March 2019

Zooplankton Community Structure in the NE Gulf of Mexico: Impacts of Environmental Variability and the Deepwater Horizon Oil Spill

Kate M. Dubickas
University of South Florida, kdubickas@mail.usf.edu

Scholar Commons Citation
Dubickas, Kate M., "Zooplankton Community Structure in the NE Gulf of Mexico: Impacts of Environmental Variability and the Deepwater Horizon Oil Spill" (2019). *USF Tampa Graduate Theses and Dissertations.*
https://digitalcommons.usf.edu/etd/7780

Zooplankton Community Structure in the NE Gulf of Mexico: Impacts of Environmental Variability and the Deepwater Horizon Oil Spill

by

Kate M. Dubickas

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science Biological Oceanography
College of Marine Science
University of South Florida

Major Professor: Kendra Daly, Ph.D
Major Co-Advisor: Pamela Hallock Muller, Ph.D.
Mark Luther, Ph.D.
Claire Paris. Ph.D.
Dave Jones, Ph.D.

Date of Approval:
March 14, 2019

Keywords: beta diversity, Centropages, ecosystem resiliency, Mississippi River, multivariate, river discharge

DEDICATION

To my mother, for giving me both roots and wings. I am a culmination of experiences and opportunities that without you, I would suffer from not having.

And to Adam Iben for being such an influential figure in helping me to see the world and myself as a multi-disciplinary expression riddled with perception and speckled with art, intrigue, and data.

ACKNOWLEDGEMENTS

This thesis would not have been possible if not for the generous support in acquiring data, insights on development, and countless comments and feedback on both my research products and personal growth throughout this process.

I am grateful for my advisor, Dr. Kendra Daly who assisted most in all these endeavors, guided me through the research progress and shared with me her wealth of knowledge. Additionally, I am also grateful to my committee members Drs. Pam Hallock Muller, Mark Luther and Claire Paris for their edits, efforts, and advice.

A special thank you to Dr. Pam Hallock Muller is deserved. She unflinchingly stepped into this project in the throws of its last four months but leaned in full-force. She personifies, in a variety of ways, what it means to be a good friend, collaborator, and student advisor.

I thank Drs. Joanne Lyczkowski-Shultz and Glenn Zapfe at NOAA’s Southeast Fisheries Science Center and Jeff Tester of The Gulf States Marine Fisheries Commission for access to the pre-DWH oil spill SEAMAP zooplankton samples and CTD data that were collected between 2005 and 2009. For their help in acquiring and managing large datasets for other environmental data, my gratitude goes out to Dr. Z. George Xue and Yanda Dan Ou at Louisiana State University, and Dr. Dan Otis and Kelly Vasbinder at USF College of Marine Science.

Thank you to my lab mate Megan Ferguson whose experience and efforts were incalculable in heading up and collaborating with in developing much of the ZooScan portions of this project and Erin Hagen for proofreading whatever version of anything I’ve written from high school to today.

A sincerest appreciation goes out to my late committee member, Dr. David Jones who spent many hours between class meetings and office hours helping me to code and understand multivariate statistics. While he may no longer be with us, the lessons I learned from him poignantly embody what it means to stand upon the shoulders of giants. His MATLAB® multivariate statistics package, FATHOM, has rendered a wide variety of data analysis techniques attainable and understandable to scores of graduate students and researchers; his legacy lives on with us.

Finally, I'd like to thank Dr. Mya Breitbert for assisting me in my preparing a competitive application package for the National Science Foundation Graduate Research Fellowship, the NSF GRFP, The Oceanography Camp for Girls Fellowship, and the USF College of Marine Science for financially supporting me. And finally, I'd like to thank Dr. Naar, Brittany Sheehy, Sami Francis and the USF College of Marine Science community at large for all playing a role in creating the inclusive, encouraging community housed within our graduate school.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

In the northeastern Gulf of Mexico, relating changes in zooplankton communities to environmental factors is crucial to understanding the marine ecosystem and impacts of perturbations such as oil spills on marine ecosystems. Zooplankton samples were collected each year between 2005–2014 in spring and summer in the vicinity of the oil spill (Deepwater Horizon) that occurred in spring 2010. Zooplankton assemblages and environmental conditions significantly differed seasonally, driven by strong variations in zooplankton at continental shelf stations, and by environmental factors including Mississippi River discharge, wind direction, temperature, and chlorophyll concentrations. Total zooplankton abundances were greatest at shelf stations, intermediate at slope stations, and lowest at offshore stations. Seasonal separation was driven by greater abundances of crab zoea, cladocerans, ostracods, and the copepod, *Eucalanus* spp. during summer. Copepods, *Centropages* spp., were significant indicators of summer conditions both before and after the oil spill.

Sub-regional comparisons in percent composition and abundances of six major non-copepod and seven copepod taxa revealed that most taxa either remained the same or significantly increased in abundance following the spill. A significant decrease in post oil spill taxa was observed only during spring for total copepods, *Eucalanaus* spp., and for salps at continental slope stations, however varying processing techniques used for zooplankton before and after the spill were employed and should be considered. . Based on our sampling periods, these results indicate that the 2010 oil spill did not significantly impact zooplankton communities in the northeastern Gulf of Mexico.

1. INTRODUCTION

1.1 Zooplankton

In the world's surface oceans, plankton comprise the base of the marine food web (Cushing, 1975; Cushing, 1995; Taucher et al., 2017). Primary producers, or phytoplankton, synthesize organic matter using radiant energy from the sun through photosynthesis. Zooplankton play a vital role in modulating the structure of pelagic phytoplankton communities and sustaining marine fisheries, by serving as the essential link connecting energy captured by phytoplankton to higher trophic levels. Some zooplankton species are herbivorous and prey directly on phytoplankton cells, while others are carnivorous and prey on other zooplankton, although many are opportunistic omnivores (Kleppel, 1993).

The structure and dynamics of zooplankton communities are influenced by complex interactions among physical, chemical, and biological processes, as well as by the physiology and behavior of the organisms themselves (Daly and Smith, 1993). Biological characteristics of zooplankton, such as abundance of individuals and community composition, are useful metrics when identifying variations within a zooplankton community as a result of changes in their environment (Ortner, et al. 1989; Kleppel, 1993).

In the upper 200 m of the northeastern Gulf of Mexico (NEGOM), zooplankton abundance generally increases landward (Hopkins, 1982), while biodiversity decreases (Ortner et al., 1989). Major groups that comprise zooplankton communities throughout the NEGOM include copepods, chaetognaths, amphipods, euphausiids, decapods, ostracods, pteropods, salps, scyphozoans, larvaceans, and hydrozoans, among others (Hopkins, 1982; Ortner et al., 1989; Rathmell, 2007; Elliot et al., 2012). Copepods, which may be herbivorous, carnivorous, or omnivorous, are commonly the numerically dominant component of zooplankton communities (Hopkins, 1982; Ortner et al., 1989; Elliot et al. 2012).

Since many zooplankton consume phytoplankton, or prey on zooplankton that do, increased phytoplankton productivity increases food resources for zooplankton communities, which can sustain higher zooplankton abundances (Rathmell, 2007; Elliot et al., 2012). Seasonal studies indicate that zooplankton abundances are greatest during spring and summer months, when primary production is highest (Houde and Chitty 1976; Biggs and Ressler, 2001; Hernandez et al., 2010). Complex relationships between physical processes, light, nutrient availability, and zooplankton grazing govern phytoplankton concentrations.

1.2 Environmental Impacts on Zooplankton Habitat

Light availability, temperature, wind-driven upwelling, river discharge, and mixed layer depth exhibit natural seasonal, interannual (Gillooly and Dodson, 2000), and spatial variability (Hopkins et al., 1981) and, thus, impact the timing and extent of phytoplankton blooms. New nutrients that support phytoplankton blooms are introduced onto the continental shelf by upwelling events (Walsh et al., 2003; Martínez-López and Zavala-Hidalgo, 2009; Jones and Wiggert, 2015) or river discharge (Lohrenz et al., 1997). In general, continental shelf areas with relatively high nutrient input support higher zooplankton abundances, but lower diversity of zooplankton groups (Hopkins, 1982).

Transitional gradients of water properties and zooplankton communities are observed from continental shelf, continental slope, and oceanic regimes (Howey, 1976; Hopkins 1982; Ortner et al., 1989). Estuarine and continental shelf environments are highly influenced by coastal processes, such as river discharge, whereas shelf and slope waters are intermediate zones between coastal river-influenced regimes and wind-driven upwelling, loop current eddies, and oligotrophic oceanic waters (Chakraborty and Lohrenz, 2015).

1.2.1 Winds

Winds play an important role in creating or influencing hydrographic features that impact plankton communities by promoting wind-driven downwelling or upwelling events and by stimulating or delaying the shedding of mesoscale eddies from the Loop Current (Martínez-López and Zavala-Hidalgo, 2009). Seasonally dominant wind directions and magnitudes control much of the circulation on the shelves, while wind directions occurring over shorter-time scales within a season affect upwelling, Mississippi River plume morphology, and Loop Current variability (Morey et al., 2003; Walker et al., 2005; Zavala-Hildalgo et al., 2014).

Dominant wind directions by season and month are shown in Table 1. During spring, fall, and winter, westward winds (winds blowing from the east) dominate in the NEGOM (Jochens et al., 2002), driving the flow of surface water towards the Louisiana-Texas shelf (Feng et al., 2012). Winds with an eastward alongshore component are favorable for upwelling in this study region (Jochens et al., 2002). Upwelling-favorable winds (eastward or winds blowing from the west) moving along the continental shelf of the NEGOM interact with surface waters. Surface waters become subject to Ekman transport, resulting in a net movement off the shelf; deeper nutrient-rich waters then replace these waters (Nguyen, 2014). This often occurs in regions where the light regime is suitable for primary producers, creating an environment conducive to high productivity (Nguyen, 2014). Because of their reliance on solar radiation, phytoplankton peak abundances are usually found in the upper water column of the ocean, and also near the seafloor across shallow regions of the continental shelf where light can penetrate to the bottom.

Upwelling-favorable winds, although not seasonally dominant (Morey et al., 2003), occur over short time periods throughout the year (Zavala-Hidalgo et al., 2014).

In terms of magnitude, generally wind speeds are greatest during mid-December into early spring (May), less strong during August into December, and weakest during summer, mid-June through July, except when associated with tropical cyclone systems (Jochens et al., 2002). May serves as a transition from winter to summer, as winds are highly variable during this time.

Table 1. Seasonal wind direction in the NEGOM. Winds with an eastward alongshore component are favorable for upwelling in this study. Data compiled from Jochens et al. (2002)

Season	Months	Average Windward Direction
Winter	Dec–Feb	S to SW
Spring	Mar	N to W
Spring	Apr–May	N to NW
Spring	Jun 1–15	NW to E
Summer	Jun 16–Jul	NW to E
Summer	Aug	N to NW
Summer	Sep	W to N
Fall	Oct–Nov	S to SW

Upwelling can also occur in association with eddies shed by the Loop Current (Sturges et al., 2000). Loop Current Eddies and smaller mesoscale eddies are typically found north and west of the Loop Current (Jochens et al., 2002). While the Loop Current and its eddies are not a common occurrence in the NEGOM, they will sometimes impinge upon the continental shelf and slope regimes (Dagg and Breed, 2003). Eddies are not generated during any particular season and appear to form randomly.

The edge of the Loop Current and the centers and the edges of cyclonic and anticyclonic eddies, respectively, are considered frontal boundaries. In many ecosystems, frontal boundaries are associated with relatively greater productivity because they may bring higher nutrient water closer to the surface by uplifting the pycnocline (Müller-Karger, 2000; Sturges et al., 2000; Jochens et al., 2002; Molinero, 2008). Evidence of this relationship was observed in the northern Gulf by Biggs (1992), who noted that a mesoscale warm-core eddy, which had shed from the Loop Current, had a very oligotrophic interior while the edges were rich in nutrients and planktonic life. More importantly, substantially greater backscatter representing zooplankton biomass was detected in the upper 50 m at two sampling locations within a cold-core region separating two warm-core eddies in the Gulf of Mexico (Zimmerman and Biggs, 1999).

In addition to their importance in contributing to upwelling and zooplankton aggregations, prevailing winds also transport buoyant waters originating from coastal rivers, such as the Mississippi River, changing plankton community structures in a particular location (Nababan et al., 2011; Chakraborty and Lohrenz, 2015).

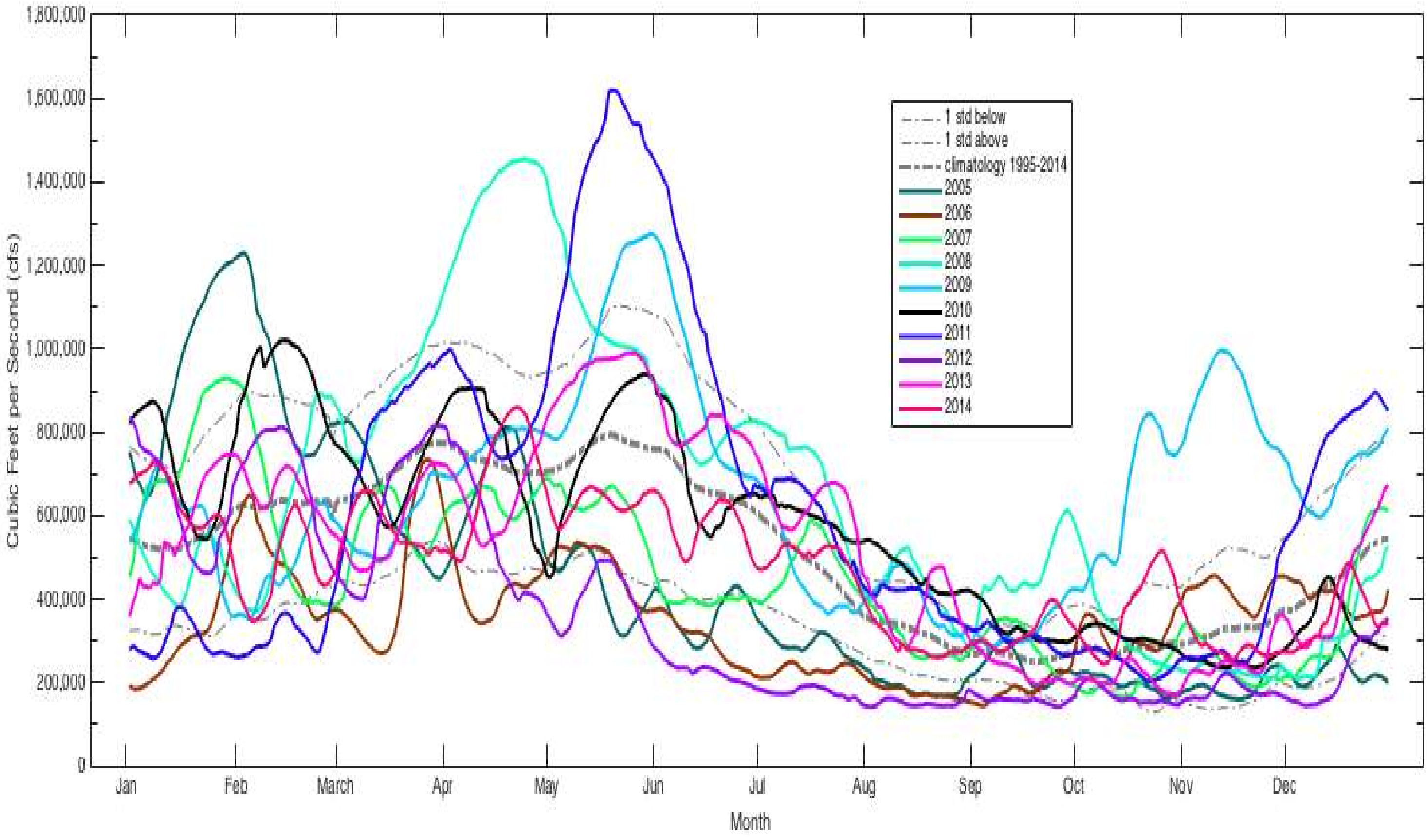

Fig. 1. Daily mean discharge and 20-year climatology of the Mississippi River 2005-2014. Discharge recorded at Tarbert Landing Latitude 31°00'30" N, Longitude 91°37'25" W.

1.2.2 River Discharge

Although river-borne nutrients significantly contribute to the variability in primary productivity in the NEGOM (Müller-Karger et al., 1991; Lohrenz et al., 2008), detailed studies relating zooplankton community assemblages to hydrographic conditions are lacking. The Mississippi River (MSR) is the predominant source for nutrient loading in the NEGOM (Walsh, 1988). Its discharge rates are of particular interest in understanding zooplankton communities because river water is enriched in dissolved nutrients (Walker et al., 2005). From data collected between 1990 and 2009, average daily total nitrogen discharge values ranged between 249–5,579 metric tons/day (Dagg and Breed, 2003). Phosphorus and nitrogen are limiting nutrients in the northern Gulf of Mexico; thus, fluvial input of these nutrients has significant effects on primary production (Dagg and Breed 2003, Lohrenz et al. 2008), and subsequently on zooplankton communities.

The MSR drains ~ 41% of the United States with 80% of that discharge entering the Gulf of Mexico (Lohrenz et al., 2008). Seasonal discharge rates of the MSR are positively correlated with snowmelt in the United States' interior. Increased outflow from the river is observed in the height of spring: March to May. Peak spring outflow typically occurs in mid-April, though maximum discharge usually occurs during the transition between spring and summer, typically between mid-May and mid-June (Fig. 1). Seasons with the lowest flow are from late summer to fall.

While intra-seasonal variation of discharge is generally predictable, interannual discharge rates are highly variable (Fig. 1). For example, in April to mid-June of 2008 and 2011, daily mean discharge rates of the MSR into the Gulf of Mexico exceeded the previous 7-year climatology (Androulidakis and Kourafalou, 2013). The greatest variability in MSR discharge between years occurs typically during spring and summer (Jochens et al., 2002). In our study, we considered spring to occur during the months of March through early June (June 15th) and summer months, late-June through September.

The flow of MSR water into the Gulf is controlled by a number of locks and diversion systems in southern Louisiana that regulate the input of freshwater, sediment, and nutrients (Walker et al., 2005). During hazardous events, the locks and diversions are opened to aid in mitigation, which was done in summer 2010 during the Deepwater Horizon oil spill and the 2011 in response to the Mississippi River Flood (USACE, 2010; USACE, 2013; Kroes et al., 2015).

1.2.3 Deepwater Horizon Oil Spill

On 20 April 2010, an explosion aboard the Deepwater Horizon oil platform resulted in a major release of Louisiana sweet crude oil into the NEGOM near the base of the continental shelf (McNutt et al., 2012). Approximately 22,0000 natural seeps in the Gulf of Mexico release a cumulative 1,500–3,800 barrels of oil per day (Joye et al., 2014). In comparison, by the time the wellhead was capped after three months, the Deepwater Horizon (DWH) oil spill had released 4.9 million barrels of oil into the Gulf (McNutt et al., 2012). Based on percent recovery values published in the Federal Interagency Solutions Group Oil Budget Calculator Science and Engineering Team Report (2010), I estimated that nearly 4 million barrels of oil remained in the environment after direct recovery efforts in the subsea from the wellhead, and burning and skimming at the surface. Large quantities of surface and subsurface oil spread as far north as the Gulf beaches in Mississippi, Alabama, and Florida and possibly as far east as the west Florida Shelf (WFS) (Reddy et al., 2012; Weisberg et al., 2016, Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016) (Fig. 2).

During the 87-day period in which the wellhead remained uncapped, at a maximum extent, 40,000 km^2 of the NEGOM was covered in oil slicks (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). In summer 2010, volatile hydrocarbons, such as benzene, toluene, ethyl benzene, xylenes (BTEX) and polycyclic aromatic hydrocarbons (PAHs), which are toxic to marine life, were detected in the upper 200 m of the water column at concentrations 160 times greater than measurements taken in years prior to the oil spill (Wade et al. 1989; Mitra and Bianchi 2003; Murawski et al., 2016). The PAHs, which are more environmentally persistent than BTEX compounds, were detected in greatest concentrations in the upper 10 m of the water column (Murawski et al., 2016, BP Gulf Science Data, 2016).

The DWH oil spill was also unique for the mitigation strategies used, including freshwater release from the MSR and massive use of sub-sea dispersants injected (SSDI) at the wellhead. Results from an Adaptive Hydraulics Modeling system from the United States Army Corps of Engineers Research and Development Center suggested that increased riverine outflow might inhibit oil intrusion to sensitive Louisiana wetland ecosystems (USACE 2010, Bianchi et al. 2011, O'Connor et al., 2016). Based on modeled scenarios, the state of Louisiana opened seven freshwater diversions and one lock along the Mississippi River to full capacity throughout the months of June and July (State of Louisiana 2010). By the end of these two months, 5.5% of the total water discharged by the Mississippi emptied freshwater and nutrients to areas in the Gulf that typically receive less than 1% of river discharge (O'Connor et al., 2016). Thus, associated with the DWH oil spill, large amounts of river-derived nutrients, freshwater, and crude oil were directly introduced into the NEGOM ecosystem.

Zooplankton live predominately in the upper 200 m of the water column (Hopkins, 1982) and, therefore, may be impacted by oil in a variety of ways. Zooplankton may experience physical or biochemical injury when exposed to oil, resulting in compromised survivorship

(Almeda, 2013; Buskey et al., 2016). Laboratory studies have shown both lethal and non-lethal impacts when copepods are exposed to oil, including decreased swimming ability (Cohen et al., 2014) which should increase predation risk and decrease the ability to catch prey, thus feeding (Cowles and Remillard, 1983), and reproduction (Olsen et al., 2013).

Using isotopic signatures, Graham et al. (2010) and Chanton et al. (2012) have shown that oil originating from the DWH oil spill entered the planktonic food-web, likely by ingestion of oil droplets (Almeda et al., 2013b) and trophic transfer from microbial organisms (Almeda et al., 2013a). While acute consequences of the spill, such as fishery closures, distressed a $5.5 billion fishing industry (NMFS, 2008), significant impacts to planktonic community abundances seemed to have been short-lived (Carassou et al., 2015; Buskey et al., 2016; Murawski et al., 2016). However, changes to community composition are largely still undetermined.

Interestingly, phytoplankton communities have shown an increase in biomass attributed to increased nutrient availability, microbial activity, and grazer mortality (Penela-Arenaz et al., 2009) after some previous oil spills (Parsons et al., 2015). For example, this type of response was observed following the Tsesis tanker spill near Stockholm, Sweden, and the wreck of Amoco Cadiz near Brittany, France (Johansson et al., 1980; Cabioch, 1981; Samain et al., 1980). Yet, decreases in zooplankton populations were reported after the Ixtoc I spill in the southwest Gulf of Mexico which lasted over nine months; although this conclusion was based largely on comparison of data collected on cruises of different seasons (Guzmán del Próo et al., 1986). Responses of plankton communities also vary widely based on species, location, season, and exposure concentrations (Abbriano et al., 2011; Ozhan and Bargu, 2014; Ozhan et al., 2014; Parsons et al., 2015; Buskey et al., 2016).

In the NEGOM, contrasting evidence of the impact of oil on plankton has been reported.

While Parsons et al. (2015) observed an 85% decrease in phytoplankton abundance and shift in species composition on the Louisiana shelf after the DWH oil spill, Hu et al. (2011) and O'Connor (2013) reported a significant positive chlorophyll anomaly, based on satellite fluorescent line-height data, to the east of the mouth of the MSR during the oil spill. Carassou et al. (2015) reported decreased abundances of some zooplankton taxa but increases of others in nearshore NEGOM waters.

Historically, plankton communities have quickly reestablished following an oil spill (Cabioch, 1981; Penela-Arenaz, 2009). Although initially plankton are adversely impacted, their short generation times and perhaps high recruitment of individuals from outside the impacted regions allow taxa to quickly return to natural population levels. Many regions impacted by oil spills show no significant changes in plankton communities over long time periods, except for changes associated with natural variability (Varela et al., 2006; Batten et al., 1998).

Carassou et al. (2015) found significant variation in zooplankton assemblages near the Alabama coast early on during the DWH oil spill (May and June 2010) compared to prior years, but these variations were no longer statically significant by July 2010. It is unknown whether oceanic zooplankton south of Alabama and on the Florida continental shelf or continental slope had a similar rapid recovery as that observed by Carassou et al. (2015). The lack of baseline (pre-DWH) data over most of the DWH spill region has impeded understanding of the consequences of the DWH oil spill (Murawski et al. 2016). Further, responses of the NEGOM's plankton communities vary greatly by location, level and duration of oil exposure, and season (Buskey et al., 2016; Murawski et al., 2016). Thus, establishing a baseline knowledge of zooplankton abundance and community composition prior to the DWH oil spill is critical for comparative studies assessing the impacts of the oil spill on NEGOM's economically important ecosystem.

The goal of my study was to explore the effects of natural seasonal and interannual environmental variability on zooplankton community structure in the NEGOM, as well as the effects of the DWH oil spill on zooplankton communities. I examined data collected on cruises during spring and summer that were carried out between 2005–2014. As noted previously, the DWH oil spill occurred in the NEGOM between May and August 2010. My study was undertaken in four phases.

1. I established baseline data for natural seasonal and interannual variation in zooplankton community structure prior to the DWH oil spill (pre-DWH) using SEAMAP samples collected between 2005–2009.
2. I assessed seasonal and interannual variation in zooplankton community structure using samples collected beginning when oil was still present in the upper 200m of the water column from the DWH oil spill (summer 2010) and in subsequent years (2011-2014); this dataset is collectively referred to as post-DWH.
3. I explored environmental variables contributing to season or year-specific variation by assembling, and performing multivariate analysis with, relevant environmental data sets, including CTD (sea water salinity, temperature, and depth) and chlorophyll data collected during the cruises, as well as MSR discharge and wind or surface current acquired from other sources.
4. Using the zooplankton and environmental data sets, I assessed the effect of DWH oil spill on zooplankton communities in the NEGOM and, when perturbed, the ability and time that the NEGOM ecosystem required to recover to pre-DWH conditions.

Using these data sets, I proposed and tested several hypotheses:

1. There will be no significant seasonal differences between spring and summer in

$H_{01.1}$ environmental conditions

$H_{01.2}$ zooplankton community structure

2. There will be no significant interannual differences during spring in

$H_{02.1}$ environmental conditions

$H_{02.2}$ zooplankton community structure

3. There will be no significant interannual differences during summer in

$H_{03.1}$ environmental conditions

$H_{03.2}$ zooplankton community structure

4. Variation in environmental conditions across years does not significantly explain any variation observed

$H_{04.1}$ in spring zooplankton community structure

$H_{04.2}$ in summer zooplankton community structure

5. There will be no significant impact of the Deepwater Horizon oil spill

$H_{03.1}$ zooplankton community structure

$H_{03.2}$ zooplankton percent composition and abundance

2. METHODS

2.1 Study Region

The study region in the NEGOM was located between latitudes 29.5°–28.5° N and longitudes 88.5°–85.5° W and spanned three sub-regions determined by bottom depth: continental shelf (20–100 m), continental slope (200–400 m), and oceanic (≥ 1,000 m). Figure 3 shows the locations of the twelve stations along two transects (DSH and PCB) that were sampled during and after the DWH oil spill and the seven stations that were sampled prior to the DWH oil spill, as part of the NOAA's Southeastern Monitoring and Assessment Program (pre-DWH) program. The station names, locations, and sub-region designations are reported in Table 2.

2.2 Sampling Methodology and Analyses

University of South Florida (USF) zooplankton samples, collectively referred to as post-DWH, were collected using bongo net tows following the SEAMAP collection methods (SEAMAP Field Operations Manual for Collection of Data, 2001). These zooplankton samples and environmental data (bottom depth, discrete depth chlorophyll, and water column profiles for CTD, chlorophyll fluorescence, dissolved oxygen, and turbidity) were collected at twelve stations on thirteen cruises between August 2010 and August 2014. This project focused on two transects lines, PCB and DSH, and the DWH site (Fig. 3). After the Deepwater Horizon event, samples collected as part of the SEAMAP program prior to then oil spill, referred to as pre-DWH, were chosen based on proximity to the post-DWH plankton collection stations.

2.2.1 Zooplankton Sampling Methodology

SEAMAP is a survey program supported by NOAA's National Marine Fisheries Service (NMFS), the Gulf States Marine Fisheries Commission, and state-level marine resource departments in Alabama, Mississippi, Louisiana, and Texas. The program first began conducting plankton tows in 1981. Stations extend from Florida to Texas, ranging from coastal to oceanic locations. While the goals of the SEAMAP surveys are to collect data on the abundance and distribution of marine organisms and associated abiotic factors, analyses have primarily focused on ichthyoplankton and other commercially important species (Knight, 2014). Therefore, not all stations are visited each cruise. Instead, stations are visited primarily during spawning periods of targeted species (spring and fall) and less frequently during summer and late fall. Twenty-four of the collected SEAMAP samples, henceforth referred to as pre-DWH, were relevant to our study region, 15 of which were collected during spring months and nine during summer.

Both the pre-DWH and USF post-DWH zooplankton samples were collected using identical methods. A 60 cm bongo net, fitted with 333 um mesh and a mechanical flowmeter, was towed in an oblique path from the surface to a depth of 200 m and back, or 2 - 5 m off the bottom at stations shallower than 200 m (Lyczkowski-Shultz and Hanisko, 2008). Bongo tow depth was determined either using an electronic depth sensor or calculated from wire paid out and wire angle (Lyczkowski-Shultz and Hanisko, 2008).

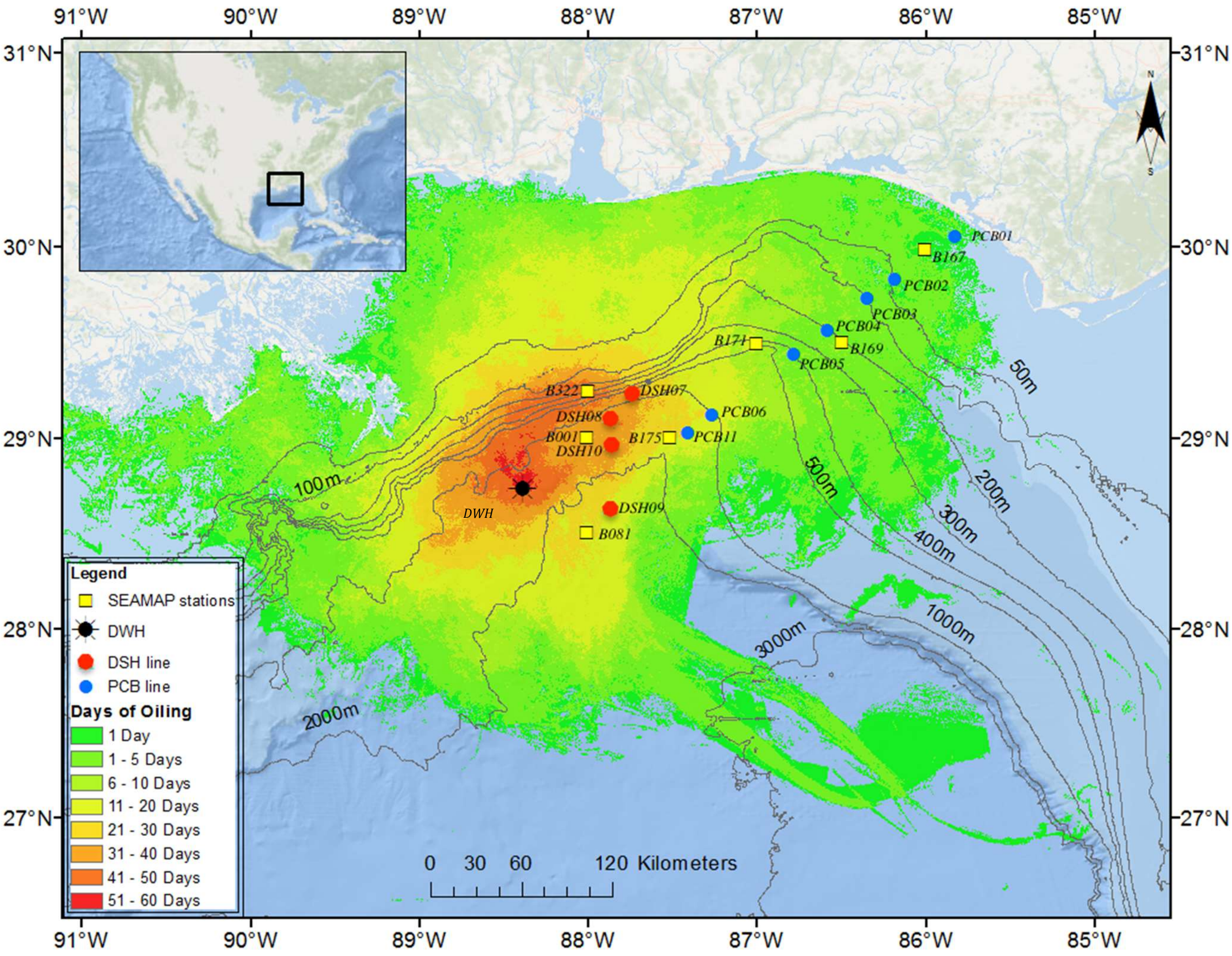

Fig. 2. Map of NEGOM sampling region showing SEAMAP pre-DWH (yellow squares) and USF post-DWH transects and stations, PCB (blue circles), DSH (red polygons), and DWH (black circle).

Table 2. Station names, coordinates, depths, and sub-regions for pre-DWH sites and post-DWH sites. B designates a pre-DWH sampling location. The first three letters of all other station names (PCB and DSH) designate the transect line for USF (post-DWH) samples. DWH is a post-DWH station named as such for its sampling location being nearest the Deepwater Horizon oilrig explosion site

Station	Latitude °N	Longitude °W	Depth (m)	Sub-Region
PCB01	30.06	-85.83	25	Continental Shelf
PCB02	29.83	-86.18	50	Continental Shelf
PCB03	29.73	-86.35	100	Continental Shelf
PCB04	29.57	-86.58	200	Continental Slope
PCB05	29.44	-86.78	400	Continental Slope
PCB06	29.13	-87.27	1000	Oceanic
PCB11	28.77	-87.29	1200	Oceanic
DSH07	29.25	-87.73	400	Continental Slope
DSH08	29.12	-87.87	1100	Oceanic
DSH09	28.64	-87.87	2300	Oceanic
DSH10	28.98	-87.87	1500	Oceanic
DWH	28.74	-88.39	1550	Oceanic
B167	30.00	-86.00	40	Continental Shelf
B169	29.50	-86.50	200	Continental Slope
B171	29.50	-87.00	350	Continental Slope
B322	29.25	-88.00	300	Continental Slope
B175	29.00	-87.50	1140	Oceanic
B081	28.50	-88.00	2200	Oceanic
B001	29.00	-88.00	1500	Oceanic

2.2.3 Zooplankton Analyses

Zooplankton abundances were calculated by identifying and enumerating dominant taxa in a subsample (such as copepods, euphausiids, chaetognaths, ostracods, etc.), multiplying by the number of splits for the subsample, and then dividing by the volume (m^3) of water filtered as determined by flowmeters. The post-DWH USF samples were analyzed microscopically to species for copepods when possible by Dawn Outrum, otherwise to genus or higher taxon for other zooplankton. However, to compare our post-DWH and pre-DWH datasets, many post-DWH zooplankton categories were collapsed into another in order to match the taxa grouping structure of the pre-DWH data.

The pre-DWH zooplankton samples were analyzed using a Hydroptic ZooScan digital imaging system. This innovative technology employs pattern recognition of zooplankter geometric shapes to allow rapid identification down to a resolution determined by a 'training set'. The training set created for this study region included the categories listed in Table 3.

Pre-DWH ZooScan sample analyses followed the methods of Gorsky et al. (2010), including sample preparation, scanning, and image processing with ZooProcess and Plankton Identifier software. First, two daily blank background images were taken, which were subsequently subtracted from the scanned zooplankton sample image. The pre-DWH samples, which were preserved in ethyl alcohol, were transferred to distilled water and split into smaller representative samples, or aliquots, using a Folsom splitter. The number of splits for a sample was determined based on visual inspection of the ability for the sample to 'fit' atop the scanning bed, without any individuals touching one another or the edges of the scanning bed. Once the appropriate aliquot size was obtained (most often 6−7 splits, i.e., 1/32nd or 1/64th of the original sample), the number of calanoid copepods present in the aliquots was counted to ensure at least 100 individuals were present. When <100 calanoid copepods were present, two scans were taken to represent that sample by scanning the final and second to final split. The purpose of this method is to obtain a representative aliquot of the original sample, since calanoid copepods often dominate Gulf of Mexico assemblages. The resulting images are saved as JPEG files. Individual zooplankton images, referred to as vignettes, were grouped by employing a created 'training set' based off of images captured by the ZooScan and processed by Plankton Identifier and

ZooProcess software (Gorsky et al. 2010).

In order to expand the ‘learning’ of the training set, vignettes (single images) were used to accurately identify the biological attributes of the samples. The training set contains folders that represent each taxonomic group of organisms or abiotic objects (Table 3). Expanding this training set required visual inspection of captured vignettes and adding each to their respective folders. Since pattern recognition software has already been applied to each sample, the last step required each automated classification to be visually validated for reliability.

