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Recovery of planktonic invertebrate communities in restored and created tidal marshes along the northern Gulf of Mexico

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ABSTRACT

A significant amount of tidal marsh restoration has occurred over the past two decades. However, restored marshes often fail to recover biological structure and ecosystem functions comparable to reference marshes. We implemented a 13-site inventory to evaluate the recovery of zooplankton and meroplankton abundance and community composition along the Mississippi and Alabama Gulf coasts. Understanding the recovery of zooplankton and meroplankton communities in restored marshes is critical, as many planktonic invertebrate species contribute to nutrient cycling and food web dynamics. We found that zooplankton and meroplankton communities in restored tidal marshes were comparable in total abundance, taxonomic richness, and taxonomic composition to communities observed in reference tidal marshes — with composition being driven mainly by surface water salinity. But zooplankton and meroplankton communities in restored marshes did have lower evenness and diversity than comparable reference marshes. These results suggest that zooplankton and meroplankton communities in restored marshes along the Mississippi and Alabama Gulf coast tend to recover after 7–34 years and support robust populations of prey items for larger, ecologically and economically-important species (e.g., fishes).

Introduction

Anthropogenic activities and global change threaten coastal wetland habitats and have resulted in an estimated loss of 50% of the world's coastal wetland habitat in the past 50 years (Mitsch and Gosselink, 1993; Duarte et al., 2013; Kirwan and Megonigal, 2013). This loss is especially problematic since coastal wetlands, such as tidal marshes, are some of the most productive ecosystems on earth and provide important ecosystem services, including supporting biodiversity of fishery and non-fishery species, improving water quality, providing flood abatement, and facilitating carbon management (Barbier et al., 2011; Zedler and Kercher, 2005).

To counteract the loss of coastal wetland habitat, and concurrent loss of ecosystem services, Section 404 of the Clean Water Act (CWA) in the United States requires that compensatory wetland mitigation (i.e., wetland restoration, establishment, or enhancement) occur when existing wetlands are damaged or destroyed. This requirement of the CWA, combined with expanded investment in coastal wetland restoration following the 2010 Deepwater Horizon incident, has led to a significant amount of coastal wetland restoration in the northern Gulf of Mexico (GOM) over the past two decades (Baumann et al., 2020).

The ecosystem services provided by restored and established (i.e., created) tidal marshes often fail to recover to levels observed in reference tidal marshes (Moreno-Mateos et al., 2012). For instance, populations of invertebrates often fail to achieve densities observed in reference marshes following restoration (Baumann et al., 2020; Moreno-Mateos et al., 2012; Craft, 2000). Restoration age; however, may influence invertebrate communities in restored marshes. Specifically, 'older' restorations tend to have more recovered invertebrate communities than 'younger' restorations (Moreno-Mateos et al., 2012).

Failure to establish invertebrate communities comparable to those in reference tidal marshes has multiple implications for the biological structure and ecosystem functions of restored and created (hereafter jointly referred to as 'restored') tidal marshes. First, several invertebrate species, especially those that burrow, are known to affect nutrient cycling in wetland soils (Baranov et al., 2016; Wang et al., 2010; Kristensen and Kostka, 2005). For example, burrowing crab communities increased the dissolved organic carbon (DOC) concentrations found in porewater extracted from soils in southern California tidal marshes

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(Walker et al., 2020). Second, aquatic invertebrates play critical roles in coastal wetland food webs — grazing on detritus and vegetation and serving as important prey resources for larger organisms like fishes and crabs (Kang et al., 2015; Parker et al., 2008). In fact, several commercially and recreationally important fish species, such as the red drum (*Sciaenops ocellatus*), rely on tidal marshes as feeding grounds, consuming a variety of macroinvertebrate species (Lellis-Dibble et al., 2008; Graff and Middleton, 2002).

Because aquatic invertebrates provide several important services, including being a vital food resource for larger ecologically and economically important species, it is essential that we understand the recovery and drivers of invertebrate community composition in restored tidal marshes. Aquatic invertebrates often recruit into tidal marshes as planktonic larvae before they settle onto the benthos and develop into their adult forms (Underwood and Fairweather, 1989). Additionally, the local composition of these aquatic invertebrate communities can depend on the local hydrology, such as surface water salinity (Bilkovic et al., 2012)—making it important to evaluate recovery in restored tidal marshes representing are range of natural salinities.

Here, we used passive collectors and vertical tows to evaluate the recovery and composition of planktonic invertebrate communities in ten restored tidal marshes relative to three reference tidal marshes along the northern GOM. Combining these distinct sampling methods (i.e., passive samplers and vertical tows), allowed us to evaluate the recovery of both meroplankton communities (i.e., zooplankton with both planktonic and benthic life stages) and the total zooplankton community. This approach is especially valuable because few studies have evaluated planktonic invertebrate recovery in the northern GOM.

Additionally, we explored how environmental conditions (i.e., relative salinity, dominant wetland vegetation) and restoration strategy affect the composition of zooplankton and meroplankton communities in restored tidal marshes located along the northern GOM. Based on previous inventories of aquatic invertebrates in restored tidal marshes, we hypothesized that the diversity and abundance of planktonic invertebrate communities would be lower in restored marshes than in reference marshes (Baumann et al., 2020; Minello and Webb Jr, 1997; Minello and Zimmerman, 1992). We also expected the recovery of zooplankton and meroplankton abundance to increase with the age of restored tidal marshes (Baumann et al., 2020; Moreno-Mateos et al., 2012). Finally, we anticipated that surface water salinity would be the main factor underlying zooplankton and meroplankton community composition in restored tidal marsh sites (Bilkovic et al., 2012).

