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Marine ecoregion and *Deepwater Horizon* oil spill affect recruitment and population structure of a salt marsh snail

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Abstract. Marine species with planktonic larvae often have high spatial and temporal variation in recruitment that leads to subsequent variation in the ecology of benthic adults. Using a combination of published and unpublished data, we compared the population structure of the salt marsh snail, *Littoraria irrorata*, between the South Atlantic Bight and the Gulf Coast of the United States to infer geographic differences in recruitment and to test the hypothesis that the *Deepwater Horizon* oil spill led to widespread recruitment failure of *L. irrorata* in Louisiana in 2010. Size-frequency distributions in both ecoregions were bimodal, with troughs in the distributions consistent with a transition from sub-adults to adults at ~13 mm in shell length as reported in the literature; however, adult snails reached larger sizes in the Gulf Coast. The ratio of sub-adults to adults was 1.5–2 times greater in the South Atlantic Bight than the Gulf Coast, consistent with higher recruitment rates in the South Atlantic Bight. Higher recruitment rates in the South Atlantic Bight could contribute to higher snail densities and reduced adult growth in this region. The ratio of sub-adults to adults in Louisiana was lower in 2011 than in previous years, and began to recover in 2012–2014, consistent with widespread recruitment failure in 2010, when large expanses of spilled oil were present in coastal waters. Our results reveal an important difference in the ecology of a key salt marsh invertebrate between the two ecoregions, and also suggest that the *Deepwater Horizon* oil spill may have caused widespread recruitment failure in this species and perhaps others with similar planktonic larval stages.

Key words: biogeography; BP Deepwater Horizon; gastropod; Littoraria; marine invertebrate; oil spill; population structure; recruitment; salt marsh; Spartina.

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Introduction

Many marine algae, invertebrates, and fish have a complex life cycle, with a small larval stage that disperses in the plankton, and a larger adult stage that is totally or relatively sedentary, and much easier to observe (Reed et al. 1988). The challenges in studying the larval stage limit our understanding of the population ecology of such species (Gaines and Bertness 1993, Jones et al. 2015). Recruitment from the planktonic into the adult stage is affected by larval production, by currents that mediate larval transport, by biotic and abiotic conditions in the water column that affect larval survival, and by conditions in the adult habitat that affect larval settlement and metamorphosis into juvenile or adult stages (Pawlik 1992, Bertness et al. 1996, Witman et al. 2010). These factors are likely to vary geographically and over time, contributing to the high spatial and temporal variation in recruitment that characterizes many marine species (Sale et al. 1984, Raimondi 1990, Witman et al. 2010, Menge et al. 2015).

Recruitment variability is best understood for marine invertebrates on rocky shores, such as barnacles and mussels, in which adults are completely sedentary and recruits can be counted soon after they settle and metamorphose from the plankton (Crisp and Barnes 1954, Connell 1985). For these species, variation in recruitment to the adult stage is often determined by near-shore currents, which tend to transport larvae toward or away from the shore, and vary in direction and strength geographically and over time depending on coastal topography and oceanographic conditions (Roughgarden et al. 1988, Connolly et al. 2001).

Measuring recruitment soon after metamorphosis from the plankton is more challenging for other taxa in which new recruits are cryptic or otherwise hard to sample (Reed et al. 1988). A well-established method for these taxa, including many marine fish, is to infer variation in recruitment from the size structure of older individuals that fall into distinct "cohorts" that resulted from past pulses of recruitment (Doherty and Fowler 1994). Here, we use this cohort-based approach to infer differences in population dynamics of the salt marsh snail *Littoraria irrorata* between the South Atlantic Bight and Gulf Coast of the United States.

Littoraria irrorata is geographically widespread and abundant in coastal salt marshes from the Mid-Atlantic through the Gulf Coast of the United States (Dayan and Dillon 1995). It is extremely important ecologically throughout its range, mediating flow of primary production into detritivore and herbivore food chains, and serving as food for higher trophic levels (Newell et al. 1989, Kemp et al. 1990, Silliman and Bertness 2002). Nevertheless, because recent *L. irrorata* recruits are cryptic, studies have largely been limited to adults that are months to over a year post-metamorphosis, and little is known about the recruitment dynamics of this species.

