CORRIGENDUM

Corrigendum: Change and recovery of coastal mesozooplankton community structure during the Deepwater Horizon oil spill (2014 Environ. Res. Lett. 9 124003)

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In the original article, the reported values for river discharge in supplement 1 were incorrect. An error was found in our conversion from ft³ s⁻¹ to m³ s⁻¹. Correct values are provided in the revised table; the error did not change our overall findings, interpretations or conclusions.

Supplementary material 1: Historical (2004 to 2009) monthly range (min–max) of environmental values compared to values observed during the oil spill year (2010). See table 2 for variables units and resolution.

| Variables                  | MAY       | June      | July      | August     |
|----------------------------|-----------|-----------|-----------|------------|
|                            | Historical| Oil spill | Historical| Oil spill  | Historical| Oil spill |
| NAO (−1.73−1.68)           | −1.49     | (−1.39−0.84) | −0.82     | (−2.15−1.13) | −0.42     | (−1.73−0.37) | −1.22     |
| SOI (−1.30−1.70)           | 1.50      | (−1.40−1.00) | 0.60      | (−1.00−0.30) | 3.00      | (−1.70−1.70) | 3.00      |
| Wind speed (3.74−5.41)     | 4.07      | (2.70−3.40) | 3.01      | (2.22−3.44)  | 3.90      | (2.24−3.71)  | 3.84      |
| u-wind (−2.99−1.12)        | −1.54     | (−1.13−1.94) | −1.00     | (−1.01−1.18) | −0.97     | (−1.15−0.70) | −0.37     |
| v-wind (−0.03−2.50)        | 1.51      | (−0.09−2.01) | 1.70      | (0.41−1.83)  | 0.99      | (−0.82−1.19) | 0.61      |
| Atmospheric pressure       | (1013.67−1018.25) | 1015.39 (1012.70−1017.03) | 1015.94 (1014.9−1017.35) | 1016.69 (1012.26−1016.69) | 1013.63 |
| Water temperature (24.80−25.99) | 26.40 (28.63−29.58) | 30.18 (29.30−30.20) | 30.53 (28.79−31.30) | 30.74      |
| River discharge (252.85−3009.72) | 2009.85 (210.82−2113.59) | 802.13 (255.13−2709.25) | 404.56 (201.22−1068.32) | 321.96      |

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Abstract
The response of mesozooplankton community structure to the Deepwater Horizon oil spill in the northern Gulf of Mexico was investigated using data from a long-term plankton survey off the coast of Alabama (USA). Environmental conditions observed in the study area during the oil spill (2010) were compared to historical observations (2005–2009), to support the contention that variations observed in zooplankton assemblage structure may be attributed to the oil spill, as opposed to natural climatic or environmental variations. Zooplankton assemblage structure observed during the oil spill period (May–August) in 2010 was then compared to historical observations from the same period (2005–2009). Significant variations were detected in assemblage structure in May and June 2010, but these changes were no longer significant by July 2010. The density of ostracods, cladocerans and echinoderm larvae were responsible for most of the differences observed, but patterns differed depending on taxa and months. Many taxa had higher densities during the oil spill year, including calanoid and cyclopoid copepods, ostracods, bivalve larvae and cladocerans, among others. Although this result is somewhat surprising, it is possible that increased microbial activity related to the infusion of oil carbon may have stimulated secondary production through microbial-zooplankton trophic linkages. Overall, results suggest that, although changes in zooplankton community composition were observed during the oil spill, variations were weak and recovery was rapid.

Online supplementary data available from stacks.iop.org/ERL/9/124003/mmedia

Keywords: assemblage structure, planktonic communities, shallow pelagic ecosystems, hydrocarbon pollution

Introduction

On 22 April 2010, an explosion occurred on the Deepwater Horizon (DWH), a deep-water oil drilling platform off the coast of Louisiana (northern Gulf of Mexico), and thereafter released an estimated 780 000 m³ of crude oil into the marine environment over a period of 85 days [1]. Approximately 25% of the released oil was either immediately recovered or burned at sea, while the remaining 75% was left to degrade in the marine environment, either naturally or enhanced by chemical dispersants [2]. Unlike accidental surface spills where most volatile components of the oil evaporate into the atmosphere, the release of oil at 1.5 km depth resulted in an extended submerged period, which allowed water-soluble portions to dissolve in the surrounding water column [3]. Over 1.7 million gallons of chemical dispersant were applied...
at the surface and at depth to emulsify the oil into small droplets and enhance bacterial degradation [4]. However, the widespread use of dispersants also increased exposure pathways of oil and dispersant to pelagic organisms, with yet largely unknown ecological consequences [5, 6].

The few studies that have addressed the impacts of the DWH oil spill on mesozooplankton suggested oil and dispersant impacted planktonic assemblages in the northern Gulf of Mexico. For example, Graham et al (2010) [7] and Chanton et al (2012) [8] used stable carbon isotope ($\delta^{13}C$) and radiocarbon ($\delta^{14}C$) tracers, respectively, to detect the introduction of oil from the DWH spill into the planktonic food web, presumably via microbial-zooplankton trophic linkages. Further, Almeda et al (2013) [6] reported increased mortality in field-collected mesozooplankton with increasing oil concentrations in mesocosm experiments, and that treatments with dispersant (either alone or with oil) resulted in the highest mortality. They also documented bioaccumulation of some polyaromatic hydrocarbons in mesozooplankton, which suggests these organisms may serve as a conduit for oil compounds to move up the food chain, as they are a major food source in pelagic environments. While these studies highlight pathways of exposure for mesozooplankton, no studies to date have examined the realized impact on mesozooplankton abundances and assemblage structure in the field [9].