Table 3. Zooplankton taxa group names used to construct the ZooScan "training set". A superscript of 1 designates groupings present in only pre-DWH samples while a superscript of 2 designates groupings only present in post-DWH samples

- *Acartia* spp.
- *Candacia* spp.
- *Centropages* spp.
- *Corycaeus* spp.
- *Eucalanus* spp.
- *Lucicutia* spp.
- *Oithona* spp.
- *Oncaea* spp.
- *Sapphirina* spp.
- *Temora* spp.
- Unknown Calanoids^{1}
- Unknown Copepods^{1}
- Amphipods
- Appendicularians
- Bivalves
- Chaetognaths
- Cladocera
- Crab Megalops
- Crab Zoea
- Crustacean Naupli
- Cumaceans^{2}
- Doliolids
- Echinoderm Larvae and Juveniles
- Eggs
- Euphausiids (Non-Larval)
- Hemichordata, *Ptychodera flava*^{2}
- Hydroid Polyps
- Isopods^{2}
- *Lucifer*
- Miscellaneous Decapod
- Miscellaneous Gelatinous
- Miscellaneous Mysids
- Ostracods
- Phyllosoma
- Polychaeta
- Pteropod *Calvolinia*
- Pteropod *Limacina*
- Pteropod, conical
- Radioloarians^{2}
- Salps
- Siphonophores
- Stomatopods
- Heteropod, *Atlantidae*
- Heteropod, Non-*Atlantidae*
- Fish Larvae
- Cyphonautes
- Miscellaneous Gastropods^{2}
- Unknown Young Malacostraca^{1}
- Holothuroidea^{2}
- Cephalopods
- Miscellaneous Pteropods

To assess zooplankton community structure, a diversity measure known as beta diversity was employed (Whittaker, 1960). Beta diversity is a measure of both the variation in the abundance and composition of zooplankton taxa among sample sites. Beta diversity considers the ratio between gamma and alpha diversity at a sample site in order to assess the similarity among sites within a sampling region (Whittaker 1960, Jost 2007). Taking Whittaker's definition into consideration, Anderson et al. (2006) proposed beta diversity as a multivariate measure of average dissimilarity of a sample comprising a group to that group's centroid where it can be now be used to measure the variability of species composition from a sampling region. For example, by employing a resemblance matrix, two sites with an identical number and types of animals present will have the same ratio between alpha (local) and gamma (regional) diversity, and will therefore be 100% identical, or have a similarity score of 1. Resemblance matrix values range between 0 and 1 and therefore beta diversity is useful for assessing the degree of community differentiation across a complex environmental gradient (Whittaker, 1960). For the purposes of this study, zooplankton community structure is synonymous with zooplankton beta diversity. Zooplankton beta diversity is being used as a measure of dissimilarity among sites based on that the taxa present (composition) and corresponding abundance for each site (i.e. sampling station).

2.2.4 Environmental Data Analyses

The influence of natural environmental variability on zooplankton community structure was assessed by analyzing a number of parameters, including surface seawater temperature, salinity, dissolved oxygen (DO), turbidity, discrete chlorophyll, and integrated chlorophyll fluorescence (0–200 m), obtained during zooplankton collection. In addition, average daily MSR discharge volume rates (3 days, 14 days, 21 days, and 30 days), and 3-day average daily wind components and magnitude were obtained from the United States Geological Survey Stream-gauging Network, and NOAA National Centers for Environmental Information, respectively. Some in-situ chlorophyll and wind values were missing from pre-DWH datasets. These missing values were supplemented with chlorophyll values and surface currents extracted from the Coupled-Ocean-Atmosphere-Wave- Sediment Transport Modeling System provided by Dr. George Xue at Louisiana State University, similar to the physical model setup described by Zang et al. (2018).

2.3 Multivariate Statistics of Pre- and Post-DWH

The relationship between environmental factors and zooplankton variability was assessed separately for both pre-DWH zooplankton communities and post-DWH zooplankton communities. Zooplankton abundance data can be found in the Supplemental Tables section.

The evaluation of the influence of environmental variability on zooplankton community structure consisted of two components. The first component assessed environmental conditions and zooplankton beta diversity separately to detect differences across seasons and years. The next component related environmental variables to changes observed in zooplankton assemblages across seasons and years.

To achieve the first component, scanned pre-DWH samples and post-DWH zooplankton data were categorized by environmental conditions and zooplankton beta diversity. These data were compared between seasons across years (i.e., spring vs. summer) and within-seasons between years (i.e., summer 20xx vs. summer 20xy) to assess significant differences. Euclidean Distance on standardized data and Bray-Curtis Dissimilarity metrics on fourth-root transformed data were used for all multivariate testing of environmental data and zooplankton data, respectively.

Euclidean distance is a dissimilarity metric calculated when analyzing continuous non-zero data of multiple variables. Euclidean distance reduces the multidimensionality of abiotic data by calculating a new single variable from the multivariate data of each site. A new single variable for each site can then be compared to another, yielding a resemblance matrix of site-to-site comparisons. Bray-Curtis dissimilarity works similarly but was used for comparing zooplankton compositional dissimilarity among sites. Bray-Curtis is more appropriate when analyzing biological data as it treats sites with missing species as ecologically similar. Bray-Curtis dissimilarities were calculated to infer the beta diversity of zooplankton groups.

Non-parametric permutation-based multivariate pairwise analysis of variance (PERMANOVA-PW), Canonical Analysis of Principal Coordinates (CAP), similarity percentages (SIMPER), and indicator values (INDVAL) were used to determine if environmental conditions ($\mathbf{X}_{\mathrm{Euc}}$) or beta diversity ($\mathbf{Y}_{\mathrm{BC}}$) were significantly different across seasons or years. All statistical analyses were conducted using MATLAB R2015a using the "Fathom" multivariate statistics toolbox for MATLAB (Jones 2017). PERMANOVA-PW tests the null hypothesis of no difference among groups' means, where significance was assessed at 1,000 permutations ($\alpha = 0.05$) of observations in either X or Y (Anderson 2001). Since the nature of this study produces multiple means to be compared at once, PERMANOVA testing is useful for comparing statistical significance among groups when group dispersions are homogeneous. All within group dispersions were tested by conducting a PERMANOVA-PW on group residuals (Anderson, 2006). When dispersions were non-homogeneous, a super-ensemble model technique (Anderson et al., 2017) recently embedded within the PERMANOVA-PW routine (unpublished) in the Fathom toolbox for MATLAB (Jones, 2017) was employed. This multivariate technique implicitly adjusts for unequal dispersions between groups, often a result of varying sample sizes between groups.

Significant PERMANOVA-PW tests were followed up with a discriminant analysis, Canonical Analysis of Principal Coordinates (CAP). This test is useful for visualizing differences among groups and determining which variables were most responsible for driving the separation of these groups (Anderson and Willis, 2003; Legendre and Legendre, 2012).

For zooplankton, similarity percentages (SIMPER) (Clarke and Warwick, 1994) and indicator values (INDVAL) (Dufrene and Legendre, 1997; De Caceres and Legendre, 2009; Legendre and Legendre, 2012; Clarke and Gorley, 2015) were employed to identify groups of zooplankton that were good discriminating species between two groups. The SIMPER routine first calculates the average dissimilarity between all pairs of groups then identifies the separate contributions of each type of zooplankton driving differences between groups. The INDVAL routine determines whether a taxon can be considered a significant indicator of a group by assessing the permutation-based significance (α) of that taxon and the ‘indicator value’ of whether that animal appeared in most of the samples comprising a group and if that animal demonstrated a higher fidelity to one group over another (Dufrene and Legendre, 1997). For this study, indicator taxa were selected only if they were both statistically significant ($\alpha = 0.05$) and if the strength, or magnitude, of its ‘indicator value’ was greater than 45.

The second component of the multivariate analyses related the influence of environmental factors to variation in zooplankton beta diversity. Distance-based Redundancy Analysis (dbRDA) in conjunction with Akaike’s Information Criterion (AIC) was used to explore these relationships. Distance-based RDA analysis assesses environmental variables to develop a combination of those criteria that best explain dissimilarities derived from the zooplankton data (Clarke and Warwick, 1994; Legendre and Anderson, 1999) and AIC determines the significance of those contributing environmental variables (Godinez-Dominguez and Freire, 2003).

2.4 Comparisons of Pre-DWH versus Post-DWH

Comparisons of pre- and post-DWH zooplankton were analyzed in two ways. First, multivariate analyses were conducted to identify changes in beta diversity between pre- and post-DWH zooplankton communities. Next, abundance and percent composition of six major zooplankton groups and seven copepod genera for pre-DWH and post-DWH were compared. Taxa included in comparative multivariate analysis of beta diversity can be found in Table 4, non-copepod taxa and copepod genera included in abundance and percent composition comparative analyses can be found in Table 5 and Table 6, respectively. Some of the six major groups (i.e. Total Copepods) represented a cumulative total of other groups. Taxa included in each of these can be found in Table 7. Because of the seasonal abundance and regional fidelity of some groups, comparisons were conducted based on seasons and sub-regions. Due to the variable sampling frequency between pre-DWH and post-DWH sampling efforts, only spring oceanic, summer continental shelf, and both spring and summer continental slope stations were analyzed. Classification of stations within each sub-region can be found in Table 2.

2.4.1 Multivariate Comparative Analyses

Principal Coordinates Analyses (PCoA) were used to organize the total variability of the multivariate beta diversity measures of pre- and post-DWH samples. Resulting ordination diagrams illustrate the total variability of beta diversity among all stations in two-dimensional space where each axis displays a percentage of the total explained variability. These ordinations are useful to determine whether distinct grouping between pre- and post-DWH samples was observed or whether substantial overlap suggested beta diversity was similar. Distance between objects indicated similarity (or dissimilarity) of zooplankton beta diversity at each station; closer objects are more similar while further apart objects are less similar. Vector biplots accompany the ordinations and depict the presence and abundance of taxa groups that explain at least 3% of total variability based on SIMPER results or deemed as significant indicators per INDVAL testing. Taxa groups displayed as arrow vectors depicted in the ordination are relative gradients with only positive ends visualized. The vectors are drawn through multivariate space and correspond to total explained variability. Objects can be superimposed onto a taxa vector arrow to estimate the presence and abundance of that animal at that station. Proximity and length of the arrow to the x-axis infers to the relative importance of that variable (Legendre and Legendre, 2012). This exploratory method was selected for assessing differences between pre-and post-DWH zooplankton communities as opposed to hypothesis-driven counterparts due to the different methodology of determining abundances of groups in samples (i.e. ZooScan versus microscopy). By assessing total variability as opposed to formulating an *a priori* hypothesis (such as done with permutation-based testing like CAP), results will offer insight into differences that may be related to zooplankton community variability or variability of the methodology.

2.4.2 Abundance and Percent Composition of Zooplankton Assemblages

Comparative analyses of pre-DWH to post-DWH were also conducted by testing the percent composition and abundances of some zooplankton groups by season and sub-region for each sampling period.

Comparisons of percent composition for some zooplankton groups were utilized in order to assess the conservation of community structure of animal abundances relative to one another. Comparisons of percent composition for pre- versus post-DWH sampling periods were first conducted using six major zooplankton groups where all copepods, Malacostraca, and pteropods, were lumped into a “Total” categories. Then, a separate analysis of just copepod abundances was conducted using the seven most common copepod genera. Percent values were computed by station by assessing the abundance of the taxon in question relative to the total abundance of all taxa groups (Table 5 and Table 6). Taxa included in the total abundance for both abundance and percent composition computations can be found in Table 7.

Additionally, comparisons of total abundances were conducted using the same six major zooplankton groups and seven common copepod genera used in the percent composition comparisons.

To assess whether pre- versus post-DWH zooplankton were significantly different, both percent compositions and abundances for each sampling period underwent Mann-Whitney-Wilcoxon significance testing.

Table 4. Taxa groups used in multivariate comparative analyses of zooplankton beta diversity between pre-DWH and post-DWH stations. Thirty-nine ‘general’ groups of zooplankton taxa present at both pre-DWH and post-DWH samples were used to compare zooplankton beta diversity of pre-DWH (2005−2009) zooplankton samples to post-DWH zooplankton samples (2010−2014) in the NEGOM

Centropages spp.
Lucicutia spp.
Temora spp.
Oithona spp.
Oncaea spp.
Corycaeus spp.
Sapphirina spp.
Candacia spp.
Eucalanus spp.
Amphipods
Cladocera
Crab Megalops
Crab Zoea
Crustacean Naupli
Euphausiids (Non-Larval)
Lucifer
Miscellaneous Decapod
Miscellaneous Mysids
Phyllosoma
Stomatopods
Ostracods
Bivalves
Heteropod, Non-Atlantidae
Echinoderm Larvae and Juveniles
Pteropod, Conical
Pteropod, C*avolinia*
Heteropod, Atlantidae
Cephalopods
Pteropod, *Limacina*
Miscellaneous Pteropod
Cyphonautes
Doliolids
Siphonophores
Chaetognaths
Eggs
Salps
Polychaeta
Appendicularians
Fish Larvae

Table 5. Zooplankton groups used in pre-DWH and post-DWH abundance and percent composition comparative analyses. Changes in abundance or percent composition of the six ‘general’ zooplankton taxa denoted with an asterisk were compared pre-DWH (2005−2009) to post-DWH (2010−2014). All taxa listed are those that comprise ‘total abundance’ for calculating percent composition

Total Copepods*	Doliolids
Chaetognaths*	Eggs
Total Malacostraca*	Fish Larvae
Ostracods*	Polychaeta
Total Pteropods*	Siphonophores
Salps*	Appendicularians
Cladoceran	Bivalves
Echinoderm Larvae and Juveniles	Cephalopods
Heteropod, Atlantidae	Cyphonautes
Heteropod, Non-Atlantidae	

Table 6. Genera of copepods used in pre-DWH and post-DWH percent composition comparative analyses. Seven genera of copepods were used to compare abundance and percent composition of copepod communities pre-DWH (2005−2009) to copepod communities post-DWH (2010−2014) in the NEGOM

Centropages spp.
Corycaeus spp.
Eucalanus spp.
Lucicutia spp.
Oithona spp.
Oncaea spp.
Temora spp.

Table 7. Zooplankton taxa groups represented in the general 'Total' categories from Table 5 used in comparisons of pre-DWH (2005−2009) to post-DWH (2010−2014)

Total Copepod	Total Malacostraca	Total Pteropods
Centropages spp.	Amphiphoda	Pteropod, *Cavolinia*
Lucicutia spp.	Miscellaneous Decapods	Pteropod, Conical
Temora spp.	Crab Zoea	Pteropod, *Limacina*
Oithona spp.	Crab Megalops	Miscellaneous Pteropods
Oncaea spp.	Phyllosoma	
Corycaeus spp.	*Lucifer*	
Eucalanus spp.	Euphausiids (non-larval)	
Unknown Calanoida	Stomatopods	
Unknown Copepod	Miscellaneous Mysids	

3. RESULTS

3.1 Diel Vertical Migration

Many zooplankton taxa exhibit diel vertical migration. Since pre-DWH and post-DWH bongo net hauls were not taken at standard times during the day or night, migrators may be present in the upper 200 m sampled at night or may have migrated outside the 200 m sampling depth during the day. To assess whether diel vertical migration confounded the estimates of total abundances in post-DWH zooplankton samples, PERMANOVA tests were run against spring day/night and summer day/night total zooplankton abundances for samples collected at stations that exceeded 200 m depth. Results indicated that day and night total zooplankton abundances were not significantly different ($p \geq 0.4$) and, therefore, all stations for all cruises were used in analyses.

3.2 Beta Diversity and Environmental Conditions

Analyses were conducted on the beta diversity of zooplankton samples and the normalized Euclidean distances of environmental data. First, the null hypothesis that beta diversity or environmental conditions were not significantly different between spring and summer seasons was tested. Second, the null hypothesis that beta diversity or environmental conditions were not significantly different between years was tested. Third, the null hypothesis of no effect of environmental conditions on the beta diversity of zooplankton was tested. The following results for both zooplankton and environmental conditions are in two sections: pre-DWH results and post-DWH. Within each section are sub-sections that include results for spring vs. summer, interannual variability, and zooplankton and environmental parameters. A third section explores comparisons between pre-DWH and post-DWH sampling periods, which includes results for pre- and post-DWH comparisons of zooplankton beta diversity, zooplankton percent composition, and zooplankton abundances by season and sub-region.

3.3 Pre-DWH Beta Diversity and Environmental Conditions

Pre-DWH zooplankton beta diversity and environmental conditions were analyzed separately. Sections herein address the null hypotheses of no significant seasonal or interannual differences in either zooplankton beta diversity or environmental conditions among pre-DWH samples.

3.3.1 Spring vs. Summer Pre-DWH Zooplankton

Beta diversity of zooplankton at pre-DWH stations was significantly different between spring and summer seasons when data from all years (2005-2009) were combined (PERMANOVA, $p = 0.025$) (Fig. 3). Results from a blind cross-validation test (Leave One Out Cross Validation Classification Success) showed that a random spring sample was successfully classified as such based on its beta diversity 93% of the time, while the success of blind summer classification was 78%. Greater presence of bivalves, ostracods, *Centropages* spp., cladocerans, echinoderm larvae and juveniles, pteropod *Limacina* spp., and stomatopods were significant indicator species of summer sampling, while a greater presence of *Eucalanus* spp. was observed during spring months. SIMPER results showed that these groups, along with crab zoea, together drove 27% of the variability between spring and summer (Fig. 4).

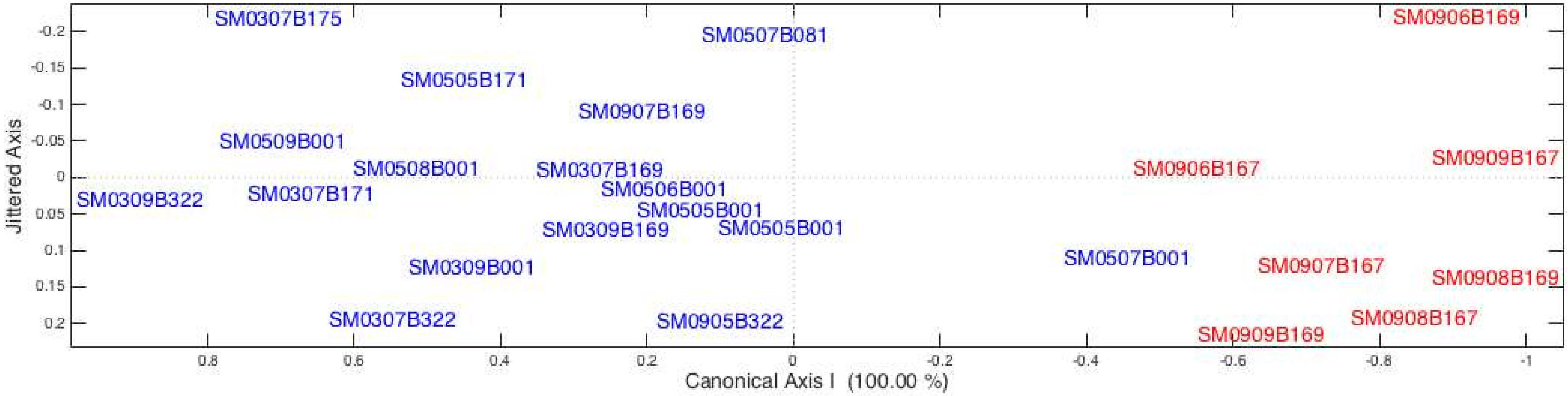

Fig. 3. CAP ordination diagram for pre-DWH zooplankton beta diversity during spring (blue) and summer (red) seasons of years 2005-2009. The canonical axes can be used to explain the total variability between each group (season) of objects; where axis I accounts for 100% of variability between groups. Any two objects' (sample site beta diversity) proximity to one another can be interpreted as similarity, with those closer being more similar and farther apart as more dissimilar. Station labeling scheme is as follows: pre-DWH SEAMAP (SM), month (mm), year (yy), station (Bnnn). There is a clear separation of zooplankton beta diversity at stations based on the season.

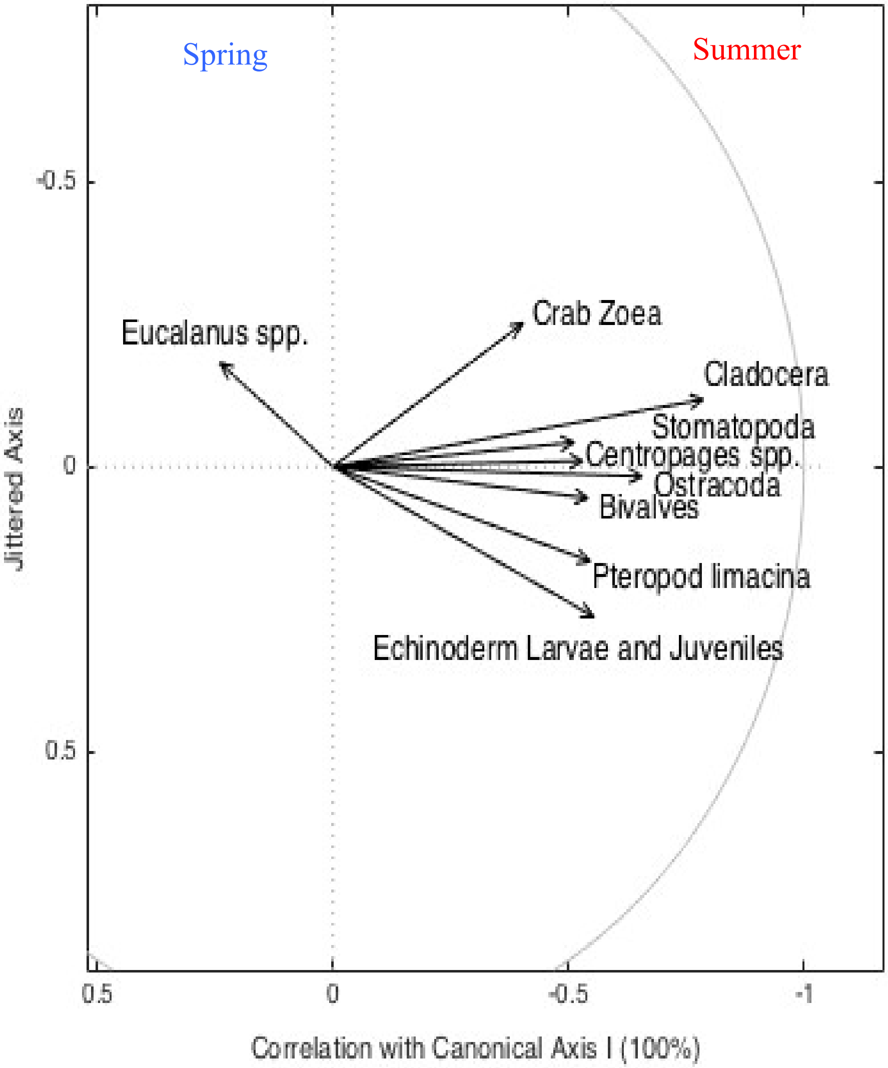

Fig. 4. CAP vector biplot for pre-DWH zooplankton beta diversity during spring and summer seasons of years 2005−2009. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 3. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 3) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors illustrate the relative importance of those taxa describing group (seasonal) separation. Summer stations have a greater presence of most taxa groups that drive seasonal differences, excluding *Eucalanus* spp., which is more prevalent in spring. Together these zooplankton taxa groups drive 27% of total variation between pre-DWH spring and summer seasons.

3.3.2 Spring & Summer Pre-DWH Interannual Zooplankton

Beta diversity within either spring or summer years were not significantly different between any pairwise years. Because groups were not significantly different, a principal coordinates analysis ordination plot was used to illustrate the total variability within spring (Fig. 5, 6) and summer (Fig. 7, 8) for pre-DWH interannual beta diversity. Results show that there was clustering of zooplankton communities by sub-regions for both spring and summer, and by year during summer, though to a lesser degree than sub-region. Particularly, continental shelf stations exhibited greater variability between years and continental slope and oceanic communities were more similar.

3.3.2.1 Spring Interannual Pre-DWH Zooplankton

Results for spring continental slope and oceanic stations revealed that groups most responsible for driving spring interannual variability were miscellaneous decapods, euphausiids, conical pteropods, miscellaneous pteropod, chaetognaths, *Eucalanus* spp., *Temora* spp., salps, crab zoea, *Lucifer*, pteropod *Limacina* spp., ostracods, crustacean nauplii, *Lucicutia* spp., and miscellaneous mysids. The single significant indicator, conical pteropods, was indicative of 2005 sampling. Spring continental slope stations B169, B171, and B322 exhibited the greatest diversity and abundance of groups responsible for driving spring interannual variability (Fig. 5, 6), though note that no inner shelf stations were visited during spring. Together, these animals drove 36% of interannual variability. Also note that the single stations representing 2006 and 2008 were substantially different along the x-axis from samples from 2005, 2007, and 2009 all of which had greater sample sizes.

3.3.2.2 Summer Interannual Pre-DWH Zooplankton

Substantial variability in zooplankton beta diversity was observed between stations and across years (Fig. 7). Taxa groups that best explain differences among summer years were most abundant at continental shelf station (B167) across years with the exception of non-larval euphausiids, which drove interannual variability at continental slope stations (B169, B322). These groups drove 41% of total summer interannual variability

Summer SIMPER results indicate ostracods, salps, crab zoea, miscellaneous pteropods, *Centropages* spp., cladocerans, miscellaneous mysids, eggs, conical pteropods, and *Eucalanus* spp. each drive at least 3% of variability. Further, it's evident that in summer (Fig. 8), continental shelf station B167 represents greater abundances of zooplankton groups, notably ostracods and *Centropages* spp., relative to continental slope and oceanic stations. However, beta diversity in sample SM0907B167 strays from this cluster of other B167 samples. This independence observed from this station can be attributed to relatively high abundance of bivalves and conical pteropods and low abundances of copepods, ostracods, and salps.

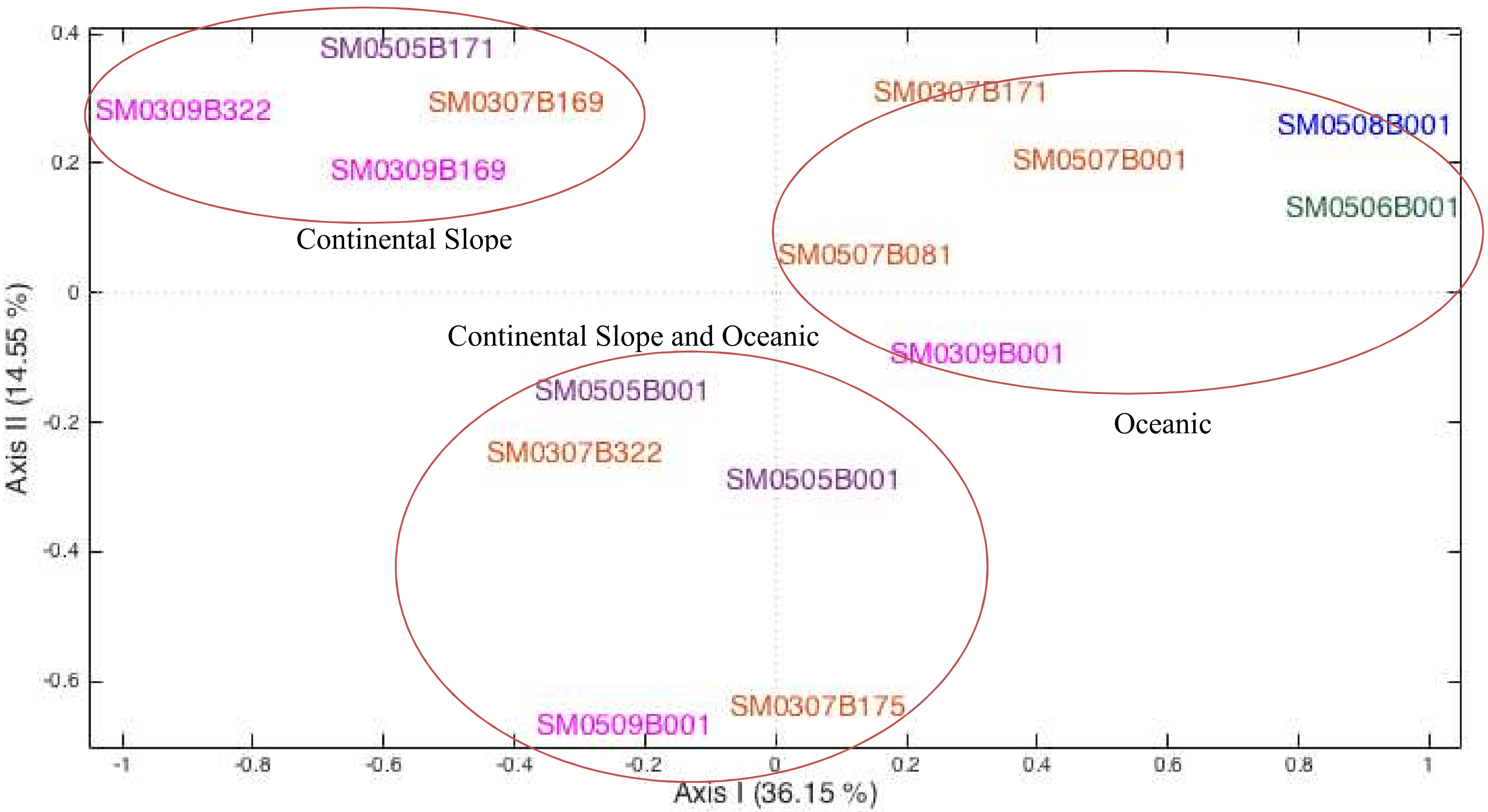

Fig. 5. PCoA ordination diagram for pre-DWH zooplankton beta diversity during spring of years 2005–2009. The axes can be used to explain the total variability between objects (site beta diversity); where axis I accounts for 36.15% and axis II accounts for 14.55% of total variability between objects. Any two objects' (sample site beta diversity) proximity to one another can be interpreted as similarity, with those closer being more similar and farther apart as more dissimilar. Station labeling scheme is as follows: pre-DWH SEAMAP (SM), month (mm), year (yy), station number (Bnnn); each year is represented as spring 2005 (purple), 2006 (green), 2007 (orange), 2008 (blue), and 2009 (pink). Depending on year, continental slope stations (B169, B171, B322) clustered separately from oceanic (B001, B081, B175), while other times they clustered together.

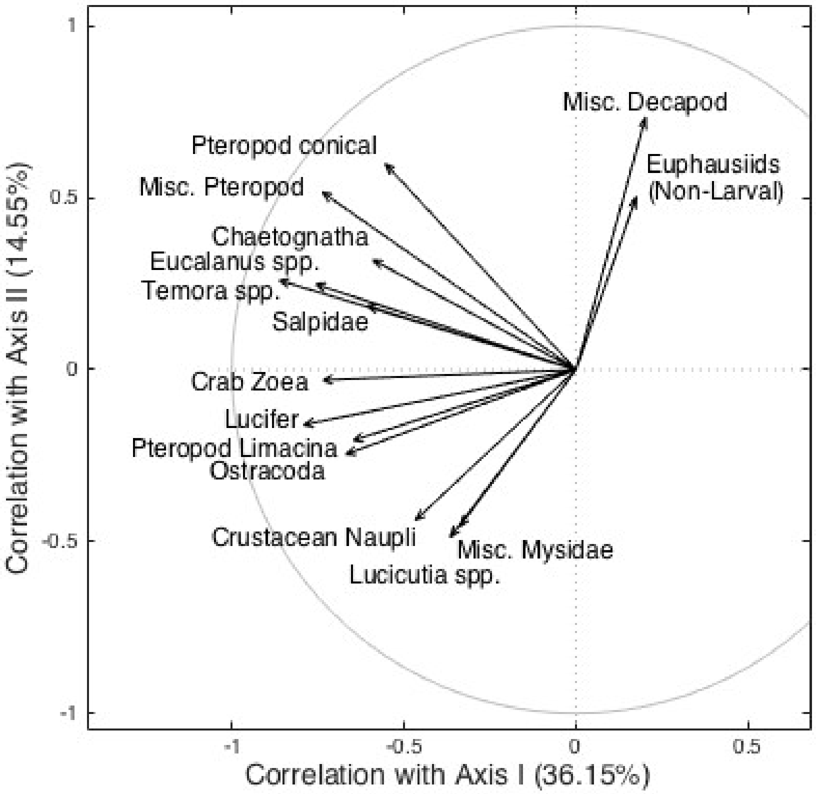

Fig 6. PCoA vector biplot for pre-DWH zooplankton beta diversity during spring of years 2005‒2009. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 5. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 5) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. Conical pteropods, indicative of 2005, were the single significant indicator group. In correspondence to Fig. 5., taxa that best explain differences among spring years were most abundant at continental slope stations while miscellaneous decapods and Euphausiids are often greater at oceanic stations.

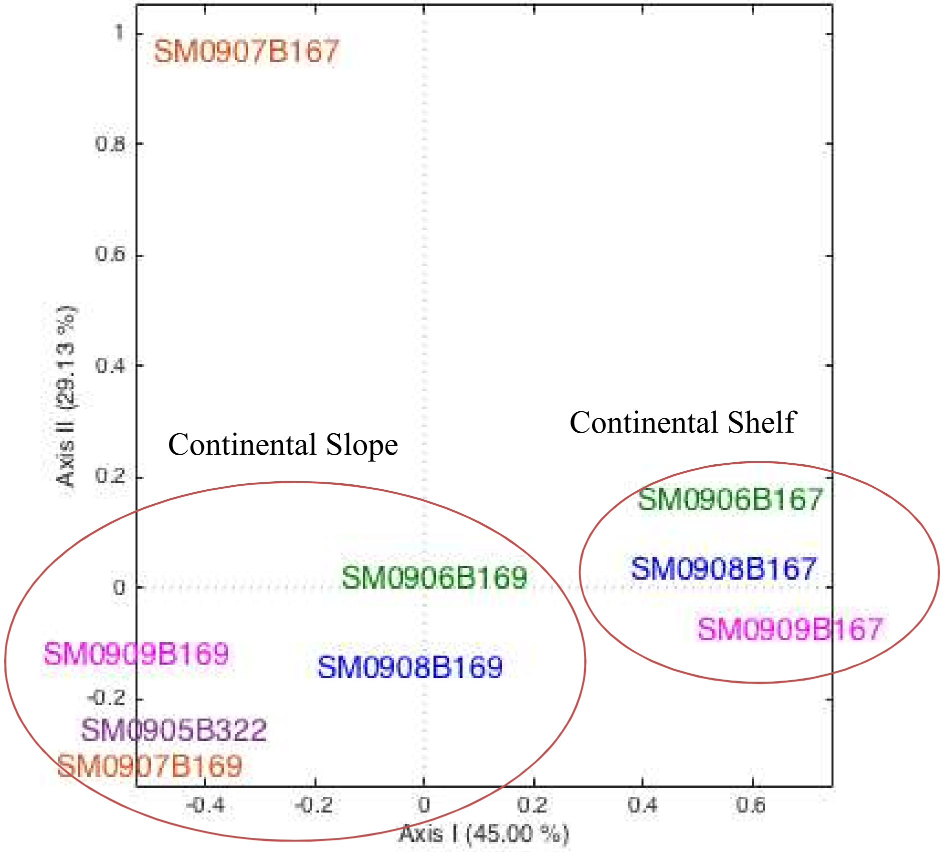

Fig 7. PCoA ordination diagram for pre-DWH zooplankton beta diversity during summer of years 2006–2009. The axes can be used to explain the total variability between objects (site beta diversity); where axis I accounts for 45% and axis II accounts for 29.13% of total variability between objects. Any two objects' (sample site beta diversity) proximity to one another can be interpreted as similarity, with those closer being more similar and farther apart as more dissimilar. Station labeling scheme is as follows: pre-DWH SEAMAP (SM), month (mm), year (yy), station number (Bnnn); each year is represented as summer 2006 (green), 2007 (orange), 2008 (blue), and 2009 (pink). Stations more strongly grouped out by sub-region as continental shelf (B167) or continental slope (B168, B322), but not annually.

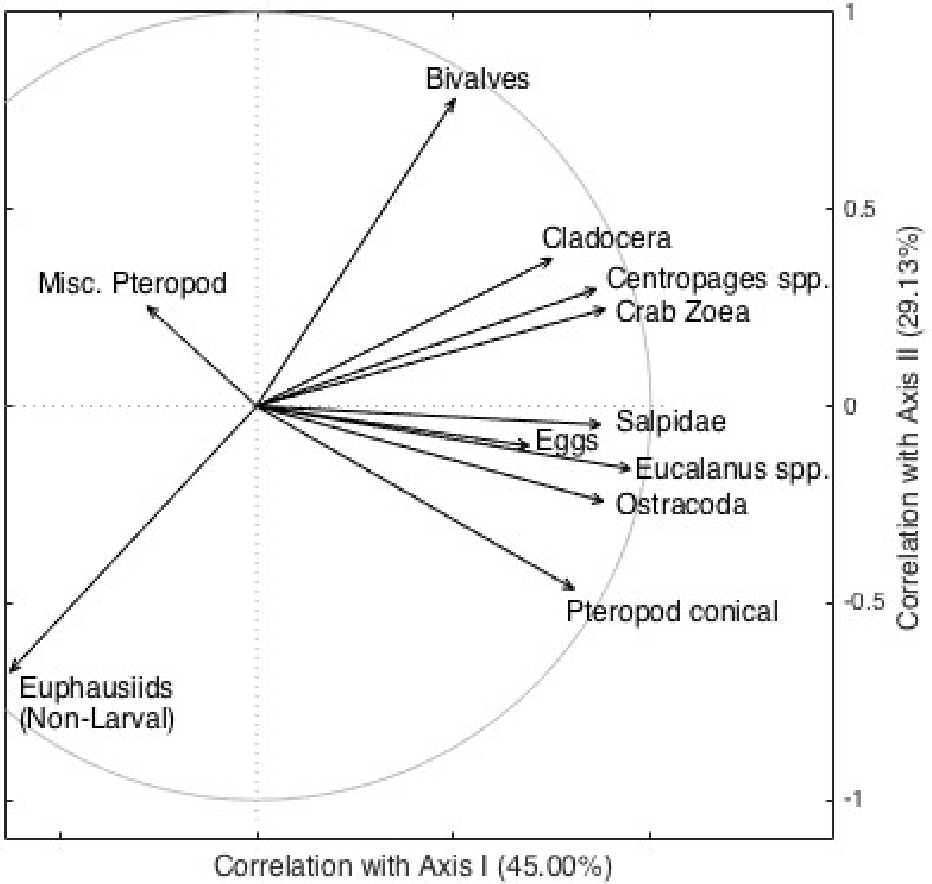

Fig 8. PCoA vector biplot for pre-DWH zooplankton beta diversity during summer of years 2006−2009. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 7. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 7) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. Taxa groups that best explain differences among summer years were most abundant at continental shelf station (B167) across years with the exception of non-larval euphausiids, which drove interannual variability at continental slope stations (B169, B322). These groups drove 41% of total summer interannual variability.

3.3.3 Spring vs. Summer Pre-DWH Environmental Conditions

Environmental conditions at pre-DWH stations were significantly different between spring and summer (PERMANOVA, p = 0.003). Seasonal differences were primarily driven by 30-day and 3-day average Mississippi River discharge, 3-day surface current magnitude, salinity, northward currents in spring, and greater surface-water temperature in summer (Fig. 9, 10).