Past efforts to evaluate the recovery of invertebrate communities in the northern GOM have 1) focused on recovery in a single restoration site (Tong et al., 2013; LaSalle, 1996), 2) been geographically restricted to restored habitats on the Texas coastline (e.g., Galveston Bay, Texas; see Minello, 2000; Minello and Webb Jr, 1997; Minello and Zimmerman, 1992), or 3) used meta-analytic approaches that limited taxonomic resolution (Baumann et al., 2020). Additionally, studies of invertebrate recovery in restored tidal marshes often focus on benthic invertebrates (e.g., snails) in 'young' restorations (e.g., <5 years old). Thus, to our knowledge, this is the first empirical inventory of planktonic invertebrate communities across multiple restored tidal marshes, varying in surface water salinity and age, along the Mississippi-Alabama Gulf coast.

Methods

Site descriptions and marsh restoration

We used a series of 13 tidal marshes in coastal wetlands along the Alabama and Mississippi, USA coast to evaluate the diversity and composition of planktonic invertebrate communities in restored tidal marshes of the northern GOM (Fig. 1). Ten of these tidal marshes had brackish surface waters ranging in salinity from 2 to 13 ppt (Table 1). The additional three marshes had fresh surface waters with a salinity of 0.1 ppt (Table 1). All tidal marsh sites were exposed to meteorologically influenced, diurnal micro tides with a maximum amplitude of 0.8 m (Schroeder et al., 2014).

Our 13 tidal marshes were mainly nested within three watersheds along the Mississippi and Alabama coastlines. Three marshes, one natural (Fowl River Natural) and two restored (Fowl River CON-1 and CON-2), were clustered along the West Fowl River (30°21′59.5″N, 88°09′33.2″W) on the western side of Mobile Bay. One natural (Grand Bay Natural) and one restored (Grand Bay Restored) marsh were located approximately 0.5 km from the mouth of Bayou Heron inside the Grand Bay National Estuarine Research Reserve (30°24′43.6″N, 88°24′19.1″W). Finally, one natural (Weeks Bay Natural) and two restored marshes (Weeks Bay Restored and Magnolia Springs) were in Weeks Bay, located on the eastern side of Mobile Bay (30°23′49.2″N 87°49′42.3″W).

Five restored marshes were located outside of these three main waterways: Perdido Beach, Helen Wood Park, Deer Island 1, Deer Island 2, and Greenwood Island. Perdido Beach is a small brackish marsh along Perdido Bay, east of Mobile Bay (30°20′28.5″N, 87°29′56.6″W). Helen Wood Park is a brackish marsh along the western coast of Mobile Bay near the mouth of Dog River (30°34′11.5″N, 88°05′06.9″W). Deer Island 1, Deer Island 2, and Greenwood Island are open-coast marshes lo-

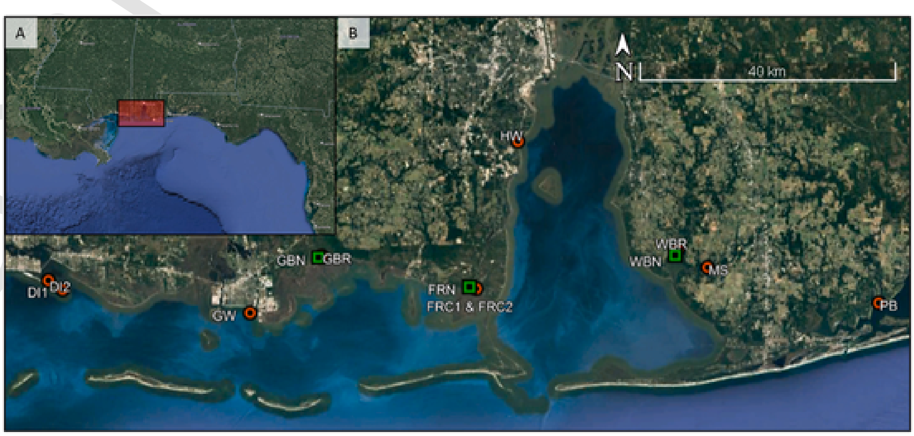

Fig. 1. Location of the study sites along the Mississippi and Alabama Gulf coast. A) Represents the broad geographic region included in the study and B) represents the individual locations of tidal marshes included in the study. Restored tidal marshes are marked with orange circles. Natural, reference tidal marshes are marked with green squares. Marsh abbreviations: DI1 Deer Island 1, DI2 Deer Island 2, FRC1 Fowl River CON1, FRC2 Fowl River CON-2, FRN Fowl River Natural, GBN Grand Bay Natural, GBR Grand Bay Restored, GW Greenwood Island, HW Helen Wood Park, MS Magnolia Springs, PB Perdido Beach, WBN Weeks Bay Natural, WBR Weeks Bay Restored. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Summary of restored tidal marsh characteristics and paired reference tidal marshes used to calculate planktonic invertebrate community recovery trajectories.

Restored tidal marsh	Age	Salinity (ppt)	Relative salinity	Dominant plant species	Restoration technique	Reference tidal marsh	Reference dominant plant species	Reference salinity (ppt)
Fowl River CON-1	34	4.6	Low brackish	*Juncus roemerianus*	Mitigation	Fowl River Natural	*Juncus roemerianus*	5.4
Fowl River CON-2	34	4.8	Low brackish	*Juncus roemerianus*	Mitigation	Fowl River Natural	*Juncus roemerianus*	5.4
Helen Wood Park	19	2.2	Low brackish	*Spartina alterniflora*	Living shoreline	Fowl River Natural	*Juncus roemerianus*	5.4
Deer Island 1	7	10.7	High brackish	*Spartina patens*	Beneficial use	Grand Bay Natural	*Juncus roemerianus*	6.0
Deer Island 2	19	9.61	High brackish	*Spartina alterniflora*	Beneficial use	Grand Bay Natural	*Juncus roemerianus*	6.0
Greenwood Island	14	13.3	High brackish	*Spartina alterniflora*	Beneficial use	Grand Bay Natural	*Juncus roemerianus*	6.0
Grand Bay Restored	17	6.5	Low brackish	*Juncus roemerianus*	Living shoreline	Grand Bay Natural	*Juncus roemerianus*	6.0
Perdido Beach	7	6.9	Low brackish	*Juncus roemerianus*	Living shoreline	Grand Bay Natural	*Juncus roemerianus*	6.0
Magnolia Springs	13	0.1	Fresh	*Juncus effusus*	Living shoreline	Weeks Bay Natural	*Juncus roemerianus*	0.1
Weeks Bay Restored	11	0.1	Fresh	*Juncus roemerianus*	Living shoreline	Weeks Bay Natural	*Juncus roemerianus*	0.1

cated west of Mobile Bay along the Mississippi coastline (Deer Island 1 and 2: 30°22′17.8″N, 88°50′07.5″W; Greenwood Island: 30°20′00.1″N, 88°31′00.7″W).

