011; Sylvan et al., 2006).

Classical depictions of the biological pump ignore sediments that receive large amounts of POM from surface blooms of phytoplankton (Azam et al., 1983). This is largely because a linear relationship has not been described relating benthic nutrient fluxes as a nutrient source for recycled primary production. In strong upwelling areas along continental shelves on the Benguela coast, benthic fluxes are inconsequential relative to the nutrients delivered from beneath the mixed layer (Calvert and Price, 1971). Conversely, in the upwelling system off central Chile sediments are an important nitrogen sources for the water column during El Nino years (Graco et al., 2006). In the Gulf of Mexico coastal eutrophication occurs as series of pulses associated with the delivery of freshwater and dissolved nutrients from Mississippi Atchafalaya River System (MARS) springtime runoff. Current nutracentric paradigms dictate that episodic nutrient delivery creates and maintains a large hypoxic zone that lasts well beyond these fluvial pulses (Rabalais et al., 2007; Turner et al., 2008), despite clear evidence of nutrient limitation in the surface waters of the shelf (Quigg et al., 2011; Sylvan et al., 2006; Sylvan et al., 2007).

Perhaps then the focus in these regions should shift to the interplay of biology, chemistry and physics that makes the lower water column figure prominently in ecosystem function. Figs. 3.4-3.6 show high concentrations of nutrients beneath the pycnocline as a result of benthic effluxes. Due to the density stratification that characterizes the continental shelf during summer these nutrients are not normally available to the stressed surface phytoplankton population. Nutrient limitation in surface waters was eased in July 2005 when the pycnocline deepened ostensibly mixing

nutrients upward (DiMarco et al., 2009) stimulating productivity throughout the water column (Fig. 3.8). Model perturbations that simulated a well-mixed water column increased the mixing of nitrogen to the surface layer from zero to 0.06 and 0.08 g-N m^{-3} d^{-1} in Zones C and D, respectively. Physical mixing at the end of summer also redistributes nutrients from bottom to surface seen in model simulations but is also evident in the drop of C:N below Redfield limitation (Fig. 3.9). With this in mind it would seem that the 'blue' (minimal surface productivity and increased light penetration) regions of the western shelf regions might be dominated by subsurface processes rather than plume processes that define the eastern Louisiana shelf.

Through combined investigations I have sought to integrate a sedimentary component of the biological pump that demonstrates the importance of remineralized nutrients to sustaining biological productivity and associated respiration necessary for bottom water hypoxia. Ammonium is the predominant form of nitrogen released by sediments during periods of low oxygen (Lehrter et al., 2011; Lin et al., 2011; Nunnally et al., In Review) and is an attractive molecule for prokaryotes and eukaryotes alike. In this instance ammonium stimulates primary production, provides nitrifiers with substrate and is easily assimilated by other microbes. All of these ecosystem processes use oxygen for biochemical reactions or provide substrate for respiration, adding to the causes of hypoxia.

Spatio-temporal patterns of benthic nutrient regeneration outlined by Nunnally et al. (In Review) highlight the importance of ammonium regeneration during the long hypoxic season in relation to the total nitrogen input by MARS. Suboxic conditions can

diminish the capability of sediments to remove nitrogen through denitrification, returning it to the lower water column in a biologically attractive molecule creating a positive feedback. This is important because current strategies for ameliorating hypoxia in the Gulf of Mexico focus on reducing riverine N loads in the hopes of reducing eutrophic conditions. This data driven modeling effort shows that benthic-pelagic coupling is an important loop in regenerated primary production leading us to revisit the Rowe and Chapman (2002) conceptual diagram of hypoxia for the region (Fig. 3.10). This paper outlines the necessary environmental conditions that must be satisfied for this to occur; namely a sediment source of nutrients, a deep euphotic zone and minimal loss of nutrients to the surface layer. Our updated conceptual diagram (Fig. 3.10) emphasizes the preeminent role of the benthos and the sub-pycnocline water column to hypoxic mechanisms on the western Louisiana continental shelf.

3.6 Conclusions

Denitrification is the dominant global sink of fixed nitrogen (Codispoti et al., 2001) Shelves are considered major sites for denitrification on global biogeochemical scales due to the high amount of organic matter that they receive (Devol, 1991). Suboxic conditions associated with hypoxic areas ostensibly increases their importance as sites of N removal, however recent research in the GoMHZ has shown that while denitrification is still important, return of ammonium to the system creates a positive feedback loop. That loop is benthic-pelagic coupling defined as the stimulation/support of primary production through a regenerated nutrient pathway originating in the sediments.

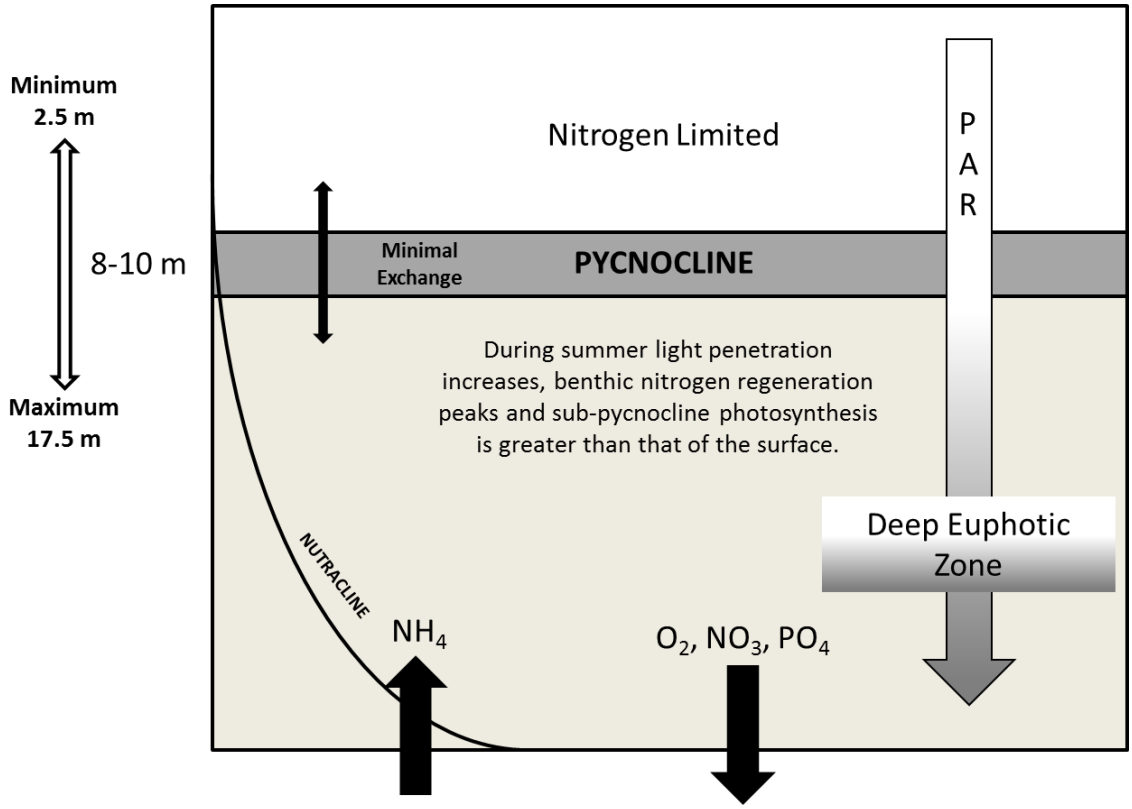


Fig. 3.10. Conceptual diagram of ecosystem processes for far West regions of the Gulf of Mexico Hypoxic Zone with emphasis on sub-pycnocline mechanisms that enhance productivity and maintain bottom water hypoxia. PAR arrow represents Photosynthetically Active Radiation. Arrow outside of box represents the changing position of the pycnocline in Zones C and D, showing maximum, minimum and average depth encountered during this study.

It must be kept in mind that all models are inaccurate, even a simple one as this, but some models can be helpful. The particular effort to partition ammonium utilization in bottom waters by microbes and phytoplankton hint at the competitive interaction that differs from those in surface waters. Profiles of dissolved nutrients indicate a rich sub-

surface layer that does not become nutrient limited even after river input to the continental shelf that stimulates surface productivity has diminished. Sufficient light levels are all that is needed to stimulate bottom water photosynthesis as sediment nutrient fluxes prevent these far west stations from nutrient limitation. Thus within a tightly coupled sub-pycnocline water column nutrients are regenerated in sediments, fuel primary production, providing substrates for respiration creating a positive feedback loop that maintains summer hypoxia West of Atchafalaya Bay.

CHAPTER IV

MACROFAUNA COMMUNITY DYNAMICS IN THE NORTHERN GULF OF MEXICO HYPOXIC ZONE: DIVERSITY, ABUNDANCE AND BIOMASS IN THE "DEAD ZONE"

4.1 Overview

Summertime hypoxia on the Louisiana continental shelf is harmful for large portions of the coastal marine biosphere and is avoided by mobile fauna. Sediment dwelling infauna cannot escape the stress associated with low oxygen concentrations and either persist or perish. Oceanographic surveys within the northern Gulf of Mexico Hypoxic Zone (GoMHZ) attempted to determine the impacts on macrofaunal benthos associated with coastal hypoxia. From 2004 to 2005 macrofauna communities were adapted to hypoxic conditions and deleterious effects were difficult to detect. The polychaete, *Parprionospio pinnata*, was the dominant species during all 5 sample years and polychaetes accounted for 98% of species identified during 2004-2005 but only 82% during 2007-2009. Species-Abundance-Biomass (SAB) curves showed poorer, simple macrofauna communities near the Mississippi River in 2004-2005 and healthier, complex communities in the western regions of the shelf.

Physical scouring during hurricanes Katrina and Rita in 2005 severely restructured species composition and the 'new' assemblage were apparently more vulnerable to hypoxia because the mean macrofauna abundance of 5228 ± 372 ind. m^{-2} prior to hurricane activity in 2005 dropped to 1886 ± 432 ind. m^{-2} afterwards. Total

number of species, Simpson's (d) and Shannon-Weiner (H') Diversity Indices all decreased significantly following the hurricane disturbance.

4.2 Introduction

Stressors in the marine environment influence the diversity and abundance of biological communities. Species successions in response to anthropogenic or natural stress determine the overall biodiversity within an ecosystem. Faunal diversity rises and falls as a function of the timing, severity and type of stress exhibited; recovery responses are also dictated by the nature of the event (Gaston, 1985). Responses to stress can be predicted based on the spatial gradient associated with the type of disturbance (Pearson and Rosenberg, 1978). Organic enrichment either as pollution or input of organic matter (OM) can be easily measured but the resulting impacts to the ecosystem in the form of hypoxia/anoxia are equivocal. The physical mixing and stratification of the water column ultimately determine if eutrophic processes lead to reduced oxygen near the sea floor that impact infaunal organisms (Gray et al., 2002). In the northern Gulf of Mexico channelized input from the Mississippi River high in nutrients derived from Midwest agriculture stimulates biological productivity on the continental shelf (Rabalais et al., 2002). During spring and early summer when the Mississippi and Atchafalaya River System (MARS) discharge peaks, coastal hydrographic and topographic forcing creates strong stratification between fresh river water and denser ocean water that produce large areas of hypoxic bottom water (DiMarco et al., 2009; Wiseman et al., 1997).

The northern Gulf of Mexico Hypoxic Zone (GoMHZ) is frequently referred to as the "Dead Zone," since mobile organisms actively avoid the region or die due to low

oxygen or sulphide poisoning. Benthic infauna are unable to change locations and must endure multiple months of hypoxic bottom water oxygen concentrations (< 2.0 mg L^{-1}). Despite the intense study this region receives, a clear gradient of organic input to the sea floor has never been shown, which is consistent with other studies that have struggled to find a clear link between nutrient input and the vertical flux of particulate organic matter (POM) (Gray et al., 2002). Current monitoring programs consistently map low oxygen conditions over a vast area (16,700 km^2 from 2000-2007 (Turner et al., 2008) but the shelf-wide measurements of hypoxia/anoxia are made at points in time rather than on a continuous basis. This leaves researchers guessing as to what conditions benthic organisms actually face on a day to day basis. Internal shelf waves change the position of the pycnocline and aerate the sea floor (DiMarco et al., 2009) making hypoxia an intermittent stressor of unknown duration and intensity, which are important factors in determining overall hypoxic effect (Seitz et al., 2009). At GoMHZ locations where continuous bottom water oxygen concentration is monitored the number of days of low oxygen have a significant negative effect on the macrobenthos (Baustian and Rabalais, 2009).