3.3.4 Spring & Summer Pre-DWH Interannual Environmental Conditions

Cluster analyses indicated that although interannual environmental conditions varied, no pairwise groupings of years were significantly different within spring or summer years. While regional grouping was prevalent in zooplankton beta diversity, the same was not true of environmental conditions. Though not significant, there was a stronger grouping effect based on environmental conditions between years, but not any strong indication that regions grouped.

3.3.5 Zooplankton and Environmental Conditions Pre-DWH

The null hypothesis of no significant effect of environmental data on the pre-DWH beta diversity of zooplankton was tested using a distance-based redundancy analysis (dbRDA) separately for each season. Neither spring nor summer results were significant and thus the null could not be rejected.

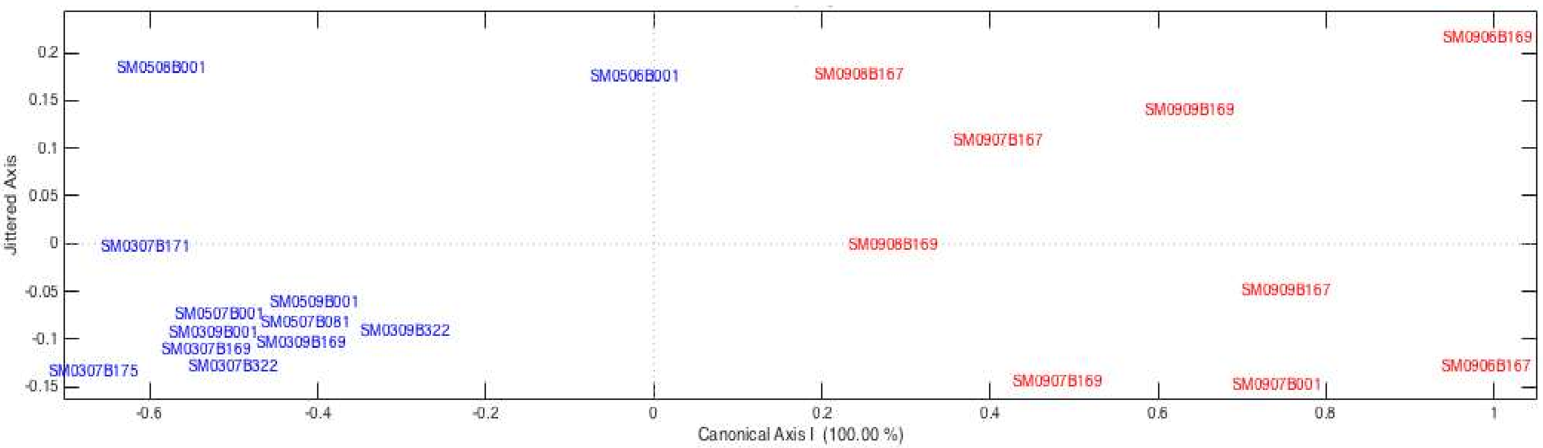

Fig. 9. CAP ordination diagram for pre-DWH environmental data during spring (blue) and summer (red) from 2005–2009. The canonical axes can be used to explain the total variability between each group (season) of objects (sample sites); where axis I accounts for 100% of variability between groups. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther apart as more dissimilar. Station labeling scheme is as follows: pre-DWH SEAMAP (SM), month (mm), year (yy), site (Bnnn). Data used in the analysis include CTD, MODIS satellite, USGS stream-gauging network, NOAA buoy, and NCAR reanalysis products. This ordination shows clear separation of spring and summer seasons.

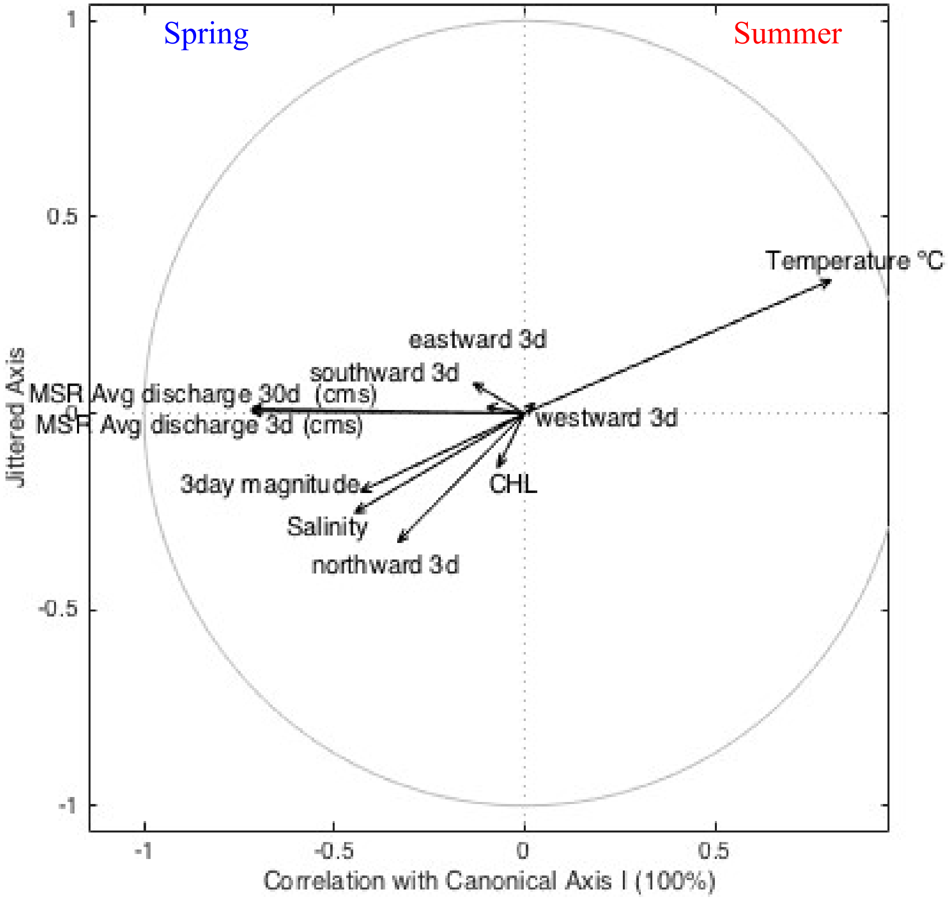

Fig. 10. CAP vector biplot for pre-DWH environmental conditions during spring and summer seasons of years 2005–2009. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 9. Each vector represents abiotic variables used to describe physical-chemical conditions at a sampling site. The intersection of an object's orthogonal projection (Fig. 9) with a vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining seasonal variability. Longer vectors illustrate the relative importance of those parameters describing group separation. Data used in the analysis include CTD, MODIS satellite, USGS stream-gauging network, NOAA buoy, and NCAR reanalysis products. Greater 30-day and 3-day average Mississippi River discharge, 3-day surface current magnitude, salinity, and northward currents in spring and higher surface-water temperature in summer drove seasonal differences.

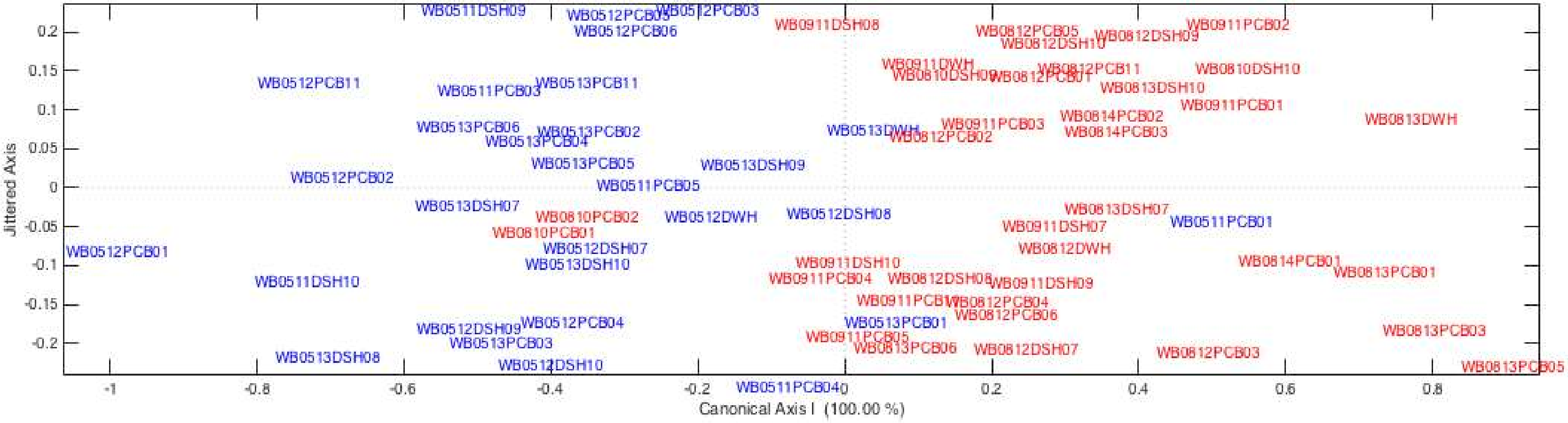

Fig. 11. CAP ordination diagram for post-DWH zooplankton beta diversity during spring (blue) and summer (red) of years 2010–2014. The canonical axes can be used to explain the total variability between each group (season) of objects (sample site beta diversity); where axis I accounts for 100% of variability between groups. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther apart as more dissimilar. Station labeling scheme is as follows: post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Zooplankton beta diversity at sites is significantly separated by season.

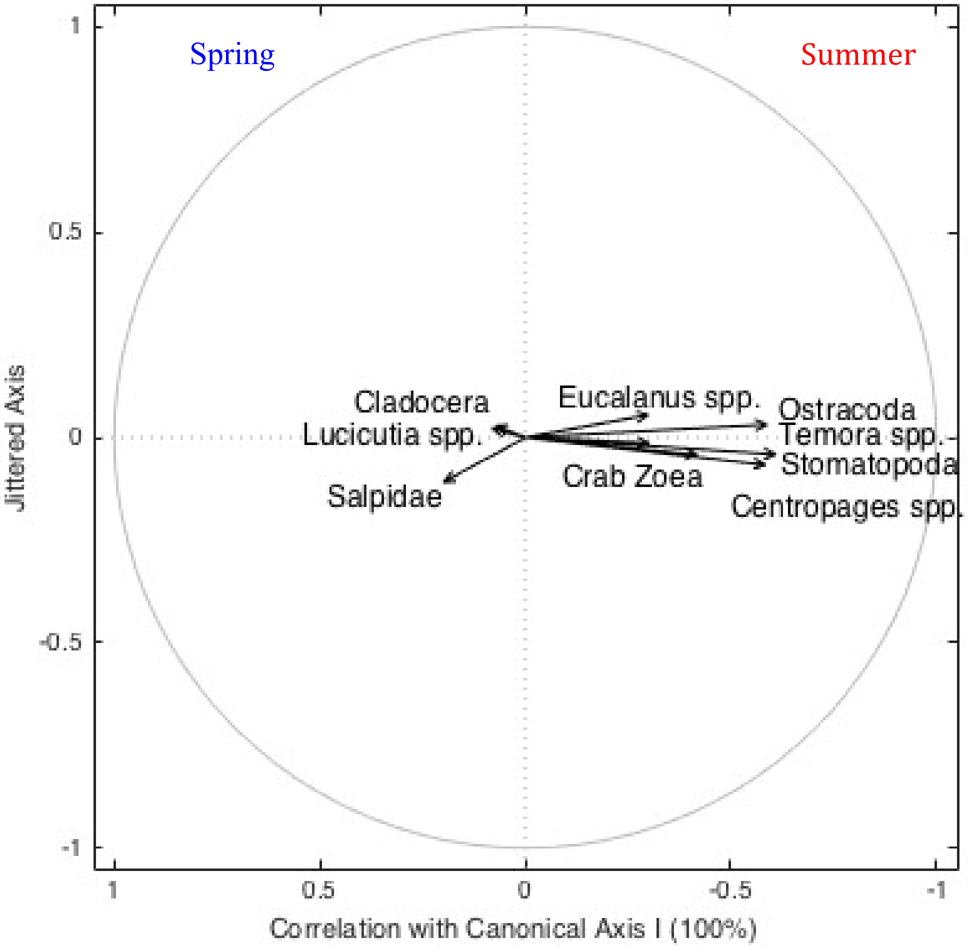

Fig 12. **CAP vector biplot for post-DWH zooplankton beta diversity during spring and summer seasons of years 2010−2014.** Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 11. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 11) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining seasonal variability. Longer vectors illustrate the relative importance of those taxa describing group separation. Summer stations have a greater presence of most taxa groups while spring had greater abundances of *Lucicutia* spp., cladocerans. Together these zooplankton taxa groups drove 27% of total variation between post-DWH spring and summer seasons.

3.4 Post-DWH Beta Diversity and Environmental Conditions

Post-DWH zooplankton beta diversity and environmental conditions were analyzed separately. Sections herein address the null hypotheses of no significant seasonal or interannual differences in either zooplankton beta diversity or environmental conditions among post-DWH samples.

3.4.1 Spring vs. Summer Post-DWH Zooplankton

Based on results from a non-parametric PERMANOVA test, zooplankton beta diversity of spring assemblages were significantly different from those in summer ($p = 0.001$) (Fig. 11), similar to the pre-DWH results. Results from a blind cross-validation test (Leave One Out Cross Validation Classification Success) showed that a random spring sample was successfully classified as such based on its beta diversity 81% of the time, while the success of blind summer classification was 92%. Indicator value results showed that the presence of crab zoea, stomatopods, and *Centropages* spp. across summer stations made these taxa significant indicators of summer sampling, though spring had no significant indicators. However, salps, cladocerans, and *Lucicutia* spp. had greater abundances in spring. SIMPER results showed that taxa most responsible for the separation of seasons were *Centropages* spp., ostracods, *Temora* spp., cladocerans, salps, *Eucalanus* spp., and *Lucicutia* spp., which together drove nearly 27% of the variability between spring and summer (Fig. 12).

3.4.2 Spring & Summer Post-DWH Interannual Zooplankton

Below are results that address the null hypotheses that (1) zooplankton beta diversity is not significantly different between any spring or (2) summer post-DWH years.

3.4.2.1 Spring Interannual Post-DWH Zooplankton

When spring stations were grouped by year, PERMANOVA results showed that zooplankton beta diversity was not significantly different between any two years. However, despite the high variability in beta diversity, some differences among spring years were notable (Fig. 13, 14). During spring months of years 2011-2013, the changes in abundances of ostracods, *Centropages* spp., *Temora* spp., cladocerans, and salps drove 24% of the total interannual variability. Spring 2011 had greater abundances of zooplankton in general relative to other years observed, and several groups had exceptionally high abundances. In 2011, the total abundances of *Centropages* spp. at PCB01 and PCB03 was nearly six times greater than that of 2012 and 38 times greater than 2013. Similarly, the average abundance of *Centropages* spp. across all spring stations was nearly nine times greater in 2011 than 2012, and almost 15 times greater than 2013. Abundances of cladocerans at PCB01 and PCB03 showed a similar trend; 2011 abundances were nearly 67 times greater than 2012 and almost nine times greater than 2013. While relative changes in the abundances of *Temora* spp. across sampling stations within a year was less drastic, the presence of nearly 100 total individuals /m^3 at PCB01 and PCB03 in 2011 compared to their absence at the same stations in 2012 is noteworthy. Lastly, cladoceran abundances were highest in 2011 and 2013. Conversely, salps, a significant indicator of spring 2012, exhibited average abundances for all stations of over 150 individuals/m^3, while less than one individual/m^3 in 2011 and less than three individuals/m^3 in 2013 were observed. Across years, abundances of *Lucicutia* spp. and euphausiids were greater at continental slope and oceanic stations relative to continental shelf stations. Despite these large differences in abundances for some groups in different years, the beta diversity of the 64 zooplankton groups across all sampling stations during spring in all years did not reveal any significant pairwise groupings between years.

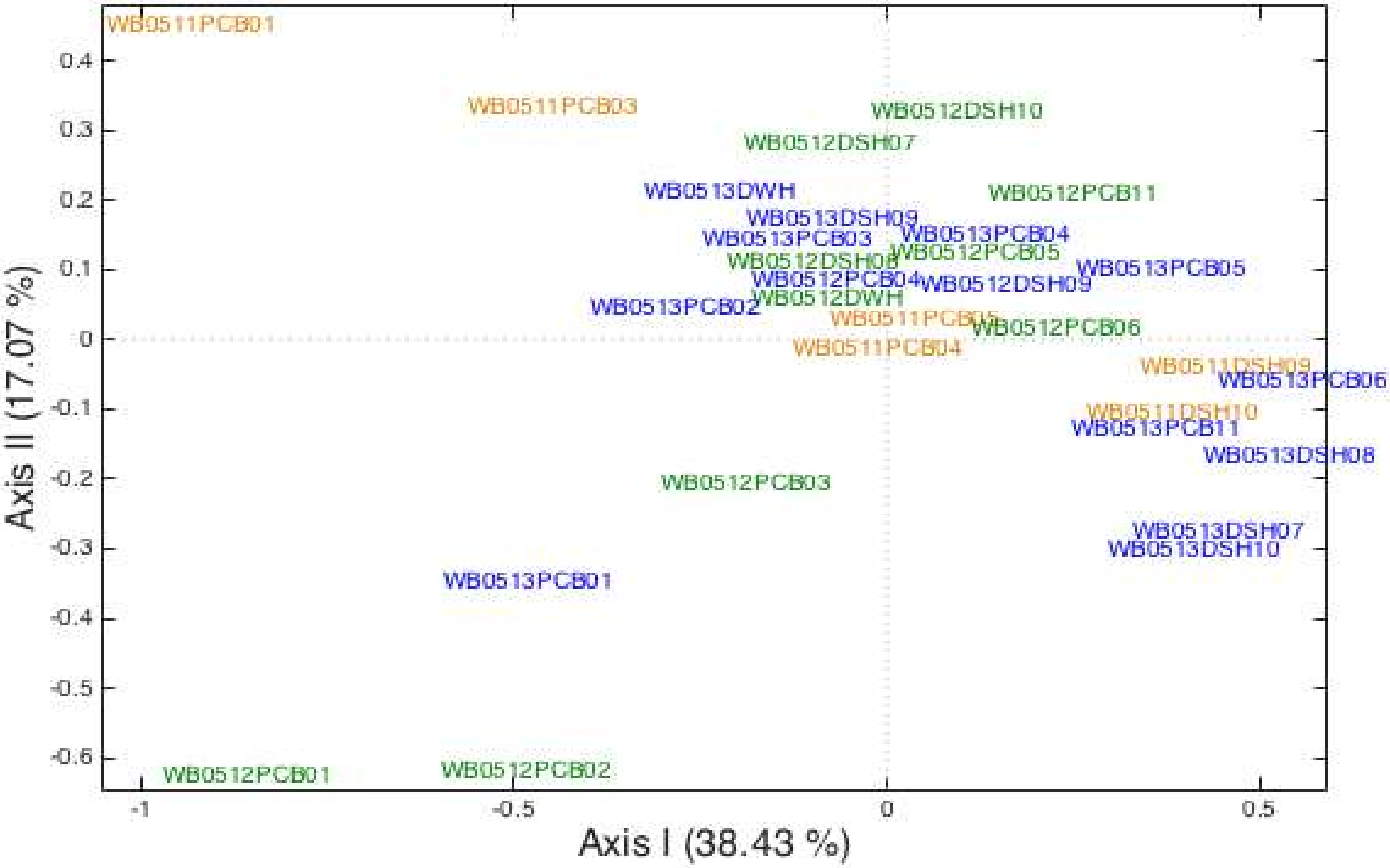

Fig. 13. PCoA ordination diagram for post-DWH zooplankton beta diversity during spring of years 2011−2013. The axes can be used to explain the total variability between objects (sample site beta diversity); where axis I accounts for 38.43% and axis II accounts for 17.07% of total variability between objects. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Each year is represented as spring 2011 (orange), 2012 (green), and 2013 (blue). No year is significantly different from another; however, a large amount of variability in seen among years, especially at continental shelf stations PCB01, PCB02, and PCB03.

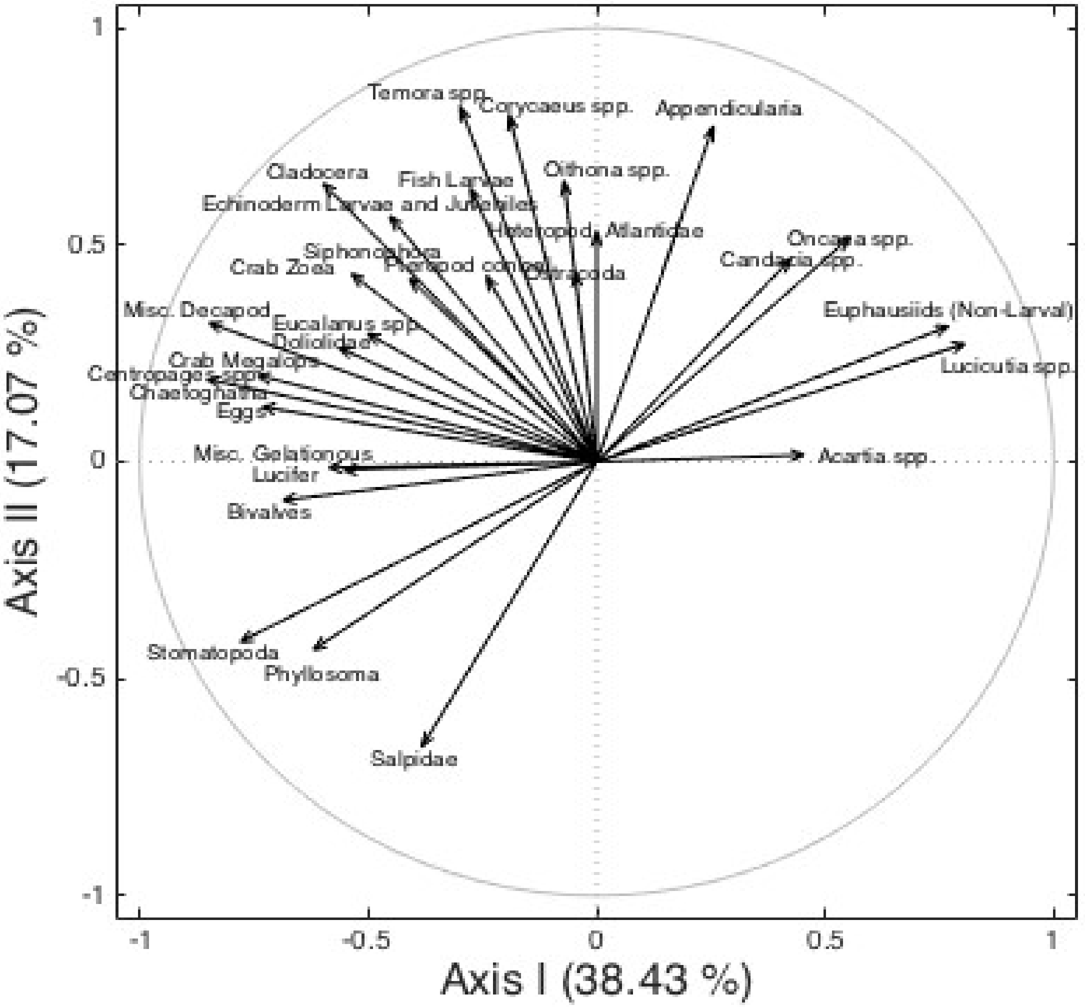

Fig. 14. PCoA vector biplot for post-DWH zooplankton beta diversity during spring of years 2011−2013. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 13. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 13) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. Taxa groups that best explain differences among spring years were most abundant at continental shelf stations (PCB01, PCB02, and PCB03). These groups drove 24% of total summer interannual variability.

3.4.2.2 Summer Interannual Post-DWH Zooplankton

Results from pairwise PERMANOVA tests between years 2010−2013 in summer show that each year stood out as significantly different from except 2010. The table below provides resulting p-values from pairwise testing of beta diversity for all years (Table 9).

Table 8. Significant p-values and non-significant (ns) results from pairwise PERMANOVA testing on post-DWH zooplankton beta diversity during summer of years 2010−2013. Significance was considered α<0.05. 2010 was not significantly different from any year though there was significant interannual variability among many other years

	2010	2011	2012	2013
2010	--	ns	ns	ns
2011	ns	--	0.002	0.001
2012	ns	0.002	--	0.002
2013	ns	0.001	0.002	--

Interestingly, the beta diversity of summer zooplankton during the oil spill (2010) was not significantly different from any year. Beta diversity of zooplankton assemblages tended to be distinct by year (Fig. 15). Stomatopods, *Centropages* spp., *Acartia* spp., ostracods, salps, chaetognaths, and doliolids together drove nearly 30% of total interannual variation. While stomatopods, ostracods, and *Centropages* spp. abundances were typically greater at continental shelf stations (PCB01, PCB02, PCB03) relative to continental slope and oceanic stations, greatest abundances and interannual variability was observed at PCB01. Abundances of these taxa were markedly high during 2010 and 2011 relative to follow-on years. In 2010, the abundance of ostracods at PCB01 was nearly twice that of 2012 and the abundance of *Centropages* spp. was more than two times greater than that of the year with the next highest abundance, 2011. High counts of ostracods, and *Centropages* spp. were also observed at PCB01 in 2011. In addition, *Temora* spp. were observed in high numbers at both PCB01 and across the entire continental shelf region. The average abundance of *Temora* spp. at continental shelf stations in 2011 was 654 individuals/m^3 compared to the average range of 10–22 individuals/m^3 from all other years. The 2011 average continental shelf abundance of chaetognaths was also notably high at 180 individuals/m^3, driven largely by the high abundance of individuals observed at PCB01. Across years, presence of *Lucicutia* spp. was most common and abundances relatively stable at continental slope and oceanic stations and mostly absent or in low abundances at continental shelf stations.

Several post-DWH summer years had significant indicator taxa (Fig. 16). Cladocerans and *Temora* spp. were significant indicators of 2011, Cyphonautes were indicative of 2012, and stomatopods and *Acartia* spp., were indicative of 2013.

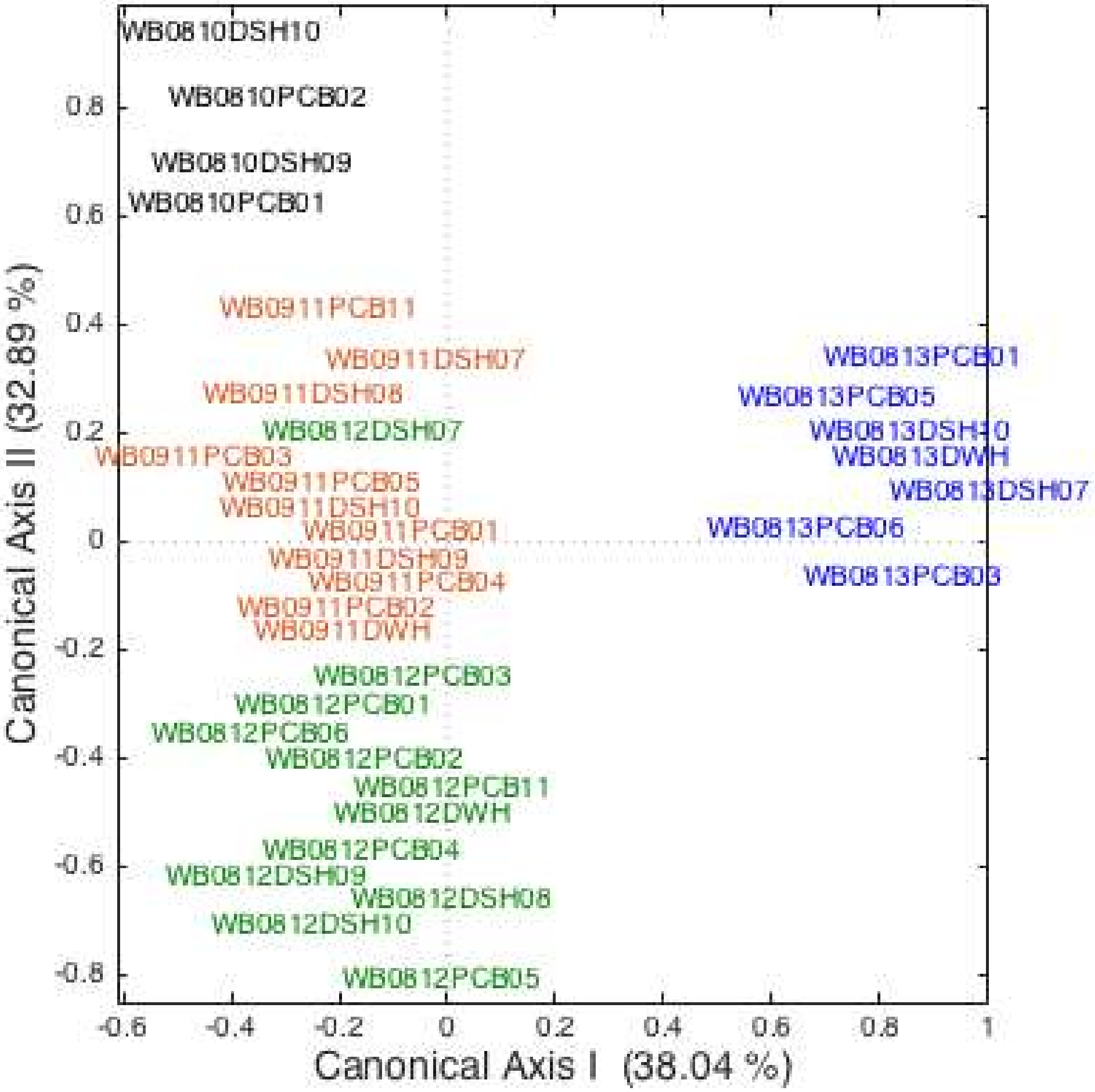

Fig. 15. CAP ordination diagram for post-DWH zooplankton beta diversity during summer of years 2010–2013. The canonical axes can be used to explain the total variability between each group (years) of objects; where canonical axis I accounts for 38.04% and canonical axis II accounts for 32.89% of variability between groups. Any two objects' (sample site beta diversity) proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn). DWH is the Deepwater Horizon oilrig explosion site. Each year is represented as summer 2010 (black), 2011 (orange), 2012 (green), and 2013 (blue). 2010 is not significantly different from any years while 2011 and 2012 are different from all years except 2010.

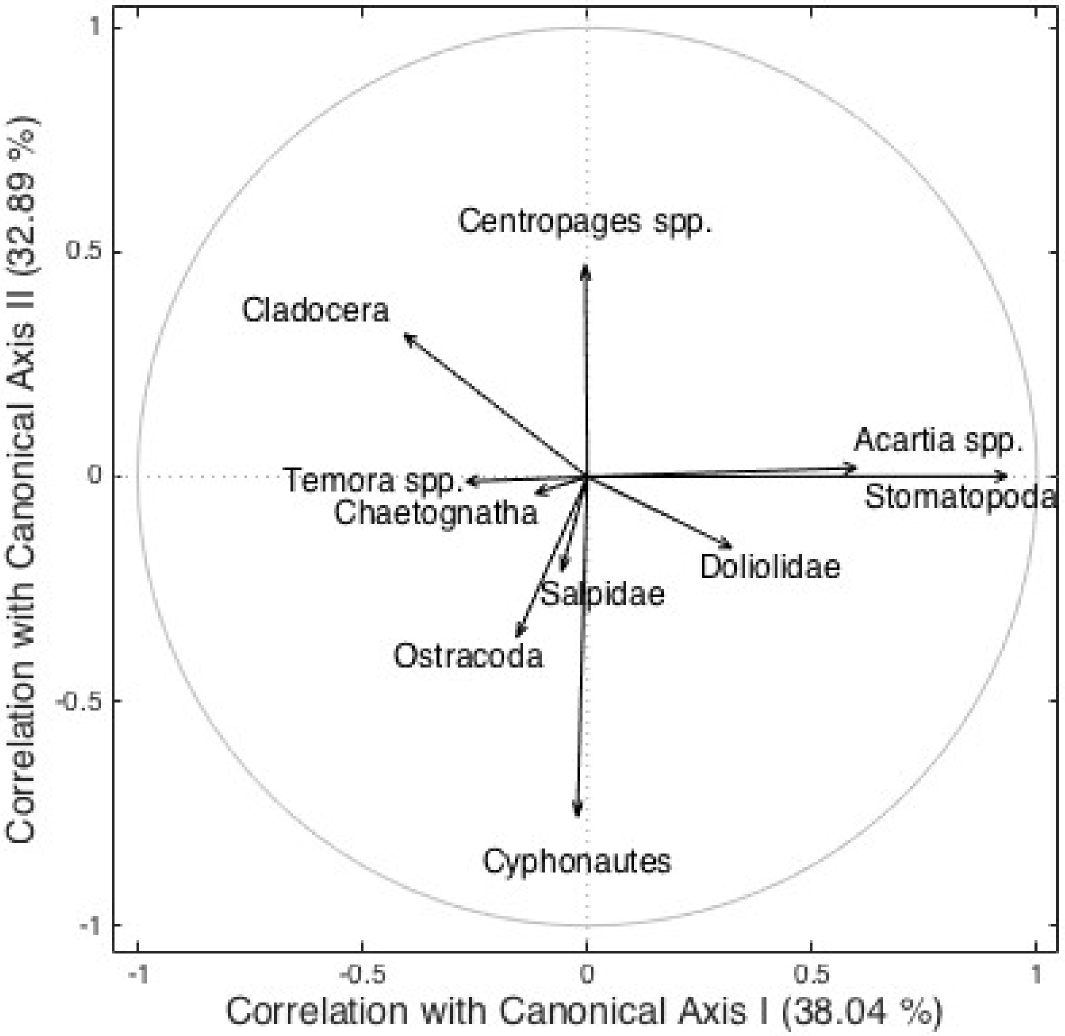

Fig. 16. **CAP vector biplot for post-DWH zooplankton beta diversity during summer of years 2010-2013.** Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 15. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 15) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors illustrate the relative importance of those taxa describing group separation. While most years had significant indicator animals, 2010 did not. However, 2010 and 2011 had notably high abundances of *Centropages* spp. and cladocerans.

3.4.3 Spring vs. Summer Post-DWH Environmental Conditions

When grouped by season, results from a non-parametric PERMANOVA test revealed that environmental conditions in spring varied significantly from those observed in summer ($p = 0.001$) (Fig. 17). The classification success of spring and summer environmental conditions was 98% and 97%, respectively. Seasonal differences were driven primarily by greater Mississippi River average discharge, 3-day wind magnitude, salinity, and westward winds in spring and greater temperature and chlorophyll in summer (Fig. 18). Mississippi River discharge was highest during springtime, while temperature and chlorophyll were higher during summer. Conditions in spring 2012 however did group nearest summer stations, which can be attributed to significantly low Mississippi River discharge during sampling months.

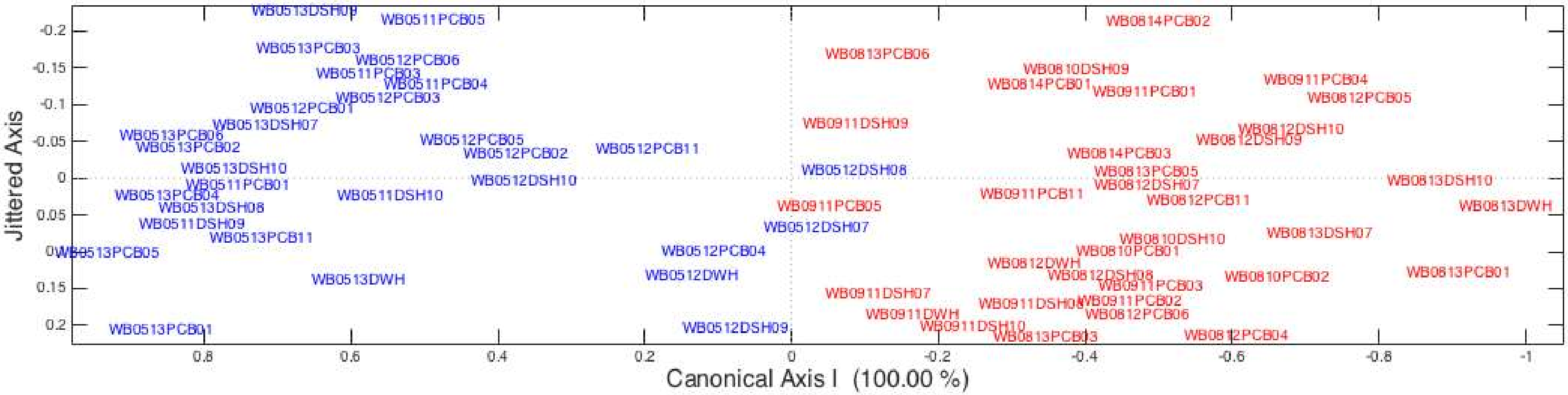

Fig. 17. CAP ordination diagram for post-DWH environmental data during spring (blue) and summer (red) seasons of years 2010−2014. The canonical axes can be used to explain the total variability between each group (season) of objects (sample sites); where axis I accounts for 100% of variability between groups. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther apart as more dissimilar Vessel (WB=R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn). DWH is the Deepwater Horizon oilrig explosion site. Data used in the analysis include CTD, MODIS satellite, USGS stream-gauging network, and NOAA buoy products. Environmental conditions at stations are highly distinct based on season with a clear separation of spring (left) from summer (right) though some overlap was observed for spring 2012 grouping nearer summer conditions.