Mesozooplankton provide a crucial link between primary producers and consumers within planktonic food webs. Many species (e.g., calanoid and cyclopoid copepods and nauplii) are the primary prey for larval fishes [10], and thus their availability and abundance have important fish recruitment implications. As such, information on zooplankton response to the DWH oil spill is critical for the estimation of the oil spill impacts on coastal open water ecosystems in the northern Gulf of Mexico [5]. The goal of this study is to examine variations in mesozooplankton community structure in response to the DWH oil spill, based on data from a unique, long-term plankton survey conducted within the impact region. Specifically, we (1) resolved potential changes in mesozooplankton assemblage structure during and shortly after the oil spill, as compared to historic, pre-spill data; and (2) quantified taxon-specific changes in abundance in response to the DWH event.

Material and methods

Field collections

All plankton samples were collected at two sites, stations T20 and T35, located approximately 20 km and 30 km south of Dauphin Island, respectively, as part of the Fisheries Oceanography of Coastal Alabama (FOCAL) plankton survey [11] (figure 1). Stations T20 and T35 were impacted by pulses of oil during the DWH spill, and were the same stations sampled by Graham et al (2010) [7]. Plankton samples were collected monthly during daytime hours using a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS; Open Seas Instrumentation, Musquodoboit Harbor, Nova Scotia) with a 0.25 m² mouth opening. Full details on the BIONESS sampling protocols are provided in Hernandez et al (2011) [11] and Carassou et al (2012) [12]. In short, the BIONESS was fished obliquely from the surface to the bottom with a 0.202 mm mesh net, and then towed up the water column to collect depth-discrete samples using 0.333 mm mesh nets. For this study, only oblique samples that integrated the entire water column (approximately 1–18 m and 1–33 m depth at stations T20 and T35, respectively) using a 0.202 mm mesh net were used for analysis. Upon retrieval, net contents were rinsed, filtered on a 0.149 mm sieve, and preserved in a 5% borate-buffered formalin-seawater solution for 48 h, before being transferred to 70% ethanol in the laboratory. A total of 50 oblique plankton samples were collected before the oil spill (hereafter grouped as ‘historic samples’) between May and August 2005–2009 at station T20, and between May and August 2007–2009 at station T35 (table 1). The frequency of sampling was increased at T20 and T35 from monthly to twice-monthly during the oil spill (between May and August 2010), to detect possible changes in planktonic communities, resulting in a total of 38 samples collected during or shortly after the oil spill (table 1).

Zooplankton processing

Each sample was split twice using a Folsom plankton splitter, generating four aliquots, from which one was randomly selected for zooplankton processing. The contents of the quarter aliquots were poured into a graduated beaker and mixed for one minute with an aquarium air bubbler. After mixing, smaller plankton aliquots were removed using a Stempel pipette (1, 2, 5 or 10 ml). Suitable aliquot volumes were achieved when counts of at least 200 copepods and 200 non-copepod organisms were reached. Zooplankton were classified into one of 24 taxonomic groups and counted under a stereomicroscope.

Environmental data

A suite of climatic indices and environmental variables were compared between 2007–2009, pre-spill seasons, and 2010, oil spill season, to explore the possibility that variations in mesozooplankton assemblage structure may have varied in response to natural environmental and climatic sources of variations. Descriptions of data sources and processing are detailed in Carassou et al (2011) [13]. A total of eight environmental variables were gathered from the National Oceanic and Atmospheric Administration (NOAA) National Weather Service Climate Prediction Center [14], NOAA National Data Buoy Center (stations 42 007 and DPIA1 [15]), and the United States Geological Survey (USGS) websites [16, 17]. These variables described both large-scale climatic conditions (i.e., North Atlantic Oscillation and Southern Oscillation Indices) and local weather and water column factors (i.e., wind conditions, atmospheric pressure, river discharge, water temperature and salinity) (table 2). Large-scale climatic data were provided at monthly intervals. Other data on local weather and water column conditions were
collected at hourly intervals. Daily river discharge data were collected from two USGS gaging stations in the Alabama River (Claiborne Lock and Dam [16]) and in the Tombigbee River (Coffeeville Lock and Dam [17]). Their sum was used as total freshwater discharge into Mobile Bay [18]. All environmental data were expressed as monthly averages for analyses.

Data analysis

Environmental conditions during the DWH oil spill period were compared with seasonal historic (pre-spill) conditions using normed Principal Component Analysis (correlation PCA [19]), in which historic data were used as the main observations, and data from the oil spill year as supplementary observations. This allowed for a visual assessment of environmental conditions during the DWH oil spill relative to the range of natural variability that historically characterized

Table 1. Number of oblique plankton samples (0.202 mm mesh) collected from May to August in 2010 (oil spill year) and during previous years (historic data) at sites T20 and T35 on the Alabama shelf. Locations for study sites are depicted in figure 1.

| Months  | T20 | T35 |
|---------|-----|-----|
| May     | 9   | 4   |
| June    | 7   | 10  |
| July    | 7   | 5   |
| August  | 7   | 4   |
| Total   | 30  | 23  |

Table 2. Climatic and environmental factors examined, with their respective units and sources. Measurement stations are depicted in figure 1.