The ten restored tidal marshes included in our study were developed using three distinct strategies. The two restored tidal marshes along the West Fowl River (Fowl River CON-1 and CON-2) were created in the 1980's as mitigation efforts for a coal and grain facility by harvesting pine savanna habitat, excavating topsoil down to the water table to allow for hydrological connectivity with the West Fowl River, and planting the area with native marsh plants (Table 1; Vittor et al., 1987). Five of the restored tidal marshes were living shorelines (Grand Bay Restored, Helen Wood Park, Weeks Bay Restored, Magnolia Springs, Perdido Beach; Table 1) that range in age from 7 to 19 years old and are green infrastructure planted with native marsh plants. Finally, three of our restored tidal marshes were created 7–19 years ago by the Mississippi Department of Marine Resources through the beneficial use of dredge materials (Deer Island 1, Deer Island 2, and Greenwood Island; Table 1). Specifically, these beneficial use marshes were built by spreading dredge material to establish a marsh platform and allowing vegetation to naturally populate the site.

Most (n = 9) of our tidal marshes had plant communities dominated by native rushes in the genus *Juncus*. Eight of these marshes were composed mainly of *J. roemerianus* (a common species in oligohaline and brackish marshes of the northern GOM) and one was composed of *J. effusus* (a common species in oligohaline marshes of the GOM; Table 1). The remaining four marshes (Helen Wood Park, Deer Island 1, Deer Island 2, and Greenwood Island) had plant communities dominated by *Spartina alterniflora* and *S. patens* (Table 1), grasses common in brackish and saline marshes along the Atlantic and Gulf coasts. In our study, tidal marshes dominated by *Juncus* species were mainly oligohaline, while marshes dominated by *Spartina* species are mainly brackish. At all tidal marshes, dominant plant communities covered 30–95% of the marsh surface (Cherry *unpublished data*).

Invertebrate surveys

At all 13 tidal marshes we surveyed subtidal invertebrate communities using a combination of passive collectors and vertical plankton tows. We used passive collectors to target benthically-recruiting meroplankton communities (e.g., swimming crabs; Metcalf et al., 1995; Rakocinski et al., 2003). Vertical plankton tows were used to target the total zooplankton community, which are commonly monitored in restored tidal marshes to understand the availability of prey resources for higher trophic levels (Kimmerer et al., 2018). Both survey techniques were deployed in ~0.5 m of water at every marsh between July and August 2021. We sampled in the late summer since this is when the abundance of juvenile fishes, known to consume zooplankton communities in tidal marshes, peaks throughout Mobile Bay (Carassou et al., 2011).

Passive Collectors: We deployed three cylindrical passive hog's hair collectors at each tidal marsh site. Specifically, the collectors consisted of a 25 cm × 20 cm piece of hog's hair (Rheem Dust & Pollen High Performance Indoor Air Filter) zip tied around a 76 cm long PVC pipe with a 3.8 cm diameter. Passive hog's hair collectors have frequently and successfully been used to monitor meroplankton communities in tidal habitats (Metcalf et al., 1995; Rakocinski et al., 2003). We deployed the passive collectors in the shallow subtidal adjacent to the tidal marsh platform by inserting the sampler's PVC into the soil until only the portion covered by the hog's hair was above the soil. This standardized the portion of the water column that interacted with our passive samplers across tidal marsh sites— the bottom 25 cm of the water column. We chose this orientation to maximize the colonization of our passive collectors by both intertidal and subtidal meroplankton. While our sample size of three collectors per marsh is small, past studies using passive hog's hair collectors have suggested that three replicates is sufficient to characterize recruiting meroplankton communities (Metcalf et al., 1995).

Passive collectors were deployed in July 2021 and were collected two weeks later in August 2021. Upon collection, we placed each individual passive collector in a 1 L glass mason jar filled with 70% ethanol. Collectors remained preserved in 70% ethanol until they were processed by rinsing the hog's hair filter with 70% ethanol for 5 min, with the rinse ethanol and storage ethanol from the mason jar collected in a 33 cm × 23 cm glass pan with a 1 cm × 1 cm grid on the bottom. We let the ethanol in the glass pan settle for 5 min before we scanned the pan for any macroinvertebrates (e.g., snails, juvenile crabs, shrimp). When macroinvertebrates were found, they were identified to the lowest taxonomic group possible using a standard key (Heard, 1982), counted, and removed from the sample at this time. We then surveyed the remaining ethanol for microinvertebrates by randomly sampling at least three, 1 cm^2 grids in the glass pan for identification. We sampled more than three grid samples if the third subsample included two or more taxa that had not previously been observed on the collector. All microinvertebrates were identified under a dissecting microscope to the lowest taxonomic group possible using a standard key (Heard, 1982). After identification, proportions of each taxonomic group in the subsamples were extrapolated to total density of each taxon per m^2.

