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The effects of experimental oil-contaminated marine snow on meiofauna in a microcosm

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ABSTRACT

During an oil spill, a marine oil snow sedimentation and flocculent accumulation (MOSSFA) event can transport oil residue to the seafloor. Microcosm experiments were used to test the effects of oil residues on meiofaunal abundance and the nematode:copepod ratio under different oil concentrations and in the presence and absence of marine snow. Total meiofaunal abundance was 1.7 times higher in the presence of snow regardless of oil concentration. The nematode:copepod ratio was 13.9 times lower in the snow treatment regardless of the oil concentration. Copepod abundance was 24.3 times higher in marine snow treatments and 4.3 times higher at the highest oil concentration. Nematode abundance was 1.7 times lower at the highest oil concentration. The result of the experiment was an enrichment effect. The lack of a toxic response in the experiments may be attributable to relatively low oil concentrations, weathering processes, and the absence of chemically dispersed oil.

1. Introduction

In the offshore marine environment, sedimentation typically increases the availability of organic matter to the benthos, leading to an enrichment effect on diversity and abundance. Organic matter deposition from the surface is the main source of food to the deep-sea environment (Gage and Tyler, 1991). Research suggests that the rate of organic matter accumulation to the seafloor increased after the Deepwater Horizon (DWH) oil spill (Ziervogel et al., 2012; Schrope, 2013; White et al., 2012; Brooks et al., 2015). The spill caused organic matter in the form of marine snow to transport large quantities of oil to the deep-sea floor through a marine oil snow sedimentation and flocculent accumulation (MOSSFA) event. The MOSSFA event resulted from the stress response of plankton and microorganisms at the ocean surface to oil and dispersant exposure. This exposure caused microorganisms and plankton to emit exopolymeric substances that facilitated the aggregation of oil and of lithogenous and biogenous particles (Passow et al., 2012; Ziervogel et al., 2012; Passow, 2014; Daly et al., 2016; Van Eenennaam et al., 2016), which subsequently sank to the sea floor. The result was higher oil concentrations in the deep-sea area surrounding the DWH wellhead with estimates ranging from 3,200 (Valentine et al., 2014) to ~33,000 km^2 (Romero et al., 2015, 2017; Schwing et al., 2015).

Meiofauna (retained on 31–63 μm sieves) are widely used to assess environmental conditions (Giere, 2009). After the DWH oil spill, meiofauna had increased abundance, decreased diversity, and increased nematode dominance in a 309.7 km^2 area around the DWH wellhead (Baguley et al., 2015). Four years after the spill, the deep-sea benthic community abundance recovered, but decreased diversity was still observed in the offshore affected zone (Reuscher et al., 2017). In contrast, the meiofauna had largely recovered four years after the spill in a Louisiana Salt marsh (Fleeger et al., 2015).

The increase in abundance and dominance of nematodes after the DWH spill reflects a balance between organic enrichment and toxicity. A combined toxicity-enrichment effect has been found in many studies that investigated exposure to oil (Kineman et al., 1980; Spies and Des Marais, 1983; Spies et al., 1988; Olsgard and Gray, 1995; Peterson et al., 1996; Jewett et al., 1999; Washburn et al., 2016). A toxicity effect is one that lowers abundance and diversity, whereas enrichment results in high abundance and low diversity (Jacobs, 1980; Sanders et al., 1980; Spies et al., 1988; Jewett et al., 1999; Washburn et al., 2017). The combined toxicity-enrichment effect observed after the DWH spill may be attributable to the interactive effects of sinking marine snow and oil residue resulting from MOSSFA.