| Source                                           | Variables                      | Unit      |
|--------------------------------------------------|--------------------------------|-----------|
| NOAA National Weather Service Climate Prediction Center [14] | El Niño Southern Oscillation Index (SOI) | —         |
| NOAA National Data Buoy Center Stations 42 007 and DPIA1 [15] | North Atlantic Oscillation index (NAO) | —         |
|                                                  | Water temperature              | °C        |
|                                                  | Wind speed (amplitude)         | m s⁻¹     |
|                                                  | Along-shore wind (u-wind)      | m s⁻¹     |
|                                                  | Cross-shore wind (v-wind)      | m s⁻¹     |
|                                                  | Atmospheric pressure           | bar       |
| USGS National Water Information System, Claiborne and Coffeeville Lock and Dams [16, 17] | River discharge               | m³ s⁻¹    |

Figure 1. Sites of zooplankton sampling (stars) and environmental measurements (filled circles) in Alabama coastal waters. The extent of oil pollution in the study area during different months in 2010 is given in Graham et al (2010) [7]. The white star in the top-left insert indicates the approximate location of the DWH site.
the area during this period of the year. Convex hulls were used to group observations by months, and the relative position of group centroids was used to assess if and how oil spill season conditions differed from historical conditions.

Zooplankton abundance data were standardized with the volume of water filtered, providing estimates of zooplankton density (number.m$^{-3}$) for each taxon in each sample. Density data were log(x + 1) transformed before analysis to reduce the weight of dominant taxa relative to rare ones [20]. Zooplankton assemblage structure observed during the DWH oil spill at each sampling site was then compared with seasonal historical assemblage structure using Correspondence Analyses (CA [19]), in which historical data were used as the main observations, and data from the oil spill year as supplementary observations. This allowed for a visual assessment of zooplankton assemblage structure observed at the two study sites during the DWH oil spill relative to the range of natural variability which characterized these assemblages at this period of the year. Convex hulls were used to group observations by months, and the relative position of group centroids was used to explore if and how zooplankton assemblages differed during the oil spill as compared to historical observations.

Analyses of Similarity (ANOSIM) were used to statistically test for differences in the relative composition of zooplankton assemblages between historical and oil spill years by month and location. Values of $R$ statistics were used to assess the strength of these differences, on a scale of 0 (indistinguishable) to 1 [21]. Analyses of Contribution to the Dissimilarity (SIMPER) were used to identify the taxa responsible for differences in assemblage composition. Variations in the mean density of those taxa, and of major zooplankton larval fish prey, i.e., calanoid and cyclopoid copepods, between historical and oil spill months were then individually tested through Mann–Whitney non-parametric tests [20].

Results

Environmental conditions

Approximately 54% of the variability in environmental conditions during May, June, July and August 2004–2009 was explained by the two first components of the PCA (figure 2). Historical observations from May were generally characterized by strong winds, high river discharge, low water temperature and weak along-shore winds. Conversely, along-shore winds were dominant, sea water was warm, and river discharge and wind speed were low in August (figure 2). June and July were characterized by intermediate conditions. Observations from 2010 (during DWH) fell within the range of historical values, as monthly centroids positioned within the convex hulls formed by historical values each month, with the exception of July (figure 2). In July 2010, values for SOI, wind speed and water temperature were indeed slightly higher than usual (supplementary material 1). However, the difference appeared minor with regards to the large variability characterizing historical values (figure 2; supplementary material 1). Overall, regional environmental conditions during the oil spill year were very similar to those in previous years.
Zooplankton assemblages

Among the 24 taxa identified in zooplankton samples, calanoid and cyclopoid copepods, chaetognaths, cladocerans, doliolids, and ostracods were consistently the most abundant (supplementary material 2). The two first axes of the Correspondence Analysis explained approximately 35% and 44% of the variance in zooplankton assemblage composition at sites T20 and T35, respectively (figure 3).

At site T20, polychaetes and barnacle cyprids were more abundant in May, whereas euphausiid protozoa and decapod larvae were more abundant in July and August (figures 3(a) and (b)). The centroid for May 2010 fell outside of the convex hulls formed by historical data (figures 3(a) and (b)), suggesting a significant difference in assemblage composition. Conversely, centroids for June, July and August 2010 fell within convex hulls formed by historical samples, indicating little if no variation in assemblage composition during the oil spill year for these months.

At site T35, barnacle nauplii, euphausiid protozoa and decapod larvae were abundant in May and June, while mysid shrimps and pteropods were abundant in August (figures 3(c) and (d)). Centroids for May, June and July 2010 fell outside of the convex hulls formed by historic data, suggesting a probable change in assemblage composition during the oil spill. Conversely, the centroid for August 2010 fell within the convex hulls formed by historic values (figures 3(c) and (d)).

ANOSIM confirmed significant, albeit weak, variations in mesozooplankton assemblage composition during the oil spill years as compared to historic years. Mesozooplankton assemblages were different during the oil spill at both sites when all months were combined together ($R < 0.2$; table 3).
Assemblages significantly diverged from historic values in May and June 2010 at both sites, but were not different in July and August (table 3). Differences in May and June 2010 were stronger at site T35 than at site T20, with the strongest difference detected at site T35 in June 2010 (table 3).

Taxa responsible for differences observed between oil spill and historical samples varied depending on sites and months. When all months were combined together, ostracods, cladocerans and echinoderms contributed the most to differences between historic and oil spill samples at both sites. When months were analyzed separately, barnacle nauplii, bivalve larvae, cladocerans, doliolids, echinoderms, euphausiid protozoa, mysid shrimps, polychaetes, calanoid and cyclopoid copepods often contributed to more than 5% of differences between oil spill and historic samples.

