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Nekton assemblage structure in natural and created marsh-edge habitats of the Guadalupe Estuary, Texas, USA

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Abstract

Natural and created *Spartina* brackish marsh habitats in the Guadalupe Estuary, adjacent to the Aransas National Wildlife Refuge, Texas, USA were surveyed during spring, summer, and fall 2004 to evaluate the equivalence of nekton assemblages in an old (>30 years) created marsh. During each season, six replicate samples were collected in each marsh type using a 1-m^2 drop sampler. Multivariate analysis revealed significant differences in nekton assemblage structure among marsh type, both within and across seasons. Species richness was significantly higher in the natural marsh in spring and summer but not in fall. Several species that were dominant in the natural marsh but rare or absent in the created marsh had strong correlations with the presence of oyster substrate that was only encountered in natural marsh samples. Although cumulative richness was greater in the natural marsh, eight species were collected only from the created marsh. Shrimp and fish biomass was significantly higher in natural marsh. Analysis of the density, biomass and size structure of three commercially important crustaceans indicated that the created marsh supported similar biomass of some species (white shrimp, blue crab); however, the size structure of some populations was variable among marshes (blue crab, brown shrimp). We conclude that lower substrate complexity (specifically oyster) and soil organic content in the created marsh reduced measures of nekton similarity and recommend that these features be addressed in future restoration efforts.

Keywords: decapod crustacean; dredge spoil; oyster; restoration; *Spartina alterniflora*; Gulf of Mexico; Texas

1. Introduction

Salt marshes along the Atlantic and Gulf coasts of the United States are productive environments that play significant roles in providing essential ecosystem services (Boesch and Turner, 1984; McIvor and Rozas, 1996; Kneib, 2003; Minello et al., 2003). Over 90% of the commercial fishery catches by weight for the southeastern Atlantic and Gulf coasts are comprised of estuarine-dependent species that rely on coastal wetlands for reproduction, nursery habitat, food resources and migration (Chambers, 1992). Many studies have demonstrated that *Spartina* marshes in Gulf of Mexico (GOM) estuaries support high densities of juvenile and adult fishes and decapod crustaceans (Zimmerman and Minello, 1984; Baltz et al., 1993; Rozas and Reed, 1993; Minello and Webb, 1997; Howe et al., 1999). In particular, vegetated marsh edge supports relatively higher densities of economically-valued species when compared with adjacent marsh habitats, such as inner marsh and nonvegetated marsh edge (Minello et al., 1991; Baltz et al., 1993; Peterson and Turner, 1994).

Natural marsh habitats have experienced extensive losses in total area over the past half-century due to coastal development and submergence (Mitsch and Gosselink, 2000). Marsh loss in GOM estuaries has triggered various restoration efforts including the intentional planting of *Spartina alterniflora* on deposits of dredge materials (Minello and Webb, 1997). Considerable controversy exists regarding the ability of dredge spoil marshes to duplicate natural habitats, and whether created marshes become more similar to natural marshes over time (Streever, 2000). For nekton (fish and decapod

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crustaceans), created marshes appear to provide a reduced support function (Minello and Zimmerman, 1992; Minello and Webb, 1997; Minello, 2000) and local factors such as variability in natural target assemblages may influence the time required for created marshes to reach equivalence with adjacent reference sites (Minello, 2000). Because restoration activities have occurred over a relatively short time period, few opportunities exist to examine long-term marsh development (Streever, 2000; Callaway, 2005). Callaway (2005) suggested that unintentional restorations can be used to assess marsh development over longer time periods and provide insight into what factors are limiting the development of created marshes.

We evaluated nekton assemblage structure in an old (>30 years) dredge spoil marsh that was unintentionally created during the construction of the Gulf Intra-Coastal Waterway (GIWW) through the Guadalupe Estuary, Texas. The objectives of our study were to: (1) compare species richness, assemblage structure and biomass of fish and decapod crustaceans (hereafter referred to as nekton) between the created marsh and an adjacent natural reference marsh across three seasons, (2) identify environmental variables and habitat features that may be limiting the development of created marsh nekton assemblages, and (3) compare abundance, biomass and size structure of three economically-valued crustacean species between the created and natural marsh across seasons. The created marsh was predicted to support similar nekton assemblages due to the long time period since marsh creation, and the null hypothesis tested for all response variables was no significant difference between created and natural marsh.