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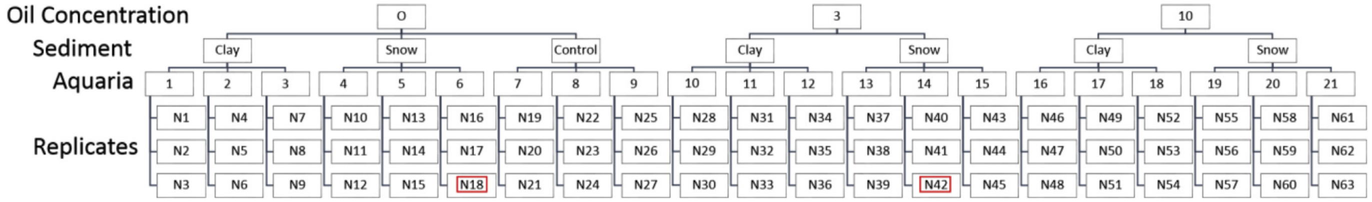

Fig. 1. Experimental design. Oil concentrations in g/m^2. The rectangles around replicates N18 and N42 indicate that these samples were lost during processing.

The nematode:copepod (N:C) ratio has become a common method for evaluating organic enrichment and chemical pollution. Nematodes usually dominate the meiofauna, and the second most abundant group is the copepods. A higher N:C ratio is believed to indicate chemically and organically polluted locations (Raffaelli and Mason, 1981) because copepods, specifically harpacticoids, are more sensitive to pollutants than are nematodes (Montagna et al., 1987, 1989; Peterson et al., 1996; Giere, 2009; Ansari et al., 2010; Elarbaoui et al., 2015). The N:C ratio has proven to work well in the Gulf of Mexico with the classification of drilling activities (Montagna and Harper, 1996), and the effects of the DWH oil spill (Montagna et al., 2013; Baguley et al., 2015).

Determining the effect of the DWH oil spill or predicting effects of future oil spills in the offshore environment on the benthic community requires identifying the interactive effects of sinking marine snow and oil residues on the seafloor. Microcosm experiments are useful for determining the interactive effects because they avoid the common complications of field experiments, such as inadequate reference sites, high natural variability, and the great spatial and temporal variability associated with benthic animals (Edwards et al., 1966; Heip et al., 1985; Coull, 1988). Previous microcosm experiments designed to test the impacts of MOSSFA on amphipods (*Corophium volutator*) and gastropods (*Hydrobia ulvae*) found that survival of both macroinvertebrates was lower in the presence of oil-contaminated marine snow (Van Eenennaam et al., 2018). The present study used a microcosm experiment examining amphipod and gastropod recovery from oil-contaminated marine snow to explore meiofaunal recovery following a MOSSFA event including abundance and nematode: copepod ratios.

2. Methods

We studied the effects of MOSSFA on the soft-bottom meiofaunal community using an experimental approach designed to accumulate oil residues gradually on the surface of the sediments in the form of marine snow or clay (Van Eenennaam et al., 2019). Our experiment is a followup to Van Eenennaam et al. (2018), which contains details of the experimental setup, and it is briefly described below.

2.1. Experimental design

The experimental setup followed the methods descriped in Rahsepar et al. (2017), Van Eenennaam et al. (2018), and Van Eenennaam et al. (2019). Twenty-one glass aquaria containing no silicone rubber and measuring 25 × 25 × 25 cm were used as microcosms. The aquaria were stored under climate-controlled conditions at 14 °C. The regime of 16 h of light and 8 h of darkness was maintained with flourescent tubes. Each aquarium contained a 5-cm layer of natural, uncontaminated sediment collected at low tide from the top 10 cm of an intertidal mudflat in the Dutch Wadden sea, the Netherlands (approximate location: 52° 56.112′ N, 4° 59.976′ E). The sediment (approximately 6% organic matter) was rinsed through a 1 mm sieve, which both infaunal macrofauna (300–500 μm) and meiofauna (45–63 μm) passed through, and pooled and split before being added to the aquaria. The initial abundance of meiofaunal organisms was unknown but sediments for all treatments were collected from one location, pooled, and split equally, so the abundance is presumed to be uniform among samples. In addition, a 15-cm layer of natural seawater, the same salinity as the intertidal mud flat, collected from Eastern Scheldt and filtered through 0.45 μm mesh, was added to each aquarium. After the microcosms settled for one day, other invertebrates were added (*Corophium volutator*, *Hydrobia ulvae*) to each aquarium (Van Eenennaam et al., 2019).

