

Recovery of the salt marsh periwinkle (*Littoraria irrorata*) 9 years after the Deepwater Horizon oil spill: Size matters

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ARTICLE INFO

Keywords:

Littoraria irrorata

Salt marsh

Marsh periwinkle

Deepwater Horizon oil spill

Ecological impacts

Ecological recovery

ABSTRACT

Prior studies indicated salt marsh periwinkles (*Littoraria irrorata*) were strongly impacted in heavily oiled marshes for at least 5 years following the Deepwater Horizon oil spill. Here, we detail longer-term effects and recovery over nine years. Our analysis found that neither density nor population size structure recovered at heavily oiled sites where snails were smaller and variability in size structure and density was increased. Total aboveground live plant biomass and stem density remained lower over time in heavily oiled marshes, and we speculate that the resulting more open canopy stimulated benthic microalgal production contributing to high spring periwinkle densities or that the lower stem density reduced the ability of subadults and small adults to escape predation. Our data indicate that periwinkle population recovery may take one to two decades after the oil spill at moderately oiled and heavily oiled sites, respectively.

1. Introduction

The Deepwater Horizon (DWH) oil spill made landfall in coastal wetland areas as emulsions of crude oil (Lin et al., 2016), having toxic, smothering, and fouling effects on shoreline vegetation and associated organisms (Baker et al., 2017). Extensive areas of wetland shoreline were oiled (Nixon et al., 2016) with approximately 95% of the oiled wetlands occurring in Louisiana. The heaviest oiling was most widespread in northern Barataria Bay where the salt marshes are dominated by *Spartina alterniflora* and *Juncus roemerianus* (Michel et al., 2013; Zengel et al., 2015). Lin et al. (2016) documented the impacts of the DWH oil spill on salt marsh vegetation in our study sites, finding that *S. alterniflora* aboveground biomass recovered within 2 to 3 years, but other aspects of the community showed limited or no recovery (Hester et al., 2016; Lin and Mendelssohn, 2012; Silliman et al., 2012; Zengel et al., 2014, 2015). While many studies examined the impacts of the DWH oil spill on salt marsh animals for 2 years or less (McCall and Pennings, 2012; Pennings et al., 2016; Silliman et al., 2012; Whitehead et al., 2011; Zengel et al., 2014, 2015), our group has been studying

impacts of the DWH oil spill on vegetation, soil parameters, microbes, benthic microalgae, infauna, and epifauna over the last 9 years (Fleeger et al., 2015, 2017, 2019; Deis et al., 2017; Lin et al., 2016; Zengel et al., 2016, 2017). These long-term studies have emphasized the importance of the recovery of the foundation species *S. alterniflora* and *J. roemerianus* to the recovery of other organisms within the salt marsh ecosystem.

Littoraria irrorata, the salt marsh periwinkle, is a conspicuous gastropod widespread in coastal salt marshes from the mid-Atlantic through the Gulf coast of the United States (Silliman and Zieman, 2001; Stagg and Mendelssohn, 2012; Pennings et al., 2016; Failon et al., 2020) and is an important species in the salt marsh food web (McCann et al., 2017). Through its feeding activity, *L. irrorata* influences marsh vegetation, organic matter and nutrient cycling, microbial communities, other invertebrates, and ecosystem productivity (Zengel et al., 2017). Some researchers have indicated that *L. irrorata* has potential to exert top-down control regulating plant productivity (Silliman and Zieman, 2001; Silliman et al., 2005), at times potentially contributing to marsh vegetation die-back events (Silliman et al., 2005). However,

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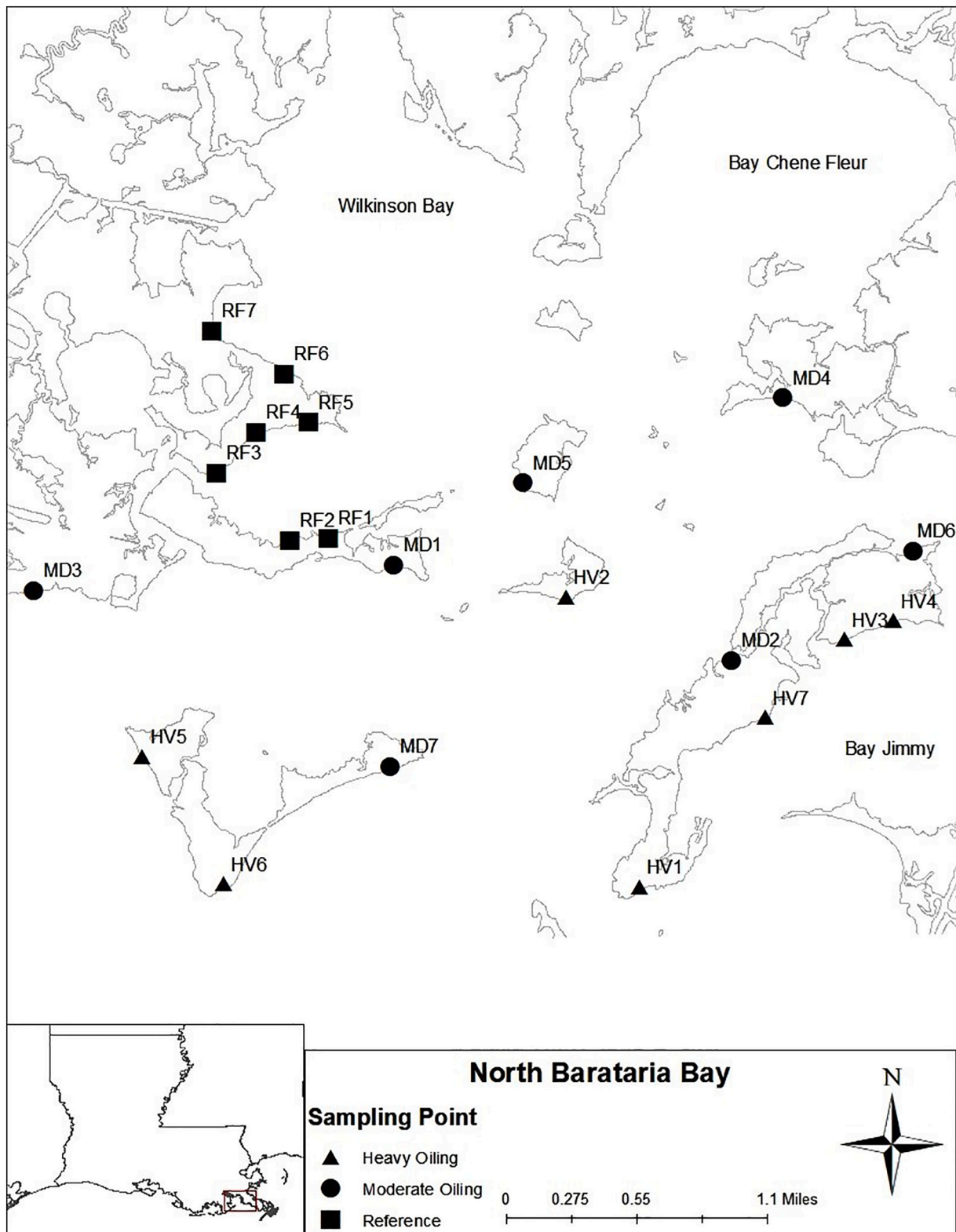


Fig. 1. Location of the twenty-one sampling stations in Barataria Bay, Louisiana.