We compared the population structure of *L. irrorata* populations between the South Atlantic Bight and the Gulf Coast of the United States. These two regions support relatively similar salt marsh communities, with the flora dominated by smooth cordgrass, *Spartina alterniflora*, black needlerush, *Juncus roemerianus*, and a handful of other plant species, and the fauna dominated by the same or congeneric species of crabs, snails, and insects (Kunza and Pennings 2008, McCall and Pennings 2012, McFarlin et al. 2015). However, these similarities may belie underlying differences in abiotic forcing between the two regions. The South Atlantic Bight is mesotidal, with a tidal range of one to three meters. In contrast, the Gulf Coast is microtidal, with a tidal range of less than one meter. Because meteorological forcing can add or subtract several decimeters to coastal sea level, meteorological and lunar forcing of sea level are of a similar magnitude in the Gulf Coast, with the result that the tidal regime is often irregular and wind

driven, with extended periods of flooded or drained conditions (Feng and Li 2010). In addition, much of the Gulf Coast experiences more freshwater input from rivers, particularly in Louisiana, such that coastal waters are often variable in salinity and well below full-strength seawater (Visser et al. 2006). This variation in oceanographic and riverine forcing is likely to affect the structure and function of Gulf Coast vs. South Atlantic Bight salt marsh communities (Kunza and Pennings 2008, McCall and Pennings 2012, McFarlin et al. 2015).

We used size-frequency distributions of sub-adult and adult *L. irrorata* to infer differences in recruitment between the two geographic regions. We also examined variation in size-frequency distributions in Louisiana over time to look for evidence that the 2010 *Deepwater Horizon* oil spill affected *L. irrorata* recruitment. During the oil spill, the cumulative extent of surface water oiling was ≥130,000 km^2 (Goni et al. 2015, MacDonald et al. 2015). Combined with low salinities associated with river water releases enacted in response to the spill (Bianchi et al. 2011), surface oiling could have affected the 2010 larval cohort of *L. irrorata* throughout much of coastal Louisiana (Bingham 1972*a*, Fodrie and Heck 2011, Mendelssohn et al. 2012, Fodrie et al. 2014). No direct measurements of *L. irrorata* recruitment in the Gulf Coast have been conducted, either before or in response to the 2010 *Deepwater Horizon* oil spill, so direct evidence of oil effects on recruitment does not exist. If, however, recruitment in 2010 was low, we would expect to see a depleted size class of *L. irrorata* in 2011 size distributions at Louisiana sites that were not affected by direct shoreline oiling.

METHODS

Study species

The gastropod *L. irrorata* occurs from New York to Texas, excluding southern Florida (Dayan and Dillon 1995). It is abundant in coastal salt marshes dominated by smooth cordgrass, *S. alterniflora*, and black needlerush, *J. roemerianus*, with typical reported densities ranging from 20 to 300 m^{-2}, and occasional densities of >1000 m^{-2} (e.g., in marsh die-off areas) (Silliman and Zieman 2001, Silliman et al. 2005, Schalles et al. 2013, McFarlin et al. 2015, Zengel et al. 2016). At typical densities, *L. irrorata* is an important detritivore, shredding fungal-colonized dead *S. alterniflora*, supporting organic matter and nutrient cycling, and supporting marsh–estuarine food chains (Newell et al. 1989, Kemp et al. 1990, Newell and Bärlocher 1993). If *L. irrorata* reaches densities of 500 m^{-2} or more, its feeding activities suppress growth of *S. alterniflora* (Silliman and Zieman 2001, Silliman and Bertness 2002, Silliman et al. 2005). *Littoraria irrorata* also serves as an important food source for a wide variety of consumers, including fish, crabs, turtles, birds, and mammals (Silliman and Bertness 2002, Soomdat et al. 2014).

The duration of the planktonic larval stage of *L. irrorata* has not been measured directly, but is estimated at 3–11 weeks based on studies of related species (Reid 1989). Recent post-metamorphic recruits occupy different microhabitats than adults (Stiven and Hunter 1976). Snails that have recently metamorphosed from the plankton are cryptic and occur hidden between the leaf sheath and the lower stem of *S. alterniflora* shoots, or in curled senescent or dead leaves. When *L. irrorata* grow to 4–6 mm in shell length, they move into the open, living on *S. alterniflora* stems and exposed leaves, as well as on the marsh substrate. Because they are much more easily seen after they move to these microhabitats, the vast majority of studies of *L. irrorata* either under-sample the smallest size ranges, or specifically limit sampling to snails that are ≥5–6 mm long. We are aware of no published studies that directly measure variation in *L. irrorata* recruitment, other than early qualitative descriptions (Odum and Smalley 1959) and recent comparisons among areas with different shoreline oiling, cleanup, and restoration treatments (Zengel et al. 2014, 2015).