The experiment was designed to test the effect of sinking oil residues mixed with clay or marine snow. The oil was provided by BP and was chemically similar to the oil released during the DWH event (BP Gulf Science Data, 2017a, 2017b; 2017c). Before addition to the microcosm the oil was weathered for 24 h in a dark room at 14 °C to allow evaporation of the lighter hydrocarbons (to mimic the weathered oil that sank from the surface to the seafloor as MOSSFA). Kaolin clay was used (hydrated aluminum silicate, CAS 1332-58-7, Sigma Aldrich) as mineral particles for oil residues to adsorb to. The amount of clay added was 3.2 g in all treatments except for the control (no clay added). Artificial marine snow was prepared from alginate (7.6 g), phytoplankton paste (6 g), and kaoline clay (3.2 g) according to the method of Van Eenennaam et al. (2018). This composistion corresponds to that of the marine snow detected after the DWH spill (Van Eenennaam et al., 2016).

The experiment ran for 80 days with a total of 7 treatments and 3 replicates. Treatments included: control (no additions), clay without oil (0 g oil/m^2; Oil-0, clay), marine snow without oil (0 g oil/m^2; Oil-0, snow), clay with low concentration of oil (3 g oil/m^2; Oil-3, clay), marine snow with low concentration of oil (3 g oil/m^2; Oil-3, snow), clay with high concentration of oil (10 g oil/m^2; Oil-10, clay), and marine snow with high concentration of oil (10 g oil/m^2; Oil-10, snow) (Fig. 1). On the basis of Romero et al. (2017), 10 g oil/m^2 was chosen as a realistic high concentration and 3 g oil/m^2 as a realistic lower concentration, as ~300 km^2 of the area contaminated with DWH oil residues in the deep-sea (located at depths > 200 m) were found to contain concentrations of oil residues in the range of 1–43 g oil/m^2, equivalent to ~0.04–1.66 g PAH/m^2 because DWH oil contains about 3.9% polycyclic aromatic hydrocarbons (PAH) based on Reddy et al. (2011).

The aquaria were aerated in the top 5 cm of the water column and 25% of the water from each microcosm was replaced once a week. Care was taken not to disturb the sediment surface. Four days after the addition of the amphipods and the gastropods the kaolin clay, marine snow, and oil were added to the corresponding treatments. Additions were carried out over a 4-day period sensu Van Eenennaam et al. (2019). That is, 25% of the total amount of each additive (freshly prepared in the case of marine snow) was added each day to mimic field conditions, instead of a single deposition that was used in earlier experiments (Van Eenennaam et al., 2018). Our analysis was performed in conjunction with the analysis of other aspects of the benthic community within the same experiment including the macrofauna (Van Eenennaam et al., 2019) and the foraminiferan community (Schwing et al., in progress), which will be reported on separately.

2.2. Meiofauna

Meiofauna in the microcosms were not counted at the beginning of the experiment, although they were presumably uniform across all microcosms. At day 80 of the experiment, three replicate sediment cores with an inner diameter of 1.9 cm were taken from each of the 21 aquaria and preserved in 70% ethanol. Each core was then rinsed

Table 1
Average abundance per sample (count) across treatments (oil concentration or sediment type) for specific taxa. Taxa are either class or order level.

Size class	Phylum	Taxa	Oil and sediment treatments						
			$0\ g/m^2$			$3\ g/m^2$		$10\ g/m^2$	
			Control	Clay	Snow	Clay	Snow	Clay	Snow
Macrofauna	Annelida	Oligochaeta	0.1	0.1	0.3	0	0.1	0.1	0
Macrofauna	Annelida	Polychaeta	0.6	0.1	0	0	0	0.2	0
Macrofauna	Crustacea	Amphipoda	0.6	0.7	0.9	0.3	0.2	0.1	0
Meiofauna	Crustacea	Copepoda	1.9	2.4	21.6	1.9	48.4	6.4	67.1
Macrofauna	Crustacea	Isopoda	0	0.2	0	0	0	0	0
Meiofauna	Crustacea	Ostracoda	0	0.4	0.4	0	0	0.1	0.1
Macrofauna	Mollusca	Bivalvia	0	0.1	0	0	0	0	0
Macrofauna	Mollusca	Gastropoda	0	0.2	0	0.3	0.4	0.3	0.5
Meiofauna	Kinoryncha		0.1	0.1	0	0	0	0	0
Meiofauna	Nematoda		114.2	90	158.8	72.9	68.3	80	78
Macrofauna	Nemertea		0.1	0	0	0	0	0	0