Earlier evaluations of benthic macroinfaunal response to environmental variations have noted changes in total fauna biomass (Gray, 1974), as well as changes in faunal groups and individual species represented (Sanders, 1968). Pearson and Rosenberg (1978) described a succession of structural changes following disturbances, and this sequence may govern the assemblages in hypoxic areas. Regularly occurring seasonal hypoxia can lead to reduced body size, limited bioturbation due to shallow

dwelling, rapid growth rates and annual life cycles (Levin et al., 2009). Changes in faunal attributes alter trophic structures and food web services, including loss of accompanied by alterations of biogeochemical function. Along a gradient of organic inputs (or biotic stressors) benthic macrofauna communities decrease in complexity as species in close proximity to enrichment are faced with low oxygen, sulfide and acidic conditions (Pearson and Rosenberg, 1978).

Investigations of stressed macrobenthic communities in the northern Gulf of Mexico are not limited to hypoxia associated with the Mississippi-Atchafalaya River System (MARS), but also include hypoxia beneath the Brazos River plume along the Texas coast and associated with brine diffusers in coastal Louisiana (Gaston, 1985; Gaston et al., 1985; Harper et al., 1991; Harper et al., 1981) which all confirmed that hypoxia stress results in a decrease in diversity, species richness and total abundance of organisms. A "peak of opportunists" coincided with highest biomass of a proliferation of small species. Enrichment opportunists such as the amphipod, *Ampelisca abdita* appear in response to increased food (Harper et al., 1991; Soliman and Rowe, 2008). Polychaetes can be resistant to hypoxic stress (Boesch and Rosenberg, 1981) and species that proliferate during hypoxia are often a subset of the normoxic community (Montagna and Froeschke, 2009). The final or most distal successional point in space and time is usually characterized by the greatest species richness. Gaston (1985) noted that the earliest colonizers during this stage died due to hypoxia, creating a lag in the return to a normal, highly-diverse community. Harper et al. (1991) noted that successional changes occurred about every 3 months, with one dominant replaced by another, which

prolonged recovery for 2 years inshore near the river mouth. Further offshore this regular sequence was not observed and the community returned to a healthy, or pre-stress, state in 1 year.

In their proposed model of faunal succession along gradients of organic input Pearson and Rosenberg (1978) outlined three community features identifiable from abundance, biomass and species data. The "peak of opportunists" (PO) is located at peak biomass and represents influx of small opportunistic species that briefly inflate total community mass. The ecotone occurs at low community abundance, biomass and species. Ecotones are areas of habitat overlap in which species from each community are represented and also includes unique species. The final stage is the transition which coincides with greatest species richness. When plotted along an environmental gradient, Species-Abundance-Biomass (SAB) curves allow investigators to pinpoint these stages.

As part of the NOAA funded Mechanisms Controlling Hypoxia (MCH) project regular cruises during 2004-2005 and 2007-2009 were made to the region of Louisiana continental shelf affected by seasonal hypoxia associated with MARS. This paper examines the consequences of coastal hypoxia for macrofauna communities along a spatial gradient moving away from the Mississippi River and over the course of several full hypoxic seasons. Species lists for five major taxa (Amphipoda, Bivalvia, Cumacea, Gastropoda and Polychaeta) were assembled to address the changes in community diversity caused by hypoxia. To our surprise we were also given the opportunity to address these structural components in the wake of Hurricanes Katrina and Rita that passed over our study areas in late August 2005. Three questions will be addressed

based on our findings: (1) Are macroinfaunal communities spatially distinct from one another based on the distance from MARS input and severity of seasonal hypoxia? (2) Does hypoxic stress cause decreased abundance and biomass of macroinfauna? and (3) Does benthic biodiversity rebound equally from severe hypoxia and storm events?

4.3 Materials and Methods

4.3.1 Study Area and Sampling Program

The northern Gulf of Mexico continental shelf receives freshwater from the Mississippi-Atchafalaya River System (MARS) entering the gulf at Southwest Pass and Atchafalaya Bay. Freshwater plumes track westward along the coast creating theoretical zones of hypoxic potential that can each be characterized by unique biological, chemical and physical characteristics (Rowe and Chapman, 2002). Conceptual zones can be classified as brown (A), green (B) and blue (C) which correspond to the distance from MARS related impacts on surface processes. Zone D was added as a set of far West stations in 2005. Sediment incubation experiments were made at the center of each of these zones (A, B, C and D) (Fig. 4.1) with the captured macrofauna retained for faunal analysis. No MCH cruises occurred in 2006, which is unfortunate since only 5 days after the final sample was taken Hurricane Katrina passed over the Louisiana continental shelf with a peak wind velocity of 175 mph (282 kph). Katrina and Hurricane Rita, a month later, together removed 2 to 15 cm of seabed (Allison et al., 2007)and resuspended surface sediments in depths shallower than 20 meters (Goni et al., 2007) affecting our entire study area (After this point Pre-Katrina and Post-Katrina will be used to refer to these late summer storm disturbances).

The Mechanisms Controlling Hypoxia (MCH) project made regular cruises to the Louisiana continental shelf during two multi-year blocks, 2004-2005 and 2007-2009. Timing of cruises was planned to observe temporal changes related to the onset, duration and breakup of hypoxic conditions within the conceptual zones. Weather and interesting physical phenomenon dictated irregular sampling; consequently not every zone was visited on a regular basis with the exception of Zone C. In excess of 100 replicate cores were collected for faunal analysis in Zones A (19), B (26), C (41) and D (21) and during four hypoxic seasons, Pre-Hypoxia (32), Early Hypoxia (27), Late Hypoxia (44) and Post Hypoxia (6). Initial MCH cruises in 2004-2005 focused on the entire shelf routinely visiting Zones A, B and C, with Zone D added during June of 2005 when hypoxic bottom waters was detected west of Zone C, after diverting to avoid Hurricane Dennis. Regular MCH cruises resumed during 2007-2009 but efforts were focused on the far west zones of C and D.

Regular hydrographic measurements were made at each station. Hydrographic data and nutrient concentrations were obtained using a Seabird 911 CTD system deployed with a twelve bottle rosette for discrete water, sampling at different depths. Instrumentation included a Seabird SBE- 43 oxygen probe, Chelsea CStar transmissometer, Chelsea Aqua 3 fluorometer, Seatech LS6000 Optical Backscatter unit, and Biospherical/ Licor irradiance sensor. Discrete measurements (surface, bottom and 5-m increments) of nutrients and dissolved oxygen concentration were made using Winkler titration and 6 channel autoanalyzer (NO_3^-/NO_2^-, H_2SiO_3, PO_4^-, NH_4^+, and Urea) using standard protocols (GERG-TAMU).

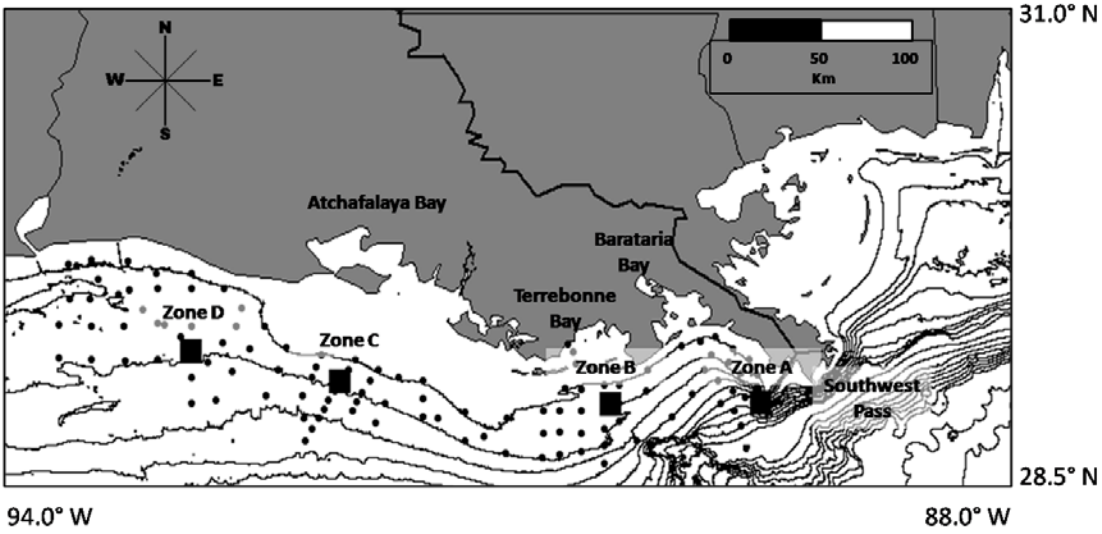


Fig. 4.1. Map of the Mechanisms Controlling Hypoxia BMIC incubation stations within the Northern Gulf of Mexico Hypoxic Zone on the Louisiana continental shelf. The Mississippi River enters the Gulf at Southwest Pass. The Atchafalaya River flows through Atchafalaya Bay before entering the Gulf. The small dots represent grid of CTD and oxygen profiles (DiMarco et al., 2009).

4.3.2 Macrofauna Collection

Benthic samples were collected using a 0.2 m^2 GOMEX box core that retained overlying bottom water. Upon recovery, Batch Microincubation Chambers (BMICs) (0.015 m2) were used to take sub-cores for ship-board incubation experiments. After the termination of BMIC experiments sediments were washed and macrofauna retained on a 0.5 mm sieve and preserved in a 10% formalin-seawater solution buffered with borax to prevent shell loss. Macrofauna samples were stained in Rose-Bengal for 24 hours, sorted to major taxonomic group and placed in 70% ethanol for preservation. The

five dominant macrofaunal taxa [amphipods (by Yousra Soliman), bivalves (by Clifton Charles Nunnnally), cumaceans (by Clifton Charles Nunnally), gastropods (by Clifton Charles Nunnnally), and polychaetes (by Fangyuan Qu)] were identified to family or better by the corresponding authors. Abundances of polychaetes, mollusks (bivalves and gastropods), and crustaceans (amphipods, cumaceans, decapods, harpacticoids, isopods, mysids, ostracods and tanaidaceans) were determined for each replicate core sample.

Polychaete biomass was determined by weighing the sorted sample. Wet weight was measured using a Sartorius CP2P balance. Once macrofauna were removed from ethanol they were dry blotted on a paper towel for 30 seconds and then moved to the balance. Amphipods and cumaceans were too few and too light to weigh reliably. Bivalve and gastropod biomasses were also problematic because they exhibited various states of decalcification.

4.3.3 Data Analysis

Differences in macrofauna community abundance, number of taxa, biomass, polychaete biomass, number of polychaete species, abundance of polychaetes, mollusks and crustaceans, and calculated diversity measures (e.g. d, J', H') was made using SPSS statistical software package (Version 16). Variables that were normally distributed and had homogenous variances were assessed using one-way ANOVAs using LSD post-hoc tests to determine significant groups. Non-normal distribution of variables was tested using Kruskal-Wallis (KW) tests to determine significant differences and Mann-Whitney U (MW) tests to determine significant post-hoc groupings. Significance associated with these tests is usually based on a p-value of 0.05, but biases in the temporal and spatial

sampling in the 2 sampling blocks (2004-2005 and 2007-2009) make it prudent to use the more stringent p-value of 0.01 when assigning significance to non-parametric tests.

Species Richness, Simpsons Diversity Index (d), Eveness (J') and the Shannon-Weiner Diversity Index were calculated for species data of Amphipods, Bivalves, Cumaceans, Gastropods and Polychaetes using PRIMER Version 6 (Clarke and Warwick, 2001). Species abundance data were square root transformed and normalized before constructing an intra-location resemblance matrix. Average species abundance per core was used to calculate Bray-Curtis similarities (Bray and Curtis, 1957) for direct comparison of faunal compositions among study areas. From these data CLUSTER analysis and non-metric multidimensional scaling (nMDS) were performed in PRIMER to examine relationships among species distributions. CLUSTER analysis uses hierarchical relationships to calculate and test diversity indices based on the taxonomic relations among species producing a dendrogram of groups based in Bray-Curtis similarity. nMDS plots use ordination techniques to examine sample relationships within a 2-dimensional plane. Relative distances between samples represent faunal similarity in nMDS plots. Environmental data corresponding to species abundances were transformed (logarithmic) and normalized to calculate Euclidean distances that created an environmental matrix. The created matrix utilized in a principal component analysis (PCA) to summarize patterns in species composition related to environmental variables. MDA and PCA plots were generated with PRIMER Version 6.