Significant differences in mesozooplankton densities were observed between the historic (pre-spill) period and the oil spill year, though patterns were highly variable both within and among taxa and stations. When the whole study period was considered, significant differences between historical and oil spill values were observed for barnacle nauplii, euphausiid protozoa, ostracods, polychaetes, calanoid and cyclopoid copepods at station T20, and for mysid shrimps and cyclopoid copepods at station T35 (table 4; figures 4 and 5).

When months were considered separately, most significant differences in densities of individual taxa were observed in June (table 4; figures 4 and 5), and in most instances, taxon densities were significantly higher during the oil spill year than in previous years (e.g., euphausiid protozoa, mysid shrimps, calanoid and cyclopoid copepods at station T20, and bivalve larvae, cladocerans, ostracods, calanoid and cyclopoid copepods at station T35). Mesozooplankton found in lower densities during the oil spill year included barnacle nauplii (June) and ostracods, calanoid and cyclopoid copepods at station T20, and bivalve larvae, cladocerans, ostracods, calanoid and cyclopoid copepods at station T35.

### Discussion

One of the major challenges in assessing DWH impacts on the northern Gulf of Mexico ecosystem is teasing apart variability in response to the oil spill and dispersant

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**Table 3.** Analyses of similarity (ANOSIM) comparing the composition of zooplankton assemblages observed from May to August between 2010 (oil spill year) and previous years (historical data) at stations T20 and T35 in the Alabama inner shelf. Corresponding number of observations are reported in table 1. When significant differences were detected ($P<0.05$), the list of taxa contributing to at least 5% of the dissimilarity (SIMPER), are listed. Taxa codes are given in supplementary material 2.

|   | T20          |       | T35          |       |
|---|--------------|-------|--------------|-------|
|   | ANOSIM       | SIMPER | ANOSIM       | SIMPER |
|   | $R$          | $P$   | $R$          | $P$   |
|   | Taxa Contrib (%) |       | Taxa Contrib (%) |       |
| All combined | 0.120 | 0.006 | 0.085 | 0.033 |
|               | ostra  | 6.95  | ostra        | 6.84  |
|               | clado  | 5.81  | clado        | 6.42  |
|               | echin  | 5.50  | echin        | 6.12  |
|               | polyc  | 5.43  | polyc        | 5.85  |
|               | uppz   | 5.34  | uppz         | 5.67  |
|               | hydro  | 5.05  | hydro        | 5.08  |
|               | myssh  | 5.04  | myssh        | 5.04  |
| May           | 0.410 | 0.015 | 0.600 | 0.036 |
|               | ostra  | 6.80  | dolio        | 10.22 |
|               | polyc  | 6.39  | clado        | 9.54  |
|               | bacyp  | 5.56  | echin        | 7.64  |
|               | ptero  | 5.47  | myssh        | 7.56  |
|               | uppz   | 5.23  | banau        | 6.43  |
|               | myssh  | 5.20  | chaet        | 5.95  |
|               | amphi  | 5.10  | larvc        | 5.72  |
|               | siphon | 5.08  |              |       |
|               | gasla  | 5.04  |              |       |
| June          | 0.318 | 0.002 | 0.688 | 0.008 |
|               | ostra  | 7.76  | ostra        | 11.47 |
|               | uppz   | 6.55  | echin        | 7.86  |
|               | clado  | 6.25  | odcla        | 6.83  |
|               | bivla  | 6.01  | uppz         | 5.61  |
|               | odcla  | 5.97  | bivla        | 5.37  |
|               | echin  | 5.74  |              |       |
|               | banau  | 5.30  |              |       |
|               | polyc  | 5.02  |              |       |
| July          | 0.150 | 0.117 | 0.194 | 0.135 |
| August        | 0.222 | 0.094 | 0.225 | 0.127 |
Table 4. Mann–Whitney non-parametric tests of differences in mean densities between historical and oil spill observations for the ten taxa contributing the most to variations in the relative composition of zooplankton assemblages, and for dominant copepod groups (see figure 3 and table 3 for assemblage analysis). Monthly mean densities for the ten taxa and for calanoid and cyclopoid copepods are plotted in figures 4 and 5, respectively, and global means are given in supplementary material 2. When significant differences are detected ($P < 0.05$, in bold), the direction of change relative to historic conditions (2005–2009) is indicated by arrows.