through a 45-μm sieve and stained with Rose Bengal mixed in 70% ethanol. The samples were left to stain overnight at 4 °C. All samples were hand sorted under a dissecting microscope at 120× magnification. During processing, two samples were lost (N18 and N42), so the 0-Snow-6 and 3-Snow-14 treatments only had two replicates (Fig. 1). No distinction was made between the different taxa's orders, ages, or sizes; all were combined into one category, with the exception of amphipods and isopods (Table 1). We calculated the N:C ratio by dividing the sum of all nematodes in a sample by the sum of all copepods. When the copepod count was zero the nematode count was used as the ratio value (Lee et al., 2001).

2.3. Statistical analyses

The experiment was a partially heirarchial incomplete block design (Fig. 1). The two-way design included two main treatments: oil concentration (0, 3, and 10 g/m^2) and sediment (clay, snow, or a control with nothing). Experiments were repeated in three aquaria, but each aquarium was unique and nested within the oil x organic matter interaction term. The statistical model therefore is $Y_{ijkl} = \mu + \alpha_j + \beta_k + \alpha\beta_{jk} + \gamma_{l(jkl)} + \epsilon_{(i)jkl}$, where Y_{ijkl} is the dependent response variable, μ is the overall sample mean, α_j is the main fixed effect for oil. $j = 1, 2$, or 3 for the three concentrations, β_k is the main fixed effect for organic matter, where $k = 1$, 2, or 3 for the clay, marine snow, or control; $\alpha\beta_{jk}$ is the main fixed effect for the interaction between oil and organic matter, and $\gamma_{l(jk)}$ is the main effect for aquaria that are nested (or unique) to the oil x organic matter interaction. A random effect is denoted by the parentheses around the subscript *jk* that represents the 21 aquaria, and $\epsilon_{(i)jkl}$ is the random error term for each of the *i* replicate measurements within cells.

2.3.1. Univariate analyses

To test for differences in meiofaunal communities among treatments, we used four dependent variables: total abundance of meiofauna, N:C, nematode abundance, and copepod abundance. Univariate analysis of variance (ANOVA) was performed and the ANOVA assumptions tested with PROC GLM in SAS 14.3 (SAS, 2017). A post-hoc comparison test was performed with Tukey's Honestly Significant Difference (HSD) test across all possible comparisons among means.

2.3.2. Multivariate analyses

Multivariate analyses of macrofauna and meiofauna community structure were performed with Primer-e version 7 (Clarke and Gorley, 2015). Before analysis the counts were square-root transformed, then a resemblance matrix was created with Bray-Curtis Similarity between samples. From the resemblance matrix, a non-metric multi-dimensional scaling (nMDS) plot with 1000 restarts and a minimum stress of 0.01 was created. In addition, we ran a cluster analysis to determine the degree of similarity between samples. Within this test a similarity profile analysis (SIMPROF) was generated to identify the statistically significant groupings.