Vertical Tows: To compare the meroplankton composition on the passive collectors to that available in the zooplankton, we conducted three vertical tows at each site in August 2021. Each vertical tow was conducted in habitat adjacent to the passive collectors [depth = 0.3–0.8 m; volume = 2.4 ± 0.2 L (mean ± 1SE)] using a plankton net with a 30 cm diameter opening and 80 μm Nitex Nylon mesh. Tow volume differed slightly between marshes because marshes varied in their local hydrology. However, zooplankton abundance and diversity were unaffected by tow volume (Table S1). Samples were preserved in 70% ethanol until processed in the laboratory. We chose to use vertical tows, rather than horizontal tows, because we wanted to sample the same section of the water column that was in contact with our passive collectors to facilitate comparisons of these distinct datasets.

We processed all vertical tows by emptying the full sample into a 33 cm × 23 cm glass pan with a 1 cm × 1 cm grid on the bottom. We let the sample in the glass pan settle for 5 min before we randomly sampled at least three, 1 cm ^{2} grids in the glass pan for species composition and density. We sampled more than three grid samples if the third subsample included two or more taxa that had not previously been observed in the sample. We identified all organisms to the lowest taxonomic group possible using a dissecting microscope and a standard key for the northern GOM (Heard, 1982). After identification, proportions of each taxonomic group in the subsamples were extrapolated to total density of each taxon per m^3.

Statistical analysis

Recovery trajectories: We calculated the total abundance, species richness, species evenness, and Shannon Index of zooplankton and meroplankton communities observed on each passive collector (n = 3) and in each vertical tow (n = 3) collected at every tidal marsh site. Species richness was calculated using the Margalef index, species evenness was calculated using Pielou's evenness index, and Shannon Index was calculated using a log base 'e' (Margalef, 1958; Pielou, 1966). We had to exclude one of the 10 restored sites (Helen Wood Park) from our passive collector dataset because two of the collectors deployed at this site were damaged.

To evaluate the recovery of invertebrate communities in tidal marshes along the northern GOM, we calculated the recovery trajectories of planktonic invertebrate total abundance, species richness, species evenness, and Shannon Index using the approach described by Moreno-Mateos et al. (2012). Prior to the analysis, we paired all restored tidal marshes with the most comparable reference tidal marsh sampled. Pairings were based on the relative surface water salinity (Table 1). We chose to group reference and restored tidal marshes based on surface water salinity because prior studies indicated that salinity influences invertebrate community structure (see Bilkovic et al., 2012). We obtained response ratios for all diversity indices at each restored tidal marsh site using the equation:

$$\ln\left(\frac{Xrest + 1}{Xref + 1}\right)$$

Xrest is the mean value observed in the restored marsh and *Xref* is the mean value observed in the reference marsh (Millenium Ecosystem Assessment, 2005; Moreno-Mateos et al., 2012). The value "1" was added to the numerator and denominator to avoid zeros (Moreno-Mateos et al., 2012). Positive response ratios thus indicate that restored marsh zooplankton and meroplankton communities outperform reference marsh communities, while negative response ratios indicate that restored marsh zooplankton and meroplankton communities lag reference marsh communities. We chose to calculate the response ratio, rather than directly compare diversity indices between restored and reference tidal marshes, because salinity can affect the diversity of marsh planktonic invertebrate communities (Brock et al., 2005) — making direct comparisons between fresh and brackish tidal marshes problematic.

We evaluated if the response ratios calculated for each diversity index (i.e., total abundance, species richness, species evenness, and Shannon Index) were different from zero, indicating that planktonic invertebrate communities in restored marshes deviate from those in reference marshes, using a series of Wilcoxon Rank tests. Additionally, to compare our findings with past studies (i.e., Baumann et al., 2020; Moreno-Mateos et al., 2012), we evaluated the impacts of restored marsh age on the response ratios of total invertebrate abundance in each of our datasets (passive collectors and vertical tows) using Pearson's r correlations. Wilcoxon Rank tests and Pearson's r correlations were run in Jamovi version 1.8. (The Jamovi Project, 2021; R Core Team, 2021).

Community composition: We compared the taxonomic composition of planktonic invertebrate communities between restored marshes and reference marshes using nonparametric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM). We chose this approach because our abundance data was based on counts that were not normally-distributed and were zero-inflated. The ANOSIM was based on a similarity matrix built using square-root transformed Bray-Curtis coefficients of species counts that were standardized by the total invertebrate abundance at each site. We evaluated the significance of our ANOSIMs using a threshold p-value of $p \leq 0.05$. If the *R* value was ≥ 0.50, we assumed that the model captured significant differences between invertebrate communities in restored and reference sites (Clarke and Warwick, 2001). Additionally, we employed SIMPER analysis (similarity percentages procedure) using the same Bray-Curtis similarity matrix as our ANOSIM analysis to identify which taxa were driving dissimilarity of planktonic invertebrate communities in restored and reference tidal marshes.

To further evaluate the factors driving planktonic invertebrate community composition in restored tidal marshes, we ran additional NMDS and ANOSIM analyses evaluating the impacts of 1) surface water salinity (Fresh, Low brackish, or High brackish), 2) dominant vegetation type (*Juncus* or *Spartina*), and 3) restoration or creation strategy implemented (Beneficial use, Mitigation, or Living Shoreline) on the ten restored tidal marshes in our dataset. We classified sites as fresh/oligohaline if their salinity was below 1.5 ppt, low brackish if their salinity was 1.5–7 ppt, and high brackish if their salinity was above 7 ppt. We chose to bin our sites, rather than consider salinity as a continuous variable, because our site salinities clearly fell into three distinct groupings. Additionally, we classified tidal marshes dominated by *J. roemerianus* and *J. effusus* as *Juncus* since both species are indicative of fresh and 'low brackish' tidal marshes in the GOM. Additionally, we classified tidal marshes dominated by *S. alterniflora* and *S. patens* as *Spartina* because both species are indicative of brackish and saline tidal marshes in the GOM.

Each ANOSIM was based on a similarity matrix built using square-root transformed Bray-Curtis coefficients of species counts that were standardized by the total invertebrate abundance at each tidal marsh. We evaluated the significance of our ANOSIMs using the same criteria previously outlined and used SIMPER analyses (based on Bray-Curtis similarity matrices) to understand taxon dissimilarity. All NMDS, ANOSIM, and SIMPER analyses were performed using PRIMER 7 software (Clarke and Gorley, 2015).

