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Contribution to the Theme Section
'Response of nearshore ecosystems to the Deepwater Horizon oil spill'

Five years of *Deepwater Horizon* oil spill effects on marsh periwinkles *Littoraria irrorata*

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ABSTRACT: The *Deepwater Horizon* spill (2010) was the largest marine oil spill in US waters to date and one of the largest worldwide. To examine effects of the oil spill on an important salt marsh species over time, we conducted a meta-analysis on marsh periwinkles *Littoraria irrorata* using published and unpublished sources spanning more than 5 yr (2010–2015), including newly available Natural Resources Damage Assessment (NRDA) and Gulf of Mexico Research Initiative (GoMRI) data sets. We tested the hypotheses that the spill decreased mean periwinkle density, reduced mean snail shell length, and changed periwinkle size distribution. Averaged across multiple studies, sites, marsh zones (edge versus interior), and years, our synthesis revealed a negative effect of heavy oiling on periwinkles. Snail densities were reduced by 73% in heavily oiled sites across all study-zone-by-year combinations, including adverse effects for both the oiled marsh edge and oiled marsh interior, with impacts observed over more than 5 yr. Mean periwinkle shell length was somewhat reduced at the oiled marsh edge in a few cases; however, periwinkle size distributions displayed greater relative proportions of smaller adults and sub-adults, and fewer large adults, across all years. Given the spatial and temporal extent of data analyzed, this synthesis provides evidence that the *Deepwater Horizon* spill suppressed populations of marsh periwinkles in heavily oiled marshes for over 5 yr, and that impacts were ongoing and recovery was incomplete, likely affecting other ecosystem components, including marsh productivity, organic matter and nutrient cycling, marsh–estuarine food webs, and associated predators.

KEY WORDS: *Deepwater Horizon* · Oil spill · Salt marsh · Marsh periwinkle · *Littoraria irrorata* · Ecological impacts · Ecological recovery · Gulf of Mexico

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INTRODUCTION

The *Deepwater Horizon* oil spill (2010) was the largest marine oil spill in US waters to date and one of the largest worldwide: over 3 million barrels of crude oil were released into the Gulf of Mexico (US District Court 2015) and over 2100 km of coastal shorelines were oiled (Michel et al. 2013, Nixon et al. 2016). The impacts of this oil spill on salt marsh vegetation have been well documented (Lin & Mendels-

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sohn 2012, Silliman et al. 2012, Zengel et al. 2015, 2016a, Lin et al. 2016, Hester et al. 2016). In comparison, the impacts of this spill on salt marsh macroinvertebrates have received less attention (although see Zengel et al. 2016a, a single-year Natural Resources Damage Assessment [NRDA] study on marsh periwinkles; and Zengel et al. 2016b on fiddler crabs [*Uca* spp.]). As a further step in understanding the effects of this oil spill on salt marsh macroinvertebrates, we assessed multi-year effects of the *Deepwater Horizon* oil spill on marsh periwinkles *Littoraria irrorata*, the dominant gastropod (snail) species in salt marshes in the Gulf region, and an important secondary consumer and prey species.

Marsh periwinkles are abundant salt marsh residents and have important influences on marsh vegetation, organic matter and nutrient cycling, microbial communities, other invertebrates, and ecosystem productivity (Zengel et al. 2016a and references therein). For example, periwinkle grazing plays a key role in the shredding and decomposition of senescent and standing dead *Spartina alterniflora* plant leaves, thereby influencing organic matter and nutrient cycling and marsh–estuarine food webs (Newell et al. 1989, Kemp et al. 1990, Hensel & Silliman 2013). Periwinkle grazing may also regulate plant productivity, and in some cases may contribute to marsh vegetation die-back events (Silliman & Zieman 2001, Silliman et al. 2005). Marsh periwinkles are also important prey for many species of commercial, recreational, and conservation interest, including blue crab *Callinectes sapidus*, diamondback terrapin *Malaclemys terrapin*, clapper rail *Rallus longirostris*, and perhaps seaside sparrow *Ammodramus maritimus* (Hamilton 1976, Heard 1982, Tucker et al. 1995). Accordingly, oil spill impacts on periwinkles could affect overall marsh structure and function and a variety of other marsh and estuarine species.

A few studies have documented impacts on marsh periwinkles following prior oil spills, with effects including increased mortality, reduced density, reduced recruitment, and altered snail size distributions (Hershner & Moore 1977, Hershner & Lake 1980, Krebs & Tanner 1981, Lee et al. 1981). However, each of these spills differed from the *Deepwater Horizon* incident in several important ways: (1) all were located outside the Gulf of Mexico region; (2) all were shallow, nearshore spills or experimental oil applications that rapidly affected shorelines, whereas oil from the offshore *Deepwater Horizon* release weathered at sea for 2 wk or more before reaching shore; (3) all were spills of refined products, including No. 6 and No. 2 fuel oils, which differ from crude oils in terms of their chemistry and ecological fate and effects (Michel & Rutherford 2014); and (4) all affected relatively small areas of salt marsh compared to the widespread shoreline oiling observed during the *Deepwater Horizon* event. These differences could result in varying ecological responses to oiling.

