POLYCHAETE ANNELID DYNAMICS IN THE NORTHERN GULF OF MEXICO, FROM SHALLOW WATER TO THE DEEP-SEA

A Dissertation

by

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ABSTRACT

Polychaete annelids dominated the macrobenthos in sediments located 5 to 9 km from the Deep Water Horizon (DWH) Oil Spill site five months after the event. Numbers of species, abundance, and biodiversity indices in the polychaete taxa were significantly lower than pre-spill values from similar depths in the eastern Gulf of Mexico (GoM). Both non-selective and selective deposit feeders were the most frequent feeding guilds, but their abundances were significantly lower. An increase in the number of carnivorous Sigalionidae may be a response to an accumulation of petroleum hydrocarbons on the sediment. The concentration of oil in the sediments was low and the source of the oil remains equivocal. Multivariate analyses illustrated the differences between communities near the DWH and those from prior studies in similar deep GoM habitats. In summary, Deep Water Horizon oil spill appears to have had a measurable impact on the polychaetes.

A time series of benthic samples from 2004 to 2012 has been utilized to assess the influence of hypoxia on the mean sizes (wet weight) of polychaeteannelid worms.While the mean body size over the entire study was 3.99±4.66 mg wet weight per individual, the mean ranged from 2.97±2.87 mg during consistently hypoxic conditions (< 2 mg/L)to a high of 7.13±7.60 mg ($p < 0.01$)under oxic conditions (> 2 mg/L). The decline in size was due to the elimination of large species under hypoxic conditions, not a reduction in size within species. At 'severe' levels of hypoxia (< 1 mg/L), the smallest species also declined in abundance, whereas the ubiquitous ‘medium sized’ *Paraprionospio pinnata* flourished.

The infaunal benthos of the upper continental slope, a transition zone between the dynamic continental shelf and the deep sea, has been sampled in 1983-85 and then again in 2000-02 at nine locations. The polychaete annelid worms, the dominant taxon within the samples, exhibited remarkable stability in abundance, diversity, depth-related zonation,and species composition (> 35% similarity in species) over that period. At 7 of the 9 locations, single appearances of several dominant species resulted in the 1983-85 samples being more abundant but less diverse than the 2000-02 survey.

DEDICATION

To my parents

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CHAPTER I

INTRODUCTION

1.1 General overview

The sea floor of the open ocean, especially in the deep sea, continues to remain obscure, even though it is our world's largest continuous habitat. While the overall biomass and densities of major biotic groups (the benthos) are fairly well-known (Rex and Etter, 2010), rates of biotic processes and responses to environmental changes, including stressors, are unknown and continue to defy prediction. The set of four principal chapters (manuscripts) in this dissertation are using the species composition of the dominant macro-infaunal group, the polychaete annelid worms, to explore how sea floor communities might be responding to oil spills (Ch 2), climate change (or lack thereof) (Ch 3), the stress of low oxygen that results from eutrophication on continental shelves (Diaz and Rosenberg, 2008) (Ch 4). Polychaete (Phylum Annelida) worms are generally the most dominant and representative taxa in marine benthic communities. They contribute about half of the total infauna abundance from shallow water to deep sea, (Sanders et al., 1965; Nephin et al., 2014). Organic enrichment, hypoxia, hurricanes, oil spills, bottom trawling, heavy metals, climate change and other anthropogenic or natural disturbances and stress can have deleterious effects on marine benthic communities (Yeo and Risk, 1979; Rabalais et al., 2001a; Dernie et al., 2003; Aronson et al., 2007; Ryu et al., 2011; Venturini et al., 2011; Lee and Lin, 2013).

A classic conceptual model indicating the successional stagesof soft bottom benthic fauna along disturbance gradientswas proposed by Pearson and Rosenberg (1978). Their model describes the change in abundance, species composition and biomass along organic enrichment gradients. Opportunistic species, generally polychaetes, dominate the first stage of recovery, resulting in large numbers of individuals and low numbers of species. The most widely recognized opportunistic polychaetes are the *Capitella capitata* complex (Tsutsumi, 1987; Samuelson, 2001). This model has been applied widely (Rhoads and Germano, 1986) but challenges to it exist (Brooks et al., 2004; Keeley et al., 2013).

Compared with shallow water, studies on deep-sea polychaeteshave focused mainly on bathymetric distribution patterns, species zonation, responses to seasonality and long-term change. High diversity in deep-sea benthos compared to shallow water was tentatively explained by niche heterogeneity, but none of the various explanations of diversity gradientsis yet wholely satisfactory (Gage, 2004). Parabolic distribution patterns of species diversity (the ‘mid-depth maximum or MDM) with depth observed in the deep Atlantic and Gulf of Mexico (Rex and Etter, 2010) and species zonation are known to be correlated with depth (Narayanaswamy et al., 2005; Carvalho et al., 2013) but explanations for the patterns vary (Carney, 2005; Wei et al., 2010).

The accumulation of deep-sea data and potential global climate change have triggered research of how deep-sea benthos respond to long-term change. A long-term change in benthic community oxygen consumption and abundance in the deep Pacific has been attributed to seasonality of food supply and decadal declines in productivity (Lauerman et al., 1996; Ruhl, 2007).

A parallel long-term set of observations was located in the Porcupine Abyssal Plain (PAP), NE Atlantic. Soto et al., (2010) used a 9-year study data to illustrate the variability in abyssal polychaete community and food supply was once again suggested as the main factor that regulated the change in deposit feeding polychaetes. These companion studies led to a search for similar long-term alternations in deep habitats using the polychaetes as indicators of what could be happening at the species level.

1.2 Polychaete studies on the northern Gulf of Mexico (<200m)

Polychaete assemblages in the shallow water of the Gulf of Mexico, as a dominant component of the macroinfaunal community, have been investigated extensively. Early studies on shallow water polychaetes in Gulf of Mexico focused on taxonomy, species distributions and life history. To date the most comprehensive key to polychaetes of Gulf of Mexico continental shelf (depth ranged from 10-200m) was prepared by Uebelacker and Johnson (1984), with fourteen authors. More than 500 polychaetes representing 288 genera were recorded and described, making this shelf one of the best known in the world.

This seven-volume set of books was compiled from five studies conducted from 1975 to 1981: the Mississippi-Alabama-Florida (MAFLA) Outer Continental Shelf study; South Texas Outer Continental Shelf Study (STOCS); The Ecological Investigations of Petroleum Production Platforms in the Central Gulf (CTGLF); The IXTOC Oil Spill Assessment study off southern Texas; and the Southwest Florida Shelf Ecosystems study(SOFLA). A morphological description and the distribution of each species are presented.

An updated taxonomic summary and checklist of polychaetes is also a significant component of the monograph on the biota of the Gulf of Mexico edited by Felder and Camp (2009), expanding the list to 800 species, including some from the deepsea. Characteristic habitats, depth distribution and geographic range are presented briefly in the checklist.

The hypoxic zone of the northern Gulf of Mexico (Turner et al., 2008) has also received extensive investigations that included polychaetes (Harper Jr. et al., 1981; Gaston, 1985; Rabalais et al., 2001a; Baustian and Rabalais, 2009). Rabalais et al., (2001b) for example summarized the progressive change in fauna (from nekton to benthic) as a response to decreasing oxygen concentration. For polychaetes, when oxygen concentration decreased from 1.5 mg/L to 1 mg/L, upward emergence from the sediment was observed (e.g. *Lumbrineris* sp.). When oxygen depletion was more severe (1-0.5mg/L), moribund polychaetes were found lying motionless on the bottom. Survival of some polychaetes during several hypoxic events(such as *Ampharete*sp. A) and dominance of opportunistic polychaetes (especially *Paraprionospio pinnata*) after hypoxia have also been documented (Rabalais et al., 2001a; Baustian and Rabalais, 2009; Levin et al., 2009).

While the causes of the hypoxia off Louisiana remain somewhat controversial, many investigators are convinced that ecosystem services (principally commercial and recreational fishing) are impaired by low oxygen stress. However, it is not a ‘dead sea’, as is often quoted in the popular media. This inspired a consideration of the special biological characteristics of the species that are capable of surviving and even flourishing under the persistent stress of low oxygen. So, Chapter 3 is devoted to the hypothesis that only small organisms, and in particular the polychaetes, are selected for by low oxygen.

1.3 The deep benthos of the northern Gulf of Mexico (>200m)

Systematic investigations across the continental slope began with the fisheries explorations of the R/V OREGON II. In the 1960’s, Willis Pequegnat and his students conducted extensive sampling over the entire GoM, but only minor attention was given to the smaller infauna such as the polychaetes (Pequegnat et al., 1990).

As interest in offshore fossil fuel exploration intensified in the GoM, deep benthic investigations evolved into systematic sampling supported by the Bureau of Land

Management (BLM), or the Minerals Management Service (MMS) from the federal government. Reports of all such studies (now the Bureau of Ocean Energy Management (BOEM) are available on-line at a BOEM website. The wealth of knowledge now available on the deep northern Gulf of Mexico continental margin is a product of the US Department of the Interior’s persistent interest in protecting potentially fragile habitats and rare communities, even though the ecosystem services at great depths may be limited.

Two extensive investigations: the Northern Gulf of Mexico Continental Slope – NGoMCS in 1980's and Deep Gulf of Mexico Benthos-DGoMB study from 2000-2002. (Rowe and Kennicutt, 2008), or publications (including theses and dissertations) associated with them, have provided extensive species lists from all the numerous locations, including the polychaetes.

The two studies also visited some of the same locations, thus providing an opportunity to consider how the benthos might have changed over this time period; this has lead to Chapter 4 on how the polychaete species composition and community parameters vary, or not, over a ca. 20 year period. This chapter relies heavily on the work of Dr. Guinn Fain Hubbard, now deceased. It includes his species lists in his PhD dissertation (Hubbard, 1995). Additionally, he mentored Dr. Yuning Wang, whose dissertation investigated the polychaetes in the latter 2000 to 2003 (DGOMB) study. Together, Hubbard and Wang created a voucher collection of the two extensive collections of polychaetes, but they never published a comparison of the material. How communities vary over time, in light of climate change and anthropogenic disturbances, has not been documented in the GoM. Thus, these two databases have been used to investigate possible variations in species composition and community parameters over a two-decade interval using their extensive polychaete species data and the voucher collections maintained at TAMUG.

1.4 Thesis outline

Previous works provided an incredibly valuable background database to further summarize and generalize on the detailed dynamics of polychaete assemblages under conditions whose effects are poorly documented. The second chapter,"Polychaete Annelid (segmented worms) Abundance and Species Composition in the Proximity (6 to 9 km) of the Deep Water Horizon (DWH) Oil Spill in the Deep Gulf of Mexico" was motivated by the Deep Water Horizon oil spill in 2010 at about 1500m depth. We assessed the influence of this oil spill by comparing the post oil spill polychaete data (five months after the oil spill) to the pre oil spill data from previous studies. This is the first species-level investigation of the spill effectsat the species level of which we are aware.

The third chapter,"Polychaete Annelid Biomass Size Spectra: The Effects of Hypoxia Stress" focused on the mean sizes of species of polychaetes in the northern Gulf of

Mexico hypoxic zone. In dealing with the relationship between low oxygen and body size, the study utilized a normalized biomass size spectra (NBSS) at geographically separated locations along the 10 to 20 meter isobaths over an 8 year time period (2004-2012), exploring the idea that small organisms can survive hypoxia substantially better than larger ones.

The forth chapter"Decadal-scale Variations in the Polychaete Annelid Populations on the Upper Continental Slope of the Northern Gulf of Mexico" considered the overlap or recurrence in species populations of the upper continental slope Gulf of Mexico over a 2 decade long period.

CHAPTER II

POLYCHAETE ANNELID (SEGMENTED WORMS) ABUNDANCE AND SPECIES COMPOSITION IN THE PROXIMITY (6 TO 9 KM) OF THE DEEP WATER HORIZON OIL SPILL IN THE DEEP GULF OF MEXICO

2.1 Introduction

The deepwater horizon (DWH) oil spill began on April 20, 2010, in the Gulf of Mexico at ~ 1500m depth (Fig. 2.1.). Effects on some groups, such as vertebrates (Antonio et al., 2011; Whitehead et al., 2011), benthic microbial eukaryotes (Bik et al., 2012), and benthic macrofauna and meiofauna (Montagna et al., 2013) have been reported, but the overall initial and long-term influences of this unprecedented alteration of the deep-water ecosystem are emerging more slowly. The influence of oil on marine animals is known to vary according to the amount, concentration, duration of exposure and location (Gin et al., 2001; Ingole et al., 2006).

Generally, benthic animals can be affected by the toxic effects of PAHs (Polycyclic aromatic hydrocarbons) and organic enrichment (Mohammad, 1974; Gomez Gesteira and Dauvin, 2005). Oil spills, fossil fuel combustion and terrigenous combustion of biomass introduce PAHs into the marine environment. The hydrophobic nature of PAHs makes them prone to deposition in marine sediment where they can be concentrated in marine invertebrates, especially deposit-feeders (Meador et al., 1995; Giessing et al., 2003; Soliman and Wade, 2008). The meager metabolism of PAHs and bioaccumulation in invertebrates can affect entire foodwebs (Somero, 1992). Organic enrichment often leads to proliferation of opportunistic species (Conlan et al., 2004), but different taxonomic groups can have a variety of positive and negative responses to oil. The numerically dominant polychaete annelids (segmented worms) appear to be among the most responsive among all the sea floor taxa and therefore have been adopted as pollution indicators (Gomez Gesteira and Dauvin, 2000; Dean, 2008). If oil were deposited on the sea floor around the DWH event site (White et al., 2012), then this contamination might be reflected in an alteration of functional feeding types, as well as species composition.

Montagna et al., (2013) were able to define a benthic footprint around the Deep Water Horizon blowout using the ratio of nematode worms to harpacticoid copepod crustaceans in multicores. Changes in species composition were not documented.

Benthic community distributions in the deep Gulf of Mexico are fairly well-known. For example, the biomass, abundance, species composition, and biodiversity can be predicted as a function of location and depth (Rowe et al., 1974; Pequegnat et al, 1990; Wang, 2004; Baguley et al., 2006a and b; Baguley et al., 2008; Sharma et al., 2011; Wei et al., 2010; 2012a and b; Carvalho et al., 2013). We thus hypothesized that the sediment infaunal species composition, abundance and biodiversity would be useful indicators of the impact of and eventual recovery from the spill by comparing the ‘new’ post-spill fauna with the extensive historical database. Thus, the aims of the current paper are to 1) present the species composition, feeding type, and community structure of deep-sea polychaete species in close proximity (5 to 9 km) to the Deep Water Horizon oil spill site and 2) compare the post-spill species composition with the extensive information in the large pre-spill database, particularly within the dominant polychaete worm assemblages.

2.2 Materials and methods

2.2.1 Sampling methods

DWH samples were obtained on Sept. 25, 2010, five months after the oil spill began and thus two months after it was terminated, during a research mission of the Motor Yacht Arctic Sunrise. Sampling locations were opportunistic and based solely on proximity to the DWH event site and available wire time during the mission. Three locations were sampled within 5 to 9 km from the well head (Numbers 15, 17, 18; Fig. 2.1. a-b) at the following locations: 28.70N x 88.44W; 28.83N x 88.34W; and 28.79N x 88.29W, respectively. These locations were within the "moderately impacted area" of the footprint defined by Montagna et al., (2013).Three replicates were taken at each site for a total of 9 samples. Their depth ranged from 1189 to 1397 m. The samples were taken with a GOMEX box corer (Boland and Rowe, 1991) that covered an area of 0.2 m^2, but removal of subsamples reduced the total area to 0.18 m^2. The subsamples were taken with polycarbonate tubes; the total oil equivalents (TOE) and the PAH data presented in this paper were measured on a single sub-core from each core. The total area of the sub-samples amounted to 0.02 m^2. The surface 15 cm of sediments in each core, minus the subsamples, were sieved at sea through 300 micrometer mesh stainless sieves and then fixed with 10% buffered formalin in filtered sea water. Then, in the lab, each of the nine samples was stained with 5% Rose Bengal for 24 hours and sorted to major taxa using a dissecting microscope. Polychaetes were further identified to species or lowest possible taxonomic level. Samples were preserved in 70% ETOH following sorting.

Four of the nine samples (15-1, 17-1, 17-2 and 18-2) were leaking sea water from the bottom jaws on recovery of the corer, and these have been noted in the Results (Table 2.1.).

2.2.2 Pre-oil spill historical database

For comparison, we utilized pre-oil spill polychaete species data from nine locations sampled during the Deep Gulf of Mexico Benthos (DGoMB) study sampled in 2000 to 2002 (Rowe and Kennicutt, 2008; Wei et al., 2010). These sites were all on the continental slope adjacent to the DWH region (Fig.2.1.a, Table 2.1.).They were not at precisely the same location as the DWH samples, and their depth ranged from 334-1825 m, with two replicates per site, except for the HiPro location with only one. Two visits were made to S36 in DeSoto Canyon: June, 2000 and 2001. Detailed information on these locations can be found in a set of papers in a special volume of Deep-Sea Research

II (Rowe and Kennicutt, 2008), with additional faunal analyses presented in Wei et al., (2010; 2012 a and b) and Carvalho et al., (2013). Polychaete species lists can be found in Hubbard (1995) and Wang (2004).Voucher specimens of each species identified by name and each species designated by letter are retained presently in working voucher collections at Texas A&M at Galveston.

2.2.3 Total oil equivalents and polycyclic aromatic hydrocarbons analysis

The top 2 cm of one sub-core from each location were used for Total Oil Equivalents (TOE) and Polycyclic Aromatic Hydrocarbons (PAH) analyses. Estimates of total oil equivalents (TOE) of DWH oil were based on the maximum intensity (MI) measured at an excitation wavelength of 260 nm and an emission wavelength of 370 nm (Wade et al., 2011) corresponding to MI from a sample of DWH oil (Sample QA10OIL01 from NIST). The analysis of PAHs used the NOAA NS&T Methods (Wade et al., 1993; Qian et al., 1998). Sediment samples were oven dried at 40°C, mixed with hydromatrix and extracted with methylene chloride in an Automated Solvent Extractor (ASE). The sample extracts along with procedural blanks were then analyzed by total scanning fluorescence. Samples were diluted, when necessary, to minimize quenching effects. Sample extracts (including matrix spike and duplicate) were reduced in volume to 1 ml and separated from possible interfering compounds using silica/alumina columns. The purified extracts were analyzed on an Agilent 6890/5973 gas chromatograph with a mass selective detector (GC/MS) using a selected ion detection technique. The GC/MS was calibrated with known concentrations of analytes at five different concentration levels and the average relative response factors of the analytes were used for PAH concentration determination. Concentrations of PAHs are reported as nanogram/gram (ng/g) on a dry weight basis for sediment samples. Both non-alkylated (parent PAHs) and alkylated PAHs are reported (Wade et al., 2008).

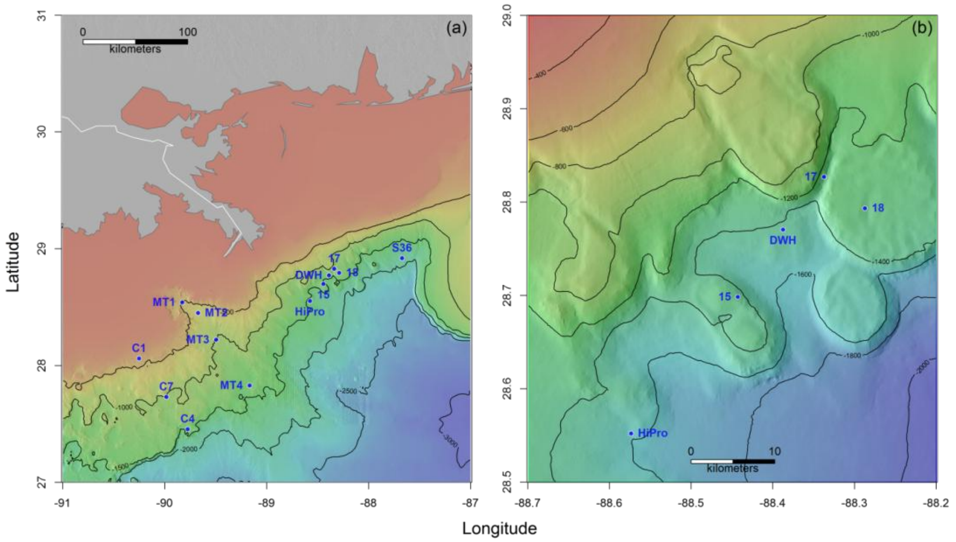

Fig.2.1 (a) Locations of historical sampling and (b) Post DWH spill sampling sites at 15, 17, and 18 (see 2.1. and 2.2.).

2.2.4 Data analysis

Biodiversity was estimated using Margalef's richness index (d) (Margalef, 1968), Pielou's evenness index (*j'*) (Pielou, 1975) and the rarefaction index Es(n) (Sanders, 1968), where Es(n) is the expected number of species in a sample of n individuals.

A species-sample matrix was square-root or forth-root transformed before multivariate analysis. Primer 6.0 was employed to calculate d, j' and Es(100). Cluster Analysis was utilized to illustrate differences in shared species between locations (the Bray-Curtis similarity measure).A Student's t-test was used to compare means. Polychaete feeding types were determined based on categories described by Fauchald and Jumars (1979). Regression plots were created by SigmaPlot 10.0.

2.3 Results

2.3.1 Polychaete abundance, species composition and alpha diversity

In total, 1035 individual polychaetes were found in the DWH samples; they belonged to 32 families and 165 species. The average abundance was 636.0 inds/m^2 (Table 2.1). Sample 18-1 had both the highest number of species and abundance, whereas 15-2 had the lowest number of species and 18-2 had the fewest individuals.

Table 2.1 Number of polychaete species (S), individuals (N), abundance and diversities of DWH, along with similar information in the continental slope database (the DGoMB study). In the historical data (DGoMB), 1C1-1 refers to a station C1, replicate 1,on Cruise 1(2000), 2-S36-2 refers station S36, replicate 2, on Cruise 2 (2001).“all” indicates that all DWH samples are included in statistical test;“remove washed” indicates analysis without the four samples that leaked sea water; d is Margalef’s richness index, j’ is Pielou’s evenness index and Es(n) is Es(100) Rarefaction Index with 100 individuals. A Student’s t-test was adopted to test the differences between the means of those parameters in the two sets of data. All locations are pictured in Fig. 2.1 a and b.