Results

Based on absolute and extrapolated counts, passive collectors captured 760,297 meroplankton (Table S2). The most abundant taxa collected on the passive collectors were Branchiopoda (19%), Ostracoda (18%), and Malacostraca (17%). Similarly, our vertical tows collected 780,365 total zooplankton (Table S3), most of which were crustation nauplii (54%) and rotifers in the family Asplanchnidae (24%).

Recovery trajectories of planktonic invertebrate communities in restored marshes

The total abundance of planktonic invertebrates on passive collectors and in vertical tows was greater in restored marshes than in reference marshes (passive collector: W = 45.0, p = 0.004; vertical tow: W = 53.0, p = 0.006; Fig. 2A and B). In fact, all restored marshes had greater abundances of zooplankton and meroplankton than their paired reference sites (indicated by positive response ratios) except Perdido Beach, which had a lower abundance of zooplankton in its vertical tows than its paired reference marsh (Grand Bay Natural).

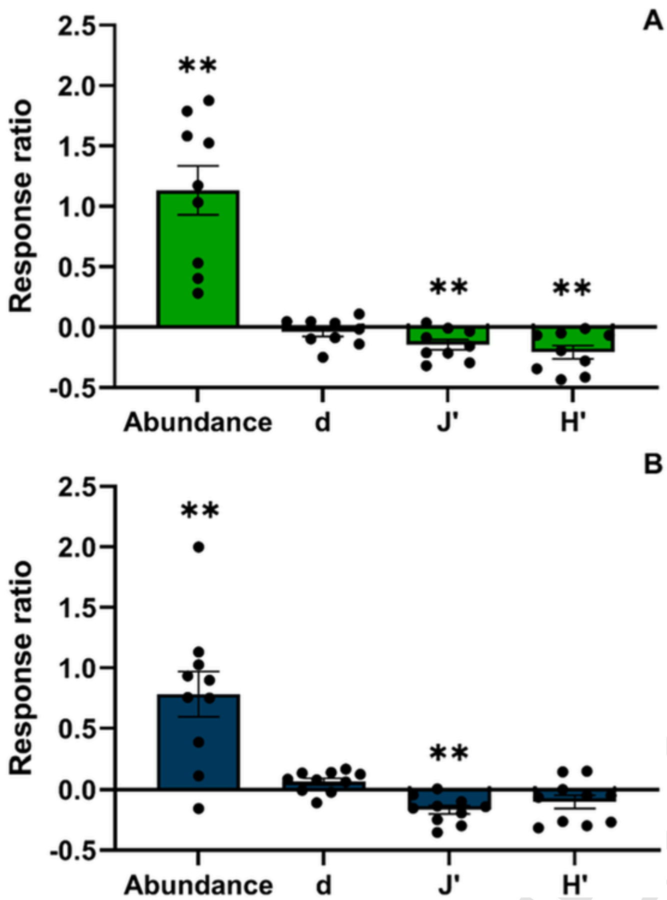

Fig. 2. Response ratios (mean ± 1SE) representing recovery trajectories of diversity indices (d represents species richness, J′ represents species evenness, and H′ represents the Shannon Index) for **A)** meroplankton communities settled on passive collectors and **B)** zooplankton communities in vertical tows along the Mississippi and Alabama Gulf coasts. Asterisks (**) represent response ratios are significantly different from 0 (i.e., restored marshes are different than reference marshes) at α = 0.05.

Zooplankton and meroplankton communities in restored marshes have developed similar species richness (passive collector: W = 16.0, p = 0.496; vertical tow: W = 46.0, p = 0.064; Fig. 2A and B) to reference tidal marshes. However, planktonic invertebrate communities in restored tidal marshes were less even (passive collector: W = 3.0, p = 0.020; vertical tow: W = 1.0, p = 0.004) and tended to have lower Shannon indices (passive collector: W = 0.0, p = 0.004; vertical tow: W = 12.0, p = 0.131) than their reference marsh sites (Fig. 2A and B). Only a single restored tidal marsh in the passive sampler dataset (i.e., Fowl River CON-2) and vertical tow dataset (i.e., Weeks Bay Restored) had greater community evenness than its paired reference site. Additionally, only three sites (Greenwood Island, Perdido Beach, and Weeks Bay Restored), all in the vertical tow dataset, had Shannon indices greater than their reference sites.

We observed no effect of restored tidal marsh age on the response ratios for total planktonic invertebrate abundance (passive collectors: r = 0.284, p = 0.459; vertical tows: r = 0.292, p = 0.413), possibly due to our sites being relatively older (7–34 years old, mean age = 17.5 years old; Fig. 3).

Planktonic invertebrate community composition in restored versus reference marshes

The composition of planktonic invertebrate communities found on passive collectors and in vertical tows were similar between restored

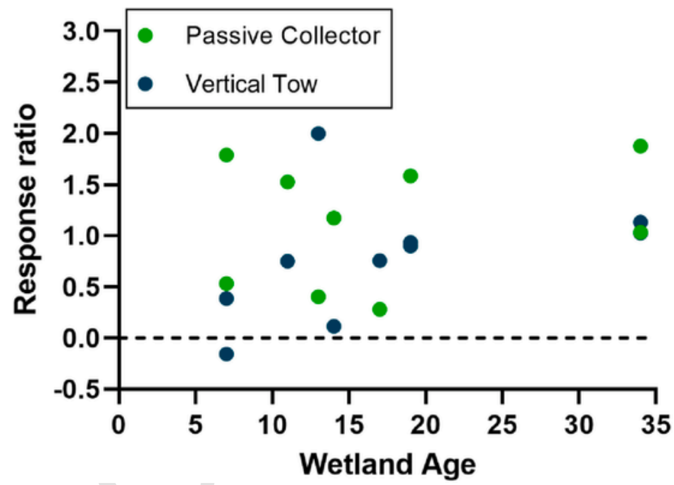

Fig. 3. Relationship between response ratios of planktonic invertebrate total abundance on passive collectors (green) and in vertical tows (blue) and the age of the restoration site. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

tidal marshes and reference marshes along the Alabama and Mississippi Gulf coast (passive collector: $R^2 = -0.149$, p = 0.850; vertical tow: $R^2 = 0.185$, p = 0.143; Fig. 4A and B).

