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Resilience of the zooplankton community in the northeast Gulf of Mexico during and after the Deepwater Horizon oil spill

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ABSTRACT

We evaluated the resilience of the zooplankton community to the Deepwater Horizon oil spill in the northeast Gulf of Mexico, by assessing abundance, biomass, spatial distribution, species composition, and diversity indices during spring, summer, and winter, May 2010 to August 2014. SEAMAP samples collected between spring and summer 2005–2009 were analyzed as a baseline. Our results did not indicate that there was a long-term impact from the oil spill, but did demonstrate that environmental variability and riverine processes strongly governed zooplankton community dynamics. Zooplankton abundances during the oil spill (spring 2010) were not significantly different from abundances during spring 2011 and 2012. Summer 2010 abundances were the highest observed for the 2005 to 2014 period, due to high river discharge, high chlorophyll, and aggregation in eddies. High densities of the dinoflagellate, *Noctiluca*, during the oil spill, and the copepod, *Centropages velificatus*, and larvaceans in all years, suggest that these taxa warrant further investigation. Ecosystem connectivity (zooplankton transport by currents into the oil spill region), high fecundity, relatively short generation times, and refugia in deeper depths are key factors in zooplankton resilience to major perturbations. This study serves as a baseline for assessment of future impacts to this system.

1. Introduction

Eutrophication, trophic cascades due to overfishing (Walsh et al., 2011), and the Deepwater Horizon (DWH) oil spill during 2010 have impacted the zooplankton community in the northeastern Gulf of Mexico (NEGOM). The DWH oil spill was the largest environmental perturbation in the Gulf of Mexico and the largest oil spill in the history of the petroleum industry (McNutt et al., 2012). Between when it began on April 20, 2010 and ended on July 20, 2010, 4.9 million barrels of oil were released. Based on satellite images, the oil spill ultimately covered up to 149,000 km² of surface area over shelf and off-shelf regions (MacDonald et al., 2015) (Fig. 1).

The Gulf of Mexico (GOM) is a marginal sea of the Atlantic Ocean and has been designated as a Large Marine Ecosystem by NOAA's Office of Science and Technology. Near surface circulation in the eastern GOM is

dominated by the energetic Loop Current, which enters from the Caribbean and facilitates exchange of oceanic species with the GOM (Biggs and Ressler, 2001). Although the Loop Current rarely occurs far enough north to directly affect NEGOM circulation, there can be indirect effects from strong currents that are generated when the Loop Current interacts with the West Florida Shelf (Vukovich et al., 1979; Hetland et al., 1999). The NEGOM is the most productive region in the Gulf of Mexico (Walsh et al., 1989; Okolodkov, 2003), where circulation and primary and secondary production are strongly influenced by large river systems, particularly the Mississippi River, but also the Atchafalaya, Mobile, and Apalachicola rivers, and numerous bays and estuaries (Lohrenz et al., 1997; Jochens et al., 2002; Dagg and Breed, 2008). High river discharge enhances stratification and coastal jets along frontal boundaries, and increases nutrients, resulting in increased phytoplankton availability for zooplankton (Jochens and DiMarco, 2008;

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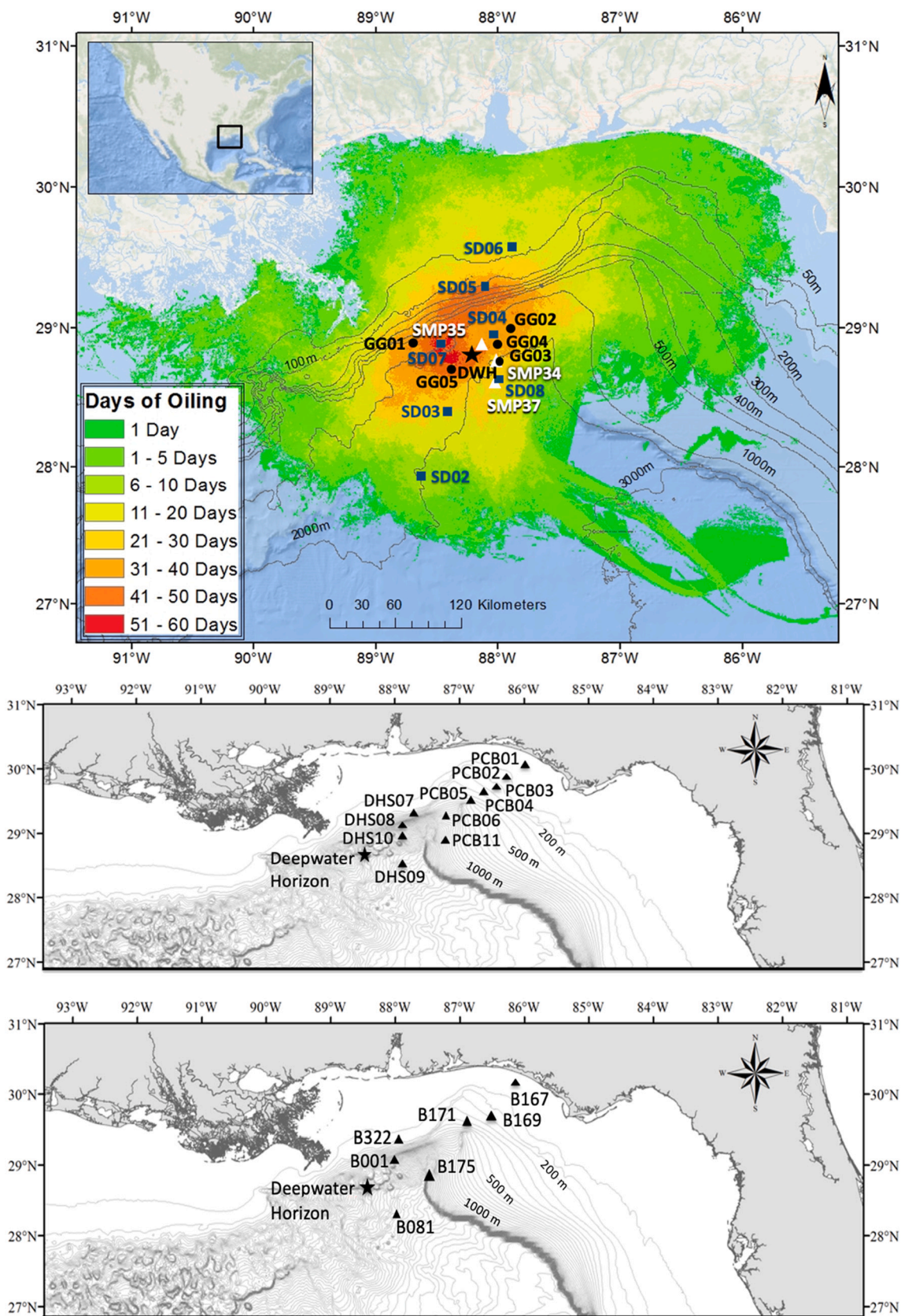


Fig. 1. Station locations for data collected prior to, during, and after the DWH oil spill. Stations occupied during May, June, and September 2010 are shown in the top panel, with extent of oil shown as days of oil detected at the surface; red is heavier oil exposure, green is light oil exposure. The locations of post-oil spill stations (August 2010–August 2014) are shown in the middle panel, and pre-oil spill SEAMAP stations (2005–2009) are shown in the bottom panel. The stars designate the DWH platform site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Nababan et al., 2011). Although the nutrient-rich Mississippi River plume frequently moves westward along the shallow Louisiana-Texas shelf leading to hypoxic conditions (Rabalais et al., 2007), during periods when winds blowing towards the north or the east dominate in summer, low salinity surface water is transported to the east towards the De Soto Canyon (Schiller et al., 2011).

While much of the GOM is oligotrophic, the NEGOM can have high chlorophyll concentrations near shore and intermediate to high chlorophyll concentrations over the shelf and in off-shelf regions influenced by the Mississippi River plume (Belabbassi et al., 2005; Lohrenz et al., 2008; Nababan et al., 2011). In addition, the shelf slope regions east of the Mississippi River delta and near the De Soto Canyon frequently have cyclonic or anticyclonic eddies, with diameters of 30 to 50 km, that persist for weeks to several months during summer (Jochens and DiMarco, 2008; Schiller et al., 2011). These eddies influence biological productivity via cross-margin flow, entrainment of low salinity shelf water, and uplift of isopycnals and nutrient fields by cyclonic eddies and at the periphery of anticyclonic eddies (Muller-Karger et al., 1991; Belabbassi et al., 2005). Higher chlorophyll, macrozooplankton, and larval fish concentrations have been observed in the meandering turbidity fronts of the Mississippi River plume in comparison to inside the plume or in shelf waters (Grimes and Finucane, 1991; Hitchcock et al., 1997). High concentrations of copepod larval stages also have been observed in mid-field plume waters, indicating that the environment is favorable for copepod production (Dagg and Whitley, 1991). Hence, the plume, fronts, and eddies can act to retain and aggregate phytoplankton, zooplankton, and fish larvae.

During the DWH oil spill, the Mississippi River diversionary channels were opened for several months with the intent that the freshwater would help prevent oil from reaching sensitive coastal areas (Bianchi et al., 2011; O'Connor et al., 2016). The 2010 above average discharge rates, along with northward winds, resulted in a freshwater lens covering much of the offshore region to the east of the Mississippi River delta during July and August. Subsequently, an unusually high phytoplankton bloom was detected by satellite measurements over a > 11,000 km² area in the NEGOM during August 2010, which disappeared by September (Hu et al., 2011). Chlorophyll concentrations were higher (anomaly: >1 mg m⁻³ of chlorophyll *a*) than the previous eight years, including other years of high river discharge. Chakraborty et al. (this issue) also reported that chlorophyll concentrations remained elevated through the following fall and winter and diatoms declined on the shelf, but increased off shelf, in comparison to previous years. Therefore, complex ecosystem interactions in the lower trophic food web occurred during and after the oil spill.

Marine zooplankton play an important role in governing ocean production and mediating biogeochemical cycles (Longhurst and Harrison, 1989; Barse, 1995). Zooplankton also are essential to sustaining fisheries, as they are the dominant prey for larval, juvenile, and some adult fish, and most fish species spend their earliest life history stages as zooplankton (Cushing, 1995). Indeed, the northern Gulf of Mexico fisheries is one of the largest in the world (NMFS, 2011). Despite the ecological importance of zooplankton, there was little baseline data in the NEGOM prior to the Deepwater Horizon oil spill. A review by Iverson and Hopkins (1981) reported that the highest zooplankton abundances (760–2757 individuals per m³) and biomass occur near shore and decrease offshore. In contrast, the lowest diversity is near shore and increases seaward. Abundances are typically lowest in winter. Copepods are usually the dominant taxa (Ortner et al., 1989), but other groups, such as chaetognaths, larvaceans, ostracods, hydromedusae, and euphausiids also make important contributions in the upper 200 m of the water column (Iverson and Hopkins, 1981). Off-shelf zooplankton abundances are lower and typical of other oligotrophic regions; however, zooplankton may have higher densities at the edges of the Loop Current and Loop Current eddies (Biggs and Ressler, 2001).

Lethal and sublethal effects of oil on marine zooplankton are a function of many factors, including exposure time, oil type and

concentration, salinity, temperature, food availability, and organism size and life history stage (Moore and Dwyer, 1974). Water column concentrations of oil (TPAH50 = sum of 50 individual polycyclic aromatic hydrocarbon concentration measurements) measured in the Gulf of Mexico following the DWH oil spill exceeded levels (TPAH50: 0.5 µg L⁻¹) known to cause lethal and sublethal effects in plankton (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). TPAH concentrations in the region of the released oil averaged 43 µg L⁻¹ in the upper 10 m, 0.4 µg L⁻¹ in the upper 100 m, and 0.2 µg L⁻¹ between 100 and 200 m of the water column (Murawski et al., 2016). High oil concentrations also were observed in the cone of oil rising from the seafloor and in the deep oil plumes, which occurred primarily between 1000 and 1400 m depth (Camilli et al., 2010). Surface oil was still detectable by mid-August 2010. Because zooplankton typically are most abundant in near surface waters (Iverson and Hopkins, 1981), they are sensitive to many environmental perturbations and are particularly vulnerable to crude oil pollution (National Research Council, 2003 National Research Council, 2003).

A number of recent laboratory studies using common zooplankton collected in the Gulf of Mexico have confirmed that Louisiana Sweet crude oil, a surrogate for the Macondo (MC252) crude oil released in the DWH oil spill, and the dispersant, Corexit 9500, have sublethal and lethal impacts on microzooplankton and mesozooplankton (Ortmann et al., 2012; Almeda et al., 2013a, 2013b, 2014b, 2014c; Olsen et al., 2013; Cohen et al., 2014; Peiffer and Cohen, 2015). The sensitivity to hydrocarbons varied between different taxa and developmental stages. In addition, some zooplankton (e.g., dinoflagellates, gelatinous doliolids, copepods) ingest oil and egest oil in fecal pellets (Lee et al., 2012; Almeda et al., 2014a, 2016), which may be reingested by other particle feeding zooplankton. For example, the heterotrophic dinoflagellates, *Noctiluca scintillans* and *Gyrodinium spirale*, ingested oil levels equivalent to 17% to 100% of crude oil concentrations at 1 µL L⁻¹ (Almeda et al., 2014a). Oil carbon also was incorporated by the lower trophic food web through biodegradation by bacteria (Graham et al., 2010; Chanton et al., 2012; Cherrier et al., 2014). In addition, there was an unanticipated sedimentation of oil-associated marine snow (which includes fecal pellets) to the seafloor during the oil spill (Daly et al., 2016). Since some zooplankton, such as euphausiids and copepods, feed on marine snow aggregates (Dilling and Alldredge, 2000; Lombard et al., 2013), even zooplankton that occurred deeper in the water column could have been exposed to oil as a result of sinking oil associated with marine snow and fecal pellets or by vertically migrating through the deep oil plumes (Quintana-Rizzo et al., 2015). Thus, in addition to the direct and indirect impacts of oil to individuals, zooplankton may have contributed to the flux of oil from the surface to the seafloor through the egestion of oil in sinking fecal pellets and in the transfer of toxic petroleum hydrocarbons to higher trophic levels in the marine food web through ingestion of oil carbon and subsequent predation.

Resilience in marine ecosystems is the capacity of a system to resist change to its structure, function, and feedbacks during and after a disturbance, and the system's ability to recover from a disturbance (Folke et al., 2004). Since these properties are difficult to measure in the field, Bernhardt and Leslie (2013) Bernhardt and Leslie (2013) recommended tracking population size and species diversity over time. Diversity is a key factor in resilience as it increases the variety of possible responses to disturbances and the probability that a species can compensate for other more vulnerable species. Ecosystem connectivity also is critical to community persistence, as the movement of organisms between regions of disturbance may reduce the risk of local extinction.

Here, we evaluate the impact of the DWH oil spill and resilience of the zooplankton community in the NEGOM, by assessing the abundance, biomass, spatial distribution, species composition, and diversity indices of zooplankton during spring, summer, and winter between May 2010 and August 2014. Particular challenges included the fact that there was little zooplankton baseline data and that the assessment of oil impacts had to be evaluated within the context of large temporal and spatial

ecosystem complexity.

2. Methods

2.1. Study area and environmental data

The study site was located in the NE Gulf of Mexico, bounded on the west by the mouth of the Mississippi River (ca. 89°W) and to the east by the Florida coastline near the De Soto Canyon (85°W) and between 28.5 and 30°N latitude. Fig. 1 shows the location of stations prior to, during, and after the oil spill. The 200 m isobath shows the edge of the continental shelf and, therefore, which stations are on the shelf and which ones are off the shelf. Tables 1 and 2 list the research cruises and provide information on associated environmental parameters during each cruise. The May–June 2010 oil spill cruise and all of the SEAMAP cruises were conducted aboard the RV *Gordon Gunter*. The September 2010 cruise was aboard the MV *Specialty Diver*; all other cruises were aboard the RV *Weatherbird II*. Not all stations or tows were completed on each cruise, due to ship or equipment issues or inclement weather, such as a tropical storm in August 2010, which ended that cruise prematurely.

Environmental data (e.g., temperature, salinity, dissolved oxygen, chlorophyll fluorescence, turbidity) were collected by CTD casts at each station. In addition, environmental data were collected simultaneously with the Shadowed Image Profiling and Evaluation Recorder (SIPPER) imaging system (Samson et al., 2001; Remsen et al., 2004) during each deployment. Sensors included a Seabird 19Plus CTD, Seabird SBE43 oxygen sensor, and WET Labs FLNTURTD chlorophyll fluorescence and turbidity, and a transmissometer. Sensors were calibrated at Sea-Bird Scientific and WET Labs and then integrated into the SIPPER towed

platform. During the SMP751001 cruise, the CTD sampling pump was turned off in the presence of surface oil slicks between May 14–15, 2010 at the recommendation of Sea-Bird Scientific. This prevented the collection of salinity and temperature records for three SIPPER deployments (SMP751001–34 to SMP751001–37). As a proxy for those deployments, we utilized the temperature and salinity record from Station 60 collected by the RV *Pelican* on May 14, 2010, approximately 3.7 km from the wellhead. Discrete chlorophyll samples were collected during post DWH cruises in 2 L amber bottles, using tygon tubing without mesh, at depths between 2 and 500 m and analyzed following the methods of Holm-Hansen et al. (1965). Since discrete chlorophyll data compared reasonably well with chlorophyll fluorescence sensor data (median R^2 : 0.72, range: 0.546–0.927, $p < 0.01$) at each station and the sensor data have a higher vertical resolution, chlorophyll fluorescence data were used for all of the profile plots.

2.2. Zooplankton collection and analyses

Zooplankton were collected using three methods: (1) camera images using the towed SIPPER system during and after the oil spill (May 2010–August 2014), (2) Bongo tows collected after the oil wellhead was capped (August 2010 – August 2014), and (3) Bongo tows collected as part of the Southeast Area Monitoring and Assessment Program (SEAMAP) prior to the oil spill (2005–2009). Only the SIPPER system was deployed during the oil spill, as nets would have been oiled and contaminated collected zooplankton.

2.2.1. SIPPER system

The SIPPER camera imaging system was developed at the University

Table 1

Zooplankton cruises during and after the DWH oil spill, with associated mean (n; range) of surface temperature and salinity, and the geometric mean (n, range) for integrated chlorophyll fluorescence (0–100 m) and integrated zooplankton (2–100 m) for different stations in the NE Gulf of Mexico.