		Depth(m)	S	N	Abundance(inds/m^2)	d	J'	Es(100)
	15-1*	1397	24	96	530.9	5.04	0.77	24
	15-2		22	42	232.3	5.62	0.93	22
	15-3		30	95	525.4	6.37	0.91	30
	17-1*	1189	41	114	630.5	8.45	0.87	38.3
	17-2*		29	50	276.5	7.16	0.95	29
	17-3		60	199	1100.5	11.15	0.85	40.3
	18-1	1318	64	306	1692.3	11.01	0.83	36.9
	18-2*		25	36	199.1	6.7	0.94	25
	18-3		39	97	536.5	8.31	0.89	39
DWH	Mean		37	115	636	7.75	0.88	31.6
	Std.Deviation				453.12	2.06	0.06	6.72
Historical Database (DGoMB)	1C 1-1	334	47	298	1727.5	8.07	0.86	32
	1C 1-5		49	122	707.2	9.99	0.92	44.4
	1C 4-1	1455	56	209	1211.6	10.3	0.86	40.2
	1C 4-2		53	199	1153.6	9.82	0.85	38.8
	1C 7-1	1080	61	302	1750.7	10.51	0.81	38.1
	1C 7-2		71	250	1449.3	12.68	0.87	45.1
	1MT1-3	482	66	612	3547.8	10.13	0.76	32
	1MT1-4		71	474	2747.8	11.36	0.79	34.8
	1MT2-1	676	60	590	3420.3	9.25	0.8	31.1
	1MT2-4		58	499	2892.7	9.17	0.8	31.7
	1MT3-1	983	95	411	2382.6	15.62	0.82	44.4
	1MT3-2		63	379	2197.1	10.44	0.86	38

Table 2.1 continued

		Depth(m)	S	N	Abundance(inds/m^2)	d	J'	Es(100)
Historical	1MT4-1	1401	65	261	1513	11.5	0.87	41.6
Database	1MT4-2		56	197	1142	10.41	0.88	40.4
(DGoMB)	1S36-1	1825	87	544	3153.6	13.65	0.76	38.5
	2S36-2		62	404	2342	10.16	0.77	33.6
	2HiPro-1	1574	62	414	2400	10.12	0.79	32
	Mean		64	363	2102.3	10.78	0.83	37.5
	Std.Deviation				833.37	1.74	0.05	4.71
	All		0	0	0	0.001	0.016	0.048
p	*remove washed		0.008	0.007	0.005	0.034	0.031	0.019

All measured biological variables (number of species, abundance, and diversity) were significantly different (lower) between DWH in 2010 and the historical database (Table 2.1), with the exception of Evenness, j’, which was higher, meaning the individuals were more evenly distributed among the species present.

None of the dominant species in the samples was the same as those in the database (Table 2.2). In both sets, the most dominant species were in the family Maldanidae, but the species were different. The *Sthenelais* sp., in the family Sigalionidae, was abundant at the DWH site, but not in the older data. While the sigalionid *Sthenelais* sp. was the 2ndmost abundant post-event species, the most abundant species (*Pholoe* sp.B) of this family ranked 57th among all the species in the database. The spionids had no prominent species in the proximity of the DWH site, but were prominent in the database (Table 2.2).

Table 2.2 Dominant species of post-spill 2010 DWH and the pre-spill 2000 DGoMB studies.

	Family	Species	Average Abundance(inds/m^2)
DWH	Maldanidae	*Micromaldane* sp.	73.1
	Sigalionidae	*Sthenelais* sp.	52.8
	Maldanidae	*Maldane* sp. A	45.5
	Paraonidae	*Aricidea* sp.3	39.9
	Syllidae	*Exogone* sp. 3	30.1
	Cossuridae	*Cossura delta*	29.5
Historical Database	Maldanidae	*Maldanidae* sp.	179.7
	Spionidae	*Spionidae* sp.	176.3
	Paraonidae	*Aricidea suecica*	101.6
	Spionidae	*Prionospio cirrifera*	73.7
	Paraonidae	*Aedicira* sp.	65.5

2.3.2 Feeding types

The non-selective deposit feeders, selective deposit feeders and suspension filter feeders were significantly lower after the event compared to the historical data (Table 2.3). The abundances of carnivores, scavengers and omnivores were not significantly different however.

The two dominant families, Capitellidae and Paraonidae, are both considered to be non-selective deposit feeders, but only the Paraonidae decreased significantly. Of the selective deposit feeders (Cirratulidae, Maldanidae and Spionidae),only the Spionidae dropped in abundance after the spill. The Family Sigalionidae was significantly higher in the post-event samples due largely to *Sthenelais* sp. (Table 2.4), the only family with higher abundances in the post-event samples. Scavengers (S) and suspension feeders (SF) were rare in both historical and DWH assemblages. No change could be detected in the omnivorous Syllidae.

2.3.3 Total oil equivalents and polycyclic aromatic hydrocarbons

Total oil equivalents (TOE) ranged from 50 up to 850ug/g of sediments, while the corresponding PAH ranged from 100 up to 1000ng/g of sediment (Fig. 2.2, Table 2.5). A linear relationship between the two was highly significant. Total PAH (TPAH) concentration in our samples near the footprint averaged 417.5±247.1 ng/g. Fifteen selected PAH (ng/g) in the DWH samples are listed in Table 2.5.The total PAH in the database (Wade et al., 2008) prior to the spill declined with depth (Fig. 2.3). Most of the post-event values were above the 95% confidence interval of the historical values at the depths sampled in this study (1.2 to 1.4 km), reinforcing other observations of DWH-derived oil and PAH in or near the ‘footprint’of the event (Montagna et al., 2013). Only two of the values at the 9 sites were on or below the regression line.

Table 2.3. Mean abundance (inds/m^2) of each feeding type. C = Carnivore, NSDF = Non-selective deposit feeder, O = Omnivore, S = Scavenger, SDF=Selective deposit feeder and SF = Suspension filter feeding. A Student's t-test was used to test differencesin means of the abundances of each feeding guild in the post-spill data and the historical database.

Survey	C	NSDF	O	S	SDF	SF
DWH	110	228	86	1.23	204	1.8
DGoMB	148.6	780.7	212.8	8.31	914.3	37.7
p	0.305	0.003	0.05	0.146	0.001	0.003

Table 2.4. Mean abundance (inds/m^2) of dominant families. Siga. (Sigalionidae), Capi. (Capitellidae), Para. (Paraonidae), Cirra. (Cirratulidae), Sylli. (Syllidae), Mald. (Maldanidae) and Spio.(Spionidae). Student's t test used to test the null hypothesis that the relative (%) mean abundance of each dominant family were the same in pre and post event data.

Survey	Siga.	Capi.	Para.	Cirra.	Mald.	Spio.	Sylli.
DWH	57.1	86.6	86.6	30.1	121.7	32.6	64.5
DGoMB	25.9	100.2	481.5	91.7	232.2	476	127.8
p	0.007	0.735	0.003	0.063	0.269	0.011	0.134

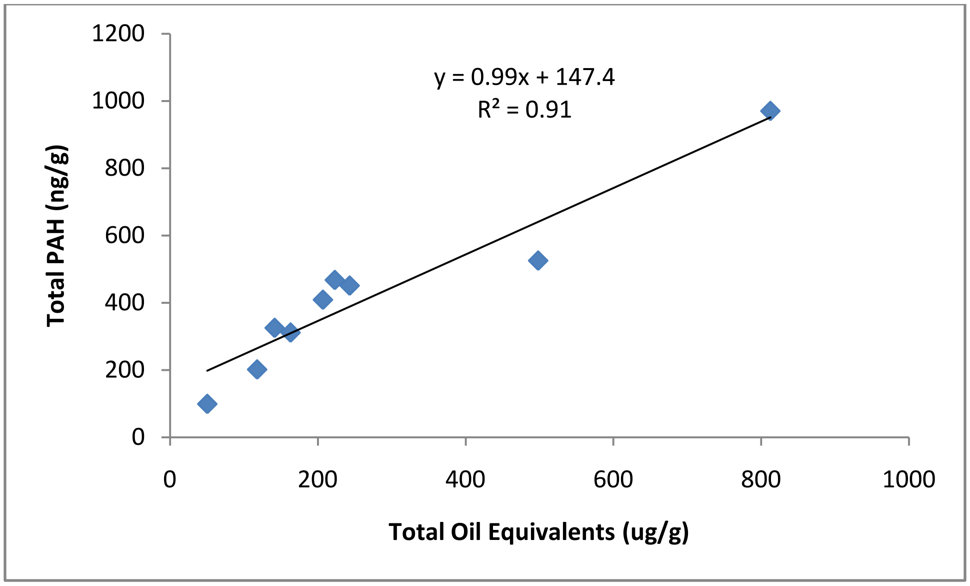

Fig. 2.2 Total PAH as a function of "total oil equivalents" from subsamples of the nine cores near (5 to 9 km) the DWH well head (Fig. 2.1).

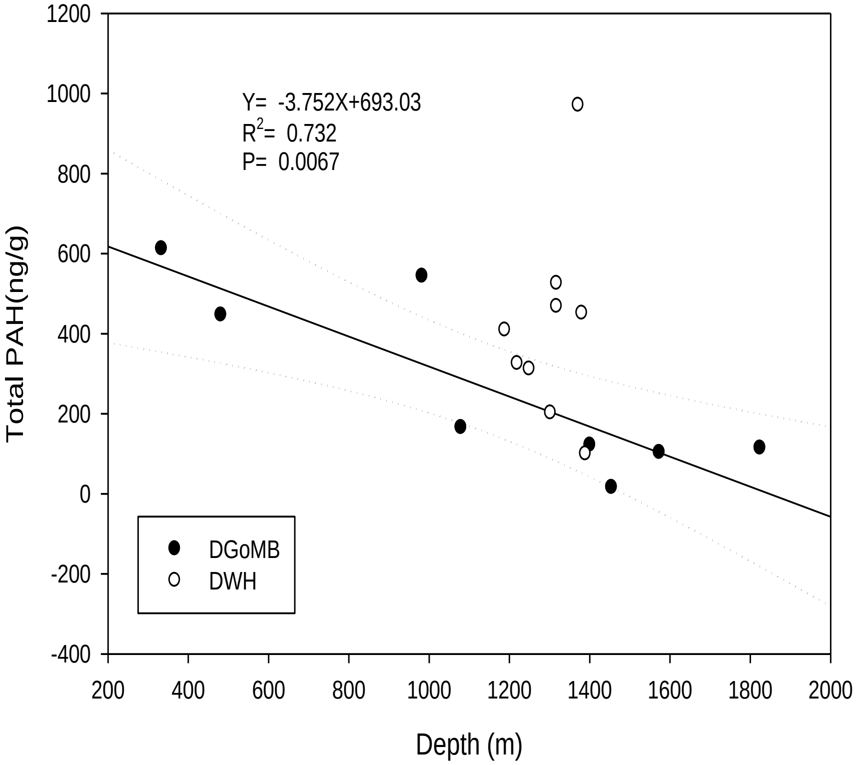

Fig. 2.3 Total PAH in the DWH samples compared to that in the historical samples (DGoMB samples in Wade et al., 2008) plotted as a function of depth. The linear regression (solid line) is encompassed by the 95% confidence interval (dashed lines) of the pre-event data.

Table 2.5 Total PAH (TPAH) and fifteen selected PAH (ng/g) in the DWH location subsamples.

		TPAH	NAPH	ACENAPL	C1FLUOR	C3FLUOR	C1PHAN	DIBEN	C1DIBEN
DWH	15-1	969.8	3.7	0.8	10.1	56.2	38.9	1.1	9.7
	15-2	98.9	0.5	0.3	0.8	0	2	0.3	1
	15-3	450.6	3.7	1.3	2.3	12.7	9.3	0.4	2.3
	17-1	408.6	3	0.4	3	21.4	12	0.4	3.3
	17-2	311.1	1.7	0.5	1.5	11.6	7.4	0	1.9
	17-3	325	2.4	0.7	3	14.4	10.1	0.3	3.3
	18-1	467.3	4.1	1.5	2.6	12.4	11.7	0.6	2.5
	18-2	201.3	2.5	0.5	1.1	6.2	2.8	0.2	0.9
	18-3	525	2.3	0.8	2.3	18.5	7.4	0.4	2
	Mean	417.5	2.7	0.8	3	17.1	11.3	0.4	3
	Std.Deviation	247.1	1.1	0.4	2.8	16	10.9	0.3	2.6

		C1FLPY	CHRYSEN	C1CHRYS	BENKFLU	BENAPYR	DBAHANT	D26NAPH	M1PHEN
DWH	15-1	39.8	8.8	53.2	1.9	4.4	1.4	4.9	18.8
	15-2	7.3	3.7	3.6	0.9	1.1	0.5	0.2	1.3
	15-3	27.3	4.5	20.1	1.8	9.6	1	1.9	2.6
	17-1	31.8	4.1	20.1	0.9	4	0.5	1.4	7.2
	17-2	21	3.2	15.7	1	1.7	0.4	0.7	3.7
	17-3	21	3.4	16.3	1.6	2.1	0.7	1.1	23
	18-1	39.2	6.9	24.8	2.8	4.3	1.6	2	4
	18-2	13.6	3	9.7	1	13.2	0.4	0.7	2
	18-3	20.8	15.4	35.4	1	1.4	0.7	0.7	3.8
	Mean	24.6	5.9	22.1	1.4	4.6	0.8	1.5	7.4
	Std.Deviation	11	4.1	14.7	0.6	4.1	0.4	1.4	7.9

2.3.4 Multivariate analysis comparing post and pre event polychaete species

The species composition with in or near the DWH oiled footprint was very different from the historical samples (Fig. 2.4). Likewise, the abundances were higher prior to the event (Fig. 2.5). The species encountered in our samples were remarkably similar (40 to 50%), but were much less similar with the database (<20%) in shared species. The species grouped on the right were all at depths of 1 km or less whereas the central group sites were all at depths between 1 and 2 km.

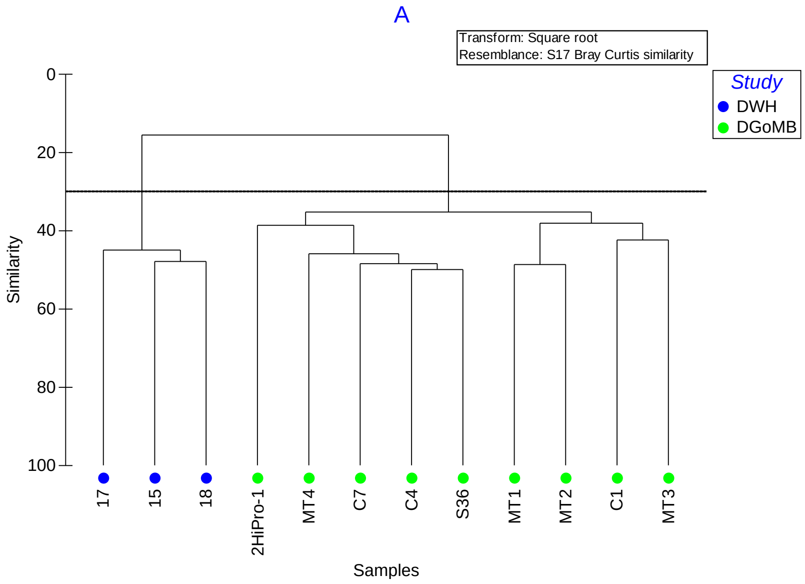

Fig. 2.4 Dendrogram of Bray-Curtis similarities.

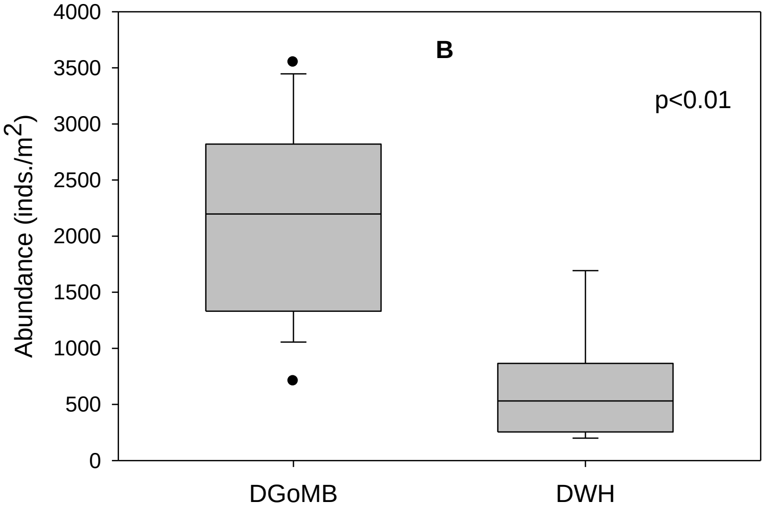

Fig. 2.5 Whisker plots of polychaete abundances (ind./m^2) of historical (DGoMB) and post-event (DWH) continental slope samples.

2.4 Discussion

2.4.1 The influence of the DWH oil spill on the polychaete assemblage

The preeminent questions are whether the oil on the sea floor in or near the DWH site was a product of the event, and secondly did that oil cause the changes observed in the polychaete assemblage. Along with the linear relationship between TOE and total PAH, there was also a strong correlation between fluorescence and total PAH reported for water column samples in the plume at the oil spill location (Wade et al., 2011). The PAH composition in the water samples was predominantly petrogenic and thus derived from oil, based on the relative abundance of parent and alkylated PAH. Weathering appeared to have occurred based on the percentage contributions of total napthalenes (TN= naphthalene+C1+C2+C3+C4) compared to total phenanthrenes/anthracenes (TP/A= phenanthrene+anthracene+C1+C2+C3+C4). The TN and total TP/A accounted for 57% and 21% respectively of the total PAH in DWH oil (OSAT, 2010). In our sediment material the TN and TP/A accounted for 2 to 5% and 18to 32% respectively of the total PAH, and this lower percentage of TN likely reflects loss due to the high solubility of napthalenes in water. This weathering may have occurred prior to deposition because weathered oil had been reported in the water column (Wade et al., 2008). There were also pyrogenic PAH present that may have originated from the fire at the platform, burning of oil at the surface, atmospheric deposition and/or transport from continental sources**.** The Operational Science Advisory Team demonstrated that PAH concentrations were higher in sediment samples collected in the footprint of the blow out site 4-6 months after the spill (OSAT, 2010), as reported by Montagna et al., (2013). However the PAH we detected were from a mixed source.

In the OSAT report, post-oil spill sediment samples that exceeded prior historical benchmarks (in Wade et al., 2008) were all located within 0.33-2.7 km of the spill site. Samples however above reference levels were found out to 10 km from the well head. White et al., (2012) observed impacts of DWH oil on deep-sea coral 11km southwest of the DWH well head three to four months after the flow was capped, within the linear distance in which we observed a decline in abundance and diversity and a change in dominant species.

As might be expected, the non-selective deposit feeding Capitellidae were relatively pollution-resistant. On the other hand, the percentage of carnivores was correlated positively with an increase in PAH and organic content in Todosos Santos Bay, Brazil (Venturini and Tommasi, 2004), as in our DWH samples, suggesting that carnivorous species are somehow immune to the stress other groups experienced.

Continental slopes are notoriously variable in time and space (Levin and Sibuet, 2011), and the effects of natural oil seeps, seasonality, topography and bottom currents cannot be excluded. Hubbard (1995) for example observed what he thought could be seasonal variation in polychaete abundances at the "C" locations. Thus our observations could be responses to seasonality in the surface water that is transferred to the sea floor in yet-to-be-observed particle fluxes (Rowe, 2013). Unstable sediments of the shelf and upper slope export organic matter to deep water (Bianchi et al., 2006) and massive slumps can smother mid-slope habitats (Santschi and Rowe, 2008), both of which could also give rise to large differences in species composition. An initial decrease in sensitive species has often been observed in shallow-water oil spills (Sanders et al., 1980), followed by recruitment of opportunistic species, especially capitellids adapted to survive and sometimes to even flourish in organically enriched sediments. Habitats recover but this can take years, based on long-term shallow water observations (Dutrieux et al., 1989; Dauvin, 1998; Gomez Gesteira and Dauvin, 2000; Kingston, 2002; Gomez Gesteira et al., 2003).The unprecedented depth and amount of oil injected into the deep ocean make predicting the recovery difficult. The lower diversity and abundance five months after the spill is a single point on a temporal continuum, but where this remote habitat is in the continuum remains unknown. A more exhaustive longitudinal study is needed to document succession of dominant macrofaunal species that may have been exposed to deep-water contamination by the DWH event (Whitehead et al., 2011).

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CHAPTER III

POLYCHAETE ANNELID BIOMASS SIZE SPECTRA, THE EFFECTS OF HYPOXIA STRESS

3.1 Introduction

The northern Gulf of Mexico continental shelf just to the west of the Mississippi River delta experiences wide-spread hypoxia seasonally (Rabalais et al., 2002). Hypoxia (dissolved oxygen < 2mg/L) results from two synergistic factors: the summer vertical stratification of the water column that prevents the mixing of oxygen into deep water (Wiseman et al., 1997) and the demand for oxygen by the decomposition of organic matter below the pycnocline (Turner and Rabalais, 1994; Rabalais et al., 2002). Since the benthic infauna is less mobile than demersal crustaceans and fishes, they are 'trapped' in deep and near-bottom water and thus susceptible to low oxygen stress. The negative effects of hypoxia on coastal benthos (decline of biodiversity, abundance, biomass and bioturbation) have been broadly recognized (Harper Jr. et al., 1981; Gaston, 1985; Diaz and Rosenberg, 2008).Many of the few species that can survive intermittent low oxygen stress are small polychaete annelid worms, the most common taxon among all benthic macrofauna (Carvalho et al., 2013; Chivers et al., 2013), but we know little about how these organisms are able to persist under such stress.

Body size is a quantifiable trait that reflects a species' evolution and ecological relationships (Damuth, 1991; White et al., 2007; Clauset and Erwin, 2008; Rakocinski, 2009; Magurran et al., 2013). Food availability (Polloni et al., 1979), latitude (Linse et al., 2006), and even oxygen levels (Chapelle and Peck, 1999), among others, are assumed to affect body size. The relationship between oxygen and body size has been discussed acrossa wide range of diverse groups (McClain and Rex, 2001; Harrison and Haddad, 2011; Clapham and Karr, 2012).

It is reasonable that smaller animals with large surface area to volume ratios would be better able to absorb oxygen in low concentrations (Singer, 2006). It has also been suggested that small organisms may be less vulnerable to disturbance because of their high birth rate and diminished demand for resources (Etienne et al., 2012). Thus we are suggesting that small size in the polychaetes may be one trait that allows them to persist during hypoxic conditions. To pursue this idea, we have generated a set of data on polychaete sizes across a broad range of inter-annual and seasonal oxygen concentrations.

The relationship between size and low oxygen stress is not necessarily simple and direct. The stress could eliminate large species in general, leaving only small species to survive. Alternatively, size could decline within a species. Or, given wide and divergent functional morphology within the entire taxa, the survival may be independent of size.

The survivors may possess some morphological or physiological talents that make them capable of utilizing what little oxygen is available.

Generation of biomass size spectra (BSS) is a simple, timesaving way to compare the structure of assemblages or populations (Saiz-Salinas and Ramos, 1999), a method first proposed by Sheldon and Parsons (1967) for particulate matter. Size spectra of populations (Warwick and Price, 1975) and assemblages (Quiroga et al., 2005) have historically provided significant insights into growth rates and secondary production, especially within the benthos. Size spectra have provided insights on survival in stressful habitats, such as oxygen minimum zones (OMZ) (Quiroga et al., 2005).

Variations in configuration and shape of simple size distribution spectra are sometimes difficult to quantify and compare (Sprules and Munawar, 1986). To obviatethis problem, Platt and Denman (1977, 1978) suggested constructing ‘normalized biomass size spectra’ (NBSS) that would facilitate comparisons of size distributions between different communities (Sprules and Munawar, 1986). We therefore have adopted the NBSS to compare sizes in the assemblages of polychaetes in our time series.

For most animal communities, NBSS is a linear plot with a negative slope that represents abundant but small organisms with relatively high total biomass down to large organisms that are fewer in number but lower in total biomass. The greater the dominance of the small size classes, the steeper the slope.

The slope and intercept of an NBSS are utilized in the comparison of the size structure of communities from different habitats (Quiroga et al., 2005; Clauset and Erwin, 2008). For example, a steep slope of the regression illustrates an assemblage dominated by small-sized organisms and thus a modest slope suggests greater importance of larger individuals.