| Taxa                  | Month       | W statistic | $P$  | W statistic | $P$  |
|-----------------------|-------------|-------------|------|-------------|------|
| Barnacle nauplii      | May–August  | 470.0       | 0.018| 146.0       | 0.893|
|                       | May         | 18.0        | 1.000| 1.0         | 0.072|
|                       | June        | 58.0        | 0.014| 9.0         | 0.898|
|                       | July        | 25.0        | 0.225| 14.0        | 0.240|
|                       | August      | 13.0        | 0.921| NA          | NA   |
| Bivalve larvae        | May–August  | 309.0       | 0.529| 120.0       | 0.324|
|                       | May         | 8.0         | 0.142| 4.0         | 0.371|
|                       | June        | 43.0        | 0.221| 0.0         | 0.020|
|                       | July        | 6.0         | 0.074| 7.5         | 0.623|
|                       | August      | 11.0        | 0.637| 19.0        | 0.034|
| Cladocerans           | May–August  | 259.0       | 0.125| 166.0       | 0.602|
|                       | May         | 12.0        | 0.394| 13.5        | 0.081|
|                       | June        | 24.0        | 0.304| 1.0         | 0.037|
|                       | July        | 14.0        | 0.626| 12.0        | 0.712|
|                       | August      | 14.0        | 1.000| 15.0        | 0.270|
| Doliolids             | May–August  | 284.0       | 0.278| 198.0       | 0.112|
|                       | May         | 24.0        | 0.395| 15.0        | 0.032|
|                       | June        | 35.0        | 1.000| 14.0        | 0.389|
|                       | July        | 10.0        | 0.256| 11.0        | 0.903|
|                       | August      | 2.0         | 0.030| 8.5         | 0.806|
| Echinoderms           | May–August  | 249.0       | 0.085| 111.0       | 0.192|
|                       | May         | 6.0         | 0.075| 3.0         | 0.204|
|                       | June        | 15.0        | 0.056| 2.0         | 0.062|
|                       | July        | 15.0        | 0.741| 12.0        | 0.709|
|                       | August      | 21.0        | 0.218| 12.0        | 0.713|
| Euphausiid protozoa   | May–August  | 181.0       | 0.003| 135.0       | 0.628|
|                       | May         | 10.0        | 0.243| 5.0         | 0.551|
|                       | June        | 12.0        | 0.027| 11.5        | 0.806|
|                       | July        | 10.0        | 0.256| 13.0        | 0.540|
|                       | August      | 12.5        | 0.850| 4.0         | 0.171|
| Mysid shrimps         | May–August  | 258.0       | 0.109| 74.5        | 0.001|
|                       | May         | 19.0        | 0.931| 0.0         | 0.017|
|                       | June        | 6.0         | 0.005| 5.0         | 0.131|
|                       | July        | 17.0        | 1.000| 7.5         | 0.371|
|                       | August      | 14.5        | 1.000| 6.0         | 0.308|
| Ostracods             | May–August  | 546.0       | <0.001| 95.5        | 0.071|
|                       | May         | 34.0        | 0.017| 10.0        | 0.551|
|                       | June        | 64.0        | 0.005| 0.0         | 0.019|
|                       | July        | 18.0        | 1.000| 7.0         | 0.539|
|                       | August      | 20.5        | 0.216| 11.0        | 0.903|
application from natural environmental ‘noise’. Mesozooplankton assemblage composition and abundance are often highly variable, largely a result of spatial and temporal variability in oceanographic conditions [22]. At seasonal scales, temperature, salinity and nutrient availability often drive primary and secondary production, thus factors such as freshwater discharge can play a significant role in structuring communities [23, 24]. Decadal patterns have also been observed, in particular related to warming trends that have impacted zooplankton distributions and phenology [25, 26]. These factors, as well as other anthropogenic factors already impacted zooplankton distributions and phenology [25, 26]. Decadal patterns have also been observed, in particular related to warming trends that have impacted zooplankton distributions and phenology [25, 26]. These factors, as well as other anthropogenic factors already impacted zooplankton distributions and phenology [25, 26].

Due to the highly variable nature of our sampling region, we cannot absolutely link observed changes in zooplankton assemblage structure with the DWH oil spill. However, our observations in zooplankton community composition were in response to the DWH oil spill, having eliminated many other probable factors.

The combination of analytical methods used in this study revealed some significant variations in zooplankton assemblage composition during the DWH oil spill on the Alabama shelf, particularly in May and June 2010, the period when the oil pollution was the most severe on the Alabama shelf [7]. A variety of taxa contributed in explaining these variations, with different patterns depending on taxa, sites and months. Overall, responses were taxon-specific, with no consistent pattern. Most changes observed within zooplankton assemblage structure were either weak in strength, or did not last more than a few months, with assemblages returning to the structure observed before the spill as soon as July 2010. These findings are consistent with previous studies which emphasized a low response of planktonic communities to other oil spills including the ‘Prestige’ spill in the Bay of Biscay [27], the ‘Sea Empress’ oil spill in the Irish Sea [28] or the ‘Tsesis’ spill in the Baltic Sea [29]. Further, these results are not surprising given the known patchy distribution of zooplankton assemblages, which increases natural variability associated with zooplankton abundance data, especially on relatively short, seasonal scales [30]. Overall, however, our analyses identified significant changes in zooplankton community composition that may be attributed to the DWH oil spill, as well as the taxa which responded most to the oil spill, and provided a preliminary estimation of the period of direct incidence of pollution on the structure of zooplankton communities in the region.

Although the depth-integrated structure of the assemblages did not change much, there may have been significant variations in vertical structure. There is evidence to suggest that zooplankton can detect and possibly avoid areas with high concentrations of hydrocarbons [5, 31]. Much of the oil in our sampling region was observed at the surface [32, 33].