Size-frequency distributions of *L. irrorata* are often bi- or tri-modal (Hamilton 1978, Soomdat et al. 2014, Zengel et al. 2014). Measured growth rates of *L. irrorata*, coupled with studies of other snails, suggest that these modes represent age classes. Among the observed modes/age classes, different life-history stages can be defined. Sexual anatomy is first visible in snails of about 6 mm in shell length (Bingham 1972*b*). The smallest mating individuals reported are about 13–14 mm long (Hamilton 1978). The largest snails in most populations range from 20 to 26 mm in shell length, although the largest

reported size in the literature is 32 mm (Kaplan 1988). Accordingly, we define three life-history stages: juveniles (<6 mm), sub-adults (6–13 mm), and adults (>13 mm); these stages are similar to those defined by others based on the same evidence (Hamilton 1978, Stagg and Mendelsohn 2012, Zengel et al. 2015, 2016). Given estimates of growth (Bingham 1972c, Stiven and Hunter 1976), juvenile snails would be <1 year of age (recruited from the plankton in the current year), sub-adults would average about one year of age (recruited in the prior year), and adults would be approximately 2 years and older.

Data

We obtained size-frequency distributions of *L. irrorata* from the South Atlantic Bight and the Gulf Coast from multiple sites in multiple years. We identified data sets by searching the literature for studies on *L. irrorata*, and by consulting with estuarine ecologists who work in these geographic regions. For literature studies, we attempted to obtain the original data set from the authors; if this was not possible, we extracted information from published figures.

We limited our comparisons to studies from the South Atlantic Bight (defined as North Carolina, South Carolina, and Georgia; we found no relevant studies from northeast Florida), and the Gulf Coast (we found relevant studies from the Florida Panhandle, Alabama, Louisiana, and Texas, but not Mississippi). In the Gulf Coast, we excluded sites from 2010 and later with heavy-to-moderate shoreline oiling from the *Deepwater Horizon* oil spill, limiting our analysis to sites that showed no visual evidence of oiling, or, in a few cases, to sites with light, non-persistent oiling, intact vegetation structure, and typical *L. irrorata* densities. The latter condition allowed us to expand our coverage in Louisiana estuaries where shoreline oiling was more widespread. As an example, for the current study, we only used reference sites from the Zengel et al. (2016) natural resource damage assessment study examining shoreline oiling and cleanup treatment effects on *L. irrorata*. Because most studies do not thoroughly search plant stems for recent recruits, frequency data in these studies for snails <6 mm in length are unreliable. We therefore left-censored the data, omitting all snails smaller than 6 mm. Data from different marsh zones at each site (if specified) were pooled without weighting for abundance in each zone, which was often not known. For each site in each year, we then calculated the proportion of sub-adults (the ratio of sub-adults to sub-adults plus adults) as a simple index of recruitment in the previous season. Because the value of this index depends not only on recruitment, but also on survival and growth rates of the sub-adult size class and densities of the adult size class, its values must be interpreted with caution. As described below, we conducted sensitivity analyses to assess whether variation in growth rates between geographic regions might affect our results, and return to this point in the discussion.

Most of the data sets that we found were collected during the summer and fall months of the year (defined here as June–November). A small number of data sets, however, were collected during the winter and spring months (December–May). A preliminary comparison of the data found no difference in the proportion of sub-adults by season in the South Atlantic Bight, but some evidence that the proportion of sub-adults was lower in the winter and spring than in the summer and fall in the Gulf Coast (results not shown). Such a result would be expected if recruitment has a seasonal peak. Because we had only a few samples from winter and spring ($n = 6$), we elected to exclude these and standardize our analyses to include only data collected in the fall and summer.