Factors affecting planktonic invertebrate community composition in restored marshes

The dominant plant species in restored marshes did affect the composition of meroplankton communities on passive collectors ($R^2 = 0.420$, p = 0.036; Fig. S1). However, since we had to exclude Helen Wood Park from the passive collector dataset (two collectors were damaged), the dominant plant community at each site covaries entirely with surface water salinity. Specifically, all fresh and low brackish restored marshes were dominated by *Juncus* spp. and all high brackish restored marshes were dominated by *Spartina* spp.—suggesting that this pattern may be driven by differences in the surface water salinity at these sites. Dominant plant species did not affect the composition of the total zooplankton community in vertical tows ($R^2 = 0.103$, p = 0.219; Fig. S2) at restored marshes along the northern GOM.

Relative surface water salinity at restored tidal marshes affected the composition of meroplankton communities on passive collectors ($R^2 = 0.569$, p = 0.010; Fig. 5). The effect of surface water salinity was most apparent between restored marshes in fresh versus low brackish conditions ($R^2 = 0.679$, p = 0.067). The dissimilarity in passive collector meroplankton communities was mainly driven by the presence of large populations of Branchiopoda, Ostracoda, and Insecta (mainly in the family Chironomidae) in freshwater marshes and by populations of Copepoda, Thecostraca (mainly in the family Chthamalidae), and Malacostraca (mainly in the family Corophiidae) in low brackish marshes. Restored marshes in fresh and high brackish conditions also tended to differ in their meroplankton communities on passive collectors ($R^2 = 1.00$, p = 0.100); however, the small sample sizes of these groups (fresh: n = 2; high brackish: n = 3) likely prevented statistical significance. Meroplankton communities on passive collectors in high brackish and low brackish restored marshes were the most similar, since both were characterized by the presence of large populations of Malacostraca from the family Corophiidae.

Surface water salinity at restored tidal marshes also affected the composition of the total zooplankton community in vertical tows ($R^2 = 0.415$, p = 0.046; Fig. 6). This effect was most evident between fresh and low brackish marshes ($R^2 = 0.873$, p = 0.048). Dissimilarity between vertical tow zooplankton communities was driven mainly by

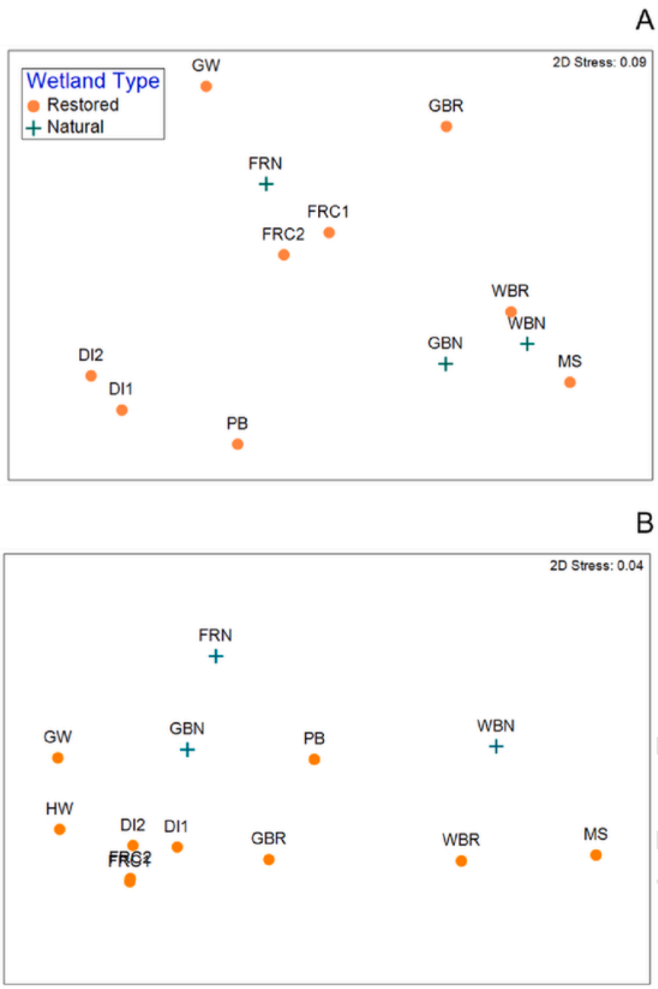

Fig. 4. Non-metric Multi-Dimensional Scaling (NMDS) ordinations of planktonic invertebrate communities **A)** on passive samplers and **B)** in vertical tows at restored (i.e., restored and created) and reference tidal marshes along the Mississippi and Alabama Gulf coasts. Marsh abbreviations: DI1 Deer Island 1, DI2 Deer Island 2, FRC1 Fowl River CON1, FRC2 Fowl River CON-2, FRN Fowl River Natural, GBN Grand Bay Natural, GBR Grand Bay Restored, GW Greenwood Island, HW Helen Wood Park, MS Magnolia Springs, PB Perdido Beach, WBN Weeks Bay Natural, WBR Weeks Bay Restored.

the presence of large populations of Monogononta (mainly in the families Asplanchnidae and Branchionidae) in freshwater marshes and by populations of Copepoda and crustacean nauplii in low brackish marshes. Restored marshes in fresh and high brackish conditions also tended to differ in the composition of the zooplankton community in vertical tows ($R^2 = 1.00$, $p = 0.100$); however, the small sample sizes of these groups (fresh: $n = 2$; high brackish: $n = 3$) likely prevented statistical significance. Zooplankton communities in vertical tows from high brackish and low brackish restored marshes were the most similar, both being defined by large populations of Copepoda and crustacean nauplii.