Date	Cruise	Temperature (°C)	Salinity	Integrated chl. (mg m ⁻²)	Integrated zooplankton (individuals m ⁻²)
Oil spill cruises					
<i>Spring</i>					
5/05/10–5/17/10	SMP751001	25.3 (4; 24.5–25.7)	ND	45.3 (3; 37.1–62.1)	261,229 (2; 206,433–330,571)
5/29/10–6/3/10	GG100200	27.6 (7; 26.7–28.2)	34.9 (7; 33.3–35.8)	38.6 (4; 27.1–51.5)	210,671 (4; 150,884–311,518)
<i>Post DWH cruises</i>					
<i>Spring</i>					
5/03/11–5/09/11	WB0511	20.6 (9; 15.6–23.9)	35.5 (9; 33.7–36.6)	27.4 (4; 27.9–31.8)	157,026 (7; 111,454–264,215)
5/07/12–5/15/12	WB0512	24.5 (11; 23.1–26.4)	34.8 (11; 32.8–35.8)	33.3 (5; 25.1–40.3)	206,542 (6; 152,900–340,900)
5/14/13–5/22/13	WB0513	23.5 (12; 21.8–24.9)	35.6 (12; 33.4–36.5)	70.1 (8; 63.7–80.2)	ND
5/29/14–6/6/14	WB0514	26.4 (6; 25.4–28.5)	34.3 (6; 30.1–36.1)	36.2 (6; 31.4–45.2)	ND
<i>Post DWH cruises</i>					
<i>Summer</i>					
8/06/10–8/16/10	WB0810	30.8 (5; 30.1–31.3)	28.1 (5; 23.3–31.4)	40.4 (3; 25.9–85.4)	270,799 (1)
9/10/10–9/15/10	SD010	29.8 (10; 29.5–30.2)	32.5 (10; 30.2–35.9)	31.5 (3; 25.9–40.4)	460,178 (6; 351,121–441,016)
9/20/11–9/28/11	WB0911	28.3 (16; 27.6–28.9)	32.6 (16; 30.5–34.7)	32.3 (5; 29.2–38.7)	171,747 (5; 112,434–254,228)
8/1/12–8/10/12	WB0812	29.6 (12; 29.0–30.7)	33.4 (12; 30.4–34.9)	32.6 (9; 26.7–39.6)	159,738 (8; 106,804–194,768)
8/5/13–08/11/13	WB0813	29.1 (12; 26.6–30.5)	28.6 (11; 24.5–33.7)	20.5 (7; 9.1–38.6)	264,586 (7; 162,825–426,776)
8/6/14–8/12/14	WB0814	30.4 (10; 29.7–31.1)	31.5 (10; 28.4–36.2)	38.3 (7; 33.8–49.6)	143,207 (7; 92,833–198,384)
<i>Post DWH cruises</i>					
<i>Winter</i>					
2/17/11–2/22/11	WB0211	19.6 (11; 18.4–21.4)	36.1 (11; 34.2–36.5)	32.0 (6; 24.5–50.7)	ND
2/15/12–2/24/12	WB0212	19.8 (11; 17.0–21.6)	35.9 (11; 35.0–36.8)	42.0 (7; 30.4–60.6)	423,953 (6; 215,129–1,120,371)
2/04/13–2/11/13	WB0213	19.8 (7; 16.6–20.9)	35.1 (7; 33.8–36.2)	38.0 (2; 34.2–42.3)	231,846 (2; 221,246–242,767)

n is number of stations; ND is no data available; Integrated chlorophyll and Integrated zooplankton values only include stations >100 m; Integrated zooplankton values are from SIPPER tows; *conductivity sensor turned off.

Table 2

Pre-DWH oil spill cruises, with associated surface temperature and salinity, integrated chlorophyll fluorescence (0–100 m), and geometric mean (n ; range) of total zooplankton abundance from SEAMAP Bongo tows for different stations in the NE Gulf of Mexico. n is number of stations; ND is no data available.

Date	SEAMAP cruise #	Stations	Temperature (°C)	Salinity	Integrated chlorophyll (mg m ⁻²)	Total zooplankton (individuals m ⁻³)
5/7/05–5/29/05	51, 52	B001, B171	ND	ND	ND	282 (3*; 202–381)
9/11/05	55	B322	24.3	35.1	ND	126
5/6/06	62	B001	25.1	36.5	105	52
9/21/06	64	B167, B169	29.9	35.8	67.3	308
3/18/07–3/28/07	72	B169, B171, B175, B 322	19.2, 20.8, 24.5, 23.1	36.0, 36.4, 36.4, 36.3	93.8, 145	219 (2; 214–402 [†])
5/28/07	73	B081, B001	27.5, 26.7	36.3, 36.5	ND	124 (4; 155–332)
9/16/07–9/17/07	75	B167, B169	31.7, 31.5	36.5, 36.4	ND	77 (2; 101–147)
5/28/08–5/30/08	82	B001	26.9	35.9	102	75 (2; 57 [†] –97)
9/29/08	84	B167, B169	27.9	36.2	112	500
3/3/09–3/13/09	901	B169, B322, B001	22.3, 21.6, 22.1	36.3, 36.4, 36.2	ND	385 (2; 239–760 [†])
5/5/09–5/29/09	902	B001	27.6	ND	92.5	202 (3; 137–655)
9/5/09–9/9/09	904	B167, B169	28.8	33.1	102	913 (2; 105–1721 [†])

*B001 sampled twice; [†]denotes total zooplankton for Sta. B167 which was 33 m deep, all other stations > 200 m.

of South Florida to sample plankton and suspended particles in the ocean. An earlier version of the SIPPER was described in Remsen et al. (2004). For this study, SIPPER used a high speed Dalsa Piranha-2 line-scan camera to image plankton, as water flowed through a 100 cm² sampling tube. A unique property of continuously scanning cameras is that they use a single line of sensor pixels to successively build a high resolution, two-dimensional image, as the object in the flow field moves past the line of pixels in the image sensor. A pseudo-collimated LED generated light sheet of white light only illuminated the field of view in the sampling tube to image the shadows and outlines of resolvable particles. The optical resolution was approximately 65 μm. SIPPER was towed at speeds between 2 and 3 knots in an oblique profile through the water column, spending approximately equal amounts of time at one-meter depth intervals between the surface and 300 m or within 5–10 m above the seafloor at shallower stations. The water flow through the sampling tube varied, but was generally about one meter per second, and was quantified continuously to an accuracy of 1.5%.

Images were analyzed using a customized software package called the Plankton Image Classification and Extraction Software (PICES) (Kramer et al., 2011). Briefly, image classification involved both automated classification and manual image labeling. Initial classifications into 70 different classes (marine snow, phytoplankton, zooplankton, fish, etc.) were predicted for each image using a multi-class feature selection (MFS) support vector machine (SVM). The predicted images were then visually validated. After all deployments were validated and added to the training library, a final comprehensive MFS-SVM classifier was rebuilt and run on all deployments using the new training library. Lastly, a dual classifier (MFS-SVM and binary feature selection classifiers) was run to reduce the rate of false positives and provide more accurate abundance estimations, especially in regions of low relative abundance (Kramer et al., 2011). Dual classifiers were run on each deployment using the most common image classes in that deployment. The performance of the dual classifier was assessed by comparing validated random subsets of images from 18 selected deployments totaling 125,483 images against predictions from the classifier using resulting confusion matrices. These analyses resulted in an estimated overall accuracy of 78.2%. Final abundances of taxa are reported as individuals m⁻³ at each 1 m depth interval based on the SIPPER flowmeter estimated volume of water imaged. Eight SIPPER tows were completed during the oil spill near the DWH wellhead during May and June 2010, of which six tows could be used for integrated total zooplankton

calculations shown in Table 1. During the SMP751001 cruise, sea conditions prevented effective SIPPER sampling in the upper 2 m in the vicinity of the wellhead. Therefore, zooplankton were integrated between 2 and 100 m, to avoid possible incorporation of near surface bubbles in estimates. The SIPPER images classes used to compare spring and summer 2010 zooplankton are shown in Table 3. Weighted mean depths (WMD) also were calculated for each SIPPER image class using the following equation:

$$WMD = \frac{\sum n_s d_s}{\sum n_s}$$

where d is the mean depth of the sampled depth interval s , and n is the abundance (individuals m⁻³).

2.2.2. Pre-oil spill SEAMAP Bongo samples

Because there was little zooplankton baseline data prior to the oil spill, we analyzed a subset of SEAMAP plankton samples collected by the NOAA/NMFS Pascagoula, MS lab (J. Lyczkowski-Shultz and G. Zapfe, pers. comm.) (Fig. 1). Only 24 SEAMAP samples coincided with our seasonal time periods and approximate station locations; usually only one to four stations per SEAMAP cruise (Table 2). CTD data also were not available for many cruises. SEAMAP Bongo tows (61 cm frame, 333 μm mesh nets) followed standard procedures described in Ford and Rester (2001). Net tows were made between 0 and 200 m, or to about 10 m above the seafloor at shallower stations. Samples were preserved in 10% formalin and then transferred to 95% ethanol solution within 48 h. We assessed the abundance of zooplankton taxa in these samples using a Hydroptic Zooscan digital imaging system with Plankton Identifier and ZooProcess software following the methods of Gorsky et al. (2010). The zooplankton taxa identified and used for comparisons with post oil spill data are shown in Table 4.

2.2.3. Post-oil spill Bongo tows

Bongo tows (61 cm diameter dual net frames, 333 μm mesh nets) followed the SEAMAP methods (0–200 m tows) (Ford and Rester, 2001). Samples were preserved using 10% sodium borate buffered formalin. Zooplankton from the left net were identified microscopically and plankton from the right net were analyzed for biomass (mg dry weight). For the identification samples, all large non-copepod taxa (e.g. sergestid shrimp, myctophids, euphausiids, etc.) were sorted from the entire sample and identified. The remaining sample was split using a Folsom

Table 3

Total integrated abundances (individuals m^{-2} , 2–100 m) of zooplankton taxa with associated weighted mean depths (WMD) for oil spill (May–June 2010) and post-oil spill (August–September 2010) SIPPER tows.

SIPPER image class	Oil spill abundance mean \pm SE	Post-oil spill abundance mean \pm SE	Oil spill WMD (m)	Post-spill WMD (m)
Protist_ acantharia	13,934 \pm 2340	13,652 \pm 1579	28 \pm 2	34 \pm 2
Protist_ noctiluca	37,733 \pm 12,612	20,793 \pm 3318	44 \pm 5	56 \pm 2
Protist_ radiolarians	16,634 \pm 3402	1083 \pm 259*	49 \pm 4	58 \pm 2
Protist_ unknown	3158 \pm 391	4783 \pm 567	36 \pm 2	36 \pm 1
Chaetognath	22,637 \pm 1420	23,901 \pm 2894	43 \pm 4	41 \pm 3
Crustacean_ copepod_ calanoid	32,823 \pm 2208	24,359 \pm 3759	33 \pm 3	36 \pm 2
Crustacean_ copepod_ oithona	11,490 \pm 427	12,071 \pm 969	45 \pm 2	45 \pm 1
Crustacean_ copepod_ poecilostomatoid	25,615 \pm 3924	21,232 \pm 3098	34 \pm 3	39 \pm 2
Crustacean_ ostracod	812 \pm 160	1852 \pm 248 [†]	52 \pm 3	51 \pm 2
Echinoderm_ bipinnaria	947 \pm 250	4030 \pm 904*	33 \pm 4	14 \pm 1*
Echinoderm_ plutei	261 \pm 75	3524 \pm 471*	35 \pm 2	44 \pm 1
Gelatinous_ hydromedusae_ other	10,224 \pm 2560	9495 \pm 1515	30 \pm 2	28 \pm 2
Gelatinous_ hydromedusae_ small	9460 \pm 2867*	5300 \pm 2536	29 \pm 3	26 \pm 3
Gelatinous_ siphonophore	2202 \pm 362	1896 \pm 326	43 \pm 3	45 \pm 2
Gelatinous_ tunicate_ doliolid	1112 \pm 282	5128 \pm 1952*	34 \pm 2	35 \pm 4
Larvacean	38,089 \pm 3680	54,528 \pm 8203	38 \pm 2	37 \pm 3
Total protists	129,673 \pm 55,017	42,883 \pm 4554	39 \pm 3	46 \pm 2
Total copepods	48,681 \pm 2684	46,752 \pm 8160	36 \pm 3	39 \pm 2
Total gelatinous zooplankton	25,201 \pm 4193	23,915 \pm 6196	32 \pm 2	29 \pm 3
Total zooplankton	170,323 \pm 10,338	176,611 \pm 23,906	36 \pm 3	37 \pm 2

SE is standard error; *indicates station group is significantly different from all other groups; [†]significant difference between oil and post-spill values.

Table 4

Taxa identified using Zooscan image analysis of pre-oil spill SEAMAP Bongo tows (2005–2009) and used in multivariate statistical analysis comparisons with zooplankton collected in post-oil spill Bongo tows (2010–2014).

<i>Centropages</i> spp.	Crab megalopae	Pteropod, <i>Cavolinia</i> spp.
<i>Lucicutia</i> spp.	Euphausiids (juv./adults)	Pteropod, <i>Limacina</i> spp.
<i>Temora</i> spp.	<i>Lucifer</i> spp.	Miscellaneous pteropods
<i>Oithona</i> spp.	Miscellaneous decapods	Cephalopods
<i>Oncaea</i> spp.	Mysids	Cyphonautes
<i>Corycaeus</i> spp.	Phyllosoma (lobster larvae)	Doliolids
<i>Sapphirina</i> spp.	Stomatopods	Siphonophores
<i>Candacia</i> spp.	Ostracods	Chaetognaths
<i>Eucalanus</i> spp.	Bivalve larvae	Miscellaneous eggs
Crustacean nauplii	Echinoderm larvae/juveniles	Salps
Amphipods	Heteropod, non-Atlantidae	Polychaete worms
Cladocera	Heteropod, Atlantidae	Larvaceans
Crab zoea	Pteropod, Conical	Fish larvae

splitter to between 1/8 and 1/1024, depending on the abundance of calanoid copepods. On average, about 240 copepods were identified in splits. Calanoid copepods were identified to the lowest possible taxon and to developmental stage when possible using a Wild dissecting microscope and an Olympus compound microscope, as needed. Non-calanoid copepods (e.g. *Oncaea*, *Oithona*) were identified to genera, but not staged. Small non-copepod taxa (e.g. ostracods, cladocerans, larvaceans, echinoderm larvae) also were removed from the split and identified to group or species and enumerated. Abundance (individuals m^{-3}) was determined as the number in the full sample or split, times the split correction factor, and then divided by Bongo net water volume filtered values determined from flow meters for each specific tow.

2.2.4. Zooplankton biomass

Biomass (mg dry weight) was determined for Bongo samples collected between February 2011 and August 2014. At sea, zooplankton were gently backwashed onto a large 100 μ m sieve using filtered seawater, rinsed briefly with distilled water, blotted dry, then stored at -20 °C in glass or plastic containers. In the lab, samples were freeze-dried, then transferred to combusted, pre-weighed aluminium foil, dried at 60 °C, and weighed on a Mettler UMX2 microbalance.

2.3. Statistical analyses

SIPPER and Bongo tows occurred at any time of the day or night, depending on the cruise track and rate at which station activities were completed. Because many zooplankton vertically migrate (Hopkins, 1982), tows in deep water (> 200 m) may have more migrators in the upper 200 m at night and fewer during the day; thereby, biasing the abundance of migrating taxa. Hopkins (1982), however, showed that most of the dominant zooplankton groups, such as copepods, chaetognaths, ostracods, larvaceans, and gastropods, had day and night biomass peaks in the upper 50 m, although some individuals occurred deeper in the water column. Euphausiids were an exception, with daytime peaks below 300 m. We compared total zooplankton in spring day/night samples and summer day/night samples and determined that none of the comparisons were significantly different [Bongo tows: PERMANOVA test, $p \geq 0.4$ (Dubickas, 2019); SIPPER tows, A. Remsen, pers. comm]. Therefore, all tows were used in analyses regardless of time of collection.

Data were tested for normality and then appropriate statistical tests were performed at a significance level of $\alpha = 0.05$. Basic statistics, one-way ANOVAs, non-parametric Mann-Whitney U tests, Kruskal-Wallis ANOVAs, and Scheffe post-hoc comparison among group tests were calculated using StatPlus. Differences in SIPPER image class abundance and weighted mean depth were tested by Kruskal-Wallis ANOVAs, with significant differences among groups identified by a Dunn test using Matlab software.

The impacts of environmental variability on zooplankton were assessed using several multivariate statistical approaches using a Matlab R2015a FATHOM toolbox (Jones, 2017), as described in Dubickas (2019). Briefly, environmental conditions were assessed using the following parameters: sea surface temperature, salinity, dissolved oxygen, turbidity, discrete chlorophyll, and integrated chlorophyll fluorescence. Average daily Mississippi River discharge volume rates (3 days, 14 days, 21 days, and 30 days), and 3-day average daily wind components and magnitude also were obtained from the United States Geological Survey Stream-gauging Network, and NOAA National Centers for Environmental Information, respectively. Missing chlorophyll values from pre-DWH SEAMAP data and surface current data were obtained from the Coupled-Ocean-Atmosphere-Wave-Sediment Transport Modeling System provided by Dr. George Xue at Louisiana State

University, as described in Zang et al. (2018). Euclidean Distance was used for environmental data and Bray-Curtis Dissimilarity metrics on fourth-root transformed zooplankton data were used for all multivariate testing. Beta diversity was used to quantify zooplankton abundance and compositional similarity/differences between sites, seasons, and years (Whittaker, 1960). 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 whether environmental conditions or beta diversity were significantly different across seasons or years and, if so, which variables were most responsible for driving the separation of these groups (Legendre and Legendre, 2012). Distance-based Redundancy Analysis (dbRDA) tests were used with Akaike's Information Criterion (AIC) to investigate the effect of environmental variables on dissimilarities in the beta diversity zooplankton data (Clarke and Warwick, 1994). AIC values were used to determine the relative importance of environmental variables (Godínez-Domínguez and Freire, 2003).

3. Results

3.1. Environmental data

The cruises during May and June 2010 occurred in the region of relatively high surface oil (0–20 m geometric mean for total PAH: $0.087 \mu\text{g L}^{-1}$, range: $0.01\text{--}10,474 \mu\text{g L}^{-1}$; <https://www.diver.orr.noaa.gov>). Extensive oil slicks and sheen were visible at the surface at stations 3.7 to 11 km from the wellhead. Stations were not occupied closer to the wellhead, so as not to interfere with oil spill response activities. August and September 2010 had lower ($24\text{--}298 \text{ ng L}^{-1}$; Paul et al., 2013), but still detectable oil concentrations in the vicinity of the DWH wellhead.

The monthly and interannual variability of Mississippi River discharge rates are shown in Fig. 2. River discharge is typically highest in spring and lowest in fall. Spring and summer 2010 had higher than average river discharge rates, which occurred over an unusually extended period of time due to the opening of diversionary channels during the oil spill. The highest discharge rate occurred in spring 2011, although summer 2011 rates were only slightly higher than the monthly climatology. The lowest discharge was during 2012 in both spring and summer, when flows were below the mean. Spring and summer 2013 was another year that had higher than mean flow, while 2014 was an average year (close to the mean flow).

Environmental parameters for cruises in different seasons and years are shown in Tables 1 and 2. Post-oil spill, the mean ($\pm 1\text{SD}$, n) sea surface temperature during spring was $24.2 \pm 2.61 \text{ }^\circ\text{C}$ ($n = 49$), with temperatures significantly warmer in summer ($29.4 \pm 1.01 \text{ }^\circ\text{C}$, $n = 65$)

and significantly cooler in winter ($19.7 \pm 1.31 \text{ }^\circ\text{C}$, $n = 29$) (one-way ANOVA, Scheffe test, $p < 0.001$). The mean sea surface salinity during spring was 35.1 ± 1.31 ($n = 45$), summer was 31.5 ± 2.84 ($n = 64$), and winter was 35.8 ± 0.720 ($n = 29$). The lower salinities (<31) during spring and summer (Table 1) are evidence of Mississippi River outflow water spreading over the study area. Mean summer salinities were significantly lower than spring and winter values (one-way ANOVA, Scheffe test, $p < 0.001$), but spring and winter salinities were not significantly different ($p > 0.05$). The geometric mean (range, n) integrated chlorophyll concentration (0–100 m) for spring was 45.3 ($25.1\text{--}80.2 \text{ mg m}^{-2}$, $n = 30$), summer was 33.0 ($9.1\text{--}85.4 \text{ mg m}^{-2}$, $n = 34$), and winter was 38.5 ($24.5\text{--}60.6 \text{ mg m}^{-2}$, $n = 15$). Spring and summer chlorophyll concentrations were significantly different (Kruskal-Wallis ANOVA, Scheffe test, $p = 0.004$), but not significantly different from winter (Scheffe test, $p > 0.05$). February and May frequently had deep chlorophyll maxima (chlorophyll $>1.0 \mu\text{g L}^{-1}$) between 38 and 88 m depth (Fig. 3), while chlorophyll maxima off shelf during summer tended to be near surface, often in a low salinity surface layer when the Mississippi River outflow was high (e.g., 2010 and 2013). During summer along the PCB line over the Florida shelf, chlorophyll concentrations were usually highest near the sea floor between near shore and about 40 m depth and then chlorophyll formed a layer in the water column at about that depth extending off shelf (e.g., August 2012, Fig. 3).