Thus, according to the Pearson and Rosenberg (1978) model, a community dominated by small opportunists following a disturbance would have a steep slope but the slope would rise during recovery as the small opportunists are replaced by larger organisms. In general, the intercept and the height of the regression line above the x axis are a function of total biomass. The departure from a statistically significant negative regression is thought to be a function of departure from steady state (Sprules and Munawar,1986; Saiz-Salinas and Ramos, 1999; Kerr and Dickie, 2001; Gómez-Canchong et al., 2013).

In this paper, we will 1) construct polychaete size spectra across a time series (2004 to 2012) at four locations along a 50 km transect within a narrow depth range (11 to ca. 20 m) in the northern Gulf of Mexico; and 2) explore the influence of seasonal hypoxia on polychaete body size structure under a. oxic, b. hypoxic and c. severely hypoxic conditions.

3.2 Methods

3.2.1 Sampling strategies

The sampling in this study began in 2004 and extended somewhat regularly until 2012. The locations were placed close to the entrance of the river onto the continental shelf (Fig. 3.1) and extended to the west in a narrow line encompassing the 10 to 20 m isobaths (Fig. 3.1). This pattern conformed to sampling sites occupied by the Mechanisms Controlling Hypoxia project (MCH) that has attempted to make consistent, repeated sampling of the same locations from early Spring, with the onset of stratification, through to late summer, when hypoxia is often most intense (Fig. 3.1, Table 3.1). The locations were place in an attempt to compare the intensity and the causes of hypoxia at what have been termed the ‘brown’ (A), ‘green’ (B) and ‘blue’ zones along the extension of the river plume as it flows and disperses from east to west (Rowe and Chapman, 2002).

Oxygen concentrations in the water column were profiled using a SeaBird 911 CTD from the surface to 1 to 2 meters above bottom. The CTD was equipped with a SB43 oxygen electrode, as well as conductivity and thermistor probes. A rosette of 12 Niskin bottles caught individual water samples that were analyzed for plant pigments, salinity, dissolved oxygen and inorganic nutrients. Near-bottom (ca. < 0.5 m) water samples were taken using a four-bottle sampler that tripped when a trigger weight encountered the mud. MCH data are available through NODC under Accession No. 0088164.

Three sub-cores (pseudo-replicates) with a diameter of 13.9 cm each were taken from a single 0.2 m^2 GOMEX box corer at each location on each cruise. These sub-cores were initially incubated for several hours in a water bath aboard ship to determine sediment community oxygen consumption and nutrient regeneration (Nunnally et al., 2013).The entire volume of sediment of each sub-core was then sieved through 0.5 mm stainless steel mesh to remove the macrofauna. In 2012 three replicate 0.1 m^2 GOMEX box cores were taken at each of two sites (Fig 3.1, Table3.1). The surface 15 cm of each of these was also sieved through 0.5 mm stainless steel mesh. Following the sieving at sea, all samples were fixed aboard ship with 10% buffered formalin in filtered sea water.

3.2.2 Sample and data processing

In the lab, the sieved and formalin-fixed biota of the subcore samples were stained with 5% Rose Bengal for 24 hours and the stained invertebrates were sorted to lowest possible taxonomic level using a dissecting microscope. Samples were preserved in 70% ETOH following sorting. The sorted polychaete annelid worm fractions were then

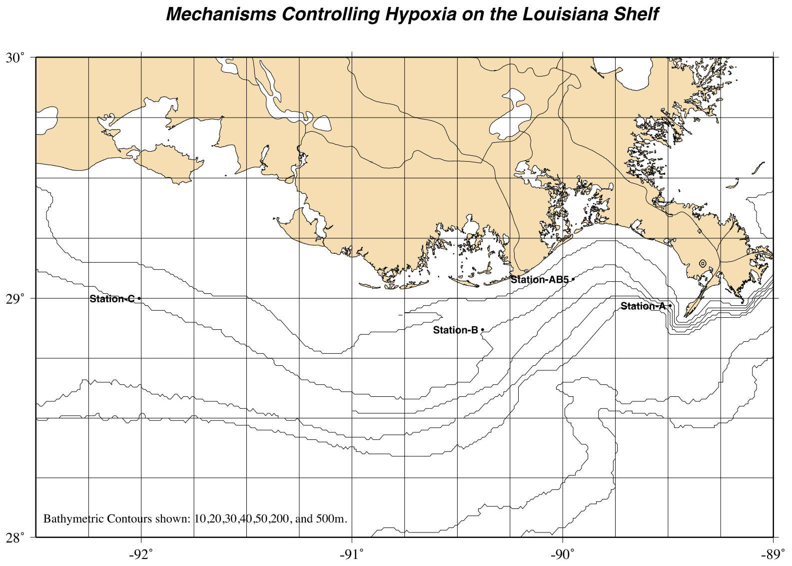

Fig. 3.1 Sampling sites in Gulf of Mexico hypoxic zone on Louisiana continental shelf.

Table 3.1 Sampling locations and depths of each site.

	Location	Depth (m)	Cruises
A	28.97 N,89.49 W	11.2	I to XIV
B	28.87 N,90.38 W	20.3	I to XV
C	29.00 N,92.01 W	19.5	I to XV
AB5	29.08 N,89.95 W	18.0	XIV & XV

sorted again to the identified species. The polychaetes accounted for 50 to 75% of the total numbers of invertebrates sampled.

Total wet weight (mg) of each polychaete species was obtained by weighing the sorted samples on a Sartorius CP2P & OHAUS AS260D balance after blotting on a paper towel for 30 seconds. Mean body weight of individuals of each ‘small’ species in each sub-core was then calculated by dividing the total weight of the species by the number of individuals in the sub-core. Individuals of large species were weighed separately.

A species-sample matrix was constructed and the species abundance data were fourth-root transformed prior to multivariate analyses. CLUSTER was carried out using PRIMER 6.0. SIMPROF (Similarity Profile) was used simultaneously with CLUSTER to test the significance ($p<0.05$) of differences between clusters (Clarke et al., 2008). SIMPER estimated the contribution of each species to a faunal group and the contribution of each species to the dissimilarity between faunal groups. The species that contributed the most to a group was considered a “characteristic” species (Clarke and Warwick, 2001). Regressions were drawn by SigmaPlot 10.0 and Excel 2007. Best-fit regression models were chosen based on the Adjust R^2 and numbers of variables. Significant differences between the means of abundances was assessed with a one-way analysis of variance (ANOVA).

Biomass size spectra (BSS) and Normalized Biomass Size Spectra (NBSS) were constructed in 14 logarithmic ($\log_2$) biomass (mg wet weight) size classes. NBSS is a graph of the biomass of a size category [m(s)] divided by the 'width' of that size category(ΔS= difference between the upper and lower boundaries of the size class) in $\log_2$ units on the dependent or y axis as a function of size categories in $\log_2$ units on the independent or x axis. In the figures, we simplified $m(s)/\Delta s$ to M(s), that is $M(s)=m(s)/\Delta s$ (Platt and Denman, 1977; 1978). Analysis of covariance (ANCOVA) was used to test the significance of differences of the slope and intercept of the NBSS linear regression lines. All statistical tests were performed with SPSS 17.0.

3.3 Results

3.3.1 Oxygen concentrations

Oxygen in the bottom water varied appreciably over the course of the sampling (Fig. 3.2). Hypoxia occurred to some degree during six of the cruises but in Spring (cruise I and VIII) all the sites were oxic. The highest single concentration overall was 6.76 mg/L at the most distant site in early Spring (C, March 07,VIII), whereas the lowest was 0.12 mg/L in late Summer (B and AB5, August 09, XIV). June 04 (II) had the lowest mean oxygen concentration, 1.15 mg/L, while the highest mean was 5.74 mg/L in March 07, VIII (Fig. 3.2). In general, as expected, higher values were located at the greatest distance from the river (C) during Spring (March and April) whereas the lowest were in mid to late summer and close to the river (A, AB5 and B). Site B has been investigated for several decades and the variations in time and space have been the subject of numerous publications (Rabalais et al., 2001 a, b; 2002; Baustian and Rabalais, 2009; Quinones-Rivera et al., 2010). All these and other MCH data are available through NODC under Accession No. 0088164.

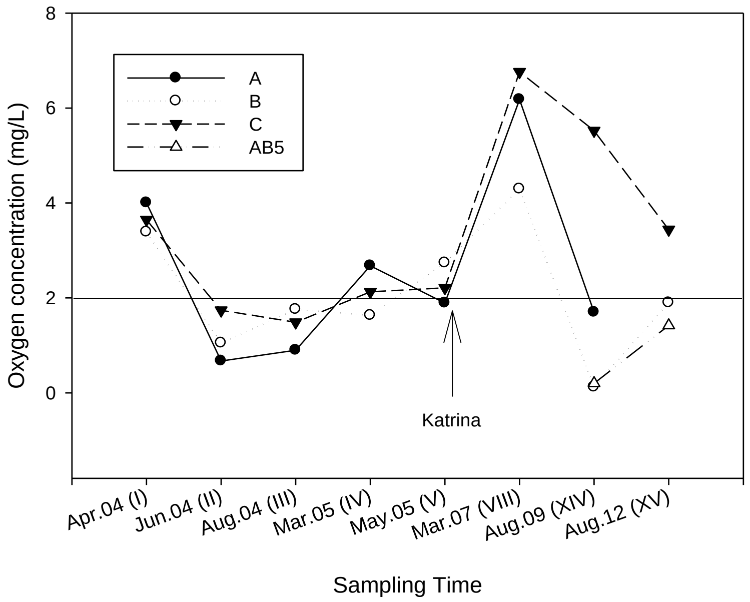

Fig. 3.2 Near-bottom oxygen concentrations at each sampling site from April 2004 to August 2012, with the horizontal line indicating the 2mg/L hypoxia threshold. Concentrations below 2mg/L were considered hypoxic whereas those below 1 mg/L were categorized as ‘severe hypoxia’.

3.3.2 Distribution of mean animal sizes

From the 64 samples utilized, we measured a mean abundance of 2746 ind. polychaetes/m^2 (±2258) and these amounted to 6.9 gm wet weight/m^2 (±5.3). There was a significant relationship between mean body size and bottom oxygen concentration (Fig. 3.3): higher oxygen meant bigger worms. Mean body size ranged from 0.6 mg to 30 mg, with an average value of 3.99 mg per worm (±4.7). The high extreme mean (30 mg) was sampled in August, 2009, Cruise XIV, and included the large bamboo worms *Clymenella torquata* and *Asychis elongatus*.

Throughout most of the early sampling period (2004-05), the average body size of the polychaete populations sampled was 2.97 mg ±2.87); however in 2007-09 the total mean body size rose to 7.13 mg±7.60) ($p<0.01$). By 2012, this value dropped back to 2.85 mg±2.97), but this latter mean was not significantly different ($p > 0.05$) from any of the prior values.

If the entire time series is arbitrarily divided into three time blocks (2004-05, 2007-09 and 2012), the mean total wet weight biomass for all the polychaetes in the samples was 7.6 (±5.9), 6.3 (±4.4) and 4.7 (±2.7) g/m^2. Statistically however these values were not different ($p>0.05$). Thus, while sizes may have changed, depending on conditions, the total biomass was relatively high and constant over time. Mean abundances during the early intense hypoxia was 3321 (± 2447) inds./m^2, whereas abundance was down to

1246 ± 1072 inds./m^{2}in the sampling two years later ($p<0.01$). Seven years later (2012) abundance was at an intermediate level (2226 ±1049 inds./m^2).

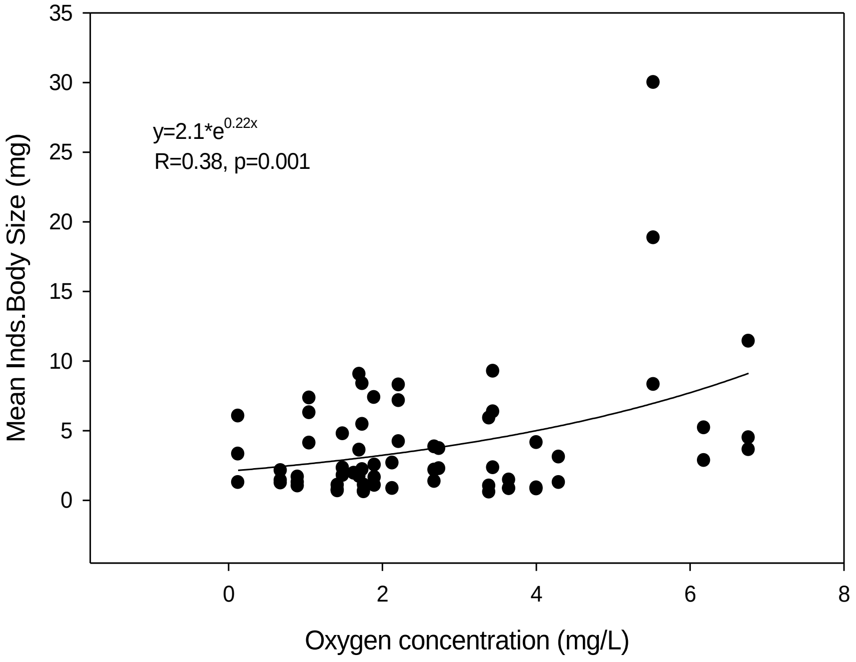

Fig. 3.3.Exponential relationship between mean body size of polychaetes and bottom oxygen concentration at each of the 64 sites in all cruises.

3.3.2 Biomass size spectra

The biomass size spectra have been plotted at the three different categories of oxygen concentration: oxic, hypoxic and severely hypoxic (Fig. 3.4). When oxygen was higher than 2 mg/L, large worms were present in size classes 7 (64-128mg) and 8 (128-256 mg). When oxygen concentration was lower than 2 mg/L, species in size class 7 and 8 disappeared, but when oxygen dropped down below 1 mg/L, another two size classes (5 and 6) also disappeared. That is, ultimately, there were no big worms when oxygen was severely low. On the other hand, the smallest worms were eliminated too at the tiniest sizes (size classes -1 down to -5), leaving only intermediate sized species (size classes 0 to 4).

The three spectra had some similar peaks within the same size classes (0, 3 and 5, Fig. 3.4); the exception was the large numbers in very small size class (-3) at oxygen lower than 2mg/L (red line, Fig. 3.4).

Species in that size class (-3) were mostly *Cossura soyeri*, *Levinsenia gracilis*, *Prionospio cristata*, and *Magelona sp.H*. This peak indicates that these relatively small species flourished under hypoxic conditions, but then, as the hypoxia worsened, they too declined (green line).

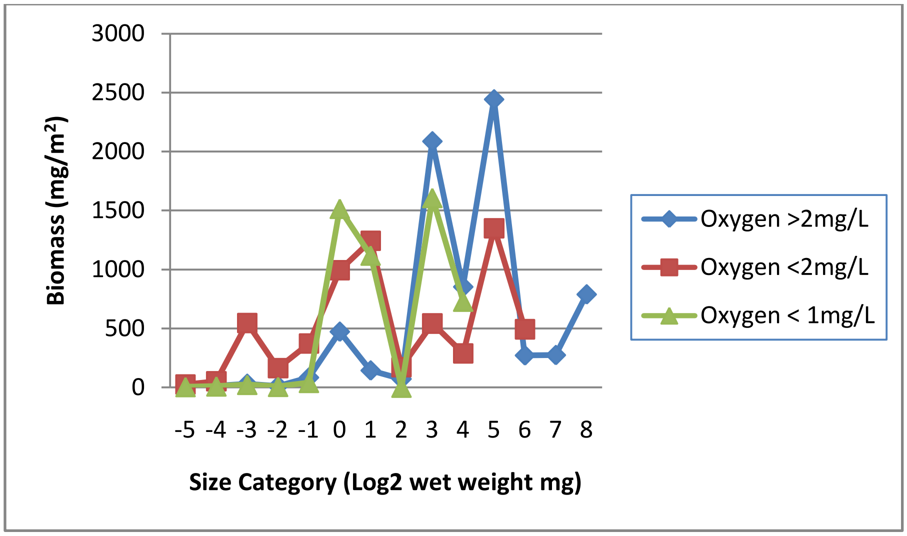

Fig. 3.4 Polychaete biomass size structure (BSS) under different oxygen concentrations, as indicated. The y axisis total wet weight biomass under each line; the x axis is the size categories, as indicated.

3.3.3 Normalized biomass size spectra

The slopes of the normalized biomass size spectra (NBSS) of both oxic and hypoxic (oxygen <2 mg/L) conditions were significant ($p<0.05$) (Fig. 3.5). The slope of hypoxic (oxygen <2mg/L) NBSS appeared to be slightly more negative than the slope for oxic conditions, but the difference was not significant (-0.68 vs -0.51 , $p>0.05$). When oxygen was below 1mg/L, the NBSS regression fit was very low($R^2 \approx 0$) with no apparent slope ($p>0.05$). This reflects the elimination of both the largest and smallest species under these severe conditions.

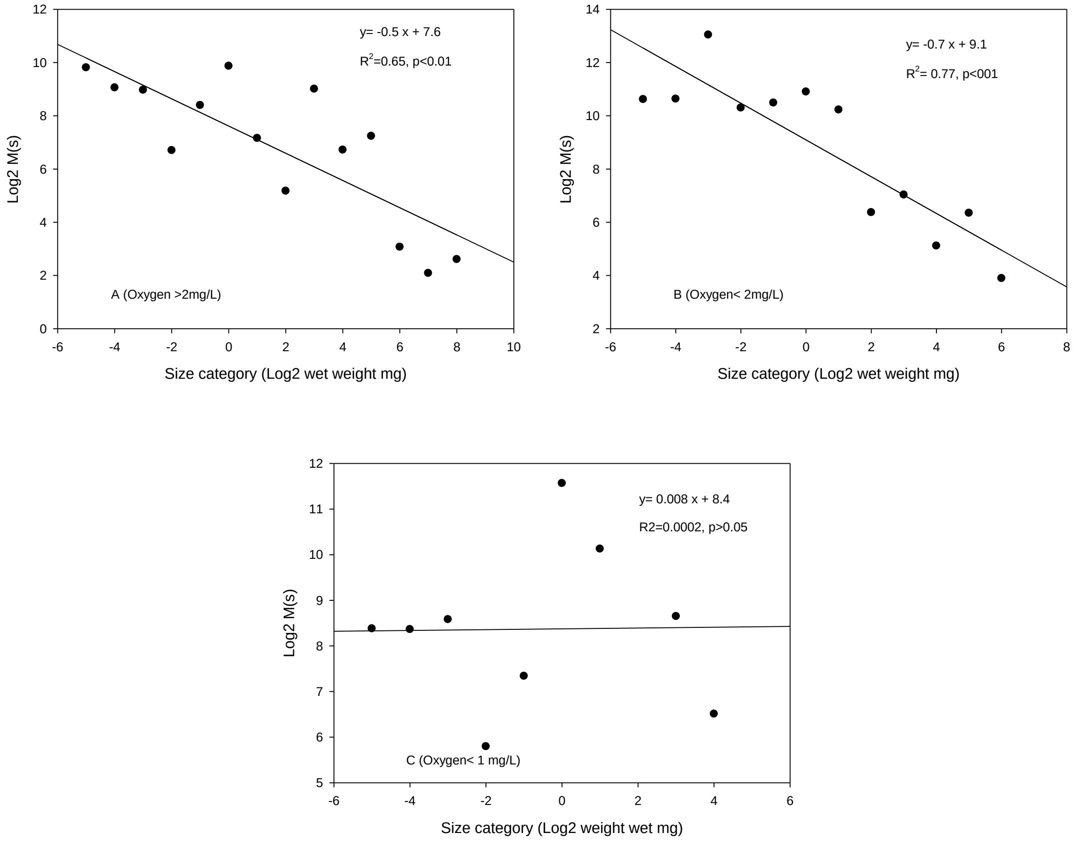

Fig. 3.5. Normalized biomass size spectra (NBSS, see text) under different oxygen concentrations :A. oxygen concentration >2mg/L; B. < 2mg/L and C. < 1 mg/L . Note the differences in axes in each graph.

3.3.4 Species composition across the time series

Similarity analysis of the entire species list from all samples indicated that there were five faunal groups with similar species (> 40% similarity, $p<0.05$). The most inclusive or recurring group (on the left of Fig. 3.6) consisted of 18 ‘times’ and ‘locations’at A, B, and C sites from 2004 to 2009 in both Spring and Summer. The other four groups involved only 7 times and locations. The three samples taken in August 2012 stood out by themselves. The other three groups included only one or two sites taken in August, with the exception of a single sampling in April at site A adjacent to the river’s entrance onto the continental shelf (Fig. 3.6).

The mixing of species assemblages at all locations and seasons into Group 1 implies that the fauna in general was rather uniform; however there is some suggestion in the sub-groups that the fauna might be partitioned into ‘zones A, B and C’ as suggested in Rowe and Chapman (2002). The A's, C's and B's tend to be clustered together from left to right (Fig. 3.6). On the left most of the group was close to the river mouth (A), whereas many in the next sub-group were at C, the most distant location, with B in the middle. These species sub-groups thus tend to reflect location rather than season or oxygen concentration. The distinctiveness of August 2012 at AB5, B and C indicates that this period was also slightly different in species composition, as was inferred from the size data.

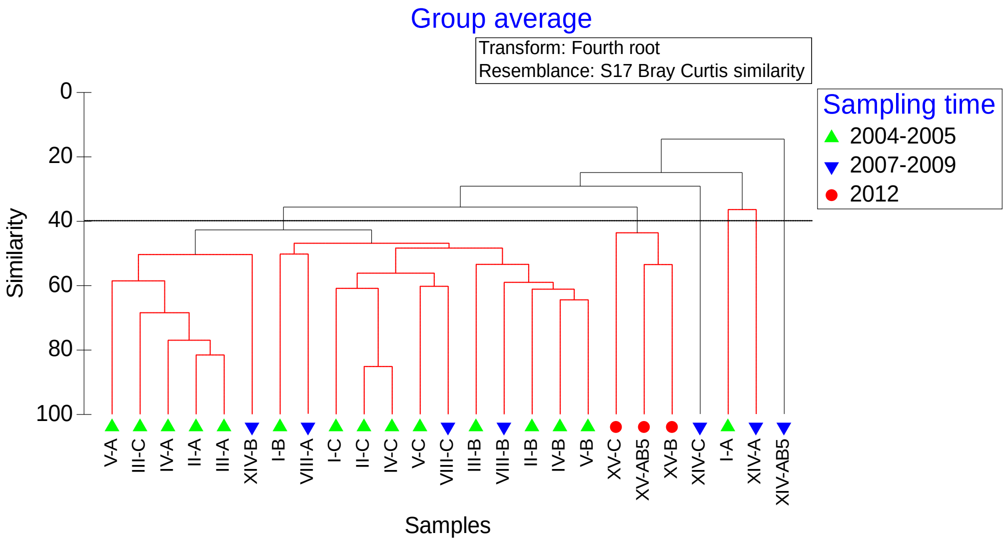

Fig. 3.6 Cluster dendrogram with Simprof test of all sites sampled from 2004-2012. Cruise numbers and site names are shown under each colored symbols ("I-A" means site A in cruise I). Green 2004-2005, blue 2007-2009, red dots 2012. Red lines mean there was no reliable statistical difference (p>0.05) between the relationships, while black lines indicate significant clusters (p<0.05). At the 40% similarity level, the samples clustered into 5 groups.

All the samples however were remarkably similar, based on the > 40% similarity in composition. *P.pinnata* has long been recognized as the most common polychaete inhabiting the Gulf of Mexico Hypoxic zone (Rabalais et al., 2001a) and likewise its remarkable abundance dominated Groups 1 and 2 (Fig. 3.6). *P.pinnata* and *Mediomastus californiensis* appeared in nearly every sample throughout the study and their abundance accounted for more than half of the total abundance everywhere. The characteristic species of Group 1 (Fig. 3.6) were all deposit feeders (both selective and non-selective), while Group 2 included carnivores, omnivores, and deposit feeders (Fauchald and Jumars, 1979).