4.4 Results

4.4.1 Macrofauna Patterns

Variation from year to year in the abundance, diversity and biomass of the macrofauna on the Louisiana continental shelf was great. All years of data were significantly different from one another (KW: $p < 0.01$). Hurricanes Katrina and Rita also played a significant role in structuring of the benthos during the study periods, significantly altering macrofauna community structure after the events (KW: $p < 0.01$). Highest recorded macrofauna abundance, 16,400 ind. m^{-2}, occurred in Zone C during Late Hypoxia and lowest total abundance (no macrofauna) occurred in Zone B during Post Hypoxia. Not surprisingly the highest (80.3 g m^{-2}) and lowest (0.0 g m^{-2}) biomass coincided with these spatial and temporal samplings during the second sampling block after the hurricane disturbance. The five dominant taxa identified to species (Amphipoda, Bivalvia, Cumacea, Gastropoda, and Polychaeta) accounted for 98% of the population during 2004-2005, but accounted for only 82% after the hurricanes (KW: $p = 0.007$). Mollusks and crustaceans were the 2 dominant macrofauna taxa, after the polychaetes, accounting for 22 and 5% of the total community. These groups did not change in their respective contribution to total fauna between sampling blocks. Ampeliscid amphipods accounted for 76% of amphipods found during both study periods.

Differences in community parameters were assessed for spatial (Zone), temporal (Season) and environmental (Oxygen Concentration) trends. Only crustacean abundance was significantly different when tested for differences between oxic and suboxic

conditions, with a greater abundance of crustaceans during oxic conditions (319 ± 58 versus 151 ± 26 ind. m^{-2}). No significant differences between zones were found for total macrofauna abundance, number of taxa groups, number of polychaete species, polychaete biomass, polychaete abundance and crustacean abundance. Individual polychaete biomass was significantly greater in Zone C compared to Zones A, B and D (KW: $p = 0.001$; MW: $p < 0.01$) (Table 4.1). Abundance of mollusks was significantly different between zones with Zone A having less mollusks per square meter than Zones B, C and D (KW: $p = 0.002$; MW: $p < 0.001$).

Total community abundance, polychaete biomass, polychaete abundance and mollusk abundance all differed significantly between hypoxic seasons (KW: $p < 0.01$). Total macrofauna abundance and polychaete abundance were significantly greater during Pre-Hypoxia, Early Hypoxia and Late Hypoxia (3622 ± 563, 4522 ± 627, and 3746 ± 544 ind. m^{-2}, respectively) when compared to Post Hypoxia (540 ± 447 ind. m^{-2})(MW: $p < 0.01$) (Table 4.2). Polychaete biomass was significantly greater during Pre-Hypoxia, Early Hypoxia and Late Hypoxia periods (5.6 ± 0.8, 9.4 ± 1.4, and 9.4 ± 2.1 g m^{-2}, respectively) when compared to Post Hypoxia (1.6 ± 0.7 g m^{-2})(MW: $p < 0.01$).

Table 4.1. Macrofauna and polychaete community parameters for all study zones.

	Zone	Abundance (# m^{-2})	S	Polychaete Biomass (g m^{-2})	Individual Polychaete Mass (mg)	Polychaete Abundance (# m^{-2})	Polychaete Species	Molluscan Abundance (# m^{-2})	Crustacean Abundance (# m^{-2})
Zone A	Mean	2491.2	4.2	4.39	2.6	2045.7	6.0	146.3	241.6
	N	19	19	18	19	19	19	19	19
	Std. Deviation	1419.5	2.1	3.02	2.4	1258.9	3.2	287.4	227.1
	Std. Error of Mean	325.7	0.5	0.71	0.6	288.8	0.7	65.9	52.1
	Minimum	329.0	1.0	0.55	0.0	263.2	2.0	0.0	0.0
	Maximum	6240.0	9.0	10.2	9.0	5460.5	16.0	960.0	723.7
Zone B	Mean	3779.6	5.2	6.27	3.7	2688.5	7.2	967.5	198.4
	N	26	26	22	25	26	26	26	26
	Std. Deviation	2761.4	2.3	6.13	7.4	2180.9	4.6	925.1	244.1
	Std. Error of Mean	541.6	0.5	1.31	1.5	427.7	0.9	181.4	47.9
	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	9760.0	10.0	20.03	35.1	7280.0	16.0	2880.0	855.3
Zone C	Mean	4244.8	5.4	10.52	8.1	2134.1	8.5	738.9	281.3
	N	41	40	39	41	41	41	41	41
	Std. Deviation	3944.5	2.8	13.05	9.1	2051.6	5.7	886.7	411.8
	Std. Error of Mean	616.0	0.4	2.09	1.4	320.4	0.9	138.4	64.3
	Minimum	160.0	1.0	0.02	0.0	65.8	1.0	0.0	0.0
	Maximum	16400.0	11.0	80.30	40.2	9120.0	22.0	3947.4	2080.0
Zone D	Mean	4033.1	4.9	7.29	3.7	2017.7	9.0	1604.5	128.6
	N	21	21	18	18	21	21	21	21
	Std. Deviation	4020.1	3.1	7.80	3.7	2166.6	9.0	1724.1	199.1
	Std. Error of Mean	877.3	0.7	1.84	0.9	472.8	2.0	376.2	43.4
	Minimum	80.0	1.0	0.26	0.7	0.0	0.0	0.0	0.0
	Maximum	10080.0	11.00	24.23	17.2	6400.0	26.0	4802.63	640.0
Total	Mean	3740.7	5.1	7.86	5.4	2197.4	7.8	838.5	231.8
	N	110	109	100	106	110	110	110	110
	Std. Deviation	3348.7	2.6	9.58	7.3	1967.2	5.9	1123.9	311.7
	Std. Error of Mean	319.3	0.3	0.96	0.7	187.6	0.6	107.2	29.7
	Minimum	0.0	0.0	0.01	0.0	0.0	0.0	0.0	0.0
	Maximum	16400.0	11.0	80.30	40.2	9120.0	26.0	4802.6	2080.0

4.4.2 Polychaete Dynamics and Species-Abundance-Biomass (SAB) Curves

From 2004 to 2005 polychaetes accounted for 73% of total macrofauna abundance compared to only 53% in 2007 to 2009 ($p = 0.001$). Polychaete mean abundance was significantly greater in 2004-2005 at 3373 ± 240 ind. m^{-2} (mean ± standard error) compared to 751 ± 122 ind. m^{-2} in 2007-2009 (KW: $p < 0.001$). Likewise polychaete biomass and number of species per sample before Katrina (8.7 ± 0.9 g m^{-2} and 11 ± 0.8 species, respectively) were significantly greater than after (6.7 ± 1.9 g m^{-2} and 4 ± 0.5 species, respectively) (KW: $p = 0.006$ and $p < 0.001$, respectively). Interestingly, the mean individual size of polychaetes was significantly greater in the years after Katrina, increasing from 2.7 ± 0.3 mg prior to the hurricanes to 9.8 ± 1.6 mg afterwards (KW: $p < 0.001$). Dominance among polychaete species and families also changed after the hurricanes except for *Paraprionospio pinnata* which was numerically dominant during both regimes. Prior to Hurricanes Katrina and Rita three species accounted for 53% of polychaete species, *P. pinnata*, *Mediomastus californiensis*, and *Aricidea sp.1*; after the hurricanes these 3 species accounted for only 37% of total polychaetes with *P. pinnata* accounting for 29 and 30% before and after, respectively (Table 4.1). Four families (Capitellidae, Maldanidae, Paraonidae and Spionidae) composed 66 and 68% of the polychaetes during 2004-2005 and 2007-2009, respectively. The relative percent composition changed between these groups after hurricane activity, with Capitellids showing the greatest decrease, 17.3% to 9.6%, and Maldanids the greatest increase, 4.8% to 16.0% (Table 4.3).

Table 4.2. Macrofauna and polychaete community parameters for all hypoxic seasons.

	Season	Abundance (# m^{-2})	S	Polychaete Biomass (g m^{-2})	Individual Polychaete Mass (mg)	Polychaete Abundance (# m^{-2})	Polychaete Species	Molluscan Abundance (# m^{-2})	Crustacean Abundance (# m^{-2})
Pre-Hypoxia	Mean	3622.5	6.0	5.64	6.0	2023.9	8.1	609.0	353.1
	N	32	32	29	32	32	32	32	32
	Std. Deviation	3186.2	2.8	4.55	9.0	194.1	5.1	855.1	442.0
	Std. Error of Mean	563.2	0.5	0.84	1.6	350.7	0.9	151.2	78.1
	Minimum	320.0	2.0	0.38	0.0	65.8	1.0	0.0	0.0
	Maximum	10986.8	11.0	17.31	33.2	9120.0	22.0	3920.0	2080.0
Early Hypoxia	Mean	4522.3	5.3	9.43	5.0	2785.7	9.4	1317.4	265.9
	N	27	27	24	26	27	27	27	27
	Std. Deviation	3258.0	2.5	6.62	7.1	1912.0	6.3	1420.1	245.1
	Std. Error of Mean	627.0	0.5	1.35	1.4	368.0	1.2	273.3	47.2
	Minimum	0.0	0.0	0.00	0.0	0.0	0.0	0.0	0.0
	Maximum	9760.00	9.00	22.76	35.05	7280.00	24.00	4240.00	800.00
Late Hypoxia	Mean	3746.2	4.2	9.42	5.8	2222.6	7.1	826.0	120.3
	N	44	43	40	41	44	44	44	44
	Std. Deviation	3611.0	2.3	13.34	8.6	2011.5	6.3	1087.9	189.3
	Std. Error of Mean	544.4	0.4	2.11	1.3	303.2	0.9	164.0	28.5
	Minimum	80.0	1.0	0.26	0.0	0.0	0.0	0.0	0.0
	Maximum	16400.0	10.0	80.30	40.2	6720.0	26.0	4802.6	79.5
Post Hypoxia	Mean	540.2	4.3	1.60	6.9	236.8	2.7	181.9	72.9
	N	6	6	6	6	6	6	6	6
	Std. Deviation	446.7	2.7	1.76	4.4	233.2	2.3	201.4	66.0
	Std. Error of Mean	182.4	1.1	0.72	1.8	95.2	0.9	82.2	26.9
	Minimum	160.0	2.0	0.02	0.11	65.8	1.0	0.0	0.0
	Maximum	1360.0	9.0	4.05	13.3	640.0	6.0	560.0	160.0
Total	Mean	3689.6	5.1	7.87	5.8	2163.0	7.7	828.6	229.7
	N	112	111	102	108	112	112	112	112
	Std. Deviation	3340.1	2.6	9.52	8.1	1966.3	5.9	1116.1	309.3
	Std. Error of Mean	315.6	0.2	0.94	0.8	185.8	0.6	105.5	29.2
	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	16400.0	11.0	80.30	40.2	9120.0	26.0	4802.6	2080.0

Species-Abundance-Biomass curves are generally used to outline community properties along a gradient of increasing organic input. We can utilize similar curves to evaluate polychaete community changes in relation to apparent gradients of organic input (Zones) and hypoxic intensity (Seasons). Polychaetes not only represent the dominant taxa found within this study but are also hearty to the affects hypoxic conditions incur, persisting longer than other taxa. Knowing the large differences between study blocks that are ostensibly the result of hurricane impacts on the continental shelf caused by Katrina and Rita four SAB curves were created (Fig. 4.2). Polychaete community changes that occurred during 2004-2005 are shown along gradients of organic input (Fig. 4.2a) and hypoxic intensity (Fig. 4.2b). Polychaete community changes that occurred during 2007-2009 are shown along gradients of organic input (Fig. 4.2c) and hypoxic intensity (Fig. 4.2d).Organic input increases moving to the left on the x-axis in Figs. 4.2a and 4.2c and hypoxic intensity increases moving to the right in Figs. 4.2b and 4.2d.

The most striking difference between sampling periods is the higher polychaete abundances in 2004-2005. Polychaete biomass and number of species in 2007-2009 were slightly lower but can be plotted on the same scale. Also noticeable are the upward trend when moving to the right on SAB curves of 2004-2005 and the downward trend in 2007-2009. In 2004-2005 the number of species, abundance and biomass all increased moving away from the Mississippi River (Fig. 4.2a) with the peak of opportunists (PO) coming in Zone B. The number of species and polychaete biomass increased along with hypoxic intensity in 2004-2005 (Fig. 4.2b) with the peak of opportunists (PO) occurring

during Late Hypoxia and the ecotone becoming established between Early and Late Hypoxia. Polychaete abundance increased with hypoxic duration but experienced a decline during Post Hypoxia. Transition points during 2004-2005 (the regions of the curves that increase towards the highest species richness) occurred between Zones C and D (Fig. 4.2a) and during the time from Late to Post Hypoxia (Fig. 4.2b).

Table 4.3. Relative contribution of polychaete species and families to total polychaete diversity during the periods of 2004-2005 (Pre Hurricane) and 2007-2009 (Post Hurricane).