Multivariate analyses indicated that pre-oil spill spring and summer environmental conditions between 2005 and 2009 were significantly different (PERMANOVA, $p = 0.003$), due to 30-day and 3-day average Mississippi River discharge, 3-day surface current magnitude, salinity, northward currents in spring, and greater surface-water temperatures in summer. No pairwise groupings of years were significantly different within spring or summer, probably due to the limited data available.

Multivariate environmental data analyses of post-oil spill years only evaluated differences between spring 2011–2013 and summer 2010–2013. Environmental conditions in spring were significantly different than those in summer (PERMANOVA test, $p = 0.001$), driven primarily by higher Mississippi River average discharge, 3-day wind magnitude, salinity, and westward (i.e., blowing towards the west) winds in spring, and higher temperatures and chlorophyll concentrations in summer. Each spring (2011–2013) was significantly different from each other ($p < 0.05$), primarily due to differences in Mississippi River discharge, temperature, chlorophyll, turbidity, wind magnitude, and wind direction. Summer 2010 and 2013 were not significantly different due to similar river discharge rates, but these years were significantly different ($p < 0.05$) from 2011 and 2012, primarily due to lower river discharge, followed by differences in chlorophyll, salinity, and temperature in 2011 and 2012.

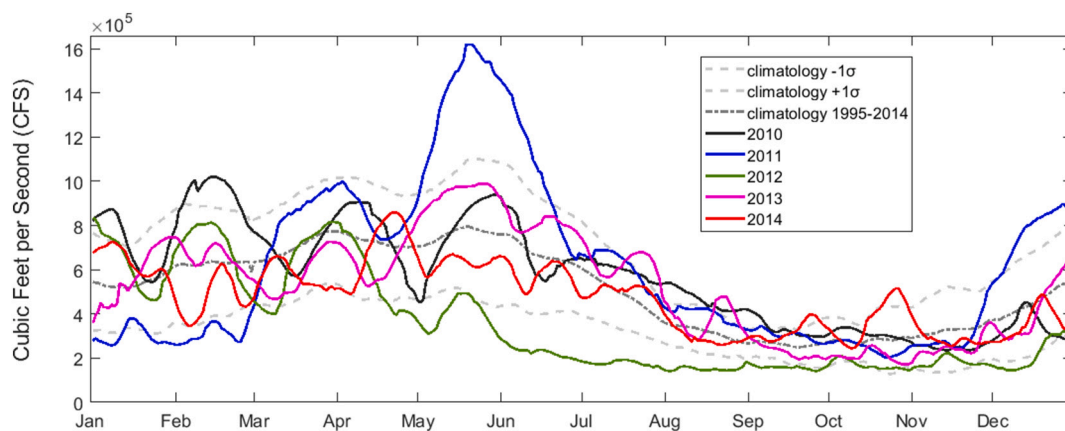


Fig. 2. Monthly Mississippi River discharge rates (cubic feet per second) at Tarbert Landing from 2010 to 2014, with the 20-year climatology mean \pm SD (1995–2014).

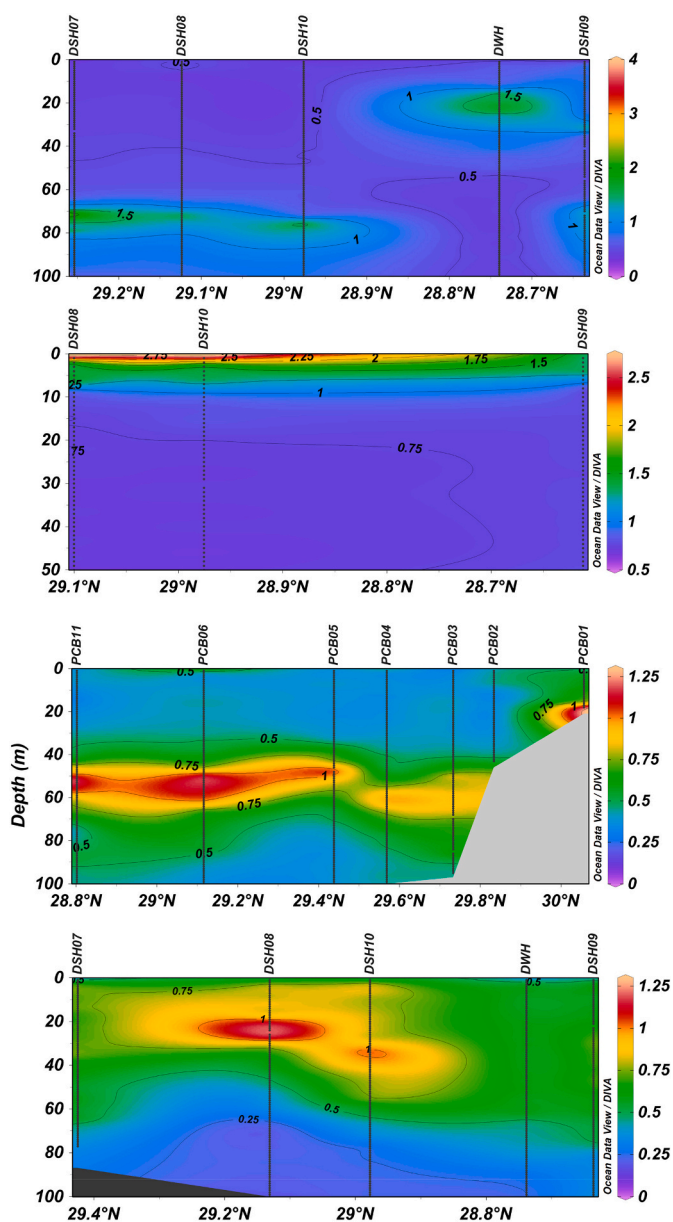


Fig. 3. Distribution patterns of chlorophyll fluorescence for May 2013, DSH stations (top panel), August 2010, DSH stations (upper middle panel), August 2012, PCB stations (lower middle panel), and February 2012, DSH stations (bottom panel). DSH stations are in a north-south orientation; PCB stations are in an east-west orientation.

3.2. Comparison of SIPPER and Bongo net results

There are advantages and disadvantages associated with each method. Bongo net tows are relatively simple to deploy in a short period of time, can be deployed in marginal weather conditions, and allow species identification, but provide no information on the vertical distribution of zooplankton. Small and/or soft-bodied zooplankton may be extruded through the mesh nets or damaged during collection. Camera systems, on the other hand, are more technologically complicated, have longer deployment times, cannot be deployed in marginal weather conditions, only a few taxa can be distinguished to species, but they usually detect higher abundances, particularly of fragile taxa, and provide detailed vertical resolution of zooplankton taxa (Remsen et al., 2004). During this study, the dominant taxa were similar in both SIPPER and Bongo tows. A comparison of the ratio of SIPPER abundance to

Bongo abundance for some of the dominant taxa [total copepods (4.3), ostracods (7.3), cladocerans (3.9), total Eumalacostraca (1.3), echinoderm larvae (7.9)] during August 2010 showed that SIPPER abundances were usually less than a factor of eight higher than that observed in Bongo tows. In contrast, small and soft-bodied taxa were substantially higher in SIPPER tows [e.g., *Oithona* spp. copepods (18.3), chaetognaths (17), larvaceans (79.8), gelatinous zooplankton (45)], owing to the standard, but relatively large Bongo net mesh size (333 μm) used. Consequently, the results from the two sampling approaches were evaluated separately.

3.3. SIPPER: zooplankton during and after the DWH oil spill

3.3.1. SIPPER: zooplankton behavior during the oil spill

SIPPER images from May–June 2010 were evaluated for any detectable differences in behaviors, such as feeding, locomotion, orientation, and reproduction. No observable differences in behavior in any zooplankton groups were identified in the vicinity of oil. In the upper 20 m of the water column where hydrocarbon concentrations were highest, predation behavior was observed by amphipods, chaetognaths, hydromedusae, ctenophores, pteropods, and squids (e.g., Fig. 4). Larvaceans were detected in their houses with visible pre-filters and ctenophores were imaged with tentacles extended in a feeding position. Many fish, shrimp, and other Eumalacostracans were observed in consistent orientation postures, suggesting that they controlled their position and may not have been stressed. *Lucifer* and other shrimps were sometimes imaged in an escape posture, indicating that they were aware of the SIPPER sampling tube. In addition, feeding behavior by a number of the hydromedusae, *Aglaura hemistoma*, was observed near surface, moving the tips of their tentacles in a circular motion as reported by Colin et al. (2005). SIPPER images from the late May–June 2010 cruise indicated that the straight-shelled pteropod, *Creseis* spp., which produces mucus strings to collect food particles, had dark brown guts and what appeared to be oil on its shell. This was confirmed by a neuston net collected immediately after the SIPPER deployment.

3.3.2. SIPPER: comparison of zooplankton during and after the DWH oil spill

Taxa that had maximum concentrations in the upper 20 m of the water column where oil concentrations were highest could have been strongly affected by the oil spill. SIPPER data revealed that 39% (geometric mean; range: 9–99%) of the zooplankton community in the upper 100 m occurred between 0 and 20 m during May and June 2010 (Fig. 5) and, therefore, was likely exposed to relatively high oil concentrations. Despite this, total integrated zooplankton showed no significant difference (Kruskal-Wallis ANOVA, $p = 0.064$) in abundances and weighted mean depths of zooplankton between May–June and summer after the wellhead was capped (August–September 2010) (Table 3). Also, spring 2010 total integrated zooplankton densities were not significantly different (Kruskal-Wallis ANOVA, $p = 0.065$) than integrated densities observed in the following two spring seasons (May 2011 and May 2012) (Table 1). The geometric mean (range) total integrated zooplankton abundances for all SIPPER tows during each season were spring: 192,177 individuals m^{-2} (111,454–340,900 individuals m^{-2}), summer: 214,400 (92,833–683,530 individuals m^{-2}), and winter: 364,576 (215,129–543,844 individuals m^{-2}). Winter integrated densities were significantly higher (Kruskal-Wallis ANOVA, $p = 0.041$) than spring and summer values; however, this difference may have been due, in part, to unusually high larvacean densities (609,261 individuals m^{-2} , 55% of total zooplankton) at PCB06 during February 2012. In fact, winter 2012 in general had high larvacean concentrations that were, on average, 40% of the total zooplankton, while total copepods also were about 40%.

The same zooplankton classes were observed during and after the oil spill (see Zooplankton Percent Composition section below; Table 3). During May–June 2010, large protists that could be resolved by SIPPER

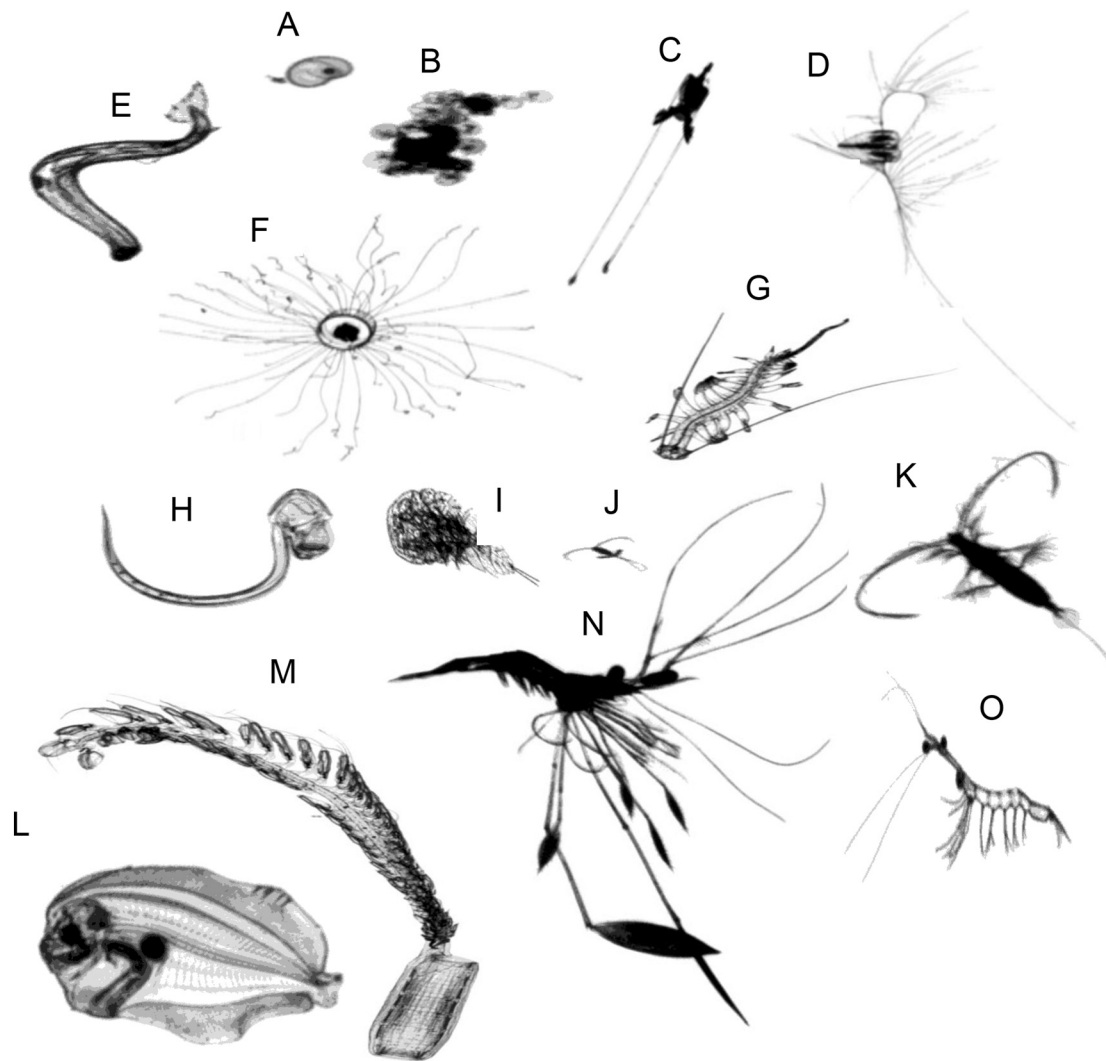


Fig. 4. SIPPER images showing zooplankton exhibiting normal behavior in the upper 20 m of the water column at oil-impacted stations during May 2010 (A - F) and during August 2010 at various depths (G - O). *Noctiluca*: (A) free and (B) attached to marine-oil-snow, (C) pteropod *Cavolinia* with tentacles extended, (D) cydippid ctenophore with tentacles extended, (E) chaetognath, (F) feeding behavior of the hydromedusae, *Aglaura hemistoma*, (G) pelagic polychaete, *Tomopteris*, (H) larvacean, (I) calanoid copepod, *Copilia*, (J) cyclopoid copepod, *Oithona*, (K) calanoid copepod, *Eucalanus*, (L) larval flat fish, (M) doliolid, (N) Eumalacostracan crustacean, and (O) sergestid shrimp, *Lucifer*. Size not necessarily to scale.

included spiny acantharians, foraminifera, the dinoflagellate, *Noctiluca*, and other large dinoflagellates, and radiolarians. Twelve mesozooplankton groups formed 89–98% of the total zooplankton imaged (Table 3), including: calanoid copepods, cyclopoid copepods (*Oithona* spp.), poecilostomatoid copepods (a suborder of Cyclopoida, e.g., *Oncaea*, *Farranula*, *Corycaeus*), chaetognaths, ostracods, echinoderm larvae, hydromedusae, siphonophores, doliolids, and larvaceans. Total copepods had the highest abundances followed by larvaceans. There was evidence of year-round secondary production based on images of larval classes. Copepod nauplii were present during every season, with the highest abundances during spring 2010 (maxima: 359 individuals m^{-3}). Echinoderm bipinnaria larvae were the most abundant larval class imaged and some individuals were present at most stations in every season, particularly at outer shelf and off-shelf stations. The highest maximum Echinoderm larval abundances occurred during spring (772 individuals m^{-3}) and summer (1064 individuals m^{-3}) 2010.

The vertical distribution of mesozooplankton taxa was variable between stations during the oil spill (Fig. 5). Calanoid copepods had maxima in the upper 20 m and weighted mean depths between 33 and 45 m (Table 3). Cyclopoid and poecilostomatoid copepods also frequently had maxima in the upper 20 m, with deeper maxima at some

stations. Chaetognaths had maxima in the upper 40 m early in May and were more evenly distributed through the water column later in May, with a weighted mean depth of 43 m. Hydromedusae also had maxima in the upper 20 m in early May and multiple depth maxima in late May–June. Similarly, larvaceans had high abundances in the upper 20 m of the water column. Overall, however, the weighted mean depths of these dominant zooplankton groups were deeper than the maximum oil concentrations in the upper 20 m. The remaining zooplankton groups, ostracods, doliolids, echinoderm larvae, and siphonophores, were common, but not abundant. Most siphonophores were small calyco-phorans, but other groups, including physonects and cystonects, also were observed.