Studies that measured relatively few snails may have done a poor job estimating the proportion of sub-adults. We therefore restricted our analyses to data sets consisting of at least 35 snails. In some cases, single studies sampled at multiple, nearby sites within a single year, or at the same site on multiple dates within a single year. To achieve the 35 snail threshold while including only one data point per study/site/yr, we pooled data across nearby sites or dates using the following rules. (1) If sites within a study were sampled on multiple dates within a year, the fall data were used. If fewer than 35 snails were sampled in fall, then summer data for the same site were also included. (2) If a site still had fewer than 35 snails, data from nearby sites (within 5000 m) from within the same study were pooled and treated as a single site/yr. If necessary, multiple sites were allowed to pool in this fashion, creating a "daisy-chain" of merged sites.

(3) Regardless of the number of snails sampled, sites within 500 m of each other were pooled as a single site even if the original investigator treated them as separate entities. To examine whether setting the cutoff at 35 affected the results, we repeated the pooling procedure and statistical analyses using cutoffs of 50 and 20 snails per site per date. Each resulting data point for a given site in a given year was treated as an independent replicate in the analyses.

Using the cutoff of 35 snails per site per date, we ended up with 86 data points for the South Atlantic Bight, covering the time period 1989–2013, and 31 data points for the Gulf Coast, covering the time period 1974–2014 (Appendix S1: Table S1). We visually compared the size-frequency distributions for the two regions by pooling all of the data of individual snail measurements within each region. For the size-frequency analysis, data were pooled directly without weighting and snails <6 mm were censored as above. Studies which provided data in the format of ranges of snail lengths were not included in this analysis.

We conducted two analyses with these data. First, we compared the proportion of sub-adults between the South Atlantic Bight and the Gulf Coast, using a non-parametric Mann–Whitney U test. We also ran this analysis using only data from the Gulf Coast prior to 2011 to rule out the potential effect of the oil spill on the geographic comparison. Second, to evaluate the potential impact of the 2010 *Deepwater Horizon* oil spill on recruitment in Louisiana, we compared the proportion of sub-adults that would have recruited before the oil spill (pre-2011); the proportion in 2011 (when individuals that had recruited in 2010 would have entered the sub-adult class); and the proportion in subsequent years to evaluate recovery. Because we studied only sites with no substantial oiling, any effects of oil would have occurred during the planktonic stage, not post-recruitment. We restricted the analyses of potential oil spill effects and recovery to sites in Louisiana because there were no 2011 data from other Gulf Coast states, and because estuarine oiling was most widespread, intense, and prolonged in Louisiana waters. For all analyses, we used non-parametric tests because distributions were often non-normal; however, in most cases results were similar using parametric tests (data

not shown). For all analyses, we considered tests with $P < 0.05$ to be statistically significant.

RESULTS

We collected size frequency data on *L. irrorata* from sites representing a considerable proportion of both the South Atlantic Bight and the Gulf Coast, with an emphasis on Georgia and Louisiana, respectively, excluding sites that suffered heavy direct oiling from the *Deepwater Horizon* oil spill (Table 1, Fig. 1). The size-frequency distributions from individual studies in the two regions (snails <6 mm not included) were often bimodal, with the trough between the modes consistent with the 13 mm cutoff that we used to separate sub-adults and adults. This bimodal pattern is still evident but less dramatic when all the data were combined (Fig. 2) due to variation among studies in the precise location of the modes and trough. Adult snails from the Gulf Coast grew considerably larger than those from the South Atlantic Bight (Fig. 2).

In the South Atlantic Bight, sub-adult snails typically comprised 48% of the post-juvenile size distribution (Fig. 3a). This was roughly two times greater than in the Gulf Coast, where sub-adults were typically only 25% of the post-juvenile size distribution (Mann–Whitney U test, $P < 0.001$). Our conclusions were similar if only pre-spill data from the Gulf Coast were used (Fig. 3b, Mann–Whitney U test, $P = 0.03$) or when a cutoff of 50 or 20 snails per site per date was used (Appendix S1: Table S2). Additionally, when we remove 2010 and 2011 data from both regions, representing observations with possible

Table 1. Number of data points (site-years after pooling using 35 observations as a minimum criteria) as a function of geographic region, state, and time period.