Five published studies have reported on the effects of the *Deepwater Horizon* oil spill on marsh periwinkles (McCall & Pennings 2012, Silliman et al. 2012, Zengel et al. 2014, 2015, 2016a). However, each of these studies either primarily focused on other topics (e.g. insects, vegetation, erosion), or was limited in timing, duration, number of sites studied, or specific locations and conditions examined relative to marsh periwinkles. Zengel et al. (2016a) was a detailed treatment of periwinkle impacts spanning a large number of sites, a relatively large area of oiled shoreline, and both the marsh edge and interior. However, that study only covered a single year of sampling (2011), thereby limiting the ability to examine longer-term periwinkle impacts and recovery. Because natural populations can be quite variable in space and time, it can be difficult in many cases for individual studies to clearly identify population and community changes even after large oil spills, hence the need for integration of data across multiple studies (Fodrie et al. 2014). Here, we synthesize results of these 5 studies and other ongoing work in a meta-analysis, using published and unpublished sources spanning more than 5 yr, including newly available Natural Resources Damage Assessment (NRDA) and Gulf of Mexico Research Initiative (GoMRI) (Deis et al. 2015) data. We tested the hypotheses that the oil spill reduced periwinkle density (snail abundance), reduced mean periwinkle shell length (snail size), and altered periwinkle size distributions in salt marshes that were heavily oiled. Using these results, we also examined prior projections of periwinkle recovery time frames based on studies published to date (see Zengel et al. 2014, 2015, 2016a).

METHODS

Studies

We synthesized all published periwinkle data comparing heavily oiled and reference sites collected after the spill (April 2010) and additional unpublished data, including large NRDA and GoMRI data sets (Table 1). Detailed methods are included in each of the published studies and are available for the

Table 1. Summary of marsh periwinkle data sources used in the meta-analysis. Zones 1, 2, and 3 refer to the oiled marsh edge, the oiled marsh interior, and the marsh interior inland of heavy oiling, respectively. NRDA: Natural Resources Damage Assessment

Source	Years	Zones	Density	Shell length	References/Notes
Silliman	2010–2013	1–2	X	–	Silliman et al. 2012, including unpubl. data
Pennings	2010–2011	3	X	–	McCall & Pennings 2012
NRDA	2011	1–3	X	X	Zengel et al. 2016a
Zengel	2011–2015	1	X	X[a]	Zengel et al. 2014, 2015, including unpubl. data
Deis	2012–2015	1	X	X	Deis et al. 2015, including unpubl. data

[a] 2012–2015 only

GoMRI data (Deis et al. 2015). Study sites were widely distributed throughout the northern Gulf of Mexico (Louisiana, Mississippi, Alabama), with numerous sites concentrated in southeastern Louisiana (Barataria and Terrebonne Bays), where salt marsh oiling was most widespread and severe (Fig. 1). No known studies were excluded from our analyses.

Sites were categorized as oiled or reference by the primary investigators using somewhat different criteria, but all the studies described visibly oiled sites with heavy oiling. The vast majority of the oiled sites corresponded to the NRDA 'heavier persistent oiling' category, defined as marsh shorelines with heavy to moderate visible oiling that persisted on the shoreline for 3 mo or longer (Nixon et al. 2016). All studies reported that their reference sites had no visible oiling or impacted vegetation at the time data were collected.

Some of the oiled sites had active, intensive shoreline cleanup treatments applied as part of the *Deepwater Horizon* emergency response, involving manual and mechanical removal of oiled wrack, raking and cutting of oiled marsh vegetation, and raking and scraping of oil deposits from the marsh substrate (Zengel et al. 2015, 2016a)—note that all or nearly all oiled sites likely had passive treatment involving sorbent boom deployment just seaward of the marsh edge, often followed by boom stranding in the marsh and subsequent retrieval operations; both oiled and reference sites may have had protective booming, including both hard and sorbent boom deployment and stranding. Because we were interested in examining the overall impacts of the oil spill, including effects of oiling and any associated shoreline treatment, and because some sources did not describe whether sites were actively treated, we pooled all oiled sites into a single category regardless of whether they were actively treated (averaged across sampling years, ~27% of oiled sites were known to have had active shoreline cleanup treatments).

Nearly all sites, reference and oiled, were located in mainland herbaceous salt marsh with muddy organic soils. A few sites were located in back barrier island salt marsh and may have had somewhat sandier soils. The salt marsh vegetation at all sites was naturally dominated by *Spartina alterniflora* and in some cases *Juncus roemerianus*, the typical salt marsh species in the region. Reference versus oiled sites within studies were compared by their respective investigators across metrics such as soils, salinity, vegetation types etc., and were found to be generally similar in terms of habitat for marsh periwinkles, other than oiling conditions and subsequent impacts on the marsh habitat (we consider 1 possible exception in the 'Discussion').