Kiehn and Morris (2009) found no support for top-down control of marsh plant productivity by *L. irrorata*. In another study, Atkins et al. (2015) found that the effect of *L. irrorata* on *S. alterniflora* biomass may be “context-dependent”, i.e. the effect varies in space and time with variation in periwinkle size-structure and density. Several studies (Deis et al., 2017; Kiehn and Morris, 2009; Stagg and Mendelsohn, 2012)

conclude that *L. irrorata* abundance, growth rate, and survival are positively correlated with *S. alterniflora* abundance. *L. irrorata* moves up and down plant stems with the tide for predator avoidance, feeding, and thermoregulation (Bingham, 1972; Henry et al., 1993; Hovel et al., 2001; Rietl et al., 2018; Vaugh and Fisher, 1988; Warren, 1985; Williams and Appel, 1989). The presence of *J. roemerianus* can be

important to both *L. irrorata* and *S. alterniflora*. Hughes (2012) found that a mixed assemblage of *J. roemerianus* and *S. alterniflora* benefits both *L. irrorata* and *S. alterniflora* by *J. roemerianus* providing *L. irrorata* refuge from predation (Failon et al., 2020) and *S. alterniflora* relief from periwinkle herbivory resulting in less loss of plant biomass. The blue crab (*Callinectes sapidus*) is a primary predator of periwinkles near the marsh edge (Carrol et al., 2018; Rietl et al., 2018; Schindler et al., 1994).

Studies conducted in the first few months to years after the DWH spill on *L. irrorata* populations (Silliman et al., 2012; Zengel et al., 2014, 2015, 2016) found density reductions of 80 to 90% at the oiled marsh edge and concluded from age and growth (i.e., shell length) data that recovery of the population structure would take several years to a decade or more once habitat conditions were suitable to support normal periwinkle life-history functions. Subsequent studies (Deis et al., 2017; Zengel et al., 2017) found variations in *L. irrorata* densities at different oiling levels. Zengel et al. (2017) found that density at heavily oiled sites remained reduced over at least 5 years; whereas, Deis et al. (2017) found densities were not significantly different between reference and heavily oiled sites at 5 years, and that density was consistently highest at moderately oiled sites. Both studies found that heavily oiled sites displayed a greater relative proportion of smaller adults and subadults, with fewer large adults as compared to reference sites. Deis et al. (2017) reported mean size of *L. irrorata* at moderately oiled sites similar to those at reference sites from 36 to 54 mo, but statistically smaller at moderately oiled sites at 60 and 66 mo after oiling.

In this study, we investigate the ongoing recovery of *L. irrorata* following the DWH oil spill (April 20, 2010) at moderately and heavily oiled locations from 30 mo (2.5 years; October 2012) through 108 mo (9 years; May 2019) after the spill. We hypothesized that greater oiling intensity would increase detrimental effects on population size structure of *L. irrorata* and slow recovery as compared to reference conditions. Zengel et al. (2016) proposed a definition for recovery of *L. irrorata* at oiled sites as attaining a density and shell size distribution similar to reference areas and the re-establishment of adult components of the population following successful recruitment. Zengel et al. (2016) estimated that recovery would occur 3 to 5 years after oiling and habitat conditions in heavily impacted areas were suitable to support periwinkle recruitment, immigration, survival, and growth and could take as long as 10 years or more to re-establish the largest/oldest snails in the population, if starting from new recruits. Our current study adds to the prior meta-analysis by Zengel et al. (2017) and previous study data in Deis et al. (2017) by providing finer detail on a key dataset included in the meta-analyses, and by extending the duration of periwinkle recovery data to 9 years post-spill. We combine our periwinkle findings with data collected by our study team on salt marsh plants and benthic macroalgae to hypothesize potential mechanisms contributing to periwinkle recovery dynamics.

2. Methods

Sampling sites were established in November 2011 (the DWH oil spill arrived in the study area in June 2010) within an approximate 8 by 5-km area along saltmarsh shorelines in Wilkinson Bay and Bay Jimmy in northern Barataria Bay, Louisiana, USA between coordinates N 29.44060° - 29.47459°, W 89.88492° - 89.94647° (Fig. 1). Shoreline Cleanup Assessment Technique (SCAT) data (Michel et al., 2013; Zengel and Michel, 2013), our own field observations, and total petroleum hydrocarbon (TPH) concentration data collected after the spill, but prior to 2011 (Lin and Mendelsohn, 2012), were used to assign sites to one of three oiling intensity levels: reference (no oiling, RF), moderately oiled (MD), and heavily oiled (HV). Seven replicate locations were identified within each oiling intensity level (i.e., $n = 7/\text{oiling level}$). Virtually all shorelines in the geographical area of moderate and heavy oiling [in and around Bay Jimmy (Fig. 1)] likely had some degree of oil exposure, even if small. Therefore, we felt that it was not prudent to

randomly and completely intersperse reference and oiled sites. Instead, we located reference sites in close proximity to each other (Fig. 1) in an area ~1 km from the nearest oiled sites. Kokaly et al. (2013) found no evidence of oiling at our reference sites using 2010 imagery, and Atlas et al. (2015) sampled hydrocarbon concentrations at a site between our sites RF4 and RF5 and found DWH oil and background TPH (0.2–0.3 mg g⁻¹) concentrations similar to that at our reference sites (0.3 ± 0.3 mg g⁻¹).

L. irrorata were sampled on 15 dates approximately bi-annually from 30 (October 2012) to 108 mo (May 2019) after the spill, generally in the spring (April to June) and fall (September to November). TPH and plant community parameters were concurrently sampled (see Lin and Mendelsohn, 2012 and Lin et al., 2016 for additional details).

2.1. TPH analysis

Surface soils (0 to 2 cm) were collected from each site on each collection date. Samples were extracted with dichloromethane (DCM) and analyzed gravimetrically as per Lin and Mendelsohn (2012) and Lin et al. (2016). DCM extracts were transferred to pre-weighed dishes, where the DCM was evaporated, and unevaporated petroleum hydrocarbon residues remaining in the dishes were weighed to the nearest 0.0001 g. TPH concentration was calculated and expressed as mg g⁻¹ dry soil.