Ostracod was the only image class that had significantly increased integrated abundances between May–June 2010 and August–September 2010 (Table 3). However, ostracods also increased between spring and summer in follow-on years; thus, the result was not unusual. Some interesting differences were observed for other taxa. Of particular note, unattached *Noctiluca* was the most abundant (up to 30,354 m^{-3}) taxa at the surface and in the upper 38 m of the water column, with many additional individuals observed in association with marine snow aggregates during the early May cruise (Figs. 4, 5). Two weeks later on the

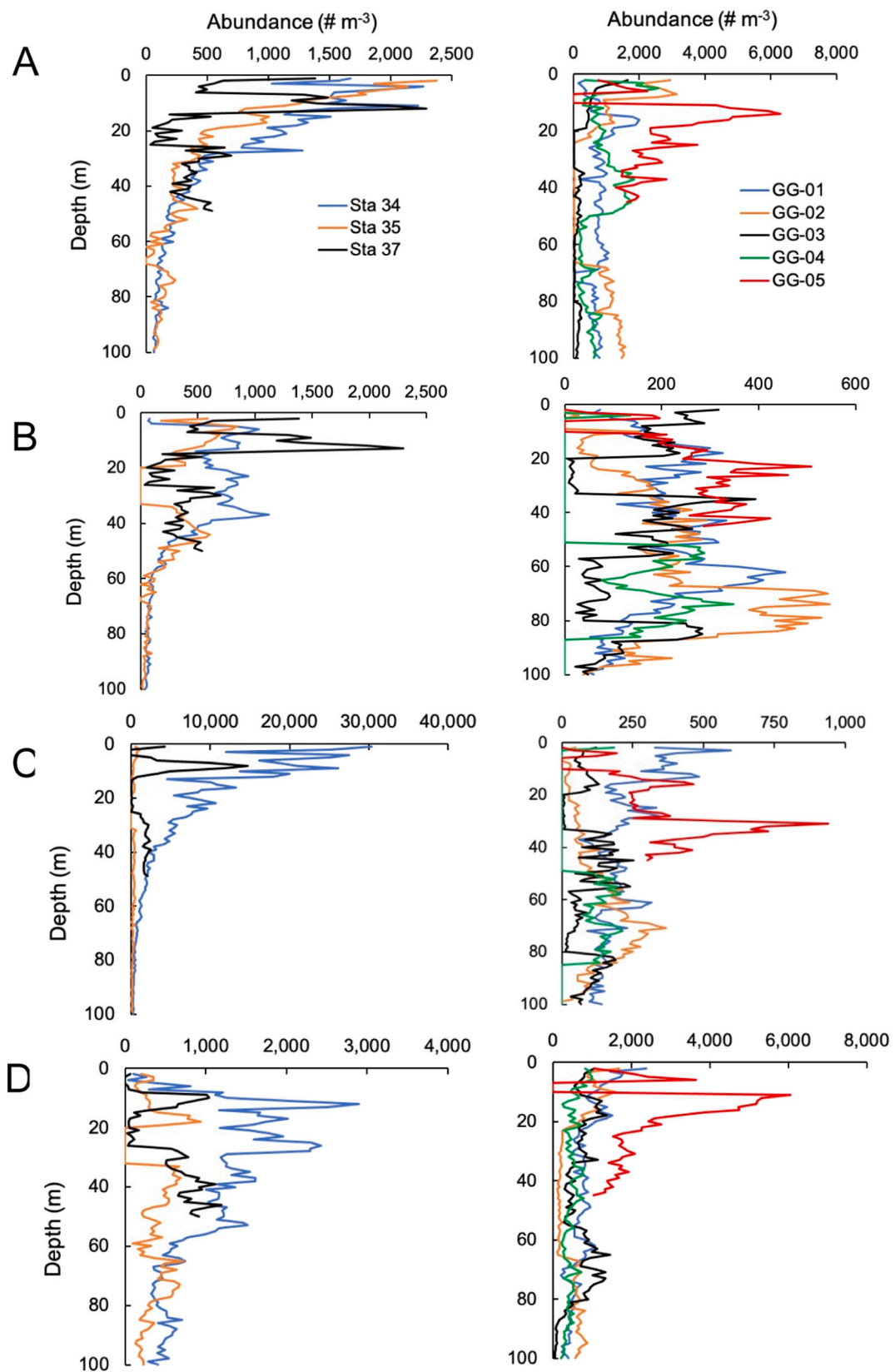


Fig. 5. Vertical distributions of abundance (individual m^{-3}) at different stations for (A) calanoid copepods, (B) chaetognaths, (C) *Noctiluca* sp., and (D) larvaceans, during the oil spill between 5 and 17 May (left panels) and 29 May – 3 June 2010 (right panels).

late May–June cruise, abundances were lower and individuals occurred deeper (51 m) in the water column. In spring 2011 and 2012, *Noctiluca* abundances were $< 1190 \text{ m}^{-3}$ and maximum densities were deeper (36–89 m) in the water column similar to the profiles observed in late May 2010. *Trichodesmium* colonies increased between spring and summer 2010, with maximum abundances increasing from 100s m^{-3} during May–June to $>1000 \text{ m}^{-3}$ during August, and $> 4000 \text{ m}^{-3}$ during September, but this same pattern was observed in 2011 and 2012.

Other less common zooplankton groups included the sergestid shrimp, *Lucifer*, Thecosomatous cone-shaped pteropods, consisting mainly of the genera *Clio* and *Creseis*, and fish eggs and larvae. *Lucifer* abundance maxima occurred in the upper 20 m (weighted mean depth of 13 m) during both the early May and late May–June cruises; however, total abundance declined by 1910%. In contrast in early May, pteropod maxima occurred in discrete layers at depths between 30 and 70 m at concentrations greater than $1000 \text{ individuals m}^{-3}$, while during late May–June abundances were much lower, with maximum concentrations ranging from 25 to $150 \text{ individual m}^{-3}$. Fish eggs were another group that occurred near surface. High concentrations of fish eggs were observed in early May in a patchy distribution between 4 and 7 m depth over several kilometers as SIPPER was towed along the boundary of the DWH exclusion zone.

3.3.3. SIPPER: zooplankton percent composition during summer 2010–2014

The dominant zooplankton classes ($> 5\%$ of the total community) observed on the shelf during summer were similar to those at the off-shelf stations with a few differences (Fig. 6). On-shelf classes (geometric means) included, calanoid copepods (17%), *Oithona* copepods (7%), poecilostomatoid copepods (8%), larvaceans (23%), chaetognaths (11%), and ostracods (8%). These classes accounted for 75–85% of the total zooplankton imaged over the shelf for each cruise, of which these copepod classes totaled 32%. Adding other SIPPER copepod classes together (e.g., unknown copepods, nauplii, *Copilia*, etc.) would only have added an additional 3% to a total copepod category at both on-shelf and off-shelf stations. Small hydromedusae and doliolids, which were among the dominant classes off shelf were, on average, $< 3\%$ of the total zooplankton on shelf. The percent composition of dominant classes at on-shelf stations was not significantly different (Kruskal-Wallis ANOVA, $p = 0.969$) between years.

The dominant classes observed during summer at off-shelf stations were: calanoid copepods (overall geometric mean: 20%), *Oithona*

copepods (8%), poecilostomatoid copepods (12%), larvaceans (28%), chaetognaths (9%), small hydromedusae (5%), and doliolids (3%). Together, these groups made up 88–89% of the images observed during each cruise, of which copepods were 40%. Calanoid copepods were abundant at all stations and years and their percent composition (13–24%), varied by less than a factor of two, while small hydromedusae (2.5–20%) and doliolids (1.2–10%) were abundant only in some years. The carnivorous chaetognath had geometric mean integrated abundances ranging from a minimum of $13,530 \text{ individuals m}^{-2}$ in 2011 to a maximum of $23,058 \text{ individuals m}^{-2}$ in 2013, which was a relatively stable percent composition of 7.5 to 11% for all years. Larvacean geometric mean integrated abundances ranged from a minimum in 2011 ($47,396 \text{ individuals m}^{-2}$) to a maximum in 2013 ($88,586 \text{ individuals m}^{-2}$), with an overall 25 to 35% variation in percent composition. The small particle-feeding copepods, *Oithona* (6.8–10%) also maintained a relatively narrow range of percent composition values. Overall, the percent composition of dominant classes at off-shelf stations was not significantly different (Kruskal-Wallis ANOVA, $p = 0.915$) between years. Thus, there was no detectable difference in percent composition of zooplankton classes during summer 2010 after the wellhead was capped and follow-on years.

Mean winter and spring percent composition of some classes also were remarkably consistent. Chaetognaths ranged from 6 to 10% in winter and 13–14% in spring, *Oithona* were 6–9% and 7–9%, and poecilostomatoid copepods were 7–9% and 7–10%, respectively. Calanoid copepods were somewhat lower in winter (17–18%), but spring (21–22%) values were similar to that in summer. In contrast, larvacean percent composition was more variable during winter than in spring and summer (winter: 24–40%; spring: 23–35%).

3.3.4. SIPPER: influence of environmental variability on zooplankton abundance

The influence of Mississippi River outflow on the interannual variability of zooplankton abundance and vertical distribution during summer in the NEGOM can be seen in Figs. 7–9. Integrated zooplankton abundances were higher during 2010 and 2013, when river discharge was relatively high (see Fig. 2), compared to abundances during lower river flow years (Fig. 7). Despite the oil spill, integrated zooplankton abundance from SIPPER tows was significantly higher during 2010 than all other years, including 2013 (Kruskal-Wallis ANOVA, $p = 0.0005$), while none of the other years were significantly different ($p > 0.05$) from each other. The Mississippi River plume also influenced the vertical

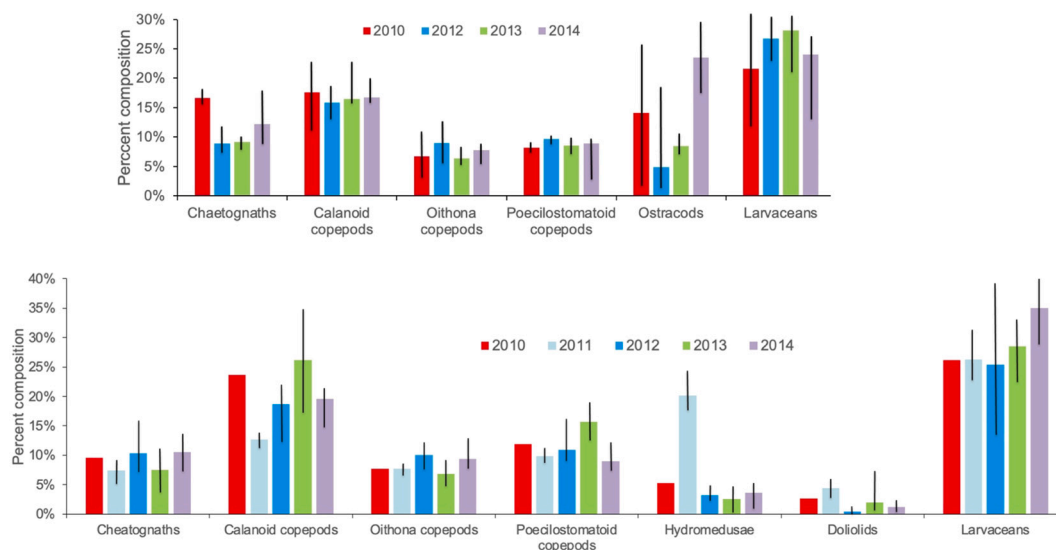


Fig. 6. Interannual variability in the geometric mean (range) percent composition of dominant zooplankton taxa in SIPPER tows at on-shelf stations (upper panel) and off-shelf stations (lower panel) during summer 2010–2014.

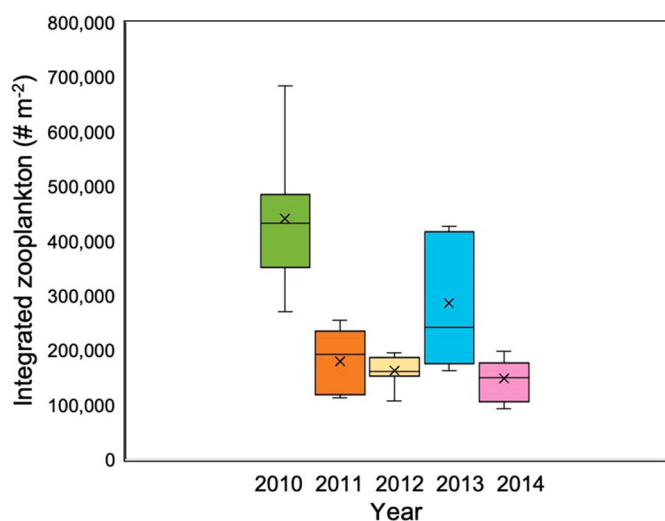


Fig. 7. Box-Whisker plots of interannual variability of integrated zooplankton abundance (individuals m^{-2} , 2–100 m) for SIPPER tows during summer (August and September 2010–2014). X is the mean, the horizontal line is the median, boxes are the first and third quartiles, and extended lines are the minimum and maximum values for each year.

distribution and magnitude of chlorophyll and zooplankton in the region. During a lower river flow summer (e.g., September 2011, Fig. 8), surface salinities were > 32 , shallow pycnoclines had variable depths, chlorophyll maxima occurred between 28 and 57 m, and chlorophyll concentrations were primarily $< 1 \text{ mg } m^{-3}$. Zooplankton had maximum concentrations near surface and secondary maxima (26–48 m) in the vicinity of the depths of chlorophyll maxima. In contrast during summer 2013, when there was high river discharge, river plume water covered much of the off-shelf study area forming a lens of low salinity (< 32) water near surface, which led to very shallow pycnoclines (Fig. 9). Chlorophyll maxima occurred in the upper 5 m of the water column, with 2-fold higher concentrations than was observed during 2011. Zooplankton maxima also occurred in the upper 5 m, with densities 3.4 to 5.8 times higher than those in 2011.

Although years with higher chlorophyll led to higher zooplankton abundances overall, there was wide range of spatial variability between stations and not a clear relationship between these two variables. Integrated zooplankton during spring (2010 to 2014) had a positive linear relationship with integrated chlorophyll fluorescence, but chlorophyll only explained about 13% of the variability in zooplankton abundance (Fig. 10). In contrast, integrated chlorophyll and integrated zooplankton had a negative relationship during summer, with integrated chlorophyll accounting for 30% of the variability in zooplankton. There was no relationship during winter, likely due to the limited availability of data.

3.4. Bongo tows: zooplankton community structure post-oil spill

3.4.1. Bongo tows: zooplankton abundance post-oil spill

Seasonal changes in total zooplankton abundance and distribution after the oil spill (August 2010–August 2014) are shown in Fig. 11. Spring and summer zooplankton abundances were highest near shore (PCB01, 25 m depth), declined towards the outer shelf (PCB03, 100 m), and then were lower and variable at PCB04 (200 m), shelf slope, and off-shelf (> 200 m) stations. During August 2010 just after the DWH well-head was capped, the maximum total zooplankton abundance at PCB01 was 1636 individuals m^{-3} , which was the third highest abundance observed overall. August 2010 abundances at DSH off-shelf stations were slightly lower (122 and 147 individuals m^{-3}) than subsequent years. The two highest abundances overall occurred during spring and summer 2011 at PCB01 (4619 and 3276 individuals m^{-3} , respectively).

The mean spring off-shelf abundance [geometric mean (range): 282 (113–568 individuals m^{-3})], was similar to the mean summer off-shelf abundance [geometric mean (range): 288 (122–726 individuals m^{-3})]. Although winter 2011 had the highest zooplankton abundance at the near shore site (PCB01, 807 individuals m^{-3}), similar to spring and summer distributions, winter 2012 and 2013 had highest abundances at mid- and outer-shelf stations (2012: 1353 individuals m^{-3} ; 2013: 1000 individuals m^{-3}). Surprisingly, the mean off-shelf winter abundance [geometric mean (range): 234 (114–599 individuals m^{-3})] was similar to spring and summer values. Overall, there was no significant difference between seasons in total zooplankton abundances at shelf (Kruskal-Wallis ANOVA, $p = 0.389$) and off-shelf stations (Kruskal-Wallis ANOVA, $p = 0.737$).

3.4.2. Bongo tows: zooplankton biomass post-oil spill

Biomass of total zooplankton showed similar spatial and temporal patterns as abundance data (Fig. 12). During spring and summer, the highest biomass values were near shore (PCB01), while during winter the highest values were further out on the shelf (PCB02). In contrast to abundance, however, the maximum biomass concentrations occurred in spring 2012, due to a large number of salps that were collected in the Bongo nets. The geometric mean (range) biomass concentrations were not significantly different (Kruskal-Wallis ANOVA, $p = 0.972$) between seasons: spring was $14.1 \text{ mg } m^{-3}$ (2.12–567 $\text{mg } m^{-3}$), summer was $15.4 \text{ mg } m^{-3}$ (6.1–107 $\text{mg } m^{-3}$), and winter was $11.5 \text{ mg } m^{-3}$ (0.472–67.5 $\text{mg } m^{-3}$). More than 90% of the values fell between 0.472 and 28.9 $\text{mg } m^{-3}$.

3.4.3. Bongo tows: zooplankton species composition post-oil spill

Although the composition of the zooplankton community varied between stations, seasons, and years, the dominant zooplankton group was usually copepods (geometric mean of all cruises: 54%). The mean percent composition of copepods (both calanoid and non-calanoid) of the total zooplankton community was not significantly different between seasons (one-way ANOVA, $p = 0.750$) [geometric mean (range); spring: 51.2% (6.15–63.2%); summer: 54.4% (24.2–90.3%); winter: 56.6% (35.8–81.7%)]. About 70% of the stations had copepod percent composition values between 50 and 70%. However, near shore stations frequently (50% of the tows) had copepod percent composition values $< 50\%$, particularly during spring and summer, when other taxa (e.g., larvaceans, doliolids, ostracods, and salps) had episodic, large aggregations. During August 2010, only four bongo tows were completed before a tropical storm ended the cruise. Of those stations, the zooplankton community at PCB02 had an unusually high percent of copepods (90.3%), while PCB01 and the off-shelf stations with the greatest oil exposure were typical of other summer values (PCB01: 53.5%, DSH09: 66.1%, DSH10: 75.9%).

Ninety-six species, 20 genera (e.g., *Oithona* spp.), and 19 groups (e.g., unknown calanoid copepods) of copepods were identified in Bongo tows. During August 2010, the most abundant copepods were *Centropages velificatus*, *Subeucalanus pileatus*, *Oithona* spp., *Corycaeus* spp., *Temora turbinata*, *Labidocera* spp., *Acartia danae*, *Oncaea* spp., and *Copilia* spp. (Fig. 13). *Centropages velificatus* had the highest densities of any zooplankton and was unusually abundant near shore during August 2010 (PCB01: 731, PCB02: 235 individuals m^{-3}) and May 2011 (PCB01: 1284 individuals m^{-3}), it was the second most abundant species after *Temora turbinata* in September 2011 (PCB01: 643 individuals m^{-3}) (Fig. 14), and occurred in lower abundances at deep-water stations (Figs. 13–15). *Centropages velificatus* also was the dominant near shore species during August 2012, August 2013, and August 2014, although at lower densities than during August 2010 (Fig. 15). Winter abundances were very low even near shore (8.56–37.1 individuals m^{-3}). Low concentrations of copepodite stages (C1–C5) were present at on-shelf and off-shelf stations during all seasons, with C4 and C5 being the dominant juvenile stages during spring and summer. Male:female ratios near shore during spring and summer ranged from 0.70–1.05. A different suite of

