



Recovery of Salt Marsh Invertebrates Following Habitat Restoration: Implications for Marsh Restoration in the Northern Gulf of Mexico

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Abstract

Recovery following salt marsh restoration in the northern Gulf of Mexico is investigated using meta-analysis for two salt marsh indicator invertebrates, the periwinkle snail (*Littoraria irrorata*) and amphipod crustaceans (Amphipoda). These invertebrates serve key marsh ecosystem functions including facilitating nutrient cycling and serving as prey for larger ecologically and economically important species. Recovery of periwinkles in restored marshes compared to reference sites is quantified by progression in population density and, because the species is long-lived (~10 years), in terms of biomass added per unit area each year following restoration. Amphipods are shorter-lived with high annual turnover; thus, recovery through time is estimated by the density of individuals rather than by biomass. The results of the analyses indicate progressive periwinkle recovery to equivalence with reference systems by year 4 in terms of density and year 6 with respect to annual biomass addition, while amphipod densities do not fully recover in the first 20 years following restoration. Although periwinkle recovery in terms of annual biomass addition reaches equivalence by year 6, the development of an age class structure characteristic of reference marshes would likely take longer because of the relatively long lifespan for this species. In addition to providing insight into the benefits of salt marsh restoration in the northern Gulf of Mexico, the approach described can be applied more generally to restoration scaling in a natural resource damage assessment context.

Keywords Meta-analysis · Snail · Crustacean · Macroinvertebrate · Amphipoda · Littorinidae

Introduction

A primary objective of coastal restoration is to create habitat that provides the types of ecological services characteristic of natural systems. Developing realistic and quantifiable goals on the basis of these services is central to planning wetland restoration projects. As coastal wetlands

provide a wide range of ecosystem services (Mitsch et al. 2015), there are numerous metrics that could be used to set project goals, determine the magnitude of restoration necessary to meet project goals, and monitor progress. Growth and population development of marsh fauna can inform restoration on a resource (e.g., species or group of species) specific basis.

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Lower trophic level consumers in the *Spartina alterniflora* salt marsh, such as the epifaunal gastropod marsh periwinkle snail (*Littoraria irrorata*) and amphipods (order Amphipoda), facilitate nutrient cycling, graze senescing organic matter and vegetation, and represent prey items for larger species such as crabs and fish (Gustafson et al. 2006; Graca et al. Graça et al. 2000; Gonzalez and Burkart González and Burkart 2004; Hamilton 1976; Kemp et al. 1990). Because many ecologically and economically important species depend upon coastal marshes for nursery functions and provision of food and shelter, improving our understanding of how prey items such as periwinkles and amphipods develop following habitat restoration has broad implications. Periwinkles, amphipods, and other invertebrates serve important roles in the marsh ecosystem; therefore, they can be viewed as indicators of overall marsh health, productivity, and recovery from disturbance.

Approximately 2000 km of shoreline from Texas to the Florida panhandle were oiled as a result of the 2010 *Deepwater Horizon* incident in the northern Gulf of Mexico (GOM) resulting in losses to resources in the estuarine coastal wetland complex including salt marsh vegetation and faunal inhabitants (Lin and Mendelssohn 2012; RamanaRao et al. 2012; Silliman et al. 2012; Biber et al. 2014; Zengel et al. 2014, 2015, 2017; Hester et al. 2016; Powers and Scyphers 2016; DWH Trustees 2016). A significant amount of salt marsh restoration in the northern GOM is expected in the coming decade following the settlement between British Petroleum and the US public. The anticipated restoration emphasizes the importance of understanding the ecological benefits associated with wetland restoration projects. Numerous studies have investigated marsh habitat development on the basis of faunal presence in the GOM (e.g., Minello and Zimmerman 1992; Minello et al. 1994; LaSalle 1996; Minello and Webb Minello and Webb Jr. 1997; Tong et al. 2013). In this study, an approach is presented to improve the understanding of how periwinkles and amphipods repopulate the marsh following restoration using statistical recovery trajectories developed from the results of individual studies conducted in the region. Recovery trajectories describe how quickly ecosystem components return to a level of functioning similar to appropriate reference, or natural, systems following restoration (Moreno-Mateos et al. 2012). Recovery of these invertebrates is quantified as the change in the periwinkle density through time, the annual addition of new periwinkle biomass, and the change in amphipod density through time following habitat restoration.

A particular challenge that restoration project managers and stakeholders are often faced with is a lack of available data to guide restoration decisions. The approaches presented in this study provide insights into how limited ecological data can be used to develop an understanding of how marsh invertebrates recover following restoration. Further, the quantitative recovery of periwinkles and amphipods or other marsh

taxa can be used in a resource equivalency analysis (REA; similar to Habitat Equivalency Analysis (HEA); Unsworth and Bishop 1994; NOAA 1995, 1999; Strange et al. 2002; Dunford et al. 2004) to estimate species-specific benefits per unit area of a marsh restoration project. Together with information on other aspects of marsh restoration, the results discussed here are used in a REA model in a companion study (Fricano et al. in review, this issue.).