Geographic region	State	Pre-2011	2011	Post-2011
South Atlantic Bight	NC	4	0	0
South Atlantic Bight	SC	4	0	0
South Atlantic Bight	GA	60	6	12
Gulf Coast	FL	4	0	0
Gulf Coast	AL	0	0	3
Gulf Coast	LA	8	8	6
Gulf Coast	TX	2	0	0

Note: A more complete breakdown of the data is presented in Appendix S1: Table S1.
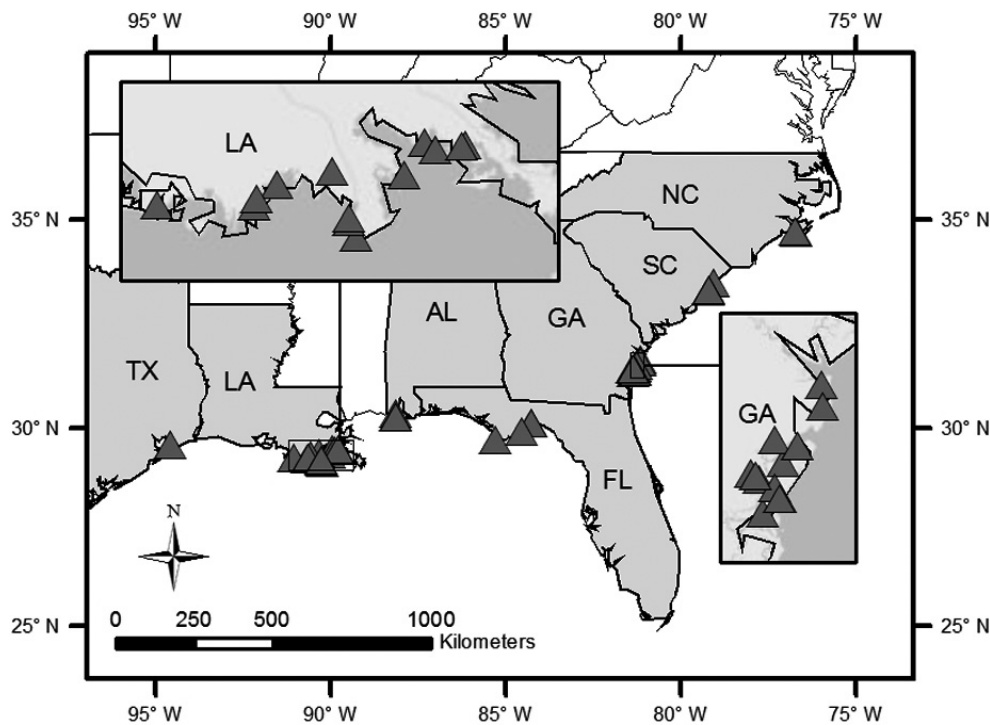
Fig. 1. Map showing geographic locations of all study sites on the Gulf Coast and South Atlantic Bight of the United States. State codes from left to right are TX: Texas; LA: Louisiana; AL: Alabama; FL: Florida; GA: Georgia; SC: South Carolina; NC: North Carolina. Insets show the distribution of sites in LA and GA in more detail. More information about study sites is provided in Appendix S1: Table S1.

direct effects from the oil spill, the comparison remains significant (Mann–Whitney U test, $P = 0.011$).

To evaluate the possibility that snails in the South Atlantic Bight were growing more slowly than snails in the Gulf Coast, we repeated the comparison between regions using either a 12 or an 11 mm cutoff for the transition from sub-adults to adults in the South Atlantic Bight while retaining the 13 mm cutoff for the Gulf Coast. Results were again significant (Mann–Whitney U test; 11 mm cutoff, $P = 0.006$; 12 mm cutoff, $P < 0.001$). If we made the test even more conservative, however, by both altering the size threshold and limiting the comparison to pre-oil spill years, the difference between regions was no longer significant (Appendix S1: Table S3, comparisons 2–5).

There was a large reduction in the proportion of sub-adults in Louisiana in 2011: The proportion of sub-adults was only 4%, one-tenth of that in previous years (Fig. 4, Kruskal–Wallis (a non-parametric equivalent to ANOVA) with Dunn post hoc pairwise test, $P < 0.001$). The reduction in 2011 remained significant if a cutoff of 50 or 20 snails per site per date was used (Appendix S1: Table S2). The sub-adult ratio largely recovered in the following years, although the post-2011 time period was not significantly different from 2011 due to low replication ($P = 0.08$). In the South Atlantic Bight, the proportion of sub-adults also differed between the pre-2011 and 2011 time periods (Kruskal–Wallis with Dunn post hoc pairwise test, $P = 0.04$), but with 2011 having a high, rather than low, proportion of sub-adults (Appendix S1: Fig. S1).