The composition of planktonic invertebrate communities within restored tidal marshes was unaffected by the restoration technique implemented for both our passive collector and vertical tow datasets (passive collector: $R^2 = 0.246$, $p = 0.140$; vertical tow: $R^2 = 0.023$, $p = 0.396$; Figs. S3–S4). However, this conclusion should be considered with caution since 1) the sample sizes for beneficial use ($n = 3$) and mitigation ($n = 2$) marshes were small, 2) restoration technique was confounded by relative salinity (Table 1), and 3) restored marshes in our dataset were relatively older (i.e., 7–34 years old).

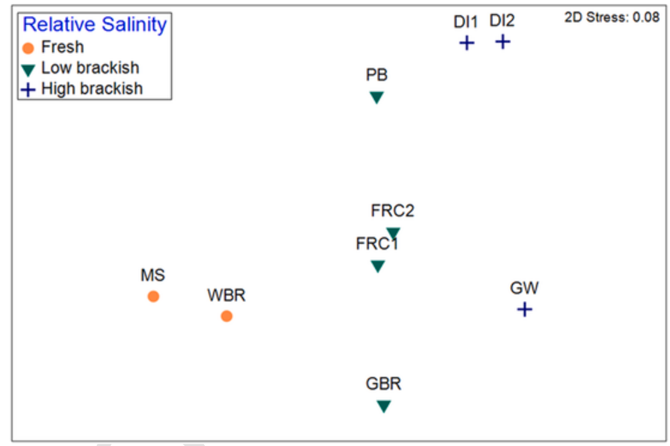

Fig. 5. Non-metric Multi-Dimensional Scaling (NMDS) ordinations of meroplankton communities on passive samplers at restored (i.e., restored and created) tidal marshes characterized by fresh, low brackish, and high brackish surface water salinity. Marsh abbreviations: DI1 Deer Island 1, DI2 Deer Island 2, FRC1 Fowl River CON1, FRC2 Fowl River CON-2, GBR Grand Bay Restored, GW Greenwood Island, MS Magnolia Springs, PB Perdido Beach, WBR Weeks Bay Restored.

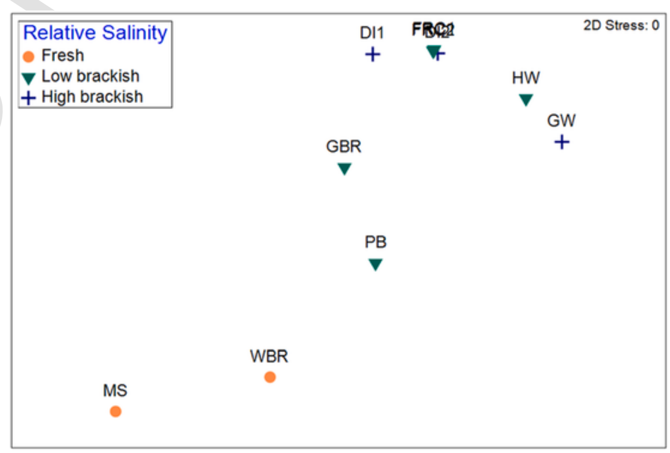

Fig. 6. Non-metric Multi-Dimensional Scaling (NMDS) ordinations of zooplankton communities in vertical tows at restored (i.e., restored and created) tidal marshes characterized by fresh, low brackish, and high brackish surface water salinity. Marsh abbreviations: DI1 Deer Island 1, DI2 Deer Island 2, FRC1 Fowl River CON1, FRC2 Fowl River CON-2, GBR Grand Bay Restored, GW Greenwood Island, HW Helen Wood Park, MS Magnolia Springs, PB Perdido Beach, WBR Weeks Bay Restored.

Discussion

Contrary to past studies (e.g., Baumann et al., 2020; Minello, 2000; Minello and Webb Jr, 1997; Minello and Zimmerman, 1992), zooplankton and meroplankton communities in restored tidal marshes had greater abundances and similar taxonomic richness to communities observed in reference tidal marshes. In fact, the meroplankton community (i.e., on passive collectors) and the total zooplankton community (i.e., in in vertical tows) at restored marshes had 2.5 and 3.4-times, respectively, the total planktonic invertebrate abundance observed in reference tidal marshes. Restored marshes did, however, have lower zooplankton and meroplankton community evenness and diversity (based on Shannon Index) than comparable reference marshes. Despite depressed evenness and diversity, the taxonomic composition of zooplankton and meroplankton communities was similar between restored marshes and reference marshes, with community composition in restored marshes being driven mainly by the local surface water salinity.

This suggests that tidal marsh restorations along the Mississippi-Alabama coastline tend to recover zooplankton and meroplankton communities after as little as 7 years.

The high abundances of zooplankton and meroplankton in restored marshes appear to be driven by large populations of single species at each site. For example, at Magnolia Springs and Weeks Bay Restored, two fresh marshes, we observed 11,783 and 33,050 *Daphnia* (i.e., Branchiopoda) individuals on passive collectors, respectively, while we only observed 1307 *Daphnia* individuals at the reference fresh marsh (i.e., Weeks Bay Natural; Table S1). Similarly, in meroplankton communities at low brackish and high brackish restored tidal marshes, we observed populations of Corophiidae (i.e., Malacostraca) that were 4–35-times larger than populations observed at the comparable reference low brackish and high brackish marshes (i.e., Fowl River Natural and Grand Bay Natural). Zooplankton communities in vertical tows also supported this trend. For instance, all restored tidal marshes had larger populations of crustacean nauplii than their relative reference marshes [restored marshes: 12,709 ± 1918 nauplius m^{-3} (mean ± 1SE); reference marshes: 3196 ± 1297 nauplius m^{-3}]. The dominance of restored tidal marsh zooplankton and meroplankton communities by single taxa suggests that restored marshes may differ functionally from reference marshes.