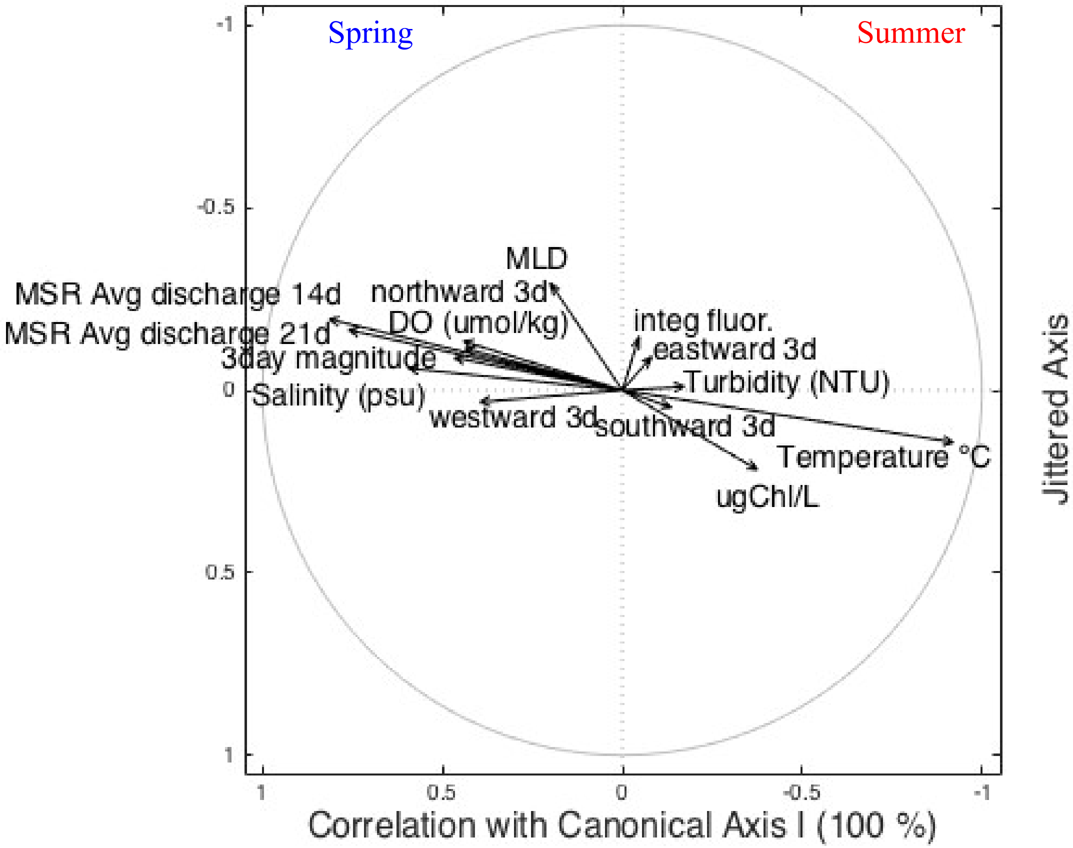

Fig. 18. CAP vector biplot for post-DWH environmental conditions during spring and summer seasons of years 2010‒2014. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 17. Each vector represents abiotic variables used to describe physical-chemical conditions at a sampling site. The intersection of an object's orthogonal projection (Fig. 17) with a vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining seasonal variability. Longer vectors illustrate the relative importance of those parameters describing group separation. Seasonal differences were driven by greater 21-day and 14-day average Mississippi River discharge, 3-day average wind magnitude, higher salinity, and westward winds in spring and greater surface-water temperature and surface chlorophyll in summer. Data used in analysis includes CTD, MODIS satellite, USGS stream-gauging network, and NOAA buoy products.

3.4.4 Spring & Summer Post-DWH Interannual Environmental Conditions

Pairwise groupings between years were analyzed using a nonparametric PERMANOVA to test the null hypothesis that environmental conditions were not significantly different between any combinations of years. The tables below provide instances of when environmental conditions between years were statistically significant (Table 9 and Table 10).

3.4.4.1 Spring Interannual Post-DWH Environmental Conditions

Environmental conditions between all spring years varied significantly (Fig. 19). Parameters that drove interannual differences were Mississippi River discharge, temperature, chlorophyll, turbidity, wind magnitude, and wind directions (Fig. 20). Unlike zooplankton beta diversity results which indicated a greater affinity of station groupings based on location, environmental conditions at spring stations tended to cluster more strongly with other stations of the same year, as opposed to the same location between years.

Table 9. Significant p-values and non-significant (ns) results from pairwise PERMANOVA testing on post-DWH environmental conditions during spring of years 2011−2013. Significance was considered α<0.05. Environmental conditions were significantly different between each spring year.

	2011	2012	2013
2011	--	0.003	0.008
2012	0.003	--	0.001
2013	0.008	0.001	--

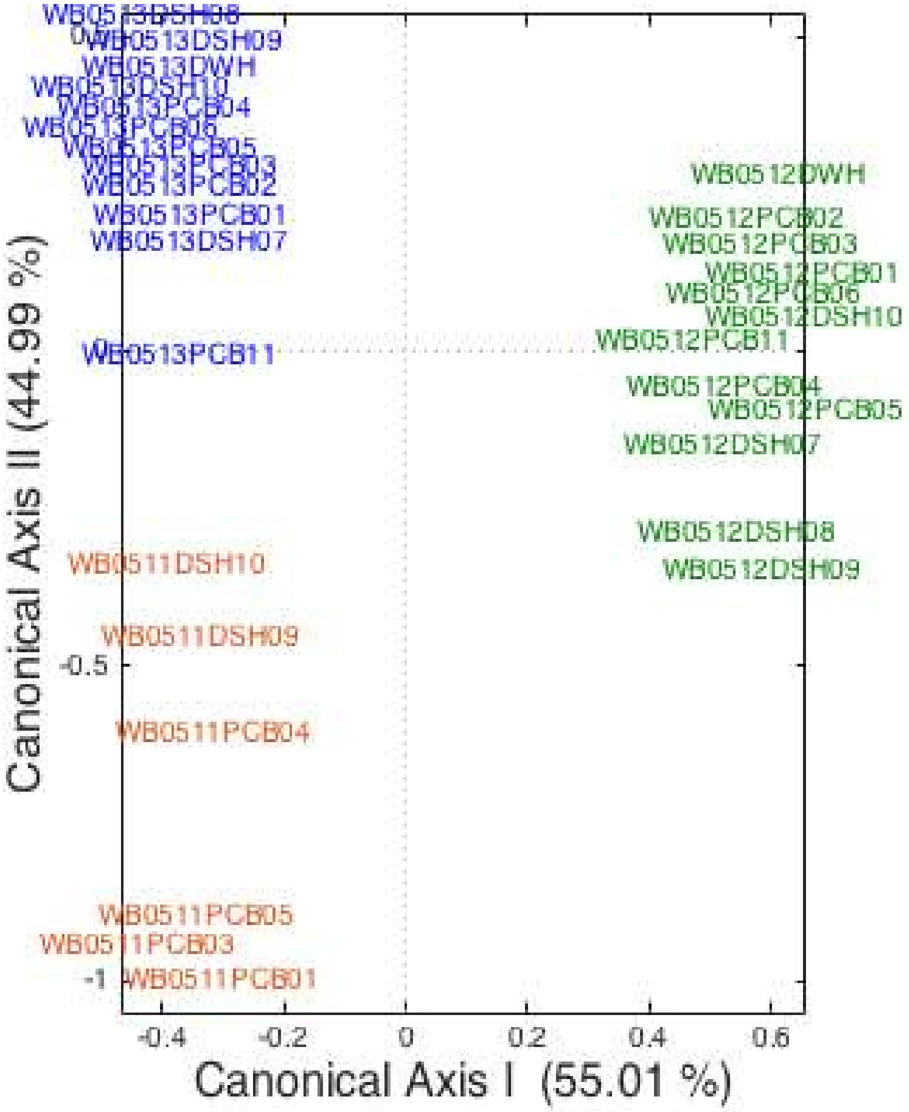

Fig. 19. CAP ordination diagram for post-DWH environmental conditions during spring of years 2011−2013. The canonical axes can be used to explain the total variability between each group (years) of objects; where canonical axis I accounts for 55.01% and canonical axis II accounts for 44.99% of variability between groups. Any two objects' (sample site environment) proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Each year is represented as spring 2011 (orange), 2012

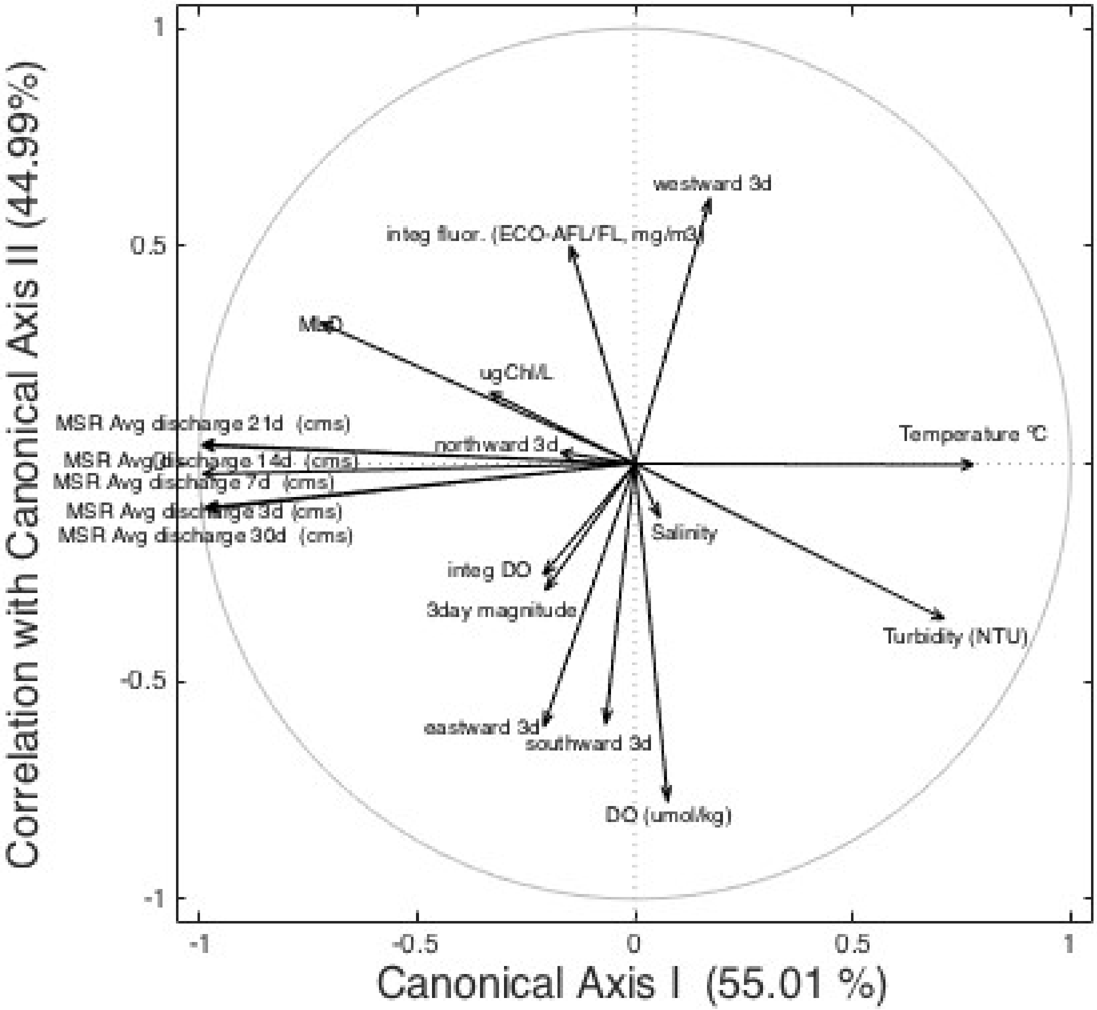

Fig 20. **CAP vector biplot for post-DWH environmental conditions during spring of years 2011–2013.** Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 19. Each vector represents an abiotic variable used to describe physical-chemical conditions at a sampling site. The intersection of an object's orthogonal projection (Fig. 19) with a vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors illustrate the relative importance of those taxa describing group separation. Average Mississippi River discharge, temperature, chlorophyll, 3-day average wind magnitude, and varying wind directions drove interannual differences. Data used in the analysis include CTD, MODIS satellite, USGS stream-gauging network, and NOAA buoy products.

3.4.4.2 Summer Interannual Post-DWH Environmental Conditions

Environmental conditions between summer years varied significantly (Fig. 21). Average Mississippi River discharge most strongly drove interannual differences between summer years along with chlorophyll, salinity, and temperature (Fig. 22). Summer 2012 had significantly low Mississippi River average discharge throughout summer; this year was the only instance of significant difference between all other summer years. Conversely, summer 2010 and 2013 exhibited the highest summer discharge and though not significantly different from one another due to comparable discharge rates, they were significantly different from 2011 and 2012, which had lower discharge rates.

Table 10. Significant p-values and non-significant (ns) results from pairwise PERMANOVA testing on post-DWH environmental conditions during summer of years 2010−2013. Significance was considered α<0.05. Environmental conditions were significantly different between most summer years

	2010	2011	2012	2013
2010	--	0.035	0.001	ns
2011	0.035	--	0.041	0.015
2012	0.001	0.041	--	0.021
2013	ns	0.015	0.021	--

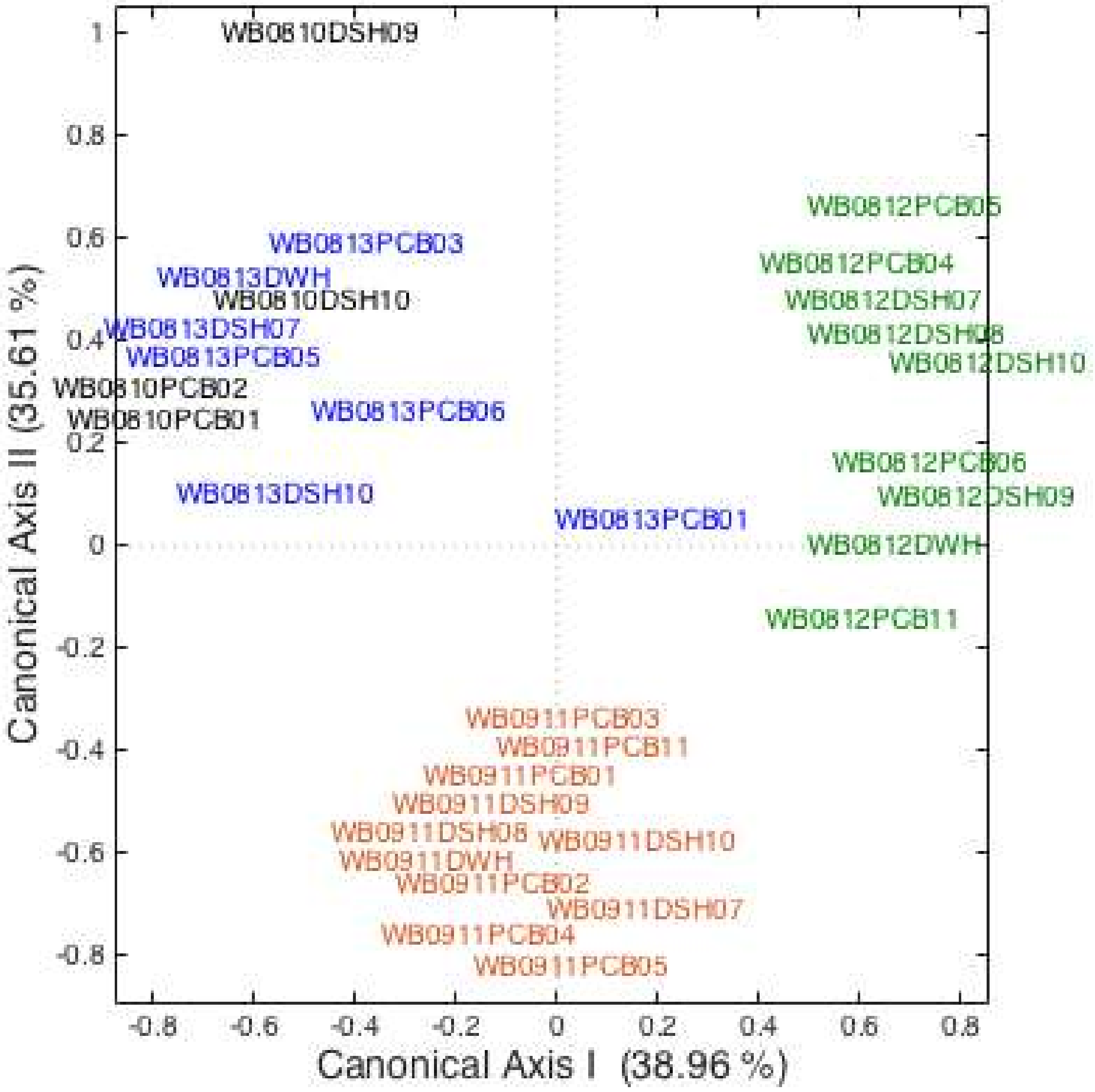

Fig. 21. CAP ordination diagram for post-DWH environmental conditions during summer of years 2010−2013. The canonical axes can be used to explain the total variability between each group (years) of objects; where canonical axis I accounts for 38.96% and canonical axis II accounts for 35.61% of variability between groups. Any two objects' (sample site environment) proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Each year is represented as summer 2010 (black), 2011 (orange), 2012 (green), and 2013 (blue). Environmental conditions at stations tended to cluster strongly by year and not by station location. Most summer years were significantly different excluding 2010 from 2013.

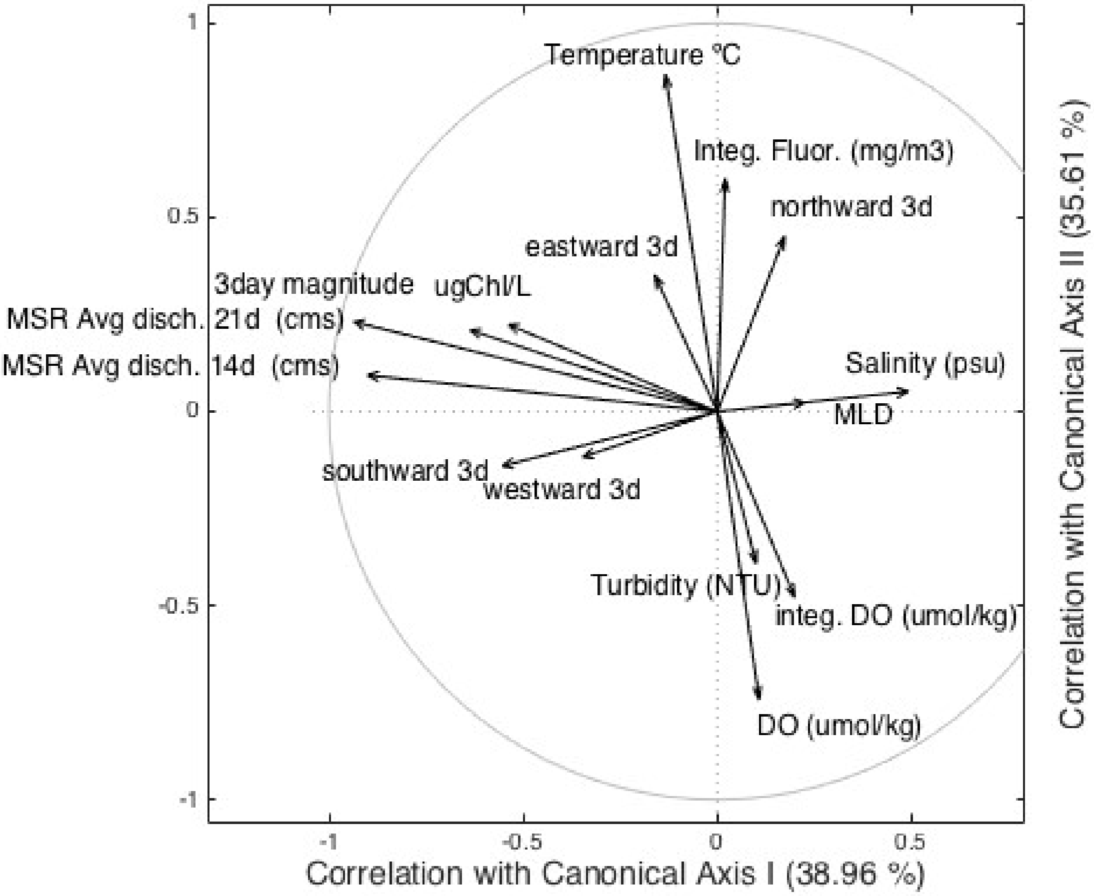

Fig 22. **CAP vector biplot for post-DWH environmental conditions during summer of years 2010–2013.** Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig. 21. Each vector represents an abiotic variable used to describe physical-chemical conditions at a sampling site. The intersection of an object's orthogonal projection (Fig. 21) with a vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors illustrate the relative importance of those taxa describing group separation. Summer interannual differences were driven by 14-day and 21-day average Mississippi River discharge, wind direction and magnitude, temperature, and chlorophyll. Significant differences were observed between most pairwise summer years, although 2010 and 2013 both had high Mississippi River discharge. Data used in the analysis include CTD, MODIS satellite, USGS stream-gauging network, NOAA buoy, and NCAR reanalysis products.

3.4.4.3 Zooplankton and Environmental Conditions Post-DWH

The null hypothesis of no significant effect of environmental data on the beta diversity of zooplankton was tested using a distance-based redundancy analysis (dbRDA) separately for each season. Both spring and summer results were significant (p = 0.001) and indicated that close to three quarters of the variability of beta diversity in zooplankton communities in spring (77%) and summer (74%) was accounted for by variability in the environmental data. For differences between years during spring, results based on the Akaike's Information Criterion (AIC) test indicated that surface chlorophyll and integrated fluorescence were the significant variables explaining the variability in spring zooplankton beta diversity. In summer, an AIC test indicated that integrated fluorescence, 21-day average Mississippi River discharge, and 7-day average Mississippi River discharge were the significant variables explaining summer beta diversity. While temperature was an important indicator driving the separation of seasons, within in a season, results did not indicate it was significant in explaining variability within zooplankton beta diversity.

Additionally, considering that abundances of *Centropages* spp. stood out as anomalously high in 2010 and 2011, we tested whether any correlation existed between *Centropages* spp. abundances and El Niño Southern Oscillation (ENSO) indices similar to work done by Mazzocchi et al. (2007) in relation to North Atlantic Oscillation. Based on a Spearman's ranked correlation test, no correlation (r = -0.22, p = 0.35) was observed for either positive or negative multivariate ENSO indices obtained from NOAA's Earth System Research Lab Physical Science Division (Fig. 23).

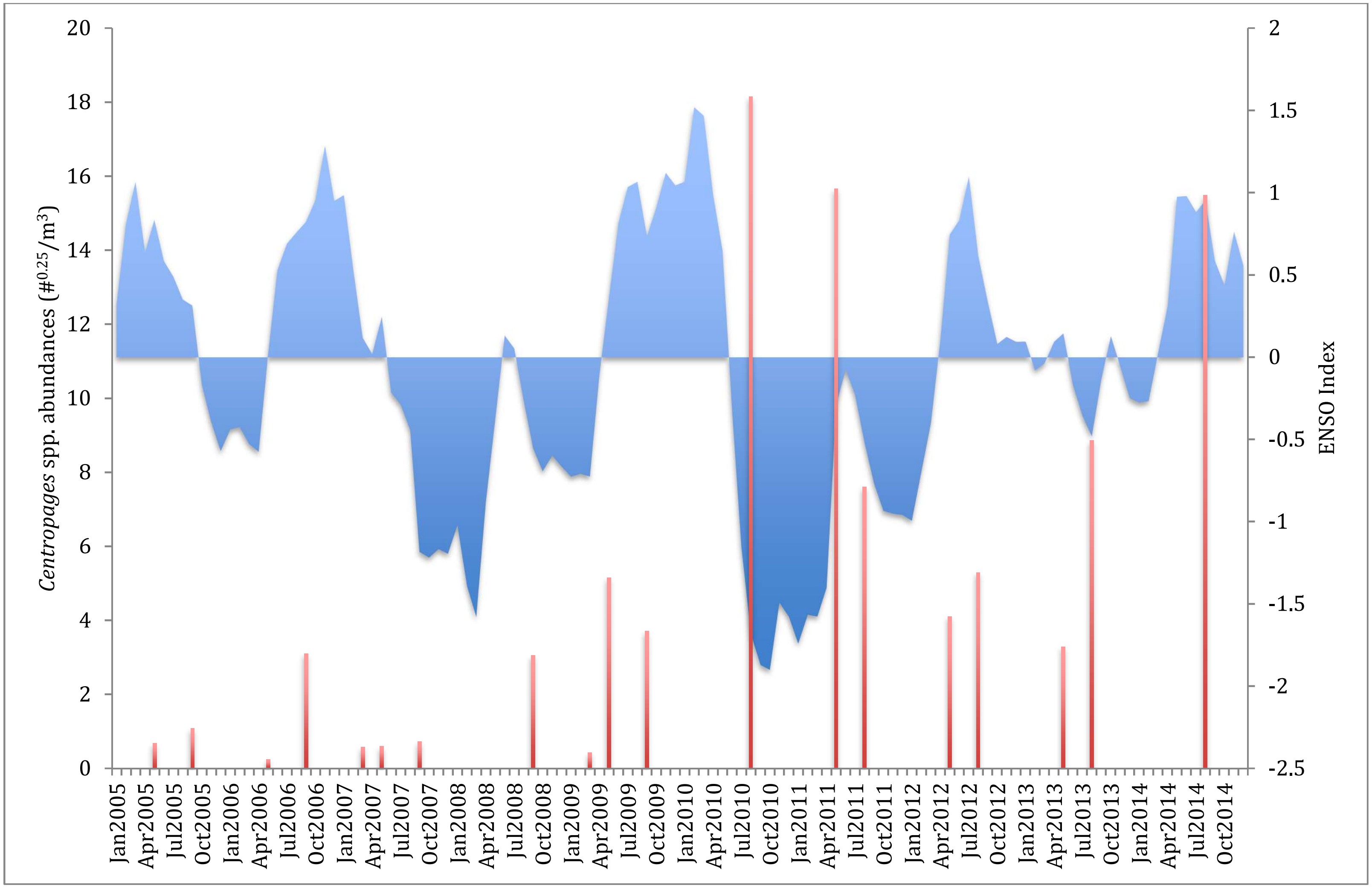

Fig. 23. Comparison of El Niño Southern Oscillation Indices and fourth-root transformed *Centropages* spp. abundances 2005–2014. No pattern is evident between El Nino Southern Oscillation indices (blue) and fourth root transformed *Centropages* spp. abundances (red) in the NEGOM 2005-2014. El Niño Southern Oscillation Indices were obtained from NOAA's Earth's Systems Research Lab.

3.5 Pre-DWH & Post-DWH Zooplankton Comparisons

Lastly, direct comparisons between pre- and post-DWH zooplankton beta diversity, abundances, and percent composition of taxa groups were done by analyzing differences in zooplankton assemblages during spring and summer at three sub-regions: continental shelf, continental slope, and oceanic stations. Stations included in each sub-region can be found in Tables 6 and 7.

While the previous sections assessed pre- and post- beta diversity as separate datasets largely to accommodate for differing zooplankton processing techniques (ZooScan vs. Miscroscopy), the following direct comparisons of beta diversity combined the pre- and post-DWH zooplankton data as a single dataset representing samples from 2005–2014. However, comparisons of abundances and percent composition between pre- versus post-DWH zooplankton taxa were done by grouping all pre-DWH data together (2005–2009) and testing the pre-DWH zooplankton abundances and percent composition against a combined post-DWH zooplankton group, representing years 2010–2014.

Note that comparisons were only made between sampling periods when both pre- and post- stations were represented for each sub-region. Therefore, due to lack of pre-DWH sampling at continental shelf stations in spring and oceanic stations in summer, comparisons were made only for spring oceanic, summer continental shelf, and both spring and summer continental slope stations sub-regions. Results of pre- and post-DWH comparisons are organized by season (i.e. spring then summer) then sub-region relative to increasing distance from shore (i.e. continental shelf followed by continental slope then oceanic).

3.5.1 Pre- & Post-DWH Comparisons of Beta Diversity Summary

In general, multivariate ordinations of zooplankton beta diversity suggest that pre- and post-DWH samples clustered separately by sampling period along the x-axis, which typically explained ~30% of the total variability among sites. Across sub-regions and seasons, a greater presence of taxa groups including a greater number of indicator taxa and higher abundances were observed at post-DWH sites. Across all sub-regions, miscellaneous decapods was a significant indicator group of post-DWH samples and *Lucicutia* spp. was a significant indicator of post-DWH continental slope stations. However, along the y-axis, which explained 20% – 30% of total variability, much overlap was observed between pre- and post-DWH. This suggests that based on the length and number of taxa vectors closest to the x-axis, the beta diversity of pre-DWH samples was substantially different from that of post-DWH samples. However, pre- and post-DWH beta diversity was actually similar relative to taxa vectors represented in the y-direction. In general, results suggest that multivariate analyses of pre- and post-DWH zooplankton beta diversity may be more revealing in differences relative to methodology of zooplankton processing and not necessarily the ecology of the assemblages.

3.5.1.1 Spring Continental Slope Beta Diversity Comparisons

Principal coordinates analysis of spring continental slope stations show distinct grouping of zooplankton beta diversity between pre- and post-DWH samples along the x-axis, which explains 35.15% of the total variability among stations. However, substantial overlap of the groups is also observed along the y-axis, which explains 24.24% of total variability (Fig. 24). Indicator value test results showed that the post-DWH samples had five significant indicator taxa including cladocerans, cyphonautes, euphausiids, miscellaneous decapods, and *Lucicutia* spp. Four taxa groups were significantly indicative of pre-DWH samples had including *Salps*, crab zoea, conical pteropods, *Eucalanus* spp. These animals in addition to *Centropages* spp., *Lucifer*, and crustacean nauplii drove 37.8% of variability between pre- and post-DWH samples (Fig. 25).

3.5.1.2 Spring Oceanic Beta Diversity Comparisons

Principal coordinates analysis of spring oceanic stations show distinct groupings of zooplankton beta diversity between pre- and post-DWH samples. However, along the x-axis where 36.14% of the total variability is explained, substantial overlap of beta diversity is observed. Overlap is also observed along the y-axis that explains 21.32% of total variability (Fig. 26), suggesting that assemblages present at pre- and post- are quite similar. Indicator value test results showed that the post-DWH group had seven significant indicator taxa groups while pre-DWH had only one. Significant indicators of post-DWH sampling were euphausiids*, Candacia* spp.*,* doliolids, miscellaneous decapods*, Lucicutia* spp.*,* cyphonautes whereas salps was the single significant indicator of pre-DWH sampling (Fig. 27). These taxa, along with *Centropages* spp, euphausiids, *Temora* spp., appendicularians, eggs, cladocerans, and *Eucalanus* spp., accounted for 51% of variability between pre-DWH and post-DWH sampling.

3.5.1.3 Summer Continental Shelf Beta Diversity Comparisons

Principal coordinates analysis of summer continental shelf stations show an overlap of zooplankton beta diversity between pre- and post-DWH samples. Along the x-axis 29.58% of the total variability is explained. The dissimilarity of the single standout station, SM0907B167, is separated from other stations by the particularly low abundances of zooplankton taxa at that year. Otherwise, overlap of the other pre-DWH stations with post-DWH stations suggests beta diversity among pre- and post- samples is similar (Fig. 28). Indicator value test results showed that the post-DWH group had seven significant indicator taxa groups while pre-DWH had only one. Significant indicators of post-DWH sampling were *Centropages* spp., *Corycaeus* spp., crustacean nauplii, miscellaneous decapods, while crab zoea was indicative of pre-DWH stations. These taxa along with ostracods, salps, cladocerans, *Temora* spp., *Eucalanus* spp., stomatopods, siphonophores, conical pteropods, and *Oithona* spp., together drove 55% of variability between pre-DWH and post-DWH sampling (Fig. 29).

3.5.1.4 Summer Continental Slope Beta Diversity Comparisons

Principal coordinates analysis of summer continental slope stations show distinct grouping of zooplankton beta diversity between pre- and post-DWH samples along the x-axis, which explains 31.45% of the total variability among stations. However, substantial overlap of the groups can be observed along the y-axis, which explains 26.16% of total variability (Fig. 30). *Centropages* spp., cyphonautes, eggs, appendicularians, *Lucicutia* spp., cladocerans, doliolids, crustacean nauplii, miscellaneous decapods, and ostracods together drive 41% of the separation of zooplankton beta diversity between pre- and post-DWH samples. Only one zooplankton group, eggs, was significantly indicative of pre-DWH samples though *Centropages* spp., miscellaneous decapods, doliolids, and *Lucicutia* spp. were significant indicator animals of post-DWH continental slope stations during summer (Fig. 31). The single station that substantially strayed from the others along the y-axis, WB0813PCB05, did so due to its high abundances of stomatopods and doliolids.

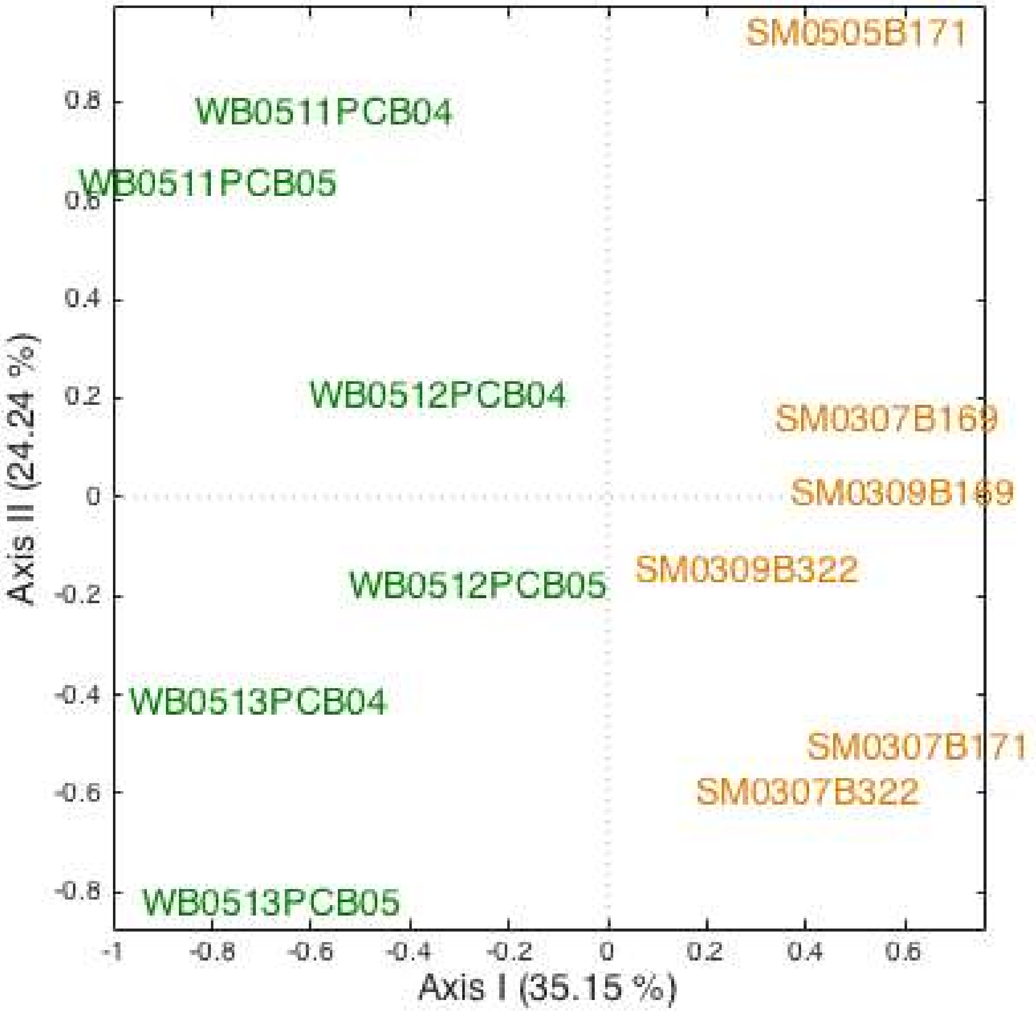

Fig. 24. PCoA ordination diagram for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during spring at continental slope stations of years 2007−2013. The axes can be used to explain the total variability between objects (sample site beta diversity); where axis I accounts for 35.15% and axis II accounts for 24.24% of total variability between objects. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows pre-DWH SEAMAP (SM), month (mm), year (yy), station (Bnnn) or post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB, or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Post-DWH stations show greater dispersion and distinct separation of pre- and post-DWH samples are evident along the x-direction, however not along the y-axis.

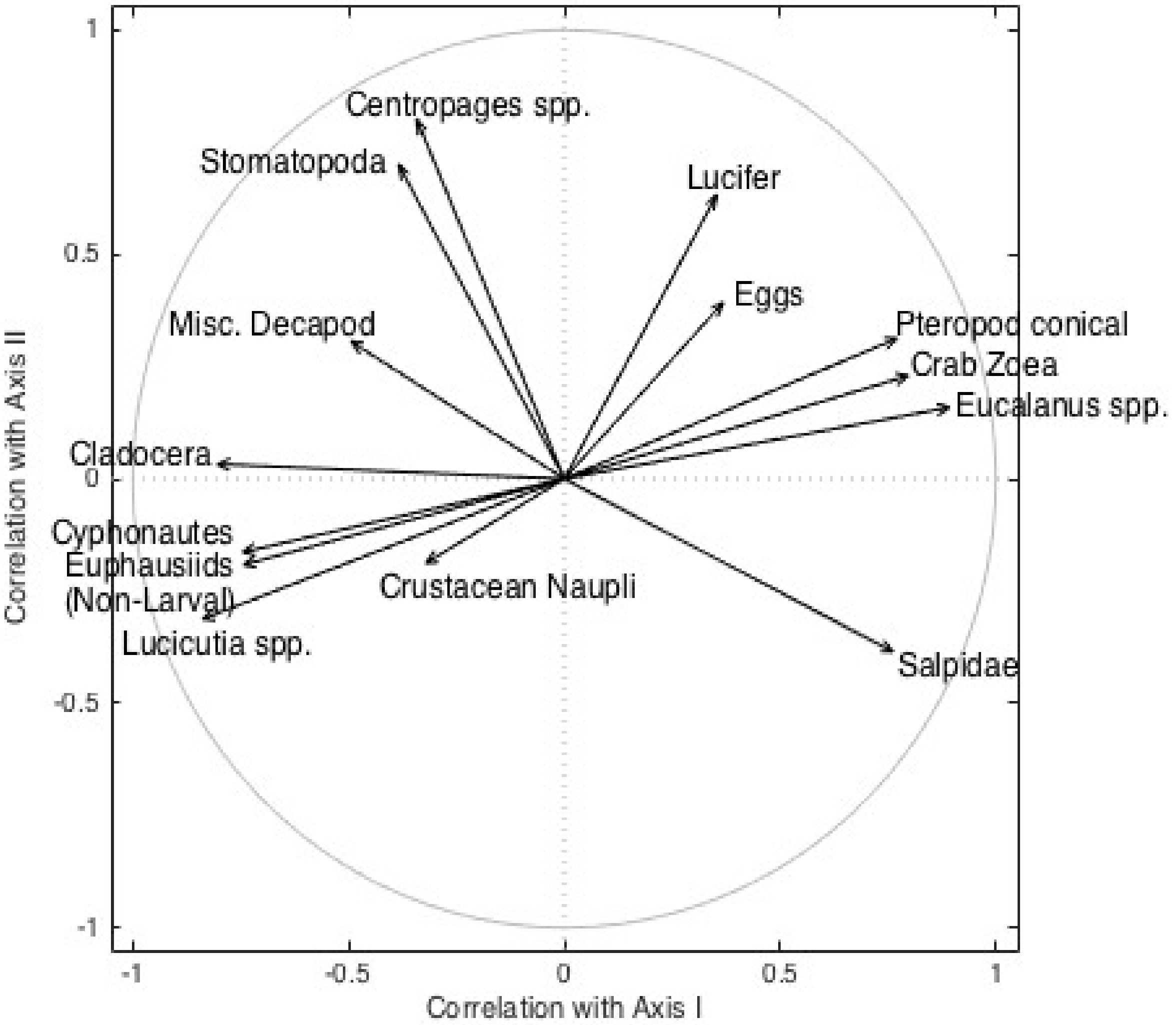

Fig. 25. PCoA vector biplot for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during spring at continental slope stations of years 2005–2013. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 24. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) values ≥ 3% and significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 24) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. A variety of taxa groups were important for explaining differences between spring pre- and post-DWH assemblages. Salps and cladocerans drove 12% of separation between pre- and post-DWH samples and were significant indicators of pre- and post- sampling, respectively.