Methods

Literature Review

A literature review was conducted in the fall of 2014 through spring of 2015 to compile data characterizing densities (i.e., number of individuals m^{-2}) of periwinkles and amphipods in (a) appropriate reference *S. alterniflora* marshes and (b) at salt marsh sites that were subject to prior restoration. An appropriate reference marsh is operationally defined as a system that has not been subject to past restoration and is not known to have experienced recent physical disturbance or contamination (Fricano et al., in review, this issue.). Further, an appropriate reference marsh should be representative of the geographic region in which restoration is expected to occur. For periwinkle densities in reference marshes, studies were sought characterizing populations in salt marshes located in Louisiana. Because literature was more limited for amphipods, studies conducted in northern Gulf of Mexico (Texas, Louisiana, Mississippi, Alabama, and west Florida) salt marshes were used to develop reference densities. Given the even more limited availability of restoration studies, a geographic range of the US Atlantic coast and northern Gulf of Mexico was used for the development of the recovery trajectories for both taxa. Only studies that compared restored marsh sites with local reference marshes were included in the recovery trajectory literature review.

The review considered published, unpublished, and gray literature (e.g., theses, dissertations, and technical reports) and was conducted using common literature search engines (e.g., Google Scholar) as well as discussions with subject matter experts. To identify studies with relevant information, a set of search terms was used that included, for example, common and scientific names of the fauna, Gulf of Mexico, US Atlantic coast, salt marsh/*S. alterniflora*, restoration, restored/created marsh, density, and recruitment (Table 1).

For the development of recovery trajectories, restoration types included salt marsh creation, hydrologic restoration, and experimental treatments that closely mimic marsh restoration (Table 2). In these restoration types, *S. alterniflora* regrowth was either facilitated by transplanting or seeding, or allowed to re-seed and grow naturally. Restoration at sites previously subjected to oil exposure was not considered in

Table 1 Summary of the terms used in the literature search for the periwinkle snail and amphipod groups. Reasonable combinations of a primary search term and secondary terms were used to query the Google Scholar search engine. Subject matter experts were consulted to verify that the literature search included all relevant studies within the respective geographical range selected for the two invertebrate groups

Primary search terms	Secondary search terms
Periwinkle literature review	
Fauna	Created marsh
Gastropod	Density
Invertebrates	Fauna assemblages
<i>Littorina irrorata</i>	Gulf of Mexico
Periwinkle	Oiled marsh
	Recruitment
	Restoration
	Restored marsh
	Size distribution
	<i>Spartina alterniflora</i>
Amphipod literature review	
Ampeliscidae	Created marsh
Amphipoda	Density
Amphipods	Fauna assemblages
Corophiidae	Gulf of Mexico
Fauna	Oiled marsh
Gammaridae	Recruitment
Invertebrates	Restoration
Talitridae	Restored marsh
	Size distribution
	<i>Spartina alterniflora</i>
	US Atlantic

the literature review. Measures of periwinkle and amphipod densities were extracted for sites with a defined post-restoration age at sampling along with a paired observation from a nearby or adjacent reference marsh. In general, periwinkle densities reported in the literature represent the sub-adult (6–13-mm shell length, ~1–1.5 years old) and adult (>13-mm shell length, ~>1.5 years old) populations (Zengel et al. 2015). Densities of juveniles (0–1 year old) are typically not measured in field studies; therefore, their densities were estimated using methods described below. Common amphipod families reported include Ampeliscidae, Caprellidea, Corophiidae, Gammaridae, and Talitridae.

For each relevant study, data were compiled on location, size of the marsh, type of restoration project, form of revegetation, site elevation, year of restoration, time since restoration, sampling technique, sampling distance from the marsh edge, number of samples and variability of the reported density, and density measurements at the restored and corresponding reference sites. Because the amphipod literature search was not conducted for a specific species, densities were often reported for multiple species or at varying taxonomic levels (e.g., order, family, or species as the lowest taxonomic level reported); therefore, information was also compiled on the taxonomic level presented in the study. This information was used to determine a total amphipod density of the measurements. For example, some studies quantified amphipods on a

species level and also provided a total quantity representing the sum across all species observed. In this case, the total amphipod density was used in the analysis. Other studies reported densities only on the species level; in these cases, a sum of the densities was computed and used as the total amphipod density. However, because amphipod densities in restored and references systems were compared within studies, differences in either taxonomic level or target species across studies were normalized for the recovery trajectory.