The dominance of restored marshes' planktonic invertebrate communities by large populations of a single taxa also explains why these sites had lower evenness and diversity than reference marshes. In fact, only a single restored site in each dataset (i.e., passive collectors and vertical tows) had a planktonic invertebrate community that was as even as the zooplankton community in their respective reference marsh. Lower community evenness in restored marshes could impact ecosystem services, such as the availability of prey species for ecologically and economically important species. For instance, if ecosystem services and functions are driven by the abundance of the dominant species, then lower community evenness may promote these ecosystem services (Hillebrand et al., 2008; Nijs and Roy, 2000). Given that the dominant taxon observed in restored tidal marshes along the Mississippi and Alabama Gulf coast were all common prey items of ecologically and economically-important species (Sperfeld et al., 2020; Mattila and Bonsdorff, 1989), it is possible that lower zooplankton and meroplankton community evenness may facilitate the nursery habitat functions of these restored marsh sites by allowing large populations of prey to persist (Gray et al., 2002).

Previous inventories of aquatic invertebrate abundance in restored marshes have commonly observed greater recovery in older restorations (Baumann et al., 2020; Moreno-Mateos et al., 2012). However, we found no relationship between restored marsh age and the recovery of planktonic invertebrate communities. This is likely because the restored marshes sampled in this study were relatively old, with ages ranging from 7 to 34 years old (mean age = 17.5 years old). In fact, several studies suggest that invertebrate communities in restored marshes begin to statistically converge with invertebrate communities in reference marshes after 4–10 years (Lu et al., 2021; Baumann et al., 2020; Moreno-Mateos et al., 2012). Our analysis further supports this observation since the taxonomic composition of zooplankton and meroplankton communities was similar between restored and reference tidal marshes in our datasets. This convergence is likely facilitated by the dispersal abilities of many zooplankton taxa, which can be moved to restored sites by other animals and flowing water (Figuerola et al., 2005, Levin and Talley, 2002).

While zooplankton and meroplankton communities in restored marshes were compositionally similar to those in reference marshes, we observed distinct zooplankton and meroplankton communities across our restored marsh sites. These differences were largely explained by marsh surface water salinity. Specifically, freshwater restored marshes were characterized by Branchiopoda, Ostracoda, and Monogononta, while low brackish and high brackish restored marshes were characterized by Copepoda, Malacostraca, Decapoda, and Thecostraca. The dominant marsh plant community also influenced the composition of meroplankton communities settling on passive collectors; however, since tidal marsh plant communities are shaped by local salinity, salinity is likely also underlying this relationship (Flynn et al., 1995; McKee and Mendelssohn, 1989; Bertness and Ellison, 1987). The finding that salinity structures meroplankton communities in restored marshes is not surprising, as past studies in natural marshes suggest that changes in surface water salinity can have direct consequences for benthic invertebrate community composition (Bilkovic et al., 2012; Brock et al., 2005; Holland et al., 1987). However, confirming that similar processes underlie zooplankton and meroplankton community composition in restored marshes allows for better predictions of restoration outcomes, especially regarding the ecosystem functions expected to develop at newly restored tidal marshes.

Zooplankton and meroplankton community composition was unaffected by the restoration technique implemented. However, this conclusion should be considered cautiously since our analysis included only a small group of older restored marshes that varied in local salinity. Previous studies have suggested that restoration technique may account for some of the variability in aquatic invertebrate recovery across restored marshes (Baumann et al., 2020), but there have been few empirical tests supporting this claim. Restoration technique should affect aquatic invertebrate recovery if restored marshes established via distinct techniques (e.g., living shorelines versus mitigation) develop organic matter at different rates, as many invertebrate communities are tied to marsh soil formation (Craft, 2000). However, this may be less important for the recovery of zooplankton and meroplankton than the recovery of benthic invertebrate communities. Thus, a valuable next step would be to rigorously evaluate the impacts of restoration techniques on organic matter development and aquatic invertebrate (including zooplankton and meroplankton) recovery in restored tidal marshes.

Our findings suggest that the composition and abundance of zooplankton and meroplankton communities recover after 7–34 years in restored tidal marshes along the Mississippi and Alabama Gulf coasts. Additionally, the composition of zooplankton and meroplankton communities in restored marshes depends mainly on the surface water salinity. Zooplankton and meroplankton community composition was unaffected by the restoration or creation technique implemented. However, all the restored marshes included in this study were hydrologically connected to rivers or bays that should facilitate zooplankton recruitment— which may not be the case for restored marshes with limited hydrological connection to natural waterways (for discussion of nearshore hydrology and invertebrate recruitment see Underwood and Fairweather, 1989). Together with the suite of other studies evaluating the recovery of invertebrate communities at single sites (Tong et al., 2013; LaSalle, 1996), on targeted taxa (Baumann et al., 2020), and in neighboring geographic regions (e.g., Galveston Bay, Texas; see Minello, 2000; Minello and Webb Jr, 1997; Minello and Zimmerman, 1992), this inventory provides robust predictions regarding the development and composition of zooplankton and meroplankton communities in restored tidal marshes. Predicting the composition of zooplankton communities at restoration sites is essential for restoration success, as restorations often aim to establish habitats with ample invertebrate prey resources for threatened and endangered species as well as locally-important fisheries.

Uncited References

CRediT authorship contribution statement

S. Rinehart : Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J.M. Dybiec :** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **E. Fromenthal :** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **T. Ledford :** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **B. Mortazavi :** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **J.A. Cherry :** Writing – review & editing, Software, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have no conflicts of interest to declare.

Data availability

Recovery of planktonic invertebrate communities in restored and created tidal marshes along the northern Gulf of Mexico. (Original data) (Dryad)

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108417.

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