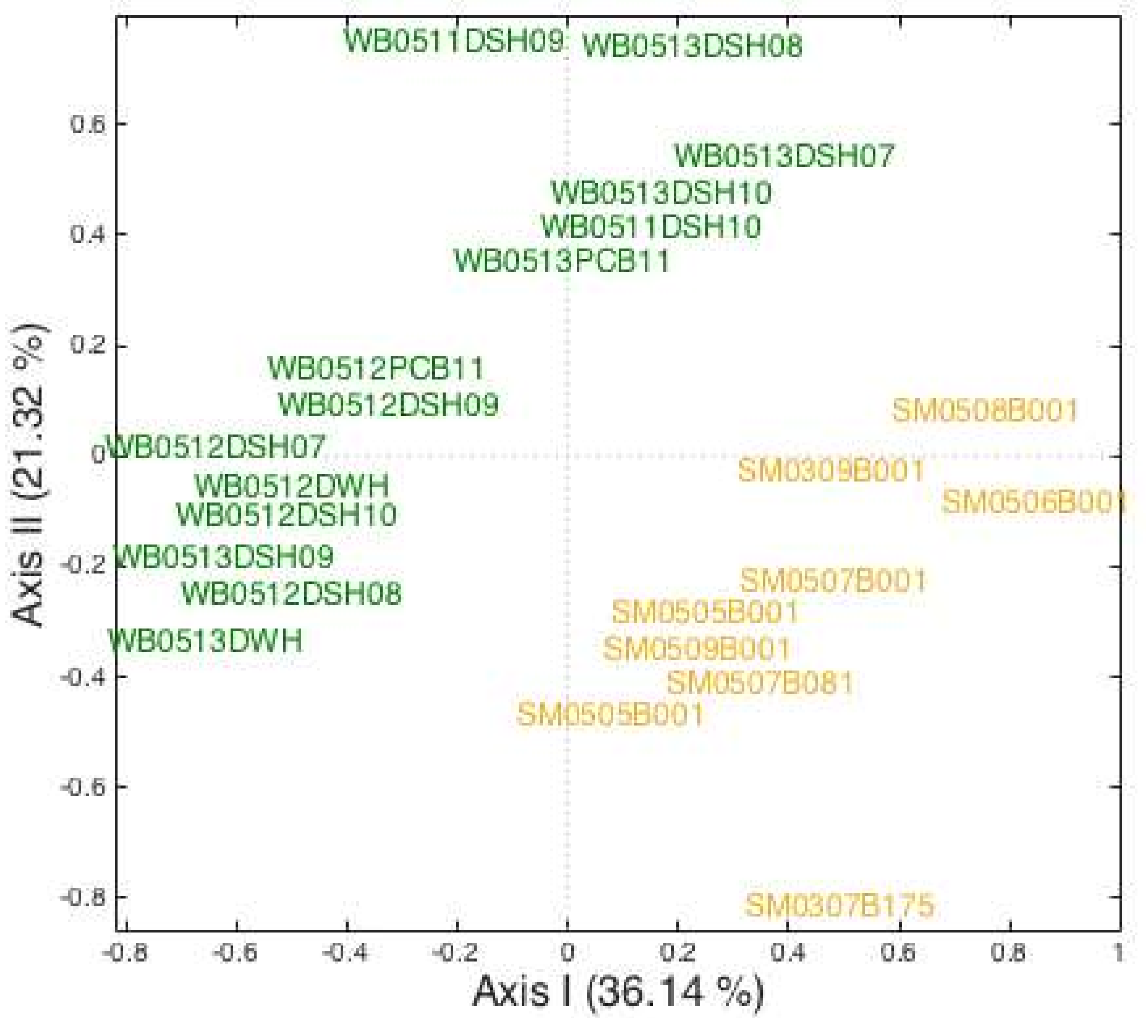

Fig. 26. PCoA ordination diagram for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during spring at oceanic stations of years 2005−2013. The axes can be used to explain the total variability between objects (sample site beta diversity); where axis I accounts for 36.14% and axis II accounts for 21.32% of total variability between objects. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows pre-DWH SEAMAP (SM), month (mm), year (yy), station (Bnnn) or post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB, or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Distinct separation of pre- and post-DWH samples is evident along the x-direction, however not along the y-axis.

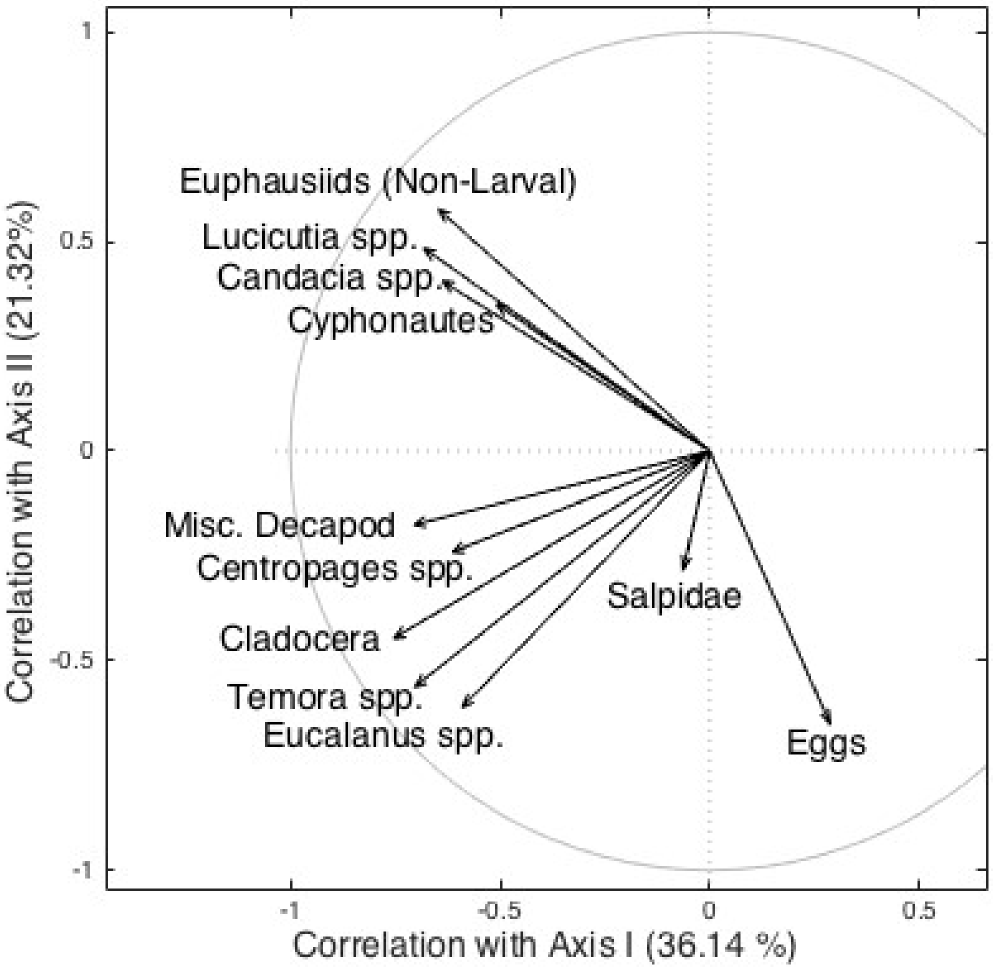

Fig. 27. PCoA vector biplot for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during spring at oceanic stations of years 2005–2013. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 26. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) values ≥ 3% and significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 26) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. Post-DWH sites have greater overall abundances and diversity than pre-DWH sites. *Centropages* spp. accounts for 5.5% of group separation while salps were significantly indicative of pre-DWH samples and euphausiids of post-DWH samples.

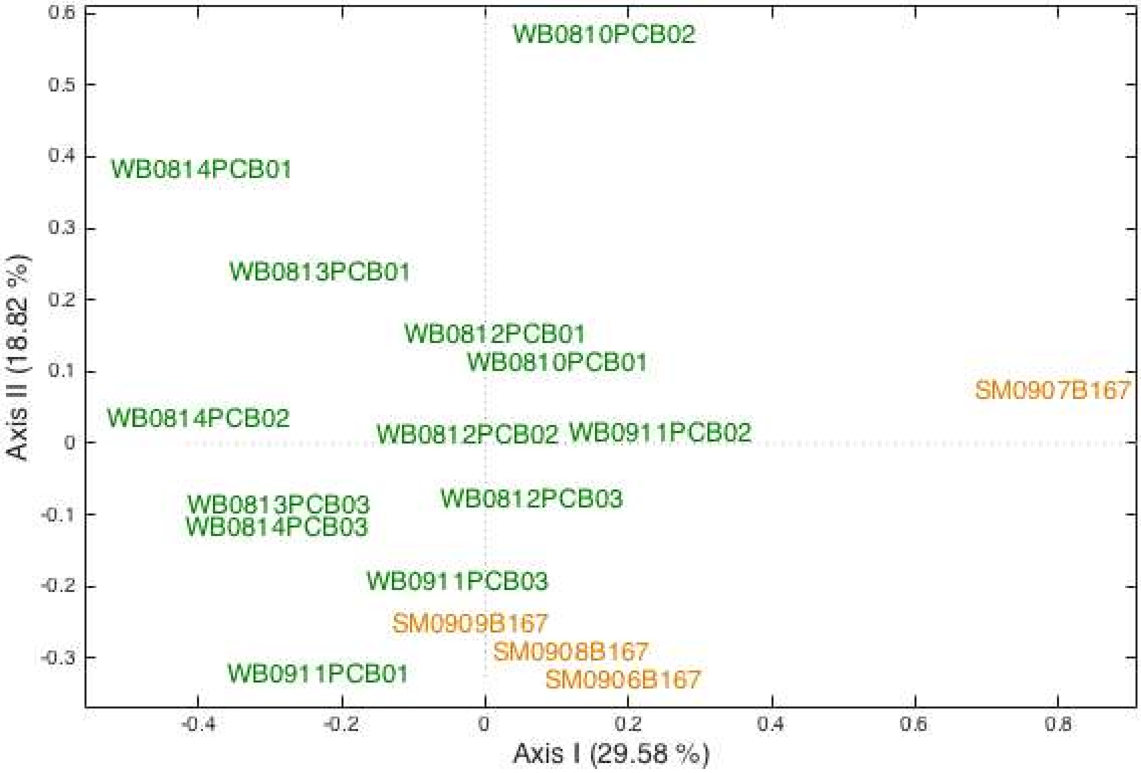

Fig. 28. PCoA ordination diagram for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during summer at continental shelf stations of years 2006−2014. The axes can be used to explain the total variability between objects (sample site beta diversity); where axis I accounts for 29.58% and axis II accounts for 18.82% of total variability between objects. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows pre-DWH SEAMAP (SM), month (mm), year (yy), station (Bnnn) or post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB, or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Post-DWH stations show greater dispersion though overlap between pre- and post-DWH samples is evident along the x-direction and the y-axis.

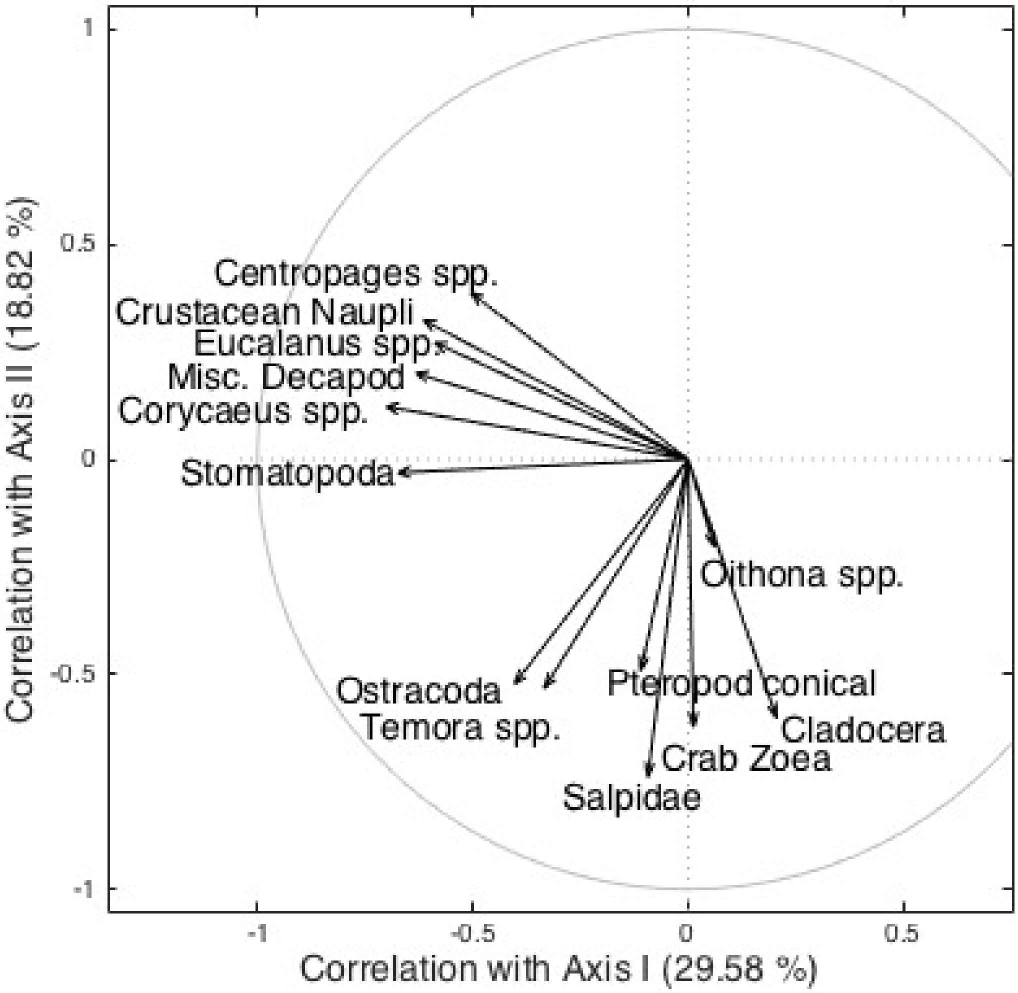

Fig. 29. PCoA vector biplot for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during summer at continental shelf stations of years 2006−2014. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 28. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) values ≥ 3% or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 28) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. Beta diversity of summer continental shelf stations have substantial variability based on year. *Centropages* spp. drove 6% of separation between pre- and post-DWH samples and were a significant indicator of post-DWH sampling, while crab zoea was the only taxa significantly indicative of the pre-DWH sampling period.

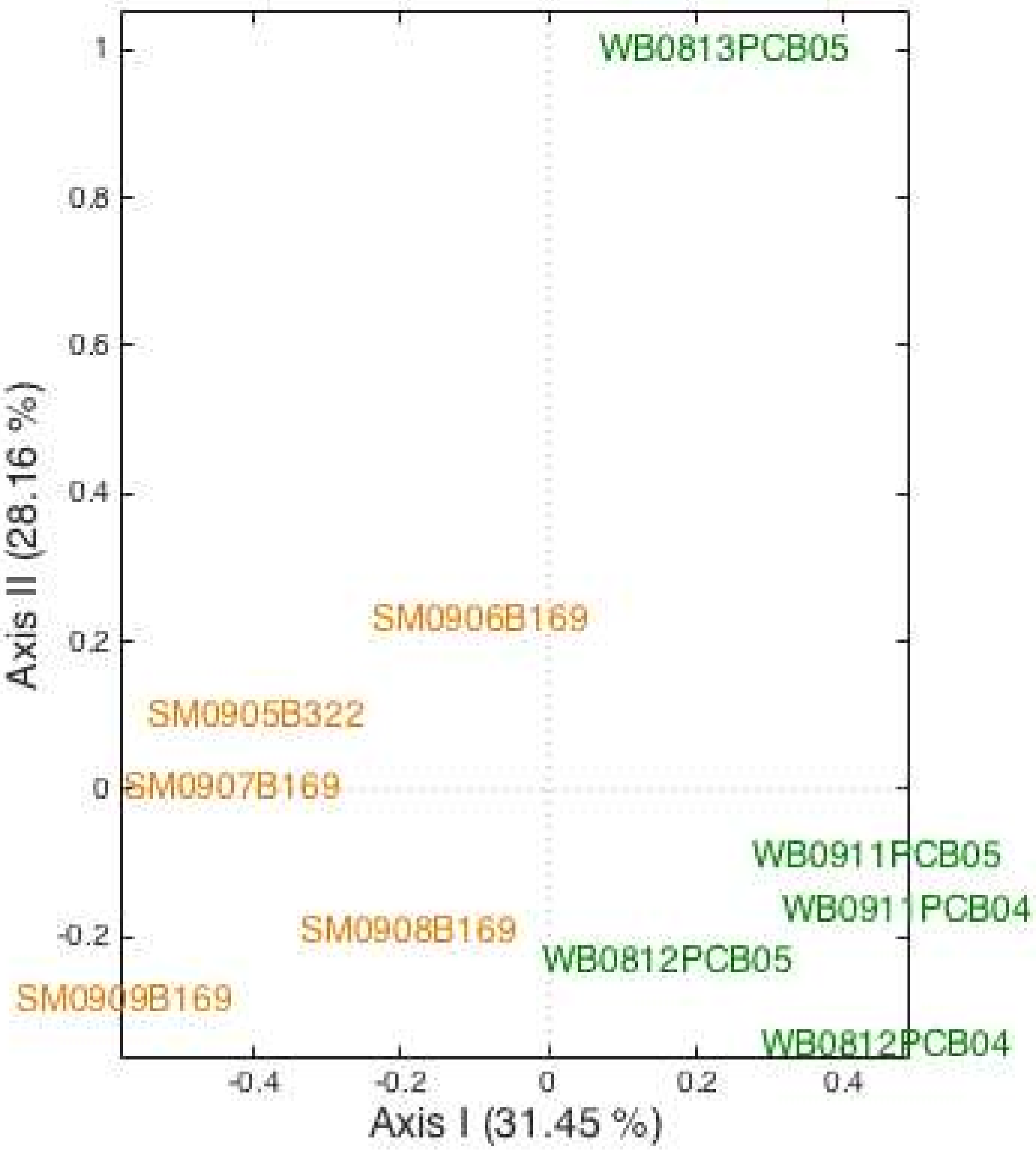

Fig. 30. PCoA ordination diagram for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during summer at continental slope stations of years 2005–2013. The axes can be used to explain the total variability between objects (sample site beta diversity); where axis I accounts for 31.45% and axis II accounts for 28.16% of total variability between objects. Any two objects' proximity to one another can be interpreted as similarity, with those closer being more similar and farther part as more dissimilar. Station labeling scheme is as follows pre-DWH SEAMAP (SM), month (mm), year (yy), station (Bnnn) or post-DWH Vessel (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB, or DSH), site number (nn). DWH is the Deepwater Horizon explosion site. Distinct groupings between pre- and post-DWH samples are evident along the x-axis while dispersion. Aside from WB0813PCB05, beta diversity of samples are similar along the y-axis.

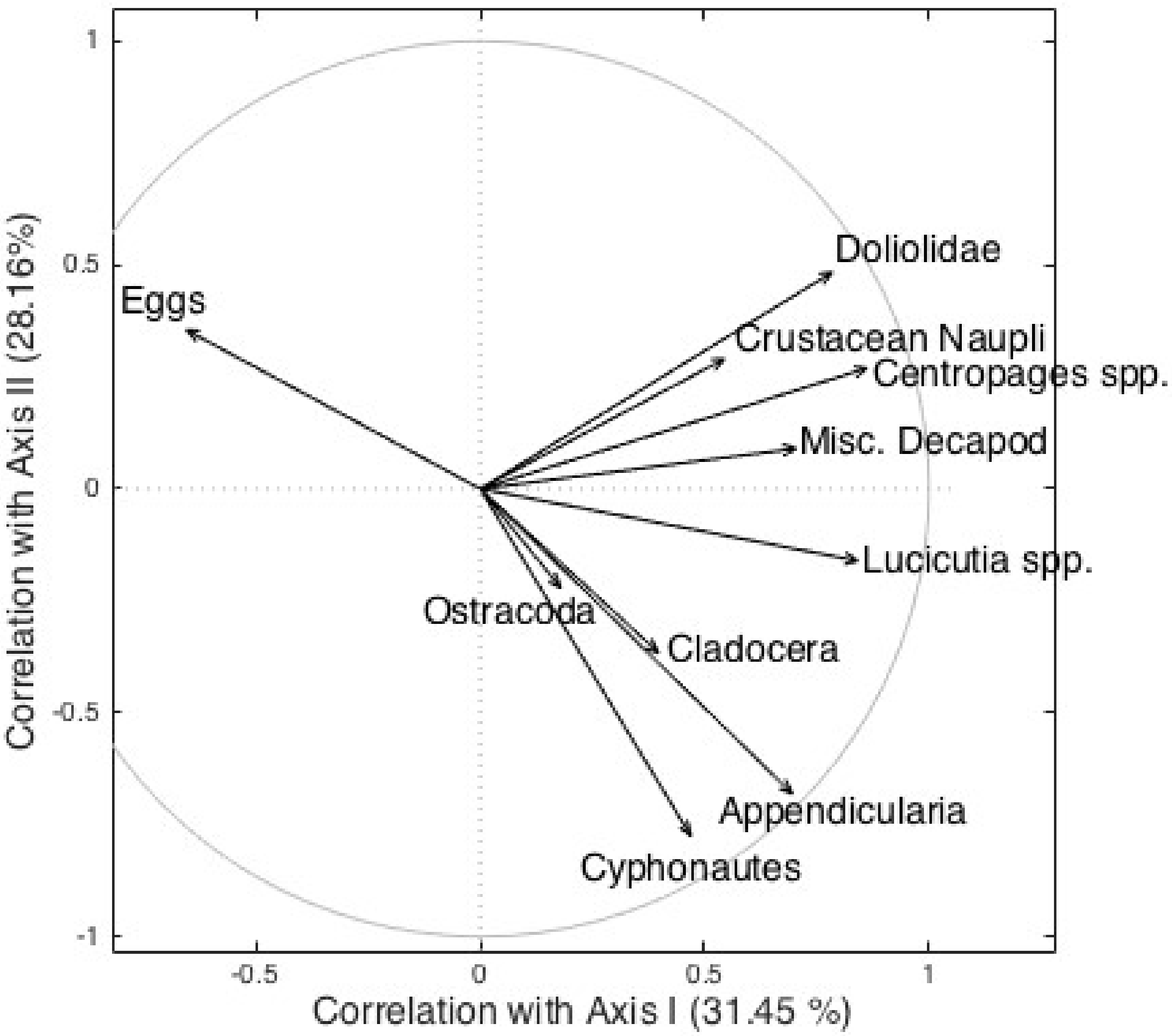

Fig. 31. PCoA vector biplot for pre-DWH (yellow) and post-DWH (green) zooplankton beta diversity during summer at continental slope stations of years 2005−2013. Vectors depicted are relative gradients with only positive ends visualized and correspond to the ordination in Fig 30. Each vector represents a zooplankton taxon important in explaining variability from similarity percentage (SIMPER) values ≥ 3% or significant indicator value results (INDVAL). The intersection of an object's orthogonal projection (Fig. 30) with a taxon vector gradient is equal to that object's modeled estimate relative to that descriptor. Longer vectors closer to the x-axis are of greater importance in explaining total variability. *Centropages* spp. and miscellaneous decapods, significant indicators of post-DWH samples, drove 8% of separation between pre- and post-DWH samples, while eggs were a significant indicator of pre-DWH sampling. In general, post-DWH samples had greater diversity and abundance of most zooplankton taxa.

3.5.2 Pre- & Post-DWH Comparisons of Zooplankton Percent Composition and Abundances Summary

Percent composition and abundance for six ‘general’ zooplankton groups and seven common copepod genera for pre-DWH samples from all years were compared to post-DWH samples from all years based on seasons and sub-regions (Table 5, 6, 7). Total copepods, chaetognaths, ostracods, and salps comprised the largest portion of zooplankton assemblages by percent and by count. *Eucalanus* spp. and *Oithona* spp. made up large portions of copepod assemblages across all sub-regions, *Centropages* spp. dominated continental shelf assemblages and *Lucicutia* spp. dominated oceanic assemblages. Many taxa exhibited statistically significant increases in either percent composition or abundance from pre- to post-DWH, however only *Eucalanus* spp., total copepods, and salps at spring continental slope stations and salps at summer shelf stations significantly decreased in both abundance and percent composition (Table 11 and 12). Oceanic stations, which were exposed to oil for the greatest number of days during the Deepwater Horizon oil spill, showed mostly either significant increases in a variety of taxa or no changes at all (Table 12), with the exception of a decrease in *Eucalanus* spp. and total copepods. *Temora* spp. and ostracods were the only groups that never showed any significant changes between sampling periods while *Oncaea* spp., total pteropods, and chaetognaths showed a significant change (always an increase) only once for either percent composition or abundance.

Results from comparisons of taxa percent composition indicated that interannual variability was high across sub-regions. However, Mann-Whitney-Wilcoxon testing of pre- versus post- percent compositions revealed that most taxa remained stable (Table 11). In total, fifty-two Mann-Whitney tests were conducted testing the percent composition of pre- versus post-DWH data. Of those 52, seven showed significant increases in percent composition of groups and eight showed significant decreases. Spring continental slope stations hosted the greatest number of significant differences between pre- and post- percent compositions; four out of the thirteen taxa tested exhibited significant increases in percent composition while significant decreases were observed for the remaining three. However, the only groups that exhibited a significant decrease in percent composition between pre- and post samples at sub-regions of both seasons were *Eucalanus* spp. and salps.

Comparisons of abundances for each of the six 'general' zooplankton groups and seven common copepod genera from all years based on seasons and sub-regions (Table 5A,B, 6) also indicated that interannual variability in abundance was relatively high, although most groups remained unchanged between pre- and post-DWH sampling periods (Table 12). Overall, there were more instances of increases in abundances than changes in percent composition. Of the eighteen significant differences observed out of the 52 comparisons between pre- and post-DWH taxa, 12 were significant increases in abundances while only six were significant decreases. The following sections is information on specific taxa groups that changed based on season and sub-region; p-values for each Mann-Whitney test conducted on percent composition or abundances can be found in Tables 11 and 12.

3.5.2.1 Spring Continental Slope Zooplankton Percent Composition

The greatest frequency of significant changes in percent composition of taxa was observed on the continental slope during spring. Increases in percent compositions from pre- to post-DWH were observed for *Lucicutia* spp., *Oithona* spp., *Corycaues* spp., and chaetognaths while significant decreases were observed for *Eucalanus* spp., total copepods, total malacostraca, and salps (Table 11).

3.5.2.2 Spring Oceanic Zooplankton Percent Composition

Significant increases were observed only in *Lucicutia* spp. in this sub-region, whereas significant decreases in both *Eucalanus* spp. and total copepods were observed from pre- to post-DWH spring oceanic samples.

3.5.2.3 Summer Continental Shelf Zooplankton Percent Composition

Only a significant increase in percent composition of total copepods was observed between pre- and post-DWH summer continental shelf samples however significant decreases were observed for *Oithona* spp., *Eucalanus* spp., and salps.

3.5.2.4 Summer Continental Slope Zooplankton Percent Composition

Summer continental slope taxa exhibited the least amount of significant variability between pre- and post- percent compositions. The single significant difference observed was for *Centropages* spp., which made up a greater portion of post-DWH samples than pre-DWH, likely attributed to its high abundances observed at PCB04 and PCB05 in summer 2011 and 2013.

3.5.2.5 Spring Continental Slope Zooplankton Abundances

Significant differences in abundances at spring continental slope stations mimic those for changes in percent composition; counts of *Lucicutia* spp. increased while *Eucalanus* spp., total copepods, and salps decreased.

3.5.2.6 Spring Oceanic Zooplankton Abundances

This sub-region exhibited greater number of instances where significant changes were observed between pre- and post-DWH sampling; however, they were all increases in abundance. These groups included the copepods *Lucicutia* spp., *Oithona* spp., *Oncaea* spp., and *Corycaues* spp., and non-copepod groups total Malacostraca and chaetognaths.

3.5.2.7 Summer Continental Shelf Zooplankton Abundances

This sub-region overall had the greater abundances relative to other sub-regions. In comparing pre- to post-DWH summer continental shelf samples, *Centropages* spp., *Corycaeus* spp., and total copepods showed significant increases in abundances while salps exhibited a significant decrease in abundance.

3.5.2.8 Summer Continental Slope Zooplankton Abundances

At summer continental slope stations, although *Centropages* spp. and *Lucicutia* spp. abundances significantly increased, total copepods and total Malacostraca significantly decreased.

Table 11. Significant p-values and non-significant results from Mann-Whitney-Wilcoxon testing of pre-DWH versus post-DWH percent composition comparative analyses by season and sub-region. A significant increase in percent composition of taxa from pre- to post- is denoted in bold while a significant decrease is italicized; non-significant results are denoted as 'ns'

	Spring Continental Slope	Spring Oceanic	Summer Continental Shelf	Summer Continental Slope
Centropages spp.	ns	ns	ns	**0.032**
Lucicutia spp.	**0.004**	**0.002**	ns	ns
Temora spp.	ns	ns	ns	ns
Oithona spp.	**0.09**	ns	*0.023*	ns
Oncaea spp.	ns	ns	ns	ns
Corycaeus spp.	**0.09**	ns	ns	ns
Eucalanus spp.	*0.004*	*0.004*	*0.048*	ns
Total Copepod	*0.002*	*0.007*	**0.006**	ns
Total Malacostraca	*0.002*	ns	ns	ns
Ostracods	ns	ns	ns	ns
Total Pteropods	ns	ns	ns	ns
Chaetognaths	**0.015**	ns	ns	ns
Salps	*0.015*	ns	*0.01*	ns

Table 12. Significant p-values and non-significant results from Mann-Whitney-Wilcoxon testing of pre-DWH versus post-DWH raw abundance comparative analyses by season and sub-region. A significant increase in percent composition of a taxa from pre- to post- is denoted in bold while a significant decrease is italicized; non-significant results are denoted as 'ns'

	Spring Continental Slope	Spring Oceanic	Summer Continental Shelf	Summer Continental Slope
Centropages spp.	ns	ns	**0.003**	**0.008**
Lucicutia spp.	**0.004**	**0.001**	ns	**0.008**
Temora spp.	ns	ns	ns	ns
Oithona spp.	ns	**0.02**	ns	ns
Oncaea spp.	ns	**0.02**	ns	ns
Corycaeus spp.	ns	**0.004**	**0.009**	ns
Eucalanus spp.	*0.002*	ns	ns	ns
Total Copepod	*0.02*	ns	**0.045**	*0.032*
Total Malacostraca	ns	**0.041**	ns	*0.06*
Ostracods	ns	ns	ns	ns
Total Pteropods	*0.04*	ns	ns	ns
Chaetognaths	ns	**0.015**	ns	ns
Salps	**0.004**	ns	*0.08*	ns

4. DISCUSSION

The goal of this study was to understand the natural seasonal and interannual effects of environmental variability on zooplankton community structure in the NEGOM in relation to the DWH oil spill. To assess the impact of the oil spill on zooplankton communities, a post-DWH baseline of zooplankton beta diversity was established for the NEGOM, a relatively understudied ocean region, utilizing samples collected between 2010–2014, and then the post-DWH results were compared to the pre-DWH data provided by SEAMAP, collected between 2005–2009. Zooplankton samples and a variety of environmental parameters including temperature, wind components and magnitude, salinity, dissolved oxygen, discrete chlorophyll, integrated fluorescence, mixed layer depth, and turbidity were used to evaluate changes in zooplankton beta diversity, abundances, and percent composition for pre- and post-DWH sampling periods. An analysis of environmental conditions and zooplankton community structure indicated that the NEGOM is a complex and highly variable oceanographic region linked closely to seasonal and interannual changes in river discharge and related effects such as seawater temperature, chlorophyll, and turbidity. The Mississippi river dominates environmental conditions and strongly impacts marine chemical and biological properties in this region. Additionally, our data suggest that the DWH oil spill did not significantly alter zooplankton communities in this study region in the years following the oil spill.

4.1 Seasonal Trends in Environmental Conditions and Zooplankton Communities

4.1.1 Environmental Influences on Beta Diversity

Rivers are a significant source of nutrients in the NEGOM (Lohrenz et al., 1990; Lohrenz et al., 1997; Jochens et al., 2002; Belabbassi et al., 2005). Our results corroborate other work that the presence of Mississippi River water is the primary driver for significant seasonal and interannual variation in environmental conditions observed in our study region (Walker, 1996; Lohrenz 1997; Dagg and Breed, 2003; Salisbury et al., 2004; Jones and Wiggert, 2015; Huang et al., 2013). The presence of river water at study sites supported higher chlorophyll concentrations (Riley, 1937; Dagg et al., 1988; Ortner et al., 1989; Lohrenz et al., 1997; Dagg and Breed, 2003; Wawrik et al. 2003, Chakraborty and Lohrenz, 2015; and others), a proxy for phytoplankton biomass and food resource for zooplankton, therefore significantly impacting zooplankton communities (Bogdanov et al., 1968; Howey, 1976; Dagg, 1988; Ortner et al., 1989; Dagg, 1995; Dagg and Breed, 2003).

In addition to river discharge, prevailing winds also influenced regional oceanographic conditions (Walker, 1996; Jochens et al., 2002; Salisbury et al., 2004; Belabbassi et al., 2005; Martinez-Lopez and Zavala-Hidalgo, 2009). Varying river discharge rates did not solely dictate seasonal and interannual differences observed in zooplankton communities and environmental conditions. Prevailing winds also were responsible for river plume morphology and introduction of river waters to our study area (Walker, 1996; Jochens et al., 2002; Morey et al., 2003; Belabbassi et al., 2005; Martinez-Lopez and Zavala-Hidalgo, 2009; Huang et al., 2013). For example, though seasonal results indicated that river discharge was greatest in spring, spring salinities throughout our study region were not indicative of river water presence. It is only when we consider prevailing winds that can we elucidate seasonal differences.

Typically, Mississippi River waters exiting through the bird's foot delta flow westward and northward due to southward and westward winds, respectively (Walker et al., 1996; Jochens et al., 2002; Walker et al., 2005; Morey et al., 2003; Androulidakis et al., 2015). Thus the fluvial discharge often becomes 'trapped' along the continental shelf west of its origin, contributing to the well-known late spring hypoxia events on the Louisiana-Texas shelf (Walker et al., 2005). While westward winds dominate in spring (Jochens et al., 2002; Walker et al., 2005), northeastward winds, prevalent in summer, can move the Mississippi River plume eastward of the delta (Walker et al., 1996; Belabbassi et al., 2005).

The dominant environmental conditions during spring months included the average Mississippi River discharge, 3-day average wind magnitude, salinity, northward currents (pre-DWH), and westward winds (post-DWH), while during summer months higher surface temperatures and lower salinities were dominant environmental forcings. Salinity measurements of <31 psu, associated with river-influenced Gulf of Mexico water (Chakraborty and Lohrenz, 2015), were not present at pre-DWH or post-DWH stations during spring, but were observed at a number of summer stations.

In the NEGOM, the Mississippi River is the largest source of low-salinity water (Nowlin et al., 2000) and nutrients during summer (Belabbassi et al., 2005) and is associated with greater phytoplankton concentrations (Dagg et al., 1988; Ortner et al., 1989; Lohrenz et al., 1997; Wawrik et al. 2003, Chakraborty and Lohrenz, 2015). In my study, distance-based redundancy analysis results revealed that Mississippi River discharge and chlorophyll concentrations were significant environmental predictors explaining summer zooplankton beta diversity, but not during spring. Despite greater Mississippi River discharge during spring, the lack of low salinity surface water at stations during spring and dominant westward wind direction illustrated that

Mississippi River waters moved to the west and did not impact the study area. Instead during summer, winds weakened and switched direction, moving the Mississippi River plume waters into our sampling region, impacting biological communities.

Additionally, summer eastward winds are favorable for coastal upwelling (Jochens et al., 2002; Nguyen, 2014), and contribute to circulation features, such as slope eddies, that also deliver nutrients to the euphotic zone (Belabbassi et al. 2005, Nguyen, 2014). Summer winds also contribute to cross-shelf transport of chlorophyll-rich river water (Morey et al., 2003; Jochens and DiMarco, 2008; Jones and Wiggert, 2015) especially towards the western side of the DeSoto Canyon due to presence of anticyclonic eddies (Morey et al., 2003; Wang et al., 2003; Chassignet et al., 2005). While the uniqueness of summer wind fields relative to spring were major proponents in explaining significant seasonal differences in environmental conditions and zooplankton beta diversity, temperature also contributed to seasonal differences.