Data Analysis

Average Reference Densities

An average density representing appropriate reference marshes was calculated for periwinkles (sub-adults and adults) and for total amphipods. Given the limited availability of data, total amphipod densities were computed for each site despite likely differences in life history, distribution, and habitat amongst the taxa reported. Specifically, a mean, weighted by the number of samples associated with each observation, was determined using all periwinkle density estimates in appropriate reference marshes in Louisiana and all total amphipod densities from northern GOM reference marshes. Reference densities were also used for the recovery trajectories when those studies also collected paired measurements at restoration sites.

Recovery Trajectories-Statistical Approach

The recovery trajectory for each invertebrate group describes repopulation through time following restoration of a salt marsh. Similar to the approach described in Moreno-Mateos et al. (2012), a response ratio (RR) was calculated for each paired observation:

$$RR_i = \left(\frac{\text{Restored Mean} + 0.01}{\text{Reference Mean} + 0.01} \right)_i \quad (1)$$

A paired observation is defined as the faunal density at a restored or created marsh or experimental site (Restored Mean) with a corresponding observation from a reference location reported in the same study (Reference Mean). A response ratio of one indicates equal densities in the restored and reference site. A small positive value (0.01) was added to numerator and denominator to prevent the occurrence of a zero value. Moreno-Mateos et al. (2012) added one to the numerator and denominator to prevent occurrence of a zero value but because invertebrate densities can be quite low, especially in the early years after restoration, we selected a value of 0.01 instead to minimize bias in the estimates. Response ratios were categorized into 1-year bins based on respective ages of the restored marsh at sampling. The

Table 2 Literature sources used to develop appropriate reference densities and recovery trajectories. Symbols indicate which metric (periwinkle recovery trajectory, periwinkle reference density, amphipod recovery trajectory, or amphipod reference density) the literature sources support. Dashes in brief description of restoration indicate the literature source is not a marsh restoration study, but data contributes to a reference density calculation

Literature source	State	Restoration type	Table or figure	Periwinkle recovery	Periwinkle reference	Amphipod recovery	Amphipod reference	Brief description of restoration literature
Alexander 1976	Louisiana	—	Table 1	•	—	—	—	Fiddler crab and periwinkle colonization of sediment amended <i>Spartina alterniflora</i> transplants.
Cain and Cohen 2014	Georgia	Experimental	Table 3	•	—	—	—	Recovery of vegetation and macrofauna following a pipeline construction project in an intertidal salt marsh.
Knott et al. 1997	South Carolina	Marsh creation/disturbance recovery	Figure 5	•	—	—	—	Evaluation of the physical and biotic characteristics of a created wetland in comparison to a natural adjacent marsh.
LaSalle 1996	Mississippi	Marsh creation	Table 13	•	—	—	—	Macrofauna recovery in a created <i>Spartina alterniflora</i> salt marsh.
Levin et al. 1996	North Carolina	Marsh creation	Table 1	•	—	—	—	—
McCall and Pennings 2012	Louisiana	—	Pers. comm.	•	—	—	—	—
McFarlin 2012	Louisiana	—	Figure 2.2	•	—	—	—	—
Minello and Zimmerman 1992	Texas	Marsh creation	Table 3	•	•	•	•	Fish and decapod crustacean use of created <i>Spartina alterniflora</i> marshes.
Minello and Webb, Jr. 1997	Texas	Marsh creation	Pers. comm.	•	•	•	•	Nekton and aquatic fauna use of several created salt marshes from three to 15 years in age.
Deepwater Horizon NRDA 2011 ¹	Louisiana	—	—	•	—	—	—	—
Roberts 1991	Florida	Marsh creation	Table 10	•	—	—	—	Faunal use of a created <i>Spartina alterniflora</i> salt marsh.
Silliman et al. 2005, 2012	Louisiana	—	Table 2 (2005), Table S3 (2012)	•	•	•	•	—
Spicer 2007	Louisiana	—	—	•	—	—	—	—
Swamy et al. 2002	Connecticut	Hydrologic restoration	Table 5	•	•	•	•	Salt marsh recovery through restored tidal connection of formerly impounded sites.
Tong et al. 2013	Louisiana	Experimental	Table 1	•	•	•	•	Analysis of the effects of various levels of sediment slurry application on the restoration of vegetation and macroinvertebrates in a degraded <i>Spartina alterniflora</i> salt marsh.
Warren et al. 2002	Connecticut	Hydrologic restoration	Table 4	•	•	•	•	Salt marsh recovery through restored tidal connection of formerly impounded sites.
Zengel et al. 2014, 2015	Louisiana	—	Pers. comm.	•	—	—	—	—