2.2. Live aboveground plant biomass and stem density

Live aboveground plant biomass and live stem density were estimated from a single haphazardly located-0.25 m (m)² quadrat at each sampling site. All plants rooted within the quadrat were clipped to the ground surface and separated into live and dead components by species (mostly *S. alterniflora* and *J. roemerianus*). Live stem density was determined by counting the number of intact living stems by species. Living plant aboveground biomass was weighed after drying to a constant mass at 60 °C. See Lin and Mendelsohn (2012) and Lin et al. (2016) for additional details.

2.3. Littoraria irrorata sampling

To quantify *L. irrorata* density and shell length, three 0.25 m² quadrats were haphazardly placed approximately 1 m landward from the marsh edge at each site and within 5 m of the site location stake. We collected *L. irrorata* from the marsh surface or attached to the vegetation within the quadrat. Juvenile *L. irrorata* were sometimes discovered in the leaf bracts and furled, dead leaves of *S. alterniflora* (Stiven and Hunter, 1976; Crist and Banta, 1983). Although juveniles were inconsistently observed, and although they are not included as an independent size category in most analyses (Zengel et al., 2016), we report data here on density for completeness. *L. irrorata* shell length, from the base of the aperture to the top point of the shell, was measured to the nearest millimeter using calipers. Once measured, *L. irrorata* were returned to the sampled quadrat.

L. irrorata were grouped by shell length into putative age classes: juveniles (< 6 millimeters (mm)); sub-adults (6 to 13 mm); and adults (> 13 mm) following Bingham, 1972; Hamilton, 1978; Stagg and Mendelsohn, 2012; Zengel et al., 2014, 2016. We additionally classified snails > 20 mm as “large adults.” The large adult size category represents those individuals greater than the approximate mean shell length for RF sites in this study as well as from other study sites not subject to oiling across Louisiana (Zengel et al., 2016; Rietl et al., 2018). Length-frequency distributions of *L. irrorata* are often bi- or trimodal with the modes representing age class (Hamilton, 1978; Pennings et al., 2016; Zengel et al., 2014, 2016). Based on growth estimates (Stiven and Hunter, 1976), juveniles are considered to be less than one year, sub-adults approximately one year, small adults ~2–5 years (Pennings et al., 2016) and large adults > 5 years old.

Evaluating changes in shell size over time by comparing size frequency histograms is a powerful technique to determine oiling impacts and to estimate recovery trajectories of gastropods (Pennings et al., 2016; Zengel et al., 2014, 2016, 2017).

2.4. Statistical analysis

All statistical analyses were conducted using Statistical Analysis Systems (SAS, version 9.2, SAS Institute, Cary, NC). Generalized Linear Mixed Models (PROC GLIMMIX) were used to individually test the dependent variables – total, large adult, small adult, and subadult *L. irrorata* density. The main effects were oiling intensity level, sampling period, and oiling intensity level x sampling period interaction. Variance was pooled and a log transformation of the value plus one [e.g., $\log(L. irrorata\text{Total} + 1)$] was performed. Log of the value plus one transformed data with pooled variances met the assumption for normality (based on the Shapiro-Wilk test) for all tests. Tukey's post-hoc test was used for pairwise comparisons. One-way Analysis of Variance (ANOVA) was used for pairwise comparisons of sampling period intervals to examine data trends between oiling intensity levels over time periods.

A two-way Mixed Model ANOVA was used to identify the effects of oiling intensity level, sample date, and the oiling intensity level x sampling period interaction on the total, *S. alterniflora* and *J. roemerianus* live aboveground biomass and live stem density. A square root transformation was performed to meet the assumption of normality.

A Mixed Model ANOVA with and *L. irrorata* mean shell length as the dependent variable was used to compare mean shell length for each sample date, oiling intensity level, and oiling intensity level x sampling period interaction. All results were highly significant (see Results) including the interaction indicating that the oiling intensity level patterns were different over sampling periods. Tukey adjusted range test and a character graphic was used to investigate mean length of the oiling intensity levels over time with the mean shell length of the RF sites to around 20 mm mean length. MD sites showed a shallower increase below that of RF sites. HV sites showed an increase well below that of either RF or HV sites. These trends associated with *L. irrorata* length and oiling intensity level were assessed with a quadratic regression mixed model Analysis of Covariance (ANCOVA) using oiling intensity level as the class variable and Trend (see below) as the covariable. Sampling periods for each sampling year were pooled to generate an annual trend rate (Trend) and the variable Trend was adjusted to "0" at the beginning of sampling. Because a curvature in mean length data for the oiling levels was noted, an annual Trend squared term (Trend²) was added to the model. The model was calculated two ways; an effects model tested for differences among means and a means model provided estimates of the means. The effects model tested for significant differences among the variables - trends, oiling intensity levels, and interaction of trends and oiling intensity levels. The means model provided estimates for all parameters (tested for a difference from zero, not from each other) and standard errors. The estimates of intercept and slope were used to generate the trend model (Fig. 6) from the beginning of the study (30 months after the spill) to the last sampling period (108 months after the spill).

Density data were standardized to individuals m^{-2} for presentation. Statistical significance was defined as $p \leq 0.05$ and p -values are reported to two decimal places. In cases where $p = 0.00$, the p -value was reported as $p < 0.01$. All error terms were expressed as standard error (SE) with $n = 7$ for each oiling level for each sampling time.

3. Results

3.1. TPH

Sites were well differentiated by TPH data supporting the establishment of the three oiling levels (Table 1). Mean TPH through all

Table 1

Mean (\pm SE, $n = 7$) total petroleum hydrocarbons (mg TPH g^{-1} soil) at reference (RF), moderately oiled (MD) and heavily oiled (HV) study sites in northern Barataria Bay, LA through 97 months following the DWH oil spill.

Months after spill	Reference sites	Moderately oiled sites	Heavily oiled sites
30	0.2 \pm 0.05	4.0 \pm 1.8	62.0 \pm 28.5
36	0.3 \pm 0.08	20.8 \pm 11.6	151.8 \pm 59.0
40	0.3 \pm 0.04	2.6 \pm 1.1	51.0 \pm 43.5
42	0.2 \pm 0.05	3.4 \pm 1.1	130.0 \pm 50.7
48	0.3 \pm 0.06	3.2 \pm 1.6	99.9 \pm 52.2
54	0.2 \pm 0.04	5.9 \pm 3.5	101.8 \pm 49.2
62	0.5 \pm 0.07	6.5 \pm 3.6	121.7 \pm 51.9
66	0.2 \pm 0.10	1.8 \pm 0.8	132.4 \pm 65.4
74	0.5 \pm 0.11	1.7 \pm 0.5	173.7 \pm 46.2
78	0.2 \pm 0.08	2.2 \pm 1.2	129.5 \pm 37.7
85	0.7 \pm 0.21	2.0 \pm 1.1	137.4 \pm 23.6
90	0.4 \pm 0.12	1.4 \pm 0.4	98.2 \pm 42.6
97	0.3 \pm 0.04	1.1 \pm 0.3	63.1 \pm 31.2

sampling periods was 0.3 \pm 0.3 mg g^{-1} at RF, 4.4 \pm 1.1 mg g^{-1} at MD, and 111.7 \pm 12.5 mg g^{-1} at HV sites. TPH at HV sites declined from approximately 500 mg g^{-1} at 9 mo after the spill as reported in Lin et al. (2016), to about 30 to 100 mg g^{-1} 97 mo after the spill. Similarly, MD sites declined from approximately 70 mg g^{-1} 9 mo after the spill (Lin et al., 2016) to between 1 and 2 mg g^{-1} 97 mo after the spill.