3. Results

Total meiofaunal abundance differed significantly with sediment type ($P\text{-value} = 0.0136$) and among replicate aquaria ($P\text{-value} = 0.0381$) (Table 2). Total meiofaunal abundance was 1.7 times higher in the marine snow than in the clay treatment (Table 2). The N:C ratio differed significantly with sediment ($P\text{-value} = 0.0007$) and among replicate aquaria ($P\text{-value} = 0.0214$) (Table 2). N:C was 13.9 times higher in control than snow treatments and 6.8 times higher in clay than snow treatments (Table 2). Nematodes and copepods together accounted for 99% of meiofauna total abundance (Table 1). Nematode abundance differed significantly with oil ($P\text{-value} = 0.0112$) (Table 2). Nematode abundance was 1.7 times higher in 0 g/m^2 than 3 g/m^2 and 10 g/m^2 (Table 2, Fig. 2). Copepod abundance differed significantly with oil ($P\text{-value} = 0.0411$) and sediment ($P\text{-value} = < 0.0001$) (Table 2). Copepod abundance was up to 4.3 times higher in 10 g/m^2 than 0 g/m^2 (Table 2, Fig. 2). Copepod abundance was up to 24.3 times higher in snow than in control and clay treatments (Table 2, Fig. 2).

The nMDS plot of meiofaunal and macrofaunal community structure has three groups at 70% similarity. The first group contains the majority of the snow treatments with oil. The second group contains only one of the clay without oil replicates. The final group contains all other treatments (control, clay, and snow without oil) (Fig. 3). The difference in similarity was not significant according to the cluster analysis and associated SIMPROF test ($P\text{-Value} = 0.2160$).

4. Discussion

Our experiment was inspired by the DWH event because of the occurrence of MOSSFA, but it was performed under laboratory conditions with estuarine organisms. Therefore, although we want to interpret the findings in the context of understanding deep-sea patterns after the DWH oil spill, we must be cognizant that we are testing mechanisms under different conditions. In addition, the experiment was designed to test the effects of MOSSFA on *Corophium volutator* and *Hydrobia*. The decision to investigate differences in meiofauna among the treatment levels was made only at the end of the experiment, which is why initial meiofauna values were not determined. However, because all sediment was collected from one location and was pooled and split before use, we assume that all the aquaria started at approximately the same abundance and diversity level of meiofauna and that the treatments were responsible for differences at the end of the experiment. It is important

Table 2

ANOVA results for (A) total abundance of meiofauna, N:C (nematode:copepod ratio), Nematoda abundance, and Copepoda abundance. DF = degrees of freedom. (B) Tukey's HSD test for abundance and sediment. (C) Tukey's HSD test for N:C and sediment. (D) Tukey's HSD test for Nematoda abundance and oil. (E) Tukey's HSD test for Copepoda abundance and oil. (E) Tukey's HSD test for Copepoda abundance and sediment.

A				P-Value			
	F-Test	Source	DF	Abundance	N:C	Nematoda	Copepoda
1	1/4	Oil	2	0.225	0.1265	0.0112	0.0411
2	2/4	Sediment	2	0.0136	0.0007	0.3434	<0.0001
3	3/4	Oil x Sediment	2	0.6175	0.1983	0.0728	0.0866
4	4/5	Aquaria(Oil x Sediment)	14	0.0318	0.0214	0.1979	0.2891
		Error	40				

B		Abundance (n/sample)	
Mean	146.36	116.22	84.22
Treatment	Snow	Control	Clay

C		N:C	
Mean	78.04	38.37	5.62
Treatment	Control	Clay	Snow

D		Nematoda Abundance	
Mean	119.54	79.06	70.61
Treatment	0 g/m^2	10 g/m^2	3 g/m^2