Discussion

We found a higher proportion of sub-adults in South Atlantic Bight vs. Gulf Coast populations of *L. irrorata*, suggesting consistently higher rates of recruitment in the South Atlantic Bight. A number of factors could cause this result, ranging
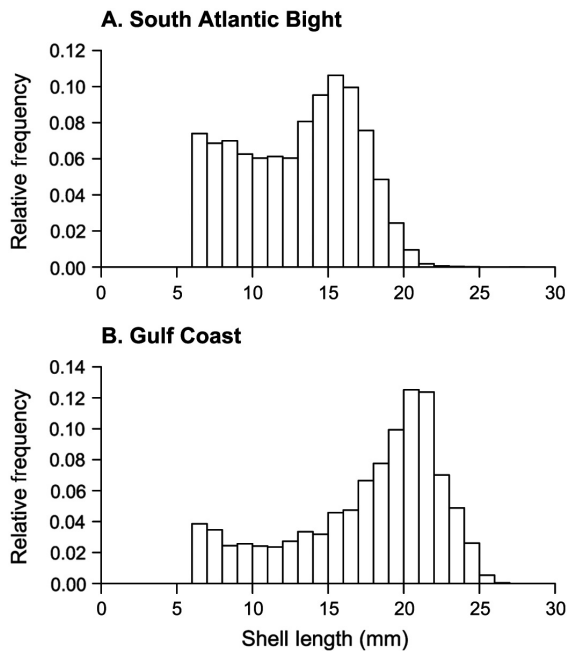
Fig. 2. Size-frequency distributions for *Littoraria irrorata* from (A) the South Atlantic Bight (n = 16,446) and (B) the Gulf Coast (n = 4873); all data combined. Tick marks indicate the lower range of each bar (e.g., the first bar in both panels represents snails 6–6.9 mm in length). Snails <6 mm in length were censored. Individual collections typically show stronger bimodal patterns that are partially blurred when collections from multiple sites and dates are combined.

consistent with the somewhat higher population densities of *L. irrorata* typically reported from the former region, and especially for Georgia vs. Louisiana (Silliman and Zieman 2001, Silliman et al. 2005, McFarlin et al. 2015). Higher densities could lead to lower adult growth rates and consequently smaller adults (Fig. 2) due to greater intraspecific competition, although climatic differences or other factors could also play a role. The ecological roles of most species are density-dependent, and comparative studies of both *L. irrorata* and other marine invertebrates between high- and low-recruitment (and density) sites have found important differences in the ecological role that these species consequently play (Witman et al. 2010, Atkins et al. 2015, Menge

from differences in larval production, water current patterns, conditions in the water column, tidal flooding of the marsh, marsh elevation and geomorphology, the propensity of larvae to metamorphose when encountering the marsh, and post-recruitment growth and survival. We lack the data to evaluate these possibilities; consequently, our discussion of potential mechanisms is necessarily speculative. All the potential mechanisms, however, suggest testable hypotheses for future studies. Future studies should focus not just on *L. irrorata*, but also on other marine invertebrates shared between the two geographic regions, to determine whether our findings are idiosyncratic to *L. irrorata* or general across the community of marine invertebrates with planktonic larvae.

Our evidence of higher recruitment rates in the South Atlantic Bight vs. the Gulf Coast is
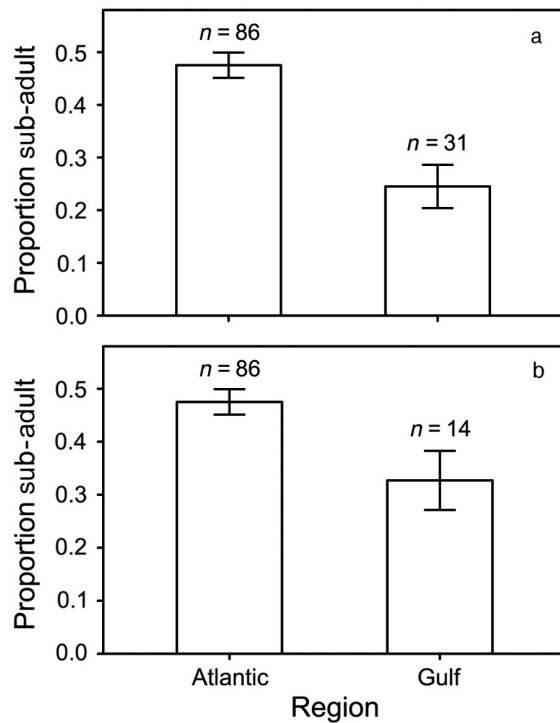