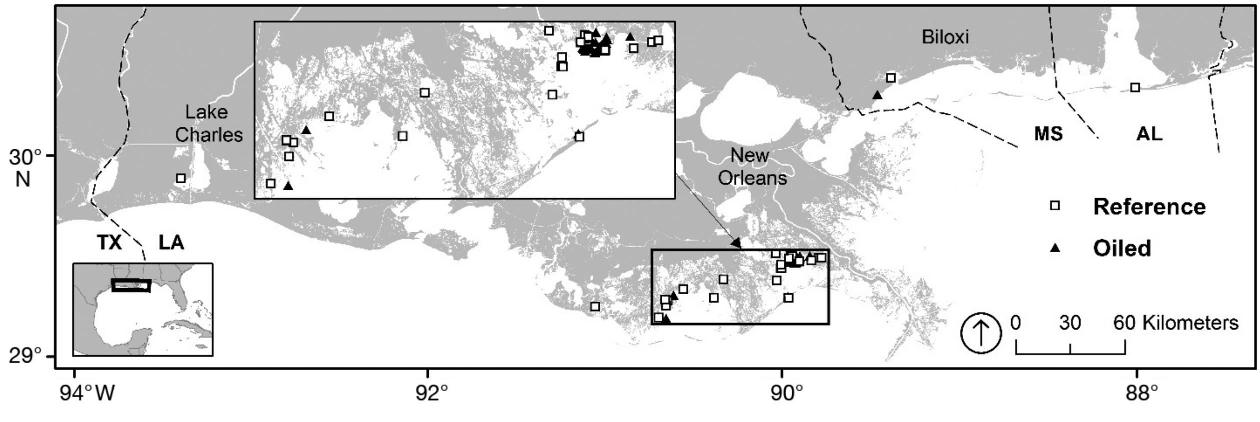

Fig. 1. Study area in the Gulf of Mexico showing locations of reference and oiled sampling sites

Marsh zones

Oil was deposited most heavily along the seaward edge of marshes, with gross visible oiling typically limited to ~10–20 m from the shoreline, though oiling extended further into the marsh in some areas (Lin & Mendelssohn 2012, Silliman et al. 2012, Kokaly et al. 2013, Michel et al. 2013, Zengel et al. 2015, 2016a). Marsh periwinkles also naturally vary in distribution and abundance between the marsh edge and interior (Zengel et al. 2016a). We therefore divided the data into 3 'marsh zones'. Zone 1 was defined as the seaward marsh edge, where oiling was typically heaviest (~0–6 m from the shoreline, depending on oiling width across shore). Zone 2 was defined as the marsh interior within the main oiling band (~6–15 m from the shoreline, depending on oiling width). Zone 3 was defined as the marsh interior a few meters landward (inland) of the main oiling band, with light to no visible oiling. Designations for marsh edge versus marsh interior were similar to those in Peterson & Turner (1994). Due to shoreline erosion (~1–3 m yr^{-1}), sampling position relative to distance from the shoreline was not static over time; however, even in later sampling years, Zone 1 sampling sites were still located within the shoreline widths most affected by oiling and most similar to earlier Zone 1 locations (and these sites had not yet eroded beyond the areas with heaviest oiling). In some cases, Zone 1 sites in later years may have been similar to locations that would have originally been considered Zone 2. In all cases, zones at the reference sites were located at distances similar to those of the oiled sites.

Periwinkle density

All studies estimated periwinkle abundance based on density counts of snails on the marsh vegetation and substrate using 0.25–1 m^2 quadrats (reported as no. periwinkles m^{-2}). Most, but not all, sampling was conducted in summer and early fall. Preliminary analysis showed no major indications of seasonality in the density data, so we did not exclude any sampling dates. Where one study sampled 2 or more times per year (Deis et al. 2015), we used an annual average for each site. We were able to compile density data for 22 study-zone-by-year combinations. We analyzed these data in 2 ways. First, we compared periwinkle mean density between oiled and reference sites using a *t*-test for each study-zone-by-year combination. Data were $\log(x + 0.1)$ transformed prior to analysis to improve normality, and Welch's statistic was used where variances were unequal. We also analyzed the untransformed data using a nonparametric Mann-Whitney *U*-test (MWU test). Second, we estimated the overall effect of the oil spill using natural log (ln; hereafter, simply 'log') response ratios, using the natural log of the ratio of mean periwinkle density at oiled sites to mean periwinkle density at reference sites for each study-zone-by-year combination (ln[mean density oiled/mean density reference]) (after Hedges et al. 1999, Zengel et al. 2016b). The log response ratio is zero if oiled and reference sites are identical, and negative if periwinkle densities are lower at oiled sites. We compared the log response ratio to zero across all study-zone-by-year combinations using a 1-sample *t*-test and a nonparametric Wilcoxon signed rank test. Back-calculating from the log response ratio, we determined the mean response ratio and asymmetric 95% confidence intervals calculated from the *t*-test and converted these to an estimate of mean proportional reduction in periwinkle density with oiling (with lower 95% confidence boundary). For all analyses, we defined statistical significance as $p \leq 0.10$ based on guidance from Mapstone (1995) for balancing Type I and Type II errors during environmental impact studies. All statistical tests across the study were 1-tailed.