| Table 4. (Continued.) |
|-----------------------|
| Taxa                  | Month     | U statistic | P   | T20      | U statistic | P   |
| Other decapods, larvae| May–August| 299.0       | 0.413 | 145.0    | 0.880 |
|                       | May       | 22.0        | 0.583 | 6.0      | 0.766 |
|                       | June      | 28.5        | 0.555 | 20.0     | 0.020 |
|                       | July      | 23.0        | 0.417 | 0.0      | 0.018 |
| Polychaetes           | August    | 1.0         | 0.018 | 15.0     | 0.262 |
|                       | May–August| 176.0       | <0.001 | 124.0    | 0.394 |
|                       | May       | 0.0         | 0.007 | 9.0      | 0.766 |
| Calanoid copepods     | June      | 21.0        | 0.184 | 12.0     | 0.713 |
|                       | July      | 4.0         | 0.035 | 5.0      | 0.262 |
|                       | August    | 7.0         | 0.218 | 10.0     | 1.000 |
| Cyclopoid copepods    | May–August| 175.0       | 0.002 | 131.0    | 0.538 |
|                       | May       | 10.0        | 0.246 | 9.0      | 0.766 |
|                       | June      | 18.0        | 0.107 | 2.0      | 0.066 |
|                       | July      | 6.0         | 0.074 | 16.0     | 0.178 |
|                       | August    | 1.0         | 0.018 | 0.0      | 0.020 |
|                       | May–August| 119.0       | <0.001 | 51.0     | 0.001 |
|                       | May       | 0.0         | 0.007 | 0.0      | 0.037 |
|                       | June      | 0.0         | <0.001 | 0.0      | 0.020 |
|                       | July      | 9.0         | 0.194 | 2.0      | 0.066 |
|                       | August    | 9.0         | 0.395 | 8.0      | 0.713 |
thus zooplankton may have migrated to deeper waters in response. Further, bottom hypoxic conditions were observed during the spill, presumably a result of bacterial breakdown of oil [34]. Previous observations from the Gulf of Mexico ‘dead zone’ suggest mesozooplankton also migrate to avoid hypoxic waters [35]. Therefore, if zooplankton were faced with the combined effect of surface hydrocarbons and bottom hypoxia, this may have effectively compressed the organisms into the middle water column. The present study is based on oblique tows, and thus cannot address these hypotheses; however, depth-discrete samples from the FOCAL survey are being processed to examine zooplankton vertical behaviors during the oil spill.

Our study suggests that many zooplankton taxa were present in significantly higher abundances during the oil spill period relative to historic observations, a result that contradicts expectations of higher mortalities based on laboratory responses to contamination [6] and field surveys in the wake of other oil spills, such as the 1979 Ixtoc-1 oil spill in the southern Gulf of Mexico [36]. One possible explanation is

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**Figure 4.** Monthly mean densities of ten taxa shown to contribute at least 5% of variations in zooplankton assemblage structure between historical (2004–2009) and oil spill (2010) samples in two sites from coastal Alabama. Blue bars represent historical values while gray bars are values observed during the oil spill season. Error bars are standard errors. Results of taxa-specific tests are given in table 4. Asterisks indicate significant differences. Study sites are depicted in figure 1.
that the zooplankton population increased in response to elevated primary productivity (i.e., bottom-up control). Satellite measurements after the spill provided evidence for elevated chlorophyll-a concentrations in the northeastern Gulf of Mexico [37]. However, this anomaly occurred only in August 2010, and was centered further offshore and to the east of our sampling region. Further, chlorophyll data collected during the oil spill at our two sampling locations (T20 and T35) varied little from June through July, and did not show evidence of bloom conditions [7], which suggests this hypothesis is not a likely explanation for increased abundances for some taxa.

A second possible explanation for increased zooplankton abundances in the wake of the DWH oil spill is that management actions in response to the spill may have impacted the food web (including zooplankton abundances) via top-down control processes. At the peak of the DWH oil spill, approximately 229,270 km² of US federal waters in the Gulf of Mexico were closed to recreational and commercial harvesting [38]. This unprecedented release of fishing pressure could have resulted in cascading indirect effects [39]. For example, large piscivores released from fishing mortality likely increased in abundance (and size), and subsequently exerted greater predation pressure on smaller, zooplanktivorous fishes, thus releasing zooplankton populations. Estimates of DWH impacts on adult fish abundances were lacking particularly for shelf and offshore species, therefore the relative importance of bottom-up and top-down controls in food webs after the oil spill remain unknown.

A third possible explanation is that the higher abundances of some zooplankton may be attributed to an increase in the abundance and activity of oil-degrading bacteria in response to oil pollution in the water column [40], which presumably enhanced microbial-zooplankton trophic linkages, and therefore contributed in stimulating secondary production, as suggested by Graham et al (2010) [7] and Chanton et al (2012) [8]. However, other zooplankton taxa had lower densities during the oil spill period. These contrasting responses might be attributable to multiple causes that are difficult to disentangle, such as species-specific resistance to oil pollution, predation rates, and competitive advantages in feeding [41].

Our field-based observations of zooplankton further highlight the disconnect between expectations based on organismal responses to the DWH oil spill versus natural populations [42]. For example, numerous exposure studies on small coastal fishes (primarily Fundulus grandis) suggest negative impacts on an individual level [43, 44, 45], however field observations from coastal habitats suggest fish population abundances were stable, or in some instances greater, after the oil spill [42, 46]. There is also evidence to suggest that commercially important shrimp species (Farfantepeneus aztecus and Litopenaeus setiferus) from impacted areas increased in abundance after the spill, and mean size of shrimp was unchanged, even though previous lab studies suggest decapods are negatively impacted by contaminants present in oil [47]. Compensatory processes and complex interactions in marine ecosystems may lessen the overall impact of large disturbances at a population level [42], however as in the case of Pacific herring following the Exxon Valdez spill, latent effects may exist within populations.

**Figure 5.** Monthly mean densities of major larval fish prey, i.e., calanoid (top) and cyclopoid (bottom) copepods between historical (2004–2009) and oil spill (2010) samples in two sites from coastal Alabama. Blue bars represent historical values while gray bars are values observed during the oil spill season. Error bars are standard errors. Results of taxa-specific tests are given in table 4. Asterisks indicate significant differences. Study sites are depicted in figure 1.
therefore continued biological monitoring in northern Gulf of Mexico ecosystem is advisable.