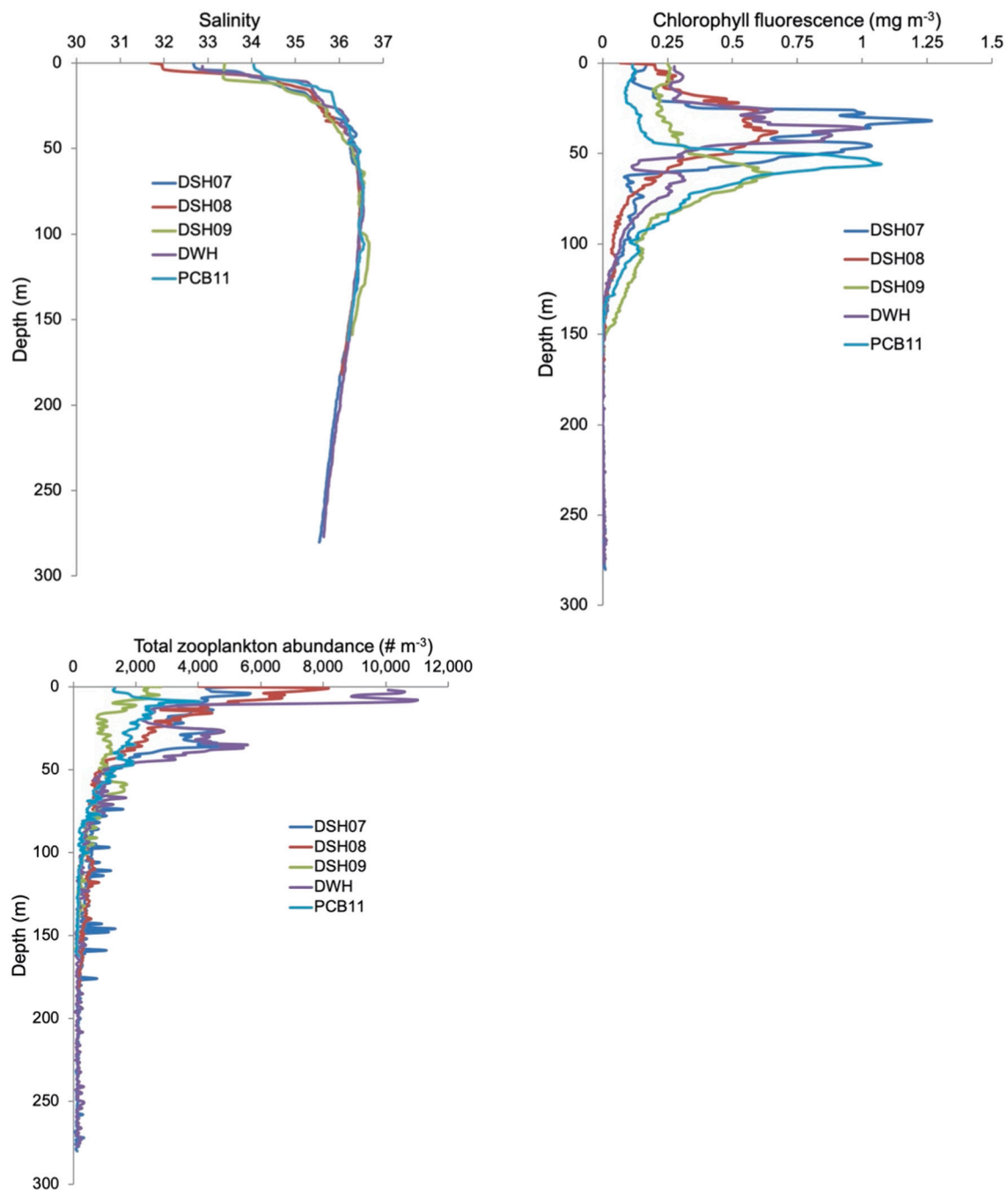


Fig. 8. Vertical profiles of salinity, chlorophyll fluorescence (mg m^{-3}), and total zooplankton abundance (individuals m^{-3}) for SIPPER stations during September 2011, when Mississippi River discharge was relatively low.

copepods dominated the system in winter, typically *Paracalanus* spp., *Corycaeus* spp., *Oithona* spp., *Ctenocalanus vanus*, *Oncaea* spp., *Nannocalanus minor*, and *Clausocalanus furcatus* (Fig. 14). *Paracalanus* spp. (262 individuals m^{-3}) followed by *Corycaeus* spp. (87 individuals m^{-3}) were the numerically dominant genera at the near shore station in February 2011, while *Oithona* spp. (maximum: 165 individuals m^{-3}) were usually the dominant genera at other stations on and off shelf. Densities of most other species were usually low at all stations during winter (< 50 individuals m^{-3}). Given the natural seasonal variability, there was no evidence that any of the dominant copepod species or genera declined or disappeared from the system following the oil spill.

One hundred and fourteen categories (1 species, 10 genera, and 103 other taxonomic categories) were identified for other zooplankton taxa

(not copepods). The spatial, seasonal, and interannual distribution of other taxa (Fig. 16) showed the same patterns as the distributions of total zooplankton and copepods. The highest abundances occurred near shore and decreased at off-shelf stations. August 2010, when low concentrations of oil were still detectable, had the third highest abundance at the near shore station (PCB01), while May and September 2011 had the highest abundances. During August 2010, PCB01 species composition was dominated by ostracods (444 individuals m^{-3}) and chaetognaths (113 individuals m^{-3}), whereas during May 2011 the dominant taxa were a more diverse group: doliolids (631 individuals m^{-3}), chaetognaths (592 individuals m^{-3}), cladocerans (388 individuals m^{-3}), ostracods (340 individuals m^{-3}), decapods (286 individuals m^{-3}), and echinoderm larvae (162 individuals m^{-3}). During September 2011, the

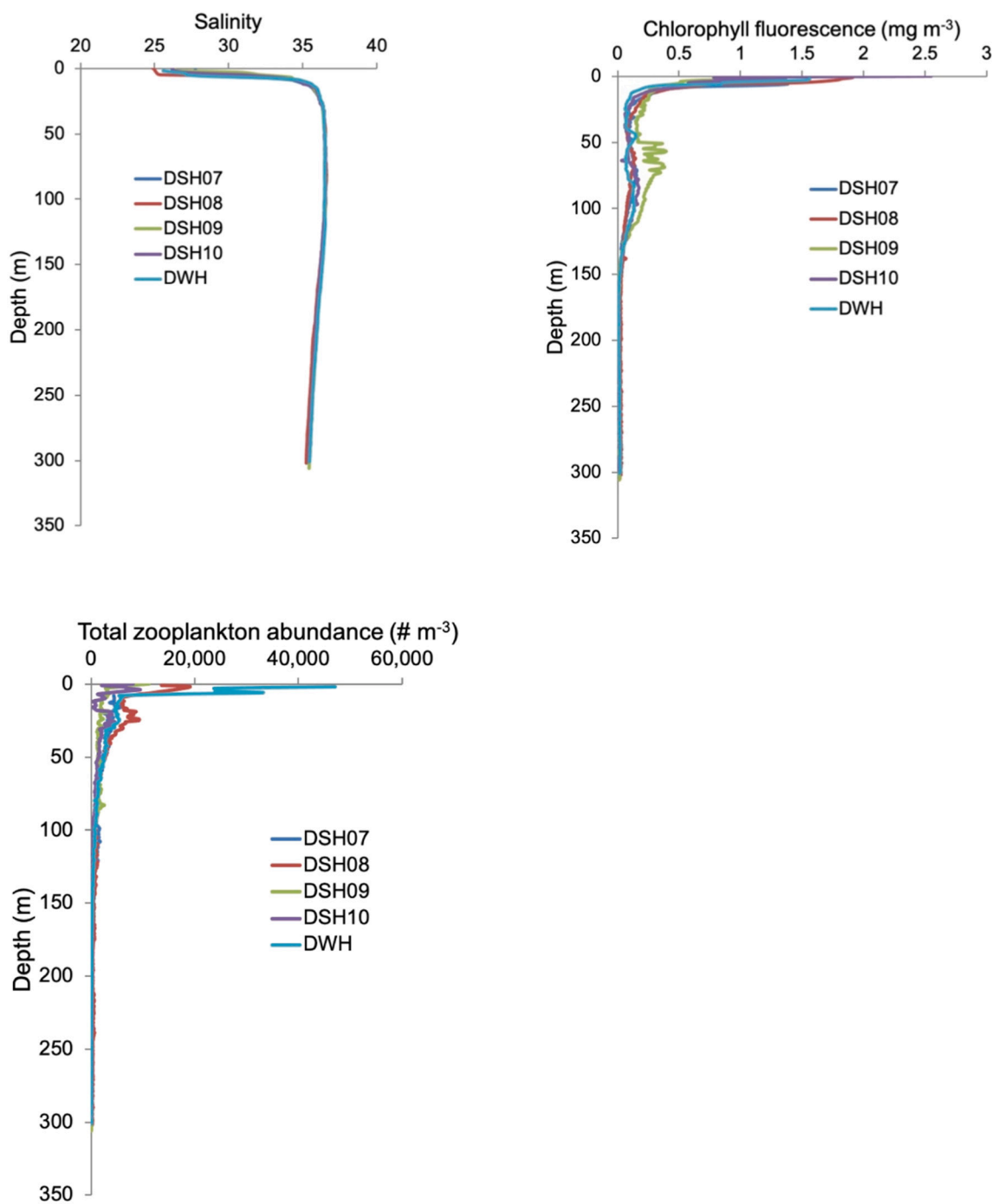


Fig. 9. Vertical profiles of salinity, chlorophyll fluorescence (mg m^{-3}), and total zooplankton abundance (individuals m^{-3}) for SIPPER stations during August 2013, when Mississippi River discharge was high.

taxa with the highest densities included ostracods (947 individuals m^{-3}), chaetognaths (324 individuals m^{-3}), larvaceans (238 individuals m^{-3}), and cladocerans (114 individuals m^{-3}). Off-shelf stations had lower abundances than shelf stations. The most frequently abundant taxa off shelf and at all stations during winter were larvaceans, chaetognaths, ostracods, doliolids, foraminifera, and other gelatinous zooplankton. There was no evidence that any of the dominant zooplankton taxa declined or disappeared from the system following the oil spill.

3.4.4. Bongo tows: zooplankton diversity indices post-oil spill

Patterns in biological diversity were assessed using different indices

to evaluate both species richness and evenness (similarity in species abundance), including species rank abundance, Shannon, Inverse Simpson, and Gini Simpson indices. Changes in species rank abundance of copepods for different stations during the first year after the oil spill are shown in Fig. 17. Species rank abundance plots visualize species richness and evenness, where the steep slopes of lines indicate low evenness (dissimilarity in abundance) and shallow slopes indicate high evenness. Species richness was low and assemblages were less even at inner shelf stations. Off-shelf stations had shallower slopes, indicating there were a few species with high densities, a larger number of species with intermediate densities, and a few species with low, similar densities. August 2010 deep-water stations had a lower species rank

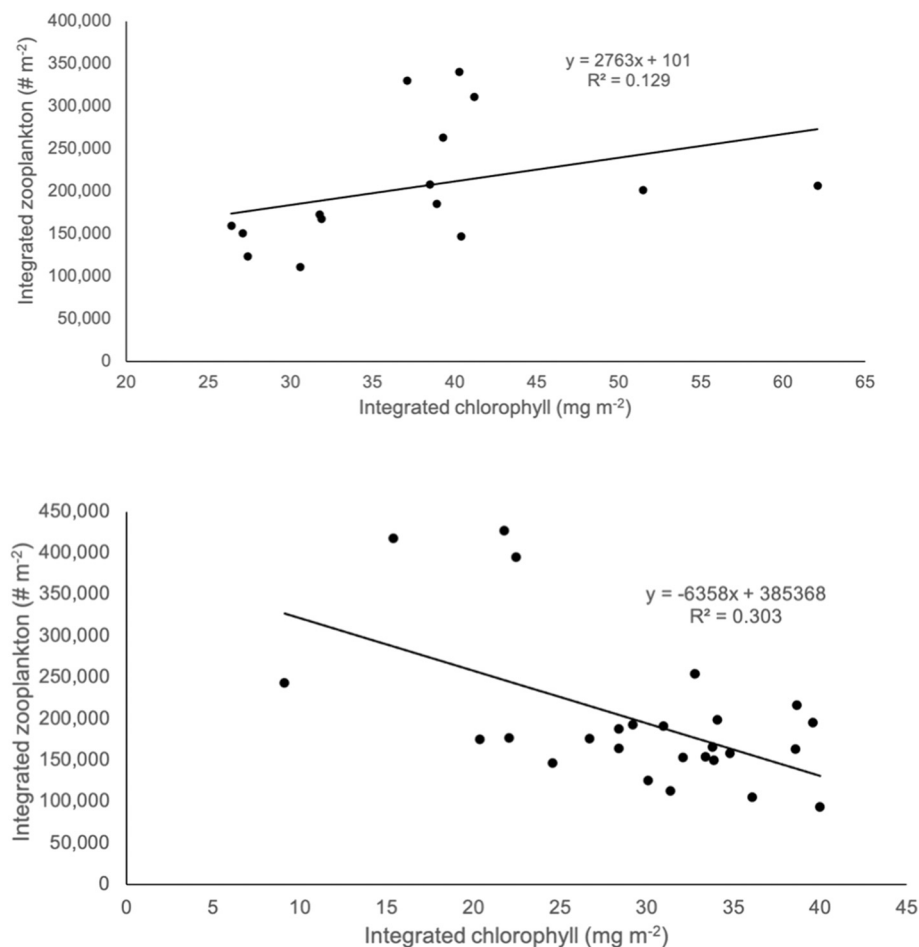


Fig. 10. Linear regression of SIPPER integrated zooplankton (individuals m^{-2} ; 2–100 m) on integrated chlorophyll fluorescence ($mg\ m^{-2}$, 0–100 m) during spring (upper panel) and summer (lower panel), between 2010 and 2014.

abundance than that in May and August 2011. The additional number of species present during spring and summer 2011 were all relatively rare species that were sporadically present at low densities, such as *Calocalanus pavoninus*, *Paracandacia simplex*, *Centropages caribbeanensis*, *Eucalanus sewelli*, *Haloptilus longicirrus*, and *Rhincalanus cornutus*. Thus, it was uncertain whether the lower species rank abundance in August 2010 was due to the oil spill or spatial variability of rare species.

Plots of the Shannon index also showed that diversity was lowest near shore and highest over the shelf slope and in deep water off shelf (Fig. 18). Although only the Shannon index is shown here, all of the diversity indices showed similar distribution patterns. August 2010 had one of the lowest Shannon indices near shore where *Centropages* densities were high, but off-shelf values, where zooplankton had the greatest exposure to oil, showed a broad range, with values that were both lower and higher than other years. Winter diversity values over the shelf did not show as steep a slope (i.e., higher diversity near shore) as values during spring and summer. Despite these differences, Shannon indices were not significantly different between years within spring, summer, and winter (Kruskal-Wallis ANOVA, $p > 0.05$). Indices also were not significantly different between seasons (Kruskal-Wallis ANOVA, $p = 0.098$).

Multivariate analyses indicated zooplankton beta diversity, which takes into account both abundance and species composition, was primarily influenced by surface chlorophyll and integrated chlorophyll during spring, while integrated chlorophyll, 21-day average Mississippi River discharge, and 7-day average Mississippi River discharge rates were important during summer (AIC, $p = 0.001$). Multivariate analyses also demonstrated that zooplankton beta diversity was significantly

different (PERMANOVA test, $p = 0.001$) between spring (2011–2013) and summer (2010–2013). SIMPER results revealed that the important taxa separating seasons were *Centropages* spp., ostracods, *Temora* spp., cladocerans, salps, *Eucalanus* spp., and *Lucicutia* spp., which accounted for about 27% of the variability between spring and summer. PERMANOVA results also showed that zooplankton beta diversity during spring was not significantly different ($p > 0.05$) between any two years, despite the fact that spring 2011 had much higher abundances of zooplankton near shore compared to other years. In contrast, zooplankton beta diversity was significantly different (PERMANOVA tests, $p < 0.05$) between all years in summer, except 2010. Thus, there was no significant difference ($p > 0.05$) in beta diversity just after the oil spill (summer 2010) and follow-on years. SIMPER results indicated that stomatopods, *Centropages* spp., *Acartia* spp., ostracods, salps, chaetognaths, and doliolids accounted for nearly 30% of total interannual variation during summer.

3.5. SEAMAP Bongo tows: zooplankton abundance pre-spill (2005–2009)

Zooplankton at the near shore SEAMAP station (B167) were identified to species/taxa by microscopic analyses for summer 2006 and 2009 and by Zooscan image analysis the other years, to determine whether *Centropages velificatus* was a dominate species during the pre-oil spill years, as well as the post-oil spill years. During September 2006, the top three dominant copepod species were *C. velificatus* (80 individuals m^{-3}), *Subeucalanus pileatus* (35.7 individuals m^{-3}), and *Oithona* spp. (8.9 individuals m^{-3}) and in September 2009 they were *Subeucalanus pileatus*

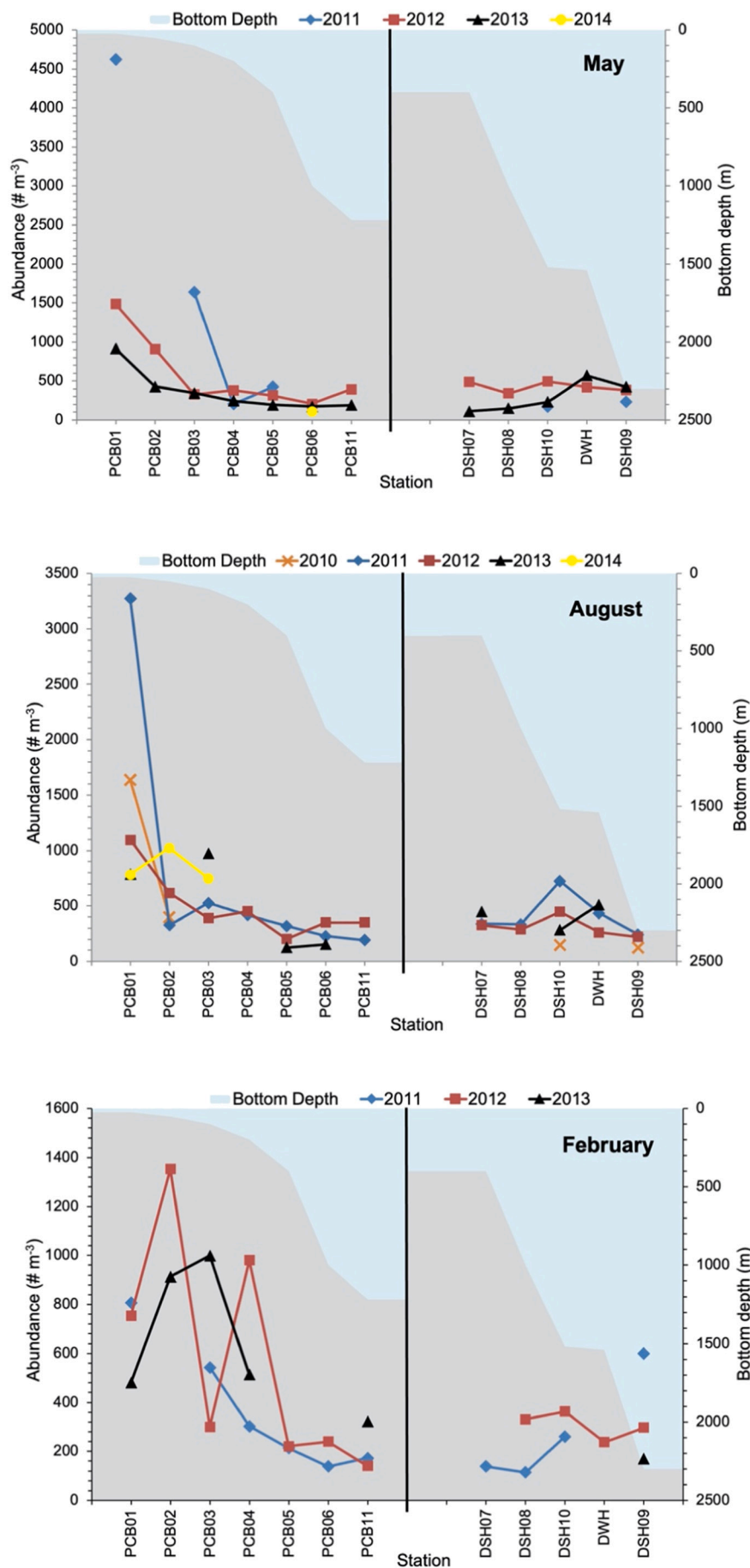


Fig. 11. Total zooplankton abundance (individuals m⁻³) from Bongo tows at post-oil spill stations during spring, summer, and winter (August 2010 – August 2014). The depth of the seafloor at each station is shown in brown, the depth of the water column is in blue. Abundances at PCB stations over the Florida shelf and De Soto Canyon are on the left; abundances at DSH stations south of Mobile Bay are on the right. Note changes in scale on the left y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(85.3 individuals m^{-3}), followed by *Oithona* spp. (87.4 individuals m^{-3}) and *C. velificatus* (75 individuals m^{-3}). During September 2007 and 2008, *Centropages* spp. was the dominant copepod at 20 and 32 individuals m^{-3} , respectively. Overall, the pre-spill summer abundances of *C. velificatus* at the near shore station were significantly lower (Mann-Whitney *U* test, $p = 0.012$) than the post-spill summer densities (range: 80–731 individuals m^{-3}).