E		Copepoda Abundance	
Mean	35	25.17	8.15
Treatment	10 g/m^2	3 g/m^2	0 g/m^2

F		Copepoda Abundance	
Mean	45.84	3.6	1.89
Treatment	Snow	Clay	Control

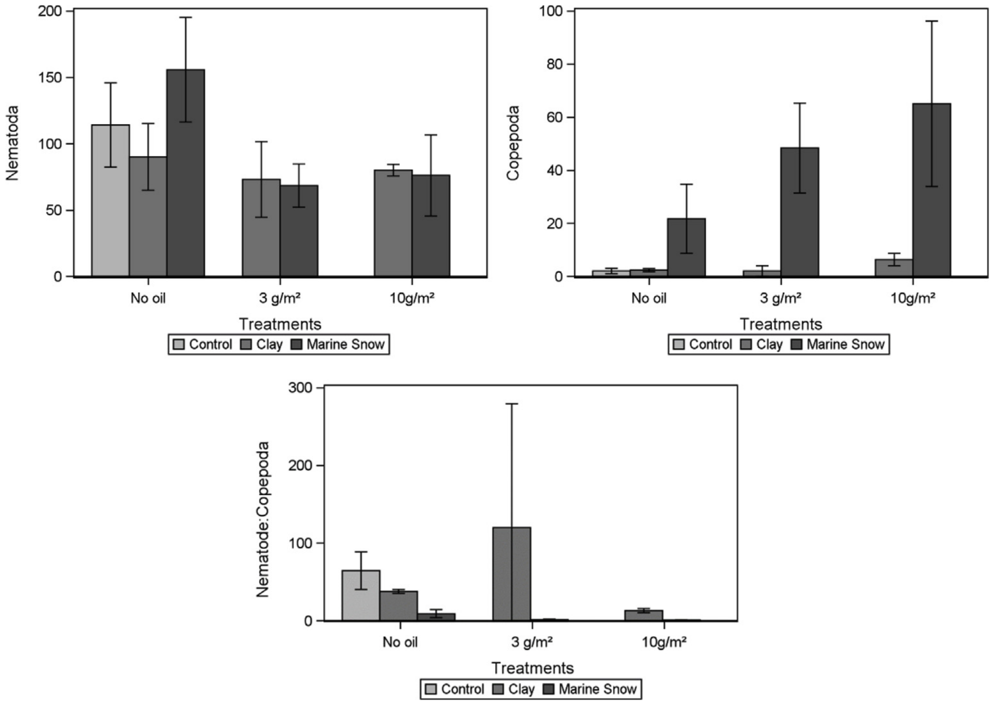

Fig. 2. Abundance averaged acrossed replicate cores and aquaria for Nematoda, Copepoda, and the nematode:copepod ratio. Error bars are standard deviation.

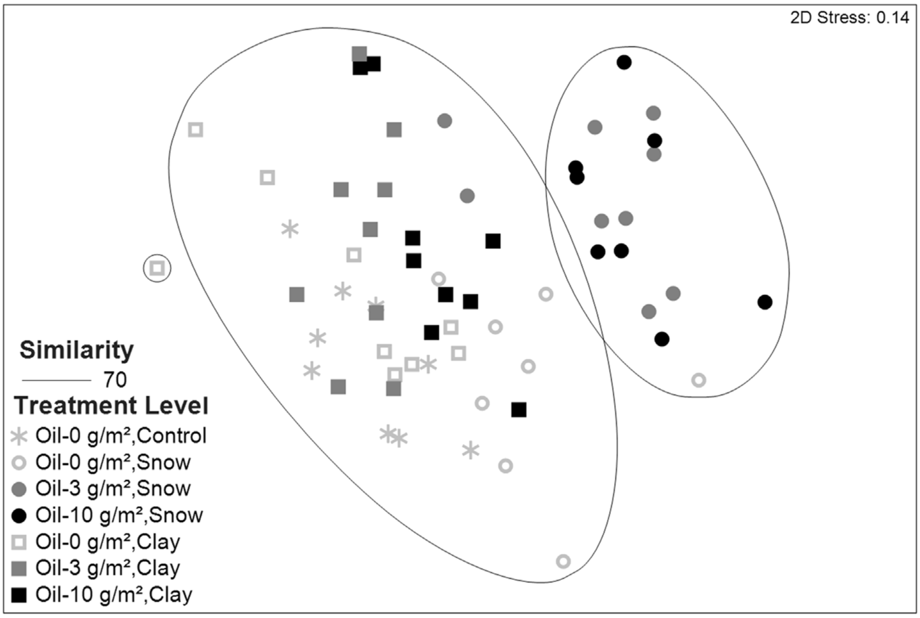

Fig. 3. nMDS plot of meiofaunal and macrofauna community structure for all replicates within aquaria by treatment level, and with a sample similarity overlay.

to note that differences were found among replicate aquaria. However, replicate aquaria are pseudoreplicates so this difference does not matter. The differences likely arise from different trajectories over time in each aquaria, which could be due to small differences in the initial conditions that become amplified.