Conclusion

Our results indicate a significant but short-term impact of DWH oil spill on the structure of zooplankton assemblages in our study region. Although the recovery in assemblage structure to historic conditions was relatively rapid, such a change may have significant consequences on other components of shallow pelagic ecosystems. The feeding success of fish larval stages is indeed a crucial determinant of fish recruitment success and therefore fish year-class strength [48, 49]. Variability in the types and abundances of mesozooplankton prey, combined with taxon-specific feeding preferences, may have created short-term, ‘match-mismatch’ dynamics in the planktonic food web. While many of the mesozooplankton taxa were significantly more abundant during the oil spill period than in previous years, further work is needed to determine larval fish diet preferences with regards to these changes in mesozooplankton abundance and community structure, as well as subsequent larval fish growth and condition. Also, our analysis to date does not include information on the size-spectra of zooplankton, which may be more telling than abundances with regards to their availability to larval fish predators. These and other indirect effects of detected changes in the planktonic community structure need to be investigated in further detail before final conclusions can be drawn about the long-term effect of the DWH incident on fisheries production in the northern Gulf of Mexico.

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References

[1] Adcroft A, Hallberg R, Dunne J P, Samuels B J, Galt J A, Barke C H and Payton D 2010 Simulations of underwater plumes of dissolved oil in the Gulf of Mexico Geophys. Res. Lett. 37 L18605

[2] Kerr R A 2010 A lot of oil on the loose, not so much to be found Science 329 734–5

[3] Reddy C M et al 2012 Composition and fate of gas and oil released to the water column during the Deepwater Horizon oil spill Proc. Natl. Acad. Sci. USA 109 20229–34

[4] NOAA (National Oceanic and Atmospheric Administration) 2012 The Future of Dispersant use in Oil Spill Response Initiative (Coastal Response Research Center)

[5] Abbriano R M, Carranza M M, Hogle S L, Levin R A, Netburn A N, Seto K L, Snyder S M and SI0 280 Francks P J S 2011 Deepwater Horizon oil spill: a review of the planktonic response Oceanogr. 24 294–301

[6] Almeda R, Warnabough Z, Wang Z, Hyatt C, Liu Z and Buskey E J 2013 Interactions between zooplankton and crude oil: toxic effects and bioaccumulation of polycyclic aromatic hydrocarbons PLoS ONE 8 e67212

[7] Graham W M, Condon R H, Carmichael R H, D’Ambra I, Patterson H K, Linn L J and Hernandez F Jr 2010 Oil carbon entered the coastal planktonic food web during the Deepwater Horizon oil spill Environ. Res. Lett. 5 045301

[8] Chanton J P, Cherrier J, Wilson R M, Sarkoodee-Adoo J, Bosman S, Mickle A and Graham W M 2012 Radiocarbon evidence that carbon from the Deepwater Horizon spill entered the planktonic food web of the Gulf of Mexico Environ. Res. Lett. 7 045303

[9] Cohen J H, McCormick L R and Burkhardt S M 2014 Effects of dispersant and oil on survival and swimming activity in a marine copepod B. Environ. Contam. Tox. 92 381–7

[10] Llopiz J K 2013 Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: a literature synthesis J. Mar. Syst. 109 69–77

[11] Hernandez F Jr, Carassou L, Muffelman S, Powers S P and Graham W M 2011 Comparison of two plankton net mesh sizes for ichthyoplankton collection in the northern Gulf of Mexico Fish. Res. 108 327–35

[12] Carassou L, Hernandez F J, Powers S P and Graham W M 2012 Cross-shore, seasonal, and depth-related structure of ichthyoplankton assemblages in coastal Alabama T. Am. Fish. Soc. 141 1137–50

[13] Carassou L, Dzwonkowski B, Hernandez F J, Powers S P, Park K, Graham W M and Mareska J 2011 Environmental influences on juvenile fish abundances in a river-dominated coastal system Mar. Coast. Fish. Dyn. Manag. Ecosyst. Sci. 3 411–27

[14] NOAA (National Oceanic and Atmospheric Administration) 2010 National Weather Service, Climate Prediction Center. NOAA NWS CPC (www.cpc.ncep.noaa.gov) Accessed December 2010

[15] NOAA (National Oceanic and Atmospheric Administration) 2010 National Data Buoy Center. NOAA NDBC (www.ndbc.noaa.gov) Accessed December 2010

[16] USGS (United States Geological Survey) 2010 Alabama River at Clairborne Lock and Dam near Monroeville, Alabama. National Water Information System, USGS 024284000 (www.waterdata.usgs.gov/usa/nwis/uv?site_no=024284000) Accessed December 2010

[17] USGS (United States Geological Survey) 2010 Tombigbee River at Coffeeville Lock and Dam, near Coffeeville, Alabama. National Water Information System, USGS 02469761 (www.waterdata.usgs.gov/usa/nwis/uv?site_no=02469761) Accessed December 2010

[18] Park K, Kim C K and Schroeder W 2007 Temporal variability in summertime bottom hypoxia in shallow areas of Mobile Bay, Alabama Estuar. Coasts 30 54–65