The highest pre-spill total zooplankton abundance (1721 individuals m^{-3}) occurred during September 2009 at the near-shore station (B167) (Table 2). The geometric mean (range) total zooplankton abundance was 193 (52–655 individuals m^{-3}) during spring and 232 (57–1721 individuals m^{-3}) during summer, compared to post-spill densities in bongo tows [spring: 381 (113–4619 individuals m^{-3}); summer: 406 (122–3276 individuals m^{-3})]. The average pre-spill Bongo tow abundances were within the range of the post-oil spill densities; however, some pre-spill abundances were lower than any observed after the oil spill, when no tows had <100 individuals m^{-3} . Pre-spill spring total zooplankton abundances were significantly lower (Mann-Whitney *U* test, $p = 0.005$) than the post-spill abundances, but summer concentrations were not significantly different before and after the oil spill ($p = 0.074$). The geometric mean (range) percent composition of copepods during spring was 65% (55–76%) and during summer was 33% (16–64%). The spring composition was not significantly different (Mann-Whitney *U* test, $p = 0.09$) than post-spill values, but summer was significantly lower ($p = 0.019$) than post-spill percentages.

Pre-spill zooplankton beta diversity was significantly different (PERMANOVA, $p = 0.025$) between spring and summer seasons when data from all years (2005–2009) were considered. Higher concentrations of *Eucalanus* spp. were observed during spring, while higher concentrations of bivalves, ostracods, *Centropages* spp., cladocerans, echinoderm larvae and juveniles, pteropod *Limacina* spp., and stomatopods were significant indicator species for summer. SIMPER results showed that these groups, along with crab zoea, accounted for 27% of the variability between spring and summer. Beta diversity was not significantly different ($p > 0.05$) between years within spring or summer, likely due to the limited number of Bongo tows available.

3.6. Bongo tows: influence of environmental variability on pre- and post-oil spill zooplankton beta diversity

The impacts of environmental variability on zooplankton beta diversity during the pre-spill period (2005–2009) were not significant for either spring or summer. However, environmental variability did significantly (distance-based redundancy test, $p = 0.001$) affect beta diversity during post-oil spill spring and summer seasons, accounting for 77% of the variability in zooplankton beta diversity during spring and 74% during summer. Akaike's Information Criterion (AIC) test revealed that surface chlorophyll and integrated chlorophyll fluorescence were critical factors that explained variability in spring zooplankton beta diversity, while integrated chlorophyll fluorescence, 21-day average Mississippi River discharge, and 7-day average Mississippi River discharge were the significant factors explaining variability in summer zooplankton beta diversity.

4. Discussion

4.1. Zooplankton abundance and biomass

Total zooplankton abundances were highly variable spatially, seasonally, and interannually in the northeastern Gulf of Mexico (NEGOM) (Figs. 7, 11). Zooplankton collected in Bongo tows were used to show cross-shelf spatial and temporal patterns, as more Bongo tows were completed than SIPPER tows. Zooplankton abundances were highest near shore in spring and summer, where chlorophyll concentrations are highest (Nababan et al., 2011), and decreased off shelf. The highest near shore abundances occurred in spring (4619 individuals

m^{-3}) and summer (3276 individuals m^{-3}) 2011, followed by summer 2010 (1636 individuals m^{-3}). Despite the large interannual differences near shore, seasonal geometric mean abundances (range: 113–726 individuals m^{-3}) were not significantly different among shelf stations ($p = 0.389$) or among off-shelf stations ($p = 0.737$) in Bongo tows, probably due to the patchy nature of zooplankton. GOM zooplankton abundances in sequential net tows may vary by one to two orders of magnitude on the shelf (Iverson and Hopkins (1981) and by a factor of five off shelf (Rathmell, 2007). Bongo and SIPPER densities could not be directly compared, as SIPPER abundance estimates were much higher than that in Bongo tows, owing to SIPPER's enhanced detection of small and fragile zooplankton. The geometric mean (range) zooplankton abundance for all SIPPER off-shelf tows was 2211 individuals m^{-3} (947–11,432 individuals m^{-3}), while Bongo abundances were typically an order of magnitude lower (Fig. 11). Near shore, SIPPER total zooplankton abundance at PCB01 was much higher than that in Bongo tows. For example, during August 2010 SIPPER densities ranged from 4826 individuals m^{-3} at the surface with the highest concentrations (15,153–18,919 individuals m^{-3}) in the bottom four meters (19–22 m), which was much higher than the total Bongo abundance of 1636 individuals m^{-3} (Fig. 11). Remsen et al. (2004) compared SIPPER and net results, using a high-resolution sampling net (162 μm mesh), which collected zooplankton from the same volumes of water that SIPPER imaged. These authors demonstrated that zooplankton densities in nets were similar to values previously published; however, nets greatly underestimated larvacean, doliolid, protoctist, and cnidarian/ctenophore abundance by 300%, 379%, 522%, and 1200%, respectively, compared to SIPPER results. Thus, zooplankton abundance and composition from our Bongo net results are likely under-estimates, particularly for gelatinous zooplankton.

Direct comparison of zooplankton abundance and biomass with previous net studies is also hampered by the use of different types of nets, different net mesh sizes, studies at different times of the year, and different locations. In addition, biomass is often reported as displacement volumes or wet biomass instead of dry weight. Nevertheless, previous studies in the NEGOM and West Florida Shelf generally observed similar spatial and temporal patterns of zooplankton abundance as our study, with highest abundances and the greatest annual variation in abundance occurring near shore or associated with the Mississippi River plume, and highest abundances occurring during spring and summer (Houde and Chitty, 1976; Iverson and Hopkins, 1981; Ortner et al., 1989). Zooplankton abundances reported for near shore and Mississippi River sites using smaller mesh nets or pumps are within the range of SIPPER densities. Lester (2005), reported maximum abundances (15,179 individuals m^{-3} ; 153 μm mesh Bongo net) near shore off Tampa Bay, during summer and fall, with lower densities in winter. Ortner et al. (1989) observed higher copepod densities (3124 individuals m^{-3} ; 333 μm mesh, MOCNESS net) in the Mississippi River plume during spring and lower densities in winter; lower spring densities (1059 individuals m^{-3}) also occurred on the Florida shelf. Carassou et al. (2014) documented a maximum calanoid copepod density of ca. 10,000 individuals m^{-3} (333 μm mesh, BIONESS net) during June 2010 at near shore sites adjacent to Mobile Bay. The maximum abundances of other zooplankton groups varied between late spring and summer in different years (2005–2010). There are few reports of zooplankton dry weights for comparison. Publications reporting displacement volumes observed higher biomass near shore, decreasing offshore (Houde and Chitty, 1976) and higher displacement volumes in the Mississippi River plume compared to the Florida shelf or a deep-water station (Ortner et al., 1989). Zooplankton dry weight biomass values (maximum: 11.9 $mg m^{-3}$, integrated 0–200 m: 35.1 $mg m^{-2}$) during summer at an off-shelf station (Hopkins, 1982) were within the range of our summer off-shelf biomass values (geometric mean, range: 12.8 $mg m^{-3}$, 6.24–34.5 $mg m^{-3}$). A study on the Alabama and north Florida shelves using a 200 μm mesh net observed zooplankton biomass values of 101 and 189 mg dry weight m^{-3} , respectively (Iverson and Hopkins, 1981). Sutor and Dagg

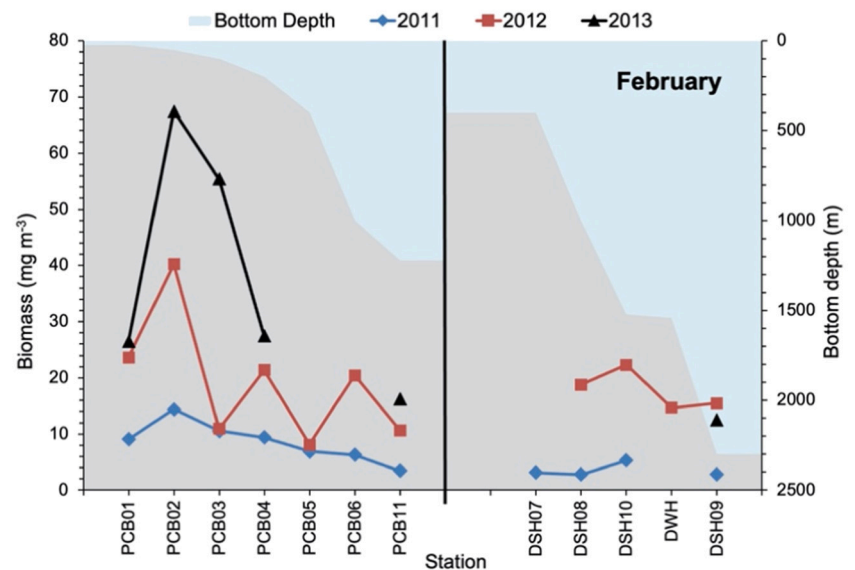
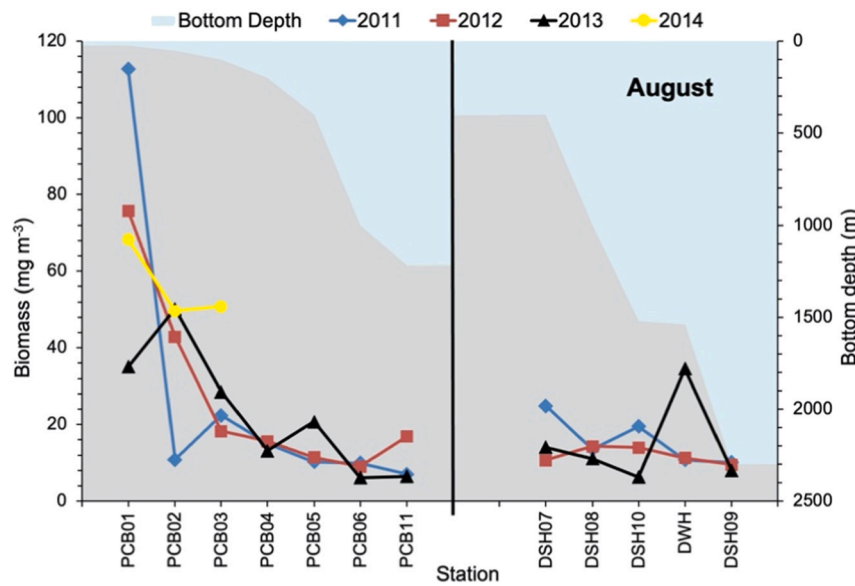
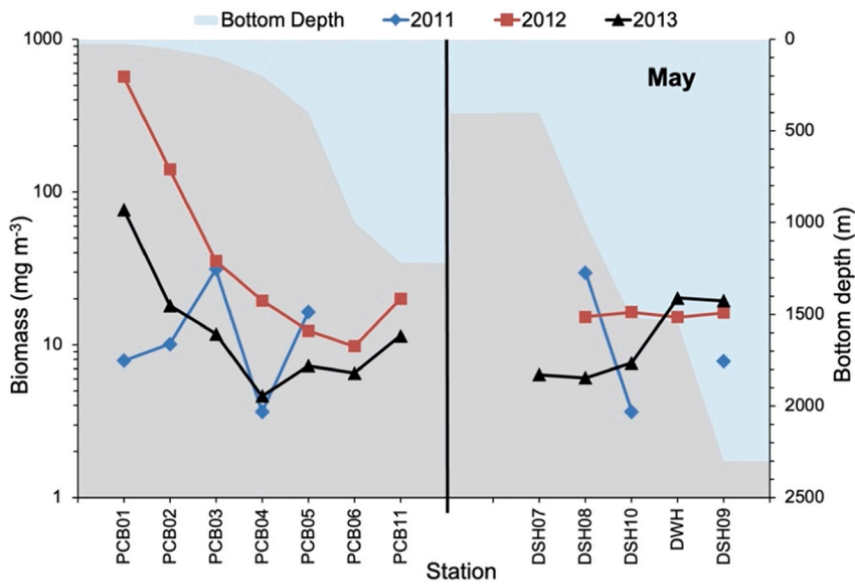


Fig. 12. Total zooplankton biomass (mg m^{-3}) concentrations from Bongo tows at post-oil spill stations during spring, summer, and winter (February 2011 – August 2014). The depth of the seafloor at each station is shown in brown, the depth of the water column is in blue. Biomass at PCB stations over the Florida shelf and De Soto Canyon are on the left; biomass at DSH stations south of Mobile Bay are on the right. Note changes in scale on the left y-axis (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

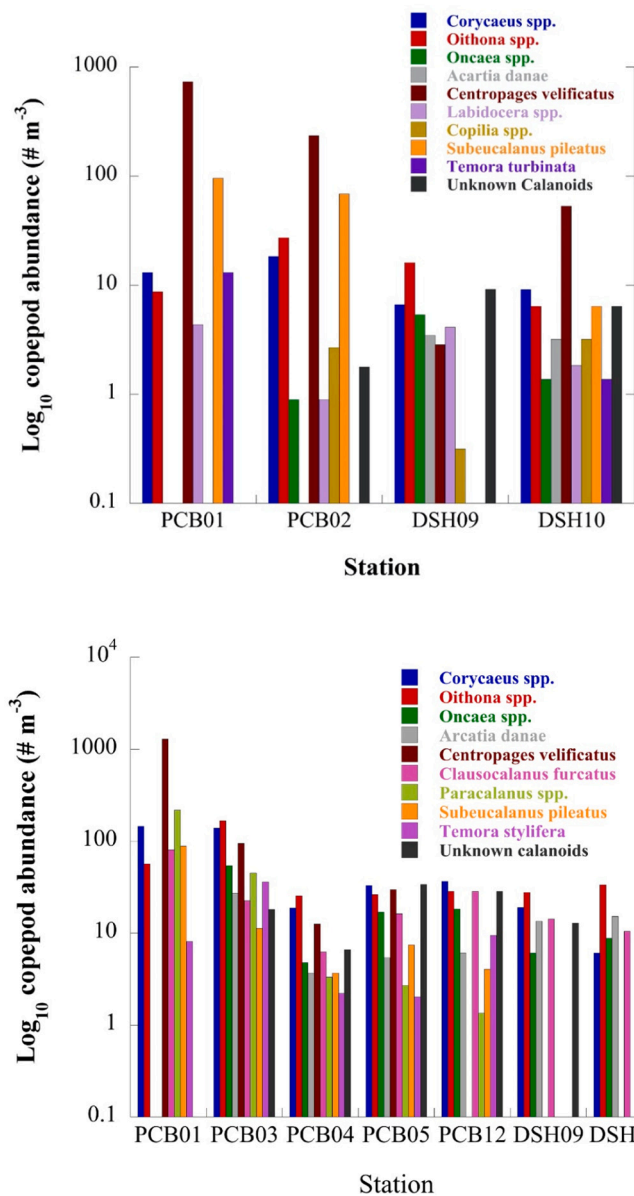


Fig. 13. Abundance (individuals m^{-3}) of dominant copepods at near-shore to off-shelf stations during August 2010 (upper panel) and May 2011 (lower panel).

(2008) used a pump to collect zooplankton and observed a similar range of densities (maxima: ca. 7000 individuals m^{-3}) and biomass (< 5 to ca. 28 $mg\ m^{-3}$) measurements in the upper 40 m of the far-field Mississippi River plume on the Louisiana shelf. Collectively, these studies indicate that our observed spatial and temporal patterns of zooplankton are consistent with previous studies and that SIPPER abundances at near-shore sites are within the range of abundances collected by nets with a smaller mesh size and pumps.

The SIPPER's off-shelf integrated zooplankton abundances were slightly, but significantly, higher ($p < 0.05$) during winter than densities in spring and summer (Table 1), in contrast to most previous investigations (e.g., Iverson and Hopkins, 1981; Lester, 2005). Secondary production occurs all year round in this subtropical system, although production is expected to be highest during summer when seawater temperature and phytoplankton concentrations peak, which is supported by the fact that copepod nauplii have an order of magnitude higher densities during summer than during winter (Dagg and Whitledge, 1991). The presence of zooplankton larval stages in SIPPER

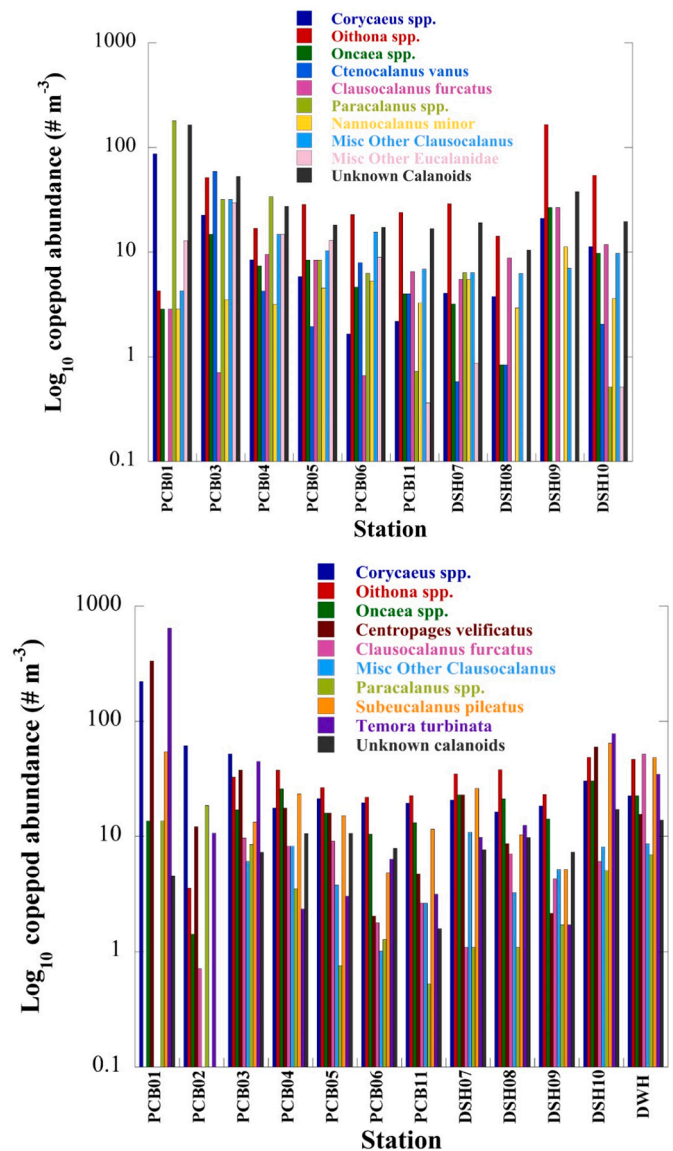


Fig. 14. Abundance (individuals m^{-3}) of dominant copepods at near-shore to off-shelf stations during February 2011 (upper panel) and September 2011 (lower panel).

images during all seasons provided further evidence of year-round production. Many nauplii are smaller than SIPPER's optical resolution (ca. 65 μm) and the Bongo net mesh size (333 μm) (Hopcroft et al., 1998); therefore, community numerical increases in larval stages were not well documented in our study. It is uncertain why there were such high zooplankton densities during winter; however, Okolodkov (2003) also reported higher plankton abundance and biomass in winter east of the Mississippi River estuary, which they attributed to elevated river discharge. Our relatively high integrated zooplankton densities in winter were, in part, due to high concentrations of larvae, especially the unusually high abundance of larvae (609,261 individuals m^{-2}) at PCB06 observed during February 2012. River discharge was above the mean flow (Fig. 2) and integrated chlorophyll (60.6 $mg\ m^{-2}$, 0–100 m) was relatively high at that time, which may have contributed to a rapid population growth of larvae.