3.2. Vegetation

Lin et al. (2016) found that the total live aboveground biomass at HV sites only recovered to 50% of that at RF and MD sites after 42 mo. Data extended to 102 mo indicate that this pattern continued, and values at HV remained 48 and 49% less than at RF and MD sites, respectively (Fig. 2). All oiling levels generally began a pattern of high fall and lower spring total live aboveground biomass at 48 mo that continued through 102 mo (Fig. 2), matching the expected pattern of winter senescence and spring to fall growth (Gallagher et al., 1980). The total live aboveground biomass, after 102 mo, varied across sampling periods ($p < 0.01$) and with oiling level independently ($p < 0.01$), but not with the interaction of sampling period and oiling level ($p = 0.33$). After 102 mo, *S. alterniflora* comprised 61, 53 and 86% of the total aboveground biomass at RF, MD and HV sites, respectively, and varied across sampling periods ($p < 0.01$) and with oiling level independently ($p < 0.01$), but not with the interaction of sampling period and oiling level ($p = 0.08$); *J. roemerianus* comprised 39, 47 and 14% of the total aboveground biomass at RF, MD and HV sites, respectively, and varied across sampling periods ($p < 0.01$) and with oiling level independently ($p < 0.01$), but not with the interaction of

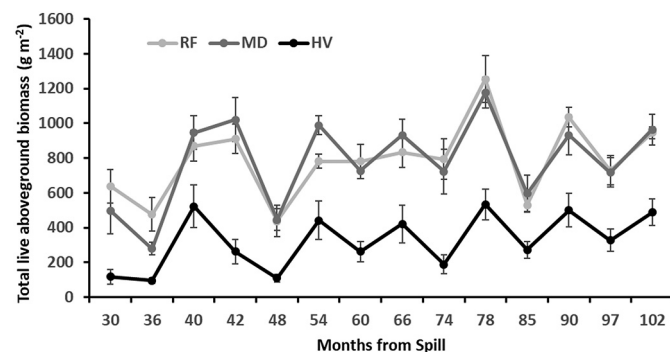


Fig. 2. Total live aboveground biomass ($g m^{-2}$) from 30 to 102 months after the DWH oil spill. Values are means (\pm SE, $n = 7$) for reference (RF), moderately oiled (MD), and heavily oiled (HV) shoreline marsh sites in northern Barataria Bay, LA.

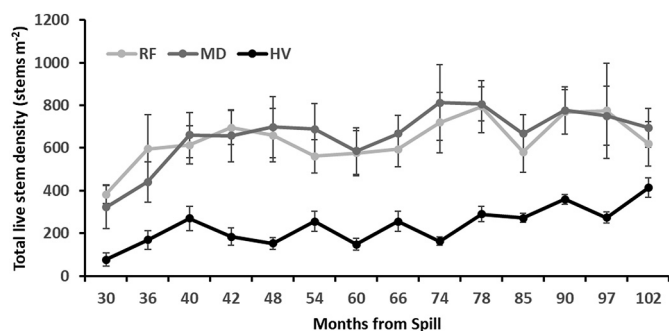


Fig. 3. Total live stem density (stems m^{-2}) from 30 to 102 months after the DWH oil spill. Values are means (\pm SE, $n = 7$) for reference (RF), moderately oiled (MD), and heavily oiled (HV) shoreline marsh sites in northern Barataria Bay, LA.

sampling period and oiling level ($p = 0.12$). The increase in live *S. alterniflora* biomass was greater over time at MD sites compared to the RF and HV sites from 40 to 66 mo.

Lin et al. (2016) found that total live stem density varied in a similar pattern as total live aboveground biomass after 42 mo. The total live stem density at the HV sites compared to the RF and MD sites was less than 50% through most of the study period, except at 102 mo when it was 66.73% and 59.54%, at RF and MD sites, respectively (Fig. 3). Total live stem density, after 102 mo, varied across sampling periods ($p < 0.01$) and with oiling level independently ($p < 0.01$), but not with the interaction of sampling period and oiling level ($p = 0.14$). After 102 mo, *S. alterniflora* comprised 33, 29 and 67% of the total live stems at RF, MD and HV sites, respectively and varied across sampling periods ($p = 0.01$) and with oiling level independently ($p < 0.01$), and with the interaction of sampling period and oiling level ($p < 0.01$); *J. roemerianus* comprised 67, 71 and 33% of the total live stems at RF, MD and HV sites, respectively, and varied across sampling periods ($p < 0.01$) and with oiling level independently ($p < 0.01$), but not with the interaction of sampling period and oiling level ($p = 0.07$). The significance of the interaction of sampling period and oiling level for *S. alterniflora* could be explained by the greater *S. alterniflora* live stem density at the HV sites compared to the RF and MD sites after 85 mo.

3.3. *Littoraria irrorata* density

L. irrorata total density over the duration of the study (Fig. 4) varied across sampling periods ($p < 0.01$) and with the interaction of sampling period and oiling level ($p < 0.01$), but not with oiling level

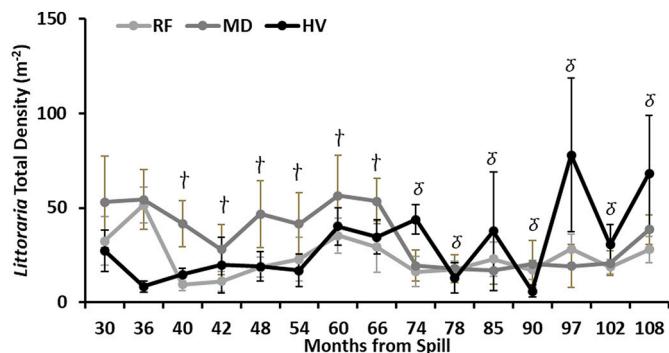


Fig. 4. Total *Littoraria irrorata* density (m^{-2}) from 30 to 108 months after the DWH oil spill. Values are means (\pm SE, $n = 7$) for reference (RF), moderately oiled (MD), and heavily oiled (HV) shoreline marsh sites in northern Barataria Bay, LA. † = a sampling period interval when MD sites had significantly higher densities than RF ($p < 0.01$) and HV ($p < 0.01$) sites. ‡ = a sampling period interval when HV sites had a significantly different (higher in spring and lower in fall) density than RF ($p < 0.01$) and MD ($p < 0.01$) sites.