2004-2005 % Contribution	2007-2009 % Contribution	Species	2004-2005 % Contribution	2007-2009 % Contribution	Family
29.0	30.3	P. pinnata	17.3	9.6	Capitellidae
12.9	3.2	M. californensis	4.8	16.0	Maldanidae
11.0	3.8	Aricidea sp. 1	12.4	8.1	Paraonidae
52.9	**37.4**	**Total**	31.5	34.8	Spionidae
			66.0	**68.6**	**Total**

In 2007-2009 polychaete community abundance and number of species declined with increasing distance from the Mississippi River (Fig. 4.2c). The PO occurred in Zone C with the large increase in biomass but dropped to its lowest point in Zone D.

Again the ecotone appeared to occur in between Zones B and C. As hypoxic intensity increased in 2007-2009 polychaete abundance and the number of species declined until Late Hypoxia but showed signs of recovery during the Post Hypoxia stage (Fig. 4.2d). Polychaete biomass peaked in Early Hypoxia corresponding to the PO and leveled out during Late and Post Hypoxia stages. The opposite position of the transition zone during 2007-2009, transitioning from more species in Zone A to less as organic input decreases (Fig. 4.2c), and losing species as hypoxic stress increases (Fig. 4.2d), illustrates the substantial difference in polychaete species composition between the two sampling periods.

4.4.3 Diversity Indices

Species richness (S) was significantly less during the 2007-09 sampling with an average of 15 species per sample before the Hurricanes Katrina and Rita and 4 species after (KW: $p < 0.001$) (Table 4.4**)**. Simpson's Index (d) and the Shannon-Weiner Index (H') decreased significantly between 2004-2005 and 2007-2009 (KW: $p < 0.001$), but evenness (J') was unaffected. J' and d were significantly different between zones (ANOVA: $p < 0.01$). J' in Zones C and D was higher than A and B ($p < 0.01$). Simpson's Index was lower in Zones A, B and C compared to Zone D ($p < 0.01$). Significant seasonal differences in evenness and H' were found between Pre, Early and Late Hypoxia and Post Hypoxia ($p < 0.01$). Post Hypoxia had a higher evenness but a lower H' compared to the earlier seasons ($p < 0.001$) (Table 4.4). Shannon-Weiner Diversity Index was significant higher during suboxic conditions versus oxic conditions (ANOVA: $p < 0.05$).

Fig. 4.2. Polychaete Species-Abundance-Biomass curves plotted along spatial (Zones) and temporal (Seasons) gradients sampled on the Louisiana continental shelf in the Northern Gulf of Mexico Hypoxic Zone: (a) 2004-2005 MCH Zones; (b) 2004-2005 Hypoxic Seasons; (c) 2007-2009 MCH Zones; (d) 2007-2009 Hypoxic Seasons. Solid lines are number of polychaete species. Dashed lines are polychaete abundance per square meter. Dotted lines are polychaete biomass per square meter. Error bars represent 1 standard error of the mean (SE).

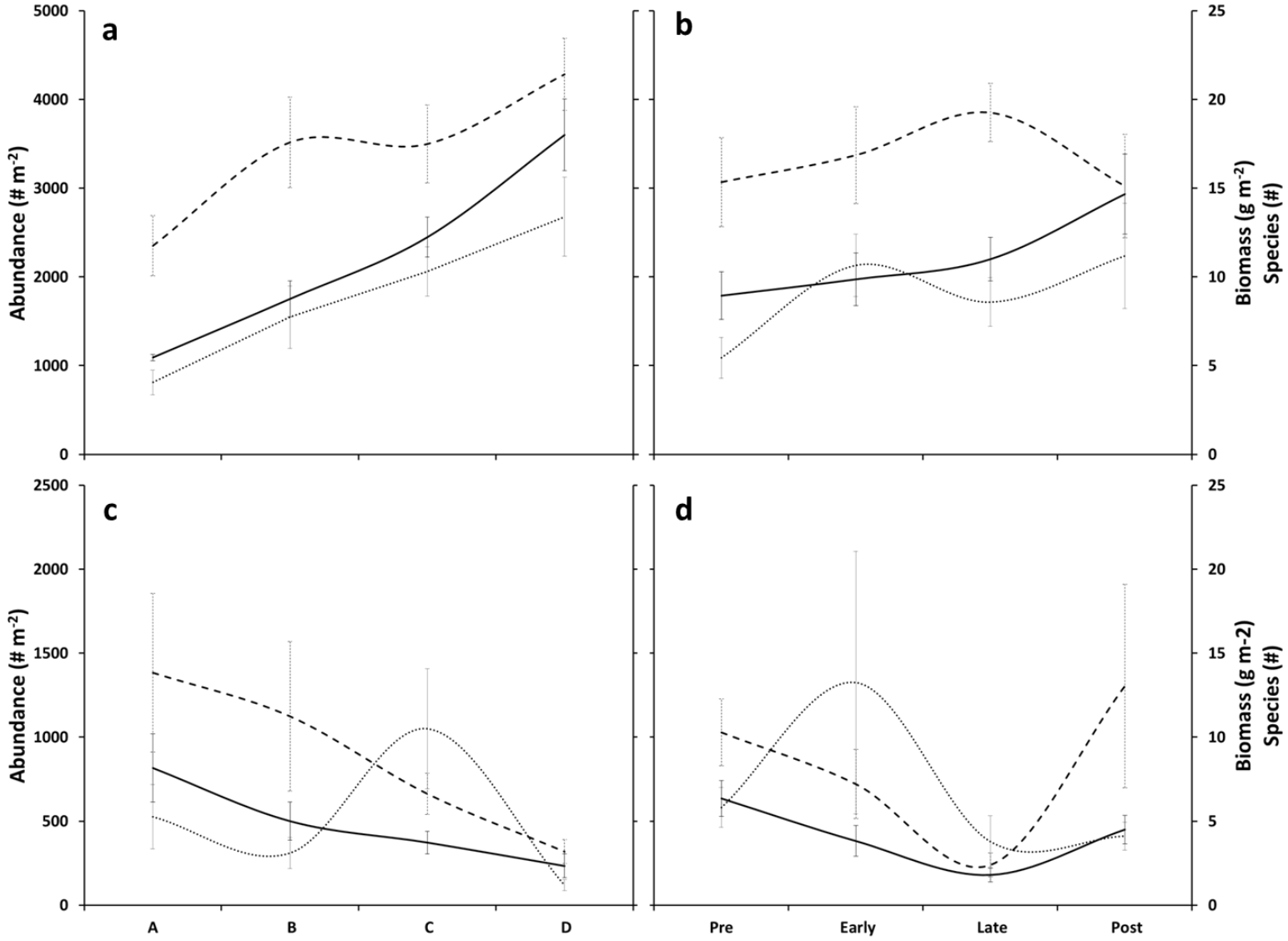
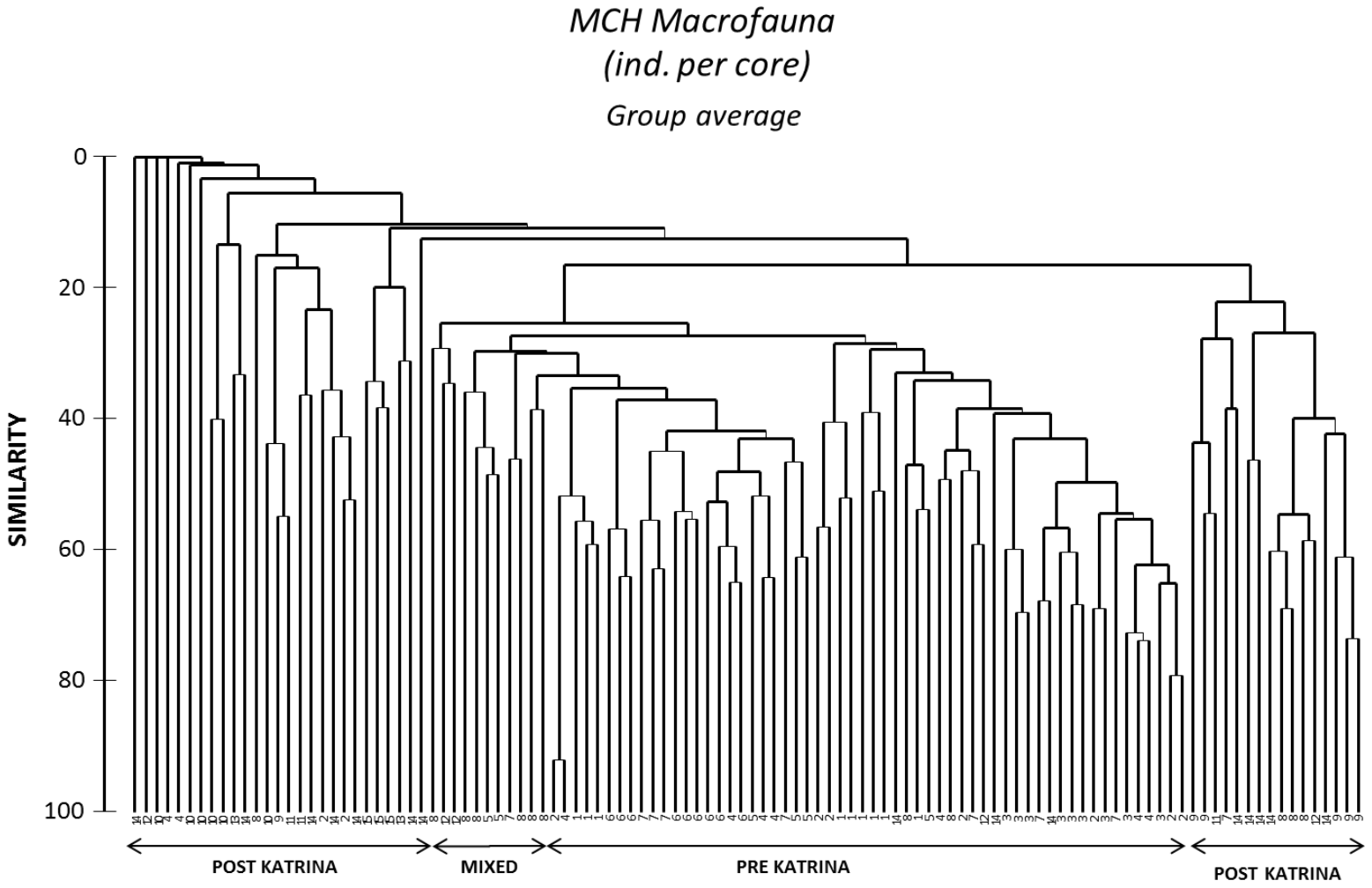

a
b
c
d
Abundance (# m-2)
Biomass (g m-2)
Species (#)
5000
4000
3000
2000
1000
0
2500
1500
500
25
20
15
10
5
A
B
C
D
Pre
Early
Late
Post

Table 4.4 Species diversity measures of dominant macrofauna species richness (S), Simpsons Diversity Index (d), Eveness (J') and Shannon-Weiner Diversity Index (H'). Each statistic is shown for study zones, seasons, oxygen concentrations and before and after hurricanes in 2005.