Shell length

A subset of studies examined snail size based on total shell length (mm) (Table 1). We were able to compile shell length data for 11 study-zone-by-year combinations. Due to seasonal effects of snail recruitment and growth, we limited our analysis to data collected in summer and early fall. We also size-censored the data, excluding juvenile snails (<6 mm shell length) from the analysis, for 2 reasons. First, small cryptic juvenile snails hidden in leaf sheaths and furled leaves were carefully sampled in some studies but not in others. Second, episodic peaks of recruitment (many very small snails) could skew or mask post-spill comparisons of mean shell length. As we did with periwinkle density, we first compared mean shell length between oiled and reference sites using a *t*-test and an MWU test for each study-zone-by-year combination, and then estimated the effect of oiling on mean shell length across all study-zone-by-year combinations by comparing the log response ratios of shell length to zero using a 1-sample *t*-test and a Wilcoxon signed rank test.

Size distribution

Size-frequency histograms were generated to examine size distribution at the marsh edge, based on shell length data from 9 study-zone-by-year combinations (Table 1, Zone 1 only). Data were pooled across studies by reference and oiling category in each year. Data were limited to summer and early fall sampling, but the data were not size-censored (the smallest sizes were retained in order to reveal recruitment patterns, if any). Life-history stages were incorporated into the histograms based on shell length ranges, with individuals <6, 6–13 and >13 mm in length defined as juveniles, subadults, and adults, respectively (after Bingham 1972, Hamilton 1978, Stagg & Mendelssohn 2012). We used Kolmogorov-Smirnov tests to determine whether differences in size-frequency distributions were statistically significant between oiled and reference sites.

RESULTS

Periwinkle density

Periwinkle densities tended to be lower at oiled sites than at reference sites for nearly all study-zone-by-year combinations (Table 2, Fig. 2). Multiple study-zone-by-year combinations had statistically significant lower periwinkle densities for the oiled versus reference sites (Table 2). No corrections of p-values were applied to address multiple tests; however, only 2 statistically significant results would have been expected by chance, but 9–11 significant results were found (regardless of which test was used, i.e. *t*-test and/or MWU test). Also, although the Zone 1 difference in 2010 reported for the Silliman data (57.6 and 0.5 snails m^{-2} for reference versus oiled, a 99% reduction in periwinkle density for the oiled sites, *t*-test p = 0.13; Table 2) was not statistically significant in our analysis, likely due to small

Table 2. Marsh periwinkle *Littoraria irrorata* density. Data include response ratios (RR) (periwinkle densities for oiled sites/periwinkle densities for reference sites), proportional reduction with oiling (reduction), and significance tests for each study-zone-by-year combination. Number of observations refers to the number of reference and oiled sites within the designated year, study, and zone. Values for the number of snails m^{-2} are means ± SE. Log (ln) response ratios (RR) less than zero indicate lower densities for oiled versus reference sites. Raw density data were $\log(x + 0.1)$ transformed for *t*-tests; non-parametric Mann-Whitney *U*-tests (MWU) are also included. Rows in **bold** indicate statistically significant differences at $p \leq 0.10$ for one or both tests. Zones 1, 2, and 3 refer to the oiled marsh edge, the oiled marsh interior, and the marsh interior inland of heavy oiling, respectively