Neresis micromma contributed most to the dissimilarity between Group 1 and 2 (3.7%). It was not common in the 2004-05 samples: only two individuals were found during those first five cruises. In the 2012 however 98 individuals were sampled (Table 3.2).

Abundance of *P.pinnata* increased from 555 ±764 inds./m^2 to 1131±1300 and 1533± 1157 inds./m^2 along the decreasing oxygen gradient. Abundance of *P.pinnata* under hypoxic conditions (<2mg/L and <1 mg/L) was significantly higher than that in oxic conditions ($p<0.05$). Abundance however of *M.californiensis* was not different within the 3 oxygen levels.

3.4 Discussion

3.4.1 Effect of hypoxia on mean animal size

The results in terms of a. the mean size of individual polychaetes (mg wet weight), b. the biomass size spectra (BSS) and c. the normalized biomass size spectra (NBSS) all denoted that animals were smaller under hypoxic conditions. Clearly, however, the

Table 3.2 Similarity percentage (SIMPER) contribution of polychaete species in each group.

Group	Species	Contri%	Cum%
1 (Av.Sim=48.32%)	*Paraprionospiopinnata*	20.17	20.17
	Mediomastuscaliforniensis	14.47	37.64
	Cossurasoyeri	12.73	47.37
	Aricidea (Acmira) sp.	11.57	58.94
2 (Av.Sim=46.98%)	*Paraprionospiopinnata*	8.55	8.55
	Mediomastuscaliforniensis	8.02	16.57
	Sthenelais sp.	6.62	23.19
	Neresismicromma	6.54	29.73
	Cossurasoyeri	6.37	36.1
1&2(Av. Dis.Sim.=64.30%)	*Neresismicromma*	3.7	3.7
	*Magelona*sp.H	2.86	6.56
	Sthenelais sp.	2.83	9.38
	Tharyxannulosus	2.8	12.18

northern Gulf of Mexico hypoxic area is not a ‘dead zone’ as is often suggested in the popular media. Animals are small but not gone; in fact some are in great abundance when oxygen is low.

A principal reason for the shift in mean size was exclusion of large-sized worms that may be more vulnerable to low oxygen physiological stress (Etienne et al., 2012), not a change in size within species. Smaller organisms with a greater surface to volume ratio may be better able to cope with low oxygen than large organisms.

This positive relationship of oxygen and size agrees with the patterns observed by McClain and Rex (2001) in turrid gastropods and ‘polar gigantism’ in amphipod crustaceans (Chapelle and Peck, 1999). Those environmental conditions were at the high end of oxygen concentrations, so comparisons are not particularly relevant to physiological stress.

The general negative slope of an NBSS reflects biomass dominance by small size classes. The relative steepness (negativity) of the slope may be a reflection of stress if low-oxygen stress favors small sizes. In our study, the NBSS slope ranged from-0.56 to -0.48, but Quiroga et al., (2005) reported a much broader range (-0.481 to -0.908) in the oxygen minimum zone (OMZ) off Chile. The OMZ however is a more permanent condition often approaching anoxia. On the other hand, Saiz-Salinas and Romas (1999) tabulated an even more negative NBSS slope along a depth gradient off Antarctica (-0.76 to -1.31), but the latter reflects the commonly observed decrease in mean size of the entire infauna that accompanies the decrease in available food as water depth increases (Polloni et al., 1979; Rowe et al., 2008).

3.4.2 The ubiquity of *Paraprionospio pinnata* and the “altered” NBSS

A very unusual NBSS regression line was generated when oxygen was lower than 1 mg/L the lack of slope may be related to stress and disturbance. Generally, if small sized animals tend to be relatively more abundant under stressful conditions (Sprules and

Munawar,1986; White et al., 2007), then the slope would steepen as the larger animals are eliminated due to low oxygen stress.The smallest-sized polychaetes in size class -5 (*Mediomastus californiensis*, *Aricidea (Acmira)*sp. and *Aricidea taylori*), theoretically would be expected to be dominant (White et al., 2007). *P.pinnata*, on the other hand (size class 0) is a medium-sized polychaete and the highest point in the 'poor' NBSS plot was in size class 0, dominated by *P.pinnata* (Table 3.3). When oxygen concentration was high, small-sized species and *P.pinnata* were almost equal in abundance. When oxygen was < 1 mg/L, the percentage of small-sized and large sized worms both declined, leaving *P.pinnata,* to flourish, with abundances 4 to 5 times more than the small-sized species. This peak in the middle attributed to *P. pinnata* contributed to the peculiar and unpredicted humped shape of the NBSS. Low oxygen did not depress dominance of *P.pinnata*. To the contrary, an increase in abundance of *P.pinnata* was encountered under moderate and severe hypoxia, reinforcing the findings of Baustian and Rabalais (2009) at Station B (their C6B). Lamont and Gage (2000) suggested that the enlargement in size and branching of the branchiae of the polychaete *Paraprionospio* sp.A on the continental slope off Oman was an adaptation to low oxygen in the OMZ. Morphological adaption of *P.pinnata* to low oxygen might be inferred from the negative relationship with oxygen concentration noted by Rabalais et al., (2001a) and Baustian and Rabalais (2009). Our data agree: *P.pinnata* actually increased when subjected to hypoxia. It is reasonable to assume that their prostomial branchial palps provide their remarkable ability to better scavenge oxygen at very low concentrations.

Table 3.3 Percentage of abundance of small sized polychaetes and *P. pinnata* under different situations.

	% Small sized (size class -6 ~ -4)	%*P. pinnata*(size class (-1~1))
2004-2005	28.7	32.5
2007-2009	8.3	34.6
Oxic (>2mg/L)	29.0	23.1
Hypoxic (<1mg/L)	13.7	62.7

CHAPTER IV

DECADAL SCALE VARIATIONS IN THE POLYCHAETE ANNELID POPULATIONS ON THE UPPER CONTINENTAL SLOPE OF THE NORTHERN GULF OF MEXICO

4.1 Introduction

The deep sea, once assumed to be a stable ecosystem, can be influenced by and responsive to food availability, sediment movement, low oxygen, variations in temperature, climate change, et al. (Smith et al., 2008, Glover et al., 2010). The upper continental slope (200 to 2000 m depths) can be particularly susceptible to near-shore processes because it is an important physical transition zone from shallow water into the deep sea.

As the transition between the highly variable shelf and the deep ocean, the fauna of the upper continental slope is tightly zoned across the depth gradient (Wei et al., 2010), This 'archibenthal zone of transition', as it has been called, is affected by continental shelf processes that export fine-grained sediment to a ‘mud line’ or depocenter in this depth interval. Additional variability is accrued by occasional warm core eddies that can affect the water column as deep as several hundred meters. Impacts of the eddies and the detrital accumulation on the fauna are not known.

If coastal eutrophication is increasing in the northern GoM (Turner et al., 2008), then some fraction of the new production is likely to be exportedtothe ‘depo center’ on the upper slope. Or the exported detritus could transit the slope to greater depths (Santschi and Rowe, 2008).

Potential fisheries resources are being sought on the upper slope world wide, but with mixed success. Upper-slope depths are sometimes characterized by large, but slow growing cold-water coral heads that are destroyed by deep trawling. Many continental slopes are the site of extensive oil and gas prospecting and production, with an occasional catastrophic event such as the 2010 BP/Transocean/Halliburton blow out in the eastern GoM.

The topography of the continental slope of the northern GoM is remarkably complex due to underlying salt deposits that form sea mount-like prominences that are adjacent to meso-scale basins (5 to 20 km across and up to 1 km or more deep). Over-burdened sediments on the slope often give rise to intermittent mass movements (slides and slumps) that leave deep scars on the upper slope and slump deposits on the continental rise or the Sigsbee Abyssal Plain. Thus, there are multiple environmental variables on the upper slope of the GoM that could cause variations in the benthic fauna in time and space. A goal of this paper is to document variations in the dominant taxon of the sedimentary infauna, the polychaete annelid worms, on the upper slope over a period of two decades.

It has been suggested that the declining supply of foodwith depth controls zonation patterns across the slope of the GoM (Wei et al., 2010). The seasonally pulsed character of organic input and other stochastic food sources (such as large whale falls) regulate the population dynamics of responding deep-sea species (Gooday et al., 1990; Kalogeropoulou et al., 2010; Soto et al., 2010; Rowe, 2013). In the GoM the seasonal variation of the input of particulate organic carbon (POC) is enhanced by surface mixing in winter (Biggs et al., 2008), not the bloom related to spring.

Emerging new evidence indicates that the biota of the deepsea might respond to environmental change (Glover and Smith, 2003; Glover et al., 2010). But time series sampling of the deep-sea fauna has been confined mainly to the abyssal NE Pacific and NE Atlantic (Smith and Druffel, 1998; Ruhl et al., 2008; Billet et al., 2010; Laguionie-Marchais et al., 2013). Deep-sea benthos also appear to respond to climate change. There is evidence for this in the fossil record of ostracods and foraminiferans (Yasuhara et al., 2014) and abrupt decreases in temperature in the Mediterranean between 1992 and 1994 were with a significant decrease in nematode abundance (Danovaro et al., 2004).

The northern Gulf of Mexico environment has seemingly been relatively stable over the past several decades (Wei et al., 2012 b). The deep water hydrographic properties (temperature, salinity, nutrients, and dissolved oxygen) are unchanged over the past 40 years (Jochens and DiMarco, 2008). Remotely sensed sea-surface chlorophyll and POC flux vary seasonally but have exhibited little inter-annual variation (Biggs et al., 2008). Thus we might expect the benthic fauna would not have changed over time. Indeed, a long-term study of the fish fauna in deep Gulf of Mexico (Wei et al., 2012 b) suggests that there has been little temporal change in zonation patterns for the last several decades.

In this paper, we attempt to assess the long-term (two decades) change in deep-sea polychaete species composition by comparing two benthic studies in the deep Gulf of Mexico: Deep Gulf of Mexico Benthos (DGoMB) program (2000-2002) and the earlier Northern Gulf of Mexico Continental Slope (NGoMCS) study (1983-1985). Determination of long-term change is important for assessing impacts of oil and gas exploration and production, possible expansion of bottom trawling off the continental shelf and the somewhat slower and perhaps more subtle effects of climate.

4.2 Methods

4.2.1 Locations selections and samples processing

All the samples were taken with a GOMEX box corer, as described by Boland and Rowe (1991). The earlier samples (1983-85) were taken with a model whose box covered an area measuring 20 x 30 cm, whereas the latter samples (2000-02) were taken with a box covering an area measuring 45 x 45 cm. The latter samples covered an area of 0.17 m^2 after sub-samples had been removed for associated sediment analyses. Sample sieving at sea utilized a 300μm mesh sieve in both studies (Hubbard, 1995; Wei et al., 2010). Sieved material was fixed in 10% buffered formalin, stained with Rose Bengal, and sorted in the laboratory to major invertebrate taxa.

The polychaete annelids in the 1983-85 were then separated to species by Guinn Fain Hubbard (Hubbard, 1995) and archived in the collections first at Texas A&M University in College Station and later at Texas A&M at Galveston, where they remain at this time. The polychaetes in the 2000-2002 samples were separated to species by Ms. Yuning Wang, under the supervision of Dr. Hubbard at the time. They too are now archived in the collections at Texas A&M at Galveston.

Nine sites (Fig. 4.1: C1,C4,C7,W1,W2,W3,W4,WC5,WC12) were sampled in both studies (1983-85 and 2000-02), representing central (C), Western (W) and West Central (WC) transects on the upper continental slope.

Locations of sampling sites were displayed in Fig. 4.1 and Table 4.1.

It is possible that the data from 1983-85 could contain variations that are responses to different seasons. Sites C1 and C4 were taken in fall 1983 and spring and fall 1984. Samples at C7 were obtained in the fall of 1984, WC5 and WC12 were sampled in the summer of 1985, and W1 to W4 were sampled in spring 1984.

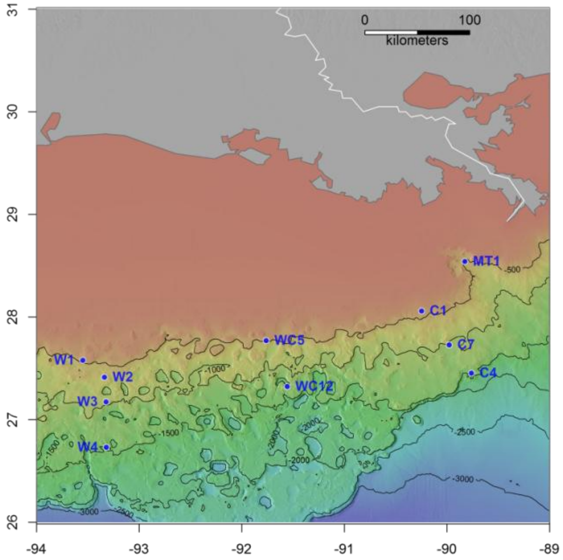

Fig. 4.1 Sampling locations at 9 sites that were repeated two times from 1983-85 to 2000 to 2002.The locations use the 2000 DGoMB designations (see Table 4.1).

Table 4.1 Locations and sampling depths of continental slope repeated sampling

DGoMB (2000 to 2003)				NGoMCS (1983 to 1985)			
Site	Lat	Lon	Depth(m)	Site	Lat	Lon	Depth(m)
C1	28.06	-90.25	335	C1	28.06	-90.25	359
C4	27.45	-89.76	1454	C4	27.47	-89.78	1412
C7	27.73	-89.98	1074	C7	27.74	-89.99	1021
W1	27.58	-93.55	379	W1	27.58	-93.55	371
W2	27.41	-93.34	625	W2	27.42	-93.34	604
W3	27.17	-93.32	860	W3	27.18	-93.32	854
W4	26.73	-93.32	1420	W4	26.74	-93.32	1410
WC5	27.77	-91.76	400	WC5	27.78	-91.77	324
WC12	27.32	-91.56	1168	WC12	27.33	-91.55	1280

There should be no seasonal response in the 2000-02 data because all the samples were obtained in June, except C7, which was sampled in May of 2000 as well.

4.2.2 Data analysis

Biodiversity was estimated for each replicate using the Rarefaction Index Es(n) (Sanders, 1968), where Es(n) is the expected number of species in a sample of n individuals. The entire species-sample matrix was square-root transformed before multivariate analysis. CLUSTER was utilized to illustrate zonation pattern via the Bray-Curtis similarity matrix. Similarity percent contribution (SIMPER) was used to find the species that contributed the most to the dissimilarities between groups.

Polychaete feeding types were determined based on categories described by Fauchald and Jumars (1979). Regression of abundance and Es(50) against depth were created by SigmaPlot 10.0.

Species distributions as a function of depth were plotted by MATLAB 2014. Es(50) and multivariate analysis were carried out by PRIMER 6.0.

Depth was used as the independent variable because most community parameters vary significantly as a function of depth or some variable that is correlated with it.

4.3 Results

4.3.1 Environmental variables

Temperature varied from ca. 10 to 13^{o} C at the shallowest upper slope locations and then descended to a stable 4^{o} C at the deepest locations at 1.4 km (Fig. 4.2). The input of detrital organic matter (POC) declined markedly across the depth gradient of the upper slope as well, from 20 to 37 mg C m^{-2} d^{-1}on the upper slope and then descends down to ca. 7 mg C m^{-2} d^{-1} at the mid-slope depths of 1.4 km (Fig. 4.3) (from Biggs et al., 2008).

Percent sand in the sediments also exhibited wide variations at the shallow sites (from ca. 1% up to 40%) but this stabilized at around 5 to 15% below about 1 km depth (Fig. 4.4).

Oxygen concentrations in the bottom water at all study sites were directly related to depth, reflecting the shallow locations where the oxygen minimum of the water column impinges on the sea floor (Fig. 4.5).

The values varied from a minimum of ca. 2.5 ml/L, which is low but not considered hypoxic, up to highs of 4.5 to 5.0 ml/L, which are characteristic of the entire GoM at all depths (> 1.5 km) (Jochens and DiMarco, 2008).

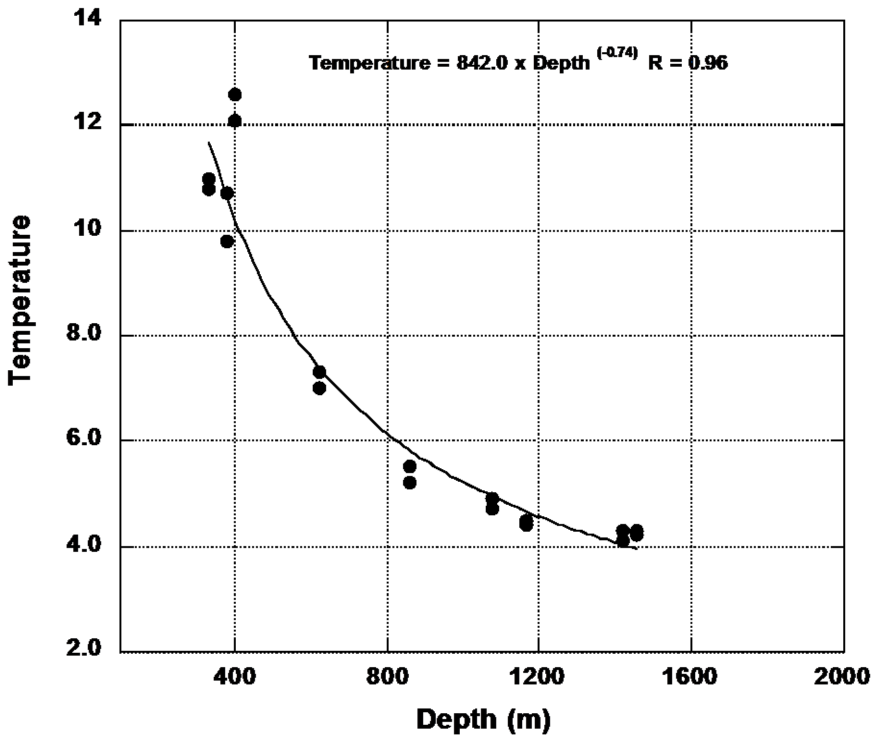

Fig. 4.2 Temperature in the bottom water at the locations sampled (Table 4.1 and Fig. 4.1).Sources: Minerals Management Services archived data available at www.BOEM.gov.

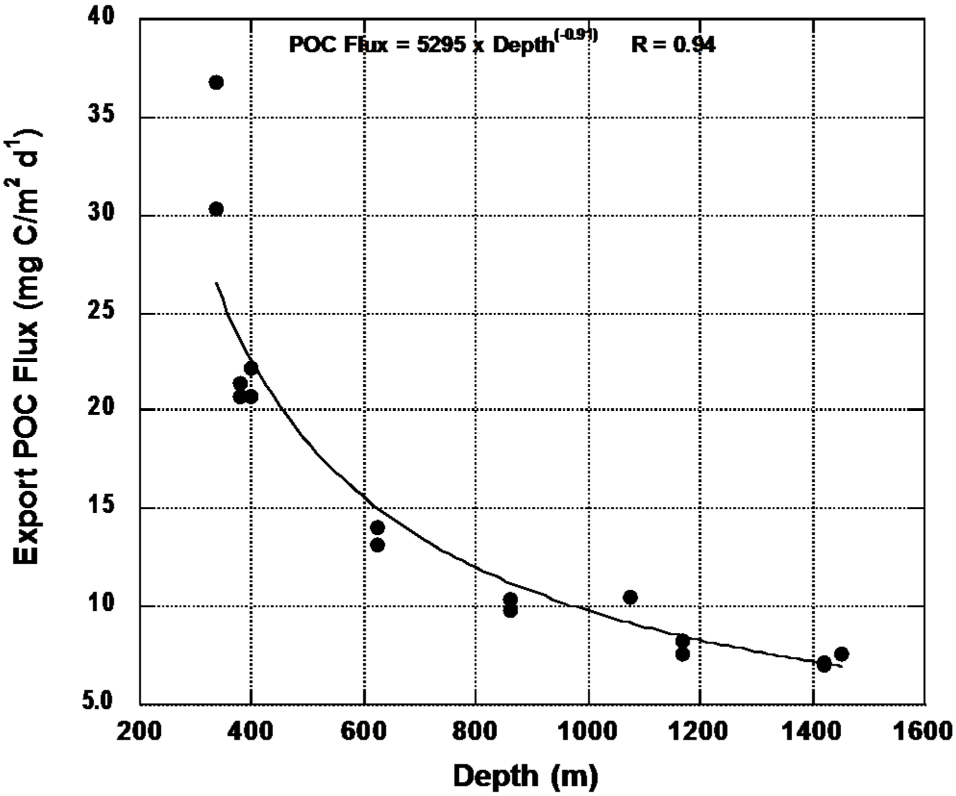

Fig. 4.3 Input of organic carbon detritus to the sea floor at the locations in Fig. 4.1 and Table 4.1 (estimated in Biggs et al., 2008).

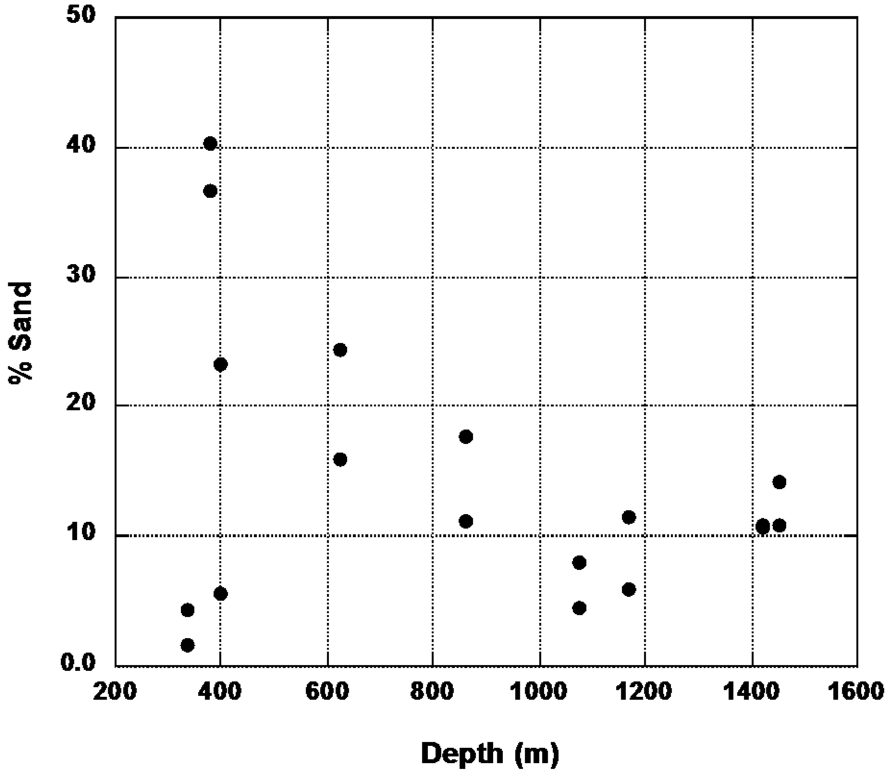

Fig. 4.4 Percent sand at each location on the upper slope (Fig. 4.1 and Table 4.1). Archived by the BOEM.gov website, from Rowe and Kennicutt, (2008) and NGoMSC at BOEM.gov.