¹ Assessment conducted in 2011 as part of the Deepwater Horizon Natural Resource Damage Assessment

response ratios were then natural log-transformed for subsequent meta-analyses. A $\ln(\text{RR})$ value of zero indicates that the density at the restored site is equal to its corresponding reference. Variance associated with each RR record was calculated using:

$$\text{Var}_{\ln\text{RR}} = \left(\frac{SE_{\text{Restored}}}{\text{Restored Mean} + 0.01} \right)^2 + \left(\frac{SE_{\text{Reference}}}{\text{Reference Mean} + 0.01} \right)^2 \quad (2)$$

where SE is the standard error associated with the respective mean. The inverse of the variance of each RR was used as the weight in the meta-analyses. Therefore, studies with higher replication and lower variance were weighted more heavily in the meta-analysis because they provide a more precise estimate of the population effect size. A random effects meta-analysis was performed using a linear mixed model with random effects of source and record within source, a fixed effect of categorical age at sampling (age bin), and weights equal to the inverses of the variances of the natural log-transformed response ratios using SAS v9.4 (SAS Institute, Cary, NC). Denominator degrees of freedom were adjusted using the Kenward-Roger method (Kenward and Roger 1997). Random effects were tested using likelihood ratio tests (χ^2 with one degree of freedom). The assumption of normality was reviewed using the conditional residuals from the fitted model. Hypothesis testing was conducted by testing whether the mean $\ln(\text{RR})$ for a given time point (age) differed from zero, i.e., whether the restored density was equivalent to that found at the reference site. The Tukey-Kramer method (Tukey 1953; Kramer 1956) of controlling the family-wise error rate was used for the multiple comparisons.

Periwinkle and Amphipod Recovery and Life History

Progressive recovery of the taxa following restoration was evaluated using metrics of periwinkle densities and biomass additions (i.e., g m^{-2}) and amphipod densities (i.e., numbers m^{-2}). Periwinkles are a long-lived species with a lifespan that can exceed 10 years (Stiven and Hunter 1976), while amphipods are a shorter-lived species with a typical lifespan of 1 year or less (Sainte-Marie 1991). Given the periwinkle community does not fully turn over each year given the species' longevity, annual mortality, and growth were considered in quantifying recovery in terms of biomass gained per year in addition to the density estimates.

Because information on periwinkle density was compiled during the literature review, density numbers were converted to biomass using average biomass for each periwinkle age class and annual mortality to estimate growth and recovery of periwinkle biomass. Zengel et al. 2015 note that

periwinkles demonstrate three post-larval age classes based on shell length: juveniles, sub-adults, and adults. We estimated an average adult whole wet weight biomass (tissue and shell) of 2 g per individual based on species-specific von Bertalanffy (Quinn and Deriso 1999) and power law growth models (Powers and Scyphers 2016). Using a linear relationship between average shell length and adult biomass, whole wet weights of 1.125 g and 0.125 g per individual were estimated for sub-adults and juveniles, respectively. Based on these relationships, each new juvenile adds 0.125 g, conversion of a juvenile to sub-adult adds 1 g, and transition of a sub-adult to adult adds 0.875 g to the marsh surface. The sum of the new biomass contributions from each of the three components (juvenile recruitment, transition of juvenile to sub-adult and transition of sub-adult to adult) represents the addition of periwinkle biomass to the marsh surface each year.

Most reported marsh densities of periwinkles represent the sub-adult and adult populations (Zengel et al. 2015). To estimate the number of juveniles in the marsh, a survivorship model was used to estimate a steady-state ratio of adult:sub-adult:juvenile. Specifically, an age class survivorship curve (Powers and Scyphers 2016) based on a natural mortality of 0.422 year^{-1} (Hoenig 1983) was applied to an arbitrary initial periwinkle population to determine predicted numbers of the initial population in each year of the 10-year life expectancy. Age class ratios were determined based on the relationship between periwinkle numbers at age 0–1 (juveniles), age 1–2 (sub-adult), and ages 2–10 (adults) resulting in a steady-state adult:sub-adult:juvenile ratio of 1.9:1:1.2. The higher proportion of adults versus sub-adults and juveniles for this species is likely due to its relatively long life, whereby the adult life stage spans a much longer time period than the other two stages.

The age class ratios were used to determine juvenile recruitment necessary in each year to achieve the adult and sub-adult densities as predicted by the recovery trajectory and average reference density. The survivorship model was then applied to juvenile recruitment in each year to quantify the numbers that undergo a transition to an older age each year resulting in an increase in new biomass to the marsh surface. Application of the ratio of adults:sub-adults:juveniles to the recovery trajectory and average reference density assumed that the populations at the restored and reference marshes are at a steady state. While this may not always be the case, it was a necessary assumption to estimate the number of juvenile periwinkles in restored and reference marshes given the lack of data on juvenile periwinkle densities.