Data source			No. observations		No. snails m^{-2}		Oiled:Reference RR			p-value	
Year	Study	Zone	Ref.	Oiled	Ref.	Oiled	RR	lnRR	Reduction	*t*-test	MWU test
2010	Silliman	1	3	3	57.6 ± 37.5	0.5 ± 0.5	0.01	−4.68	0.99	0.13	0.18
2011	Silliman	1	3	3	28.0 ± 16.2	8.7 ± 7.7	0.31	−1.17	0.69	0.13	0.20
2011	**NRDA**	**1**	**9**	**23**	**33.8 ± 13.9**	**4.6 ± 1.2**	**0.14**	**−1.99**	**0.86**	**<0.01**	**<0.01**
2011	**Zengel**	**1**	**5**	**19**	**37.0 ± 11.5**	**0.1 ± 0.1**	**0.00**	**−5.86**	**1.00**	**<0.01**	**<0.01**
2012	Silliman	1	3	3	48.0 ± 32.6	23.1 ± 18.0	0.48	−0.73	0.52	0.22	0.35
2012	**Zengel**	**1**	**5**	**19**	**183.2 ± 40.6**	**3.5 ± 1.0**	**0.02**	**−3.95**	**0.98**	**<0.01**	**<0.01**
2012	Deis	1	7	7	32.6 ± 13.0	27.4 ± 10.8	0.84	−0.17	0.16	0.32	0.47
2013	Silliman	1	3	3	8.9 ± 8.9	8.9 ± 1.8	1.00	0.00	0.00	0.85	0.82
2013	**Zengel**	**1**	**5**	**10**	**130.0 ± 27.4**	**4.1 ± 1.6**	**0.03**	**−3.46**	**0.97**	**<0.01**	**<0.01**
2013	**Deis**	**1**	**7**	**7**	**35.1 ± 5.8**	**29.0 ± 11.5**	**0.83**	**−0.19**	**0.17**	**0.01**	**0.02**
2014	**Zengel**	**1**	**5**	**10**	**97.6 ± 38.4**	**8.7 ± 2.8**	**0.09**	**−2.42**	**0.91**	**<0.01**	**<0.01**
2014	**Deis**	**1**	**7**	**7**	**62.3 ± 18.6**	**54.0 ± 16.7**	**0.87**	**−0.14**	**0.13**	**0.08**	**0.12**
2015	**Zengel**	**1**	**5**	**10**	**181.8 ± 72.8**	**12.2 ± 5.6**	**0.07**	**−2.70**	**0.93**	**<0.01**	**0.01**
2015	Deis	1	7	7	97.1 ± 23.7	112.3 ± 19.5	1.16	0.14	−0.16	0.48	0.75
2010	**Silliman**	**2**	**3**	**3**	**104.5 ± 23.1**	**48.4 ± 29.7**	**0.46**	**−0.77**	**0.54**	**0.18**	**0.10**
2011	**Silliman**	**2**	**3**	**3**	**42.7 ± 15.0**	**18.0 ± 8.0**	**0.42**	**−0.86**	**0.58**	**0.11**	**0.10**
2011	**NRDA**	**2**	**11**	**24**	**95.3 ± 28.0**	**46.0 ± 10.3**	**0.48**	**−0.73**	**0.52**	**0.04**	**0.05**
2012	Silliman	2	3	3	10.2 ± 8.9	22.5 ± 13.8	2.20	0.79	−1.20	0.62	0.75
2013	Silliman	2	3	3	28.7 ± 8.7	40.7 ± 9.8	1.42	0.35	−0.42	0.80	0.90
2010	Pennings	3	6	5	50.8 ± 23.8	64.1 ± 18.8	1.26	0.23	−0.26	0.87	0.88
2011	Pennings	3	6	6	68.5 ± 30.8	45.5 ± 11.7	0.66	−0.41	0.34	0.52	0.37
2011	NRDA	3	11	24	81.3 ± 19.7	110.8 ± 16.5	1.36	0.31	−0.36	0.68	0.84

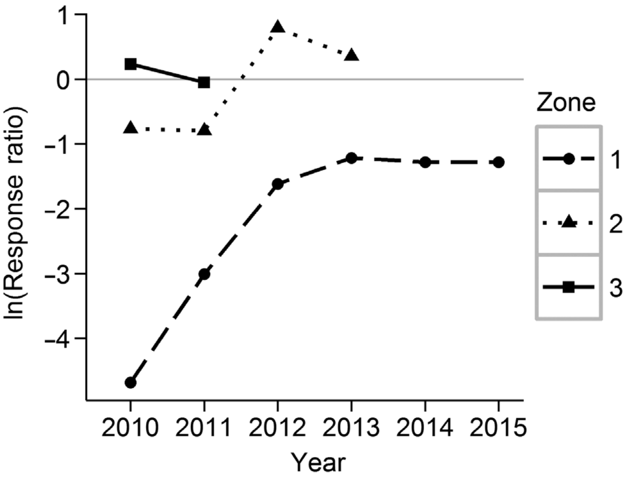

Fig. 2. Log (ln) response ratios (oiled:reference) for marsh periwinkle *Littoraria irrorata* density by zone and year. Where more than one study contributed data for any zone-by-year combination, average values were plotted. Values less than zero indicate lower periwinkle densities for oiled versus reference sites. Log response ratios were significantly lower than zero for the combined analysis across all study-zone-by-year observations (*t*-test, $p < 0.01$; Wilcoxon signed ranked test, $p < 0.01$). Zones 1, 2, and 3 refer to the oiled marsh edge, the oiled marsh interior, and the marsh interior inland of heavy oiling, respectively

sample size, this difference was statistically significant in the more complex analysis conducted by Silliman et al. (2012) ($p = 0.01$, rounded).

As a whole, log response ratios for periwinkle density were significantly different from zero, indicating that the oil spill reduced densities in the oiled sites relative to reference conditions (Fig. 2). Examining the data by zone and over time, Zone 1 differences were statistically significant across multiple studies and years, and recovery of oiled sites to reference levels was not exhibited overall (Fig. 2). Some recovery over time was observed in Zone 1; however, this leveled off and stayed below reference values during 2013–2015 (Fig. 2). Zone 2 differences were significantly different over 2010–2011 across multiple studies, with overall recovery observed by 2012 (Table 2, Fig. 2). Periwinkle densities were not affected by oiling in Zone 3 (Fig. 2). On average, periwinkle densities across all study-zone-by-year combinations were reduced by 73% in the oiled sites (95% lower confidence bound = 47% reduction).