4.1.2 Influences on Zooplankton Taxa

The Metabolic Theory of Ecology (MTE) is an ecological principle that relates growth-rate to body mass and temperature (Brown et al., 2004). While other factors, such as food availability or reproduction strategy (i.e., diapause, developmental stages) contribute to variation in growth-rates of ectotherms (Gillooly and Dodson, 2000; Lin et al., 2013), in general, MTE states generation times have a positive relationship with temperature and negative relationship with body mass (Brown et al., 2004; Hirst et al., 2003). Previous studies have explored the influence of temperature and body mass on growth rates for some zooplankton, although mostly on estuarine or coastal species.

Growth studies conducted with an experimental design closest to *in-situ* conditions using wild-caught animals with no addition of food sources were compiled into a comprehensive review by Hirst et al. (2003). In an effort to remove the effects of body size, growth rates were standardized based on μgC/individual. Of the considered zooplankton groups, chaetognaths, larvaceans, thaliaceans, planktonic crustaceans (excluding copepods), and broadcast- and sac-spawning copepods exhibited a positive relationship between temperature and growth-rates (Hirst et al., 2003), especially for juvenile copepods as a function of food saturation (Hirst and Bunker, 2003). Higher summer temperatures, in addition to the presence of river plume waters as a proxy for increased food availability, prompted faster generation times for many zooplankton groups in the NEGOM, resulting in a net increase in summer zooplankton abundances and significant differences in seasonal zooplankton beta diversity.

The CAP ordinations revealed that fewer zooplankton taxa were important for defining spring samples relative to summer. The average total abundance per station in summer was greater than spring for both datasets. Zooplankton communities also exhibited strong sub-regional differences between continental shelf, continental slope, and oceanic stations. Moving seaward by sub-region, total average abundance was greatest at continental shelf stations, intermediate at continental slope stations, and lowest at oceanic stations, a pattern previously observed for this study region in terms of biomass (Howey, 1976), zooplankton abundance (Ortner, 1989) and on the west Florida shelf (Hopkins et al., 1981). Of the significant summer-indicator groups, *Centropages* spp. and stomatopods were represented in both pre- and post-DWH datasets.

Centropages spp. is a dominant copepod typical of shallow continental shelf and river-influenced environments throughout the northern and eastern Gulf of Mexico (Howey, 1976; Hopkins et al., 1981; Turner and Tester, 1989; Ortner, 1989; Lester, 2005; Walsh, 2012; Elliot et al., 2012). While its presence is not surprising in either spring or summer, it was selected as a summer indicator due to its greater fidelity across sampling sites in summer relative to spring, possibly attributed to cross-shelf movement of river water.

The sample with the single highest abundance of *Centropages* spp., 2,569 individuals/m^3, was collected at PCB01 in spring 2011. The second highest abundance, 1,462 individuals/m^3, was recorded during summer 2010. Moreover, *Centropages* spp. abundances in summer 2010 and spring 2011 were anomalously high relative to the rest of the data. Overall, the average abundances of *Centropages* spp. tended to be slightly higher in summer, and was more frequently observed across pre- and post-DWH stations during summer. However, the range of abundances, excluding those at PCB01 summer 2010 and spring 2011, were not substantially different based on season. Abundances were highest at continental shelf stations, and also relatively high at continental slope and post-DWH oceanic stations in association with salinities close to or below 31 psu. Thus, high abundances of *Centropages* spp. is likely linked to the influence of river water.

Larval planktonic stages of stomatopods were another significant indicator of summer. Though their presence was fairly consistent between seasons, overall greater abundances were seen during summer. Larval stomatopods are common in neritic waters throughout their temperate to tropical range (Morgan and Provenzo, 1979), and are especially common in shrimping areas of the Gulf of Mexico (Hildebrand, 1954) ranging from the continental shelf (Franks et al., 1972) to oceanic waters (Hildebrand, 1954). Larval stomatopods were relatively abundant during summer across sub-regions at both continental shelf and oceanic stations.

Moreover, the presence or greater abundance of many taxa including crab zoea, cladocerans, *Eucalanus* spp., and ostracods were important for driving seasonal separation in both datasets. Previous studies have reported these groups to be most abundant at continental shelf stations (Carassou et al., 2015), though they are common throughout the study region (Franks, 1972; Howey 1976; Hopkins et al., 1981; Ortner, 1989; Turner and Tester, 1989; Walsh, 2012), sometimes with high abundances observed at continental slope and oceanic stations as well.

4.1.3 Seasonal Differences: Summary

Seasonal differences in zooplankton beta diversity were driven largely by environmental parameters, specifically Mississippi River discharge, temperature, chlorophyll, salinity, and prevailing wind direction and magnitude. Based on the results of this study, it is clear that seasonal differences in environmental conditions are strongly linked to temperature, the presence of river water, and the cascading effects of river water on zooplankton communities. Warmer summer temperatures likely shorten generation times for many zooplankton groups. Additionally, the presence of zooplankton taxa associated with continental shelf and river-influenced regions, such as *Centropages* spp. (Howey, 1976; Hopkins et al., 1981; Ortner, 1989; Lester et al., 2008; Elliot et al., 2012; Walsh, 2012) and cladocerans (Della Croce and Angelino, 1987; Walsh, 2012) at slope and oceanic sites may be indicative of the transport of coastal waters to slope and oceanic regimes due to summer wind fields.

4.2 Interannual Trends in Environmental Conditions and Zooplankton

Many of the same environmental parameters that drove seasonal differences between spring and summer zooplankton communities were also responsible for driving interannual variability in zooplankton beta diversity within a season. Significant interannual differences in environmental conditions were observed between nearly all years, associated with varying Mississippi River discharge, temperature, chlorophyll, salinity, and prevailing wind direction and magnitude. Stations exhibited greater annual fidelity based on environmental conditions than on zooplankton beta diversity. However, significant interannual differences in zooplankton communities occurred more frequently in summer compared to spring. Sub-regional groupings showed particularly strong differences at continental shelf stations for both environmental conditions and beta diversity during both spring and summer. In spring, continental shelf stations clustered separately from continental slope and oceanic stations, which commonly grouped together. This can likely be attributed to the preclusion of river water at continental slope and oceanic stations. During summer, continental slope stations and oceanic stations were more often subjected to ecological complexities associated with river plumes. Stations nearest the Mississippi River bird-foot delta exhibited transitional qualities; sometimes with environmental conditions either having low salinity and high chlorophyll likely from river discharge, or high salinity and low chlorophyll, more typical of an oceanic regime. Relative to sub-regions, especially as they relate to chlorophyll concentrations, environmental conditions in spring and summer both exhibited major differences between the heavily river-influenced continental shelf stations as compared with the continental slope and oceanic stations (El-Sayed, 1972; Ortner et al., 1989; Lohrenz et al., 1990; Qian et al., 2003; Lester, 2005; Chakraborty and Lohrenz, 2015), which consequently, drive responses by the zooplankton communities (Howey, 1976; Hopkins et al., 1981; Dagg et al., 1988; Ortner et al., 1989; Lester, 2005; Walsh, 2012).

4.2.1 Interannual Variability in Environmental Conditions and Zooplankton During Spring

During spring, there were no significant interannual differences in zooplankton beta diversity despite the high observed between years at continental shelf stations. I suspect that the lack of significant interannual differences between spring years was linked to similarities between zooplankton communities at continental slope and oceanic stations as they relate to environmental conditions. The continental shelf stations, exhibited high interannual variability in chlorophyll concentrations associated with river discharge.

Continental shelf stations are highly influenced by NEGOM rivers during spring (Jochens et al., 2002; Qian et al., 2003; Jones and Wiggert, 2015) and biological communities are more tightly coupled with physical variability in this sub-region (Biggs and Ressler, 2001). However, continental slope and oceanic locations were largely precluded from fluvial effects during spring, whether from the Mississippi River, the other two largest riverine influences in the region, Mobile Bay and the Apalachicola River (Qian et al., 2003), or numerous other smaller river discharges into the NEGOM (Jochens et al., 2002). Based on salinities during spring, our station data support previous observations that continental shelf stations experienced river influence during spring while continental slope and oceanic stations more commonly did not.

At intermediate salinities near river inputs, the introduction of new nitrate by rivers plumes can result in phytoplankton blooms (Dagg et al., 1987; Lohrenz et al., 1990; Dagg and Breed, 2003), where high rates of zooplankton grazing have also been observed (Dagg, 1995). Grazing-induced mortality by zooplankton is typically the most common end-point for marine phytoplankton (Banse, 1995; Dagg, 1995), especially gelatinous microzooplankton (Dagg 1995; Dagg and Breed, 2003), which can more quickly respond to increases in phytoplankton concentrations. However, members of the copepod community respond more slowly (Dagg, 1995) because they have higher food saturation requirements (Hirst and Bunker, 2003) and longer generation times (Dagg, 1995; Hirst et al., 2003). Riverine-influenced regions also support high abundances of some copepods species (Turner, 1984; Dagg and Breed, 2003), such as *Temora* spp. and *Centropages* spp. (Howey, 1976; Ortner et al., 1989; Dagg, 1995; Elliot et al., 2012; Lester, 2005). But as the river plume moves away from its source, the nitrate is quickly depleted by phytoplankton (Redalje et al., 1994; Lohrenz et al., 1999), primary production slows (Liu and Dagg, 2003), and the mismatch between phytoplankton growth rates and grazer-induced mortality by zooplankton necessary for bloom conditions lessens (Dagg, 1995). The copepod communities change in response to the ecological environment as the plume moves away from its source (Howey, 1976; Dagg, 1995).

However, due to prevailing wind fields in the spring season, continental slope and oceanic sub-regions are less likely to be subjected to the complex environment and ecology associated with plume waters. The NEGOM environment unassociated with river discharge is relatively oligotrophic (Qian et al., 2002; Müller-Karger et al., 2015) and interactions between phytoplankton and zooplankton communities in these regions have a closer growth-rate to grazing-mortality ratio (Banse, 1995). These ecological and environmental conditions support lower zooplankton abundances and taxa better suited to these environments such as *Candacia* spp., *Oncaea* spp., *Oithona* spp., and *Lucicutia* spp. (Howey, 1976) and euphausiids (Hopkins et al., 1981; Hopkins, 1982), also observed in our continental slope and oceanic zooplankton samples.

Looking landward, not only did continental shelf stations cluster separately from continental slope and oceanic stations from the same year, but also continental shelf stations substantially differed from one another interannually. The high interannual variability observed at continental shelf stations on the Florida shelf was likely associated with annual changes in discharge of coastal rivers closest to shelf PCB stations, especially PCB01 which exhibited the greatest interannual variability and is closest to the coastline. Regardless of wind forcing on the Mississippi River plume advecting it into our study region, discharge from rivers including the Mobile, Tombigbee, Choctawhatchee, Escambia, and Appalachicola, influence coastal and shelf locations (Gilbes et al., 1996; Walker, 1996; Gilbes et al., 2002; Jochens et al., 2002). However, annual patterns of Mississippi River discharge rates are similar for other rivers in the southeast such as the Alabama, Tombigbee, and Apalachicola (US Geological Survey, 2016), although with much smaller discharge volumes (Gilbes et al., 1996; Jochens et al., 2002). For the present study, the Mississippi River was used as a proxy for other river discharge rates. Therefore, interannual differences in southeast watershed discharge rates will be discussed in terms of the Mississippi River discharge.

The geographical extent of our study region represented in a single year ranged from continental shelf to oceanic environments. This spatial range may be useful to capture large-scale interannual differences in zooplankton beta diversity, such as those observed in summer between years. Yet, for spring, the study area may be too large to capture significant interannual differences influenced at smaller scales, such as the impacts of annual variability of river discharge on zooplankton beta diversity at continental shelf stations (Walker, 1996; Dagg and Breed, 2003). This is not surprising if we consider the dominant prevailing westward winds during spring would confine river water to the continental shelf, minimizing transport of river water to continental slope and oceanic stations, whereas northern and eastward wind components during summer would facilitate offshore transport (Walker, 1996; Morey et al., 2003; Qian et al., 2003; Belabbassi et al., 2005; Jochens and DiMarco, 2008; Jones and Wiggert, 2015).

For example, previous studies have shown substantial interannual differences in a variety of zooplankton taxa associated with river plumes or coastal regions, namely ostracods, salps, *Centropages* spp., *Temora* spp. (Turner and Tester, 1989; Ortner et al., 1989; Elliot et al., 2012), and cladocerans (Della Croce and Angelino, 1987; Hopkins, 1977; Paffenhöfer, 1984; Lester, 2005; Elliot et al., 2012).

Cladocerans are associated primarily with neritic waters (Della Croce and Angelino, 1987), where they can exhibit dramatic population growth (Paffenhöfer and Knowles, 1980), especially in spring and summer (Hopkins, 1984; Paffenhöfer, 1984; Turner and Tester, 1989). Even *Evadne tergestina*, the only cladoceran known to establish offshore populations, is regarded as estuarine and comprises dominant portions of zooplankton assemblages only within nearshore communities (Della Croce and Angelina, 1987), especially on the Florida Shelf (Hopkins, 1977; Paffenhöfer, 1984; Squires, 1984; Lester, 2005). Further, Lester (2005) reported *E. tergestina* as a dominant member of coastal zooplankton communities during *Karenia brevis* blooms, but not during non-blooms. Therefore, abundances of cladocerans were associated with years of high river discharge. In spring 2011, a time that exhibited historically high river discharge (Kroes et al., 2015), cladocerans abundances were high at continental shelf stations and low at continental slope and oceanic stations.

4.2.2 Interannual Variability in Environmental Conditions and Zooplankton During Summer

Similarly to spring, much of the interannual variability observed in summer zooplankton community structure was driven by changes at continental shelf stations linked to interannual variability of river discharge (Walker, 1996; Dagg and Breed, 2003). However, low salinities also were observed at slope and oceanic stations during summer, indicative of cross-shelf and offshore transport of river water. As a result, zooplankton beta diversity at oceanic DSH stations nearest the mouth of the Mississippi and continental slope stations sometimes exhibited transitional properties and were more closely associated with continental shelf stations than oceanic (Ortner et al., 1989), especially during years of higher river discharge rates, such as 2010 and 2013.

Although Mississippi River plume waters and cross-shelf transport of other river waters were more often present at stations across our study region during summer, river plume waters were not present at every station during summer. Zooplankton communities at slope and oceanic stations co-occurred with salinities indicative of oceanic water and were similar to previous observations that reported greater abundances of *Oithona* spp., *Candacia* spp., and *Lucicutia* spp. (Howey, 1976; Ortner et al., 1989) and euphausiids (Hopkins et al., 1981; Hopkins, 1982), typical of slope and oceanic regimes.

4.2.3 Exceptional Cases in Interannual Variability

In contrast to summer 2010 and spring 2011, 2012 had exceptionally low river discharge and relatively weak winds. Overall, low zooplankton abundances were observed, except for a salp bloom at Florida continental shelf stations in summer 2012. While salp blooms are thought to be largely unpredictable, factors that likely contribute to these events include upwelling, asexual reproduction, predation, and chlorophyll concentrations (Boera et al., 2008; Deibel and Paffenhöfer, 2009). Salps employ muscular pumping of their bodies to filter water and capture phytoplankton for feeding (Deibel and Paffenhöfer, 2009). While an introduction of new nutrients from upwelling or river discharge could contribute to greater food availability, high chlorophyll concentrations can also adversely affect salps. Harbison (1986) observed that too high a concentration of phytoplankton cells can obstruct salp feeding filters, effectively plugging their ability to feed and compromising survivorship. Further, their feeding strategy may cause a greater hydrological disturbance than other surrounding zooplankton, which may lead to increased detection of a zooplankton patch by predators and increased predation on other nearby competing zooplankton taxa (Deibel and Paffenhöfer, 2009). In 2012, despite significantly low river discharge relative to other years, the first week of May exhibited an uptick in river discharge compared to preceding months. This uptick likely introduced new nutrients that subsequently fueled a chlorophyll bloom. Considering that the observed discrete surface chlorophyll and integrated chlorophyll concentrations in 2012 were not very different from those during spring 2013, despite the significant interannual differences in river discharge between the two years, it is possible our sampling efforts captured the effects of a recent bloom of phytoplankton.

Swarms of gelatinous zooplankton are common along coastal regions of the northern Gulf of Mexico (Dagg and Breed, 2003) and their prey can respond quickly to the introduction of new nutrients. Considering river discharge was low during months leading up to our early May 2012 zooplankton sampling, it is possible that prior to our efforts, particularly low abundances of zooplankton were present, and therefore grazing by zooplankton on phytoplankton was relatively low. By asexually reproducing, salps have short generation times, especially relative to other top grazers, such as copepods that reproduce sexually (Liu and Dagg, 2003). If there was a net reduction in grazing pressure and competition for shared food resources (phytoplankton), coupled with a pulse of new nutrients, environmental conditions in May 2012 may have been suitable for a salp bloom to occur. Given the low abundances of zooplankton prior to our sampling efforts, the salp bloom captured in our 2012 samples may be a representation of an ecological advantage of salps. This example highlights the variability in zooplankton communities, especially relative to the survival strategies of specific taxa, and emphasizes how individual samples do not reflect interannual differences as they relate to the environment.

Another interesting exception to the general interannual trends discussed for spring and summer is the anomalously high zooplankton abundances, notably *Centropages* spp., at continental-shelf stations in summer 2010 and spring 2011. Environmental conditions in March

2010, before the April 2010 Deepwater Horizon oil spill, included an uncommon movement of Mississippi River plume water to the east (Huang et al., 2013). Within this region, Huang et al. observed an increase in CO_2 uptake and satellite-derived increase in chlorophyll, which they attributed to increased biological activity. Following the oil spill, high abundances of river-associated taxa, such as *Centropages* spp. (Howey, 1976; Ortner et al., 1989; Dagg, 1995; Elliot et al., 2012; Lester, 2005) and ostracods (Turner and Tester, 1989; Ortner et al., 1989; Elliot et al., 2012), were observed in August 2010, which may have been related to the spring event described by Huang et al. (2015). Had the oil spill significantly altered zooplankton community structure in the NEGOM by increasing zooplankton mortality, as predicted from laboratory experiments (Almeda, 2013; Buskey et al., 2016), such high zooplankton abundances would not have been observed.

My observations suggested the opposite, which is also consistent with previous reports that primary productivity has increased following some, but not all, oil spills (Penela-Arenaz et al., 2009; Hu et al., 2011), possibly because the oil serves as a micronutrient (Ozhan et al., 2014) and potentially leading to increased zooplankton food availability. Thus, it is difficult to determine what environmental factors contributed to the high 2010 summer zooplankton abundances (Daly et al., 2013).

4.3 The Deepwater Horizon Oil Spill

Based on laboratory studies that showed that oil exposure can compromise survivorship and can lead to zooplankton mortality (Almeda, 2013; Buskey et al., 2016), the Deepwater Horizon oil spill event unquestionably killed zooplankton in the NEGOM. Although in this study, the seasonal, interannual, and sub-regional changes in zooplankton beta diversity observed in both pre- and post-DWH samples were strongly related to natural phenomena, such as wind direction and river discharge. While beta diversity is a useful metric to assess multivariate data, such as with the many taxa that comprise zooplankton community structure, processing the pre- and post-DWH zooplankton communities using different methods (Zooscan versus microscopy) limited the comparison. For example, some pre-DWH zooplankton data acquired using a Hydroptic Zooscan were similar to that of post-DWH zooplankton data, acquired through microscopy. Conversely, abundances for other zooplankton taxa were substantially different, with greater numbers nearly always represented by samples analyzed by microscopy. This was likely a result of image quality on the Zooscan. The quality of the computer images, the problem of material adhering to individuals, and smaller copepods sometimes being hidden underneath or within larger animals and going unrecognized the scanning phase limited accurate identification of some images. Data acquired by an experienced scientist using a microscope for identification did not have such limitations. No other work has been published comparing these techniques using Gulf of Mexico samples. Hopefully these results may be useful in identifying groups that best highlight the inconsistencies between methodologies and in developing future training sets and protocols for this study region. Despite the limitations in assessing beta diversity as a metric for determining significant differences in zooplankton community structure in the NEGOM before and after the oil spill, comparison of major groups proved to be a useful way to assess such changes.

Comparisons of major taxa groups by sub-region revealed that no major groups were missing between sampling periods. While some groups exhibited significant changes in percent composition (Table 11), they were not always significantly different in abundances (Table 12), or vice versa. The greatest variability in comparisons of zooplankton percent compositions and abundances were observed at continental shelf and continental slope stations. Due to the distance of these stations from the Deepwater Horizon blowout site and having experienced only 1–10 days of oiling (Fig. 2), differences in these taxa are likely rather due to coastal processes, such as river discharge and upwelling (Schiller et al., 2011) rather than oil exposure. When comparing only oceanic sites, which fell within the 'heavily oiled' region and would therefore exhibit a greater signal of environmental distress, most zooplankton percent comparisons were not significantly different between pre- and post-DWH sampling periods. Of those that were significantly different, abundances increased for those taxa post-DWH. Zooplankton percent composition and abundances during the spill year (2010) did not stand out as significantly different from other years.

Based on these findings, there was no significant impact of the Deepwater Horizon on zooplankton communities in the NEGOM. While nearshore stations, PCB01 and PCB02, exhibited anomalously high abundances of the copepod *Centropages* spp. during summers of 2010 and 2011 and spring of 2011 (Daly et al., 2013), it is difficult to link this event directly to the spill. The anomalously high abundances of *Centropages* spp. event were, however, notable, as it extended along the shelf down the West Florida Shelf (Daly et al., 2013).

In the Mediterranean Sea, highest abundances and bi-modal peaks of *Centropages* spp. were observed during negative NAO years attributed to greater precipitation, vertical mixing, and reduced predation by gelatinous zooplankton (Mazzochi et al., 2007; Molinero et al., 2008). For our region, where El Nino-Southern Oscillation events are a more important global metric impacting annual regional changes in rainfall and its relationship with stream and river discharge (Clark et al., 2014), we found no correlation between ENSO indices and increased abundances of *Centropages* spp. (Figure 23).

Some caveats relative to this study include the sample sizes and differing methodology between sampling periods. While we observed many significant interannual differences in the post-DWH USF data, no significant differences in years were observed in the pre-DWH SEAMAP data. This is likely a result of small sample sizes (number of stations). Additionally, the nature of zooplankton sampling is coarse relative to the ecological complexity and patchy nature of these communities (Omori and Ikeda, 1976). Bongo net tows capture a finite, relatively small observation in a system where water is constantly dictating the movements of planktonic animals. Towed samples are a mere snapshot in this vast system. Further, some taxa that can be numerically important contributors to zooplankton assemblages, such as copepod nauplii and metazoans, are too small to be accurately represented using a 333 μm net or are difficult to preserve, such as gelatinous animals (Omori and Ikeda, 1976). Lastly, collection times were opportunistic based on when the ship arrived at the station. Because of this, a variety of diel vertical migration signals or net avoidance exhibited by some taxa during daytime sampling may have been overlooked. These results highlight the importance of long-term, high frequency monitoring representing a variety of sub-regions in order to achieve a more comprehensive analysis of environmental perturbations.

5. CONCLUSIONS

The collection of zooplankton and environmental parameters to assess the impact of the Deepwater Horizon oil spill began during August 2010, nearly a month following the successful capping of the wellhead. However, oil remained in the upper 200 m at that time, though none was detected during the follow-on cruises. Zooplankton communities and environmental conditions following the initial oilrig explosion and subsequent oil spill were compared to zooplankton communities predating the spill to assess the impact of the oil spill on zooplankton communities in the NEGOM.

Many previous studies have demonstrated substantial variability in both environmental conditions and zooplankton communities in the NEGOM, linked to changes in Mississippi River discharge and wind components. Though Mississippi River volumetric discharge rates tend to be higher in spring, westward winds dominate such that many of our sampling stations to the east of the mouth of the Mississippi river exhibited salinity measurements characteristic of ocean water. The influence of Mississippi River plume waters moved eastward over our sampling sites in summer, when eastward winds are most prominent. Sub-regional differences within a season were notable, especially the continental shelf stations that are exposed to river influence regardless of seasonal winds. Eastward winds, increased influence of river discharge on phytoplankton abundances, and higher seawater temperatures produced environmental conditions that supported higher zooplankton abundances and diversity than those observed in spring. Similarly, interannual variability of zooplankton communities were greater in summer than in spring samples. Previous studies have shown that higher temperatures in summer result in faster generations times for many zooplankton species, contributing to higher zooplankton abundances and diversity.

In conclusion, no significant impacts of the Deepwater Horizon oil spill on zooplankton communities in the NEGOM were found. While nearshore stations, PCB01 and PCB02, exhibited anomalously high abundances of the copepod *Centropages* spp. during summer of 2010, spring 2011, and summer 2011, it is difficult to link this event directly to the oil spill. Our post-DWH zooplankton analyses can now serve as a ‘new’ baseline for zooplankton community structure in the NEGOM. However, continued long-term, high frequency sampling of zooplankton and environmental conditions are needed in order to better understand the natural variability of this system relative to future adverse consequences from an environmental perturbation. Information on other oceanic features and phenomena, such as topography, upwelling-events, presence of eddies, and closer consideration of diel vertical migration of some taxa will be required to more effectively address interannual variability of zooplankton beta diversity across the region in addition to river discharge.

6. REFERENCES

Abbriano, R.M., Carranza, M.M., Hogle, *et al.* (2011) Deepwater Horizon oil spill: A review of the planktonic response. *Oceanography,* **24**, 294–301.

Almeda, R., Wambaugh, Z., Chai, C., *et al*. (2013a) Effects of crude oil exposure on bioaccumulation of polycyclic aromatic hydrocarbons and survival of adult and larval stages of gelatinous zooplankton. *PLoS One,* **8(10)**. *http://dx.doi.org/10.1371/ journal.pone.0074476*.

Almeda, R., Wambaugh Z., Wang Z., *et al.* (2013b) Interactions between zooplankton and crude oil: Toxic effects and bioaccumulation of polycyclic aromatic hydrocarbons. *PLoS One* **8(6)**:e67212, *http://dx.doi.org/10.1371/ journal.pone.0067212.*

Anderson, M. J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol.*, **26**, 32–46.

Anderson, M. J., and Willis, T. J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, **84**, 511–525.

Anderson, M. J., Ellingsen, K. E., and McArdle, B. H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecol. Let.,* **9**, 683–693.

Anderson, S.C., Cooper, A.B., Jensen, *et al.* (2017) Improving estimates of population status and trend with superensemble models. *Fish and Fisheries*, **18**, 732–741.

Androulidakis, Y.S. and Kourafalou, V. (2013) On the processes that influence the transport and fate of Mississippi waters under flooding outflow conditions. *Ocean Dyn.,* **63**, 143–164.

Androulidakis, Y. S., Kourafalou, V. H., and Schiller, R. V. (2015) Process studies on the evolution of the Mississippi River plume: Impact of topography, wind and discharge conditions. *Cont. Shelf Res.*, **107**, 33–49.

Banse, K. (1995). Zooplankton: Pivotal role in the control of ocean production. ICES *J. Mar. Sci*., **52**, 265–277.

Batten, S.D., Allen, R.S., and Wotton, C.M., (1998) The effects of the Sea Empress oil spill on the plankton of the southern Irish Sea. *Mar. Pollut. Bull.,* **36**, 764–774.

Belabbassi, L., Chapman, P., Nowlin Jr., *et al.* (2005). Summertime nutrient supply to near-surface waters of the northeastern Gulf of Mexico: 1998, 1999, and 2000. *Gulf Mex. Sci*, **23**, 137–160.

Bianchi, T.S., Cook, R.L., Perdue, E.M., *et al*. (2011) Impacts of diverted freshwater on dissolved organic matter and microbial communities in Barataria Bay, Louisiana, USA. *Mar. Environ. Res.,* **72**, 248–257.

Biggs, D.C. and Ressler, P.H. (2001) Distribution and abundance of phytoplankton, zooplankton, icythyoplankton, and micronekton in the Deepwater Gulf of Mexico. *Gulf Mex. Sci.,* **1**, 7–29.

Biggs, D.C. (1992) Nutrients, plankton, and productivity in a warm-core ring in the western Gulf of Mexico. *J. Geophys. Res.,* **97**, 2143–2154.

Boero, F., Bouillon, J., Gravili, C. *et al*. (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Mar. Ecol. Prog. Ser*., **356**, 299–310.

Bogdanov, V., Sokolov, I., and Khromov, N. (1968) Regions of high biological and commercial productivity in the Gulf of Mexico and Caribbean Sea. *Oceanology*, **8**, 371–380.

BP Gulf Science Data1. (2016) Chemical Analysis of Oil Samples from the Gulf of Mexico and Adjoining States from May 2010 to March 2014. Filename: WaterChemistry_W-01v02-01_xTab. *https://data.gulfresearchinitiative.org/data/BP.x750.000:0005*

Buskey, E.J., White, H.K. and Esbaugh, A.J. *(*2016) Impact of oil spills on marine life in the Gulf of Mexico: effects on plankton, nekton, and deep-sea benthos. *Oceanography,* **29**, 174–181.

Brown, J. H., Gillooly, J. F., Allen, A. P., *et al.* (2004) Toward a metabolic theory of ecology, *Ecology*, **85**, 1771–1789.

Cabioch, L. (1981) Subtidal and pelagic ecological impact. In ‘‘Amoco Cadiz Fate and Effects of the Oil Spill,’’ *Proceedings of the International Symposyum, Centre National pour l'Exploitation des Oceans*, Paris, 475–480.

Carassou, L, Hernandez, F.J., and Graham, W.M. (2015) Corrigendum: Change and recovery of coastal mesozooplankton community structure during the Deepwater Horizon oil spill (2014 *Environ. Res. Lett*. 9 124003). *Environ. Res. Lett.*, **10(4)**.

Chakraborty, S. and Lohrenz, S. E. (2015) Phytoplankton community structure in the river-influenced continental margin of the northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.,* **521**, 31–47.

Chanton, J.P., Cherrier J., Wilson R.M., *et al.* (2012) Radiocarbon evidence that carbon from the Deepwater Horizon spill entered the planktonic food web of the Gulf of Mexico *Environ. Res. Lett.,* **7**, 1–4.

Chassignet, E.P., Hurlburt, H.E., Smedstad, *et al.* (2005). Assessment of data assimilative ocean models in the Gulf of Mexico using ocean color. In W. Sturges, and A. Lugo-Fernandez (Eds.), Circulation in the Gulf of Mexico: Observations and models. *Geophys. Mono. Ser.,* 87–100. Washington, D.C.: AGU

Clark, C., Nnaji, G. A., and Huang, W. (2014) Effects of El-Niño and La-Niña sea surface temperature anomalies on annual precipitations and streamflow discharges in southeastern United States. *J. Coast. Res.*, **68**, 113–120.

Clarke, K.R. and Warwick, R. M. (1994) Change in Marine Communities: An approach to statistical analysis and interpretation. Bourne Press Ltd., Plymouth, 144 p.

Clarke, K.R., and Gorley, R.N. (2015) Primer v7: User Manual/Tutorial. PRIMER-E: Plymouth.

Cohen, J.H., McCormick, L.R., and Burkhardt, S.M. (2014) Effects of dispersant and oil on survival and swimming activity in a marine copepod. *Bull. Environ. Contam. Toxicol.,* **92**, 381–387.

Cushing, D. H. (1975) Marine Ecology and Fisheries, Cambridge University Press, Cambridge, 279 p.

Cushing, D. H. (1995) Population production and regulation in the sea, A fisheries perspective. Cambridge University Press. Cambridge, 357 p.

Cowles, T.J., and J.F. Remillard. (1983) Effects of exposure to sublethal concentration of crude oil on the copepod *Centropages hamatus*: Part I. Feeding and egg production. *Mar. Bio.,* **78**, 45–51.

Dagg, M.J. (1995) Copepod grazing and the fate of phytoplankton in the northern Gulf of Mexico. *Cont. Shelf Res.,* **15**, 1303–1317.

Dagg, M.J. (1988) Physical and biological responses to the passage of a winter storm in the coastal and inner shelf waters of the northern Gulf of Mexico. *Cont. Shelf Res.,* **8**, 167–178.

Dagg, M.J., and Breed, G.A. (2003) Biological effects of Mississippi River nitrogen on the northern Gulf of Mexico—a review and synthesis. *J. Mar. Syst.,* **43**, 133–152.

Dagg, M. J., Ortner, P. B., and Al-Yamani, F. (1988) Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico. *Fish. Bull.*, **86**, 319–330.

Daly, K.L and Smith, W.O. (1993) Physical-Biological Interactions Influencing Marine Plankton Production. *Ann. Rev. Ecol., Evol.System.,* **24**: 555–585.

Daly, K.L., Schwierzke-Wade, L., Dreger, *et al.* (2013) Plankton dynamics following the BP oil spill. Gulf of Mexico Oil Spill & Ecosystem Science Conference, New Orleans, January 23, 2013.

De Caceres, M. and Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology,* **90**, 3566–3574.

Deibel, D. and Paffenhöfer, G. A. (2009) Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). *J. Plankton Res.*, **31**, 1571–1579.

Della Croce, N. and Angelino, M. (1987) Marine cladocera in the Gulf of Mexico and the Caribbean sea. *Cahiers de biologie marine*, **2**.

Dufrene, M. and Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.,* **67**, 345–366.

Deepwater Horizon Natural Resource Damage Assessment Trustees. (2016) Final Programmatic Damage Assessment and Restoration Plan and Final Programmatic Environmental Impact Statement. Retrieved from: *http://www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan.*

El-Sayed, S.Z. (1972) Primary productivity and standing crop of phytoplankton. *Serial Atlas of the Marine Environment,* **22**, 8–13.

Elliot, D.T., Pierson, J.J. and Roman, M.R. (2012) Relationship between environmental conditions and zooplankton community structure during summer hypoxia in the northern Gulf of Mexico. *J. Plankton Res.* **34**, 602–613.

Feng, Y., DiMarco, S. F. and Jackson, G.A. (2012) Relative role of wind forcing and riverine nutrient input on the extent of hypoxia in the northern Gulf of Mexico. *Geophys. Res. Lett.* **39**, L09601, *doi:10.1029/2012GL051192.*

The Federal Interagency Solutions Group, Oil Budget Calculator Science and Engineering Team. (2010) A Report to the National Incident Command: Oil Budget Calculator Deepwater Horizon. *http://www.restorethegulf.gov/sites/default/files/documents/pdf/OilBudgetCalc_Full_HQ-Print_111110.pdf*

Franks, J. S., Christmas, J., Siler, W. L., *et al*. (1972) A Study of Nektonic and Benthic Faunas of the Shallow Gulf of Mexico Off the State of Mississippi As Related to Some Physical, Chemical, and Geological Factors. *Gulf Res. Rept.* **4**, 1–148.

Gilbes, F., Tomas, C., Walsh, J. J., and Müller-Karger, F. E. (1996) An episodic chlorophyll plume on the West Florida Shelf. *Cont. Shelf Res.*, **16**, 1201–1224.

Gilbes, F., Müller-Karger, F. E., and Del Castillo, C. E. (2002). New evidence for the West Florida Shelf plume. *Cont. Shelf Res.* **22**, 2479–2496.

Gillooly, J.F., and Dodson, S.I. (2000) The relationship of neonate mass and incubation temperature to embryonic development time in a range of animal taxa. *J. Zool.,* **251**, 369–375.

Godinez-Dominguez, E. and Freire, J. (2003) Information-theoretic approach for selection spatial and temporal models of community organization. *Mar. Ecol. Prog. Ser.,* **253**, 17–24.

Graham, W. M., Condon R.H., Carmichael, R.H., *et al.* (2010) Oil carbon entered the coastal planktonic food web during the Deepwater Horizon oil spill. *Environ. Res. Lett.,* **5**, 045301. *doi:10.1088/1748-9326/5/4/045301*

Gorsky, G., Ohman M.D., Picheral, M. *et al.* (2010) Digital zooplankton image analysis using the ZooScan integrated system. *J. Plankton Res.*, **32**, 285–303.

Grosjean, P., Picheral, M., Warembourg, C. and Gorsky, G. 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system ICES *Mar. Sci.,* **61**, 518–525.

Guzmán del Pr óo, S. A., Chávez, E.A., Alatriste, F.M., *et al.* (1986) The impact of the Ixtoc-1 oil spill on zooplankton. *J. Plankton Res*. **8**, 557–581.

Harbison, G. R., McAlister, V. L. and Gilmer, R. W. (1986) The response of the salp, *Pegea confoederata*, to high levels of particulate material: Starvation in the midst of plenty. *Limnol. Oceanogr.*, **31**, 371–382.

Hernandez, F., Powers, S., and Graham, W. (2010) Seasonal variability of ichthyoplankton abundance and assemblage composition in the northern Gulf of Mexico off Alabama. *Fish. Bull.* **108***,* 193–207.

Hildebrand, H. H. (1954) A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Pub. *Inst. Mar. Sci., Univ. Tex.* **3**, 233–366.

Hirst, A. G. and Bunker, A. J. (2003) Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol. Oceanogr.*, **48**, 1988–2010.

Hirst, A.G., Roff, J.C., and Lampitt, R.S. (2003) A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Adv. Mar. Biol.*, **44**, 1–142.

Howey, T.W. (1976) Zooplankton of the Gulf of Mexico: Distribution of Displacement Volume, Occurrence of Systematic Groups, Abundance and Diversity Among Copepods. *LSU Historical Dissertations and Theses*. 2968. *https://digitalcommons.lsu.edu/gradschool_disstheses/2968*

Hopkins, T.L. (1982) The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep Sea Res.,* **29**, 1069–1083.

Hopkins, T.L. (1977) Zooplankton distribution in surface waters of Tampa Bay, Florida. Bull. Mar. Sci., **27**, 467–478.

Hopkins, T. L., Milliken, D.M., Bell, *et al.* (1981) The landward distribution of oceanic plankton and micronekton over the west Florida continental shelf as related to their vertical distribution. *J. Plankton. Res.,* **3**, 645–658.

Houde, E.D. and Chitty, N. (1976) Seasonal abundance and distribution of zooplankton, fish eggs, and fish larvae in the eastern Gulf of Mexico. *NOAA Technical Report NMFS SSRF-701, National Oceanic and Atmospheric Administration,* United States Department of Commerce, National Marine Fisheries Service, Seattle, WA.

Huang, W. J., Cai, W. J., Castelao, *et al.* (2013) Effects of a wind-driven cross-shelf large river plume on biological production and CO2 uptake on the Gulf of Mexico during spring. *Limnol. Oceanogr.*, **58**, 1727–1735.