		S	d	J'	H' (log 2)
Zone A	Mean	8.3	2.74	0.94	2.70
	N	19	19	19	19
Zone B	Mean	10.9	3.78	0.95	2.78
	N	26	22	21	26
Zone C	Mean	12.0	3.70	0.97	3.09
	N	43	43	43	43
Zone D	Mean	13.5	4.12	0.98	2.76
	N	21	19	19	21
Pre Hypoxia	Mean	11.8	3.61	0.96	3.13
	N	32	32	32	32
Early Hypoxia	Mean	13.3	4.32	0.96	2.93
	N	27	23	22	27
Late Hypoxia	Mean	10.8	3.43	0.95	2.81
	N	44	42	42	44
Post Hypoxia	Mean	4.7	2.21	1.00	1.82
	N	6	6	6	6
Oxic	Mean	10.4	3.48	0.97	2.81
	N	52	49	49	52
Suboxic	Mean	12.2	3.74	0.95	2.95
	N	57	54	53	57
Pre Hurricane	Mean	15.4	4.33	0.95	3.47
	N	60	59	58	60
Post Hurricane	Mean	3.7	2.71	0.98	2.22
	N	52	47	47	52
Total	**Mean**	**11.3**	**3.61**	**0.96**	**2.89**
	N	**112**	**106**	**105**	**112**

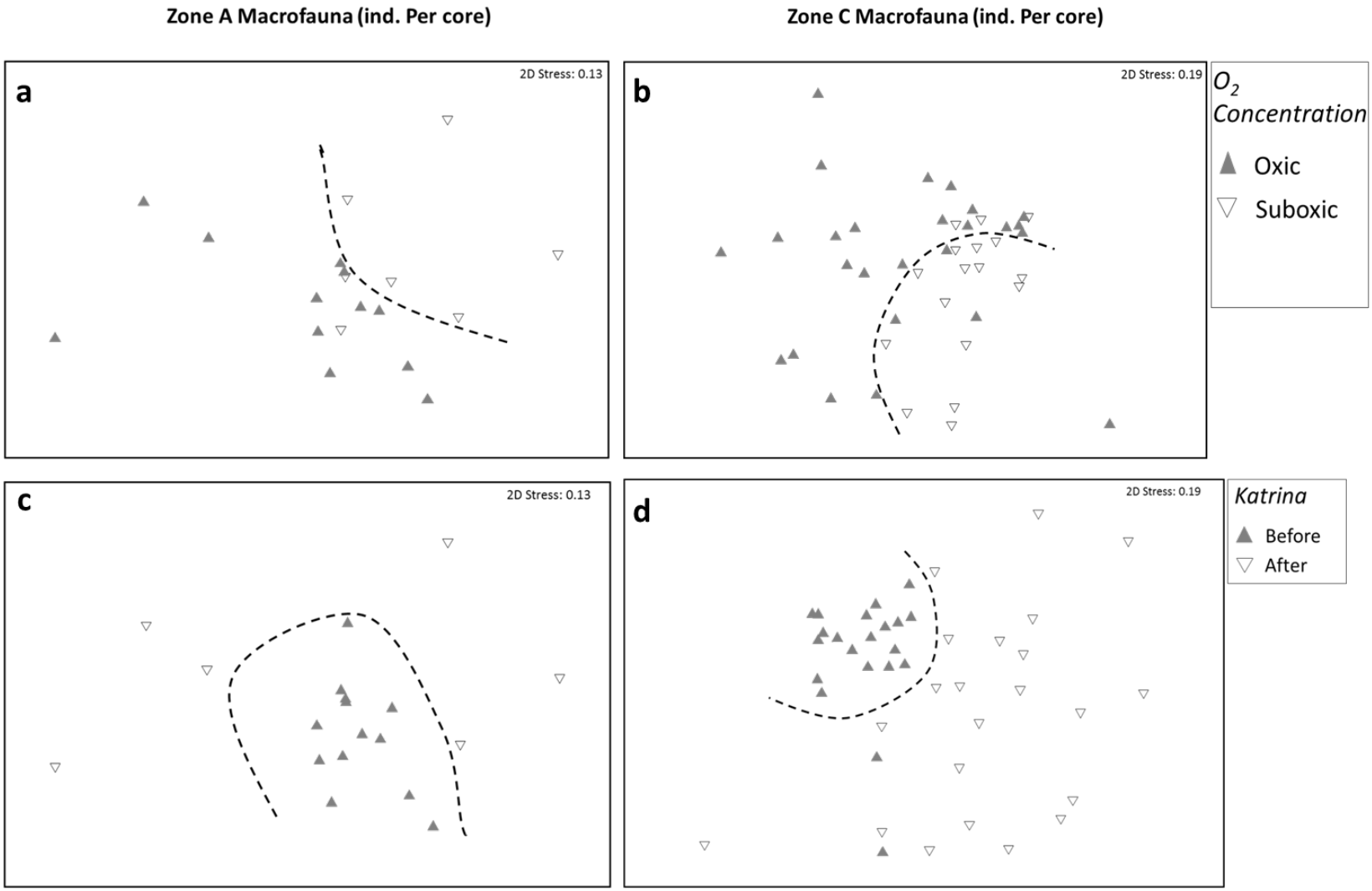
Fig. 4.3. Cluster diagram of faunal group resemblance for macrofauna replicate samples. The x-axis numbers correspond to MCH cruises and arrows denote similar groups based on sampling before or after the major hurricane events of 2005. The y-axis shows Bray-Curtis similarity (%).


MCH Macrofauna
(ind. per core)
Group average
SIMILARITY
0
20
40
60
80
100
POST KATRINA
MIXED
PRE KATRINA
POST KATRINA

4.4.4 Recurrent Groups

Cluster analysis of macrofaunal species based on Bray-Curtis similarity identified two groups at the 30% similarity level, one corresponding to sampling before Katrina and the other made after Katrina (Fig. 4.3). A mixed group clustered at the 30% level contained cruise samples both before and after Katrina. A final grouping of samples collected mostly after Katrina displayed weak similarity at only about 5%. Non-metric multidimensional scaling (nMDS) plots for Zones A and C produced identifiable groups of samples that were separated based on bottom water oxygen concentrations and in relation to timing before or after Hurricane Katrina (Fig. 4.4). Macrofauna samples affected by hypoxic conditions overlapped with normoxic samples but wide spreads between sample types clearly demonstrated different fauna groups away from neutral areas (Fig. 4.4a and 4.4b). Tightly clustered groups marked very clear differences in samples taken prior to and after Hurricane Katrina. Samples in Zones B and D were densely clustered on top of each other and showed no separation of groups for any study variable. Principal component analysis of macrofauna community association with environmental parameters (concentrations of oxygen, ammonium, nitrate, nitrite, silicate, phosphate, and urea plus depth) displayed a wide scatter among MCH zones with a majority of samples explained by depth and bottom water urea concentration (Fig. 4.5). Interestingly several samples in Zone A cluster closer to axes representing bottom water oxygen and ammonium concentrations.

Fig. 4.4. Non-metric multidimensional scaling (nMDS) of macrofaunal communities based on calculated Bray-Curtis faunal similarity. Faunal groups are separated by dashed lines. (a) Zone A faunal similarity based on oxic and suboxic conditions; (b) Zone C faunal similarity based on oxic and suboxic conditions (Upright shaded triangles represent oxic samples; inverted open triangles represent suboxic samples); (c) Zone A faunal similarity based on samples from before and after major hurricane activity in 2005; (d) Zone C faunal similarity based on samples from before and after major hurricane activity in 2005 (Upright shaded triangles represent pre-hurricane samples; inverted open triangles represent post hurricane samples).


Zone A Macrofauna (ind. Per core)
Zone C Macrofauna (ind. Per core)
a
2D Stress: 0.13
b
2D Stress: 0.19
O_2 Concentration
Oxic
Suboxic
c
2D Stress: 0.13
d
2D Stress: 0.19
Katrina
Before
After

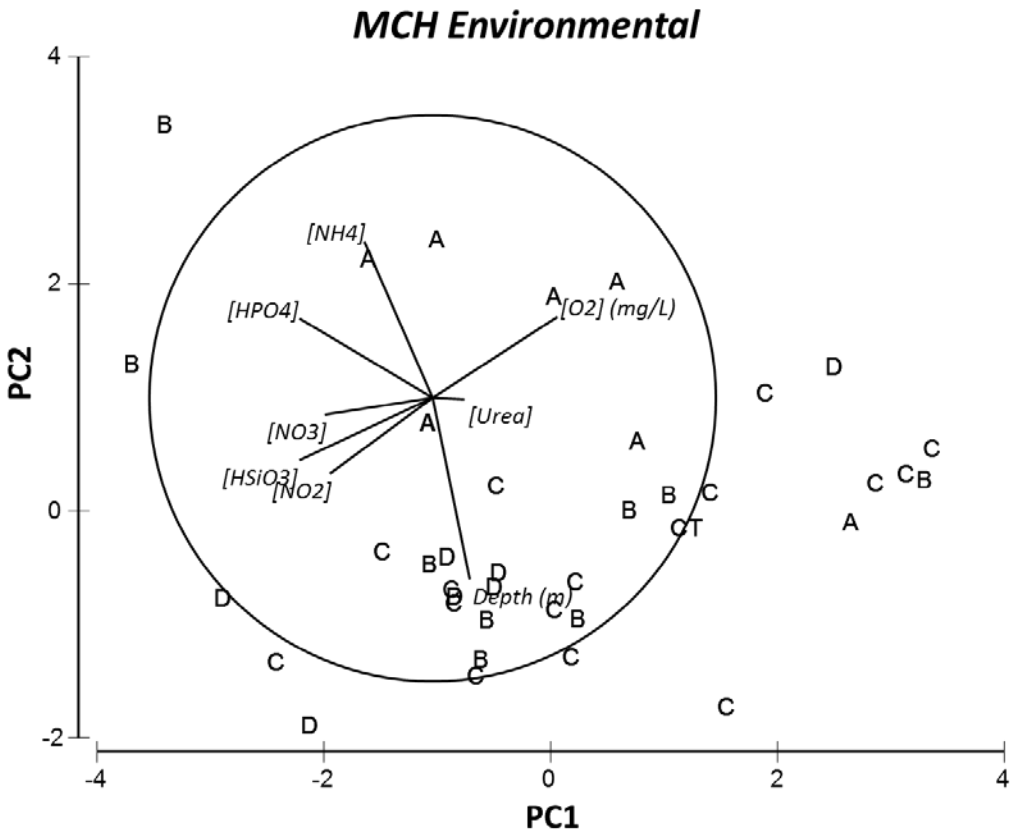


Fig. 4.5. Principal component analysis (PCA) based on 8 environmental variables. Labels represent MCH zones used during study.

4.5 Discussion

Macrofauna communities on the Louisiana continental shelf West of MARS have been subjected to large areas of seasonally hypoxic bottom waters, such that there exists no reliable record of what a healthy community would look like for this area. As this area has been subject to hypoxic events long before human exacerbation of low oxygen conditions (Swarzenski et al., 2008) it is likely that a resident fauna exists that is adapted

to hypoxia (Rhoads and Morse, 1971). For this reason no large scale patterns were found by our study and macrofauna communities showed no significant decreases along spatial gradients. During 2004-2005 our results hardly show any detrimental effects of low oxygen on the macrobenthos worthy of the "Dead Zone" moniker. Yet when describing this area to the general public or even other oceanographic researchers the hypoxic zone causes blank stares (too much editorial?). However, we were fortunate to witness the impacts of a short lived event that not only reorganized biological communities but also affected their ability to respond to organic enrichment and hypoxia.

4.5.1 Hurricane Impacted Continental Shelf System and Macrofauna

Hurricane impacts in other coastal regions have documented similar declines in abundance and species diversity followed by colonization by opportunists (Boesch et al., 1976; Mallin et al., 1999). Engle et al. (2009) found benthic taxa, abundances and H' diversity had declined in the Birdsfoot delta and along the Mississippi and Alabama coastlines 2 months after Katrina. They also noted shifts in taxa composition and dominance associated with survival and colonization of opportunists. Benthic communities impacted by Hurricane Fran (1996) in Cape Fear, North Carolina recovery was seen after 3 months. Katrina was however significantly stronger and at the time of occurrence was determined to be the sixth strongest Atlantic hurricane on record. Our results belie this fact as macrobenthic communities were still depauperate some 4 years after the storm.

Hurricane impacts on the Louisiana continental shelf redistribute sediment organic carbon offshore to the slope (Sampere et al., 2008). Hurricane Katrina removed sediments from the seabed and deposited at a magnitude greater than annual fluvial inputs from the MARS system (Allison et al., 2007; Goni et al., 2007). Significant increases in individual polychaete size that were found after the hurricanes of 2005 are likely related to the increased numbers of Maldanid polychaetes that coincided with the decrease of Capitellid polychaetes. Maldanids, or bamboo worms fall within the larger size spectrum of polychaetes and Capitellids are commonly among the smaller sized polychaetes. This change in the relative percentages of polychaetes may be related to a coarser grain size distribution that occurred as a result of seabed scouring by Hurricanes Katrina and Rita (Allison et al., 2007). Not only did taxa composition change among polychaetes but their relative contribution to total diversity decreased creating a macrofauna community more susceptible to hypoxic stress (Gray et al., 2002). Changes in diversity metrics as result of hurricane scouring the Louisiana continental shelf reflect the loss of species and decreased diversity but community evenness did not change suggesting that all taxa were affected equally.

4.5.2 Polychaete Clues that Apply the Total Macrobenthic Community

Polychaete SAB curves along a gradient of organic input during 2004-2005 clearly show the influence of abnormal environmental conditions in Zone A near the Mississippi River, causing low polychaete abundance, biomass and diversity. Abundance, biomass and number of species reached their greatest values at the other end of the gradient in Zone D (Fig. 4.2a). The pre hurricane polychaete community changed

very little along the gradient of increasing hypoxic intensity (Fig. 4.2b) suggesting the polychaete community was adapted to low oxygen conditions (Boesch and Rosenberg, 1981). The 2005 hurricanes that impacted the Louisiana coastline reorganized polychaete communities, changed their taxonomic make-up (Table 4.3) and consequently the ability to survive the long hypoxic season (Fig. 4.2d).