Shell length

Mean periwinkle shell lengths tended to be somewhat lower at oiled sites than at reference sites for more than half of the study-zone-by-year combinations, but these trends were only statistically significant for 2 comparisons (one each in Zone 1 in 2011 and 2015; Table 3, Fig. 3). For these two, mean shell lengths were 14% smaller at oiled versus reference sites (Table 3). In this case, 1 significant difference out of 11 would have been expected by chance. As a group, log response ratios for shell length were not statistically different from zero, but results did

Table 3. Marsh periwinkle *Littoraria irrorata* shell length. Data include response ratios (RR) (shell length for oiled sites/shell length for reference sites), proportional reduction with oiling (reduction), and significance tests for each study-zone-by-year combination. Number of observations refers to the number of reference and oiled sites within the designated year, study, and zone; values for shell length are means ± SE. Log (ln) response ratios (RR) less than zero indicate smaller shell lengths for oiled versus reference sites. Raw shell length data were $\log(x + 0.1)$ transformed for *t*-tests; non-parametric Mann-Whitney *U*-tests (MWU) are also included. Rows in **bold** indicate statistically significant differences at $p \leq 0.10$ for one or both tests. Zones 1, 2, and 3 refer to the oiled marsh edge, the oiled marsh interior, and the marsh interior inland of heavy oiling, respectively

Data source			No. observations		Shell length (mm)		Oiled:Reference RR			p-value	
Year	Study	Zone	Ref.	Oiled	Ref.	Oiled	RR	lnRR	Reduction	*t*-test	MWU test
2011	**NRDA**	**1**	**9**	**12**	**17.9 ± 1.3**	**15.4 ± 1.5**	**0.86**	**−0.15**	**0.14**	**0.09**	**0.12**
2012	Zengel	1	5	10	17.3 ± 0.6	16.3 ± 1.2	0.95	−0.06	0.05	0.19	0.40
2012	Deis	1	7	6	14.9 ± 1.7	16.9 ± 1.3	1.13	0.12	−0.13	0.83	0.82
2013	Zengel	1	5	8	14.2 ± 1.6	15.2 ± 2.1	1.07	0.06	−0.07	0.53	0.69
2013	Deis	1	7	7	15.9 ± 1.8	14.5 ± 1.3	0.91	−0.09	0.09	0.30	0.27
2014	Zengel	1	5	8	18.5 ± 1.1	17.9 ± 0.7	0.96	−0.04	0.04	0.34	0.18
2014	Deis	1	7	7	17.7 ± 0.7	16.7 ± 0.8	0.94	−0.06	0.06	0.17	0.19
2015	Zengel	1	5	6	19.6 ± 0.4	19.3 ± 0.8	0.99	−0.01	0.01	0.36	0.53
2015	**Deis**	**1**	**7**	**6**	**18.0 ± 0.9**	**15.5 ± 1.4**	**0.86**	**−0.15**	**0.14**	**0.09**	**0.09**
2011	NRDA	2	11	20	19.5 ± 1.1	19.8 ± 0.4	1.01	0.01	−0.01	0.64	0.34
2011	NRDA	3	11	23	20.6 ± 0.6	20.8 ± 0.2	1.01	0.01	−0.01	0.66	0.75

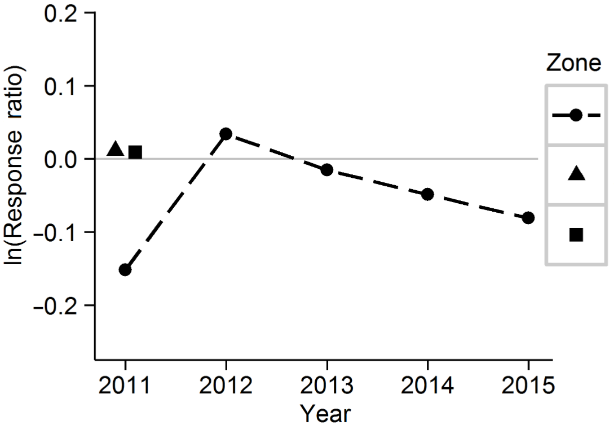

Fig. 3. Log (ln) response ratios (oiled:reference) for marsh periwinkle *Littoraria irrorata* shell length by zone and year. Values less than zero indicate smaller shell lengths for oiled versus reference sites. Log response ratios were not significantly lower than zero for the combined analysis across all study-zone-by-year observations (*t*-test, p = 0.12; Wilcoxon signed ranked test, p = 0.12). Zones 1, 2, and 3 refer to the oiled marsh edge, the oiled marsh interior, and the marsh interior inland of heavy oiling, respectively

appear to vary with time. Examining the data by zone and over time, shell length was reduced in Zone 1 in 2011, but appeared recovered by 2012 (Fig. 3). After 2012, there was a mild declining trend in shell length in Zone 1 for oiled sites compared with reference sites, with 1 record being statistically significant in 2015 (Fig. 3, Table 3). Shell size was not affected by oiling in Zones 2 or 3 (though the number of observations was limited).