Hu, C., Weisberg, R.H., Liu, Y., *et al.* (2011) Did the northeastern Gulf of Mexico become greener after the Deepwater Horizon oil spill?" *Geophys. Res. Lett.,* **38**, L09601. *doi:10.1029/2011GL047184*

Jochens, A. E., and DiMarco, S. F. (2008). Physical oceanographic conditions in the deepwater Gulf of Mexico in summer 2000–2002. *Deep Sea Res., Part II*, 55(24–26), 2541–2554.

Jochens, A. E., DiMarco, S. F., Nowlin, *et al.* (2002) Northeastern Gulf of Mexico Chemical Oceanography and Hydrography Study: Synthesis Report. *U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA.* **OCS Study MMS 2002-055,** 1–586.

Johansson, S., Larsson, U., and Boehm, P. (1980) The Thesis oil spill. Impact on the pelagic ecosystem. *Mar. Poll. Bull.,* **11***,* 284–293.

Jones, E., and Wiggert, J. (2015) Characterization of a high chlorophyll plume in the northeastern Gulf of Mexico. *Remote Sens. Environ.,* **159**, 152–166.

Jones, D. L. (2017) Fathom Toolbox for MATLAB: software for multivariate ecological and oceanographic data analysis. College of Marine Science, University of South Florida, St. Petersburg, FL, USA. *http://www.marine.usfedu/user/djones/*

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427–2439.

Joye, S.B., Teske, A. P., and Kostka, J.E. (2014) Microbial dynamics following the macondo oil well blowout across Gulf of Mexico environments. *BioScience,* **64**, 766–777.

Kleppel, G.S. (1993) On the diets of calanoid copepods. *Mar. Ecol. Prog. Ser.*, **99**, 183–195.

Knight, C.R. (2014) Taxonomy, Diversity, and Distribution Patterns of Portunid Crab Megalopae in the Northern Gulf of Mexico During Fall of 2003. *University of Southern Mississippi Master's Theses.* Paper 32.

Kourafalou, V. H. and Androulidakis, Y. S. (2013) Influence of Mississippi River induced circulation on the Deepwater Horizon oil spill transport. *J. Geophys. Res.,* **118**, 3823–3842.

Kroes, D. E., Schenk, E.R., Noe, G.B., and Benthem, A.J. (2015) Sediment and nutrient trapping as a result of a temporary Mississippi River floodplain restoration: The Morganza Spillway during the 2011 Mississippi River Flood. *Ecol. Eng.* **82**, 91–102.

Legendre, P. and Anderson, M.J., (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.,* **69**, 1–24.

Legendre, P. and Legendre, L. (2012) Numerical Ecology. *Elsevier, Amsterdam.* Vol **3**. 989 p.

Lester, K.M. (2005) Zooplankton of the West Florida Shelf: Relationships with *Karenia brevis* blooms. Ph.D Dissertation. Department of Marine Science, St. Petersburg, University of South Florida *Theses and Dissertations.* Paper 739. *http://scholarcommons.usf.edu/etd/739.*

Lester, K.M., Heil, C.A., Neely, M.B., *et al.* (2008) Zooplankton and *K. brevis* in the Gulf of Mexico. *Cont. Shelf Res.,* **28**, 19–111.

Lin, K. Y., Sastri, A. R., Gong, G. C., and Hsieh, C. H. (2013). Copepod community growth rates in relation to body size, temperature, and food availability in the East China Sea: a test of metabolic theory of ecology. *Biogeosciences*, **10**, 1877–1892.

Liu, H. and Dagg, M., (2003) Interactions between nutrients, phytoplankton growth, and grazing by micro- and meso-zooplankton in the plume of a large river. *Mar. Ecol. Prog. Ser.,* **258**, 31–42.

Lohrenz, S. E., Dagg, M.J., and Whitledge, T.E. (1990) Enhanced primary production at the plume/oceanic interface of the Mississippi River. *Cont. Shelf Res.,* **10**, 639–664.

Lohrenz, S.E., Fahnenstiel, G.L., Redalje, D.G., *et al.* (1997) Variations in primary production of northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the Mississippi River. *Mar. Ecol. Prog. Ser*., **155**, 45–54.

Lohrenz, S. E., Fahnenstiel, G. L., Redalje, D. G., *et al.* (1999). Nutrients, irradiance, and mixing as factors regulating primary production in coastal waters impacted by the Mississippi River plume. *Cont Shelf Res.*, **19**, 1113–1141.

Lohrenz, S. E., Redalje, D. G., Cai, W., *et al.* (2008) A retrospective analysis of nutrients and phytoplankton productivity in the Mississippi River plume. *Cont. Shelf Res.,* **28**, 1466–1475.

Lyczkowski-Shultz, J., Hanisko, D.S., Sulak, K.J., and Dennis III, G.D. (2004) Characterization of ichthyoplankton within the U.S. Geological Survey's Northeastern Gulf of Mexico study area—based on analysis of Southeast Area Monitoring and Assessment Program (SEAMAP) sampling surveys 1982–1999, NEGOM Ichthyoplankton Synopsis Final Report, U.S. Dept. of the Interior, USGS SIR-2004-5059.

Lyczkowski-Shultz, J. and Hanisko, D.S. (2008) A time series of observations of red snapper larvae from SEAMAP surveys 1982–2003: seasonal occurrence, distribution, abundance and size *in* Patterson, III, *et al.* (eds.). Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, MD. p. 3–23

Martínez-López, B. and Zavala-Hidalgo, J. (2009) Seasonal and interannual variability of cross-shelf transports of chlorophyll in the Gulf of Mexico. *J. Mar. Sys.,* **77**, 1–20.

Mazzocchi, M. G., Christou, E. D., Di Capua, I., *et al.* (2007) Temporal variability of Centropages typicus in the Mediterranean Sea over seasonal-to-decadal scales. *Prog. Oceanogr.*, **72**, 214–232.

McNutt, M. K., Camilli, R., Crone, T. J., *et al.* (2012). Review of flow rate estimates of the Deepwater Horizon oil spill. *PNAS*, **109**, 20260–20267.

Mitra, S. and Bianchi, T. (2003) A preliminary assessment of polycyclic aromatic hydrocarbon distributions in the lower Mississippi River and Gulf of Mexico. *Mar. Chem.,* **82**, 273–288.

Molinero, J. C., Ibanez, F., Souissi, S., *et al.* (2008) Surface patterns of zooplankton spatial variability detected by high frequency sampling in the NW Mediterranean: Role of density fronts. *J. Mar. Syst.*, **69**, 271–282.

Morey, S. L., Schroeder, W.W. O'Brien, and J.J. Zavala-Hidalgo, J. (2003) The annual cycle of riverine influence in the eastern Gulf of Mexico basin. *Geophys. Res. Lett.,***30**, 16.

Morgan, S. G. and Provenzano, A. J. (1979) Development of pelagic larvae and postlarva of *Squilla empusa* (Crustacea, Stomatopoda). *Fish. Bull.,* **77**, 61–90.

Müller -Karger, F. E. (2000) The spring 1998 northeastern Gulf of Mexico (NEGOM) cold water event: Remote sensing evidence for upwelling and for eastward advection of Mississippi water (or: How an errant Loop Current anticyclone took the NEGOM for a spin). *Gulf Mex. Sci.*, **18**, 6.

Müller -Karger, F. (1993) Chapter 8. River discharge variability including satellite-observed plume-dispersal patterns. *Climate change in the Intra-Americas sea* United Nations Environmental Programme (wider Caribbean region) and intergovernmental oceanographic commissions (Caribbean and adjacent regions), p. 162–192.

Müller-Karger, F. E., Walsh, J. J., Evans, R. H., and Meyers, M. B. (1991) On the seasonal phytoplankton concentration and sea surface temperature cycles of the Gulf of Mexico as determined by satellites. *J. Geophys. Res.: Oceans*, **96(C7)**, 12645–12665.

Müller -Karger, F. E., Smith, J.P., Werner, S., *et al.* (2015) Natural variability of surface oceanographic conditions in the oceanic Gulf of Mexico. *Prog. Oceanogr.,* **134**, 54–76.

Murawski, S.A., Fleeger, J.W., Patterson III, *et al.* (2016) How did the Deepwater Horizon oil spill affect coastal and continental shelf ecosystems of the Gulf of Mexico? *Oceanography,* **29**, 160–173.

Nababan, B., Müller-Karger, F., Hu, C., and Biggs, D. (2011) Chlorophyll variability in the northeastern Gulf of Mexico. *Internat. J. Remote Sens.,* **32**, 8373–8391.

National Marine Fisheries Service (2008) Fisheries Economics of the United States. Economics and Sociocultural Status and Status Trends Series, Silver Spring, MD, *http://www.st.nmfs.noaa.gov/st5/publication/fisheries_economics_2008.html.*

Hereinafter cited as NMFS 2010. Job and income figures include commercial fisheries for the entire state of Florida.

Nguyen, T. (2014) Variability of Cross-Slope Flow in the Desoto Canyon Region. Master's Thesis. *Florida State University Libraries, https://diginole.lib.fsu.edu/islandora/object/fsu:252867/datastream/PDF/view*

Nowlin, W. D., Jochens, A.E., Howard, M.K., *et al.* (2000) Hydrographic properties and inferred circulation over the northeastern shelves of the Gulf of Mexico during spring to midsummer of 1998. *Gulf Mex. Sci.,* **18**, 40–54.

Olsen, A.J., Nordtug, T. Altin, D., *et al.* (2013) Effects of dispersed oil on reproduction in the cold water copepod *Calanus finmarchicus (Gunnerus). Environ. Toxicol. Chem.,* **32**, 2045–2055.

Ortner, P.B., Hill, L.C., and Cummings, S.R. (1989) Zooplankton community structure and copepod species composition in the northern Gulf of Mexico. *Cont. Shelf Res.,* **9**, 387–402.

O'Connor, B. S., Müller-Karger, F. E., Nero, R. W., *et al.* (2016). The role of Mississippi River discharge in offshore phytoplankton blooming in the northeastern Gulf of Mexico during August 2010. *Remote Sens. Environ.*, **173**, 133–144.

O'Connor, B.S. (2013) Impacts of the Anomalous Mississippi River Discharge and Diversions on Phytoplankton Blooming in the Northeastern Gulf of Mexico in August 2010. Ph.D. Dissertation. Department of Marine Science, St. Petersburg, University of South Florida. *Theses and Dissertations Paper 739 http://scholarcommons.post-DWH.edu/etd/4736.*

Omori, M. and Ikeda, T. (1976) Methods in Marine Zooplankton Ecology. John Wiley and Sons: New York, 332 p.

Ozhan, K., and Bargu, S. (2014) Distinct responses of Gulf of Mexico phytoplankton communities to crude oil and the dispersant Corexit EC9500A under different nutrient regimes. *Ecotoxicology,* **23**, 370–384.

Ozhan, K., Parsons, M. L., and Bargu, S. (2014) How were phytoplankton affected by the Deepwater Horizon oil spill? *BioSciences*, **64**, 829–836.

Paffenhöfer, G.A. (1984) Food ingestion by the marine planktonic copepod *Paracalanus* in relation to abundance and size distribution of food. *Mar. Bio.*, **80**, 323–333.

Paffenhöfer, G.A., and Knowles, S.C. (1980) Omnivorousness in marine planktonic copepods. *J. Plankton Res.*, **2**, 355–365.

Parsons, M.L., Morrison, W., Rabalais, N.N., *et al.* (2015) Phytoplankton and the Macondo oil spill: A comparison of the 2010 phytoplankton assemblage to baseline conditions on the Louisiana shelf. *Enviro. Poll.*, **207**, 152–160.

Penela-Arenaz M, J. and Bellas, E. Vazquez. (2009) Effects of the Prestige oil spill on the biota of NW Spain: 5 years of learning. *Adv. Mar. Bio.,* **56**, 365–396

Qian, Y., Jochens, A.E., Kennicutt II, *et al.* (2003) Spatial and temporal variability of phytoplankton biomass and community structure over the continental margin of the northeast Gulf of Mexico based on pigment analysis. *Cont. Shelf Res.,* **23**, 1–17.

Rathmell, K. (2007) The influence of the Loop Current on the diversity, abundance, and distribution of zooplankton in the Gulf of Mexico. University of South Florida, *Graduate Theses and Dissertations.* Paper 2334. *http://scholarcommons.post-DWH.edu/etd/2334.*

Redalje, D.G., Lohrenz, S.E., and Fahnensteil, G.L., (1994) The relationship between primary production and the vertical export of particulate organic matter in a river-impacted coastal system. *Estuaries,* **17**, 829–838.

Reddy C.M., Arey, J.S., Seewald, J.S., *et al.* (2012) Composition and fate of gas and oil released to the water column during the *Deepwater Horizon* oil spill. *PNAS,* **109**, 20229–20234.

Riley, G. A. (1937) The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. *J. Mar. Res.*, **1**, 60–74.

Salisbury, J.E., Campbell, J.W., Linder, *et al.* (2004) On the seasonal correlation of surface particle fields with wind stress and Mississippi discharge in the northern Gulf of Mexico. *Deep-Sea Res. II*, **51**, 1187–1203.

Samain, J. F., Moal, J., Coum, A., *et al.* (1980) Effects of the "Amoco Cadiz" oil spill on zooplankton. *Helgoländer Meeresuntersuchungen*, **33**:BF02414748, *https://doi.org/10.1007/BF02414748*

Squires, A. P. (1984) The distribution and ecology of zooplankton in Charlotte Harbor, Florida. *Doctoral dissertation*, University of South Florida, Tampa.

Schiller, R.V., Kourafalou, V.H., Hogan, P., and Walker, N. D. (2011) The dynamics of the Mississippi River plume: Impact of topography, wind and offshore forcing on the fate of plume waters. *J. Geophys. Res.,* **116**, C06029, *doi:10.1029/2010JC006883*

SEAMAP Field Operations Manual for Collection of Data. (2001) National Marine Fisheries Service and Gulf States Fisheries Commission *http://sedarweb.org/docs/wsupp/S38_RD_15_SEAMAP_MANUAL_OCT01.pdf*

State of Louisiana (2010) Office of Coastal Protection and Restoration officials open Davis Pond diversion to full capacity to help curb oil penetration into coastal marshes. *http://emergency.louisiana.gov/Releases/07242010-alert.html.coastal.louisiana.gov/index.cfm?md=newsroom&tmp=detail&articleID=1216*

Sturges, W. and Leben, R. (2000) Frequency of ring separations from the Loop Current in the Gulf of Mexico: a revised estimate. *J. Phys. Oceanogr.,* **30**, 1814–1819.

Taucher, J., Haunost, M., Boxhammer, T., *et al.* (2017) Influence of ocean acidification on plankton community structure during a winter-to-summer succession: An imaging approach indicates that copepods can benefit from elevated CO_2 via indirect food web effects. *PLoS ONE,* **12**, e0169737. *doi:10.1371/journal.pone.0169737*

Turner, J.T. (1984) Feeding Ecology of Some Zooplankters that are Important Prey Items of Larval Fish. NOAA Technical Report National Marine Fisheries 7, Washington, D.C., 34 p.

Turner, J.T, and Tester, P.A. (1989) Zooplankton Feeding Ecology: Copepod grazing during an expatriate red tide., *in* Cosper *et al. (eds.)* Novel Phytoplankton Blooms: Causes and impacts of recurrent brown tides and other unusual blooms. Springer, Berlin, p. 359–374.

USACE (2010) Caernarvon Freshwater Diversion Project. United States Army Corps of Engineers New Orleans District. *http://www.mvn.usace.army.mil/prj/caernarvon/caernarvon.htm*

USACE (2013) Mississippi River Flood of 2011 Report. United States Army Corp of Engineers. *http://www.mvdusace.army.mil/Missions/FloodRiskManagement/RegionalFloodRiskManagementProgram/MRTPostFloodReport.aspx.*

U.S. Geological Survey (2016) National Water Information System data available on the World Wide Web (USGS Water Data for the Nation) *https://waterdata.usgs.gov/nwis/rt*

Varela, M., Bode, A., Lorenzo, J., *et al.* (2006) The effect of the Prestige oil spill on the plankton in the N-NW Spanish coast. *Mar. Poll. Bull.,* **53**, 272–286.

Wade, T.L., Ii, M.C.K and Brooks, J.M. (1989) Gulf of Mexico hydrocarbon seep communities: Part III. Aromatic hydrocarbon concentrations in organisms, sediments and water. *Mar. Environ. Res.,* **27**, 19–30.

Walker, N. D. (1996). Satellite assessment of Mississippi River plume variability: causes and predictability. *Remote Sens. Environ.,* **58**, 21–35.

Walker N.D., Wiseman, W.J., Rouse, L.J., and Babin, A. (2005) Effects of river discharge, wind stress, and slope eddies on circulation and the satellite-observed structure of the Mississippi River plume. *J. Coastal Res.*, **21**, 1228–1244

Walsh, J. J. (1988) On the Nature of Continental Shelves, Academic, San Diego, California, 508 p.

Walsh, B. M. (2012). Zooplankton population dynamics in relation to the red tide dinoflagellate *Karenia brevis* on the West Florida Shelf of the Gulf of Mexico. *Doctoral dissertation*, University of Maryland Center for Environmental Science Horn Point Laboratory.

Wang, D. P., Oey, L.Y., Ezer, T., and Hamilton, P. (2003). Near-surface currents in DeSoto Canyon (1997–99): Comparison of current meters, satellite observation, and model simulation. *J. Phys. Oceanogr.,* **33**, 313–326.

Wawrik, B., Paul, J.H., Campbell, L., *et al.* (2003) Vertical structure of the phytoplankton community associated with a coastal plume in the Gulf of Mexico. *Mar. Ecol. Prog. Ser.*, **251**, 87–101.

Weisberg, R. H., Zheng, L., Liu, Y., *et al.* (2016). Did Deepwater Horizon hydrocarbons transit to the west Florida continental shelf? *Deep Sea Res. Part II: Topical Studies in Oceanography*, **129**, 259–272.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.*, **30**, 280–338.

Zavala-Hidalgo, J., Mateos-Jasso, A., Morey, S. and Martinez-Lopez, B. (2014) The response of the Gulf of Mexico to wind and heat flux forcing: What has been learned in recent years? *Atmósfera*, **27**, 317–334.

Zang, Z., Xue, Z.G., Bao, S., *et al.* (2018) Numerical study of sediment dynamics during hurricane Gustav. *Ocean Modelling*, **126**, 29–42.

Zimmerman, R. A. and Biggs, D. C. (1999). Patterns of distribution of sound-scattering zooplankton in warm-and cold-core eddies in the Gulf of Mexico, from a narrowband acoustic Doppler current profiler survey. *J. Geophys. Res.: Oceans*, **104**, 5251–5262.

7. APPENDICES

Table 13. Table of pre-DWH untransformed zooplankton taxa and abundances by station name (SM), month (mm), year (yy), station (Bnnn), local time (central standard time), and location (latitude and longitude) of collection, taxa categories, and abundances (#/m^3) used in pre-DWH analyses

Station Name	Date sampled	Latitude	Longitude	Time (CST)
SM0905B322	9/11/05	N29 ° 15.13	W87 ° 59.90	1:25:00
SM0907B167	9/17/07	N29 ° 58.49	W86 ° 01.27	0:04:00
SM0906B167	9/21/06	N30 ° 00.06	W86 ° 00.68	8:27:00
SM0906B169	9/21/06	N29 ° 29.28	W86 ° 29.41	3:07:00
SM0907B169	9/16/07	N29 ° 29.56	W86 ° 30.74	14:04:00
SM0908B169	9/29/08	N29 ° 29.67	W86 ° 30.30	19:57:00
SM0908B167	9/29/08	N29 ° 59.43	W86 ° 00.09	11:39:00
SM0909B167	9/9/09	N29 ° 59.38	W85 ° 59.33	10:15:00
SM0909B169	9/5/09	N29 ° 30.36	W86 ° 30.19	6:58:00
SM0309B001	3/4/09	N29 ° 00.13	W88 ° 00.01	7:35:00
SM0309B322	3/3/09	N29 ° 14.96	W87 ° 59.99	14:40:00
SM0506B001	5/6/06	N28 ° 59.54	W87 ° 59.37	21:42:00
SM0507B001	5/28/07	N29 ° 00.56	W88 ° 00.56	23:02:00
SM0507B081	5/28/07	N28 ° 30.49	W88 ° 00.49	16:25:00
SM0307B322	3/28/07	N29 ° 15.48	W88 ° 00.83	22:40:00
SM0307B175	3/28/07	N29 ° 00.31	W87 ° 30.88	16:33:00
SM0307B171	3/18/07	N29 ° 30.00	W87 ° 00.02	7:47:00
SM0307B169	3/18/07	N28 ° 29.91	W86 ° 30.75	11:32:00
SM0309B169	3/13/09	N29 ° 30.45	W86 ° 29.52	21:24:00
SM0509B001	5/29/09	N28 ° 59.95	W87 ° 59.35	0:14:00
SM0508B001	5/30/08	N29 ° 00.06	W88 ° 00.30	0:05:00
SM0505B171	5/11/05	N29 ° 30.00	W87 ° 00.00	19:24:00
SM0505B001	5/29/05	N28 ° 59.75	W87 ° 59.61	23:47:00
SM0505B001	5/7/05	N29 ° 00.42	W88 ° 00.37	16:14:00

Centropages spp.	*Lucicutia* spp.	*Temora* spp.	*Oithona* spp.	*Oncaea* spp.	*Corycaeus* spp.	*Sapphirina* spp.
1.17	0.59	1.76	12.30	3.32	6.63	0.59
2.07	0.00	0.89	1.48	0.30	0.00	0.00
20.09	16.37	1.49	8.93	0.74	0.00	7.44
2.97	0.81	4.86	4.05	0.54	2.43	0.81
0.00	3.73	1.98	7.33	5.36	8.38	2.79
0.20	1.20	3.40	12.20	1.00	5.20	2.20
32.00	5.16	20.99	7.91	2.41	8.60	1.03
43.17	0.00	3.05	77.71	16.76	34.54	2.03
0.72	1.17	0.63	18.16	8.54	8.99	0.72
0.00	1.95	1.20	24.51	13.22	7.97	0.15
0.00	4.15	38.35	20.73	33.17	44.57	0.00
0.06	0.36	0.42	3.90	1.74	1.80	0.60
0.58	0.12	0.69	8.98	1.38	9.67	1.04
0.19	0.56	4.11	15.86	2.05	7.84	3.73
0.00	2.69	12.58	45.38	3.60	8.08	2.69
0.00	2.89	2.89	9.04	0.36	5.42	1.81
0.00	3.83	1.81	6.44	1.21	3.43	0.40
5.47	1.26	5.47	28.64	3.37	1.68	1.26
1.63	2.29	8.49	32.33	12.73	11.76	4.57
26.54	4.71	0.74	24.81	4.22	4.96	0.25
0.00	1.34	0.56	9.17	1.01	3.24	0.22
4.19	0.60	11.36	13.76	9.57	13.76	0.00
0.00	2.69	4.61	21.33	24.03	16.91	2.31
0.00	11.91	0.99	25.55	9.67	5.95	0.74

Candacia spp.	*Eucalanus* spp.	Unknown Copepod	Unknown Calanoid	Amphipoda	Cladocera	Crustacean Naupli
0.78	11.32	0.00	33.37	2.15	0.00	0.20
0.00	2.07	1.78	5.04	0.01	1.48	0.00
0.00	21.58	5.95	59.53	8.19	11.16	0.00
1.35	14.31	2.70	22.69	3.78	7.83	0.00
0.58	3.49	1.05	25.60	0.56	0.00	0.00
1.20	4.40	0.80	28.80	1.60	0.60	0.00
0.00	12.39	1.38	32.00	9.32	0.34	0.00
0.00	77.71	14.73	127.49	19.81	47.24	0.51
0.18	1.98	0.99	25.80	0.72	1.53	0.00
0.45	3.76	2.40	49.14	0.65	0.00	2.40
2.07	40.42	16.58	295.39	10.38	0.00	19.69
0.00	1.98	2.64	23.79	1.02	0.00	0.00
0.12	8.06	0.81	30.51	2.20	3.45	0.00
0.93	6.16	1.68	44.60	1.68	0.19	0.00
0.00	44.02	3.14	60.18	2.73	0.00	3.14
0.00	22.06	1.45	67.26	2.23	0.36	0.72
0.20	36.06	3.62	48.54	2.87	0.00	0.00
0.42	94.32	5.05	77.05	9.32	0.00	0.00
0.98	57.47	6.20	98.94	1.98	0.00	0.00
0.00	9.67	1.74	50.85	1.49	0.00	0.50
0.00	6.38	0.34	19.13	0.56	0.00	0.00
0.60	46.07	7.18	107.07	12.58	0.00	0.00
0.00	13.26	1.54	80.15	2.69	0.38	1.54
0.00	16.37	0.25	68.47	1.99	0.99	0.50

Misc. Decapod	Crab Zoea	Crab Megalops	Phyllosoma	Lucifer	Euphausiids (Non-Larval)
0.00	0.00	0.00	0.00	0.20	0.40
0.44	0.51	0.04	0.00	0.89	0.00
2.98	4.47	0.00	0.00	0.74	0.00
0.82	2.97	0.27	0.00	0.54	0.54
0.03	0.13	0.07	0.00	0.00	0.97
0.40	1.40	0.20	0.01	0.20	0.20
2.41	4.47	0.69	0.10	3.81	0.00
0.51	15.24	0.51	0.00	1.52	0.00
0.37	0.00	0.00	0.00	0.09	0.90
0.19	0.00	0.02	0.00	0.04	0.09
0.01	1.04	0.02	0.00	10.36	0.15
0.12	0.00	0.00	0.00	0.18	0.48
0.47	0.93	0.00	0.00	0.12	0.23
0.38	0.19	0.00	0.00	2.05	0.56
0.02	0.92	0.00	0.00	1.80	0.46
0.00	0.36	0.00	0.00	9.04	0.00
0.61	0.00	0.00	0.00	0.00	2.34
1.73	1.29	0.05	0.00	2.11	0.44
0.33	0.98	2.61	0.00	6.20	0.00
0.00	1.49	0.25	0.00	1.74	0.00
0.91	0.00	0.00	0.00	0.00	0.01
0.60	3.07	0.70	0.00	21.59	0.03
0.58	0.38	0.19	0.00	4.61	0.38
0.25	0.00	0.50	0.00	1.49	0.01

Unknown Young Malacostraca	Stomatopoda	Misc. Mysidae	Ostracoda	Echinoderm Larvae and Juveniles
3.51	0.00	0.00	26.15	0.20
2.07	0.07	0.00	1.78	0.59
6.70	1.49	0.74	64.00	8.19
2.97	0.27	0.00	101.00	1.62
1.98	0.01	0.25	8.56	1.98
3.00	0.02	0.00	91.00	1.60
3.10	3.85	0.00	356.13	15.83
11.68	1.02	2.03	1004.70	9.65
1.71	0.00	0.27	5.93	5.48
1.50	0.00	0.15	5.11	1.05
16.59	0.00	0.01	6.22	1.04
1.62	0.00	0.00	2.04	0.72
1.61	0.00	0.00	4.95	0.35
8.21	0.00	0.00	3.17	0.19
6.29	0.00	0.00	5.39	2.25
4.70	0.00	0.36	5.42	0.36
1.81	0.00	0.00	6.04	1.01
2.11	0.00	0.01	10.11	1.26
4.57	0.00	0.00	3.92	0.65
6.95	0.00	0.99	6.95	0.25
2.46	1.00	0.00	1.68	1.01
10.77	0.05	1.79	7.18	0.60
47.47	0.77	0.00	9.42	0.96
7.69	0.25	0.50	8.93	0.74

Heteropod, Atlantidae	Heteropod, Non-Atlantidae	Bivalves	Pteropod *Limacina* spp.	Pteropod *Cavolinia* spp.
0.00	0.00	1.17	0.78	0.00
0.00	0.00	19.56	2.07	0.00
2.98	0.00	16.37	8.19	0.00
1.35	0.00	1.62	4.59	0.27
0.00	0.00	0.12	0.59	0.01
1.00	0.00	0.40	18.00	0.00
1.38	0.00	7.91	14.11	0.00
1.02	0.00	12.19	20.83	0.00
0.00	0.00	0.27	1.17	0.00
0.00	0.00	1.50	4.36	0.00
0.00	0.00	0.00	6.22	0.00
0.06	0.00	0.30	0.30	0.00
0.00	0.01	0.00	1.73	0.00
0.76	0.00	0.56	1.31	0.00
0.45	0.00	0.45	2.25	0.01
0.37	0.00	0.36	0.72	0.01
0.21	0.00	0.41	2.01	0.00
0.44	0.00	0.42	0.42	0.02
0.33	0.00	0.98	0.65	0.00
0.00	0.00	0.74	2.48	0.00
0.00	0.00	0.00	0.11	0.00
0.05	0.00	0.60	1.21	0.00
0.58	0.00	0.19	10.95	0.00
0.25	0.00	0.50	1.24	0.00

Pteropod conical	Misc. Pteropod	Cephalopoda	Cyphonautes	Chaetognatha	Misc. Gelationous	Siphonophora
0.98	0.20	0.20	0.39	6.83	0.00	2.93
0.00	0.59	0.00	0.00	4.74	0.00	0.00
17.86	0.00	0.00	0.00	37.21	0.01	9.67
1.35	0.00	0.00	0.00	12.69	0.00	0.81
0.94	0.00	0.12	0.12	12.23	0.00	3.39
0.80	0.80	0.00	1.80	24.00	0.00	9.40
2.08	0.69	0.00	0.00	65.72	0.72	62.62
6.10	0.00	0.00	3.05	76.70	0.00	20.83
0.00	0.00	0.00	0.72	9.26	0.00	2.97
0.31	0.00	0.00	0.30	6.76	0.00	1.05
5.18	2.07	0.00	3.11	19.70	0.00	7.26
0.18	0.00	0.00	0.12	4.91	0.00	0.48
1.50	0.00	0.00	0.58	14.51	0.00	1.61
3.92	0.00	0.00	0.00	24.63	0.00	2.43
1.80	0.00	0.01	0.45	26.05	0.00	5.41
0.00	0.00	0.00	0.00	8.32	0.00	0.73
5.90	0.00	0.00	0.00	11.28	0.00	5.03
3.85	0.42	0.00	0.00	22.32	0.00	22.32
2.94	0.33	0.00	0.33	23.18	0.00	11.46
0.74	0.00	1.30	0.00	13.89	0.25	5.71
0.45	0.00	0.00	0.00	17.21	1.00	3.13
29.31	0.60	0.00	0.00	65.21	0.00	2.39
4.42	0.00	0.00	0.77	17.49	0.00	2.50
1.74	0.00	0.00	0.74	23.81	0.00	3.47

Doliolidae	Appendicularia	Salpidae	Eggs	Fish Larvae	Hydroid Polyps	Polychaeta
1.56	2.54	1.37	0.39	0.21	0.39	1.37
0.00	2.67	0.30	0.30	0.38	2.67	2.37
6.70	23.81	17.87	4.47	2.27	1.49	2.23
1.08	1.62	1.08	3.78	2.71	0.28	0.81
0.81	1.40	0.47	0.47	0.80	0.14	0.74
0.80	7.20	2.60	8.20	1.61	0.22	1.20
2.06	4.13	42.67	28.56	1.76	0.35	1.47
24.41	19.81	12.19	3.05	1.17	0.52	7.13
0.27	3.42	0.00	0.90	0.83	0.18	0.45
0.01	4.36	0.00	0.90	0.20	0.16	1.50
16.58	20.73	8.29	0.00	0.11	1.04	4.15
0.12	0.42	0.18	0.60	0.12	0.06	0.24
0.12	1.04	0.12	1.73	0.21	0.14	1.73
2.24	2.05	1.68	0.56	1.18	0.20	1.13
5.39	21.56	10.79	0.90	1.45	0.02	2.25
3.25	0.00	1.45	3.25	0.79	0.01	1.45
1.02	0.20	4.63	1.61	0.28	1.02	1.61
3.37	5.05	8.01	5.47	1.14	3.82	2.62
6.20	8.16	44.73	1.31	1.63	1.31	0.34
8.93	14.39	0.74	3.47	0.50	0.00	0.00
0.23	2.24	0.45	0.11	0.34	0.23	0.67
0.00	4.19	0.60	2.39	0.27	0.63	1.20
2.50	5.77	1.92	1.73	1.16	0.20	1.73
1.24	1.98	0.25	1.49	1.24	0.99	0.25

Table 14. Table of post-DWH untransformed zooplankton taxa and abundances by station (WB = R/V Weatherbird), month (mm), year (yy), transect (PCB or DSH), site number (nn) or DWH, which is the Deepwater Horizon explosion site, local time (central standard time), location of collection (latitude and longitude), taxa categories, and abundances (#/m^3) used in pre-DWH analyses

Station Name	Date Sampled	Latitude	Longitude	Time (CST)	*Centropages* spp.	*Lucicutia* spp.
WB0814PCB03	8/11/14	29 39.441	86 27.471	5:52	213.27	44.43
WB0814PCB02	8/11/14	29 44.145	86 20.901	9:44	368.88	17.29
WB0814PCB01	8/11/14	29 51.310	86 08.620	14:38	160.06	0.00
WB0813DWH	8/7/13	28 45.791	88 23.488	22:05	122.48	35.33
WB0813DSH10	8/8/13	28 58.111	87 51.526	9:05	54.68	12.26
WB0813DSH07	8/9/13	29 15.668	87 43.720	5:47	46.38	33.73
WB0813PCB06	8/9/13	29 07.319	87 16.033	14:15	0.86	10.76
WB0813PCB05	8/10/13	29 26.694	86 46.005	0:18	39.36	7.20
WB0813PCB03	8/10/13	29 44.009	86 20.713	14:42	52.47	3.28
WB0813PCB01	8/11/13	30 03.565	85 50.012	8:26	496.49	0.00
WB0812DWH	8/8/12	28 44.480	88 23.390	3:13	1.77	8.84
WB0812DSH10	8/8/12	28 58.324	87 51.949	14:57	9.55	12.73
WB0812DSH09	8/7/12	28 37.788	87 52.666	14:54	4.14	3.45
WB0812DSH08	8/9/12	29 07.452	87 52.213	3:19	7.01	5.26
WB0812DSH07	8/9/12	29 15.344	87 43.602	12:43	23.75	11.08
WB0812PCB11	8/7/12	28 48.160	87 18.648	1:22	1.42	5.66
WB0812PCB06	8/6/12	29 07.167	87 15.901	13:39	1.54	12.35
WB0812PCB05	8/6/12	29 26.045	86 46.453	0:55	6.16	12.31
WB0812PCB04	8/5/12	29 33.473	86 35.122	17:03	7.13	16.41
WB0812PCB03	8/5/12	29 44.170	86 20.879	10:51	93.53	0.00
WB0812PCB02	8/5/12	29 50.275	86 11.551	6:41	179.73	0.00
WB0812PCB01	8/4/12	30 03.222	85 49.884	23:39	357.24	0.00
WB0911DSH10	9/25/11	28 59.065	87 51.396	5:32	119.35	18.21

Temora spp.	*Oithona* spp.	*Oncaea* spp.	*Corycaeus* spp.	*Sapphirina* spp.	*Candacia* spp.	*Eucalanus* spp.	*Acartia* spp.
31.10	28.88	71.09	24.44	2.22	6.66	68.87	8.89
0.00	28.82	57.64	69.17	5.76	0.00	144.09	25.94
0.00	0.00	2.67	58.69	0.00	0.00	125.38	5.34
4.71	25.91	11.78	2.36	2.36	0.00	91.86	5.49
7.54	41.48	8.49	12.26	3.77	0.94	23.57	155.45
0.00	33.73	12.65	4.22	2.11	0.00	75.90	6.60
3.44	13.77	3.87	12.48	1.29	1.72	6.02	177.10
2.88	2.40	1.92	1.44	1.44	0.00	17.28	1.29
39.35	26.24	4.92	42.63	3.28	0.00	27.88	16.32
3.71	0.00	5.56	83.37	1.85	0.00	79.66	16.40
8.84	17.68	14.15	18.57	0.88	2.65	1.77	0.00
3.18	28.65	39.00	32.63	1.59	2.39	11.94	0.88
3.45	26.60	14.16	15.89	0.69	4.14	2.42	0.80
5.26	39.45	28.05	12.27	0.00	1.75	16.66	3.80
11.08	66.51	36.42	31.67	0.00	0.00	22.96	2.63
5.66	29.72	16.98	33.26	4.25	1.42	6.37	3.96
15.44	42.46	15.44	23.93	0.77	1.54	3.86	0.71
3.08	17.70	10.77	10.77	0.00	2.31	1.54	3.86
11.42	52.80	14.27	26.40	0.71	5.71	13.56	2.31
6.88	50.20	5.50	29.57	2.75	0.69	6.19	2.85
18.34	20.17	5.50	40.35	1.83	0.00	115.54	2.06
14.29	10.72	10.72	142.90	0.00	0.00	153.61	0.00
155.76	48.55	30.34	30.34	5.06	3.03	64.73	0.00

Foraminifera	Radiolarians	Amphipoda	Cladocera	Crustacean Naupli	Misc. Decapod	Crab Zoea	Crab Megalops
8.90	0.00	11.72	0.00	6.32	23.51	2.54	1.04
11.53	0.00	0.36	0.00	25.42	44.02	0.39	0.02
8.00	0.00	1.38	0.00	11.42	12.05	0.08	0.00
0.00	2.36	2.64	0.00	5.12	13.39	4.84	2.59
0.00	0.00	2.98	1.89	5.89	7.22	0.98	0.02
2.11	2.11	8.53	0.00	4.39	5.22	0.17	0.04
2.17	2.16	0.96	0.00	0.10	1.57	0.02	0.00
0.00	0.00	3.11	0.00	1.81	4.41	0.16	0.00
9.91	0.00	5.30	0.00	7.51	10.75	0.23	0.00
13.05	0.00	4.11	0.03	15.63	36.58	0.03	0.00
5.30	2.65	2.89	0.00	0.89	2.09	0.06	0.03
2.41	1.60	2.43	0.00	0.00	2.10	0.03	0.13
1.38	1.04	0.49	0.00	0.70	1.33	0.04	0.11
1.75	0.00	0.97	0.00	0.00	3.53	0.92	0.13
0.40	0.80	0.38	0.80	0.80	16.63	0.23	0.02
7.08	0.71	0.11	0.00	0.71	5.49	0.78	0.07
0.77	2.32	0.87	0.77	0.00	2.54	0.05	0.02
0.00	0.00	1.84	0.00	0.01	0.90	0.07	0.08
1.43	0.00	1.60	0.72	2.86	9.15	0.03	0.04
10.33	0.69	2.93	5.52	0.69	7.01	0.07	0.09
1.83	0.00	3.91	9.24	1.85	20.86	7.42	0.16
0.00	0.00	9.82	0.00	0.00	8.57	0.03	0.31
3.05	1.02	7.12	41.57	1.01	6.42	0.01	0.44