4.2. Zooplankton community composition and diversity

Zooplankton composition in this study also was similar to previous studies, although the dominance of any particular species was highly

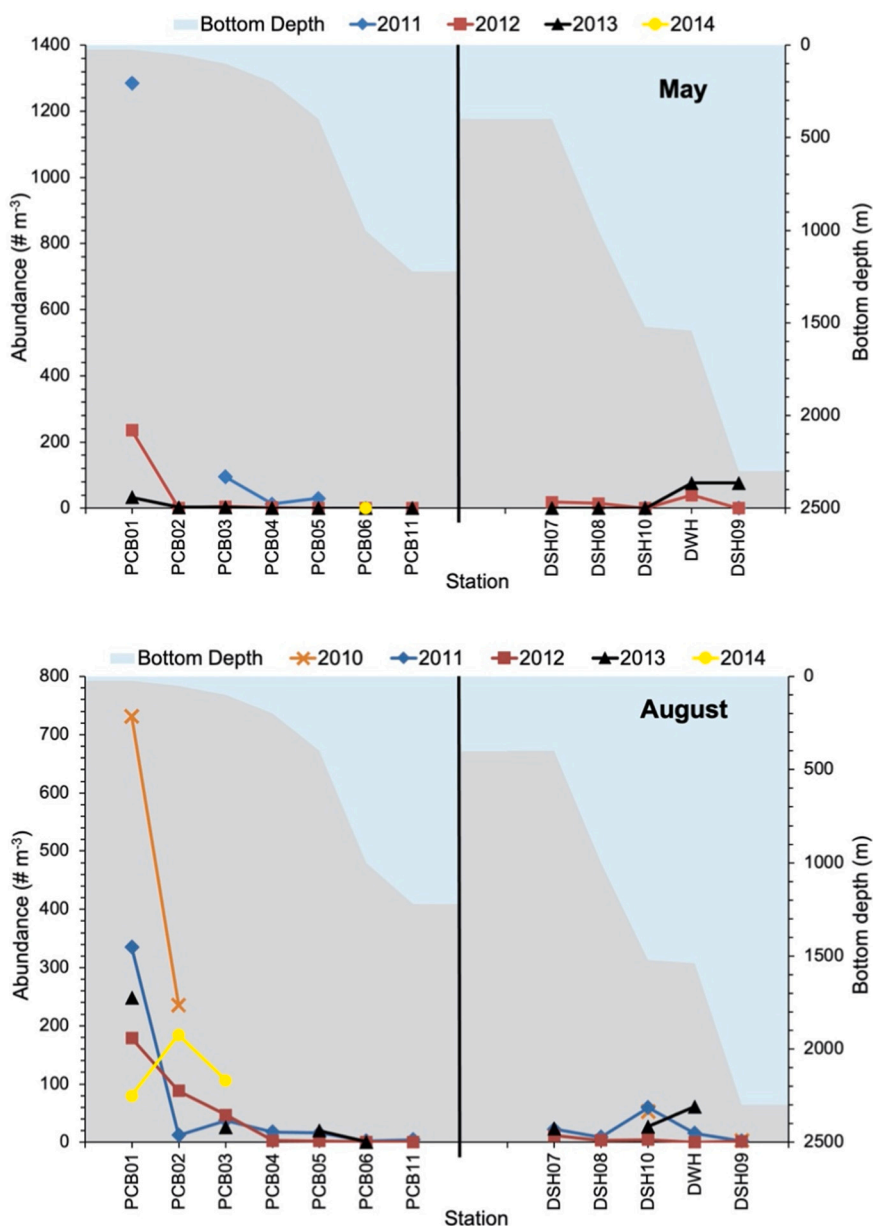


Fig. 15. Abundance (individuals m⁻³) and distribution of *Centropages velificatus* during May (upper panel) and August/September (lower panel) between 2010 and 2014. The depth of the seafloor at each station is shown in brown, the depth of the water column is in blue. Abundances at PCB stations over the Florida shelf and De Soto Canyon are on the left; abundances at DSH stations south of Mobile Bay are on the right. Note changes in scale on the left y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variable (e.g., Minello, 1980; Iverson and Hopkins, 1981; Hopkins, 1982; Lester, 2005; Rathmell, 2007; Carassou et al., 2014). In our study small and medium copepods, about 0.5 to 2.5 mm in length, were usually the dominant taxa, along with chaetognaths, larvaceans, ostracods, doliolids, cladocerans, decapods, and echinoderm larvae. Other groups, such as small hydromedusae, were episodically abundant. SIPPER would not have been able to detect aggregations of large hydromedusae, as the sampling tube was too small. The mean percent composition of total copepods (35–40%) in SIPPER tows was lower than that for the Bongo net data (51–57%), because SIPPER observed higher abundances of soft bodied zooplankton, such as larvaceans, than that in the Bongo data. Previous net studies noted that copepods were the dominant taxa at all sites, times of year, and vertically in the water column. Percent copepods on the Texas shelf averaged 61% (Minello, 1980). Hopkins (1982) showed that copepods in the central Gulf were 80% of the total zooplankton, but copepods had variable percentages with depth down to 1000 m (night range: 28.5–85.1%). Ortner et al. (1989) found that copepods were 70–75% of the total zooplankton at a central Gulf station, but up to 87% on the north Florida shelf. Another central Gulf study

noted that copepods were 60% of the total zooplankton (Rathmell, 2007), with *Oithona plumifera* frequently the dominant species and 5% of the total zooplankton, similar to our results at off-shelf stations. *Oithona* is one of the most abundant and ubiquitous copepods in the world's oceans, accounting for a substantial proportion of herbivory and omnivory in food webs, and is frequently underestimated by conventional net sampling (Turner, 1986; Gallienne and Robins, 2001). Although, our copepod percent composition values are within the range of previous studies, our average values were lower, doubtless due to our more extensive sampling over space and time and the ability of the SIPPER camera to detect more fragile organisms.

One of the more interesting results of our study was that, on average, the SIPPER percent composition of some of the dominant zooplankton groups was remarkably consistent between years, despite large changes in environmental conditions. This was particularly true for the small particle feeding copepods (e.g., *Oithona*, poecilostomatoid copepods) and carnivorous chaetognaths. Larvaceans and other gelatinous zooplankton were more variable, as they have faster generations times and can respond more rapidly to favorable environments to form

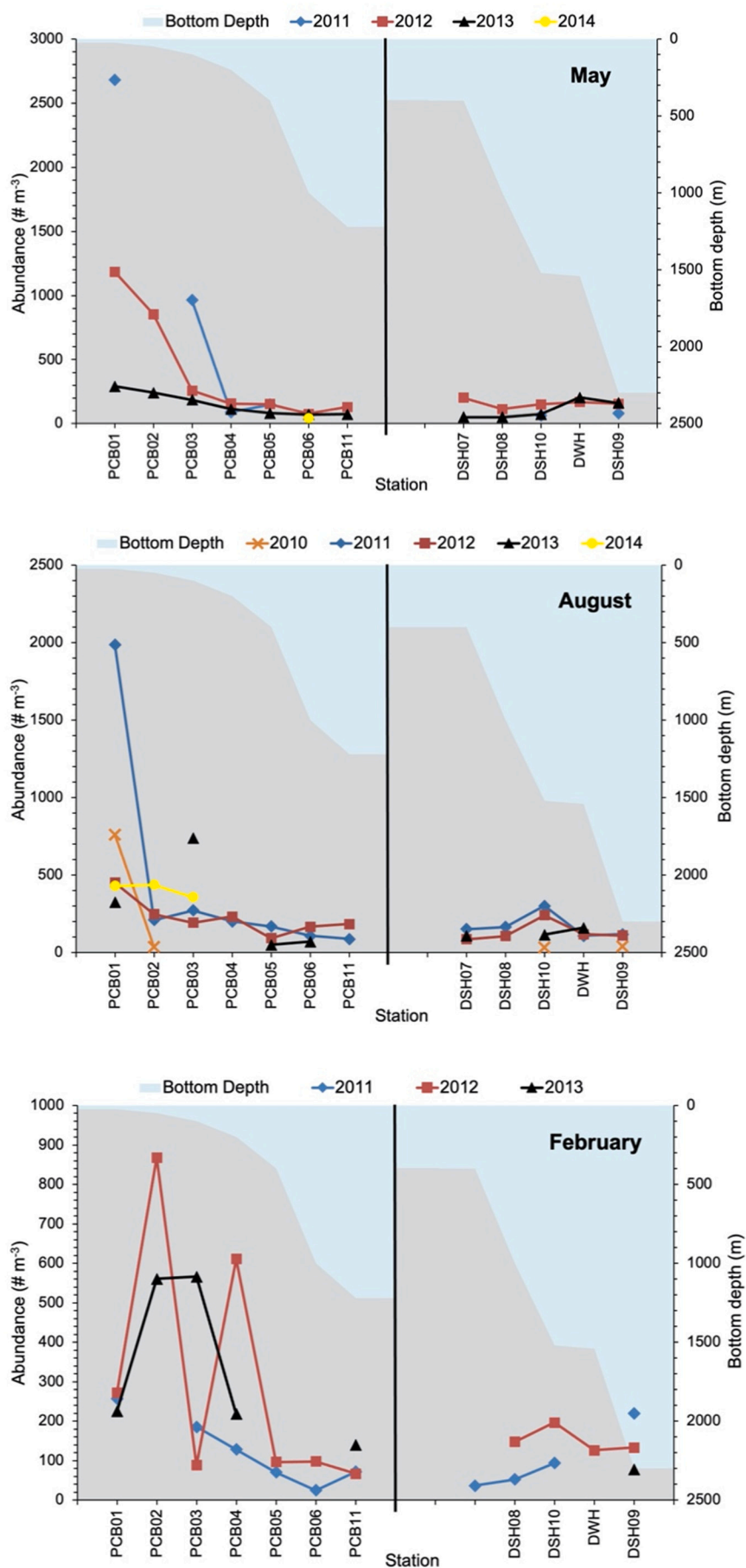


Fig. 16. Spatial, seasonal, and interannual abundance (individuals m⁻³) and distribution of total other zooplankton (non-copepods) during May (upper panel), August/September (middle panel), and February (lower panel) 2010–2014. The depth of the seafloor at each station is shown in brown, the depth of the water column is in blue. Abundances at PCB stations over the Florida shelf and De Soto Canyon are on the left; abundances at DSH stations south of Mobile Bay are on the right. Note changes in scale on the left y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

population “blooms” or they may form large aggregations in ocean fronts (Hopcroft et al., 1998; Paffenhöfer and Gibson, 1999; Graham et al., 2001).

Our biodiversity indices (species rank abundance and Shannon) were lowest near shore and highest on the outer shelf (200 m) and off shelf. Based on temperature and salinity measurements, the outer shelf was effectively oceanic water, which contributed to greater zooplankton diversity at those sites. The lowest diversity and largest seasonal changes occurred near shore during summer 2010 and spring 2011, when *Centropages velificatus* dominated the plankton community. Overall, Shannon indices were not significantly different ($p > 0.05$) between seasons or between years within each season. However, multivariate comparisons of zooplankton beta diversity indicated that spring communities were significantly different ($p = 0.001$) from those in summer and that summer communities had greater interannual diversity than spring. One caveat is that the diversity indices were based on Bongo net tow data. The common practice of only identifying zooplankton in subsampled splits to reduce sample analysis time may result in reduced numbers of rarer species, thereby impacting the accuracy of diversity indices. There are very few other studies reporting diversity measures in the northern Gulf of Mexico. Ortner et al. (1989) reported that Shannon Weaver diversity indices for the zooplankton community had a wide range in the Mississippi River plume (1.27–2.65), on the Florida shelf (1.48–2.73), and in the central Gulf (1.76–3.11), but all were within the range of our diversity indices (0.9–3.5). Minello (1980) found that species richness (range: 9–51) of adult female copepods, increased from near shore to a 73 m station on the Texas shelf, and the greatest diversity was observed during winter at that mid-shelf station. While general diversity patterns in previous studies appear to be similar to our results, more work on this important topic is needed in the Gulf of Mexico, particularly since high zooplankton diversity may contribute to resilience in this system.

Another intriguing result of our study was the exceptionally high abundances of *Centropages velificatus* near shore during 2010 and 2011. *C. velificatus* is a coastal, intermediate sized copepod, 1.6 mm in length, and broadly distributed in the Gulf of Mexico. Minello (1980) noted that *C. velificatus* was relatively common near shore (8 m) on the Texas shelf, but reported much lower densities (maximum ca. 65 individuals m^{-3}) than we observed. It was most abundant from June to October and sea surface temperature explained 14% of the variability in abundance. Cházaro-Olvera et al. (2019) reported that *C. velificatus* was one of the 10 most abundant, but never dominant, species off southern Mexico. In contrast, *C. velificatus* was the dominant near shore species in all summers of our study, except in 2009 and 2011. *C. velificatus* was 84% of the total copepod community at PCB01 in August 2010, 66% in May 2011, and ranged from 26 to 78% in the following years during spring and summer. The presence of copepodites suggested that reproduction occurred all year round, even though abundances were low in winter. It is uncertain why *C. velificatus* played such a dominant role in the coastal NEGOM and why abundances were so high during and after the DWH oil spill. *C. velificatus* is considered to be a raptorial omnivore, feeding on large phytoplankton, microzooplankton, as well as small crustaceans (Turner, 1987). *C. velificatus* can rapidly respond to favorable food conditions by turning ingested phytoplankton into egg production within 16–17 h at typical summer temperatures (Tester and Turner, 1990). In addition, *C. velificatus* releases subitaneous eggs in the NEGOM, which may hatch within a short period of time (7–10 days) or become quiescent (i.e., delayed development) and settle to the seafloor, forming a benthic egg bank (Chen and Marcus, 1997). This broadcast spawner had a higher hatching success (79–100%) during summer and fall, when adult females were present off coastal Florida, compared to other coastal species tested. Although Chen and Marcus (1997) found that benthic quiescent, subitaneous eggs had a lower hatching success, delayed hatching is presumed to be a bet-hedging strategy, which may increase the survival of offspring by extending the period over which eggs hatch. Mississippi River discharge, as a proxy for the influence of freshwater in coastal regions of the NEGOM, was unusually high in late

winter and spring 2010 and spring 2011, resulting in higher chlorophyll levels (Hu et al., 2011; Chakraborty and Lohrenz, 2015), with possible linkages to the high abundances of *C. velificatus*.

4.3. Influence of environmental conditions on zooplankton

Multivariate analyses indicated that spring environmental conditions were significantly different than those in summer ($p = 0.001$), due to higher Mississippi River discharge, wind magnitude and direction, and salinity in spring, and higher temperature and chlorophyll concentrations in summer. Zooplankton beta diversity, which incorporates differences in species abundance and composition between stations, also was significantly different ($p = 0.001$) between spring and summer, primarily influenced by surface chlorophyll and integrated chlorophyll during spring, while Mississippi River discharge rates and integrated chlorophyll were the dominant factors influencing zooplankton during summer. Overall, environmental variability explained 77% of zooplankton beta diversity in spring and 74% in summer. Physical and biological processes act together to produce and maintain the temporal and spatial patterns of zooplankton abundance, distribution, and species composition (Daly and Smith, 1993). The complex and dynamic circulation and variable biogeochemistry in the NEGOM play an important role in governing the spatial, seasonal, and interannual heterogeneity in zooplankton distributions. The two years with the highest SIPPER integrated zooplankton abundances, summer 2010 and 2013, had significantly different ($p < 0.05$) environmental conditions compared to other years, driven by higher Mississippi River discharge, lower sea surface temperature, lower salinity, and higher chlorophyll concentrations. Previous studies determined that similar environmental factors influenced chlorophyll, zooplankton, and juvenile fish distributions in this region and in the southern Gulf of Mexico, including river discharge rates, temperature, chlorophyll, wind speed, and wind-driven upwelling in near-shore areas (Jochens et al., 2002; Nababan et al., 2011; Carassou et al., 2011; Chakraborty and Lohrenz, 2015; Carassou et al., 2014; Färber Lorda et al., 2019). Thus, these environmental variables govern, to a large extent, the lower trophic food web community from phytoplankton to small fish in parts of the Gulf of Mexico.

Circulation features influenced zooplankton distributions. During the oil spill, periodic upwelling favorable winds in late spring and summer 2010 contributed to the eastward flow of the Mississippi River plume (Kourafalou and Androulidakis, 2013; Weisberg et al., 2014). Strong shelf break jets and eddies were observed during late spring and summer 2010 and again during the high river flow year in 2013 (Kourafalou and Androulidakis, 2013; Daly et al., 2020). These anticyclonic slope eddies occurred to the SE of the mouth of the Mississippi River in the vicinity of the DWH site and our nearby stations, entraining low salinity, high chlorophyll water along their peripheries. Gulf of Mexico HYCOM model simulations indicated that particles were entrained and retained in and around the core of the eddy, with lateral transport on eddy filaments and in the strong currents on the outer boundaries of the eddies (Daly et al., 2020). Typically, the interior of anticyclonic eddies in the Gulf of Mexico are biological deserts, as this is an area of convergence (Biggs and Ressler, 2001). However, this area had some of the highest abundances of zooplankton (Table 1) compared to the other lower flow years, when no eddies were detected. The combination of the Mississippi River plume, strong currents along the shelf break, and upwelling and retention by the eddy, probably contributed to the chlorophyll anomaly reported by Hu et al. (2011). It is uncertain what role the oil spill may have played in the observed unusually large chlorophyll bloom. This suite of physical and biological processes contributed to the high zooplankton abundances observed over the shelf slope and off shelf during summer 2010 (despite the oil spill) and 2013 (Fig. 7). In particular, the relatively high abundances off shelf may have been the result of aggregation by the eddy, as well as enhanced production from elevated chlorophyll.