Amphipods have a life expectancy of approximately 1 year or less (Saint-Marie 1991). Therefore, restoration was calculated as the product of percent recovery in each year from the recovery trajectory and the amphipod density in reference marshes. Brood number and fecundity over the life of the amphipod were not considered in this analysis. The number of annual amphipod broods is not relevant to the development

of the recovery trajectory because the trajectory is based on measured amphipod densities in restored and reference sites at the same point in time.

Results

Periwinkle and Amphipod Reference Densities

A total of 372 observations (number of samples) from ten sources were used to determine a mean reference density of 41 ± 34 periwinkles m^{-2} (\pm standard deviation) in Louisiana salt marshes (Table 2). The age ratios (1.9:1:1.2 adult:sub-adult:juvenile) estimated above resulted in a steady-state reference population of 27 adults, 14 sub-adults, and 18 juveniles m^{-2} .

A weighted mean reference density of 1294 ± 3303 amphipods m^{-2} (\pm standard deviation) from 325 observations for salt marshes in the northern Gulf of Mexico was estimated from three literature sources (Table 2). Variability in the amphipod density was high and likely attributable to differences in reported taxa in the literature, natural and seasonal variability in the populations, and the quality of vegetation at the sampling site. In addition, the mean density was strongly influenced by a small number of high-density measurements. The influence of the high-density measurements is illustrated by comparing the weighted mean density of 1294 amphipods m^{-2} with the data set median density of 319 individuals m^{-2} .

Periwinkle Recovery

The literature review returned seven studies, representing 53 records for which response ratios were determined (Table 2). The records were obtained from restored marsh systems in North Carolina, South Carolina, Georgia, Florida, Mississippi, and Louisiana. The data spanned a range of 0–15 years post-restoration. The meta-analysis revealed that time since restoration had a significant effect on the response ratio.

Table 3 Results of the weighted random effects model with restoration site age as a fixed effect for periwinkles. Frequency represents the number of observations in each restoration site age bin. LS mean is the least

However, the frequency of records was unevenly distributed across the age bins. Specifically, 39 of the 53 records (74%) were in the first three age bins (0–1, 1–2, and 2–3 years), while only two age bins beyond the initial three had more than one record (Table 3). The modeled least square means indicated progressive recovery of periwinkle densities over the initial 3 years and potential recovery to reference marsh densities by age 4 (Table 3; Fig. 1). After the initial 4 years, recovery was variable and inconclusive, which may be due, in part, to the limited number of observations in these age bins.

As stated previously, the periwinkle reference density calculated based on reported field measurements likely represents the sub-adult and adult population. To determine juvenile recruitment over the first 4 years, the least square means response ratios were multiplied by the reference density of 41 ± 34 individuals m^{-2} to determine the number of sub-adults and adults present in the restored marsh. The number of juveniles recruited to the marsh surface was then determined according to the age class ratios discussed above. The survivorship curve was used to repopulate the marsh surface through year 20 (Fig. 2). Based on the survivorship curve, a steady-state for juvenile recruitment, transition of juveniles to sub-adults, and transition of sub-adults to adults occurs in year 6.

As stated above, new biomass is gained through recruitment of juveniles or growth of existing individuals, which for the purpose of this analysis, is characterized by the transition of juveniles to sub-adults and transition of sub-adults to adults. Based on the biomass gained through each phase, annual addition of periwinkle biomass to the restored marsh surface was low over the initial 3 years as indicated by the low response ratios and low number of transitions to sub-adults and adults. In years 4 (5 g m^{-2}) and 5 (18 g m^{-2}), new biomass to the marsh surface increased because the number of juvenile recruits increased and there were subsequently more transitions of juveniles to sub-adults and sub-adults to adults. The maximum annual steady-state addition of biomass ($25 \text{ g m}^{-2} \text{ y}^{-1}$) occurs from years 6 to 20 (Fig. 2).

squares mean $\ln(\text{RR})$ and is reported with standard error. An alpha of 0.1 was used in the test for significance

Age bin	Frequency	LS mean $\ln(\text{RR})$	Standard error	d.f.	<i>t</i> value	<i>p</i> value ($\text{Pr} > t $)
0–1	15	−5.49	0.78	6.3	−6.99	0.0003
1–2	12	−4.31	0.85	7.5	−5.1	0.0011
2–3	12	−1.84	0.80	7.8	−2.29	0.0516
3–4	2	0.13	1.41	32.3	0.09	0.9294
4–5	1	−1.69	1.92	37.4	−0.88	0.3838
5–6	1	−4.56	1.97	42.4	−2.31	0.0258
6–7	7	−1.05	0.89	11.1	−1.17	0.2661
9–10	1	−3.94	2.43	43.0	−1.62	0.1119
12–13	1	−0.66	1.92	37.6	−0.35	0.7313
14–15	1	−0.58	1.93	38.8	−0.3	0.7641
Total	53	−3.61	0.37	52	−9.8	<0.0001