Prior to Katrina polychaete communities were healthier (higher diversity, biomass and abundance) away from the Mississippi River with less complex communities existing near the source of organic input. Post Katrina Zone A exhibited highest polychaete diversity and abundance but simpler communities were found out West. Transitional communities existed in the western zones and were characterized by increasing species before Katrina; afterwards these transitional groups were located near to the Mississippi River and were characterized by loss of species. In the Post Katrina macrobenthic world communities were structured along a gradient of food availability with the peak of opportunists occurring in Zone C rather than Zone B, flipping the SAB curves (Fig. 4.2a and c). Communities after Katrina were composed of species not adapted to low oxygen stresses and consequently fared worse during the long hypoxic season (Fig. 4.2d).

Decreased molluscan abundance in Zone A may be due to the higher sedimentation associated with the shallow depth and proximity to the Mississippi River in addition to the low oxygen and high ammonium levels that help influence biological community organization near the Mississippi River outflow (Fig. 4.5). Increased acidity associated with hypoxic areas impedes molluscan ability to produce shells (Pearson and

Rosenberg, 1978). Decreased crustacean abundance in the latter seasons of hypoxia likely represents a relative inability to cope with hypoxic conditions (Gray, 1974).

4.6 Conclusions

Spatially or temporally distinct macrofauna communities could not be distinguished within the GoMHZ which may be related to the large spread of our 4 sampling sites and impacts of large storms that interrupted our multi-year study. Gradients in time and space do not always exist in perturbed ecosystems even those with long histories of study (Maurer et al., 1993). We suggest further work in deciphering macrofauna community dynamics lay out closer spaced transects that extend away from the shoreline as well as parallel to it. Hypoxic stress does cause decreased abundance and diversity among macrofauna communities that are not adapted to deal with low oxygen, such as the communities that arose following Hurricanes Katrina and Rita. Potential bias of our multivariate species analysis could be caused by hurricane disturbance that altered taxa proportions. Before hurricanes the five taxa identified accounted for 99.1% of all macrofauna, after they accounted for only 81.6%.

SAB curves of polychaete communities do resemble the conceptual model of Pearson and Rosenberg (1978), most likely because the spatial axis is not a true gradient of organic input. As noted above, the data lack the spatial resolution to determine gradients in faunal assemblages but SAB curves prove useful in comparing macrofaunal communities before and after hurricane disturbance. The most notable of these differences are that before the hurricanes polychaete communities were resistant to

hypoxic stress but suffered due to proximity to MARS. After the hurricanes communities fared better close to MARS but were decimated by hypoxia.

Our abundance values fall within the range of previous studies from the GoMHZ (3700 ind. m^{-2} in this study compared to a range of 119-18,437 ind. m^{-2}) (Baustian and Rabalais, 2009; Rabalais et al., 2001; Rowe et al., 2002). It is likely that the stable macrofauna community we sampled during 2004-2005 is however less abundant and diverse than other shelf communities. Increased abundance, biomass and number of species after hypoxia (Fig. 4.2b and d) suggest niches were opened and competition for space decreased during hypoxia similar to findings by Powers et al. (2001) within the GoMHZ. However the long lasting deleterious effect of hurricanes reorganized the macrofauna communities in the GOMHZ to a far greater extent than 5-6 months of low oxygen concentrations, consistent with other findings of dramatic community reorganization by climatic events (1981-1984 El Nino) (Maurer et al., 1993).

CHAPTER V

SUMMARY

The hypoxic phenomenon that occurs in the northern Gulf of Mexico Hypoxic Zone (GoMHZ) on a seasonal basis is a complicated interplay of physics, chemistry, biology and geology making it an ideal conceptual system to study in a multidisciplinary project. Previously I have likened it to a natural laboratory in which to study benthic biogeochemistry and biology because of presumed subtractive effects that low oxygen stresses ostensibly create on benthic function and structure. Unlike a real laboratory the experimenter has little choice on how and when these stressors are manipulated and sometimes things just refuse to die in an orderly pattern. Even with a substantial number of replicate incubations and macrofauna samples (over 100 each) significant patterns of sediment community oxygen consumption (SCOC), nutrient regeneration and macrofauna distribution and diversity were few and far between. In this brief summary I will attempt to answer a number of hypotheses posed during this study, pose new questions generated by my findings and identify gaps in my data that hindered an overall synthesis of function and structure.

Sediments are often overlooked when investigating water column processes that impact marine ecosystem health and the GoMHZ until recently was no different. Sediments were considered to be a significant sink for oxygen and nitrogen, the two most studied elements in coastal eutrophication. Recent evidence has shown that sediments contribute very little to oxygen consumption as rates of oxygen uptake slow

under hypoxic conditions (Lehrter et al., 2011; Rowe, 2001). Studies have also revealed that less than expected amounts of denitrification occur in GoMHZ sediments with much of the nitrogen returned to the overlying water (Lehrter et al., 2011; Lin et al., 2011). This has been related to the decoupling of nitrification-denitrification in the sediments, thus reducing the role that sediments in this region have in removing fixed nitrogen.

The second chapter of this dissertation has shown that sediments are important in GoMHZ nutrient budgets as they recycle between 17-27% for nitrogen, phosphorus and silica delivered to the continental shelf by the Mississippi Atchafalaya River System (MARS) (Fig. 2.7). The nature of these transformations was not the same of nitrogen and phosphorus, with sediments acting as a net source of ammonium, releasing 1 mmol-NH_4^+ m^{-2} d^{-1}, and as a net sink for phosphorus, taking up 0.1 mmol-P m^{-2} d^{-1}. This means the hypoxic regulation of ammonium production and phosphate uptake lead to accentuated P-limitation in the GoMHZ which has been linked to increased N-pollution away from initial inputs (Howarth et al., 2011; Quigg et al., 2011).

Positive sediment feedbacks ostensibly add to ecosystem eutrophication throughout the GoMHZ, but the modeling simulation in Chapter III focused on impacts in Zones C and D. Using data of benthic remineralization and primary production that was assessed simultaneously was a relatively novel approach to answer questions about benthic-pelagic coupling that were first raised 3 decades ago (Rowe et al., 1977; Rowe et al., 1975). More importantly, results from Chapter III highlighted the importance of sub-pycnocline processes that influence hypoxic potential in the western areas of the GoMHZ which prompted a revisal of the Rowe and Chapman (2002) conceptual zones

(Fig. 3.10). Continental shelf physics were shown to have definitive impacts on nutrient distributions and the location of primary production within the water column when a deep pycnocline appeared in July of 2005. This dip in the pycnocline should have not only moved nutrients up into the N-limited surface layer but also moved oxygen toward the bottom, similar to the internal wave described in August of 2004 by DiMarco et al. (2009). As stressed in the discussion of Chapter II, it provides more impetus to determine the effect the pycnocline has on the biogeochemical processes that exist within the pycnocline and those affected by its movement.

Analysis of macrofauna communities were originally predicated on finding summertime decreases in abundance and diversity, because what else would happen to animals unable to leave the "Dead Zone." Despite their impacts on land Hurricanes Katrina and Rita proved to fortuitous since it provided another whole ecosystem stressor with which to compare to hypoxia. Again in our "natural laboratory" an unexpected accident proved to be an important research opportunity to assess damages done through the chronic stressor of a hypoxic summer versus the acute stress of a hurricane. The two disparate ecosystem stresses highlighted the existence of a macrofauna community dominated by polychaete worms that was adapted to the stress of seasonal hypoxia. It also showed how a physical disturbance reorganized a biological community impacting diversity and the ability to withstand environmental stress.

Several hypotheses were proposed, revised and dismissed during this research odyssey; eight remain and are addressed by this dissertation. In Chapter I three hypotheses were addressed: H_{01}: Spatial proximity to riverine and marsh sources of

organic carbon (OC) affects rates of oxygen consumption and nutrient regeneration. H_{02}: Temporal duration of hypoxia impacts sedimentary biogeochemistry causing hysteresis of the system. H_{03}: Biogeochemical rates are dependent on the dissolved oxygen concentration of the overlying water. Hypothesis H_{01} was confirmed by similarities of benthic fluxes in Zones A and C to each other, each in closest proximity to the Mississippi River and Atchafalaya Bay respectively, but this support was not significant. H_{02} was not clearly resolved since some fluxes peaked in Late Hypoxia after the long hypoxic season but again were not statistically significant. H_{03} was only shown to be significantly different for oxygen fluxes which were slower during suboxic conditions. In Chapter III two hypotheses were dealt with: H_{04}: Regeneration of nutrients in sediments fuel sub-pycnocline primary production and enhance water column nitrification. H_{05}: In the western regions of GoMHZ benthic-pelagic coupling acts to prolong and maintain bottom water hypoxia. H_{04} was partially accepted since the data and the results of the model showed evidence of benthic nutrient fluxes supporting sub-pycnocline primary production, but no conclusions as to the enhancement of nitrification in the water column could be made. H_{05} was not definitively proved but strong evidence of benthic fueled eutrophication and the mechanisms behind this were addressed. In Chapter IV three more hypotheses emerged: H_{06}: Macroinfaunal communities are spatially distinct from another based on the distance from MARS input and severity of seasonal hypoxia. H_{07}: Hypoxic stress cause decreased abundance and biomass of macroinfauna. H_{08}: Does benthic biodiversity can rebound equally from severe hypoxia and storm events? H_{06} was not supported as a general fauna appeared to

exist across the GoMHZ. H_{07} had two conclusions, one for each of the macrofauna communities that existed prior and after the hurricane events in 2005. During 2004-2005 a macrofauna community adapted to hypoxic stress persisted throughout the hypoxic season not significantly changing in abundance or biomass. The post hurricane macrofauna community succumbed to long term hypoxia and decreased in abundance and diversity. H_{08} was easily proven as the macrofauna community adapted to low oxygen rebounded easily while the hurricanes altered the macrofauna community to a degree that recovery was still occurring 4 years after the event.

Not all expectations were realized, most notable the blending of function and structure in the analysis of benthic biogeochemistry. This was hampered by the inability to accurately measure the biomass of the benthic community or describe the relative individual contribution of taxa to nutrient fluxes. Such a goal could be achieved with a separate lab based approach coupled with field experiments and the use of ^{7}Be isotopes to measure bioturbation activities. Despite these caveats it may still be possible to accomplish this goal with advanced multivariate techniques and selective handling of macrofauna to determine total community biomass.

Finally, two main management perspectives can be advocated based upon the research within. The first is that riverine inputs are not the only important sources of nitrogen to the GoMHZ system and benthic contributions/subtractions should be incorporated in budgets for the region. Second, when a healthy resident macrofauna community is present, dominated by hypoxia tolerant polychaete species it is NOT A

DEAD ZONE. This is important when considering the impacts that hypoxia might have on demersal fish species that are commercially important.

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APPENDIX A

Tables of Previous Investigations in the northern Gulf of Mexico

Table A1. Sediment Community Oxygen Consumption in the Northern Gulf of Mexico Hypoxic Zone. Values reported in mmol-O_2 m^{-2} d^{-1}. Rates measured under hypoxic conditions are printed in red; rates of anoxic measurements in blue.