The role of organic matter was apparent in the experimental results because significantly higher total abundances and copepod abundances were found in marine snow treatments without a significant oil × sediment interaction (Table 2). Organic-matter content in the deep-sea sediment that originates from the surface plays a key role in meiofaunal abundance because it is the main source of food to the deep-sea environment (Gage and Tyler, 1991). Meiofaunal abundances are highest when the chlorophyll *a* concentrations in the overlying water column and deposition rates are high (Baguley et al., 2006).

The striking result from the current experiment was not the increase of total meiofaunal abundance but the increase in copepods in the presence of marine snow with higher oil concentrations (Table 1, Fig. 2). This is reflected in the nematode:copepod ratio (N:C) which was significantly lower in the presence of marine snow regardless of oil concentration (Table 2). In the presence of high natural oil seeps, changes in nematode and copepod abundances have been attributed to changes in food availability with copepods feeding on microalgae and nematodes feeding on bacteria primarily (Montagna et al., 1987, 1989). It is hypothesized that the increase in copepod abundance seen in the current experiment was because they were feeding on the alginate and algae paste used to create the marine snow as well as the additional organic carbon from the oil (Spies and DesMarais, 1983; Brooks et al., 1987).

In contrast, in the current experiment nematode abundance decreased at higher oil concentrations with no sediment effect (Table 2, Fig. 2). After the DWH spill the deep-sea meiofauna exhibited biological toxicity with moderate impacts observed up to 60 km from the wellhead (Baguley et al., 2015). However, unlike the copepods the nematode abundance increased near the wellhead (Baguley et al., 2015), a striking difference from the current experiment results where copepod abundance increased and nematode abundance decreased with oil concentration (Table 2, Fig. 2). Therefore, the addition of contaminated marine snow in this experiment resulted in an enrichment response of increased total meiofauna abundance, increased copepod abundance and decreased nematode dominance as observed in the N:C ratio (Table 2). The toxicity response found near the DWH wellhead, nematode dominance increased (Baguley et al., 2015), was not observed in the present experiment.

One reason for the lack of a toxicity response in this experiment could be the use of estuarine organisms. The Gulf of Mexico coastal areas have an order of magnitude higher PAH concentrations than found in offshore continental shelf sediments (Kennicutt et al., 1996). The apparent threshold for total PAH to have toxic effects on estuarine invertebrates is about 220 ppm (Long and Morgan, 1990). In contrast, the threshold for total PAH toxic effects on the deep sea invertebrates is about 24 ppm (Balthis et al., 2017). Therefore, estuarine organisms that are always exposed to higher concentrations could be more tolerant of PAH than offshore organisms. Toxicity responses were observed after the DWH spill in a contaminated salt marsh, where total meiofauna, nematode, and copepod abundances decreased (Fleeger et al., 2015). The heavily oiled marshes had TPH concentrations exceeding 450 mg/g surface sediment (Fleeger et al., 2015), which is equivalent to 450,000 μg/g (or ppm) that is 45,000 times higher than the dose used here of 10 ppm. Therefore, shallow-water observations after the DWH accident also indicate a toxicity response but concentration levels were higher than those observed around the wellhead. The lack of a toxicity response in the current experiment could be because of increased tolerances in estuarine organisms.

The lack of a toxicity response in this experiment could be attributed to the oil concentrations used in the different treatments. The experimental concentrations were only one-fourth of the maximum range observed by Romero et al. (2017). This range was chosen because the absolute maximum from Romero et al. (2017) was only found in a very small area and the chosen concentrations were more representative. To compare oil concentrations from this experiment to field observations, we converted concentrations to ppm (Table 3). The oil concentrations in this experiment were within the range of concentrations found with severe effects to benthic organisms at a zone near the DWH wellhead (Baguley et al., 2015) (Table 3). However, experimental concentrations were in the lower range of the concentrations at which a toxicity response is highly likely to occur (Balthis et al., 2017) (Table 3). Therefore, other variables in addition to oil concentration may have affected the experimental results causing a lack of toxic response.