Fig. 1 Recovery trajectory for the periwinkle snail. Circles represent the least square means of the 1-year age bins and error bars represent standard error associated with the mean. The dashed line represents a $\ln(RR)$ of 0, which indicates statistical convergence of restored and reference density measurements

Amphipod Recovery

The literature search for studies characterizing temporal changes of amphipods in restored marshes returned five

studies representing 14 response ratio records (Table 2). The restored marshes were located in Connecticut, Louisiana, and Texas. The records were spread across nine 1-year age bins over a 21 year maximum post-restoration age. Only four age bins included more than one response ratio. In general, response ratios indicated lower amphipod densities at restored sites relative to reference. Given the large uncertainties in the model results, determining a response ratio at specific time intervals as indicated by the age bins was not appropriate (Table 4). The uncertainties were related to the low frequency of data in each age bin. The age effect was removed from the weighted random effects model to estimate an average least squares mean response ratio of 0.479 (standard error = 0.121) across all years, which compares well with a weighted mean response ratio of 0.514. The uniform response ratio was used to calculate a constant supply of 620 amphipods m^{-2} or 153 amphipods m^{-2} in each year from a reference mean density of 1294 individuals m^{-2} or median density of 319 individuals m^{-2} , respectively, in northern GOM salt marshes.

Fig. 2 a Periwinkle repopulation of the restored marsh surface for each age class (in units of individuals m^{-2}) using the recovery trajectory and survivorship model demonstrates slow but progressive recovery to reference densities after approximately a decade. **b** Annual addition of new periwinkle biomass ($g m^{-2}$) to the restored marsh surface for each age class. Annual new biomass addition is quantified by transitions of periwinkles to older age classes and not by aging of the adult population. Thus, new biomass addition peaks within a couple years of maximum juvenile recruitment to the marsh surface

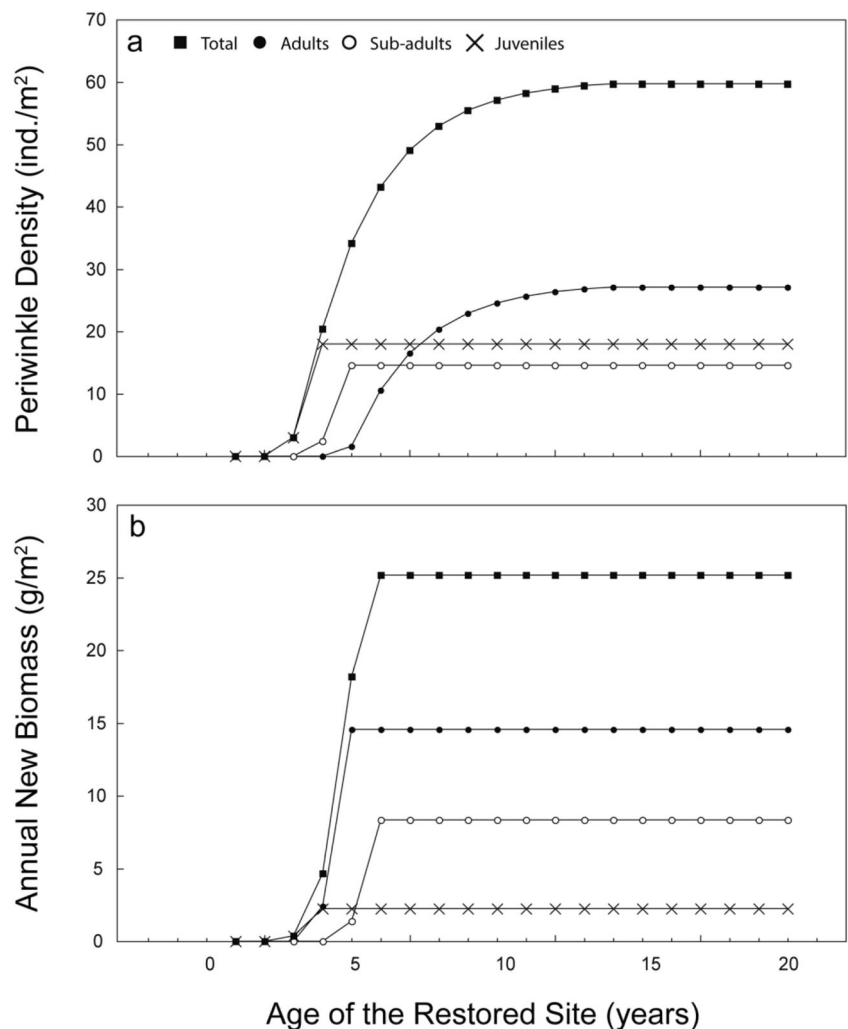


Table 4 Results of the weighted random effects model with age as a fixed effect for total amphipods. Frequency represents the number of observations in each age bin. LS mean is the least squares mean ln(RR) and is reported with standard error. An alpha of 0.1 was used in the test for significance