	[O_2] (µm)	SCOC (mmol m^{-2} d^{-1})	Depth (m)	Temperature	Salinity	Year	Month	Site	Location	Study	Relative MCH Zone	Method
	—	23	13	19.6	34	1992	April	1a	29° 00.0'; 89° 30.1'	Morse and Rowe 1999	A	Benthic Chamber
	—	24	18	28.1	30.3	!992	April	2a	29° 07.2; 89° 44.4'	Morse and Rowe 2001	A	Benthic Chamber
	168	22.8	20	20	—	1992	April	GC1	—	Rowe et al. 2002	A	Benthic Chamber
	95	6	17	20	—	1992	April	C6A	—	Rowe et al. 2002	B	Benthic Chamber
	126	24.5	20	20	—	1992	April	4	—	Rowe et al. 2002	A	Benthic Chamber
	109	22.6	17	20	—	1992	April	D2	—	Rowe et al. 2002	C	Benthic Chamber
	—	32.8	20	28.1	30.3	1992	April	2a	29° 07.2; 89° 44.4'	Miller-Way et al. 1994	A	BMIC
Mean		**22.2**										
Hypoxic	10	11	18	26.5	—	1991	July	C6A	—	Rowe et al. 2002	B	Benthic Chamber
Hypoxic	6	1.62	20	25.2	—	1991	July	C6B	—	Rowe et al. 2002	B	Benthic Chamber
	83	6.93	21	26.4	—	1991	July	C7	—	Rowe et al. 2002	B	Benthic Chamber
Hypoxic	7	5	17	26.8	—	1991	July	D2	—	Rowe et al. 2002	C	Benthic Chamber
	—	6.72	25	—	—	1990	July	BL1	—	Gardner et al. 1993	B	Benthic Chamber
	—	10.08	53	—	—	1990	July	81	—	Gardner et al. 1993	C	Benthic Chamber
	—	9.36	29	—	—	1990	July	92	—	Gardner et al. 1993	B	Benthic Chamber
	—	5.28	106	—	—	1990	July	112	—	Gardner et al. 1993	B	Benthic Chamber
Mean Oxic		**7.7**										
Mean Hypoxic		**5.9**										
	—	19	13	20	36	1994	August	1b	29° 00.0'; 89° 30.1'	Morse and Rowe 2000	A	Benthic Chamber
	—	56	19	27.2	32.1	1994	August	2b	30° 07.2; 89° 44.4'	Morse and Rowe 2002	A	Benthic Chamber
Hypoxic	—	1.9	12	28.2	28.7	1994	August	3	29° 06.5'; 89° 35.7'	Morse and Rowe 2003	A	Benthic Chamber
	130	40.1	25	28.1	—	1994	August	1	—	Rowe et al. 2002	A	Benthic Chamber
Anoxic	0	1.9	12	28.5	—	1994	August	3	—	Rowe et al. 2002	A	Benthic Chamber
Hypoxic	11	26.4	25	27.2	—	1994	August	4	—	Rowe et al. 2002	A	Benthic Chamber
Hypoxic	14	16.6	30	28.6	—	1994	August	C6B	—	Rowe et al. 2002	B	Benthic Chamber
Mean Oxic		**38.4**										
Mean Suboxic		**11.7**										

Table A2. Nutrient Fluxes from the Northern Gulf of Mexico Hypoxic Zone for the months of April, July and August (the most common dates of measurements). Values are mmol m-2 d-1. Negative values indicate flux into sediments and positive values indicate flux out of sediments. Rates presented in red were made under hypoxic conditions and rates in blue were made during anoxia.

	NH_4^+	NO_3^-	NO_2^-	$NO_3^- + NO_2^-$	$PO4^{3-}$	DIC	Depth (m)	Temperature	Salinity	Year	Month	Site	Location	Study	Relative MCH Zone
	3.7	—	—	—	0.26	35.0	13	19.6	34	1992	April	1a	29° 00.0'; 89° 30.1'	Morse and Rowe 1999	A
	3.0	—	—	—	0.024	17.0	18	28.1	30.3	!992	April	2a	29° 07.2; 89° 44.4'	Morse and Rowe 2001	A
	3.7	—	—	—	—	36	20	20	—	1992	April	GC1	—	Rowe et al. 2002	A
	1.3	—	—	-0.4	—	14	17	20	—	1992	April	C6A	—	Rowe et al. 2002	B
	3.6	—	—	-0.6	—	19	20	20	—	1992	April	4	—	Rowe et al. 2002	A
	1.4	—	—	-0.1	—	36	17	20	—	1992	April	D2	—	Rowe et al. 2002	C
	2.4	-0.21	0.082		-0.2		20	28.1	30.3	1992	April	2a	29° 07.2; 89° 44.4'	Miller-Way et al. 1994	A
Mean	**2.7**	**-0.21**	**0.082**	**-0.37**	**0.03**	**26.2**									
	2.1	—	—	-2	—	—	18	26.5	—	1991	July	C6A	—	Rowe et al. 2002	B
	2	—	—	-0.16	—	—	20	25.2	—	1991	July	C6B	—	Rowe et al. 2002	B
	4	—	—	-1.8	—	—	21	26.4	—	1991	July	C7	—	Rowe et al. 2002	B
	3.7	—	—	-1.2	—	—	17	26.8	—	1991	July	D2	—	Rowe et al. 2002	C
	1.29	0.516	-0.24	—	—	—	25	—	—	1990	July	BL1	—	Gardner et al. 1993	B
	0.369	0.204	-0.005	—	—	—	53	—	—	1990	July	81	—	Gardner et al. 1993	C
	0.794	-0.61	-0.034	—	—	—	29	—	—	1990	July	92	—	Gardner et al. 1993	B
	0.295	-0.259	0.05	—	—	—	106	—	—	1990	July	112	—	Gardner et al. 1993	B
Mean Oxic	**3.85**	**-0.037**	**-0.057**	**-1.5**											
Mean Hypoxic	**2.05**			**-1.08**											
	3.9	—	—	—	0.26	53.0	13	20	36	1994	August	1b	29° 00.0'; 89° 30.1'	Morse and Rowe 2000	A
	4.2	—	—	—	-0.41	56.0	19	27.2	32.1	1994	August	2b	30° 07.2; 89° 44.4'	Morse and Rowe 2002	A
	2.6	—	—	—	1.20	37.0	12	28.2	28.7	1994	August	3	29° 06.5'; 89° 35.7'	Morse and Rowe 2003	A
	—	—	—	-0.4	—	53	25	28.1	—	1994	August	1	—	Rowe et al. 2002	A
	2.2	—	—	-1.5	—	38	12	28.5	—	1994	August	3	—	Rowe et al. 2002	A
	4.4	—	—	-0.8	—	55	25	27.2	—	1994	August	4	—	Rowe et al. 2002	A
	0.8	—	—	-0.2	—	24	30	28.6	—	1994	August	C6B	—	Rowe et al. 2002	B
Mean Oxic	**4.1**			**-0.4**	**-0.08**										
Mean Suboxic	**2.5**			**-0.83**	**1.20**										

Table A3. Abundance, diversity and biomass of macrofauna communities studied within the Northern Gulf of Mexico Hypoxic Zone. Data shown in red are represent hypoxia at the time of sampling; data in blue are sampled from anoxic bottom water. Sieve mesh size is micrometers.

	Abundance (Ind. m^{-2})	Taxa Groups	Biomass (g C m^{-2})	Biomass (g AFDW m^{-2})	Depth	Year	Month	Site	Location	Study	MCH Zone	Sieve Size
	—	—	0.23	—	20	1992	April	GC1	—	Rowe et al. 2002	A	250
	—	—	0.01	—	17	1992	April	C6A	—	Rowe et al. 2002	B	250
	119	—	1.24	—	20	1992	April	4	—	Rowe et al. 2002	A	250
	—	—	0.49	—	17	1992	April	D2 WD3	—	Rowe et al. 2002	C	250
	8637	22	—	2.59	20	1990	April	2E	29° 07.3'; 89° 41.7'	Rabalais et al. 2001	A	500
	18437	51	—	2.92	20	1990	April	ST53 WD3	28° 51.4'; 90° 27.7	Rabalais et al. 2001	B	500
	2873	16	—	0.93	20	1991	Feb-May	2E	29° 07.3'; 89° 41.7'	Rabalais et al. 2001	A	500
	6486	22	—	1.55	20	1991	Feb-May	ST53	28° 51.4'; 90° 27.7	Rabalais et al. 2001	B	500
	2578	—	—	—	20	2004	April	C6B	28° 52.1'; 90° 28.0'	Baustian and Rabalais 2009	B	500
Mean	**27.75**	**27.75**	**0.49**	**2.00**								
	5911	—	0.68	—	18	1991	July	C6A	—	Rowe et al. 2002	B	250
	—	—	0.16	—	20	1991	July	C6B	28° 52.1'; 90° 28.0'	Rowe et al. 2002	B	250
	—	—	0.56	—	21	1991	July	C7	—	Rowe et al. 2002	B	250
	—	—	0.11	—	17	1991	July	D2	—	Rowe et al. 2002	C	250
	—	—	0.36	—	40	1990	July	100	—	Gardner et al. 1993	A	250
	—	—	1.77	—	28	1990	July	111	—	Gardner et al. 1993	B	250
	—	—	0.38	—	39	1990	July	113	—	Gardner et al. 1993	C	250
	1970	—	—	—	20	2004	July	C6B	28° 52.1'; 90° 28.0'	Baustian and Rabalais 2009	B	500
Mean Oxic	**1970**	—	**0.56**	—								
Mean Suboxic	**5911**	—	**0.68**	—								
	—	—	0.19	—	25	1994	August	1	—	Rowe et al. 2002	A	250
	—	—	0.20	—	20	1994	August	2	—	Rowe et al. 2002	A	250
	—	—	0.11	—	12	1994	August	3	—	Rowe et al. 2002	A	250
	—	—	0.12	—	25	1994	August	4	—	Rowe et al. 2002	A	250
	—	—	0.04	—	30	1994	August	C6B WD3	—	Rowe et al. 2002	B	250
	1431	12	—	0.45	20	1990	August	2E	29° 07.3'; 89° 41.7'	Rabalais et al. 2001	A	500
	730	4	—	0.23	20	1990	August	ST53	28° 51.4'; 90° 27.7	Rabalais et al. 2001	B	500
	1346	8	—	0.46	20	1990	Sept.	ST53	28° 51.4'; 90° 27.8	Rabalais et al. 2002	B	500
	800	—	—	—	20	2004	August	C6B	28° 52.1'; 90° 28.0'	Baustian and Rabalais 2009	B	500
Mean Oxic	—	—	**0.20**	—								
Mean Suboxic	1076.75	8	**0.09**	**0.38**								

APPENDIX B

Macrofauna Species List

Table B1. List of macrofauna species identified with associated taxonomic information.

Phylum	Class	Order	Family	Species
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae	Ampelisca milleri
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae	Ampelisca vadorum
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae	Ampelisca brevisimulata
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae	Ampelisca abdita
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae	Ampelisca sp
Arthropoda	Malacostraca	Amphipoda	Oedicerotidae	Monoculodes gibbosa
Arthropoda	Malacostraca	Amphipoda	Isaeidae	Photis macinerneyi
Arthropoda	Malacostraca	Amphipoda	Ischyroceridae	Ericthonius sp
Arthropoda	Malacostraca	Amphipoda		Listeriella sp
Arthropoda	Malacostraca	Amphipoda		Listeriella bernardi
Arthropoda	Malacostraca	Amphipoda	Liljeborgiidae	Liljeborgia sp
Arthropoda	Malacostraca	Amphipoda	Pariambidae	Paracaprella pusilla
Mollusca	Bivalvia	Veneroida	Semelidae	*Abra aequalis*
Mollusca	Bivalvia	Arcoida	Arcidae	Anadara spp.
Mollusca	Bivalvia	Veneroida	Tellinidae	*Angulus texanus*
Mollusca	Bivalvia	Arcoida	Noetiidae	*Arcopsis adamsi*
Mollusca	Bivalvia	Carditoida	Astartidae	*Astarte concha*
Mollusca	Bivalvia	Carditoida	Condylocartidae	*Carditopsis smithii*
Mollusca	Bivalvia	Myoida	Corbulidae	*Corbula dietziana*
Mollusca	Bivalvia	Myoida	Corbulidae	*Corbula contracta*

Phylum	Class	Order	Family	Species
Mollusca	Bivalvia	Myoida	Corbulidae	Corbula spp.
Mollusca	Bivalvia	Nuculida	Nuculidae	*Ennucula aegeensis*
Mollusca	Bivalvia	Veneroida	Semelidae	*Ervilia concentrica*
Mollusca	Bivalvia	Arcoida	Arcidae	FAMILY Arcidae
Mollusca	Bivalvia	Mytiloida	Mytilidae	FAMILY Mytilidae
Mollusca	Bivalvia	Veneroida	Veneridae	*Gemma gemma*
Mollusca	Bivalvia	Veneroida	Veneridae	*Gouldia cerina*
Mollusca	Bivalvia	Arcoida	Arcidae	*Lunarca ovalis*
Mollusca	Bivalvia	Veneroida	Tellinidae	*Macoma pulleyi*
Mollusca	Bivalvia	Veneroida	Tellinidae	*Macoma tageliformis*
Mollusca	Bivalvia	Veneroida	Tellinidae	Macoma spp.
Mollusca	Bivalvia	Veneroida	Mactridae	*Mulinia lateralis*
Mollusca	Bivalvia	Pectinoida	Pectinidae	*Nodipecten fragosus*
Mollusca	Bivalvia	Nuculida	Nuculidae	*Nucula proxima*
Mollusca	Bivalvia	Nuculanoida	Nuculanidae	*Nuculana acuta*
Mollusca	Bivalvia	Nuculanoida	Nuculanidae	*Nuculana concentrica*
Mollusca	Bivalvia	Nuculanoida	Nuculanidae	Nuculana spp.
Mollusca	Bivalvia	Lucinoida	Lucinidae	*Parvilucina crenella*
Mollusca	Bivalvia	Veneroida	Ungulinidae	*Phlyctiderma semiaspera*
Mollusca	Bivalvia	Veneroida	Ungulinidae	*Phlyctiderma soror*
Mollusca	Bivalvia	Veneroida	Veneridae	*Pitar pilula*
Arthropoda	Malacostraca	Cumacea	Nannastacidae	*Campylaspis sp. C*