Weathering processes affect the toxicity of oil by significantly changing its chemical composition. The oil in this experiment was artificially weathered through evaporation in dark conditions. This must

Table 3

Summary of polycyclic aromatic hydrocarbon (PAH) concentrations in sediment samples from field and experimental studies. The observed benthic effects represents the degree of effect as defined by the publication source. PAH = 2–6 ring polycyclic aromatic hydrocarbons, including alkylated homologs. PAH concentrations are based on dry weight. For Romero et al. (2017) the PAH values are the mean ± 95% confidence interval.

Source	Data type	Observed benthic effects	PAH (ppm)
Baguley et al. (2015)	Field Observation	Severe	1.2–47.6
Baguley et al. (2015)	Field Observation	Moderate	0.4–2.4
Baguley et al. (2015)	Field Observation	Uncertain	0.2–1.0
Baguley et al. (2015)	Field Observation	None	0.03–0.8
Romero et al. (2017)	Pre-spill field Observation	Unknown	3.8 ± 1.7
Romero et al. (2017)	Post-spill field Observation	Unknown	15.1 ± 6.7
Balthis et al. (2017)	Experiment	> 80% Probability	25
Balthis et al. (2017)	Experiment	< 20% Probability	4
Present study	Treatment 3g oil/m^2	None	3.0
Present study	Treatment 10 g oil/m^2	None	9.8

have resulted in the evaporation of the lighter, in general more toxic compounds, but photo enhanced toxicity can occur when the oil is exposed to sunlight (Alloy et al., 2015, 2016). It is thus likely that our weathered oil was less toxic compared to the oil that weathered on the surface water of the Gulf of Mexico during the spill. In addition, it is not likely that oil found on the seafloor reached the sea surface before being deposited, which would have resulted in higher concentrations of the lighter more toxic compounds than in the weathered oil used in our study.

Another difference between our experiments and field observations during the DWH oil spill is that only the effect of deposited oil was tested, while in the GoM the water column must also have contained dissolved oil compounds and possibly oil droplets, which was facilitated by the application of dispersants. Dispersants solubilize fractions of toxic hydrocarbons, which increases their bio availability (Mu et al., 2014), resulting in synergistic toxic effects between dispersants and oil (Fern et al., 2015).

In conclusion, the presence of oil in the experiment did not cause a toxic response; instead total meiofauna and copepod abundance increased while the N:C ratio and nematode abundance decreased. These findings are in contrast with observations at a salt marsh affected by DWH, where meiofauna total, nematode, and copepod abundance were lower after the spill (Fleeger et al., 2015). The experimental findings also differ from observations at the offshore site of the DWH spill, where total meiofaunal abundance and N:C ratio were higher at affected sites, indicative of a toxicity effect (Montagna et al., 2013; Baguley et al., 2015; Washburn et al., 2016; Balthis et al., 2017). In addition, results from this study indicate that the chemical composition of the weathered oil, and not only oil concentrations, are important in influencing the toxicity response and impact of oil spill in benthic environments. The lack of a toxic response in the experiments compared to field studies may be attributable to a combination of factors including relatively low oil concentrations, weathering processes, and the absence of chemical dispersed oil.

CRediT authorship contribution statement

Melissa Rohal: Writing - original draft, formal analysis, investigation. **Noe Barrera:** Investigation, writing - review and editing. **Justine S. Van Enennaam:** Investigation, Writing - review and editing, Methodology. **Edwin M. Foekema:** Writing - review and editing, Conceptualization, Methodology. **Paul A. Montagna:** Formal analysis, Writing - review and editing, supervision. **Albertinka J. Murk:** Writing - review and editing, Conceptualization, Methodology. **Marissa Pryor:** Writing - review and editing, Investigation. **Isabel C. Romero:** Formal analysis, writing - review and editing

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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Appendix A. Supplementary data

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