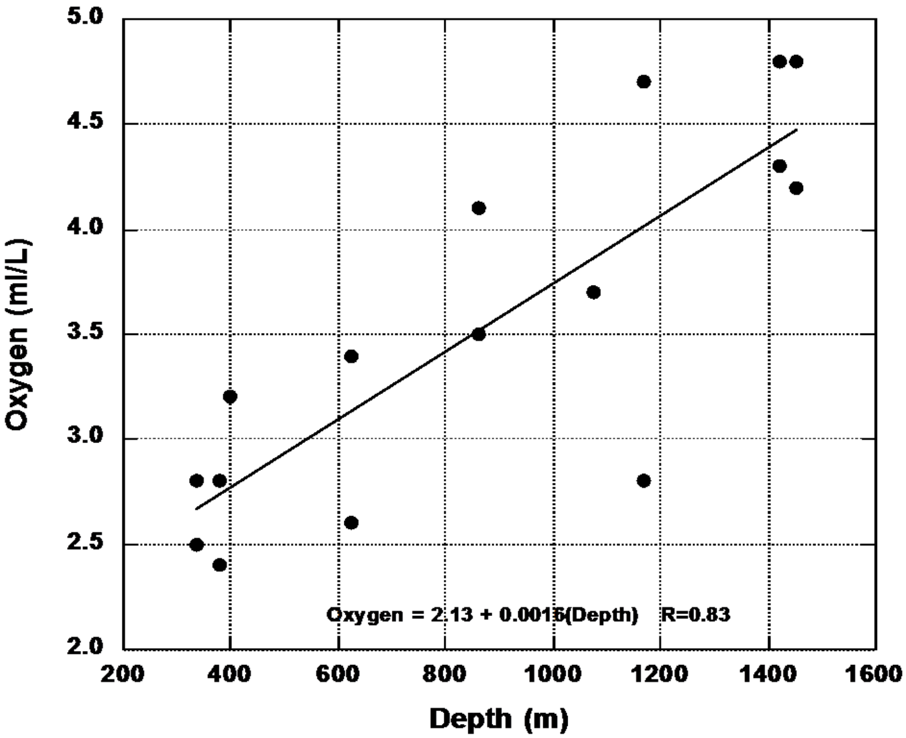

Fig. 4.5 Bottom water oxygen concentration (ml/L) at the locations in Fig. 4.1 and Table 4.1. Data from Rowe and Kennicutt (2008) as well as archived at BOEM.gov and discussed in Jochens and DiMarco (2008).

4.3.2 The fauna of the upper continental slope: transects C,W and WC

The overall mean abundances (number m^{-2}) (Fig. 4.6) and mean diversities (Es(50)) (Fig. 4.7) of the two data sets were statistically no different between 1983- 85 [NGoMCS (1707.4± 799.6 inds./m^2, Es(50)= 21.02± 3.6)] and 2000-02 [DGoMB (abundance: 1416.8± 952.0 inds./m^2, Es(50): 24.7± 4.1), ($p > 0.05$)].

The regressions of abundances and Es(50) against depth (Fig. 4.6 and 4.7) in the two time periods varied widely but the two were also not statistically different. Abundances decreased with depth linearly (Fig. 4.6), whereas diversity reached its peak value at ~900 m depth at W3 and then decreased with depth (Fig. 4.7).

Although there was no convincing statistical evidence that either of relationships were different as a function of 'time', the diversity of 8 of the 9 locations was higher in the more recent data (2000-02), whereas the abundances were higher at 7 of the 9 locations of the older data (1983-85). Likewise, the highest diversity (at W3) was among the lowest in abundances.

Of the ten dominant species (most abundant) (Table 4.2), 50% were identical within two studies: *Spionidae* sp., *Litocorsa antennata, Maldanidae* sp., *Aricidea suecica* and *Spiophanes berkeleyorum* (Table 4.2). Nine out of the ten were deposit feeders, the exception being *Litocorsa antennata*, considered omnivorous (Fig. 4.8). Deposit feeders

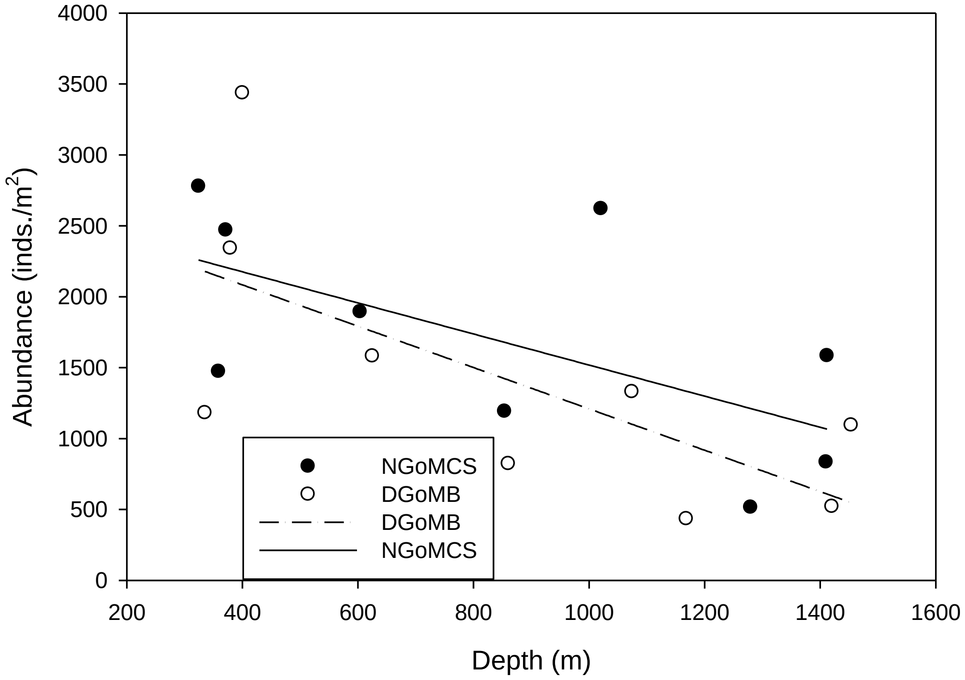

Fig. 4.6 Linear regression of polychaete abundance against depth. Black dots and solid line represent 1983-85 NGoMCS values and regression line (Y= 2919.9-1.1X, R^2= 0.37, p= 0.08). White dots and dashed line represent 2000-02 DGoMB abundances and regression line (Y= 2666.2-1.5X, R^2= 0.46, $p < 0.05$).

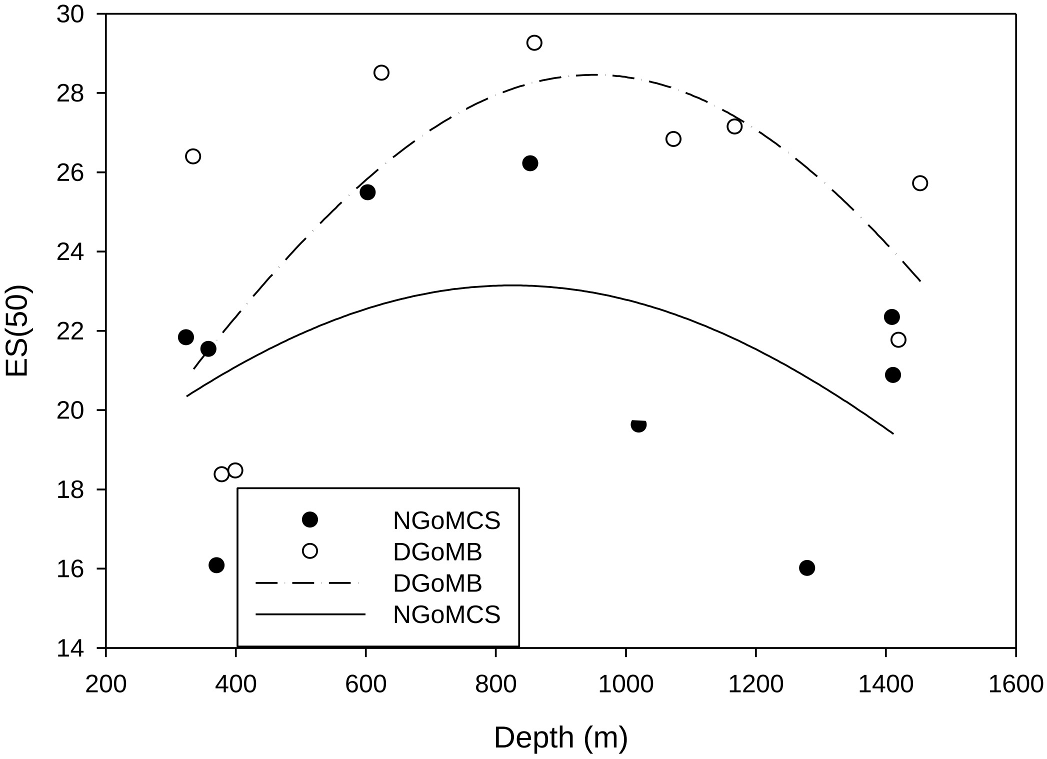

Fig. 4.7 Gaussian peak regression of polychaete diversity (Es(50)). Black dots and solid line indicate 1983-85 NGoMCS values and regression line ($Y = 23.1e^{[-0.5(\frac{X-825.2}{986.5})^2]}$, R^2=0.14,p=0.08). White dots and dashed line indicate 2000-02 DGoMB abundances and regression line ($Y = 28.5e^{[-0.5(\frac{X-950.2}{791.4})^2]}$, R^2=0.45, p<0.01)

and non-selective) constituted the majority (70%) in both studies. Shared dominant species had somewhat similar distribution patterns, with a few small differences (Fig. 4.9, Table 4.2). *Maldane* sp.A was rarely found in the more recent 2000-02 DGoMB samples, but in the older NGoMCS study it was abundant at C7, along with several at C4. *Prionospio cristata* was never sampled in the older 1983-85 samples (NGoMCS), but it reached up to1751 inds./m^2 at WC5 in 2000-02 DGoMB samples.

Another dominant species in 1983-85 was *Aurospio dibranchiate*, but it was rarely sampled in DGoMB in 2000. These high values are reflected in the high densities in Fig. 4.5. In general, the dominants occurred together along the depth gradient (Fig. 4.9), but three of them appeared only in one of the data sets (*P. cristata*, *A. dibranchiate* and *Maldane* sp A).

Multivariate analysis (CLUSTER and SIMPROF) on pooled data identified six groups ($p< 0.05$) with 35% or greater similarity in species composition (Fig. 4.10).Groups from left to right were Group 1: only D-WC5; Group 2: the 2000-02 western locations at mid-slope depths (D-W3, D-W4, D-WC12); Group 3: 1983-85 sampling at the same locations (N-W3, N-W4, N-WC12); Group 4: upper slope (< 650 m) locations with a mixture of both older and more recent samples (N-WC5, N-W1, N-W2, D-W1, D-W2); Group 5 and Group 6: all from the central transect sites but separated neatly into the older and the more recent samples (N-C1, N-C4, N-C7 versus D-C1, D-C4, D-C7). Note

Table 4.2. Dominant species and their abundances in by study date.

1983-85 NGoMCS	Ave. Abundance(inds./m^2)	2000-02 DGoMB	Ave. Abundance(inds./m^2)
Maldane sp.A	203.5	*Prionospiocristata*	139.6
Spionidae sp.	126.9	*Litocorsaantennata*	115.9
Litocorsaantennata	118.9	*Spionidae sp.*	113.7
Maldanidae sp.	71.0	*Maldanidae sp.*	80.3
Aurospiodibranchiate	55.7	*Aricideasuecica*	35.2
Aricideasuecica	53.0	*Tachytrypane sp. A*	34.3
Prionospioehlersi	46.3	*Prionospio sp.*	31.2
Ampharetidae sp.	43.8	*Tharyxmarioni*	29.4
Spiophanesberkeleyorum	36.1	*Aedicira sp.*	20.1
Prionospiocirrifera	29.4	*Spiophanesberkeleyorum*	17.4

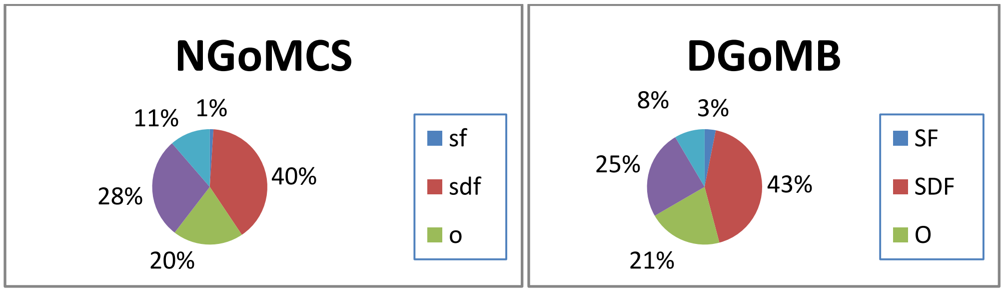

Fig. 4.8 Percentage distribution of polychaete feeding types in the older 1983-85 NGoMCS versus the more recent 2000-02 DGoMB study. The most abundant feeding types were selective deposit feeders (SDF) and non-selective deposit feeders (NSDF), which constituted about 70% total abundance in both studies. Omnivores (O),Carnivores (C) and Suspension filter feeders (SF), whose percentages were also similar between the two studies, constituted the remaining 30% of abundance.

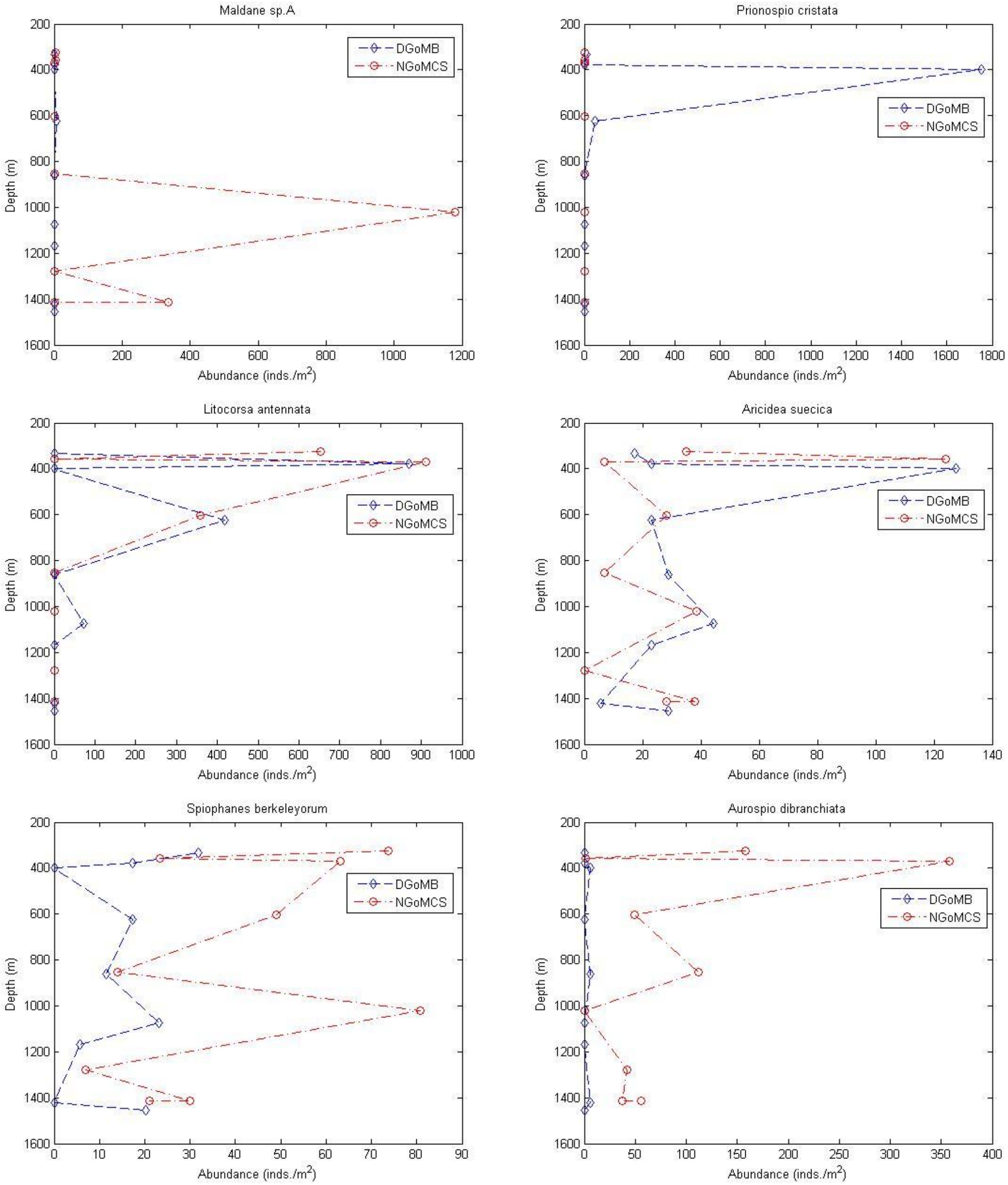

Fig. 4.9 Depth distribution of the abundances of dominant species. Blue diamonds and lines indicate more recent 2000-02 DGoMB abundances; red circles and lines indicate older 1983-85 NGoMCS abundances.

that if the similarity criterion were lowered from 35% to 22%, then all the sites would be grouped together as a single “middle to upper continental slope” group. The Central transect and middle slope sites were separated by ‘study’ (older versus more recent) but below the 35% similarity level, while the upper slope sites from the two different studies were grouped together.

According to SIMPER, the average dissimilarity between groups 2 and 3 (the 600 down to 1400 m or mid-slope sites) was 75.8%, and *Aurospio dibranchiata* contributed 5.9% to that dissimilarity while *Scolelepis* sp. contributed 4.13%. Dissimilarity between Groups 5 and 6, the central transect sites, was 74.8%. There, the bamboo worm *Maldane* sp.A contributed 19.3% to the dissimilarity.

The entire set of samples clustered into 6 significant groups at 35% similarity. The mid-slope depths cluster into two groups separated by time (D vs N in the blue squares). The upper slope however is a mixture of D and N (dark blue triangles). The central transect is split into two as well, again in terms of the 1983-85 vs 2000-02 studies. That is, while all the C line samples clustered together at > 35% similarity, they could still be clustered further by 'time' as opposed to depth. Thus the mid-slope samples of W and WC and all of C could be separated on the basis of time, whereas the upper slope of W and WC could not be separated by time.

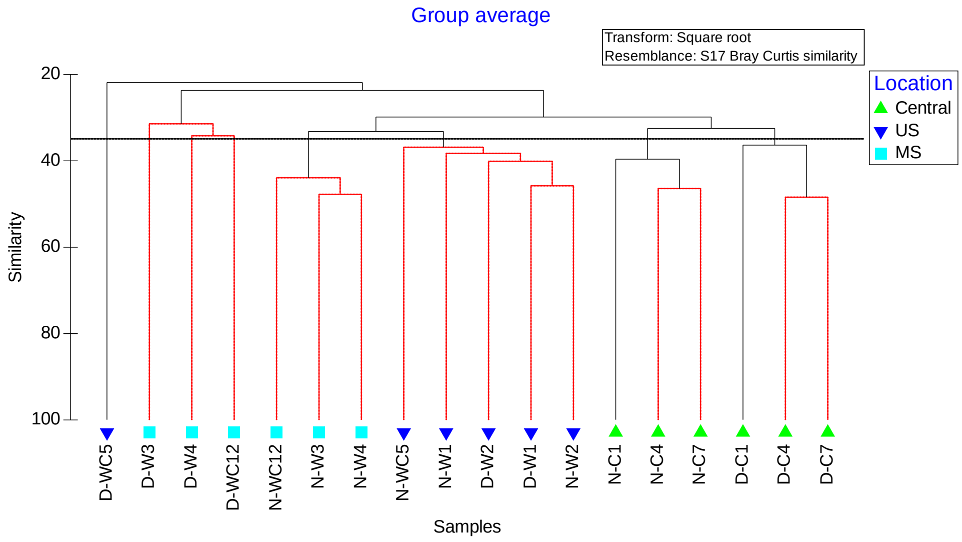

Fig. 4.10 Cluster dendrogram with Simprof test of all sites sampled. Green triangles: Central transect. Blue triangles: upper slope sites (depth shallower than 650m). Blue squares: middle slope sites (deeper than 650 m). D is 2000-02 and N is 1983-85 samples. Black lines indicate significant ($p< 0.05$) clusters, red links are not. The horizontal black line marks the 35% similarity in species between samples.

4.4 Discussion

4.4.1 Stability of deep-sea polychaete populations

The conventional descriptors of abundance, diversity and feeding types of polychaete assemblages werere markably similar between the two studies two decades apart. This implies that recruitment and mortality had remained fairly constant over that period and that no particularly significant change in the environmental conditions had occurred.

Species-level analyses however revealed some subtle but surprising differences.The separation of the two groups was not a function of a general change in the overall species composition per se, but rather of the pronounced but intermittent dominance by single species. That is, single species in great abundance caused the dissimilarities. And those species were never the same. For example: *Maldane* sp.A and *Prionospio cristata* were the two most abundant species in the two studies; their dominance resulted from a sudden peak at some sites, but in other locations their values were very low (Fig. 4 9).

The C transect sites were separated from the other two (W and WC) mainly because of high numbers of the bamboo worm *Maldane* sp.A (19.3% of dissimilarity). The single outlier on the upper slope (D-WC5) had minimal similarity with all the other groups because of its high abundance of *Prionospio cristata*, as noted in earlier work on zonation patterns (Wei et al., 2010).

4.5 Conclusions

In general, the upper and middle continental slope polychaete worm fauna remained remarkably stable (>35% similarity in species composition) for two decades, with the exceptions being unpredictable, single occurrences of dense populations of single species. The majority of the early 1983-85 samples had greater densities but lower diversity than the 2000-02 samples, but the differences were not statistically significant. Cluster analysis suggested that small changes in species composition were related to time rather than location or depth. More intense sampling in time and space will be necessary to validate observations of the constancy of populations over longer periods or to elucidate possible seasonal variations (Rowe, 2013) and estimates of secondary production (Rowe et al., 2008), but this information is important for assessing future natural or anthropogenic alternations of the upper continental slope transition zone.

CHAPTER V

CONCLUSION

Benthic communities of the continental shelf and slope undergo various types of natural or anthropogenic disturbance or stress. In shallow water, benthic communities are influenced by organic enrichment, hypoxia, hurricanes, bottom trawling, heavy metals et al. In the deep sea, where the survival of benthos relies heavily on descending organic particles, benthic communities are dynamic and can be affected by the seasonality of sinking particles, stochastic food falls, long term climate change, submarine sediment movement and accidental deep-sea oil spills. Polychaetes, as the most representative group of the benthic animals, are very responsive to the above-mentioned events. They deserve more research in their dynamic responses to various disturbances and stress.

The 2010 deepwater horizon (DWH) oil spill was unprecedented for the amount of oil released and its depth (1500m). Sediments 5 to 9 km away from the spill site were sampled five months after the event to study the community structure of potential oil-affected polychaetes in comparison with historical data to document any shifts in polychaete species composition. According to our results, the DWH oil spill had a measurable impact on polychaetes that could be demonstrated by the following evidence: 1) Numbers of species’ abundance dropped to almost half of the pre-spill levels. Diversity was also significantly lower than the historical data. 2) Deposit feeders maintained their dominance, but the abundance decreased to almost one fourth of the pre-spill values. Sigalionidae, a carnivore, increased in abundance, a possible response to the accumulation of PAHs in the sediment. 3) Radical shift in species composition after the oil spill was revealed by CLUSTER analysis.