Size distribution

Periwinkle size-frequency histograms differed between the oiled and reference sites across all years and all comparisons were statistically significant (Fig. 4). Periwinkle populations in the oiled sites had greater relative proportions of smaller adults and sub-adults, and fewer larger adults, compared with reference sites (Fig. 4). This was observed across all years continuing into 2015. In addition, in several years (2012–2014) the oiled sites also had lower relative proportions of juveniles compared with reference sites, indicating low recruitment or poor survival of early recruits at the oiled sites (Fig. 4). This was most evident in 2012, when a large peak in juveniles was observed at the reference sites, but not at the oiled sites. In 2015, more juveniles were observed at oiled sites compared with reference sites; however, this may have been due to higher water levels at the time reference sites were sampled in 1 study, interfering with sampling of the smallest snails hidden in the lower leaf sheaths.

DISCUSSION

Our analysis indicated that the *Deepwater Horizon* oil spill negatively affected marsh periwinkle populations, with ongoing effects and incomplete recovery observed more than 5 yr post-spill, especially at the oiled marsh edge. Periwinkles at oiled sites were less abundant than at reference sites. In some cases, snails

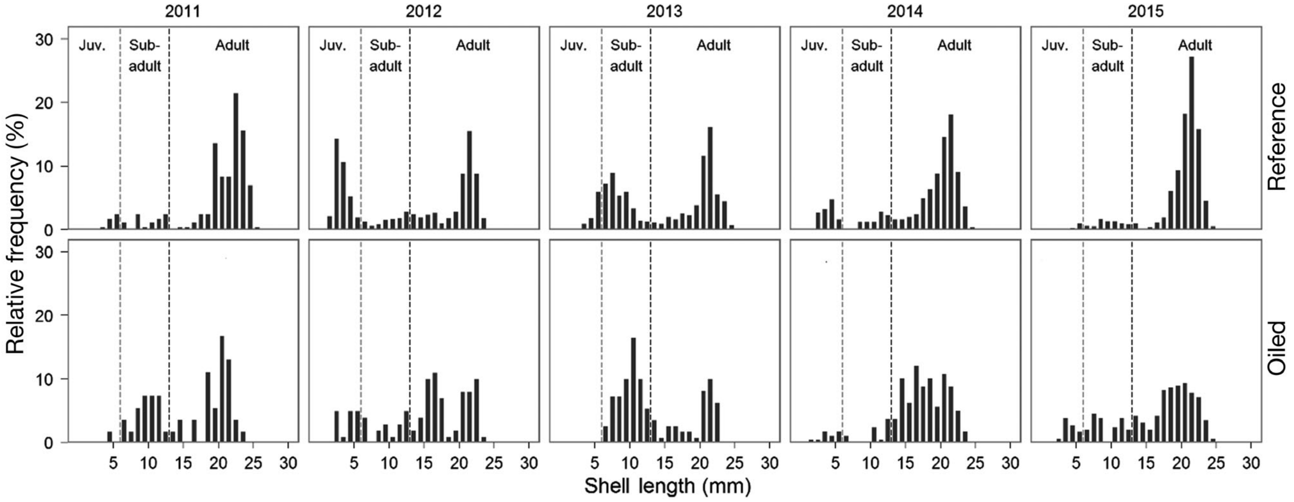

Fig. 4. Marsh periwinkle *Littoraria irrorata* size-frequency histograms for reference and oiled sites by year. Periwinkle life stage classes are defined as juveniles (<6 mm), sub-adults (6–13 mm), and adults (>13 mm). Size distributions differed between oiled and reference sites in all years (Kolmogorov-Smirnov tests, p < 0.01 for each year)

were smaller on average at the oiled sites, and more clearly, overall size distribution was altered at the oiled sites across all years, with fewer large adults and lower recruitment or poor survival of new recruits in most years, compared with reference sites.

We found clear evidence that the oil spill reduced periwinkle density at the oiled marsh edge and in the oiled marsh interior across multiple years. By 2015, more than 5 yr after initial oiling, overall periwinkle density (integrated across studies) had not recovered to reference levels at the oiled marsh edge. In contrast, densities in the oiled marsh interior appeared to have recovered by 2012. Despite initial trends toward recovery, overall periwinkle density at the oiled marsh edge leveled off below reference values during 2013–2015 (short of recovery). This may indicate that periwinkle density at the marsh edge may not fully recover or that recovery could be prolonged in some instances.

Looking at individual studies over time, densities at the Silliman et al. (2012) oiled marsh edge sites appeared 'recovered' by 2013 (reference and oiled densities were similar), though their sample sizes were small and both their reference and oiled densities in 2013 were far below typical densities in the region (see Zengel et al. 2016a). Because of this, we consider recovery at the Silliman et al. (2012) marsh edge sites to be inconclusive. Density differences between oiled and reference sites in the Deis et al. (2015) data (2012–2015) were not as large as observed elsewhere, although Deis et al. (2015) indicated that a confounding influence of greater *Juncus roemerianus* plant dominance (and less *Spartina alterniflora*) may have resulted in lower periwinkle densities at their reference sites, affecting their comparisons. Even so, densities at their oiled sites appeared recovered by 2015 and were similar to mid-range to higher values typical for the region (see Zengel et al. 2016a). However, even though densities appeared recovered in the Deis et al. (2015) data, shifts in size distributions to smaller adults and sub-adults, and fewer large adults, were evident at their oiled sites across all years, similar to those observed in our combined analysis. This is likely due to initial losses of snails across all size classes, followed by subsequent recruitment or immigration of smaller (younger) snails that had not yet grown into the larger size classes. In addition, mean shell lengths in the Deis et al. (2015) data were also significantly smaller for their oiled versus reference sites in 2015. Therefore, even though periwinkle densities may have recovered in their study, population recovery in terms of size structure had not occurred in the Deis et al. (2015) sites as of 2015.