Sea water temperature was an important environmental parameter

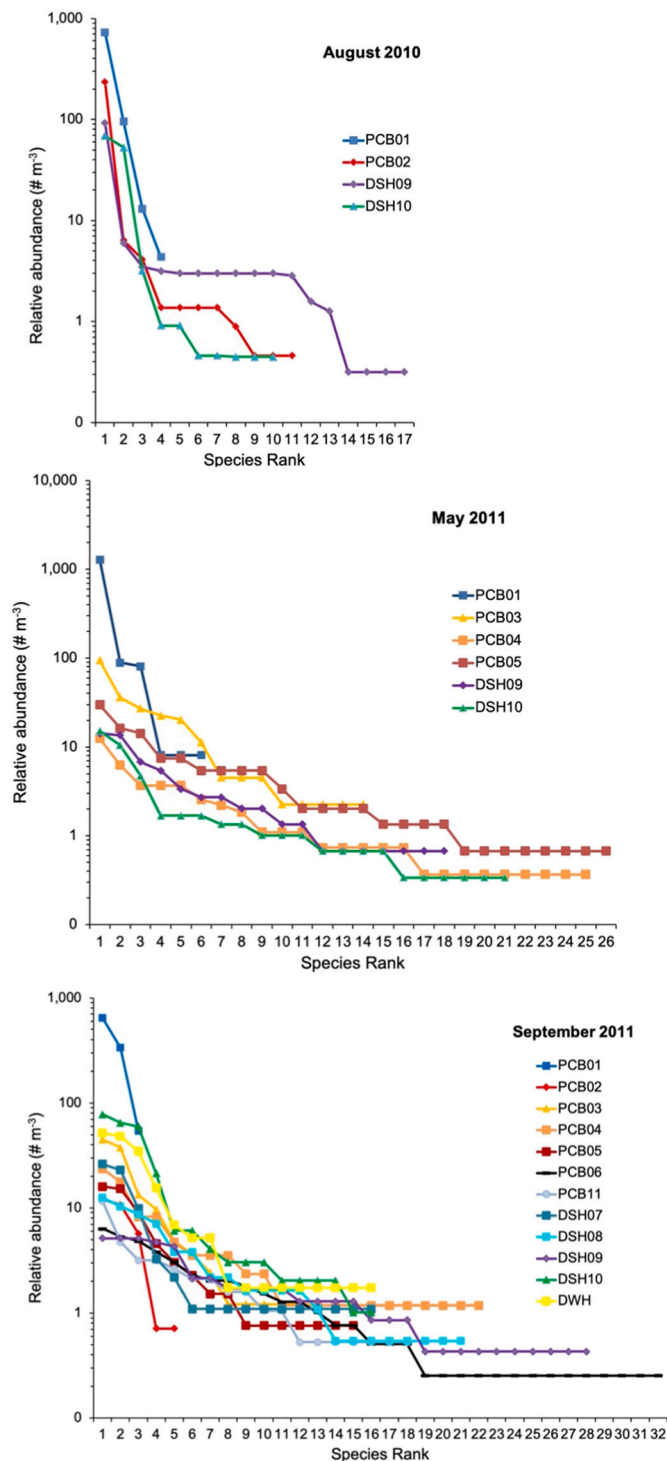


Fig. 17. Copepod species rank abundance for August 2010 and May and September 2011. Only copepods identified to species were included in the analyses (i.e., no genera spp.).

impacting zooplankton in this study. Warmer sea water temperatures result in higher growth rates for both phytoplankton and zooplankton. A review of zooplankton growth rates suggests that growth is generally temperature dependent, with growth rates increasing with higher temperatures (Hirst and Bunker, 2003). Primary and secondary production can occur all year in the NEGOM, but is higher during summer. Phytoplankton cell division rates range from 1.3 d^{-1} in March up to 2.7 d^{-1} in summer (Lohrenz et al., 1999), whereas zooplankton generation times

are on the order of weeks to months (Vargo and Hopkins, 1990), with some exceptions. For example, larvaceans can complete an entire generation (eggs to adults) in a few days or less at summer temperatures (Dagg, 1995; Hopcroft et al., 1998). High densities of ichthyoplankton during spring and summer on the Alabama shelf also were related to higher temperatures (Hernandez Jr. et al., 2010).

Chlorophyll concentrations were another important parameter impacting zooplankton and are typically used as a proxy for food availability. In our study, the vertical distribution of zooplankton was most closely linked to chlorophyll during high river flow periods, when chlorophyll and zooplankton maxima co-occurred in the low salinity surface layer (Figs. 3, 9). The highest surface chlorophyll and primary production values in the NEGOM have been reported at intermediate (20–30) salinities (Lohrenz et al., 1999), which we observed in the surface layer when river flow was high. Primary productivity maxima during summer are typically in the upper 2 m of the water column in the river plume or in the upper 10 m outside the plume (Redalje et al., 1994). When river flow was lower, chlorophyll and zooplankton were more broadly distributed through the water column (Figs. 3, 8). Zooplankton maxima were often higher in the water column than the chlorophyll maxima and may have been closer to the primary productivity maximum (Hopkins, 1982). Zooplankton had a weak, positive relationship ($R^2 = 0.129$) with chlorophyll in spring and a stronger, but negative relationship ($R^2 = 0.303$) in summer. This is not surprising as areas having high zooplankton concentrations would experience higher grazing rates, which would reduce chlorophyll concentrations (e.g., Färber Lorda et al., 2019). Indeed, field experiments indicated that copepods could ingest 14 to 62% of the daily phytoplankton production in the mid- and far-field sectors of the Mississippi River plume (Dagg, 1995). Microzooplankton have even higher feeding rates (82% of algal growth on cells $<20 \mu\text{m}$; Fahnenstiel et al., 1995).

Zooplankton food availability as determined by integrated chlorophyll concentrations, was higher in spring than in summer, but neither were significantly different than winter ($p > 0.05$). The fact that larval and juvenile stages were present during spring, summer, and winter suggests that food resources could support some secondary production year-round. Nababan et al. (2011) also noted that there was no consistent seasonal pattern in chlorophyll concentrations in this region. They observed higher chlorophyll during winter in 1998, which they attributed to high river discharge during an El Niño-Southern Oscillation (ENSO) event. Gomez et al. (2019) also determined that the strongest ENSO impact on river discharge and subsequent effect on phytoplankton was during winter-early spring. During our study, ENSO events ranged from a strong El Niño in 2010, to a strong La Niña in 2011, a moderate La Niña in 2012, and neutral ENSO indices in 2013 and 2014 based on the Oceanic Niño Index. Hence, high river flow in 2010 was associated with a strong El Niño, but not the high river flow in 2013. A caveat, however, is that high integrated chlorophyll values not resulting from high river discharge were often due to deep chlorophyll maxima. Picoplankton are typically the dominant component of the deep phytoplankton community and elevated chlorophyll concentrations are often due to an increase in the number and size of chloroplasts per cell, owing to chromatic adaptation, and not due to an increase in the number of cells (McManus and Dawson, 1994; Chakraborty and Lohrenz, 2015). Thus, high integrated chlorophyll concentrations may not always be a good indicator of food availability. In addition, zooplankton are able to detect and exploit small patches and thin layers of microplankton on vertical scales (e.g., Figs. 8 and 9). Even when chlorophyll concentrations are low, food resources may not limit zooplankton growth and reproduction as most zooplankton are omnivores. For example, many of the dominant copepods (e.g., *Centropages velificatus*, *Temora* spp., *Oithona* spp., *Corycaeus* spp.) in our study are known to consume microzooplankton and/or naupliar stages of copepods, as well as phytoplankton (Paffenhöfer and Knowles, 1980; Turner et al., 1984; Turner, 1987; Bennett and Hopkins, 1989; Stoecker and Capuzzo, 1990; Kleppel et al., 1996).

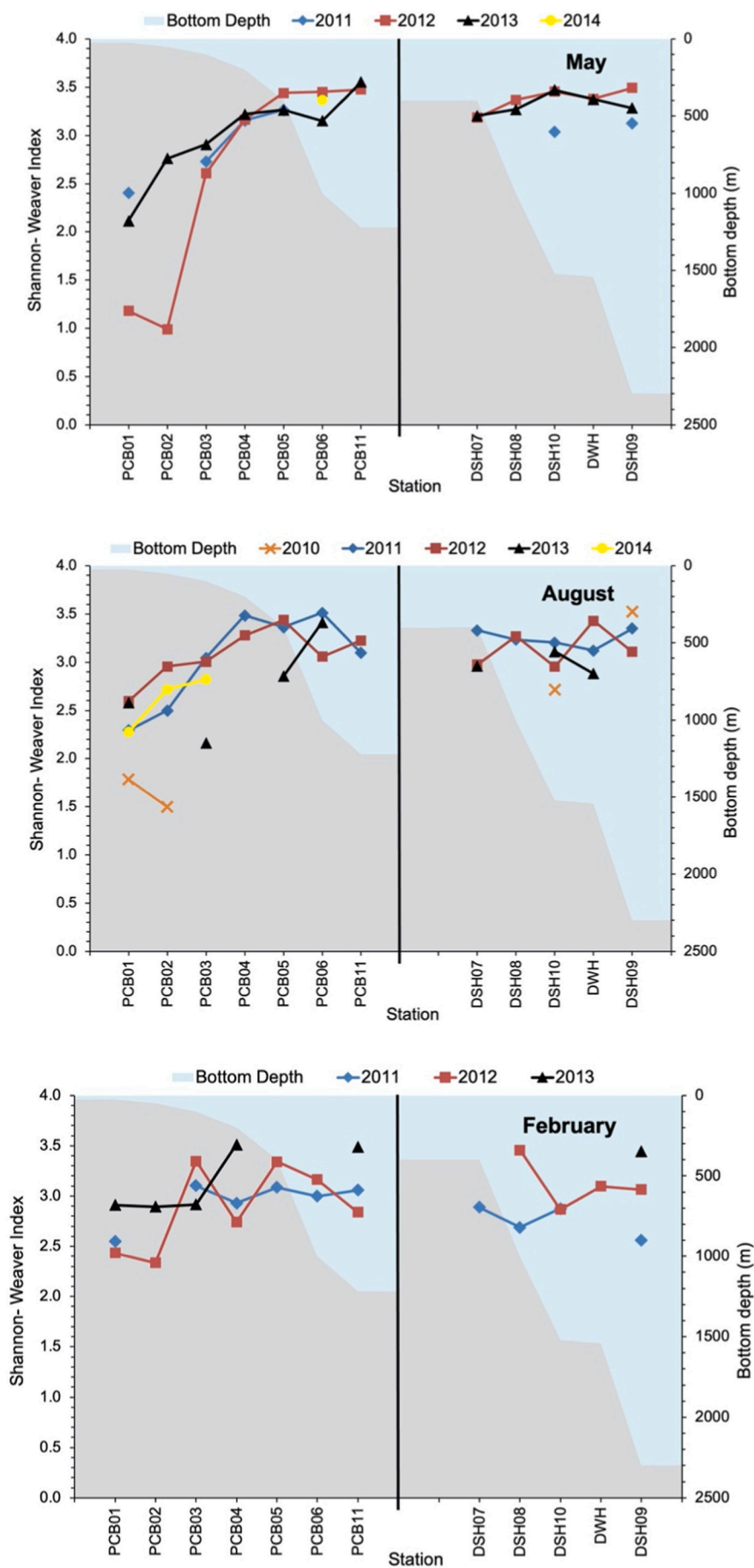


Fig. 18. Spatial, seasonal, and interannual variability of Shannon diversity indices during May, August/September, and February 2010–2014. The depth of the seafloor at each station is shown in brown, the depth of the water column is in blue. Indices at PCB stations over the Florida shelf and De Soto Canyon are on the left; indices at DSH stations south of Mobile Bay are on the right. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.4. Impacts of the Deepwater Horizon oil spill on the zooplankton community

Impacts of oil spills on zooplankton communities depend on the type and concentration of oil, the frequency and duration of exposure to that oil, the proportion of different life history stages of zooplankton exposed to oil, and the sensitivity of different taxa to oil. The [Deepwater Horizon Natural Resource Damage Assessment Trustees Report \(2016\)](#) determined that oil concentrations greater than $0.5 \mu\text{g L}^{-1}$ (ppb), which are considered toxic to marine zooplankton, were present in the upper 20 m of the water column for extended periods during our May, June, and August 2010 cruises, but concentrations were spatially variable. Based on field samples and a modeling study, the Trustees Report (2016) estimated that planktonic invertebrate mortality ranged from 37 to 68 trillion individuals overall, and 4–6% of the zooplankton community in off-shelf waters. Laboratory studies also clearly demonstrated that common Gulf of Mexico zooplankton experience sublethal and lethal impacts from exposure to oil and dispersants, including reduced rates of feeding, growth, egg production, egg hatching, development time, fecal pellet production, and impaired swimming behavior (e.g., [Almeda et al., 2013a, 2013b, 2014b, 2014c](#); [Cohen et al., 2014](#); [Lee et al., 2017](#)). In addition, little is known about the evolutionary response of organisms to crude oil. [Lee et al. \(2017\)](#) found that the common estuarine copepod, *Eurytemora affinis*, developed a tolerance to crude oil over a 2–3 year period, based on increasing survival and shorter development times between pre- and post-spill field populations. Individuals from the field population showed significant genetic variation in tolerance to oil upon which natural selection could act. Thus, impacts of oil on zooplankton communities could be highly variable and complex over a long period of time.

There is no doubt that the DWH oil spill caused mortality and sublethal effects in zooplankton. However, our sampling was not designed to track exposure of zooplankton to oil and the consequences of that exposure over time. One interesting result observed in SIPPER images was that large numbers of fish eggs at the surface during early May 2010 did not appear to have been fertilized or to have developed embryos. Instead, many appeared empty or had symmetrical dark patches along their perimeter, which could have been the remains of germinal, embryonic tissue from embryos that ceased development and were decomposing (J. Lyczkowski-Shultz and J. Incardona, pers. comm.). Another interesting result was the unusually large concentrations ($> 30,000 \text{ m}^{-3}$) of *Noctiluca* unattached in the water column in early May 2010, as well as attached to oil-associated marine snow aggregates. It is not known why these high densities were not sustained for the duration of the oil spill. Surface and subsurface dispersants were applied between May 15 and July 12, 2010 ([Kujawinski et al., 2011](#)), which may have affected the availability of oil to *Noctiluca*. [Almeda et al. \(2014a\)](#) showed that both *Noctiluca scintillans* and *Cyrodinium spirale* had a high tolerance for crude oil and dispersants in laboratory experiments. These heterotrophic dinoflagellates maintained growth rates in oil treatments that were similar to those in control treatments, and they readily ingested oil and egested fecal pellets containing crude oil. *Noctiluca* also were observed in association with the Torrey Canyon oil spill in 1967 ([Cooper, 1968](#)). *Noctiluca scintillans* is remarkable as a relatively large (200–2000 μm) single celled animal having rapid growth rates and is capable of forming large blooms (up to $9600 \text{ cells L}^{-1}$) in many regions of the world's oceans ([Gomes et al., 2014](#)). It is considered to be a harmful algal species, as it releases high concentrations of ammonium and can clog gills of other organisms. Our findings illustrate that this species may contribute to the fate of oil spills and deserves further investigation.

The overall evidence indicates that the zooplankton community was resilient to the DWH oil spill. Although about 40% of the zooplankton community (0–100 m) was concentrated in the upper 20 m of the water column in the vicinity of the oil spill and, therefore, could have been exposed to the highest oil concentrations, there was a large spatial

variability in both oil and zooplankton. The abundance of zooplankton during the oil spill in spring 2010 was not significantly different ($p > 0.05$) from abundances in the following years (2011 and 2012). Also, zooplankton abundances during summer 2010, shortly after the wellhead was capped, were the highest observed for the 2005 to 2014 period, but this was likely due to a combination of environmental effects, including high river discharge, high chlorophyll, and aggregation in eddies. The general distribution patterns and quantities of zooplankton (abundance, biomass, diversity) were similar to other years and previous publications. The dominant zooplankton taxa (species and percent composition) were similar to other years as well. Pre-spill spring total zooplankton abundances were significantly lower ($p < 0.05$) than the post-spill abundances, but summer concentrations were not significantly different ($p > 0.05$) before and after the oil spill. Similar to our study, [Carassou et al. \(2014\)](#) reported that there were significantly higher abundances ($p < 0.05$) of mesozooplankton during the oil spill compared to prior years at stations near Mobile Bay, Alabama, but they observed higher densities much earlier (May–June 2010). They also noted that there was a rapid recovery and those differences were no longer significant by July 2010, while we observed higher densities at off-shelf stations in August. [Carassou et al. \(2014\)](#) attributed the increase in abundance to an increase in microbial activity that stimulated secondary production. Thus, the oil spill did not appear to have a large adverse effect on the zooplankton community, except perhaps for short-term, local effects that we would not have detected.

In general, determining the impacts of oil spills on zooplankton communities in the field has been hampered by a lack of baseline data and the fact that zooplankton are spatially patchy and have large seasonal and interannual fluctuations in their abundance and distributions, making it difficult to separate natural and climatic variability from effects of oil. In those studies where impacts of oil spills were shown to occur (reviewed in [Teal and Howarth, 1984](#)), some spills (e.g., Amoco Cadiz) resulted in high zooplankton mortality, which showed up after 20 days, and copepods had depressed digestive enzymes. After the Tsesis oil spill in 1977 off Sweden, zooplankton declined immediately and were observed with oil in appendages or in guts for over three weeks, but the community was re-established in that time period ([Johansson et al., 1980](#)). The IXTOC-I oil spill in June 1979 was another large spill in the Gulf of Mexico. [Guzmán del Prío et al. \(1986\)](#) reported that zooplankton biomass and ecosystem indicators of diversity declined after the oil spill. However, there appeared to be considerable variability so the trends are uncertain. The persistence of oil in zooplankton also suggested that there was chronic oil pollution. During the DWH oil spill, fishing closures (i.e., more fish in the system) may have increased top down predation on zooplankton, but this did not appear to result in reduced zooplankton abundances. [Mitra et al. \(2012\)](#) also showed that zooplankton collected during August and September 2010 contained low levels of PAHs derived from the oil spill. Oil in zooplankton could have been ingested by predators or passed to new generations through their eggs, or egested in fecal pellets. Sublethal impacts are even more difficult to investigate, as ecosystem interactions are complex, non-linear, and poorly understood.

The recovery of zooplankton communities in the NEGOM was relatively rapid owing to their high abundance, high fecundity, relatively short generations times, and recruitment from other areas ([National Research Council, 2003](#)). Assuming that there was high mortality due to oil, high fecundity and relatively short generation times (weeks to months for copepods) alone would not have been able to replace zooplankton to the high densities observed during the oil spill and shortly after the wellhead was capped. Since oil concentrations were highest in the upper 20 m of the water column, zooplankton that inhabited deeper depths, and were not in the cone of rising oil and deep plumes, may have experienced a refuge from oil. Most importantly, connectivity with other regions of the Gulf of Mexico ecosystem may be the key element in zooplankton resilience in the NEGOM system. In other words, location extinction didn't occur because zooplankton are

continuously transported into the oil spill region. Backtrack simulations of passive particles using a Gulf of Mexico HYCOM model indicated that over a 30-day period during July 2010, currents carried particles to the DWH site from both the western and eastern outer reaches of the oil spill and beyond, where there was very little oiling (Daly et al., 2020). Although zooplankton do not behave like passive particles, this exercise provided some boundaries on the connectivity of current flow in this region.

5. Conclusions and knowledge gaps

Environmental variability and riverine processes strongly govern spatial, seasonal, and interannual phytoplankton and zooplankton community dynamics in the NEGOM. Zooplankton may be resilient to extreme perturbations in the NEGOM owing to ecosystem connectivity. Longer term perturbations from chronic pollution, such as oil seeps, nutrients, and overfishing could have very different, more subtle, effects. Our investigation has made a substantial contribution towards advancing understanding of zooplankton dynamics in this region; however, there continue to be gaps in our knowledge. There is little information on zooplankton functional rate measurements during any season and, therefore, it is not known if ecosystem function was impacted during the oil spill. Due to their high densities, *Centropages velificatus*, larvaceans, and *Noctiluca* may be important to ecosystem function in this region and warrant further investigation. The extent to which zooplankton contribute to the flux of oil to the seafloor through egestion of oil in fecal pellets is poorly known. Also, the role that zooplankton play conveying oil up through the food web and the subsequent impact on upper trophic level predators is not well known. This study provides baseline data to assess future perturbations to this system, including the effects of climate change.

CRedit authorship contribution statement

K. Daly: Project administration, Funding acquisition, Analysis, Visualization, Writing. **A. Remsen:** Methodology, Data collection, Analyses, Visualization, Writing. **D. Outram:** Sample analyses, Data Curation, Editing. **H. Broadbent:** Data collection, Data Curation, Analyses, Visualization, Editing. **K. Kramer:** Data collection, Software, Methodology, Analyses. **K. Dubikas:** Analyses, Visualization, Writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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