Fig. 3. The proportion of sub-adult snails in the South Atlantic Bight vs. the Gulf Coast. Numbers above bars indicate the number of data points for each region; error bars indicate 1 standard error. (a) (All years). The two regions are significantly different (Mann–Whitney U test, $P < 0.001$). (b) South Atlantic Bight (all years) vs. the Gulf Coast (pre-2011). The two regions are significantly different (Mann–Whitney U test, $P = 0.025$).
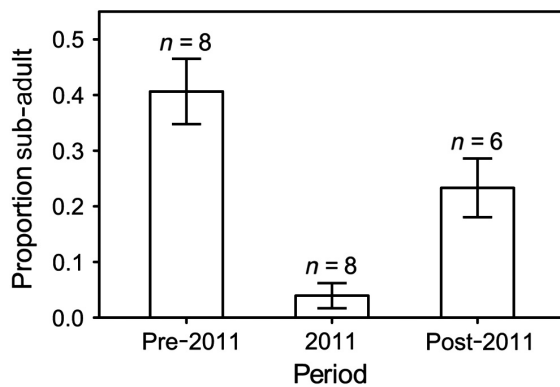
Fig. 4. The proportion of sub-adult snails in Louisiana during three time periods. Numbers above bars indicate the number of data points for each time period; error bars indicate 1 standard error. The time periods are significantly different (Kruskal–Wallis, $P < 0.001$), and 2011 is significantly different from the pre-2011 time period (Dunn post hoc pairwise tests, $P < 0.005$) but not from the post-2011 time period (Dunn post hoc pairwise tests, $P = 0.08$).

et al. 2015). In addition, it is possible that *L. irrorata* populations in the Gulf are genetically distinct from those in the South Atlantic Bight. The little direct evidence available to date does not support this hypothesis (Dayan and Dillon 1995); however, a phylogeographic break along the Florida peninsula is seen for many coastal species (Soltis et al. 2006). If the Gulf Coast populations have evolved a markedly different life-history than the Atlantic Coast populations, this might affect interpretation of geographic differences in recruitment; however, it could not explain the drop in recruitment in the Gulf associated with the oil spill that we discuss below. Thus, plastic or genetic differences in recruitment, adult densities, and size structure of *L. irrorata* between the South Atlantic Bight and Gulf Coast could affect its ecological role in the two areas. As a result, we caution against un-critically extrapolating findings of ecological studies between the two geographic regions unless snail density, biomass, and size structure are similar.

During the *Deepwater Horizon* oil spill, there was concern that surface water oiling, combined in some locations with low salinities caused by river water releases enacted in response to the spill, would affect larvae of a wide variety of marine species (Fodrie and Heck 2011, Mendelssohn et al. 2012, Fodrie et al. 2014, Jones et al. 2015). We found that the proportion of sub-adults in Louisiana *L. irrorata* populations was reduced by 90% in 2011, suggesting widespread recruitment failure in 2010. These data all come from salt marsh sites that were not directly oiled or received only light shoreline oiling. Therefore, the results are unlikely to be explained by post-metamorphic effects of shoreline oiling on settlement or survival. Rather, the most likely explanations are either that oiling caused widespread reproductive failure and mortality of adults, limiting larval production, or that widespread waterborne oiling, combined in some locations with low salinities due to river water releases, harmed planktonic larvae prior to recruitment to the marsh. Densities of adult *Littoraria* were reduced by 50–90% at heavily oiled sites (Zengel et al. 2016); effects on fecundity of survivors were not measured. Oiled sites, however, represented only 15%, and heavily oiled sites only 1% of the Louisiana marsh shoreline surveyed during the spill. Although the loss and possible reproductive failure of adults at these sites would have caused some reduction in the larval pool, this mechanism cannot explain the recovery of *Littoraria* population structure after 2011 because densities of *Littoraria* at oiled sites remained suppressed for more than a year after the spill (Zengel et al. 2015). *Deepwater Horizon* oil was toxic to some marine invertebrate and vertebrate larvae (Goodbody-Gringley et al. 2013, Incardona et al. 2014, Vignier et al. 2015), and low salinities reduce survival of *L. irrorata* larvae (Bingham 1972a). No studies, however, directly measured the abundance of *L. irrorata* larvae or immediately post-metamorphic juveniles in Louisiana during these years, so we lack any direct evidence of these putative mechanisms. Future studies, however, could evaluate the effects of oil on *L. irrorata* larvae in the laboratory to determine what concentrations affect growth and survival. The near-absence of sub-adults in 2011 did not occur throughout the entire geographic range of *L. irrorata*, because a similar comparison in the South Atlantic Bight found that 2011 had an unusually high proportion of sub-adults. Therefore, the lack of sub-adults in Louisiana in 2011 is more consistent with a local or regional cause (such as the oil