independently ($p = 0.54$). Adult density was similarly affected by sampling period ($p < 0.01$) and the interaction of sampling period and oiling level ($p = 0.01$), but not with oiling level alone ($p = 0.50$). Further separating the adult population density, large adult density was affected by sampling period ($p < 0.01$) but not oiling level ($p = 0.21$) or the interaction of sampling period and oiling level ($p = 0.74$); small adult density was affected by sampling period ($p < 0.01$) and the interaction of sampling period and oiling level ($p < 0.01$), but not oiling level alone ($p = 0.50$). Subadults varied by sampling period ($p < 0.01$), oiling level ($p = 0.01$), and with their interaction ($p = 0.04$). There was a noticeable trend of increasing total population density from 40 to 66 mo after the spill at all oiling levels (Fig. 4). Total population density at MD sites remained higher than RF or HV sites until 66 mo post spill, as noted by Deis et al. (2017). RF or HV sites increased at similar rates from 40 to 66 mo. In the period from 30 to 66 mo after the oil spill, total density varied by sampling period ($p < 0.01$), but not oiling level ($p = 0.08$) and without interaction of sampling period and oiling level ($p = 0.49$). In pairwise comparisons of sampling periods from 40 to 66 mo, MD sites had significantly higher densities than RF ($p < 0.01$) and HV ($p < 0.01$) sites. Beginning at 74 mo, and through the remainder of the study (108 mo), HV sites had a significantly different (higher in spring and lower in fall) density than RF ($p < 0.01$) and MD ($p < 0.01$) sites and began a distinctive pattern of high spring and low fall density. This pattern may have influenced the observed significance of the interaction of sampling period and oiling level.

Because of the significant interaction between of sampling period and oiling level found for each size class, trends in the total density of subadult, small adult, and large adult *L. irrorata* populations at the oiling level sites from 30 to 108 mo after the spill were examined in detail (Figs. S1, S2, and S3, respectively). The increasing trend for MD sites between 40 and 66 mo was driven by an increase in the small adult portion of the population (Fig. S2). Density at all oiling levels tended to vary regularly with lower density in the fall and higher density in the spring through much of the study period. This trend was most noticeable in the large adults beginning at 78 mo through the remainder of the study for RF and HV sites (Fig. S3). These putative seasonal trends are greater in the total population at the RF sites by the addition of small adults showing the same trends beginning at 78 mo and subadults (Fig. S2) added beginning at 90 mo (Fig. S1).

3.4. *Littoraria irrorata* shell length

Mean *L. irrorata* shell length (Fig. 5) varied across time and ranged from approximately 16 to 21 mm at RF sites, 16 to 19.5 mm at MD sites,

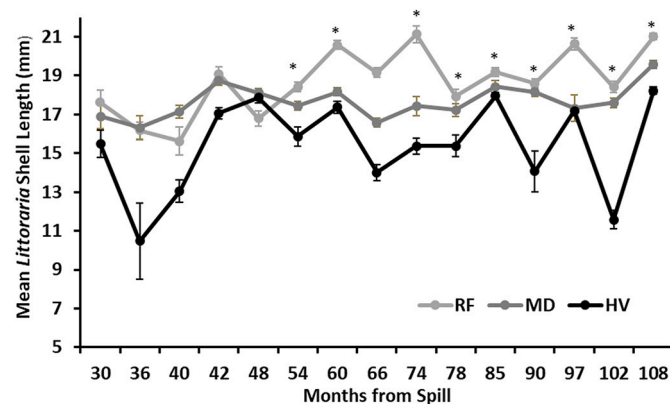


Fig. 5. Mean *Littoraria irrorata* shell length (mm) from 30 to 108 months after the DWH oil spill. Values are means of sites (\pm SE, $n = 7$) for reference (RF), moderately oiled (MD), and heavily oiled (HV) shoreline marsh sites in northern Barataria Bay, LA. * = a sampling period interval when shell length at RF sites are significantly greater than MD ($p = 0.01$) and HV sites ($p < 0.01$).

and 12 to 18 mm at HV sites. Mean shell length over the duration of the study was influenced by sampling period ($p < 0.01$), oiling intensity ($p < 0.01$), and the interaction of oiling level and sampling period ($p < 0.01$). A general trend of increasing mean shell size over time for all of the oiling levels was noticeable. This observation was most distinct at RF and MD sites. In pairwise comparisons from 30 to 108 mo, RF and MD sites mean shell lengths were not significantly different ($p = 0.48$) but were significantly greater than HV sites mean shell length ($p < 0.01$ and $p = 0.03$, respectively). There was a period of mean shell length increase for all of the oiling intensity levels from 30 to 54 mo when pairwise comparison of mean shell lengths showed no significant differences among the sites. After 54 mo, shell lengths at RF sites were significantly greater than MD and HV sites ($p = 0.01$ and $p < 0.01$, respectively); however, MD sites were not significantly greater than HV sites ($p = 0.08$). HV sites showed a tendency of a greater mean shell length in the spring and smaller mean shell length in the fall beginning at 78 mo post spill which coincides with the pattern for density mentioned above (i.e., putative seasonal patterns in shell length size and density were similar for the HV sites).

Trends in mean shell length from 30 mo to 9 years were quantified using ANCOVA with oiling level as the class variable and "Trend" as the covariable. Results revealed significant differences among oiling levels and in linear and quadratic trends for each oiling level (Table 2) providing strong support that trends over time were significant.

A separate means model was also calculated to determine if these trends differed among oiling levels; results for intercepts and slopes were significant for the RF sites (Table 3). MD and HV sites generally show a linear increase over time. Average shell length at RF sites gradually increased over the sampling period to a maximum of approximately 20 mm at 97 mo (Fig. 6). The trend line for MD sites indicates that mean shell length increased from approximately 17 mm to 19 mm over the study period. Mean shell length at HV sites showed an increasing trend over the study from approximately 14.5 mm to 16 mm.