Age bin	Frequency	LS mean ln(RR)	Standard error	d.f.	<i>t</i> value	<i>p</i> value (Pr > <i>t</i>)
1–2	1	−1.39	3.20	5	−0.43	0.68
2–3	2	−5.45	2.26	5	−2.41	0.06
4–5	3	−0.68	1.85	5	−0.37	0.73
5–6	1	−1.01	3.20	5	−0.32	0.77
6–7	2	−3.82	2.26	5	−1.69	0.15
8–9	1	−0.72	3.20	5	−0.23	0.83
12–13	1	−0.72	3.20	5	−0.23	0.83
14–15	1	−2.33	3.20	5	−0.73	0.50
20–21	2	−0.37	2.26	5	−0.16	0.88
Total	14	−1.96	0.73	13	−2.69	0.02

Discussion

Recovery of Invertebrates and Salt Marsh Function

For periwinkles, recovery in terms of density was estimated to occur in year 4 when the mean restored marsh density converged with reference, or a natural log response ratio of zero (Table 3; Fig. 1). The slower rate of periwinkle recovery during the initial 3 years following restoration may reflect limited habitat suitability, enhanced predation, or both, during the early years of restoration project establishment. Periwinkles have a close association with *S. alterniflora* (Vaughn and Fisher 1992; Hutchens and Walters 2006; Kiehn and Morris 2009). As such, early periwinkle recruitment may be dependent on sufficient aboveground vegetation, which typically occurs within the first few years following restoration (Ebbets et al. in review, this issue). At the same time, lower vegetation cover in the initial years following restoration may also result in higher predation rates, limiting the recovery rate of the periwinkle population (Warren 1985; Silliman and Bertness 2002).

The periwinkle recovery trajectory provides information only on temporal changes in the population density of periwinkles but not age structure. The species is long-lived relative to the marsh ages in the recovery trajectory; therefore, it is unlikely that a steady-state population characteristic of natural marshes is achieved in 4 years even as periwinkle densities in restored marshes approach reference densities. Because this species does not turn over annually, we incorporated elements of natural mortality, age class ratios, and changes in biomass between age classes to grow the population through time and provide insight into how much new biomass is added to the restored marsh surface each year while conforming to the recovery trajectory. In this study, it is assumed that increases in net biomass occur through juvenile settlement in the marsh followed by transitions of juveniles to sub-adults and sub-adults to adults. While the approach is simplistic in the sense that biomass gain is not accounted for as adult periwinkles grow from year to year, adult snails grow little after age 5

and therefore add little additional biomass as they age (Powers and Scyphers 2016).

For the amphipod analysis, there are too few observations to develop annual response ratios over the entire marsh restoration age spectrum. Because of the data limitation, the habitat age effect (i.e., age bins) was removed from the recovery trajectory to increase the power of the meta-analysis. This results in a mean recovery of approximately 50% over the entire age range of restored marshes available in the dataset. Soil organic matter content and nutrients are slower to recover in restored marshes and can remain lower than reference values long after vegetation establishment, which can limit production of infauna (Cammen 1975, 1976; Sacco et al. 1994; Craft et al. 1988; Minello and Zimmerman 1992; Schrama et al. 2012). Craft et al. (1988) estimated that macroorganic matter nutrient pools can approximate natural marshes 15 to 30 years following restoration. Further, Schrama et al. (2012) observed late succession emergence of nutrient cycling macrodetritivores, specifically the amphipod *Orchestia gammarellus* as the dominant species in total faunal biomass, decades after restoration in a Netherlands salt marsh. Slow development of nutrient pools and other soil metrics is supported by a literature synthesis and similar meta-analysis (Ebbets et al. in review, this issue), which may explain the slow and partial recovery of the amphipod community in restored marshes. Further, another meta-analysis found lower densities of more mobile crustaceans such as penaeid shrimp and mud crabs in restored sites compared to natural marshes a decade or more after restoration (Hollweg et al. in review, this issue).

The results of the periwinkle and amphipod recovery analyses suggest that while marsh hydrology and vegetation may establish within the first few years of marsh creation or restoration (Cammen 1976; Sacco et al. 1994; Minello and Zimmerman 1992; Schrama et al. 2012), the invertebrate community may take longer to approximate reference conditions. Given that these invertebrates serve as important prey species for larger fauna that utilize the marsh and also play an important role in enhancing nutrient cycling, the lag in recovery of

these fauna suggests that certain marsh functions may be slower to recover than others. Specifically, while a relatively young created marsh may have sufficient vegetation to provide sheltering habitat functions, it may have lower overall food provisioning and nutrient cycling functions due to lower abundance of the marsh invertebrates that contribute to these developing functions.