2. Methods

2.1. Study sites

Natural and created marshes were located in the Guadalupe Estuary, Texas, USA, adjacent to the Aransas National Wildlife Refuge (Fig. 1). The natural marsh (Sundown Island) was located in Sundown Bay (N 28°10′, W 96°52′) adjacent to the GIWW, a shipping channel maintained by the Army Corps of Engineers. The created marsh (northern Bludworth Island) was located in Mesquite Bay (N 28°10′, W 96°51′) adjacent to the GIWW, less than 1 km from the natural site (Fig. 1). Northern Bludworth Island historically contained natural marsh habitat however, disposal of dredge material during the construction of the GIWW in the early 1940s resulted in the conversion of marsh to upland habitat. Contained disposal of dredge spoil began in the early 1970s and colonization by marsh vegetation probably occurred after this period (Tom Stehn, United States Fish and Wildlife Service, personal communication).

Both marshes were characterized by a narrow (<3-m) band of *Spartina alterniflora* along the inter-tidal fringe with succulent halophytes dominating the high inter-tidal marsh plant assemblage. Widgeon-grass (*Ruppia maritima*) was encountered growing among the emergent vegetation of both marshes; however, its distribution was sparse and large clumps were rarely encountered. The substrate of Sundown Island was primarily composed of mud with patches of live oyster in the fringing vegetation, whereas Bludworth Island marsh substrate consisted primarily of sand and small (<10-cm) oyster shell fragments with areas of clay. Although live oyster was observed less than 25 m from the created marsh edge, clumps of live oyster were never encountered or observed within the vegetation fringing the created marsh. Mean tidal range over the study period was 11.7 cm.

2.2. Sampling procedures

Six replicate samples were collected at random locations within created and natural marsh sites during spring, summer, and fall 2004. Nekton was collected using a 1-m^2 drop sampler deployed from a boom mounted on a 5.1-m boat. For each sample, the boat and sampler were pushed from open water toward the marsh and the drop sampler was released when it was approximately 1 m inside the marsh–water interface. When the drop sampler failed to seal, the sample was abandoned and a new sample was initiated at a randomly chosen location at least 25 m from the abandoned sample. The sampler performed well over all substrates including clumps of live oyster, and no samples containing oyster were abandoned due to an incomplete seal.

Immediately following each drop, a suite of habitat variables was measured within the sampler. Temperature (°C), dissolved oxygen (mg l^{-1}), and salinity were measured using a YSI 85 handheld meter, and depth was recorded to the nearest centimeter. The presence or absence of live oyster substrate and attached *Ruppia maritima* was recorded, and all *Spartina alterniflora* stems (live and dead) were removed and counted. One 10-cm^3 soil core was collected for determination of percent soil organic content. Core samples were kept on ice following collection, returned to the laboratory, and frozen until analyzed. Nekton were removed from the sampler following the collection of habitat data. Three people conducted sweeps inside the drop sampler with 3.2-mm mesh dip nets until each person had conducted three consecutive sweeps that did not collect additional organisms.

All nekton were euthanized with MS-222, fixed in a 10% buffered formalin solution in the field, and transferred to 70% ethanol for storage. For each replicate sample, species were identified, counted, and weighed to the nearest 0.01 g. Three commercially important crustacean species (brown shrimp, *Farfantepenaeus aztecus*; white shrimp, *Litopenaeus setiferus*; and blue crab, *Callinectes sapidus*) were selected for analysis of size distributions. For these species, each individual was also measured to the nearest millimeter. Shrimp were measured from the tip of the rostrum to the end of the telson (total length), and carapace width was measured for blue crabs.