The Gulf of Mexico hypoxic zone is the world's second largest hypoxic region. The low oxygen stress on polychaetes' size and community structure were explored by a 8-years survey on benthic animals inhabiting the hypoxic zone using Normalized Biomass Size Spectra (NBSS). While the mean body size over the entire study was 3.99± 4.66 mg wet weight per individual, the mean ranged from 2.97± 2.87 mg during consistently hypoxic conditions (< 2 mg/L) to a high of 7.13± 7.60 mg ($p < 0.01$) under oxic conditions (> 2 mg/L). The decline in size was due to the elimination of large species under hypoxic conditions (< 2 mg/L), not a reduction in size within species. At 'severe' levels of hypoxia (< 1 mg/L), the smallest species also declined in abundance, whereas the ubiquitous 'medium sized' *Paraprionospio pinnata* flourished. The dominance of 'medium sized' *Paraprionospio pinnata* in the worst oxygen depletion condition (< 1 mg/L) eliminated the usual linear decline of the NBSS.

The upper and middle continental slope polychaete worm fauna remained remarkably stable (> 35% similarity in species composition) for two decades, with the exceptions being unpredictable, single occurrences of dense populations of single species. The majority of the early 1983-85 samples had greater densities but lower diversity than the 2000-02 samples, but the differences were not statistically significant. Cluster analysis suggested that small changes in species composition were related to time rather than location or depth. More intense sampling in time and space will be necessary to validate observations of the constancy of populations over longer periods or to elucidate possible seasonal variations and estimates of secondary production, but this information is important for assessing future natural or anthropogenic alternations of the upper continental slope transition zone.

REFERENCES

Antonio, F.J., Mendes, R.S., Thomaz, S.M., 2011. Identifying and modeling patterns of tetrapod vertebrate mortality rates in the Gulf of Mexico oil spill. Aquatic Toxicology. 105, 177-179.

Aronson, R.B., Thatje, S., Clarke, A., Peck, L.S., Blake, D.B., Wilga, C.D., Seibel, B.A., 2007. Climate change and invasibility of the Antarctic benthos. Annual Review of Ecology, Evolution, and Systematics. 38, 129-154.

Baguley, J., Montagna, P., Hyde, L., Rowe, G., 2008. Metazoan meiofauna biomass and weight-dependent respiration in the northern Gulf of Mexico deep sea. Deep-Sea Research II. 55, 2607-2616.

Baguley, J., Montagna, P., Lee, W., Hyde, L., Rowe, G., 2006a. Spatial and bathymetric trends in Harpacticoida (Copepoda) community structure in the Northern Gulf of Mexico deep sea. Journal of Experimental Marine Biology and Ecology. 320, 327-341.

Baguley, J., Montagna, P., Hyde, L., Kalke, R., Rowe, G., 2006b. Metazoan meiofauna abundance in relation to environmental variables in the northern Gulf of Mexico deep sea. Deep-Sea Research I. 53, 1344-1362.

Baustian, M.M. and Rabalais, N.N., 2009. Seasonal composition of benthic macrofauna exposed to hypoxia in the northern Gulf of Mexico. Estuaries and Coasts. 32, 975-983.

Bianchi, T.S., Allison, M.A., Canuel, E.S., McKee, B.A., Wakeham, S.B., 2006. Evidence for rapid export of riverine and shelf-derived organic matter into Mississippi Canyon. Eos Transactions American Geophysical Union. 87, 572-573.

Biggs, D.C., Hu, C., Müller-Karger, F.E., 2008. Remotely sensed sea-surface chlorophyll and POC flux at Deep Gulf of Mexico Benthos sampling stations. Deep-Sea Research II. 55, 2555-2562.

Bik, H.M., Halanych, K.M., Sharma, J., Thomas, W.K., 2012. Dramatic shifts in benthic microbial eukaryote communities following the Deepwater Horizon Oil Spill. PLoS ONE. 7, e38550.

Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, I.G., 2010. Long-term change in the abyssal NE Atlantic: The ‘Amperima Event’ revisited. Deep-Sea Research II. 57, 1406-1417.

Boland, G.S. and Rowe, G.T., 1991. Deep-sea benthic sampling with the GOMEX box corer. Limnology and Oceanography. 36, 1015-1020.

Brooks, K.M., Stierns, A.R., Backman, C., 2004. Seven year remediation study at the Carrie Bay Atlantic Salmon (*Salmo* salar) farm in the Broughton Archipelago, British Columbia, Canada. Aquaculture. 239, 81-123.

Carney, R., 2005. Zonation of deep-sea biota on continental margins. Oceanography and Marine Biology: An Annual Review. 43, 211-279.

Carvalho, R., Wei, C-L., Rowe, G.T., Schulze, A., 2013. Complex depth-related patterns in taxonomic and functional diversity of polychaetes in the Gulf of Mexico. Deep-Sea Research I. 80, 66-77.

Chapelle, G. and Peck, L., 1999. Polar gigantism dictated by oxygen availability. Nature. 399, 114-115.

Chivas, A.G., Narayanaswamy, B., Lamont, P., Dale, A., 2013. Changes in polychaete standing stock and diversity on the northern side of Senghor Seamount (NE Atlantic). Biogeosciences. 10, 3535-3546.

Clapham, M.E. and Karr, J.A., 2012. Environmental and biotic controls on the evolutionary history of insect body size. Proceedings of the National Academy of Sciences of the United States of America. 109, 10927-10930.

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology. 366, 56-69.

Clarke, K.R. and Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd ed. PRIMER-E Ltd, Plymouth, UK.

Clauset, A. and Erwin, D.H., 2008. The evolution and distribution of species body size. Science. 321, 399-401.

Conlan, K.E., Kim, S.L., Lenihan, H.S., Oliver, J.S., 2004. Benthic changes during 10 years of organic enrichment by McMurdo Station, Antarctica. Marine Pollution Bulletin. 49, 43-60.

Damuth, J., 1991. Of size and abundance. Nature. 351, 268-269.

Danovaro, R., Dell'Anno, A., Pusceddu, A., 2004. Biodiversity response to climate change in a warm deep sea. Ecology Letters. 7, 821-828.

Dauvin, J.C., 1998. The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Marine Pollution Bulletin. 36, 669-676.

Dean, H.K., 2008. The use of polychaetes (Annelida) as indicator species of marine pollution: a review. Revista de Biologia Tropical. 56, 11-38.

Dernie, K.M., Kaiser, M.J., Warwick, R.M., 2003. Recovery rates of benthic communities following physical disturbance. Journal of Animal Ecology. 72, 1043-1056.

Diaz, R.J. and Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science. 321, 926-929.

Dutrieux, E., Martin, F., Guelorget, O., 1989. Oil pollution and polychaeta in an estuarine mangrove community.Oil and Chemical Pollution. 5, 239-262.

Etienne, R.S., de Visser, S.N., Janzen, T., Olsen, J.L., Olff, H., Rosindell, J., 2012. Can clade age alone explain the relationship between body size and diversity? Focus. 6, 170-179.

Fauchald, K. and Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology- An Annual Review. 17, 193-284.

Felder, D.L. and Camp, D.K.(Eds.), 2009. Gulf of Mexico Origin, Waters, and Biota. Vol. 1, Biodiversity.1st.ed. College Station, Texas, Texas A&M University Press.

Gage, J.D., 2004. Diversity in deep-sea benthic macrofauna: the importance of local ecology, the larger scale, history and the Antarctic. Deep-Sea Research II. 51, 1689-1708.

Gaston, G.R., 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. Estuarine Coastal and Shelf Science. 20, 603-613.

Giessing, A.M.B., Mayer, L.M., Forbes, T.L., 2003. Synchronous fluorescence spectrometry of 1- hydroxypyrene: a rapid screening method for identification of PAH exposure in tissue from marine polychaetes. Marine Environmental Research. 56, 599-615.

Gin, K.Y.H., Huda, M.D.K., Lim, W.K., Tkalich, P., 2001. An oil spill-food chain interaction model for coastal waters.Marine Pollution Bulletin. 40, 590-597.

Glover, A.G., Smith, C.R., 2003. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. Environmental Conservation. 30, 219-224.

Glover, A.G., Gooday, A.J., Bailey, D.M., Billett, D.S., Chevaldonné, P., et al., 2010. Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. Advances in Marine Biology. 58, 1-95.

Gomez Gesteira, J.L. and Dauvin, J.C., 2000. Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. Marine Pollution Bulletin. 40, 1017-1027.

Gomez Gesteira, J.L., Dauvin, J.C., Salvande Fraga, M., 2003. Taxonomic level for assessing oil spill effects on soft-bottom sublittoral benthic communities. Marine Pollution Bulletin. 46, 562-572.

Gómez-Canchong, P., Blanco, J.M., Quiñones, R.A., 2013. On the use of biomass size spectra linear adjustments to design ecosystem indicators. Scientia Marina. 77, 257-268.

Gomez Gesteira, J.L. and Dauvin, J.C., 2005. Impact of the Aegean Sea oil spill on the subtidal fine sand macrobenthic community of the Ares-BetanzosRia (Northwest Spain). Marine Environmental Research. 60, 289-316.

Gooday, A.J., Turley, C.M., Allen, J.A., 1990. Responses by benthic organisms to inputs of organic material to the ocean floor: A review [and discussion}. Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences**.** 331, 119-138.

Harper Jr., D.E., McKinney, L.D., Salzer, R.R., Case, R.J., 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. Contribution in MarineScience. 24, 53-79.

Harrison, J.F. and Haddad, G.G., 2011. Effects of oxygen on growth and size: synthesis of molecular, organismal, and evolutionary studies with *Drosophila melanogaster*. The Annual Review of Physiology. 73, 95-113.

Hubbard, G.F.,1995. Benthic polychaetes from the Northern Gulf of Mexico continental slope. Doctor of Philosophy thesis. Texas A&M University, College Station, Texas.

Ingole, B., Sivadas, S., Goltekar, R., Clemente, S., Nanajkar, M., et al., 2006. Ecotoxicological effect of grounded MV River Princess on the intertidal benthic organisms off Goa. Environment International. 32, 284-291.

Jochens, A.E. and DiMarco, S.F., 2008. Physical oceanographic conditions in the deepwater Gulf of Mexico in summer 2000-2002. Deep-Sea Research II. 55, 2541-2554.

Kalogeropoulou, V., Bett, B.J., Gooday, A.J., Lampadariou, N., Martinez Arbizu, P., Vanreusel, A., 2010. Temporal changes (1989-1999) in deep-sea metazoan meiofaunal assemblages on the Porcupine Abyssal Plain, NE Atlantic. Deep-Sea Research II. 57, 1383-1395.

Keeley, N.B., Forrest, B.M., Macleod, C.K. 2013. Novel observations of benthic enrichment in contrasting flow regimes with implications for marine farm monitoring and management. Marine Pollution Bulletin. 66, 105-116.

Kerr, S. and Dickie, L., 2001. The biomass spectrum: a predator-prey theory of aquatic production. Columbia University Press, New York.

Kingston, P.F., 2002**.** Long-term Environmental Impact of Oil Spills. Spill Science & Technology Bulletin. 7, 53-61.

Laguionie-Marchais, C., Billett, D.S.M., Paterson, G.L.D., Ruhl, H.A., Soto, E.H., et al., 2013. Inter-annual dynamics of abyssal polychaete communities in the North East Pacific and North East Atlantic-A family-level study. Deep-Sea Research I. 75, 175-186.

Lamont, P.A. and Gage, J.D., 2000. Morphological responses of macrobenthic polychaetes to low oxygen on the Oman continental slope, NW Arabian Sea. Deep-Sea Research II. 47, 9-24.

Lauerman, L.M.L., Kaufmann, R.S., Smith Jr., K.L, 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I. 43, 1075-1079, 1081-1103.

Lee, L.H. and Lin, H.J., 2013. Effects of an oil spill on benthic community production and respiration on subtropical intertidal sandflats. Marine Pollution Bulletin. 73, 291-299.

Levin, L.A. and Sibuet, M., 2011. Understanding continental margin biodiversity: A new imperative. Annual Review of Marine Science. 4, 79-112.

Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., Neira, C., Rabalais, N.N., Zhang, J., 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences. 6, 2063-2098.

Linse, K., Barnes, D.K.A., Enderlein, P., 2006. Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. Deep-Sea Research II. 53, 921-931.

Magurran, A.E., Queiroz, H.L., Hercos, A.P., 2013. Relationship between evenness and body size in species rich assemblages. Biology Letters. 9, 20130856.

Margalef, R., 1968. Perspectives in Ecological Theory. University of Chicago Press, Chicago.

McClain, C.R. and Rex, M.A., 2001. The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: an application of quantile regression. Marine Biology. 139, 681-685.

Meador, J.P., Stein, J.E., Reichert, W.L., Varanasi, U., 1995. Bioaccumulation of polycyclic aromatic hydrocarbons by marine organisms. Reviews of Environmental Contamination and Toxicology. 143, 79-165.

Mohammad, M.B.M.,1974. Effect of chronic oil pollution on a polychaete. Marine Pollution Bulletin. 5, 21-24.

Montagna, P.A., Baguley, J.G., Cooksey, C., Hartwell, I., Hyde, L.J., Hyland, J.L., Kalke, R.D., Kracker, L.M., Reuscher, M., Rhodes, A.C.E., 2013. Deep-sea benthic footprint of the Deepwater Horizon Blowout. PLoS ONE. 8, e70540.

Narayanaswamy, B.E., Bett, B.J., Gage, J.D., 2005. Ecology of bathyal polychaete fauna at an Arctic-Atlantic boundary (Faroe-Shetland Channel, north-east Atlantic). Marine Biology Research. 1, 20-32.

Nephin, J., Juniper, S.K., Archambault, P., 2014. Diversity, abundance and community structure of benthic macro- and megafauna on the Beaufort shelf and slope. PLoS ONE. 9, e101556.

Nunnally, C.C., Rowe, G.T., Thornton, D.C.O., Quigg, A., 2013. Sedimentary oxygen consumption and nutrient regeneration in the Gulf of Mexico hypoxic zone. Journal of Coastal Research, Special Issue.63: Understanding and Predicting Change in the Coastal Ecosystems of the Northern Gulf of Mexico, 84-96.

OSAT, 2010. Summary report for sub-sea and sub surface oil and dispersant detection: sampling and monitoring. Operational Science Advisory Team (OSAT).

Available at: http://www.restorethegulf.gov/sites/default/files/documents/pdf/OSAT_Report_FINAL_17DEC.pdf

Pearson, T.H. and Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review. 16, 229-311.

Pequegnat, W.E., Gallaway, B.J., Pequegnat, L.H., 1990. Aspects of the ecology of the deep-water fauna of the Gulf of Mexico. American Zoologist. 30, 45-64.

Pielou, E.C., 1975. Ecological Diversity. Wiley-Interscience, New York.

Platt, T. and Denman, K., 1977. Organization in the pelagic ecosystem. Helgolander Wissenschaftliche Meeresuntersuchungen. 30, 575-581.

Platt, T. and Denman, K., 1978. The structure of pelagic ecosystems. Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer. 173, 60-65.

Polloni, P., Haedrich, R., Rowe, G.T., Clifford, C.H., 1979. The size-depth relationship in deep ocean animals. Internationale Revue der gesamten Hydrobiologie und Hydrographi. 64, 39-46.

Qian, Y., Sericano, J.L., Wade, T.L., 1998. Extraction and clean-up of sediments for trace organic analysis. In: Sampling and Analytical Methods of the National Status and Trends Program, Mussel Watch Project: 1993-1996 Update. NOAA Technical Memorandum NOS ORCA. 130, 94-97.

Quinones-Rivera, Z, Wissel, B., Rabalais, N., Justic, D., 2010. Effects of biological and physical factors on seasonal oxygen dynamics in a stratified eutrophic coastal ecosystem. Limnology and Oceanography. 55, 289-304.

Quiroga, E., Quinones, R., Palma, M., Sellanes, J., Gallardo, V.A., Gerdes, D., Rowe, G. T., 2005. Biomass size-spectra of macrobenthic communities in the oxygen minimum zone off Chile. Estuarine, Coastal and Shelf Science. 62, 217-231.

Rabalais, N.N., Smith, L.E., Harper, D.E., Justic, D., 2001a. Effects of seasonal hypoxia on continental shelf benthos. In Coastal hypoxia: Consequences for living resources and ecosystems, Coastal and Estuarine Studies. 58, Rabalais, N.N. and Turner, R.E.(Eds.), pp. 211-240, Washington, DC: American Geophysical Union.

Rabalais, N.N., Harper, Jr., D.E., Turner, R.E., 2001b. Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. In Coastal hypoxia: Consequences for living resources and ecosystems, Coastal and Estuarine Studies. 58, Rabalais, N.N. and Turner, R.E.(Eds.), pp. 115-128, Washington, DC: American Geophysical Union.

Rabalais, N.N., Turner, R.E., Scavia, D., 2002. Beyond science into policy: Gulf of Mexico hypoxia and the Mississippi River. Bioscience. 52, 129-142.

Rakocinski, C.F., 2009. Linking allometric macrobenthic processes to hypoxia using the Peters mass balance model. Journal of Experimental Marine Biology and Ecology. 381, S13-S20.

Rex, M. and Etter, R., 2010. Deep-Sea Biodiversity: Pattern and Scale. Harvard University Press, Cambridge.

Rhoads, D.C. and Germano, J.D., 1986. Interpreting long-term changes in benthic community structure: a new protocol. Hydrobiologia. 142, 291-308.

Rowe, G.T., Wei, C-H., Nunnally, C., Haedrich, R., Montagna, P., Baguley, J.G., Bernhard, J.M., Wicksten, M., Ammons, A., Briones, E.E., Soliman, Y., Deming, J.W., 2008. Comparative biomass structure and estimated carbon flow in food webs in the deep Gulf of Mexico. Deep-Sea Research II. 55, 2699-2711.

Rowe, G.T., 2013. Seasonality in deep-sea food webs- A tribute to the early works of Paul Tyler. Deep-Sea Research II. 92, 9-17.

Rowe, G.T. and Chapman, P., 2002. Continental shelf hypoxia: some nagging questions. Gulf of Mexico Science. 20, 153-160.

Rowe, G.T. and Kennicutt, M.C., 2008. Introduction to the Deep Gulf of Mexico Benthos Program. Deep Sea Research II. 55, 2536-2540.

Rowe, G.T., Polloni, P.T., Horner, S.G., 1974. Benthic biomass estimates from the northwestern Atlantic Ocean and the northern Gulf of Mexico. Deep Sea Research and Oceanographic Abstracts. 21, 641-650.

Ruhl, H.A., 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. Ecology. 88, 1250-1262.

Ruhl, H.A., Ellena, J.A., Smith, K.L., 2008. Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. Proceedings of the National Academy of Sciences. 105, 17006-17011.

Ryu, J., Khim, J.S., Kang, S.G., Kang, D., Lee, C.H., Koh, C.H., 2011. The impact of heavy metal pollution gradients in sediments on benthic macrofauna at population and community levels. Environmental Pollution. 159, 2622-2629.

Saiz-Salinas, J.I. and Ramos, A., 1999. Biomass size-spectra of macrobenthic assemblages along water depth in Antarctica. Marine Ecology Progress Series. 178, 221-227.

Samuelson, G.M., 2001. Polychaetes as indicators of environmental disturbance on subarctic tidal flats, Iqaluit, Baffin Island, Nunavut Territory. Marine Pollution Bulletin. 42, 733-741.

Sander, H.L., Hessler, R.R., Hampson, G.R., 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. Deep-sea Research. 12, 845-867.

Sanders, H.L., 1968. Marine benthic diversity: A comparative study. The American Naturalist. 102, 243-282.

Sanders, H.L., Grassle, J.F., Hampson, G.R., Morse, L.S., Garner-Price, S., Jones, C.C., 1980. Anatomy of an oil spill: Long term effects from the grounding of the barge Florida off West Falmouth, Massachusetts. Journal of Marine Research. 38, 265-380.

Sanders, H.L.,1968. Marine benthic diversity: A comparative study. The American Naturalist. 102, 243-282.

Santschi, P.H. and Rowe, G.T., 2008. Radiocarbon-derived sedimentation rates in the Gulf of Mexico. Deep-Sea Research II. 55, 2572-2576.

Sharma, J., Baguley, J., Bluhm, B., Rowe, G., 2011. Do meio- and macrobenthic nematodes differ in community composition and body weight trends with depth? PLoS ONE. 6, e14491.

Sheldon, R.W. and Parsons, T.R., 1967. A continous size spectrum from particulate matter in the sea. Journal of the Fisheries Research Board of Canada. 24, 909-915.

Singer, D., 2006. Size relationship of metabolic rate: Oxygen availability as the “missing link” between structure and function? Thermochimica Acta. 446, 20-28.

Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food limitation, ecosystem structure and climate change. Trends in Ecology and Evolution. 23, 518-528.

Smith, J.K.L. and Druffel, E.R.M., 1998. Long time-series monitoring of an abyssal site in the NE Pacific: an introduction. Deep-Sea Research II. 45, 573-586.

Soliman, Y. and Wade, T.L., 2008. Estimates of PAHs burdens in a population of ampeliscid amphipods at the head of the Mississippi Canyon (N. Gulf of Mexico). Deep-Sea Research II. 55, 2577-2584.

Somero, G.N., 1992. Biochemical ecology of deep-sea animals. Experientia. 48, 537-543.

Soto, E.H., Paterson, G.L.J., Billett, D.S.M., Hawkins, L.E., Galéron, J., Sibuet, M., 2010. Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean. Deep-Sea Research II. 57, 1396-1405.

Sprules, W.G. and Munawar, M., 1986. Plankton size spectra in relationship to ecosystem productivity, size and perturbation. Canadian Journal of Fisheries and Aquatic Sciences. 43, 1789-1794.

Tsutsumi, H., 1987. Population dynamics of Capitella capitata (Polychaeta; Capitellidae) in an organically polluted cove. Marine Ecology Progress Series. 36, 139-149.

Turner, R.E. and Rabalais, N.N., 1994. Coastal eutrophication near the Mississippi river delta. Nature. 368, 619-621.

Turner, R.E., Rabalais, N.N., Justic, D., 2008. Gulf of Mexico hypoxia: alternate states and a legacy. Environmental Science and Technology. 42, 2323-2327.

Uebelacker, J.M. and Johnson, P.G., 1984. Taxonomic Guide to the polychaetes of Northern Gulf of Mexico. Final Report to the Mineral Management Service, contract 14-12-001-29091. Barry M. Vittor&Associates, Mobile, Alabama.

Venturini, N., Pires-Vanin, A.M.S., Salhi, M., Bessonart, M., Muniz, P., 2011. Polychaete response to fresh food supply at organically enriched coastal sites: repercussion on bioturbation potential and trophic structure. Journal of Marine Systems. 88, 526-541.

Venturini, N. and Tommasi, L.R., 2004. Polycyclic aromatic hydrocarbons and changes in the trophic structure of polychaete assemblages in sediments of Todosos Santos Bay, northeastern, Brazil. Marine Pollution Bulletin. 48, 97-107.

Wade, T.L., Brooks, J.M., Kennicutt II, M.C., McDonald, T.J., Sericano, J.L., Jackson, T.J., 1993. GERG Trace Organics Contaminant Analytical Techniques. National Status and Trends Program for Marine Environmental Quality, NOAA Tech. Memo. NOS ORCA 71, Sampling and Analytical Methods of the National

Status and Trends Program National Benthic Surveillance and Mussel Watch Projects 1984-1992, Vol. IV Comprehensive Descriptions of Trace Organic Analytical Methods, Silver Spring, MD, pp. 121-129.