The Zengel et al. (2014, 2015) data showed the most prominent influence (largest effect sizes) on the lack of density recovery in later years, perhaps due to heavier or more persistent oiling in their study sites compared with others (see Zengel et al. 2015, Fleeger et al. 2015 for oiling conditions and comparison with the Deis et al. 2015 sites). The Zengel et al. (2014, 2015) oiled sites also displayed the same proportional shift towards smaller adult and sub-adult snails, and fewer large adults, observed elsewhere and in our overall analysis. In addition, the Zengel et al. (2014, 2015) data were the main source indicating low juvenile periwinkle recruitment or survival at the oiled sites compared to the reference sites. However, very few juvenile snails were recorded by Deis et al. (2015) at either their reference or oiled sites; this finding may have been influenced by confounding vegetation differences, overriding any possible effects of oiling on juvenile recruitment or survival (see previous paragraph). Beyond the differences and nuances of individual studies, we re-emphasize that our findings (integrated across all studies) indicate both an overall lack of periwinkle density recovery and the alteration of periwinkle size distribution through 2015 at the oiled marsh edge.

In the Zengel et al. (2016a) NRDA study, a definition of full recovery was proposed based on attaining both periwinkle density and size distributions similar to reference conditions. Zengel et al. (2016a) projected that full periwinkle recovery would take at least 3 to 5 yr once oiling and habitat conditions were suitable to support normal periwinkle life-history functions (e.g. recruitment, survival, growth). Considering our overall analyses in the present paper, and individual datasets extending into 2014–2015, we find that full recovery had yet to occur by 2015. In the case of the Deis et al. (2015) data, where *Spartina alterniflora* stem density and aboveground biomass (primary habitat constituents for marsh periwinkles; see Kiehn & Morris 2009, Stagg & Mendelssohn 2012, McFarlin et al. 2015) were reported to have recovered by 2012–2013 in their heavily oiled sites (Fleeger et al. 2015, Lin et al. 2016; both pertaining to the Deis et al. 2015 study), periwinkle size structure had still not recovered 2 to 3 yr later. This conforms to prior recovery projections, as well as observations that periwinkle recovery may depend on but lag vegetation recovery (Zengel et al. 2014, 2015, 2016a).

There are at least 3 reasons why recovery of marsh periwinkle populations might take several years. First, because residual oil remains on and in the marsh soils (Lin et al. 2016), remaining oil might continue to affect periwinkles at heavily oiled sites.

Second, because the snails depend on the marsh vegetation as their principal habitat (Kiehn & Morris 2009, Stagg & Mendelssohn 2012, McFarlin et al. 2015), snail recovery is unlikely until plant recovery is complete. Third, recruitment and immigration of new snails into the population and their subsequent growth to larger adults may be slow enough that it takes a number of years for the population to rebuild. Our findings that snail populations had not fully recovered as of 2015 is consistent with these hypotheses, and emphasizes the need for continued and long-term monitoring of populations affected by this and other environmental impacts.

Marsh periwinkles play important ecological roles in salt marshes (see Zengel et al. 2016a and references therein). They feed on and shred decomposing plant material, thereby stimulating the food web and accelerating nutrient cycling (Newell et al. 1989, Kemp et al. 1990, Hensel & Silliman 2013). When they are abundant, their feeding activity can regulate the growth of salt marsh plants (Silliman & Zieman 2001). They are important prey items for a variety of larger consumers, many of which are of commercial, recreational, and conservation importance (Hamilton 1976, Heard 1982, Tucker et al. 1995). Consequently, the long-lasting effects of the oil spill on marsh snails are likely to impact a variety of other species and ecological processes in the salt marsh.

We conclude that the *Deepwater Horizon* oil spill had substantial impacts on periwinkles in heavily oiled marshes, including density reductions and shifts in size structure, both spanning multiple years. Impacts were ongoing and full recovery had not occurred as of 2015, more than 5 yr post-spill. Our findings support the idea that full periwinkle recovery is likely to be a long-term process, and suggest that monitoring of snail populations should be continued. Finally, oil spill effects on marsh periwinkles are likely to impact a variety of marsh species and processes, and these implications should be considered in future studies.

Data sources. NRDA data used in this paper are publicly available at https://dwhdiver.orr.noaa.gov. GoMRI data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org (doi: 10.7266/N7FF3Q9S). Data from McCall & Pennings (2012) are publicly available at http://dx.doi.org/10.6073/pasta/8da296e41363a8fcb931d44a71264107.

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