Uncertainties

The objective of this study is to develop information on the response of biological metrics to restoration using meta-analysis. The estimation of recovery critically depends on ecological input data and assumptions (Strange et al. 2002). The recovery trajectory meta-analysis is informed by response ratio data from paired restored and reference marsh sites, which was limited for both periwinkles and amphipods. The following section discusses the caveats and uncertainties associated with the results of the meta-analyses and the variability of the data used in the development of the recovery estimates.

There is considerable variability in the data used to calculate the reference densities for both taxa. For periwinkles, density observations range from 0 to nearly 300 individuals m^{-2} , variability which is captured in a weighted standard deviation that is 84% of the mean. Amphipods densities range from three to more than 28,000 individuals m^{-2} leading to a standard deviation that is greater than the mean. Some of this uncertainty can be explained by natural spatial variability in periwinkle and amphipod populations across and within marsh systems while some may be explained by variability in study objectives and the sampling design used to estimate densities (Van Dolah 1978; Kneib 1984; Covi and Kneib 1995; Hutchins and Walters 2006). For instance, marsh position (e.g., distance from the marsh edge and elevation) can influence animal use, as most fauna tend to aggregate near the edge (Subrahmanyam et al. 1976; Minello et al. 1994; Minello, 2000). An additional potential contributor to reference density variability relates to the reporting of amphipod species. For this analysis, total amphipod densities were used; however, these estimates represent the taxa quantified in the respective study. Studies reported on different amphipod taxa and at different taxonomic levels. The lack of a standardized suite of species likely has a large effect on the mean total amphipod density and associated uncertainty here.

Grouping all amphipod species may also fail to capture any changes in the amphipod community that may occur over time as a restoration project matures. Amphipod species have different habitat preferences and feeding patterns, which could result in changes in species dominance over time that are not captured by total amphipod density (Kneib 1982; Best and Stachowicz 2014). While the total amphipod density metric does not account for potential species-level trends, grouping amphipods was necessary for this study due to the data

limitations. Likewise, combining data from the GoM and US Atlantic coasts likely introduced additional variability to the datasets. In the future as more data become available, it would be preferable to develop region-specific reference densities.

Other Considerations and Influences on Invertebrate Recovery

The recovery of periwinkles and amphipods in a restored marsh may be related to other factors aside from marsh age (Minello and Webb 1997). Hydrology is a defining characteristic of coastal wetlands and is an important influence on faunal use, including both periwinkles and amphipods (Minello et al. 1994). In comparison with natural *S. alterniflora* marshes, created marshes of Galveston Bay, Texas, were consistently higher in elevation and more irregularly flooded, thus exhibited lower nekton use due to restricted access to the marsh surface (Minello and Webb 1997). Restriction in tidal flooding of a restored marsh could reduce periwinkle recruitment or amphipod transport and result in reduced recovery for these invertebrates compared to restoration projects where tidal flooding has been fully restored. Differences in how restoration projects are designed could therefore influence the measured recovery of marsh fauna and contribute to the variability observed in this study. To the extent feasible, marsh restoration project design should consider the habitat needs and accessibility of the created marsh for the variety of faunal species that utilize natural marshes. A restoration project designed to benefit fauna should consider a suite of species or species groups, incorporate heterogeneity of elevation to create sub-habitats, and include sufficient channeling to provide critical edge zone habitat within the marsh. Further, collocation of restoration sites with or near a natural marsh should increase, for example, the dispersal probability of planktonic larvae and allow for easier migration of fauna to the newly created marsh.

Conclusion

Periwinkles and amphipods represent important taxa in the marsh ecosystem as consumers and as prey items in ecologically and economically valuable food webs. The methodology presented here represents a framework to estimate how these indicator species of marsh health develop following restoration despite limited data. Meta-analysis is a powerful tool to analyze data compiled from many different sources; however, in practice, restoration and reference site data used to inform these types of simplistic models should be as representative as possible of a potential candidate restoration or study site. Reference conditions and rate of recovery following a habitat disturbance or restoration project are likely unique to the

habitat. Therefore, consideration should be given to the tradeoffs between quantity and quality of the data used.

Aside from providing valuable insight into the development of important marsh species, the results presented here can also be used in REA framework. Fricano et al. (in review, this issue) uses the estimates developed here, along with other information on marsh development, to quantify anticipated restoration benefits of a generic marsh restoration project in coastal Louisiana. Together with related studies on the recovery of other marsh resources, this analysis provides a quantitative understanding of the ecological benefits associated with marsh restoration. It can also help inform marsh restoration efforts in the coming years intended to recover natural resource losses from the 2010 *Deepwater Horizon* incident.

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