To better evaluate changes in mean shell length, the relative frequencies of *L. irrorata* juvenile (< 6 mm), subadult (6 to 13 mm), smaller adult (13 to 20 mm), and larger adult (> 20 mm) age classes were calculated by pooling size classes into yearly intervals from 30 to 108 mo after the spill (2.5 to 9 years; Fig. 7). The relative frequency of subadults and smaller and larger adults at RF and MD sites remained nearly equally high through 36 mo after the spill. A large proportion of smaller adults occurred at all of the oiling levels from mo 36 to 42 (year 3 to 3.5) after the spill. However, the relative frequency of larger adults at MD and HV sites decreased compared to RF sites after mo 48 (year 4). The differences in the proportion of larger adults became more apparent from mo 48 to 108 (year 4 to 9) after the spill when RF sites had a higher relative frequency of larger adults than MD sites, and MD had a higher relative frequency than HV sites. The proportion of larger adults at HV sites varied little, typically less than 15% throughout the study, whereas larger adults comprised approximately 50% of the population at RF sites in most years after year 4 with the exception of year 7. The proportions of larger adults were highest for all oiling levels at 108 mo (year 9); this may be reflective of a springtime only sampling.

Table 2

Results of fixed effects ANCOVA regression model testing for oiling levels and linear and quadratic trends in the data for oiling levels.

Effect	p value
Trend	< 0.01
Oiling level	0.05
Trend*oiling level	< 0.01
Trend ²	< 0.01
Trend ² *oiling level	< 0.01

Table 3

The results of quadratic, annual rates, fixed effects ANCOVA regression means model with parameters estimated starting at zero providing intercepts and slopes with standard errors (SE) for reference (RF), moderately oiled (MD), and heavily oiled (HV) shoreline marsh sites in northern Barataria Bay, LA. (Note that MD and HV sites fit a linear model rather than a quadratic model).

Effect	Oiling levels	Estimate	SE	p value
Oiling level	HV	14.43	0.81	< 0.01
Oiling level	MD	17.16	0.76	< 0.01
Oiling level	RF	16.74	0.79	< 0.01
Trend*oiling level	HV	0.33	0.20	0.10
Trend*oiling level	MD	-0.02	0.16	0.89
Trend*oiling level	RF	1.01	0.20	< 0.01
Trend ² *oiling level	HV	-0.02	0.02	0.40
Trend ² *oiling level	MD	0.04	0.02	0.06
Trend ² *oiling level	RF	-0.08	0.03	< 0.01

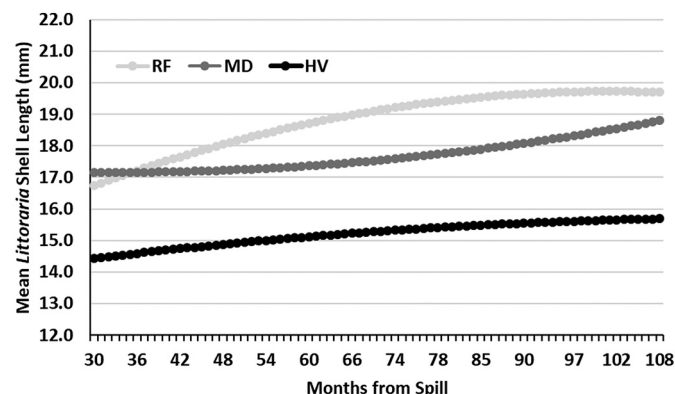


Fig. 6. The trend for the average shell length (mm) of *Littoraria irrorata* over time from the beginning of the study (30 months after the spill) to the last sampling period (108 months after the spill), provided by the slopes and intercepts of the ANCOVA regression means model in Table 3, at the reference (RF), moderately oiled (MD), and heavily oiled (HV) shoreline marsh sites in northern Barataria Bay, LA. Individual points along the trend lines represent modeled time intervals.

4. Discussion

In their meta-analysis of saltmarsh periwinkle responses and recovery on the marsh edge habitat after the DWH oil spill, Zengel et al. (2017) concluded that neither snail density nor population size structure recovered 5 years post spill. They observed a steadily increasing density for the first 3 years after the spill with only a slight increase for years 4 and 5 and that *L. irrorata* populations in the oiled sites had greater relative proportions of smaller adults and sub-adults, and fewer larger adults, compared with reference sites. Our extended analysis through 9 years also found that recovery was incomplete, and although some of the observed trends continued, other responses changed over time indicating a complex and varied recovery process. For example, we observed that from 40 to 66 mo, MD sites had the highest abundance and increases in the small adult size class suggesting that the ecological factors affecting recovery varied with oiling intensity. This positive effect on periwinkles was probably caused by the influence of *S. alterniflora* live aboveground biomass which was increased at MD relative to RF sites from 36 to 66 mo after the spill (Lin et al., 2016). Lin and Mendelsohn (2012) found that negative impacts to the co-dominant plant species *J. roemerianus* increased with oiling intensity and repeated oiling after the DWH oil spill. *S. alterniflora* live aboveground biomass was relatively higher at MD sites perhaps because *J. roemerianus* was slow to recover reducing the negative effects of interspecific competition on *S. alterniflora*. In addition, Li et al. (1990) reported that low levels of oiling ($3.33 \text{ gCm}^{-2} \text{ day}^{-1}$) stimulated *S. alterniflora*

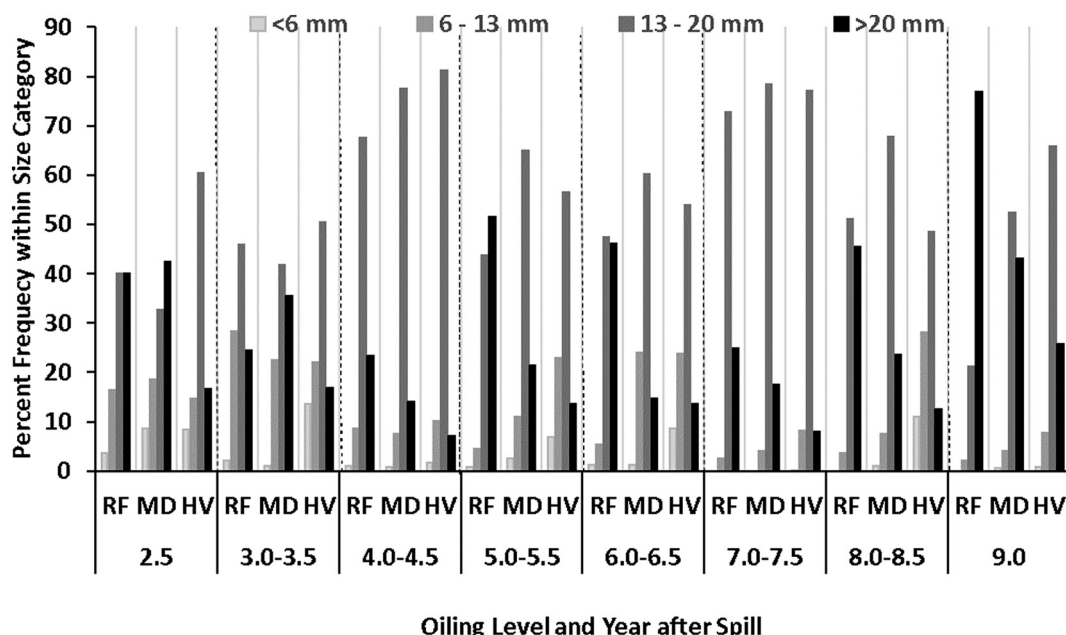


Fig. 7. The relative frequency of juvenile (< 6 mm), subadults (6 to 13 mm), small adult (13 to 20 mm), and large adult (> 20 mm) shell length categories of *Littoraria irrorata* yearly from the beginning of the study at 30 months (2.5 years) after the spill to 108 months (9 years) after the spill.

growth. *S. alterniflora* aboveground biomass and *L. irrorata* densities at MD sites both decreased relative to RF and HV sites simultaneously at 66 mo, further suggesting the initial importance of *S. alterniflora* in recovery after the oil spill.