Wade, T.L., Sweet, S.T., Sericano, J.L., Guinasso Jr. N.L., Diercks, A-R., Highsmith, R.C., Asper, V.L., Joung, D., Shiller, A.M., Lohrenz, S.E., Joye, S.B., 2011. Analyses of Water Samples from the Deepwater Horizon Oil Spill: Documentation of the Sub-Surface Plume. In Monitoring and Modeling the Deepwater Horizon Oil Spill: A Record-Breaking Enterprise, Geophysical Monograph Series, vol. 195, Liu, Y.(ed.), pp. 77–82, AGU, Washington, D.C.

Wade, T.L., Soliman, Y., Sweet, S.T., Wolff, G.A., Presley, B.J., 2008. Trace elements and polycyclic aromatic hydrocarbons (PAHs) concentrations in deep Gulf of Mexico sediments. Deep-Sea Research II. 55, 2585-2593.

Wang, Y-N., 2004. Patterns in biodiversity and distribution of benthic Polychaeta in the Mississippi Canyon, Northern Gulf of Mexico. Doctor of Philosophy thesis. Texas A&M University, College Station, Texas.

Warwick, R.M. and Price, R., 1975. Macrofauna production in an estuarine mud flat. Journal of the Marine Biological Association of the UK**.** 55, 1-18.

Wei, C-L, Rowe, G., Escobar-Briones, E., Nunnally, C., Soliman, Y., Ellis, N., 2012 a. Standing stocks and body size of deep-sea macrofauna: Predicting the baseline of 2010 Deepwater Horizon oil spill in the northern Gulf of Mexico. Deep-Sea Research I. 69, 82-99.

Wei, C-L., Rowe, G.T., Haedrich, R.L., Boland, G.S., 2012 b. Long-term observations of epibenthic fish zonation in the deep northern Gulf of Mexico. PLoS ONE. 7, e46707.

Wei, C-L., Rowe, G.T., Hubbard, G.F., Scheltema, A.H., Wilson, G.D.F., Petrescu, I, Foster, J.M., Wicksten, M.K., Chen, M., Davenport, R., Soliman, Y., Wang, Y.N., 2010. Bathymetric zonation of deep-sea macrofauna in relation to export of surface phytoplankton production. Marine Ecology Progress Series. 399, 1-14.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J., Enquist, B.J., 2007. Relationship between body size and abundance in ecology.Trends in Ecology and Evolution. 22, 323-330.

White, H.K., Hsing, P-Y., Cho, W., Shank, T.M., Cordes, E.E., Quattrini, A.M., Nelson, R.K., Camilli, R., Demopoulos, A.W.J., German, C.R., Brooks, J.M., Roberts, H.H., Shedd, W., Reddy, C.M., Fisher, C.R., 2012. Impact of the Deepwater

Horizon oil spill on a deep-water coral community in the Gulf of Mexico. Proceedings of the National Academy of Sciences of the United States of America. 109, 20303-20308.

Whitehead, A., Dubansky, B., Bodinier, C., Garcia, T.I., Miles, S., Pilley, C., Raghunathan, V., Roach, J.L., Walker, N., Walter, R.B., Rice, C.D., Galvez, F., 2011. Genomic and physiological footprint of the deepwater horizon oil spill on resident marsh fishes. Proceedings of the National Academy of Sciences of the United States of America. 109, 20298-20302.

Wiseman, W., Rabalais, N., Turner, R., Dinnel, S., MacNaughton, A., 1997. Seasonal and inter-annual variability within the Louisiana coast current: stratification and hypoxia. Journal of Marine Systems. 12, 237-248.

Yasuhara, M., Okahashi, H., Cronin, T.M., Rasmussen, T.L., Hunt, G., 2014. Response of deep-sea biodiversity to abrupt deglacial and Holocene climate changes in the North Atlantic Ocean. Global Ecology and Biogeography. 23, 957-967.

Yeo, R.K. and Risk, M.J., 1979. Intertidal catastrophes: effect of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. Journal of the Fisheries Research Board of Canada. 36, 667-669.

APPENDIX A

POLYCHAETE SPECIES LIST OF DGOMB AND DWH STUDIES

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Aberrantidae	*Aberranta sp.*	0	1	1	0	0	2	0	0	0	0	0	0
Acrocirridae	*Macrochaeta sp. A*	0	0	1	0	0	0	0	0	0	0	0	0
Acrocirridae	*sp.*	0	0	0	0	0	2	1	0	1	0	0	0
Acrocirridae	*Acrocirrus frontifilis*	0	0	0	0	0	0	0	11	0	0	0	0
Acrocirridae	*Macrochaeta clavicornis*	1	5	1	0	0	0	2	27	1	1	2	1
Acrocirridae	*Acrocirridae sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Ampharetidae	*Amphicteis sp.*	1	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	*Hobsonia sp.*	0	0	0	1	0	0	0	0	0	0	0	0
Ampharetidae	*Isolda pulchella*	0	0	0	0	0	0	1	0	0	0	0	0
Ampharetidae	*Melinna cristata*	0	0	0	4	0	0	0	0	0	0	0	0
Ampharetidae	*Amphicteis gunneri*	0	4	0	5	0	0	0	0	0	0	0	0
Ampharetidae	*Ampharete sp. A*	1	1	0	0	5	0	1	11	0	0	0	0
Ampharetidae	*Melinna maculata*	0	0	0	20	0	0	0	0	0	0	0	0
Ampharetidae	*sp.*	0	0	4	9	2	1	9	7	5	0	0	0
Ampharetidae	*Ampharete sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Ampharetidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	2	0
Ampharetidae	*sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Ampharetidae	*sp.3*	0	0	0	0	0	0	0	0	0	0	0	1
Ampharetidae	*sp.4*	0	0	0	0	0	0	0	0	0	0	0	1
Amphinomidae	*Chloeia viridis*	0	0	0	1	0	0	0	0	0	0	0	0
Amphinomidae	*Eurythoe sp. B*	0	0	0	0	0	0	1	0	0	0	0	0
Amphinomidae	*Paramphinome sp. B*	0	1	0	0	0	0	0	0	0	0	0	0
Amphinomidae	*sp.*	0	0	0	0	0	0	0	2	0	0	0	0
Amphinomidae	*Eurythoe sp. A*	0	0	1	0	1	1	0	0	0	0	0	1
Amphinomidae	*Paramphinome sp.*	0	0	0	0	0	0	0	3	1	0	0	0
Amphinomidae	*Paramphinome jeffreysii*	5	0	6	0	0	0	0	3	0	0	0	0
Amphinomidae	*Paramphinome sp. A*	0	0	6	0	0	7	4	0	0	2	0	0
Aphroditidae	*sp.*	0	1	0	0	0	0	0	0	0	0	0	0
Aphroditidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Capitellidae	*Genus K*	0	0	0	0	0	1	0	0	0	0	0	0
Capitellidae	*Genus P*	0	0	0	0	1	0	0	0	0	0	0	0
Capitellidae	*Genus Q*	0	0	0	0	0	0	0	1	0	0	0	0
Capitellidae	*Genus S*	0	0	0	0	0	0	1	0	0	0	0	0
Capitellidae	*Genus T*	0	0	0	0	0	1	0	0	0	0	0	0
Capitellidae	*Genus X*	0	0	0	1	0	0	0	0	0	0	0	0
Capitellidae	*Genus AG*	0	0	0	1	0	0	0	0	0	0	0	0
Capitellidae	*Genus AM*	0	0	0	1	0	0	0	0	0	0	0	0
Capitellidae	*Genus AN*	0	1	0	0	0	0	0	0	0	0	0	0
Capitellidae	*Genus AQ*	0	0	0	1	0	0	0	0	0	0	0	0
Capitellidae	*Heteromastus sp. A*	0	0	0	0	0	0	0	1	0	0	0	0
Capitellidae	*Paraleiocapitella sp.*	0	0	0	0	0	1	0	0	0	0	0	0
Capitellidae	*Capitella capitata*	0	0	0	0	0	1	1	0	0	3	1	4

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Capitellidae	*Genus R*	0	0	0	1	1	0	0	0	0	0	0	0
Capitellidae	*Genus Y*	0	0	0	0	1	1	0	0	0	0	0	0
Capitellidae	*Genus Z*	0	0	0	0	0	0	0	0	2	0	0	0
Capitellidae	*Genus AC*	0	0	0	0	0	0	2	0	0	0	0	0
Capitellidae	*Genus AE*	0	0	0	0	0	1	1	0	0	0	0	0
Capitellidae	*Genus AK*	0	1	0	0	0	0	1	0	0	0	0	0
Capitellidae	*Neoheteromastus sp. B*	0	0	1	0	0	1	0	0	0	0	0	0
Capitellidae	*Genus AA*	2	0	0	0	1	0	0	0	0	0	0	0
Capitellidae	*Genus AF*	0	0	0	1	0	1	0	1	0	0	0	0
Capitellidae	*Decamastus sp. A*	0	0	0	0	2	1	0	0	1	0	0	0
Capitellidae	*Genus A*	0	0	2	0	0	0	0	1	1	0	0	0
Capitellidae	*Genus C*	0	0	2	0	1	0	0	1	0	0	0	0
Capitellidae	*Neomediomastus sp. A*	3	0	0	0	0	0	0	2	0	0	0	0
Capitellidae	*Genus G*	1	0	2	0	0	0	0	0	3	0	0	0
Capitellidae	*Notomastus latericeus*	0	1	0	2	0	1	0	3	0	0	0	0
Capitellidae	*Mediomastus californiensis*	3	0	0	0	0	0	3	2	1	0	3	0
Capitellidae	*Notomastus hemipodus*	0	0	0	3	2	4	1	1	0	0	0	2
Capitellidae	*Notomastus americanus*	0	0	0	5	7	1	1	0	0	0	1	0
Capitellidae	*Barantolla sp. A*	5	0	0	0	0	1	6	0	21	0	0	0
Capitellidae	*sp.*	2	13	7	1	4	0	11	73	46	0	0	0
Capitellidae	*Genus 1*	0	0	0	0	0	0	0	0	0	7	7	13
Capitellidae	*Genus 2*	0	0	0	0	0	0	0	0	0	0	3	4
Capitellidae	*Genus 3*	0	0	0	0	0	0	0	0	0	0	1	0
Capitellidae	*Genus 4*	0	0	0	0	0	0	0	0	0	4	0	2
Capitellidae	*Genus 5*	0	0	0	0	0	0	0	0	0	1	0	0
Capitellidae	*Genus 6*	0	0	0	0	0	0	0	0	0	0	0	1
Capitellidae	*Genus 7*	0	0	0	0	0	0	0	0	0	9	2	24
Capitellidae	*Genus 8*	0	0	0	0	0	0	0	0	0	0	0	2
Capitellidae	*Genus 9*	0	0	0	0	0	0	0	0	0	0	0	2
Capitellidae	*Heteromastus sp.1*	0	0	0	0	0	0	0	0	0	4	10	15
Capitellidae	*Leiocapitella sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Capitellidae	*Leiocapitella sp.B*	0	0	0	0	0	0	0	0	0	2	0	0
Capitellidae	*Mediomastus sp.*	0	0	0	0	0	0	0	0	0	0	0	5
Capitellidae	*Notomastus sp.*	0	0	0	0	0	0	0	0	0	0	0	2
Chaetopteridae	*sp.*	0	0	1	0	0	0	0	0	0	0	0	0
Chaetopteridae	*Spiochaetopterus costarum*	0	3	0	0	0	1	0	0	1	0	0	0
Chrysopetalidae	*Dysponetus sp. B*	0	0	2	0	0	0	1	1	0	0	0	0
Cirratulidae	*Caulleriella sp. A*	0	0	0	0	0	0	1	0	0	0	0	0
Cirratulidae	*Cirriformia sp. C*	0	0	0	0	0	1	0	0	0	0	0	0
Cirratulidae	*Chaetozone sp.*	0	1	0	0	1	0	0	0	0	0	0	0
Cirratulidae	*Cirriformia sp. A*	0	0	0	0	0	2	0	0	0	0	0	0
Cirratulidae	*Cirriformia sp. B*	0	0	0	0	0	2	2	0	0	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Cirratulidae	*Chaetozone sp. A*	1	0	1	0	0	7	0	0	0	0	1	0
Cirratulidae	*sp.*	0	0	0	3	0	0	7	9	6	0	0	0
Cirratulidae	*Tharyx annulosus*	5	6	4	0	0	11	10	16	4	0	1	0
Cirratulidae	*Tharyx marioni*	16	13	9	6	45	15	22	32	11	0	0	0
Cirratulidae	*Caulleriella sp.1*	0	0	0	0	0	0	0	0	0	1	0	1
Cirratulidae	*Caulleriella sp.2*	0	0	0	0	0	0	0	0	0	1	0	0
Cirratulidae	*Chaetozone sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Cirratulidae	*Chaetozone sp.B*	0	0	0	0	0	0	0	0	0	0	1	0
Cirratulidae	*Chaetozone sp.C*	0	0	0	0	0	0	0	0	0	0	8	0
Cirratulidae	*Cirriformia sp. 1*	0	0	0	0	0	0	0	0	0	0	1	0
Cirratulidae	*Cirriformia sp. 2*	0	0	0	0	0	0	0	0	0	0	0	1
Cirratulidae	*Genus B*	0	0	0	0	0	0	0	0	0	0	1	0
Cirratulidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	2	0
Cirratulidae	*sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Cirratulidae	*sp.3*	0	0	0	0	0	0	0	0	0	0	0	4
Cirratulidae	*sp.4*	0	0	0	0	0	0	0	0	0	0	0	1
Cirratulidae	*sp.5*	0	0	0	0	0	0	0	0	0	0	0	5
Cirratulidae	*Tharyx sp.1*	0	0	0	0	0	0	0	0	0	0	13	1
Cirratulidae	*Tharyx sp.2*	0	0	0	0	0	0	0	0	0	0	1	1
Cirratulidae	*Tharyx sp.3*	0	0	0	0	0	0	0	0	0	0	0	2
Cossuridae	*Cossura alba*	1	0	0	0	0	0	0	0	0	0	0	0
Cossuridae	*sp.*	0	0	0	0	0	0	0	1	0	0	0	0
Cossuridae	*Cossura laeviseta*	0	0	0	0	2	0	0	0	0	0	0	0
Cossuridae	*Cossura sp. A*	2	0	0	0	0	4	0	0	0	0	0	1
Cossuridae	*Cossura soyeri*	1	0	0	4	18	3	0	0	0	2	0	1
Cossuridae	*Cossura delta*	3	0	0	9	96	16	1	0	21	17	27	4
Dorvilleidae	*Dorvillea sp. A*	0	0	0	0	1	0	0	0	0	0	0	0
Dorvilleidae	*Genus A*	0	0	0	0	0	1	0	0	0	0	0	0
Dorvilleidae	*Genus C*	0	0	0	0	0	1	0	0	0	0	0	0
Dorvilleidae	*Protodorvillea kefersteini*	0	0	0	0	0	0	0	1	0	0	0	0
Dorvilleidae	*Schistomeringos sp.*	0	0	0	1	0	0	0	0	0	0	0	0
Dorvilleidae	*Pettiboneia sp. B*	0	0	0	0	2	0	0	0	0	0	0	0
Dorvilleidae	*Ophryotrocha sp. A*	0	0	0	0	0	3	0	0	0	0	0	0
Dorvilleidae	*Meiodorvillea sp. B*	0	0	0	0	0	1	3	0	0	0	0	0
Dorvilleidae	*Pettiboneia sp. A*	0	0	0	4	0	0	0	0	0	0	0	0
Dorvilleidae	*Dorvillea sp. C*	0	0	0	6	0	0	0	0	0	0	0	0
Dorvilleidae	*sp.*	0	1	2	1	0	2	0	1	0	0	0	0
Dorvilleidae	*Meiodorvillea sp. A*	0	2	1	0	3	0	0	0	4	0	4	2
Dorvilleidae	*Schistomeringos rudolphi*	0	0	0	1	13	0	0	0	0	0	0	0
Dorvilleidae	*Schistomeringos sp. B*	0	0	2	11	1	0	0	0	0	0	0	0
Eunicidae	*Eunice filamentosa*	0	0	0	0	0	0	1	0	0	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Eunicidae	*Marphysa sp. A*	0	0	0	0	1	0	0	0	0	0	0	0
Eunicidae	*Palola siciliensis*	0	0	1	0	0	0	0	0	0	0	0	0
Eunicidae	*Lysidice ninetta*	2	0	0	0	0	0	0	0	0	0	0	0
Eunicidae	*sp.*	0	2	0	0	0	0	0	0	0	0	0	0
Eunicidae	*Euniphysa aculeata*	0	0	0	0	3	0	0	0	0	0	0	0
Family B	*sp.*	0	0	0	0	0	1	0	0	0	0	0	0
Fauveliopsidae	*Fauveliopsis sp.*	0	0	0	0	0	2	0	0	0	0	0	0
Fauveliopsidae	*Fauveliopsis sp. B*	0	1	3	0	2	0	2	1	0	0	0	0
Fauveliopsidae	*Fauveliopsis sp. A*	0	0	4	0	2	8	0	1	0	5	4	5
Flabelligeridae	*Brada villosa*	0	0	1	0	0	0	0	0	0	0	0	0
Flabelligeridae	*Diplocirrus sp.*	0	0	0	0	0	0	1	0	0	0	0	0
Flabelligeridae	*Pherusa sp.*	0	0	0	0	0	0	0	1	0	0	0	0
Flabelligeridae	*Diplocirrus sp. B*	0	0	2	0	0	0	0	0	0	0	0	0
Flabelligeridae	*Pherusa inflata*	0	0	0	0	2	0	0	0	0	0	0	0
Flabelligeridae	*sp.*	1	0	0	0	0	1	0	0	1	0	0	0
Flabelligeridae	*Therochaeta sp. A*	0	0	0	0	0	2	1	0	0	0	0	0
Flabelligeridae	*Diplocirrus capensis*	0	4	1	0	0	1	0	4	0	0	0	0
Flabelligeridae	*Diplocirrus sp. A*	3	0	2	0	0	0	3	2	2	0	3	3
Glyceridae	*Hemipodus sp.*	0	0	0	0	2	0	0	2	1	0	0	0
Glyceridae	*sp.*	0	0	0	0	5	0	4	0	0	0	0	0
Glyceridae	*Glycera sp.*	7	13	10	21	10	12	5	7	1	0	2	0
Glyceridae	*sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Glyceridae	*sp.2*	0	0	0	0	0	0	0	0	0	0	0	1
Glyceridae	*Goniada sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Goniadidae	*Progoniada regularis*	0	0	0	1	0	0	0	0	0	0	0	0
Goniadidae	*Goniadella sp. A*	0	1	0	0	0	0	0	1	0	0	0	0
Goniadidae	*sp.*	1	0	0	0	1	0	0	1	0	0	0	0
Hesionidae	*Gyptis sp.*	0	0	0	0	1	0	0	0	0	0	0	0
Hesionidae	*Nereimyra sp.*	1	0	0	0	0	0	0	0	0	0	0	0
Hesionidae	*sp.*	0	0	1	0	0	0	0	0	0	0	0	0
Hesionidae	*Genus A*	13	0	0	0	0	2	0	0	0	0	0	0
Hesionidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Longosomatidae	*Heterospio longissima*	0	0	1	0	39	7	0	0	2	0	0	0
Lumbrineridae	*Lumbrinerides sp.*	1	0	0	0	0	0	0	0	0	0	0	0
Lumbrineridae	*Lumbrineris brevipes*	0	0	1	0	0	0	0	0	0	1	3	2
Lumbrineridae	*Lumbrineris coccinea*	0	0	0	0	0	0	0	1	0	0	0	0
Lumbrineridae	*Lumbrineris latrielli*	0	0	0	0	1	0	0	0	0	0	0	0
Lumbrineridae	*Lumbrineris sp. A*	0	0	0	0	0	1	0	0	0	0	0	0
Lumbrineridae	*Lumbrinerides sp. A*	0	0	0	0	0	2	0	0	0	0	0	0
Lumbrineridae	*Lumbrineris sp. C*	0	0	2	0	0	0	0	0	0	0	0	0
Lumbrineridae	*Lumbrineriopsis paradoxa*	0	0	0	0	0	3	0	0	1	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Lumbrineridae	*Lumbrineris candida*	0	0	0	2	1	0	1	0	0	0	0	0
Lumbrineridae	*sp.*	0	0	0	2	0	0	0	1	1	0	0	0
Lumbrineridae	*Augeneria bidens*	0	0	0	0	4	1	0	0	0	0	0	0
Lumbrineridae	*Lumbrinerides acuta*	0	0	4	0	0	0	4	0	0	0	0	0
Lumbrineridae	*Ninoe sp. A*	1	0	0	0	1	3	1	4	1	0	2	0
Lumbrineridae	*Lumbrineris verrilli*	0	0	0	5	0	4	0	4	1	0	5	2
Lumbrineridae	*Lumbrinerides dayi*	1	3	0	0	0	0	4	16	0	0	0	0
Lumbrineridae	*Lumbrineris sp.*	0	0	0	0	0	0	0	0	0	0	0	1
Lumbrineridae	*Lumbrineris sp.B*	0	0	0	0	0	0	0	0	0	0	0	1
Magelonidae	*Magelona sp. G*	2	0	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Euclymene sp. A*	0	0	1	0	0	0	0	0	0	0	0	0
Maldanidae	*Maldane sp.*	0	1	0	0	0	0	0	0	0	0	0	0
Maldanidae	*Maldane glebifex*	0	3	0	0	0	20	0	0	0	0	0	0
Maldanidae	*Maldane sp. A*	0	0	0	0	0	0	0	0	24	19	27	28
Maldanidae	*Micromaldane sp.*	0	9	4	4	16	17	36	17	2	45	39	35
Maldanidae	*sp.*	5	72	55	8	75	73	34	166	39	0	0	0
Maldanidae	*Petaloproctus sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Maldanidae	*Petaloproctus sp.2*	0	0	0	0	0	0	0	0	0	1	0	0
Maldanidae	*sp.1Maldanidae*	0	0	0	0	0	0	0	0	0	0	3	0
Nephtyidae	*Nephtys picta*	0	0	0	0	0	1	0	1	0	0	0	0
Nephtyidae	*Nephtys sp.*	0	0	0	0	0	0	0	0	2	0	0	0
Nephtyidae	*Nephtys squamosa*	0	0	0	16	0	0	0	0	0	0	0	1
Nephtyidae	*Micronephthys minuta*	5	1	3	25	0	1	0	0	0	0	0	0
Nephtyidae	*Aglaophamus verrilli*	4	0	0	18	14	0	0	0	0	0	0	0
Nephtyidae	*sp.*	12	0	0	12	11	1	0	0	0	0	0	0
Nephtyidae	*Aglaophamus circinata*	0	0	0	0	0	0	0	0	0	2	0	0
Nephtyidae	*Micronephthys sp.1*	0	0	0	0	0	0	0	0	0	1	0	0
Nephtyidae	*Micronephthys sp.2*	0	0	0	0	0	0	0	0	0	0	0	1
Nephtyidae	*Micronephtys sp.*	0	0	0	0	0	0	0	0	0	0	0	1
Nephtyidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	1	1
Nereidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Nereididae	*Ceratocephale websteri*	0	1	0	0	0	0	0	0	0	0	0	0
Nereididae	*sp.*	0	0	2	0	0	1	0	0	0	0	0	0
Nereididae	*Gymnonereis sp.*	0	0	0	1	0	3	1	0	0	0	0	0
Nereididae	*Ceratocephale loveni*	1	1	0	0	0	3	7	0	0	0	0	0
Nereididae	*Ceratocephale oculata*	0	1	3	0	0	0	0	9	5	5	18	16
Oenonidae	*sp.*	0	0	0	0	0	1	0	1	0	0	0	0
Onuphidae	*Kinbergonuphis sp. A*	0	0	0	0	1	0	0	0	0	0	0	0
Onuphidae	*Nothria sp.*	1	0	0	0	0	0	0	0	0	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Opheliidae	*Ophelina acuminata*	0	0	0	0	1	1	0	1	0	0	0	0
Opheliidae	*Ophelina sp. C*	0	0	0	0	0	3	0	0	0	0	0	0
Opheliidae	*Tachytrypane jeffreysii*	0	0	3	0	2	0	0	0	0	0	0	0
Opheliidae	*sp.*	0	1	1	0	0	2	0	3	1	0	0	0
Opheliidae	*Armandia maculata*	0	1	3	0	0	0	4	4	0	0	0	0
Opheliidae	*Ophelina cylindricaudata*	2	0	0	0	1	5	3	2	0	0	0	12
Opheliidae	*Tachytrypane sp. A*	26	2	8	0	18	52	0	13	0	0	0	0
Opheliidae	*Ophelina sp.*	0	0	0	0	0	0	0	0	0	0	0	1
Opheliidae	*Ophelina sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Opheliidae	*sp.*	0	0	0	0	0	0	0	0	0	0	2	0
Orbiniidae	*Naineris laevigata*	0	0	0	0	0	0	1	0	0	0	0	0
Orbiniidae	*Proscoloplos sp. A*	0	0	0	0	0	1	0	0	0	0	0	0
Orbiniidae	*Scoloplos sp.*	0	1	0	0	0	0	0	0	0	0	0	0
Orbiniidae	*Leitoscoloplos sp. A*	0	0	0	0	0	0	2	0	0	0	0	0
Orbiniidae	*Orbinia americana*	0	0	0	0	0	0	4	0	0	0	0	0
Orbiniidae	*Califia calida*	1	0	1	0	1	0	1	1	0	0	0	0
Orbiniidae	*Scoloplos rubra*	0	0	0	0	0	1	0	4	0	0	0	0
Orbiniidae	*sp.*	0	1	4	0	0	0	1	0	0	0	0	0
Orbiniidae	*Leitoscoloplos fragilis*	1	0	0	0	0	0	7	0	0	0	0	0
Orbiniidae	*Leitoscoloplos robustus*	1	0	5	0	0	5	4	0	0	0	0	0
Orbiniidae	*Leitoscoloplos sp.*	0	3	4	0	0	2	0	10	0	0	0	0
Orbiniidae	*Phylo felix*	0	0	0	0	0	0	0	0	0	0	1	0
Oweniidae	*Myriochele oculata*	0	0	1	0	1	0	0	0	0	0	0	0
Oweniidae	*Myriochele sp. A*	0	1	0	0	0	0	0	3	0	0	0	0
Oweniidae	*sp.*	0	3	1	0	0	0	0	0	0	0	0	0
Oweniidae	*Myriochele heeri*	0	5	0	0	7	0	1	7	0	0	0	0
Oweniidae	*Myriowenia sp. A*	0	2	3	0	10	0	6	1	0	0	0	0
Paralacydoniidae	*Paralacydonia paradoxa*	2	1	6	2	4	14	3	0	1	2	11	6
Paraonidae	*Aricidea alisdairi*	0	0	0	1	0	0	0	0	0	0	0	0
Paraonidae	*Aricidea minuta*	0	0	0	1	0	0	0	0	0	0	0	0
Paraonidae	*Aricidea quadrilobata*	0	0	0	1	0	0	0	0	0	0	2	2
Paraonidae	*Aricidea wassi*	0	0	0	1	0	0	0	0	0	0	0	0
Paraonidae	*Cirrophorus branchiatus*	0	0	0	0	0	1	0	0	0	0	0	0
Paraonidae	*Cirrophorus forticirratus*	0	0	0	0	0	0	0	1	0	1	0	2
Paraonidae	*Cirrophorus neapolitanus*	0	0	1	0	0	0	0	0	0	0	0	0
Paraonidae	*Levinsenia oculata*	0	0	0	1	0	0	0	0	0	0	0	0
Paraonidae	*Paraonella nordica*	0	1	0	0	0	0	0	0	0	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Paraonidae	*Paraonella sp.*	0	1	0	0	0	1	0	0	0	0	0	0
Paraonidae	*Aricidea catherinae*	0	0	0	0	0	0	0	3	0	0	0	0
Paraonidae	*Levinsenia sp.*	0	0	0	0	1	0	4	0	0	0	0	0
Paraonidae	*Aricidea cerrutii*	0	1	0	0	0	4	0	0	3	0	0	0
Paraonidae	*Cirrophorus abranchiatus*	0	10	1	0	0	0	1	1	0	0	0	0
Paraonidae	*Cirrophorus lyra*	0	3	2	0	1	0	0	7	1	0	0	0
Paraonidae	*Aricidea trilobata*	0	0	0	0	1	14	2	0	0	0	0	0
Paraonidae	*Sabidius sp. A*	15	2	1	1	1	4	0	0	0	0	0	0
Paraonidae	*Sabidius cornatus*	0	0	2	4	3	11	0	0	13	0	0	0
Paraonidae	*Levinsenia brevibranchiata*	16	0	2	6	0	11	0	0	1	0	0	0
Paraonidae	*Aricidea fragilis*	0	5	2	2	8	0	9	11	0	0	3	0
Paraonidae	*Paraonella sp. A*	0	2	5	19	0	0	8	4	0	0	0	0
Paraonidae	*sp.*	4	10	6	3	13	0	0	1	1	0	0	0
Paraonidae	*Levinsenia gracilis*	6	0	2	24	6	3	1	0	1	16	1	2
Paraonidae	*Aricidea lopezi lopezi*	4	1	0	9	20	1	10	3	2	0	0	0
Paraonidae	*Aricidea mirifica*	0	0	0	0	0	0	0	1	58	0	0	0
Paraonidae	*Levinsenia oligobranchiata*	12	0	2	35	14	4	0	7	2	0	0	0
Paraonidae	*Levinsenia uncinata*	5	7	16	10	4	15	11	15	5	0	0	0
Paraonidae	*Paraonella monilaris*	0	28	10	20	7	0	15	8	0	0	0	0
Paraonidae	*Aricidea sp.*	1	0	0	0	69	3	8	8	0	0	0	0
Paraonidae	*Aricidea simplex*	14	2	5	11	23	62	0	6	24	1	14	6
Paraonidae	*Aedicira sp.*	10	10	7	66	70	0	14	3	12	0	0	0
Paraonidae	*Aricidea suecica*	6	10	20	128	51	28	8	32	15	0	0	0
Paraonidae	*Aricidea sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Paraonidae	*Aricidea sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Paraonidae	*Aricidea sp.3*	0	0	0	0	0	0	0	0	0	12	9	44
Paraonidae	*Aricidea sp.4*	0	0	0	0	0	0	0	0	0	4	0	0
Paraonidae	*Aricidea sp.5*	0	0	0	0	0	0	0	0	0	0	1	0
Paraonidae	*Aricidea sp.6*	0	0	0	0	0	0	0	0	0	0	0	1
Paraonidae	*Aricidea (Acmira) sp.C*	0	0	0	0	0	0	0	0	0	0	1	0
Paraonidae	*Aricidea (Acmira)sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Paraonidae	*Aricidea (Acmira)sp.2*	0	0	0	0	0	0	0	0	0	0	0	1
Paraonidae	*Cirrophorus americanus*	0	0	0	0	0	0	0	0	0	0	0	4
Paraonidae	*Levinsenia reducta*	0	0	0	0	0	0	0	0	0	0	0	1
Paraonidae	*Levinsenia sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Paraonidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	1	4
Paraonidae	*sp.2*	0	0	0	0	0	0	0	0	0	0	0	2
Paraonidae	*sp.3*	0	0	0	0	0	0	0	0	0	0	0	1
Paraonidae	*sp.4*	0	0	0	0	0	0	0	0	0	0	0	1