[19] Legendre P and Legendre L 1998 Numerical Ecology (Amsterdam: Elsevier)
[20] Zar J H 1999 Biostatistical Analysis 4th edn (Upper Saddle River, NJ: Prentice-Hall)
[21] Clarke K R 1993 Non parametric multivariate analysis of changes in community structure Aust. J. Ecol. 18 117–43
[22] Chen M, Chen B, Harrison P and Liu H 2011 Dynamics of mesozooplankton assemblages in subtropical coastal waters of Hong Kong: a comparative study between a eutrophic estuarine and a mesotrophic coastal site Cont. Shelf Res. 31 1075–86
[23] Roman M, Zhang X, McGilliard C and Boicourt W 2005 Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay Limnol. Oceanogr. 50 480–92
[24] Araujo H M P, Nascimento-Vieira D A, Neumann-Leitao S, Schwamborn R, Lucas A P O and Alves J P H 2008 Zooplankton community dynamics in relation to the seasonal cycle and nutrient inputs in an urban tropical estuary in Brazil Braz. J. Biol. 68 751–62
[25] Bi H, Ji R, Liu H, Jo Y H and Hare J A 2014 Decadal changes in zooplankton of the Northeast US continental shelf PLoS ONE 9 e87720
[26] Rice E, Dam H G and Stewart G 2014 Impact of climate change on estuarine zooplankton: surface water warming in long Island sound is associated with changes in copepod size and community structure Estuar. Coasts in press 1–11
[27] Varela M et al 2006 The effect of the ‘prestige’ oil spill on the plankton of the N-NW Spanish coast Mar. Poll. Bull. 53 272–86
[28] Batten S D, Allen R J S and Wotton C O M 1998 The effects of the Sea Empress oil spill on the plankton of the Southern Irish Sea Mar. Poll. Bull. 36 764–74
[29] Johansson S, Larsson U and Boehm P 1980 The tsesis oil spill impact on the pelagic ecosystem Mar. Poll. Bull. 11 284–93
[30] Omori M and Hamner W M 1982 Patchy distribution of zooplankton: behavior, population assessment and sampling problems Mar. Biol. 72 193–200
[31] Seuront L 2010 Zooplankton avoidance behaviour as a response to point sources of hydrocarbon-contaminated water Mar. Freshw. Res. 61 263–70
[32] Powers S P, Hernandez F J, Condon R H, Drymon J M and Free C M 2013 Novel pathways for injury from offshore oil spills: direct, sublethal and indirect effects of the Deepwater Horizon oil spill on pelagicSargassum communities PLoS ONE 8 e74802
[33] Szedlmayer S T and Mudrak P A 2014 Influence of age-1 conspecifics, sediment type, dissolved oxygen, and the Deepwater Horizon oil spill on recruitment of age-0 red snapper in the Northeast Gulf of Mexico during 2010 and 2011 N. Am. J. Fish. Manag. 34 443–52
[34] DISL 2010 Dauphin Island Sea Lab Scientists Report Drop in Oxygen on Alabama shelf. Available: (http://press.disl.org/6_9_10oxygentBP.htm) Accessed 10 August 2014
[35] Roman M R, Pierson J J, Kimmel D G, Boicourt W C and Zhang X 2012 Impacts of hypoxia on zooplankton spatial distributions in the northern Gulf of Mexico Estuar. Coasts 35 1261–9
[36] del Próo G S, Chávez E A, Alatriste F M, de la Campa S, De la Cruz G, Gómez L, Guadarrama R, Guerra A, Mille S and Torruco D 1986 The impact of the Ixtoc-1 oil spill on zooplankton J. Plankt. Res. 8 557–81
[37] Chuanmin H, Weisberg R H, Liu Y, Zheng L, Daly K L, English D C, Zhao J and Vargo G A 2011 Did the northeastern Gulf of Mexico become greener after the Deepwater Horizon oil spill? Geophys. Res. Lett. 38 L09601
[38] NOAA Fisheries 2010 Deepwater Horizon/BP Oil Spill: Size and Percent Coverage of Fishing Area Closures Due to BP Oil Spill. NOAA, National Marine Fisheries Service, Southeast Regional Office. Retrieved 2014–10–20 (http://sero.nmfs.noaa.gov/deepwater_horizon/size_percent_closure/index.html)
[39] Peterson C H, Rice S D, Short J W, Esler D, Bodkin J L, Ballachey B E and Irons D B 2003 Long-term ecosystem response to the Exxon Valdez oil spill Science 302 2082–6
[40] Hazen T C et al 2010 Deep-sea oil plume enriches indigenous oil-degrading bacteria Science 330 204–8
[41] Walsh G E 1978 Toxic effects of pollutants on plankton, chapter 12, Principles of Ecotoxicology ed G C Butler (New York: Wiley) pp 257–74
[42] Fodrie F J and Heck K L Jr 2011 Response of coastal fishes to the Gulf of Mexico oil disaster PLoS ONE 6 e21609
[43] Whitehead A et al 2012 Genomic and physiological footprint of the Deepwater Horizon oil spill on resident marsh fishes Proc. Natl. Acad. Sci. 109 20298–302
[44] Garcia T I, Shen Y, Crawford D, Oleksiak M F, Whitehead A and Walter R B 2012 RNA-Seq reveals complex genetic response to Deepwater Horizon oil release in Fundulus grandis BMC Genomics 13 474
[45] Dubansky B, Whitehead A, Miller J T, Rice C D and Galvez F 2013 Multitissue molecular, genomic, and developmental effects of the Deepwater Horizon oil spill on resident Gulf killifish (Fundulus grandis) Environ. Sci. Technol. 47 5074–82
[46] Moody R M, Cebrian J and Heck K L Jr 2013 Interannual recruitment dynamics for resident and transient marsh species: evidence for a lack of impact by the macondo oil spill PLoS ONE 8 e58376
[47] van der Ham J L and de Mutsert K 2014 Abundance and size of Gulf Shrimp in Louisiana’s coastal estuaries following the Deepwater Horizon oil spill PLoS ONE 9 e108884
[48] Cushing D H 1996 Towards a science of recruitment in fish populations ed O Kinne Excellence in Ecology (Oldendorf/Luhe: Ecology Institute of Oldendorf-Luhe) Book 7
[49] Fuiman L A and Werner R G (ed) 2002 Fishery Science: The Unique Contributions of Early Life Stages (Oxford: Blackwell)