Our longer-term study also revealed that the pattern of steadily increasing density and body size periwinkles over time at HV sites changed after ~5 y post spill. *L. irrorata* densities at HV sites from 74 to 108 mo became highly variable (Fig. 4) with significantly higher or lower density at HV sites compared to RF or MD sites in an apparent seasonal pattern opposite of the seasonal pattern in live aboveground biomass of the marsh vegetation. Mean size variation also began a similar seasonal-like pattern from 78 to 108 mo, most notably at RF and HV sites (Fig. 5). However, the magnitude of change in body size from season to season was much greater at HV sites than at RF sites, suggesting that variation at HV sites was becoming more like that experienced at RF sites over time but that full recovery was not yet achieved. It seems unlikely that density and body size variation was random given the similar (but opposite) pattern of seasonal variation in vegetation. There are a number of possible explanations for the larger magnitude of change from season to season in the pattern of periwinkle recovery at HV sites. For example, the slow recovery of vegetation from heavy oiling may affect seasonally variable food sources for periwinkles or influence patterns of larval recruitment, intra-marsh migration, as well as predation pressure.

HV marsh sites had much lower aboveground plant biomass and stem density than either MD or RF sites from 30 to 102 mo post spill, and both values varied between a spring low and fall high at all oiling levels (Figs. 2 and 3). The slow recovery of *J. roemerianus* at HV sites contributed to these differences (Lin et al., 2016; Lin, unpublished data). The reduced aboveground biomass and stem density would be expected to lead to a more open marsh canopy at HV sites and increased light exposure on the marsh surface enhancing benthic microalgal production, especially in the spring. Fleeger et al. (2015, 2017, 2019) found that the recovery of benthic microalgal biomass at our sampling sites was complete 2–3 years after the spill, and that benthic microalgal biomass reached much higher levels after 4–5 years at HV sites coincident with the slow recovery of plant cover. Benthic microalgae serve as an important basal food resource for many adult and juvenile infauna and possibly periwinkles. Alexander (1979) found dead *S. alterniflora* to

be a major portion of the diet of *L. irrorata*; however, benthic microalgae and meiofauna form a significant portion of their diet when available representing higher organic matter content and caloric value than detritus (Odum, 1970 in Alexander, 1979). Using stable isotope ratios, Sullivan and Moncreiff (1990) found that the primary food source of *L. irrorata* is edaphic algae. *L. irrorata* may have benefited from this food source especially in the spring at HV sites when live aboveground plant biomass was low. These observations suggest that the more open marsh at the HV sites favored benthic microalgal growth that facilitated a high density of subadult and small adult (2 to 5 years of age) *L. irrorata* (see Photograph 1).

Recruitment or migration patterns also affect *L. irrorata* abundance and size structure. For a period of approximately one year after the oil spill, recruitment was likely prevented or reduced into the HV sites; however, recruitment likely increased as *S. alterniflora* and benthic macroalgae began to return to the HV sites. We were unable to track actual recruitment into the sites and our sampling of juveniles was



Photographs 1 and 2. *Littoraria irrorata* (a) at a low tide on the marsh surface (May 2018 – 97 mo after the oil spill) (b) at a higher tide on *Spartina alterniflora* stems (May 2019 – 108 mo after the oil spill) at heavily-oiled station, HV9. Note lack of *Juncus roemerianus* in both photographs.



Photographs 1 and 2. (continued)

inconsistent. The variation in population density that we found between the size classes (Figs. S1, S2, and S3) could be due to a combination of variable recruitment and/or migration. The periodic increases in subadults (Fig. S1) could be the result of sporadic recruitment. Movement may explain increases in small adult snails into the MD and HV sites because subadults (Fig. S1) do not follow the same pattern as the small and large adults indicating that population size structure may not occur by site-specific recruitment and growth alone. Migration or movement would explain the variation in size distribution patterns described by Crist and Banta (1983); however, movement of periwinkles within the marsh proper has been little studied. Mark and recapture studies (e.g., Vaughn and Fisher, 1992) indicate little movement by both juvenile and adult *L. irrorata* (Hamilton, 1978). Studies, however, indicate that distribution of juveniles may change as they grow, from the edge to the interior (Crist and Banta, 1983; Rietl et al., 2018). If so, *L. irrorata* also may be moving from the marsh edge further into the marsh after spring resulting in the lower fall abundance. Movements at HV sites may differ because of the increased benthic algal biomass causing more subadults to stay at or migrate to HV sites.

Predation could also play a role in the seasonal-like variation of *L. irrorata* density and shell size (Failon et al., 2020). Stem density at HV sites was reduced by more than 50% compared to RF and MD sites leaving the open environment described above and fewer stems for *L. irrorata* to climb to avoid predators (see Photograph 2). *J. roemerianus* was absent from the HV sites for most of the study period and serves an alternate climbing stem for *L. irrorata* (Hughes, 2012). Predators may control both abundance and size of *L. irrorata* at the HV sites because of the lack of refuge. The predator–prey relationship between *C. sapidus* and *L. irrorata* depends on the size of both species (Hamilton, 1976; Rietl et al., 2018; Schindler et al., 1994). Through field observations and experiments, Hamilton (1976) estimated the largest size of preyed upon *L. irrorata* was 15 mm shell length which falls within the small adult age class that we found at HV sites. It is therefore plausible that the abundance swings between spring and fall at the HV sites could be the result of local immigration in the spring due to greater algal biomass and greater predation into the fall due to inability to avoid predators.

Wind/wave energy within Barataria Bay differs with the location and orientation of the site. Our heavily oiled sites experienced higher levels of wave energy during major storm events (e.g., Hurricane Katrina) which has been linked to erosion (Deis et al., 2019). Previous work on littorine snails on wave swept shores have found that body sizes are smaller than from protected shores because snails in high energy sites expend significant metabolic energy to avoid displacement (Boulding and Van Alstyne, 1993; Trussell et al., 1993). Deis et al. (2019) does find that wave energy at the HV sites during major storm

event is higher and does significant erosion. Our marsh sites, however, are generally low-energy and low-tidal amplitude (lunar driven diurnal tidal amplitudes in the region are about 30 cm) shores in which some high tides do not inundate the marsh edge. The average difference in wave energy between RF and HV sites is generally low (except during major storm events), and is unlikely to contribute significantly to observed differences in body size.