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Phyllodocidae	*Paranaitis polynoides*	0	0	0	1	0	0	0	0	0	0	0	0
Phyllodocidae	*Paranaitis speciosa*	0	1	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	*Genus A*	0	3	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	*Anaitides mucosa*	0	0	0	1	2	0	1	0	0	0	0	0
Phyllodocidae	*Mystides borealis*	0	0	0	0	2	0	2	5	0	1	0	0
Phyllodocidae	*sp.*	1	1	2	0	0	1	1	2	1	0	0	0
Phyllodocidae	*Protomystides bidentata*	1	0	2	0	0	6	1	3	2	0	1	0
Phyllodocidae	*Eteone lactea*	0	0	0	0	0	0	0	0	0	0	1	0
Phyllodocidae	*Eumida sp.1*	0	0	0	0	0	0	0	0	0	0	0	2
Phyllodocidae	*Hesionura sp. 1*	0	0	0	0	0	0	0	0	0	0	1	0
Phyllodocidae	*Paranaitis sp.1*	0	0	0	0	0	0	0	0	0	1	0	0
Phyllodocidae	*sp.1Phyllodocidae*	0	0	0	0	0	0	0	0	0	0	2	1
Phyllodocidae	*sp.2Phyllodocidae*	0	0	0	0	0	0	0	0	0	0	1	0
Phyllodocidae	*sp.3Phyllodocidae*	0	0	0	0	0	0	0	0	0	0	0	2
Pilargidae	*Ancistrosyllis sp. B*	0	0	0	0	0	1	0	0	0	0	0	0
Pilargidae	*Sigambra bassi*	1	0	0	0	0	0	0	0	0	0	0	0
Pilargidae	*sp.*	0	0	0	0	0	0	0	1	0	0	0	0
Pilargidae	*Ancistrosyllis sp. A*	1	0	0	1	0	0	0	0	0	0	0	0
Pilargidae	*Synelmis albini*	0	0	0	2	0	0	0	0	0	0	0	0
Pilargidae	*Synelmis sp. B*	0	0	0	0	1	1	0	0	0	0	0	0
Pilargidae	*Sigambra wassi*	0	0	0	3	2	0	0	0	0	0	0	0
Pilargidae	*Synelmis klatti*	3	0	3	1	5	5	4	0	1	2	0	1
Pilargidae	*Sigambra tentaculata*	3	0	0	10	15	1	0	2	0	0	0	0
Pilargidae	*Litocorsa antennata*	0	0	38	0	0	0	0	0	0	0	0	0
Pilargidae	*Ancistrosyllis sp. 1*	0	0	0	0	0	0	0	0	0	0	0	1
Pilargidae	*Pilargis sp.*	0	0	0	0	0	0	0	0	0	0	2	0
Pilargidae	*sp.1Pilargidae*	0	0	0	0	0	0	0	0	0	0	1	0
Pilargidae	*Synelmis sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Poecilochaetidae	*Poecilochaetus fulgoris*	0	0	0	0	0	0	0	1	0	0	0	0
Poecilochaetidae	*Poecilochaetus sp.*	0	0	3	0	0	0	0	0	0	0	0	0
Polychaeta	*sp.1*	0	0	0	0	0	0	0	0	0	2	1	2
Polychaeta	*sp.2*	0	0	0	0	0	0	0	0	0	0	0	1
Polychaeta	*sp.3*	0	0	0	0	0	0	0	0	0	0	0	1
Polychaeta	*sp.4*	0	0	0	0	0	0	0	0	0	0	0	1
Polynoidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	0	1
Polyodontidae	*sp.1*	0	0	0	0	0	0	0	0	0	1	0	0
Sabellariidae	*Phalacrostemma sp. A*	0	0	1	0	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. E*	0	0	0	1	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. H*	0	0	0	1	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. I*	0	1	0	0	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. N*	0	0	0	0	0	0	1	0	0	0	0	0
Sabellidae	*Fabricia sp. B*	0	1	0	0	0	0	0	0	0	0	0	0
Sabellidae	*Chone americana*	0	0	1	0	0	0	1	0	0	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Sabellidae	*Chone sp. B*	0	0	0	2	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. F*	0	0	0	2	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. G*	0	0	0	2	0	0	0	0	0	0	0	0
Sabellidae	*Euchone incolor*	0	0	4	0	0	0	0	0	0	0	0	0
Sabellidae	*Fabricia sp. A*	0	0	3	0	0	0	0	1	0	0	0	0
Sabellidae	*Chone sp.*	0	0	5	0	0	0	0	0	0	0	0	0
Sabellidae	*Chone sp. A*	1	1	1	1	0	0	0	1	0	0	0	0
Sabellidae	*sp.*	0	3	5	2	1	0	0	8	5	0	0	0
Scalibregmatidae	*Scalibregma inflatum*	0	0	0	0	0	0	0	1	0	0	0	0
Scalibregmatidae	*sp.*	0	1	0	0	0	0	0	0	0	0	0	0
Serpulidae	*Hydroides sp.1*	0	0	0	0	0	0	0	0	0	0	0	3
Sigalionidae	*Genus A*	0	0	0	1	0	0	0	0	0	0	0	0
Sigalionidae	*Pholoe sp.*	0	0	0	0	0	0	0	1	0	0	0	0
Sigalionidae	*Thalenessa sp. A*	0	0	0	0	0	1	0	0	0	0	1	0
Sigalionidae	*Pholoe sp. A*	0	0	0	0	0	2	0	0	0	0	0	0
Sigalionidae	*Pholoe sp. C*	0	0	0	1	2	0	0	0	0	0	0	0
Sigalionidae	*Ehlersileanira incisa*	0	0	3	0	1	0	0	8	0	0	0	0
Sigalionidae	*Sthenelais sp. A*	0	0	0	1	1	7	0	3	4	0	2	0
Sigalionidae	*Sthenolepis sp. A*	0	1	0	0	0	11	0	5	0	0	0	0
Sigalionidae	*Pholoe sp. B*	0	0	16	0	0	7	0	0	0	0	0	0
Sigalionidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	1	1
Sigalionidae	*sp.2*	0	0	0	0	0	0	0	0	0	0	2	0
Sigalionidae	*Sthenelais sp.*	0	0	0	0	0	0	0	0	0	15	28	43
Sphaerodoridae	*Ephesiella sp. A*	0	1	0	0	0	0	0	0	0	0	0	0
Sphaerodoridae	*Sphaerodoridium sp. A*	3	0	0	2	0	0	0	0	0	0	0	0
Sphaerodoridae	*Sphaerodoropsis sp. A*	4	0	1	1	0	0	2	0	0	0	0	0
Spionidae	*Microspio pigmentata*	0	0	0	0	0	1	0	0	0	0	0	0
Spionidae	*Nerinides*	0	0	0	0	0	1	0	0	0	0	0	0
Spionidae	*Spio sp.*	0	0	0	0	0	1	0	0	0	0	0	0
Spionidae	*Spiophanes sp. A*	0	0	0	0	0	1	0	0	0	3	1	3
Spionidae	*Streblospio sp.*	0	0	0	0	0	1	0	0	0	0	0	0
Spionidae	*Apoprionospio pygmaea*	0	0	0	2	0	0	0	0	0	0	0	0
Spionidae	*Prionospio fauchaldi*	0	0	0	2	0	0	0	0	0	0	0	0
Spionidae	*Prionospio perkinsi*	0	0	0	2	0	0	0	0	0	0	0	0
Spionidae	*Prionospio aluta?*	0	0	0	3	0	0	0	0	0	0	0	0
Spionidae	*Rhynchospio sp.*	0	0	0	0	0	3	0	0	0	0	0	0
Spionidae	*Spiophanes bombyx*	0	0	1	0	0	1	1	0	0	0	0	0
Spionidae	*Spiophanes sp.*	0	0	1	0	0	0	0	0	2	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Spionidae	*Aurospio dibranchiata*	0	0	0	2	3	0	0	0	0	0	0	0
Spionidae	*Spiophanes kroyeri*	0	0	0	4	0	0	1	0	0	0	0	0
Spionidae	*Spio pettiboneae*	0	0	1	4	0	2	0	0	0	0	0	0
Spionidae	*Malacoceros sp.*	0	0	0	0	1	6	1	0	0	0	0	0
Spionidae	*Prionospio multibranchiata*	0	0	0	3	5	0	0	0	0	0	0	0
Spionidae	*Laonice cirrata*	0	3	0	4	0	2	0	0	0	0	0	0
Spionidae	*Prionospio delta*	0	0	0	9	0	0	0	0	0	0	0	0
Spionidae	*Prionospio (Minuspio) sp. A*	1	0	2	5	0	2	0	0	0	0	0	0
Spionidae	*Prionospio (Minuspio) sp.*	0	0	0	14	0	0	0	0	0	0	0	0
Spionidae	*Genus B*	1	2	0	0	0	9	0	7	0	0	0	0
Spionidae	*Prionospio cristata*	3	0	0	18	0	0	0	0	0	0	1	0
Spionidae	*Spiophanes sp. D*	6	2	1	0	0	7	2	4	7	0	0	0
Spionidae	*Prionospio sp.*	7	0	0	13	20	9	1	1	0	0	0	0
Spionidae	*Prionospio steenstrupi*	0	0	0	51	0	1	0	0	0	0	0	1
Spionidae	*Prionospio ehlersi*	3	0	0	55	2	0	1	2	0	0	0	0
Spionidae	*Prionospio cirrobranchiata*	19	0	0	29	20	8	6	0	0	0	0	0
Spionidae	*Prionospio heterobranchia*	0	0	0	85	0	0	0	0	0	0	0	0
Spionidae	*Spiophanes berkeleyorum*	11	7	6	41	44	20	3	30	1	4	12	7
Spionidae	*Prionospio cirrifera*	26	0	0	68	77	40	5	0	0	0	0	0
Spionidae	*sp.*	40	35	62	46	92	29	39	153	21	0	0	0
Spionidae	*Polydora sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*Prionospio sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*Prionospio sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*Prionospio sp.3*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*Prionospio sp.4*	0	0	0	0	0	0	0	0	0	1	1	0
Spionidae	*Prionospio sp.5*	0	0	0	0	0	0	0	0	0	0	0	2
Spionidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*sp.3*	0	0	0	0	0	0	0	0	0	0	2	0
Spionidae	*sp.4*	0	0	0	0	0	0	0	0	0	0	1	0
Spionidae	*sp.5*	0	0	0	0	0	0	0	0	0	0	2	0
Spionidae	*sp.6*	0	0	0	0	0	0	0	0	0	1	0	0
Spionidae	*Spiophanes sp. 1*	0	0	0	0	0	0	0	0	0	0	3	0
Spionidae	*Spiophanes sp. 2*	0	0	0	0	0	0	0	0	0	0	1	1
Spirorbidae	*Spirorbis (Janua) corrugatus*	0	0	0	4	0	0	0	0	0	0	0	0
Syllidae	*Pionosyllis sp. B*	0	0	1	0	0	0	0	0	0	0	0	0
Syllidae	*Sphaerosyllis aciculata*	0	0	0	0	0	1	0	0	0	0	0	0
Syllidae	*Sphaerosyllis magnidentata*	0	0	0	0	0	0	0	1	0	0	0	0

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Syllidae	*Sphaerosyllis sp. B*	0	0	0	0	0	0	1	0	0	0	0	0
Syllidae	*Syllis (Ehlersia) cornuta*	0	0	1	0	0	0	0	0	0	0	0	0
Syllidae	*Syllis (Ehlersia) sp. A*	0	0	1	0	0	0	0	0	0	0	0	0
Syllidae	*Exogone sp. H*	0	0	2	0	0	0	0	0	0	0	0	0
Syllidae	*Exogone sp. K*	0	2	0	0	0	0	0	0	0	0	0	0
Syllidae	*Sphaerosyllis renaudae*	1	1	0	0	0	0	0	0	0	0	0	0
Syllidae	*Sphaerosyllis sp.*	0	0	1	0	0	1	0	0	0	0	0	0
Syllidae	*Exogone sp. J*	0	0	3	0	0	0	0	0	0	0	0	0
Syllidae	*Pionosyllis sp. C*	0	0	0	0	3	0	0	0	0	0	0	0
Syllidae	*Syllis (Ehlersia) ferrugina*	0	0	4	0	0	0	0	0	0	0	0	0
Syllidae	*Sphaerosyllis glandulata*	0	0	0	0	0	5	0	0	0	0	0	0
Syllidae	*Sphaerosyllis longicauda*	5	0	0	0	0	0	0	0	0	0	0	0
Syllidae	*Exogone sp. C*	0	0	5	0	0	0	1	1	0	0	0	0
Syllidae	*Exogone sp.*	1	3	0	0	0	2	2	0	0	0	0	0
Syllidae	*Sphaerosyllis taylori*	0	4	1	0	0	1	2	0	0	0	0	0
Syllidae	*Syllides floridanus*	0	0	1	0	0	9	0	0	0	0	0	0
Syllidae	*Eusyllis lamelligera*	0	0	12	0	0	0	0	0	0	0	0	0
Syllidae	*Exogone atlantica*	3	0	0	0	0	6	3	0	0	0	0	0
Syllidae	*Sphaerosyllis piriferopsis*	0	3	3	2	0	1	1	3	0	0	1	0
Syllidae	*sp.*	0	0	11	0	0	0	0	2	1	0	0	0
Syllidae	*Exogone sp. D*	4	0	3	0	0	0	8	5	1	0	0	0
Syllidae	*Exogone sp. A*	0	3	6	0	0	8	2	12	6	0	0	0
Syllidae	*Exogone longicirrus*	2	6	14	0	0	0	9	7	0	0	0	0
Syllidae	*Exogone dispar*	9	3	4	0	0	23	10	0	0	2	3	6
Syllidae	*Exogone sp. B*	0	3	8	0	0	1	9	27	2	0	0	1
Syllidae	*Exogone lourei*	0	0	0	0	0	0	0	0	0	0	1	0
Syllidae	*Exogone sp. 1*	0	0	0	0	0	0	0	0	0	8	2	24
Syllidae	*Exogone sp. 2*	0	0	0	0	0	0	0	0	0	0	3	0
Syllidae	*Exogone sp. 3*	0	0	0	0	0	0	0	0	0	16	10	23
Syllidae	*Proceraea sp.1*	0	0	0	0	0	0	0	0	0	1	0	0
Syllidae	*sp.1*	0	0	0	0	0	0	0	0	0	0	1	0
Syllidae	*sp.2*	0	0	0	0	0	0	0	0	0	0	1	0
Syllidae	*sp.3*	0	0	0	0	0	0	0	0	0	0	1	1
Syllidae	*sp.*	10	12	7	1	7	17	1	7	0	0	0	0
Terebellidae	*sp.*	1	6	6	3	5	0	3	9	0	0	0	0
Terebellidae	*Amaeana sp.1*	0	0	0	0	0	0	0	0	0	0	3	2
Terebellidae	*Polycirrus sp.B*	0	0	0	0	0	0	0	0	0	0	0	6
Trichobranchidae	*Terebellides stroemi*	0	0	0	1	0	0	0	0	0	1	2	1

Appendix A continued

		DGoMB									DWH		
Family	Species	C1	C4	C7	MT1	MT2	MT3	MT4	S36	HiPro	15	17	18
Trichobranchidae	*Terebellides sp.*	2	0	0	0	1	0	0	0	1	0	0	0
Trichobranchidae	*sp.*	0	2	0	1	0	0	0	2	0	0	0	0
Trichobranchidae	*Terebellides atlantis*	0	3	0	3	4	4	0	1	0	0	0	0
Trichobranchidae	*Terebellides distincta*	0	8	1	8	30	0	2	13	5	0	0	0