Phyllosoma	Lucifer	Euphausiids (Non-Larval)	Stomatopoda	Misc. Mysidae	Ostracoda
0.00	2.29	0.10	74.21	0.01	160.51
0.01	0.00	3.14	102.13	0.00	101.18
0.00	0.00	0.00	44.10	0.00	227.22
0.00	0.74	0.02	32.25	0.00	9.52
0.00	1.16	0.03	27.09	0.00	6.65
0.00	1.05	0.04	26.21	0.00	12.70
0.00	1.59	0.01	10.00	0.00	4.76
0.00	0.45	0.04	12.31	0.00	7.73
0.00	0.02	0.03	48.24	0.00	517.63
0.00	0.00	3.85	97.61	0.00	31.73
0.00	0.12	4.27	0.09	0.00	12.48
0.00	0.19	5.99	0.12	0.01	121.21
0.00	0.30	3.48	0.43	0.00	40.95
0.00	0.94	6.86	0.12	0.00	19.38
0.00	1.95	1.76	0.25	0.00	7.39
0.01	0.10	5.33	0.06	0.00	66.86
0.00	0.88	1.75	0.04	0.00	61.10
0.00	0.21	2.99	0.17	0.00	18.60
0.01	0.81	0.85	0.12	0.00	61.58
0.01	0.62	0.05	0.26	0.00	33.23
0.00	5.89	0.06	0.97	0.00	0.00
0.00	0.73	0.00	0.11	48.09	215.02
0.00	1.17	5.58	0.06	0.00	23.32

Echinoderm Larvae and Juveniles	Holothuroidea	Heteropod, Atlantidae	Heteropod, Non-Atlantidae	Bivalves
0.00	0.00	0.01	0.00	2.22
0.00	0.00	5.78	0.00	5.76
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.01	0.00
0.00	0.00	0.00	0.01	0.00
0.00	0.00	0.01	0.00	4.22
5.61	0.00	0.00	0.00	0.00
0.48	0.00	0.48	0.00	0.00
0.01	0.00	3.44	0.00	4.93
37.75	0.00	0.00	0.00	7.44
0.91	0.00	0.01	0.00	0.88
0.80	0.80	0.80	0.00	0.80
0.00	0.69	0.35	0.00	0.00
0.01	0.00	0.00	0.00	2.63
0.80	0.00	0.20	0.00	1.60
5.71	0.00	0.01	0.00	0.01
1.55	0.77	0.01	0.00	0.00
2.40	0.00	0.01	0.00	0.01
2.93	0.71	0.01	0.00	1.43
8.46	0.00	0.10	0.00	1.40
2.19	1.85	1.86	0.00	3.68
7.17	0.00	0.00	0.00	21.43
4.07	0.01	0.00	0.00	4.05

Misc. Gastropods	Pteropod, *Limacina* spp.	Pteropod, *Cavolinia* spp.	Pteropod, conical	Misc. Pteropod	Cephalopoda
2.23	8.92	0.05	0.06	0.00	0.03
8.69	5.81	0.07	0.02	0.00	0.00
0.00	2.67	0.13	0.29	0.00	0.00
0.01	7.10	0.00	0.05	0.00	0.01
0.00	0.00	0.01	0.01	0.00	0.00
0.00	0.02	0.00	0.02	0.00	0.01
0.87	0.01	0.00	0.00	0.00	0.01
0.00	0.00	0.01	0.04	0.00	0.01
9.84	47.66	0.18	30.23	0.06	0.04
11.12	18.61	0.03	26.40	0.01	0.00
0.00	8.91	0.03	4.49	0.00	0.02
0.00	14.36	0.00	4.81	0.00	0.01
0.00	4.16	0.03	4.59	0.88	0.01
0.00	10.56	0.00	0.01	0.00	0.01
1.60	2.20	0.00	0.41	0.00	0.01
0.71	9.25	0.02	2.90	0.00	0.03
0.01	3.87	0.00	4.64	0.00	0.01
0.00	6.19	0.02	3.92	0.72	0.01
0.00	5.01	0.01	3.60	0.69	0.00
1.38	36.89	0.53	5.75	0.00	0.02
0.04	14.76	0.32	0.04	0.00	0.00
0.03	3.63	0.00	0.00	0.00	0.06
1.02	5.06	0.00	0.01	0.00	0.03

Cyphonautes	Chaetognatha	Misc. Gelationous	Siphonophora	Doliolidae	Appendicularia	Salpidae	Eggs
0.00	69.28	2.22	9.01	4.65	0.00	31.10	2.23
0.01	141.92	8.71	3.12	8.89	37.69	31.73	2.89
0.00	109.63	0.00	14.21	3.50	34.68	0.00	2.67
2.38	21.55	9.74	4.75	80.62	2.41	0.01	0.00
0.96	20.90	1.97	2.89	45.50	9.43	0.95	0.94
2.11	31.94	4.31	8.49	6.40	10.56	0.01	0.00
3.03	21.67	0.05	3.04	2.17	13.79	2.60	1.72
0.00	1.52	2.59	0.50	26.73	0.48	0.49	0.96
1.66	44.75	4.95	3.35	8.26	16.49	0.01	0.00
5.56	33.84	28.22	2.23	0.00	18.79	0.00	3.71
17.92	20.73	1.80	10.71	1.81	14.33	0.02	0.00
15.20	26.67	0.86	13.64	3.99	20.87	0.80	0.00
7.29	6.32	0.74	9.11	1.39	21.92	0.35	0.35
24.77	16.44	0.91	2.73	4.39	7.10	0.07	0.00
1.40	32.06	1.66	1.03	1.23	5.21	0.00	0.20
16.48	32.43	2.90	2.87	3.58	13.63	0.72	0.71
15.48	42.63	0.02	3.91	0.77	15.49	0.00	0.00
12.48	17.33	1.64	5.49	2.34	9.39	1.55	0.01
27.95	35.39	3.19	8.65	5.72	37.98	0.01	0.00
19.46	28.09	2.86	8.44	4.87	6.91	0.73	0.02
37.24	52.58	12.92	18.81	16.86	9.53	0.27	5.50
3.63	90.96	7.56	3.60	0.14	25.37	0.00	21.57
1.02	31.65	9.19	19.31	69.01	47.76	1.02	0.00

Fish Larvae	Polychaeta	Hemichordata, *Ptychodera flava* (krohns larvae)
2.30	2.25	0.01
6.85	2.25	0.01
0.06	0.12	0.00
0.13	2.83	0.00
1.32	2.73	0.00
0.11	3.88	0.94
1.84	4.30	0.01
0.08	1.74	0.44
0.33	0.07	0.00
0.20	1.71	0.01
0.41	5.59	0.00
0.23	4.44	0.00
0.20	0.83	0.00
0.23	1.40	1.04
0.97	0.90	0.00
0.50	2.64	0.00
1.13	4.31	0.00
0.45	5.42	0.00
1.72	5.51	0.00
2.33	7.93	0.00
4.47	0.88	0.69
4.15	9.59	0.00
1.36	0.00	0.00

Station Name	Date Sampled	Latitude	Longitude	Time (CST)	*Centropages* spp.	*Lucicutia* spp.
WB0911DSH09	9/22/11	28 38.637	87 51.992	0:07	4.29	11.15
WB0911DSH08	9/24/11	29 07.238	87 52.390	21:31	17.39	10.87
WB0911DSH07	9/26/11	29 15.626	87 43.428	4:09	45.84	12.00
WB0911DWH	9/22/11	28 44.040	88 24.548	13:36	31.13	13.84
WB0911PCB11	9/25/11	28 48.317	87 18.596	13:05	9.48	7.90
WB0911PCB05	9/26/11	29 26.652	86 46.749	19:57	31.84	14.41
WB0911PCB04	9/27/11	29 34.081	86 34.433	3:20	35.29	18.82
WB0911PCB03	9/27/11	29 43.958	86 20.345	6:38	75.10	3.63
WB0911PCB02	9/27/11	29 50.450	86 07.753	9:35	24.22	0.00
WB0911PCB01	9/27/11	30 03.225	85 49.583	12:24	670.02	0.00
WB0810DSH10	8/10/10	28 59.400	87 50.500	10:08	106.12	8.23
WB0810DSH09	8/9/10	28 36.391	87 53.414	17:35	5.68	7.89
WB0810PCB02	8/8/10	29 49.800	86 11.200	11:00	470.47	0.00
WB0810PCB01	8/8/10	30 01.535	85 52.221	3:36	1461.84	0.00
WB0513DWH	5/16/13	28 44.743	88 23.952	18:51	152.82	20.38
WB0513DSH10	5/17/13	28 58.169	87 51.042	3:44	0.00	25.95
WB0513DSH09	5/16/13	28 37.587	87 50.644	9:13	153.75	19.80
WB0513DSH08	5/17/13	29 06.375	87 52.402	10:29	0.00	19.31
WB0513DSH07	5/17/13	29 15.112	87 43.043	17:16	0.00	9.12
WB0513PCB11	5/15/13	28 48.688	87 19.695	21:51	0.00	19.55
WB0513PCB06	5/18/13	29 07.774	87 15.928	6:52	0.00	30.51
WB0513PCB05	5/18/13	29 26.925	86 46.955	18:37	0.00	10.79
WB0513PCB04	5/18/13	29 34.088	86 35.136	20:46	2.12	19.63

Temora spp.	*Oithona* spp.	*Oncaea* spp.	*Corycaeus* spp.	*Sapphirina* spp.	*Candacia* spp.	*Eucalanus* spp.	*Acartia* spp.
12.86	23.15	14.15	18.43	1.29	0.86	7.72	1.01
28.26	38.04	21.19	16.30	1.63	3.80	13.59	1.71
21.83	34.92	22.92	20.74	1.09	0.00	31.65	1.09
69.18	46.69	22.48	22.48	0.00	3.46	58.80	2.18
10.54	22.65	13.17	19.49	1.05	0.00	16.86	1.73
10.61	26.54	15.92	21.23	1.52	1.52	19.71	0.25
9.41	37.65	25.88	17.65	3.53	1.18	32.94	0.00
90.85	32.71	16.96	52.09	1.21	0.00	18.17	3.53
22.80	3.56	1.42	61.27	0.00	0.00	0.00	0.00
1285.72	0.00	13.58	221.83	4.53	0.00	54.33	0.00
5.49	6.40	1.37	9.15	4.12	0.46	6.40	0.00
1.26	16.10	5.37	6.63	1.26	0.63	2.53	5.03
0.89	27.23	0.89	18.30	4.91	0.00	68.74	9.78
26.10	8.70	0.00	13.05	0.00	0.00	95.72	0.00
50.94	58.58	15.28	30.56	2.55	0.00	56.03	0.00
0.00	12.46	11.42	10.38	0.00	1.04	2.08	9.34
25.62	26.79	18.64	26.79	1.16	5.82	43.10	9.32
0.00	16.09	6.44	4.51	0.00	1.29	2.57	3.22
0.00	7.29	3.65	6.84	0.91	0.91	1.82	7.29
0.00	19.55	8.69	10.32	1.09	1.09	9.78	5.43
0.00	8.39	9.15	7.63	0.76	1.53	6.10	2.29
1.88	31.44	7.98	10.79	1.88	1.88	4.69	9.38
10.61	28.11	10.61	17.50	1.59	2.12	1.06	5.83

Foraminifera	Radiolarians	Amphipoda	Cladocera	Crustacean Naupli	Misc. Decapod	Crab Zoea	Crab Megalops
13.12	1.30	1.33	3.02	1.71	1.01	0.04	1.25
3.30	2.72	2.21	19.09	1.09	1.23	0.00	0.03
7.68	2.18	4.44	10.96	1.10	4.67	0.02	0.09
10.43	0.00	0.02	1.74	0.00	3.70	0.01	0.01
12.71	2.11	1.06	7.92	0.00	0.57	0.01	0.01
14.64	0.76	2.36	12.23	0.76	0.23	0.00	0.13
21.44	0.01	3.57	9.52	0.00	2.96	0.03	0.18
7.33	0.00	6.62	16.99	0.01	6.44	0.02	0.26
5.04	0.00	1.42	2.15	6.52	7.79	0.09	0.00
4.56	0.00	23.41	113.99	0.04	11.07	0.25	0.32
0.01	2.74	0.08	2.76	0.00	4.66	0.03	0.01
0.63	0.95	0.63	0.63	0.63	3.47	0.00	0.00
0.45	0.00	0.45	0.00	0.45	2.23	0.00	0.00
4.35	0.00	30.46	13.05	0.00	43.51	0.00	0.00
2.55	0.00	0.49	5.16	20.46	38.89	0.00	0.04
0.00	1.04	4.42	0.00	0.00	0.06	0.00	0.00
1.17	1.17	8.56	4.67	2.36	24.74	0.00	0.01
1.93	0.00	1.49	0.00	0.00	0.02	0.00	0.00
0.46	0.46	1.53	0.00	0.00	0.02	0.00	0.00
0.54	0.00	1.94	0.00	0.54	0.60	0.00	0.00
1.53	0.00	1.63	0.00	0.76	0.01	0.00	0.00
13.63	0.47	0.25	0.47	0.47	1.00	0.00	0.00
5.83	0.00	0.64	13.87	1.06	1.19	0.00	0.02

Phyllosoma	Lucifer	Euphausiids (Non-Larval)	Stomatopoda	Misc. Mysidae	Ostracoda
0.00	0.11	6.10	0.12	0.00	40.57
0.00	0.23	3.40	0.07	0.00	7.65
0.00	0.20	4.45	0.07	0.00	16.49
0.00	0.11	0.16	0.11	0.00	15.62
0.00	0.04	1.66	0.00	0.00	19.00
0.00	0.17	4.58	0.01	0.00	16.81
0.00	2.70	6.16	0.06	0.02	22.47
0.00	1.85	3.69	0.03	0.00	83.90
0.01	3.60	0.00	0.10	0.00	91.44
0.04	11.11	0.00	4.74	0.00	946.78
0.00	0.48	1.02	0.01	0.00	3.23
0.00	0.00	3.79	0.00	0.00	4.73
0.00	0.45	0.00	0.00	0.00	0.00
0.00	4.35	0.00	0.00	4.35	443.77
0.00	15.18	8.14	0.01	0.00	7.65
0.00	0.80	13.29	0.00	0.00	5.26
0.00	2.80	13.19	0.04	0.02	3.50
0.00	0.03	4.27	0.00	0.00	3.22
0.00	0.09	5.35	0.00	0.00	4.11
0.00	0.06	6.16	0.00	0.00	8.18
0.00	0.02	11.25	0.00	0.00	6.88
0.00	0.01	3.29	0.00	0.00	2.83
0.00	0.00	1.81	0.00	0.01	2.13

Echinoderm Larvae and Juveniles	Holothuroidea	Heteropod, Atlantidae	Heteropod, Non-Atlantidae	Bivalves
15.10	0.00	0.01	0.00	1.72
0.55	0.00	0.00	0.00	0.54
6.59	0.00	0.00	0.00	0.01
0.00	0.00	1.73	0.00	0.00
1.58	0.00	0.00	0.00	0.00
14.68	0.00	0.77	0.01	0.01
1.23	0.00	0.00	0.00	4.71
0.00	0.00	1.22	0.00	6.08
16.74	0.00	0.00	0.00	2.14
64.05	0.00	4.85	0.00	72.61
0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.32	0.00	0.32
0.45	0.00	0.00	0.00	0.00
13.05	0.00	0.00	0.00	4.35
7.64	0.00	0.01	0.01	2.55
0.00	0.00	0.01	0.00	1.04
0.00	0.00	2.37	0.00	0.00
0.65	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.46
1.09	0.00	0.01	0.00	0.00
2.29	0.00	0.01	0.00	0.00
4.72	0.00	0.01	0.01	0.00
5.32	0.00	0.01	0.00	0.00

Misc. Gastropods	Pteropod, *Limacina* spp.	Pteropod, *Cavolinia* spp.	Pteropod, conical	Misc. Pteropod	Cephalopoda
0.00	3.04	0.00	0.45	0.00	0.01
1.09	1.09	0.00	0.55	0.00	0.02
4.38	1.12	0.00	2.21	0.00	0.04
0.00	0.01	0.00	0.00	0.00	0.02
0.00	0.54	0.00	1.58	0.00	0.01
1.55	2.29	0.00	0.11	0.00	0.01
10.62	1.19	0.01	0.03	0.00	0.02
1.22	4.87	0.08	2.45	0.00	0.01
0.71	1.44	0.00	0.71	4.53	0.00
0.00	9.41	0.04	27.30	0.00	0.11
0.00	0.01	0.00	0.46	0.00	0.01
0.00	1.58	0.00	0.32	0.00	0.00
0.00	3.12	0.00	0.00	0.00	0.00
0.00	17.40	0.00	0.00	0.01	0.00
0.00	0.01	0.00	2.59	0.00	0.00
0.01	3.14	0.00	2.12	0.00	0.00
0.00	1.16	0.00	1.21	0.00	0.01
0.00	0.64	0.00	0.65	0.00	0.00
0.00	0.46	0.00	0.91	0.00	0.00
0.00	3.29	0.00	2.79	0.00	0.00
0.00	0.77	0.00	0.77	0.00	0.00
0.00	2.82	0.00	0.94	0.00	0.01
0.00	1.61	0.00	0.02	0.00	0.00

Cyphonautes	Chaetognatha	Misc. Gelationous	Siphonophora	Doliolidae	Appendicularia	Salpidae	Eggs
1.76	13.25	0.46	6.09	0.86	3.07	1.32	0.00
1.09	13.24	3.83	11.03	20.20	55.86	0.00	0.54
0.00	16.82	5.51	9.93	21.96	13.18	5.50	0.00
1.73	26.47	5.25	3.56	21.05	10.47	1.73	0.00
0.53	14.26	0.02	4.25	0.00	16.36	0.53	0.00
5.37	16.35	6.87	17.60	5.39	29.99	6.89	0.00
3.53	25.20	3.56	10.72	17.73	38.04	7.13	0.00
0.01	17.32	7.28	22.10	2.46	59.65	2.44	1.21
1.42	35.26	2.16	11.73	0.72	9.33	1.50	0.71
0.04	324.26	23.38	9.27	41.77	237.82	9.83	4.56
0.00	15.20	0.03	0.48	0.46	1.84	0.00	0.46
0.32	14.20	0.00	0.00	0.63	2.53	0.00	0.32
0.00	21.87	2.68	0.89	0.45	2.23	0.00	0.89
4.35	113.12	26.10	0.00	0.00	26.10	0.00	4.35
0.01	20.99	7.71	20.51	2.61	12.79	0.00	0.01
0.03	25.61	0.02	4.36	2.09	6.36	1.08	0.00
7.00	37.56	4.70	16.40	10.54	12.82	0.00	1.16
1.29	14.31	1.95	3.30	1.29	14.26	0.00	0.00
0.00	16.52	0.93	5.97	1.38	10.97	0.00	0.46
1.64	21.11	1.67	6.71	1.64	10.35	0.56	0.00
0.00	16.14	0.04	2.34	1.53	25.24	0.00	0.00
2.83	17.07	1.04	5.28	1.41	18.37	0.50	0.00
2.15	22.92	6.49	12.85	2.66	27.67	0.55	2.12

Fish Larvae	Polychaeta	Hemichordata, *Ptychodera flava* (krohns larvae)
0.40	12.18	0.00
0.70	2.21	0.00
1.33	9.83	0.00
0.11	9.99	0.00
0.07	3.59	0.00
1.20	4.45	0.00
0.61	4.71	0.00
4.25	1.34	0.00
0.09	9.76	0.00
0.52	4.32	0.00
0.08	18.39	0.00
1.58	0.93	0.00
0.00	1.26	0.00
4.35	0.45	0.00
0.20	5.14	0.00
0.36	1.07	0.01
1.44	1.22	0.01
0.08	0.66	0.00
0.54	0.02	0.00
1.32	1.66	0.00
0.10	0.01	0.00
1.58	1.44	0.03
1.19	2.73	0.53

Station Name	Date Sampled	Latitude	Longitude	Time (CST)	*Centropages* spp.	*Lucicutia* spp.
WB0513PCB03	5/19/13	29 43.986	86 20.239	7:40	6.02	3.01
WB0513PCB02	5/19/13	29 50.235	86 10.906	9:45	6.98	0.00
WB0513PCB01	5/19/13	30 03.672	85 49.583	20:32	66.55	0.00
WB0512DWH	5/10/12	28 45.092	88 24.050	8:16	79.96	15.99
WB0512DSH10	5/10/12	28 58.403	87 51.593	20:20	0.00	30.68
WB0512DSH09	5/9/12	28 36.528	87 51.908	23:02	0.00	33.02
WB0512DSH08	5/11/12	29 07.162	87 53.126	6:41	29.40	14.70
WB0512DSH07	5/11/12	29 15.692	87 44.907	10:51	37.65	10.04
WB0512PCB11	5/14/12	28 48.082	87 18.241	20:54	0.00	19.29
WB0512PCB06	5/14/12	29 07.158	87 16.140	14:31	0.00	18.10
WB0512PCB05	5/14/12	29 25.765	86 47.642	8:17	0.00	13.04
WB0512PCB04	5/12/12	29 34.308	86 34.442	0:17	3.77	16.01
WB0512PCB03	5/12/12	29 43.774	86 20.566	10:07	10.61	2.27
WB0512PCB02	5/13/12	29 49.997	86 10.651	12:27	3.50	0.00
WB0512PCB01	5/13/12	30 03.887	85 49.805	7:03	471.46	0.00
WB0511DSH10	5/7/11	28 59.461	87 53.166	17:27	0.00	12.17
WB0511DSH09	5/7/11	28 40.329	87 49.129	7:22	1.35	15.55
WB0511PCB05	5/6/11	29 25.473	86 47.119	1:30	59.51	12.85
WB0511PCB04	5/5/11	29 33.846	86 35.039	21:09	25.01	4.05
WB0511PCB03	5/5/11	29 44.287	86 21.276	16:43	189.23	0.00
WB0511PCB01	5/5/11	30 02.708	85 50.118	7:43	2568.80	0.00

Temora spp.	*Oithona* spp.	*Oncaea* spp.	*Corycaeus* spp.	*Sapphirina* spp.	*Candacia* spp.	*Eucalanus* spp.	*Acartia* spp.
10.54	20.33	1.51	36.14	1.51	3.76	0.00	1.51
2.33	32.58	1.16	16.29	0.00	2.33	17.45	2.33
0.00	0.00	1.85	35.12	0.00	0.00	5.55	0.00
18.66	31.98	13.33	22.65	2.67	6.66	23.99	4.00
39.44	74.50	10.96	21.91	6.57	4.38	30.68	2.19
2.36	40.09	22.41	21.23	4.72	2.36	9.43	2.36
26.13	53.90	14.70	18.78	0.00	5.72	24.50	5.72
37.65	77.81	18.82	40.16	2.51	11.29	28.86	6.27
6.43	20.90	32.15	27.33	0.00	8.04	24.11	0.00
2.34	32.11	10.51	7.01	1.75	0.58	16.35	1.75
8.70	32.17	19.13	12.17	2.61	1.74	27.82	4.35
13.18	47.07	23.54	20.71	6.59	1.88	16.01	13.18
1.52	14.78	1.90	8.34	2.65	0.00	6.07	15.54
0.00	20.10	0.00	1.75	1.75	0.00	9.61	6.12
0.00	11.46	0.00	0.00	0.00	0.00	36.01	0.00
0.68	33.47	8.79	6.09	0.00	0.00	2.71	17.58
0.00	27.73	6.09	18.94	2.03	2.03	0.00	14.88
4.06	26.37	16.91	33.14	0.00	0.00	8.12	8.12
5.88	25.37	4.78	18.76	0.00	0.37	11.03	3.68
76.59	166.70	54.06	139.67	2.25	2.25	15.77	29.29
16.16	56.55	0.00	145.40	8.08	0.00	88.86	0.00

Foraminifera	Radiolarians	Amphipoda	Cladocera	Crustacean Naupli	Misc. Decapod	Crab Zoea	Crab Megalops
3.79	0.00	1.89	55.30	0.00	2.95	0.78	0.10
1.16	0.00	0.36	47.94	0.00	60.83	0.07	0.00
0.00	0.00	3.18	0.00	0.00	16.84	0.00	0.03
1.36	4.00	2.83	1.34	0.00	4.24	0.00	0.01
6.59	0.00	8.85	8.81	2.19	2.38	0.00	0.00
10.63	1.18	3.82	1.20	0.00	3.75	0.00	0.04
0.00	0.00	5.02	4.12	1.63	5.20	0.01	0.00
20.14	2.51	3.90	7.59	0.00	6.43	0.00	0.01
8.06	0.01	9.72	1.62	0.00	0.08	0.00	0.01
7.62	0.58	3.00	2.34	0.58	0.05	0.00	0.00
20.97	5.23	4.56	0.87	0.00	2.82	0.01	0.02
1.88	0.01	9.67	16.06	0.00	7.42	0.01	0.02
39.44	1.14	3.68	7.24	0.00	12.58	0.01	0.07
0.00	0.00	1.56	3.51	0.00	12.38	0.00	0.12
3.27	0.00	2.51	0.00	0.00	5.29	0.00	0.03
9.18	0.34	3.12	0.00	0.34	0.37	0.00	0.00
6.12	0.00	2.90	0.00	0.68	0.04	0.00	0.00
10.18	0.01	4.81	0.68	2.03	2.22	0.00	0.01
1.48	1.85	4.93	2.23	0.37	1.67	0.00	0.12
251.03	2.25	133.98	97.03	0.00	27.84	0.00	0.31
0.00	0.00	0.09	388.41	0.00	285.79	48.50	0.28

Phyllosoma	Lucifer	Euphausiids (Non-Larval)	Stomatopoda	Misc. Mysidae	Ostracoda
0.00	0.85	1.04	0.14	0.00	0.00
0.00	9.69	0.09	1.24	0.02	0.00
0.00	0.95	0.00	1.33	0.00	7.42
0.00	3.23	8.35	0.02	0.00	10.69
0.00	2.39	7.56	0.02	0.00	17.57
0.00	1.60	4.43	0.00	0.00	11.87
0.00	1.01	7.57	0.03	0.00	9.81
0.00	3.09	4.02	0.01	0.00	12.58
0.00	1.85	9.31	0.00	0.00	12.89
0.00	0.08	1.65	0.00	0.00	4.10
0.00	3.58	4.00	0.01	0.02	8.74
0.00	1.29	1.18	0.02	0.15	13.24
0.00	3.12	0.43	0.54	0.00	4.18
0.04	12.19	0.01	1.17	0.00	0.01
0.13	3.40	0.00	3.73	0.00	0.00
0.00	0.21	1.71	0.00	0.04	0.00
0.00	0.72	3.94	0.01	0.03	1.36
0.00	4.94	6.13	0.01	0.01	18.31
0.00	0.70	1.53	0.05	0.08	18.09
0.00	0.63	0.34	0.11	0.00	0.00
0.03	1.39	0.00	0.03	0.03	339.72

Echinoderm Larvae and Juveniles	Holothuroidea	Heteropod, Atlantidae	Heteropod, Non-Atlantidae	Bivalves
6.08	0.00	0.01	0.00	0.00
2.33	0.00	0.00	0.00	0.00
5.55	0.00	0.00	0.00	1.85
5.34	0.00	0.00	0.01	1.33
2.20	0.00	2.20	0.00	0.00
1.20	0.00	0.01	0.01	0.00
0.82	0.00	0.83	0.00	0.82
2.53	0.00	1.26	0.00	0.00
1.61	0.00	0.00	0.01	0.00
3.52	0.00	0.59	0.01	0.58
1.74	0.00	0.00	0.00	0.01
0.94	0.00	0.02	0.00	0.00
0.00	0.00	0.01	0.00	1.52
0.00	0.00	0.00	0.00	0.87
1.66	0.00	0.00	0.00	4.91
0.34	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.68	0.00
1.36	0.00	0.01	0.00	0.00
1.10	0.00	0.00	0.00	1.10
9.11	0.00	0.01	0.00	2.30
162.16	0.00	0.13	0.00	64.66

Misc. Gastropods	Pteropod, *Limacina* spp.	Pteropod, *Cavolinia* spp.	Pteropod, conical	Misc. Pteropod	Cephalopoda
0.00	3.02	0.00	5.28	0.00	0.00
0.00	0.00	0.02	2.36	9.36	0.04
0.00	1.88	0.00	3.73	0.00	0.00
0.00	5.35	0.00	4.12	0.00	0.02
0.00	2.20	0.00	0.03	0.01	0.00
0.00	8.29	0.00	0.24	0.01	0.01
0.00	0.00	0.00	1.73	0.00	0.00
0.00	0.01	0.00	0.01	0.00	0.00
0.00	4.83	0.00	0.02	0.00	0.01
0.00	4.09	0.01	1.18	0.00	0.01
0.00	0.88	0.00	2.62	0.00	0.01
0.00	2.85	0.00	0.97	0.00	0.03
0.38	0.76	0.01	1.14	0.00	0.01
0.00	1.75	0.03	0.00	0.00	0.04
0.00	4.91	0.00	0.00	0.00	0.00
0.00	0.34	0.00	0.01	0.00	0.01
0.00	0.01	0.00	0.01	0.00	0.00
0.00	27.84	0.00	0.70	0.00	0.00
0.37	0.00	0.00	0.48	0.00	0.00
0.00	4.53	0.00	9.14	0.00	0.09
8.08	0.03	0.00	24.77	0.00	0.63

Cyphonautes	Chaetognatha	Misc. Gelationous	Siphonophora	Doliolidae	Appendicularia	Salpidae	Eggs
3.78	47.93	12.16	13.71	1.53	21.15	0.00	1.52
3.49	70.77	4.87	4.82	7.05	7.02	0.07	0.02
9.27	222.89	1.88	0.03	2.22	1.85	0.00	7.48
1.33	25.47	4.03	5.40	33.41	34.79	8.00	0.00
6.58	26.65	4.47	6.66	0.01	26.46	0.01	4.38
2.39	25.09	2.53	14.46	8.34	37.01	10.71	0.01
0.00	31.36	5.76	9.90	0.85	20.57	0.84	0.82
3.77	60.72	7.57	11.37	8.81	41.56	0.00	0.00
11.28	8.25	0.03	6.54	3.23	45.17	1.63	0.00
1.75	8.86	1.79	8.21	2.35	19.91	1.17	0.58
10.45	35.94	3.51	7.87	3.48	23.58	0.11	0.87
1.89	62.01	2.87	18.91	5.67	3.81	1.00	0.94
4.18	43.51	5.34	15.95	2.56	2.65	103.39	0.01
0.00	35.61	25.50	6.28	1.75	0.87	734.39	0.87
0.00	97.04	6.68	16.40	14.17	0.03	1015.10	21.84
2.04	14.03	2.74	3.10	1.03	21.13	0.00	0.68
0.68	26.65	2.04	2.83	1.37	26.66	0.01	0.00
2.05	57.69	0.68	1.38	0.01	1.37	0.00	0.68
3.32	41.05	2.22	1.50	0.37	2.96	0.00	0.74
6.77	308.16	0.18	36.23	2.34	65.60	0.00	6.77
0.00	591.87	16.50	41.18	631.06	56.89	0.00	258.53

Fish Larvae	Polychaeta	Hemichordata, *Ptychodera flava* (krohns larvae)
1.03	2.29	0.01
2.98	2.42	0.00
0.17	0.84	0.00
0.21	1.48	0.00
9.10	6.59	0.00
1.45	3.60	0.00
1.88	1.68	0.00
2.74	0.02	0.00
3.51	0.04	0.00
0.20	0.63	0.00
2.03	2.65	0.00
0.54	1.02	0.00
1.24	1.25	0.00
0.52	2.80	0.03
0.15	0.05	0.00
0.79	3.07	0.00
0.11	0.01	0.00
2.74	0.01	0.00
0.91	0.38	0.00
3.14	2.25	0.00
8.74	0.09	0.00

Table 15. Taxa groups used in the zooplankton beta diversity analyses
upon combining pre- and post-DWH zooplankton abundance datasets

Centropages spp.
Lucicutia spp.
Temora spp.
Oithona spp.
Oncaea spp.
Corycaeus spp.
Sapphirina spp.
Candacia spp.
Eucalanus spp.
Amphipoda
Cladocera
Crustacean Naupli
Misc. Decapod
Crab Zoea
Crab Megalops
Phyllosoma
Lucifer
Euphausiids (Non-Larval)
Stomatopoda
Misc. Mysidae
Ostracoda
Echinoderm Larvae and Juveniles
Heteropod, Atlantidae
Heteropod, Non-Atlantidae
Bivalves
Pteropod, *Limacina* spp.
Pteropod, *Cavolinia* spp.
Pteropod conical
Misc. Pteropod
Cephalopoda
Cyphonautes
Chaetognatha
Siphonophora
Doliolidae
Appendicularia
Salpidae
Eggs
Fish Larvae
Polychaeta

Table 16. List of taxa groups that comprise each of the taxa categories (bold) used in post-DWH zooplankton analyses with others in order to create the 'general grouping' categories used in zooplankton analyses

***Centropages* spp.**
Centropages caribbeanensis
Centropages hamatus
Centropages velificatus
Misc Other *Centropages*
***Lucicutia* spp.**
Lucicutia clausi
Lucicutia flavicornis
Lucicutia gaussae
Lucicutia gemina
Lucicutia ovalis
Misc Other *Lucicutia*
***Temora* spp.**
Temora longicornis
Temora stylifera
Temora turbinata

Foraminifera
Foraminifera
Radiolarians
Radiolarians
Amphipoda
Amphipoda Damaged
Amphipoda, Caprellidae
Amphipoda, Gammaridae
Amphipoda, Hyperiidae
Cladocera
Cladocera, *Penilia* spp.
Cladocera, *Evadne* spp. (Gravid)
Cladocera, *Evadne* spp. (Other)
Crustacean Naupli
Barnacle Cyprid larvae
Barnacle Naupli larvae

Stomatopoda
Stomatopoda, Mantis Shrimp
Misc. Mysidae
Misc. Mysidae
Ostracoda
Ostracoda
Echinoderm Larvae and Juveniles
Total Echinoderm Larvae and Juveniles
Holothuroidea
Holothuroidea (doliolaria larvae)
Holothuroidea (auricularia larvae)
Heteropod, Atlantidae
Heteropod, Atlantidae
Heteropod, Non-Atlantidae
Heteropod, Non-Atlantidae
Heteropod; Non-Atlantidae; Damaged

Misc. Gelatinous
Pyrosomatidae
Other Ctenophora
Ctenophora, *Beroe* spp.
Cestida Comb Jelly
Doliolidae
Doliolidae
Appendicularia
Appendicularia
Salpidae
Salpidae
Eggs
Fish Egg
Fish Larvae
Elopomorpha (leptocephalus larvae)
Mcytophidae

***Oithona* spp.**	Misc. Crustacean Naupli	**Bivalves**	Stomiiformes, Viperfish
Oithona spp.	**Misc. Decapod**	Total Bivalves	Stomiiformes, Dragonfish
***Oncaea* spp.**	Misc Other Decapods	**Misc. Gastropods**	Fish Juvenile (scales and color present)
Oncaea spp.	Sergestidae Shrimp	Misc Other Gastropoda	Syngnathiformes, Pipefish (Juvenile)
***Corycaeus* spp.**	Callinectes similis (Juvenile)	Gastropoda (veliger larvae)	Syngnathiformes, Trumpetfish (Juvenile)
Corycaeus spp.	**Crab Zoea**	**Pteropod limacina**	Misc. Fish Larvae (Preflexion)
***Sapphirina* spp.**	*Albunea* spp., Crab Zoea	Pteropod Thecosomata, *Limacina* spp.	Misc. Fish Larvae (Flexion)
Sapphirina spp.	*Lepidopa* spp., Crab Zoea	**Pteropod cavolinia**	Misc. Fish Larvae (Postflexion)
***Candacia* spp.**	*Emerita* spp., Crab Zoea	Pteropod Thecosomata, *Cavolinia* spp.	Misc. Fish Larvae (Damaged)
Candacia armata	**Crab Megalops**	**Pteropod conical**	**Polychaeta**
Candacia bipinnata	Misc. Crab Megalops	Pteropod Gymnosomata	Polychaeta
Candacia bispinosa	*Callinectes similes* (Megalops)	**Misc. Pteropod**	**Hemichordata, Ptychodera flava (krohns larvae)**
Candacia curta	**Phyllosoma**	Pteropod Gymnosomata	Hemichordata, Ptychodera flava (krohns larvae)

Table 17. Description of zooplankton and environmental variables with corresponding data resource or retrieval method used in analyses

Variable	Data Source
Integrated Dissolved Oxygen (umol/kg)	0-200m summation of Dissolved Oxygen from R/V Weatherbird CTD Roseatte and Sensor Suite
Dissolved Oxygen (umol/kg)	R/V Weatherbird CTD Roseatte and Sensor Suite
Temperature ºC	R/V Weatherbird CTD Roseatte and Sensor Suite
Salinity (psu)	R/V Weatherbird CTD Roseatte and Sensor Suite
Turbidity (NTU)	R/V Weatherbird CTD Roseatte and Sensor Suite
ugChl/L	Discrete Filtered Chlorophyll
Integ Fluor. (ECO-AFL/FL, mg/m3)	0-200m summation of Fluorescence from R/V Weatherbird CTD Roseatte and Sensor Suite
Mixed Layer Depth (m)	depth where ($\theta\bar{x} = \theta_{10m} \pm 0.2$ °C) (de Boyer Montégut et al., 2004)
Mississippi River Avg. Discharge (cubic meters per second)	Average of x days before the day of collection retrieved from United States Geological Survey Stream Gauging Network (https://waterdata.usgs.gov/usa/nwis/)
Wind Directional Components	NOAA National Data Buoy Center or reanalysis products from the National Center for Environmental Information (https://www.ndbc.noaa.gov/ or https://www.ncei.noaa.gov/)
Current Directional Components	Model products provided by Zang, Z. et al., 2018
Pre-DWH Zooplankton	SEAMAP; correspondence with Dr. Glenn Zapfe; abundances in Table 13
Post-DWH Zooplankton	Available online through GRIIDC: https://data.gulfresearchinitiative.org/