Reference sites established after oil spills are often problematic especially when data from before oiling events are unavailable. It is likely that our RF sites received trace amounts of oil from post-spill meteorological events that redistributed dissolved petroleum hydrocarbons. Fleeger et al. (2015) using the same reference sites found that abundance and diversity of meiofauna were well below regional means and indicative of effects for 1–2 years post spill. Our periwinkle data suggests that recovery of total abundance occurred within 2–3 years post spill; however, mean shell length (representative of population size distribution) may have taken 7–8 years post spill to recover at our reference sites. We feel our recovered RF sites were however representative of marshes in the area based on the composition of vegetation [strong foundation species effects of vegetation are well known to influence marsh faunal communities (Craft et al., 2003, Johnson et al., 2018)]. Nearby sites have been part of a marsh-wide monitoring program (CRMS stations, <https://lacoast.gov/crms/#>). The percent cover of the co-dominant plant species, *S. alterniflora* and *J. roemerianus*, at our 7 reference sites and CRMS stations 0237, 3590, and 0224 were quite similar (38.7 and 53%, 64 and 37%, and 39.5 and 45%) (*S. alterniflora* and *J. roemerianus*, respectively in August of 2019 [CRMS web site]) and were 48.4% for *S. alterniflora* and 41.6% for *J. roemerianus* (calculated from data from Lin et al., 2016). Over the 42-month post-spill period, *S. alterniflora* dominance varied from 27.8% to 51.7% while *Juncus* dominance varied from 39.4% to 59.2%. Further evidence that periwinkles at our RF sites are typical of the region comes from the work of Rietl et al. (2018) who measured morphological characteristics of *L. irrorata* at five marsh locations in south Louisiana between the Atchafalaya and Mississippi rivers including Barataria Bay. They found that mean shell length varied between 17.32 ± 0.21 mm and 23.31 ± 0.20 mm at all sites and that mean length in East Barataria Bay = 21.54 ± 0.11 mm. *L. irrorata* mean shell length at our RF sites was 18.42 ± 0.26 mm after 4.5 years post spill and 21.01 ± 0.16 mm at 9 years post spill. This similarity suggests that the mean shell length of our RF site periwinkles was representative of area marshes after a recovery period.

A significant amount of salt marsh restoration is expected in the Gulf of Mexico over the next decade or more as a result of the settlement from the DWH oil spill. Baumann et al. (2018) modeled re-population trajectories for *L. irrorata* from restoration studies conducted in Louisiana. Recovery was quantified as change in *L. irrorata* density through time and the annual addition of new biomass through juvenile settlement. Baumann et al. (2018) estimated that periwinkle density recovery occurred in year 4 and that maximum annual steady-state addition of biomass occurred starting at year 6. They do describe the problem with their approach for restoration projects because, as we have discussed, periwinkle recovery is dependent on vegetation recovery (i.e. for restoration projects, the growth and expansion of vegetation after planting) and vegetation recovery for restoration projects takes a period of time after initial planting. We recommend that comparison of the *L. irrorata* population density (total and size classes) along with size structure (mean shell length) at restoration sites and reference sites be employed rather than density and biomass as a simpler, non-invasive, and more informative approach to monitoring recovery of restored marsh sites.

5. Conclusions

Duarte et al. (2015) suggest that environmental degradation and recovery in coastal and estuarine ecosystems are not parallel. Recovery

often displays hysteresis as the pressures of degradation and recovery are different. Our data on periwinkles suggests that the factors that drive recovery are complex and variable over time for oil spills. Dramatic losses in *L. irrorata* populations at heavily oiled sites (Silliman et al., 2012; Zengel et al., 2016, 2017) occurred followed by steadily increasing density and population size structure for about 5 years post spill as recruitment began and environmental conditions improved. However, the recovery trajectory of *L. irrorata* responded to differences in environmental conditions and ecological opportunities and pressures as affected by the intensity of oiling. For example, initial higher densities at the MD sites in the post recovery period may be a response to a heightened recovery of *S. alterniflora*. Strong fluctuations in *L. irrorata* density and size structure at HV sites occurred from 74 to 108 mo post spill in a seasonal-like pattern at HV sites. The magnitude of these differences was much greater than at HV sites than RF sites and suggest that recovery was occurring but was not complete. We speculate that lingering effects of heavy oiling on vegetation cover have had cascading effects on periwinkles. Periwinkle density and size distribution may have responded to increases in seasonally important food resources (i.e., microalgae and meiofauna) and increased predation pressure in the more open canopy.

Periwinkle recovery at moderately and heavily oiled sites after the DWH oil spill based on population size structure was not complete after 9 years. As a rough extrapolation, it can be estimated that the MD sites may recover within approximately 11 years and HV sites may take two decades or more to recover after the DWH oil spill. Reflecting on the proposed definition for recovery of *L. irrorata* by Zengel et al. (2016), recovery is based on habitat conditions in heavily impacted areas becoming suitable to support normal levels of periwinkle recruitment, immigration, survival, and growth. The primary reason for the lack of recovery at the HV sites is that the habitat has yet to stabilize and become suitable for full *L. irrorata* population recovery as described by Zengel et al. (2016).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2020.111581>.

CRedit authorship contribution statement

Donald R. Deis: Conceptualization, Methodology, Investigation, Writing - original draft, Visualization. **John W. Fleeger:** Conceptualization, Methodology, Investigation, Writing - review & editing, Visualization. **David S. Johnson:** Writing - review & editing. **Irving A. Mendelssohn:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Qianxin Lin:** Conceptualization, Investigation, Writing - review & editing, Project administration, Funding acquisition. **Sean A. Graham:** Conceptualization, Writing - review & editing, Funding acquisition. **Scott Zengel:** Conceptualization, Methodology, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Aixin Hou:** Writing - review & 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.

Acknowledgements

Funding for this project was provided by the Gulf of Mexico Research Initiative. Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org>, and includes the following datasets doi:10.7266/N7FF3Q9S, doi:10.7266/n7-c6cb-p211, doi:10.7266/N7P849FF, doi:10.7266/N74J0CJW. This is contribution

3930 of the Virginia Institute of Marine Science, William & Mary. We would like to thank James (Jay) Geaghan, Ph.D., Professor Emeritus, Louisiana State University and Renee Price, for assistance on data analysis. We would like to thank Stefan Bourgoïn, Eric Schneider, David Loy, and Patrick Burke for assistance on sampling. The authors thank the reviewers for their critical comments that assisted in the development of the final product.

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