spill) than with a large-scale cause (such as variation in climate).

We assumed that the proportion of sub-adults in the population is a good, if indirect, measure of past recruitment success. Similar measures are widely used in other contexts, such as fisheries research, to evaluate recruitment, but they are imperfect. In particular, although we interpreted geographic and temporal differences in this ratio as reflecting variation in recruitment, an alternative possibility is that the differences were caused by variation in adult density. In theory, densities of sub-adults could be similar in the two regions, but higher adult densities in the Gulf Coast would produce a lower sub-adult ratio than in the South Atlantic Bight. We consider this alternative to be unlikely. As noted above, *L. irrorata* densities are lower in the Gulf Coast than the South Atlantic Bight, particularly for Louisiana vs. Georgia (McFarlin et al. 2015) (the central comparison in our study). Similarly, it is unlikely that the low sub-adult ratio in 2011 in Louisiana was due to unusually high densities of adults that year, because measured adult densities in reference areas were similar to literature values for other years (Zengel et al. 2016). Nevertheless, it is possible that adult survival differs geographically or over time, and this would be a useful topic for future studies to explore.

Another alternative explanation for our findings would be that sub-adult snail growth rates were higher in the Gulf Coast than in the South Atlantic Bight, and higher in Louisiana in 2010–2011 than in other years. If so, snails might exit the sub-adult size category more quickly, leading to a lower sub-adult ratio. We consider this alternative also to be unlikely because growth rates of *L. irrorata* appear similar in the Gulf of Mexico and North Carolina (Bingham 1972*c*, Stiven and Hunter 1976), and because size-frequency distributions in the South Atlantic Bight and Gulf Coast had a trough between sub-adult and adult modes that was similar between regions (Fig. 2). Additionally, we can think of no reason why sub-adult growth rates would have been elevated at un-oiled sites in Louisiana in 2010–2011 compared to other years. Nevertheless, the size-frequency distributions for the two regions show that snails reach larger sizes in the Gulf Coast than the South Atlantic Bight, which is consistent with either greater survival or more rapid growth. These differences could occur during the adult stage, in which case they would not affect our calculations. However, it is possible that sub-adult growth rates differ geographically or temporally, and this would be a useful topic for future studies to explore. We repeated our analyses using a fifteen and eight percentage smaller (11 and 12 mm) sub-adult to adult size threshold for the South Atlantic Bight (as would occur if growth was slower), and got similar results, so the differences in sub-adult growth rate between regions would have to be substantial to have explained our results.

Our findings are based on studies of a single salt marsh species, but other salt marsh invertebrates also have planktonic larvae. These other species are likely also be affected by the same factors that created differences in *L. irrorata* population structure between the South Atlantic Bight and Gulf Coast. Future studies of ribbed mussels, *Geukensia* spp., and fiddler crabs, *Uca* spp., could determine whether the differences among ecoregions that we found apply to additional species of salt marsh macroinvertebrates that have planktonic larvae.

In conclusion, our results, based on the size structure of sub-adult and adult *L. irrorata* snails, suggest that recruitment of this salt marsh snail consistently differs between South Atlantic Bight and Gulf Coast populations, and that recruitment of this species in Louisiana in 2010 was reduced by the *Deepwater Horizon* oil spill. These results suggest the possibility of important geographic differences in the population and community ecology of *L. irrorata*, and perhaps of other marine invertebrates that might show similar recruitment patterns. These results are also consistent with concerns that the *Deepwater Horizon* oil spill may have caused widespread recruitment failure of marine organisms with planktonic life-history stages in 2010.

Acknowledgments

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