Phylum	Class	Order	Family	Species
Arthropoda	Malacostraca	Cumacea	Nannastacidae	*Cumella sp. B*
Arthropoda	Malacostraca	Cumacea	Nannastacidae	*Cumella sp. G*
Arthropoda	Malacostraca	Cumacea	Nannastacidae	Cumella spp.
Arthropoda	Malacostraca	Cumacea	Diastylidae	*Diastylis sp. A*
Arthropoda	Malacostraca	Cumacea	Diastylidae	*Diastylis sp. B*
Arthropoda	Malacostraca	Cumacea	Diastylidae	*Diastylis sp. C*
Arthropoda	Malacostraca	Cumacea	Leuconidae	*Eudorella monodon*
Arthropoda	Malacostraca	Cumacea	Leuconidae	*Eudorella sp. A*
Arthropoda	Malacostraca	Cumacea	Leuconidae	*Leucon americanus*
Arthropoda	Malacostraca	Cumacea	Diastylidae	*Oxyurostylis lecroyae*
Arthropoda	Malacostraca	Cumacea	Diastylidae	*Oxyurostylis smithi*
Mollusca	Gastropoda	Littorinimorpha	Assimineidae	*Assiminea succinea*
Mollusca	Gastropoda		Pyramidellidae	*Careliopsis styliformis*
Mollusca	Gastropoda	Littorinimorpha	Personidae	*Distorsio clathrata*
Mollusca	Gastropoda	Caenogastropoda	Epitoniidae	Epitonium spp.
Mollusca	Gastropoda	Caenogastropoda	Eulimidae	Eulima spp.
Mollusca	Gastropoda		Pyramidellidae	*Eulimastoma canaliculatum*
Mollusca	Gastropoda		Pyramidellidae	Eulimastoma spp.
Mollusca	Gastropoda	Neogastropoda	Mitromorphidae	*Mitromorpha haycocki*
Mollusca	Gastropoda	Caenogastropoda	Eulimidae	*Microeulima hemphillii*
Mollusca	Gastropoda	Neogastropoda	Nassariidae	*Nassarius acutus*
Mollusca	Gastropoda	Neogastropoda	Nassariidae	*Nassarius albus*

Phylum	Class	Order	Family	Species
Mollusca	Gastropoda	Neogastropoda	Nassariidae	Nassarius spp.
Mollusca	Gastropoda	Littorinimorpha	Naticidae	*Tectonatica pusilla*
Mollusca	Gastropoda	Neogastropoda	Olivellidae	*Olivella lactea*
Mollusca	Gastropoda	Littorinimorpha	Naticidae	*Polinices spp.*
Mollusca	Gastropoda	Neogastropoda	Columbellidae	*Suturoglypta iontha*
Mollusca	Gastropoda	Neogastropoda	Terebridae	*Terebra dislocata*
Mollusca	Gastropoda	Neogastropoda	Terebridae	*Terebra protexta*
Mollusca	Gastropoda	Neogastropoda	Terebridae	*Terebra taurina*
Mollusca	Gastropoda	Neogastropoda	Terebridae	Terebra spp.
Mollusca	Gastropoda	Caenogastropoda	Turritellidae	*Turritella exoleta*
Mollusca	Gastropoda	Littorinimorpha	Tornidae	*Vitrinella helicoidea*
Mollusca	Gastropoda	Cephalaspidea	Rhizoridae	*Volvulella texasiana*
Mollusca	Gastropoda	Cephalaspidea	Rhizoridae	Volvulella spp.
Mollusca	Gastropoda	Littorinimorpha	Rissoidae	Zebina spp.
Annelida	Polychaeta	Terebellida	Ampharetidae	*Ampharete sp.A*
Annelida	Polychaeta	Terebellida	Ampharetidae	*Melinna sp.1*
Annelida	Polychaeta		Aphroditidae	Aphroditid *sp.1*
Annelida	Polychaeta		Aphroditidae	Aphroditid *sp.2*
Annelida	Polychaeta		Capitellidae	*Decamastus sp.1*
Annelida	Polychaeta		Capitellidae	Capitellidae Genus 1
Annelida	Polychaeta		Capitellidae	*Heteromastus sp.1*
Annelida	Polychaeta		Capitellidae	*Mediomastus californiensis*

Phylum	Class	Order	Family	Species
Annelida	Polychaeta		Capitellidae	*Notomastus daueri*
Annelida	Polychaeta		Capitellidae	Capitellid sp.1
Annelida	Polychaeta	Spionida	Chaetopteridae	*Spiochaetopterus costarum*
Annelida	Polychaeta	Terebellida	Cirratulidae	*Chaetozone sp.1*
Annelida	Polychaeta	Terebellida	Cirratulidae	*Chaetozone sp.2*
Annelida	Polychaeta	Terebellida	Cirratulidae	*Chaetozone sp.D*
Annelida	Polychaeta	Terebellida	Cirratulidae	*Cirriformia sp.1*
Annelida	Polychaeta	Terebellida	Cirratulidae	Cirratulid *sp.1*
Annelida	Polychaeta	Terebellida	Cirratulidae	Cirratulid *sp.2*
Annelida	Polychaeta	Terebellida	Cirratulidae	Cirratulid *sp.3*
Annelida	Polychaeta	Terebellida	Cirratulidae	Cirratulid *sp.4*
Annelida	Polychaeta	Terebellida	Cirratulidae	Cirratulid *sp.5*
Annelida	Polychaeta	Terebellida	Cirratulidae	*Tharyx annulosus*
Annelida	Polychaeta		Cossuridae	*Cossura soyeri*
Annelida	Polychaeta		Cossuridae	Coss*urid sp.1*
Annelida	Polychaeta		Dorvilleidae	*Schistomeringos rudolphii*
Annelida	Polychaeta	Phyllodocida	Eulepethidae	*Grubeulepis mexicana*
Annelida	Polychaeta		FAMILY X	FAMILY X *sp.1*
Annelida	Polychaeta	Terebellida	Flabelligeridae	*Brada villosa*
Annelida	Polychaeta	Phyllodocida	Glyceridae	*Glycera americana*
Annelida	Polychaeta	Phyllodocida	Glyceridae	*Glycera sp.C*

Phylum	Class	Order	Family	Species
Annelida	Polychaeta	Phyllodocida	Glyceridae	Glycerid *sp.1*
Annelida	Polychaeta	Phyllodocida	Goniadidae	*Glycinde solitaria*
Annelida	Polychaeta	Phyllodocida	Goniadidae	*Goniada teres*
Annelida	Polychaeta	Phyllodocida	Goniadidae	Goniadid *sp.1*
Annelida	Polychaeta	Phyllodocida	Goniadidae	Goniadid *sp.2*
Annelida	Polychaeta	Phyllodocida	Goniadidae	Goniadid *sp.3*
Annelida	Polychaeta	Phyllodocida	Hesionidae	*Gyptis brevipalpa*
Annelida	Polychaeta	Phyllodocida	Hesionidae	Hesionid *sp.1*
Annelida	Polychaeta	Eunicida	Lumbrineridae	*Lumbrineris cruzensis*
Annelida	Polychaeta	Eunicida	Lumbrineridae	*Lumbrineris ernesti*
Annelida	Polychaeta	Eunicida	Lumbrineridae	*Lumbrineris sp.B*
Annelida	Polychaeta	Eunicida	Lumbrineridae	*Lumbrineris verrilli*
Annelida	Polychaeta	Eunicida	Lumbrineridae	*Ninoe sp.B*
Annelida	Polychaeta	Eunicida	Lumbrineridae	Lumbrinerid sp.1
Annelida	Polychaeta	Eunicida	Lumbrineridae	Lumbrinerid sp.2
Annelida	Polychaeta	Spionida	Magelonidae	*Magelona sp.H*
Annelida	Polychaeta		Maldanidae	*Sabaco elongatus*
Annelida	Polychaeta		Maldanidae	*Clymenella torquata*
Annelida	Polychaeta		Maldanidae	Maldanid sp.1
Annelida	Polychaeta		Maldanidae	Maldanid sp.2
Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Aglaophamus sp.1*
Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Aglaophamus sp.2*

Phylum	Class	Order	Family	Species
Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Aglaophamus verrilli*
Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Nephtys incisa*
Annelida	Polychaeta	Phyllodocida	Nephtyidae	Nephtyid sp.1
Annelida	Polychaeta	Phyllodocida	Nereidae	Alitta succinea
Annelida	Polychaeta	Phyllodocida	Nereidae	*Nereis sp.1*
Annelida	Polychaeta	Phyllodocida	Nereidae	Nereid sp.1
Annelida	Polychaeta	Phyllodocida	Nereidae	Nereid sp.2
Annelida	Polychaeta	Phyllodocida	Nereidae	Nereid sp.3
Annelida	Polychaeta	Phyllodocida	Nereidae	*Neresis micromma*
Annelida	Polychaeta	Eunicida	Onuphidae	*Diopatra cuprea*
Annelida	Polychaeta	Eunicida	Onuphidae	*Diopatra sp.1*
Annelida	Polychaeta	Eunicida	Onuphidae	*Kinbergonuphis sp.1*
Annelida	Polychaeta	Eunicida	Onuphidae	*Mooreonuphis sp.1*
Annelida	Polychaeta	Eunicida	Onuphidae	Onuphid sp.1
Annelida	Polychaeta		Opheliidae	*Ophelina sp.1*
Annelida	Polychaeta		Opheliidae	*Armandia maculata*
Annelida	Polychaeta		Opheliidae	*Ophelina sp.2*
Annelida	Polychaeta	Sabellida	Oweniidae	*Myriowenia sp.A*
Annelida	Polychaeta	Sabellida	Oweniidae	*Owenia sp.A*
Annelida	Polychaeta		Paraonidae	*Aricidea (Acmira) sp.1*
Annelida	Polychaeta		Paraonidae	*Aricidea taylori*
Annelida	Polychaeta		Paraonidae	*Cirrophorus americanus*

Phylum	Class	Order	Family	Species
Annelida	Polychaeta		Paraonidae	*Cirrophorus forticirratus*
Annelida	Polychaeta		Paraonidae	*Levinsenia gracilis*
Annelida	Polychaeta		Paraonidae	*Levinsenia sp.1*
Annelida	Polychaeta		Paraonidae	Paraonid sp.1
Annelida	Polychaeta		Paraonidae	Paraonid sp.2
Annelida	Polychaeta		Paraonidae	Paraonid sp.3
Annelida	Polychaeta		Paraonidae	Paraonid sp.4
Annelida	Polychaeta		Pectinariidae	Pectinariid sp.1
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	*Anaitides sp.1*
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	*Genetyllis sp.1*
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	*Phyllodoce arenae*
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	Phyllodocid sp.1
Annelida	Polychaeta	Phyllodocida	Pilargidae	*Ancistrosyllis papillosa*
Annelida	Polychaeta	Phyllodocida	Pilargidae	*Sigambra tentaculata*
Annelida	Polychaeta	Spionida	Poecilochaetidae	*Poecilochaetus johnsoni*
Annelida	Polychaeta	Phyllodocida	Polynoidae	*Malmgreniella sp.B*
Annelida	Polychaeta	Phyllodocida	Polynoidae	Polynoid sp.1
Annelida	Polychaeta	Phyllodocida	Polynoidae	Polynoid sp.2
Annelida	Polychaeta	Sabellida	Sabellidae	*Megalomma bioculatum*
Annelida	Polychaeta	Sabellida	Sabellidae	Sabellid sp.1
Annelida	Polychaeta	Phyllodocida	Sigalionidae	*Sthenelais sp.1*
Annelida	Polychaeta	Spionida	Spionidae	*Malacoceros sp.1*

Phylum	Class	Order	Family	Species
Annelida	Polychaeta	Spionida	Spionidae	*Paraprionospio pinnata*
Annelida	Polychaeta	Spionida	Spionidae	*Polydora aggregata*
Annelida	Polychaeta	Spionida	Spionidae	*Polydora ligni*
Annelida	Polychaeta	Spionida	Spionidae	*Prionospio cristata*
Annelida	Polychaeta	Spionida	Spionidae	*Prionospio sp.1*
Annelida	Polychaeta	Spionida	Spionidae	*Prionospio sp.2*
Annelida	Polychaeta	Spionida	Spionidae	Spionid *sp.1*
Annelida	Polychaeta	Spionida	Spionidae	*Spiophanes missionensis*
Annelida	Polychaeta	Terebellida	Sternaspidae	*Sternaspis scutata*
Annelida	Polychaeta	Terebellida	Terebellidae	*Pista sp.1*

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