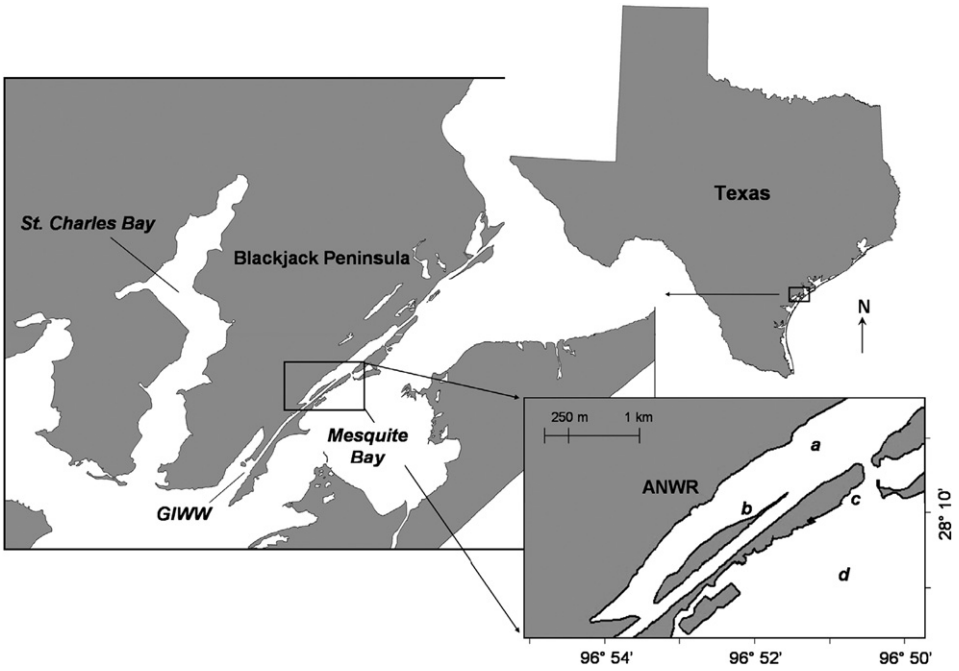

Fig. 1. Map depicting the location of the Guadalupe Estuary within Texas and the location of the natural and created marshes within the estuary. a, Sundown Bay; b, Sundown Island (natural marsh); c, northern Bludworth Island (created marsh); d, Mesquite Bay; ANWR, Aransas National Wildlife Refuge.

2.3. Data analysis

Rarefaction was used to estimate species richness in each marsh based on the total number of individuals collected in each season and to determine if the number of samples collected with the drop sampler was sufficient to characterize marsh nekton assemblages. Species richness (observed richness), abundance and biomass values for each replicate drop sample were used for statistical comparisons. Abundance and biomass values were log transformed $[\log_{10}(x+1)]$ and species richness was square root transformed prior to statistical analysis in order to meet the assumptions of parametric statistical procedures. Square root transformation was chosen for species richness because it performs well with count data (Zar, 1999). Normality was tested using the Martinez–Iglewicz test, and homogeneity of variance was tested using the modified Levene test. Transformed data met the assumptions of equal variance and normality and parametric procedures were used for statistical comparisons. Differences among marsh type were tested using repeated-measures analysis of variance (rmANOVA) where marsh type was the categorical variable and season was the repeated variable. Significance levels were adjusted using the Bonferroni algorithm to account for the use of response variables in multiple tests ($\alpha_{\text{adjusted}} = 0.017$). Differences in size distributions of the three crustacean species were tested using the Kolmogorov–Smirnov two-sample test where individuals from each marsh type were aggregated across seasons. Rarefaction curves were constructed using Eco Sim (Gotelli and Entsminger, 2006) and rmANOVA tests were performed using NCSS 2000 (Number Cruncher Statistical Systems, 2000).

Two-sample *t*-tests were performed to test for differences in environmental and habitat variables among marshes with the exception of categorical variables (oyster and sea grass presence/absence). To examine the relationship between environmental variables, richness and aggregate groupings of nekton, Pearson product moment correlations were calculated using Bonferroni corrected *P* values to adjust for multiple comparisons ($\alpha_{\text{adjusted}} = 0.003$). All environmental and habitat variables listed in Table 1 were included in the correlation analysis.

Correspondence analysis (CA) of the species-by-replicate matrix was used to examine variation in species relative abundances among marsh type and season. Multi-response permutation procedures (MRPP) were performed to test the null hypothesis of no difference in nekton assemblage structure between the natural and created marsh based on species relative abundances both within and among seasons. MRPP is a non-parametric technique used to test the significance of a priori sample groupings when the data violate the assumptions of parametric procedures such as multivariate analysis of variance. When significant sample groupings were detected, pairwise comparisons were made using Bonferroni corrected *P* values ($\alpha_{\text{adjusted}} = 0.004$).

Canonical correspondence analysis (CCA) was used to identify environmental variables and habitat features correlated with species relative abundances. This direct gradient technique ordinates species and sample scores along gradients of environmental variation. All habitat and environmental variables were included in the CCA (Table 1) but only significant, non-redundant variables were retained for interpretation. Rare species were down weighted in both CA and CCA to limit their influence in the ordinations. Both CA and CCA

Table 1
Means and standard errors of environmental variables measured in the created and natural marsh during spring, summer and fall 2004

Parameter	Spring		Summer		Fall	
	Natural	Created	Natural	Created	Natural	Created
Temperature (°C)	25.2 (0.8)	24.6 (0.2)	32.0 (0.8)	34.8 (0.5)	27.1 (0.3)	27.2 (0.3)
Salinity	7.6 (1.7)	13.7 (<0.1)	8.0 (0.6)	6.0 (0.1)	14.3 (<0.1)	13.9 (<0.1)
Dissolved oxygen (mg l^{-1})	7.42 (0.25)	7.51 (0.13)	7.27 (0.66)	9.14 (0.26)	5.64 (0.16)	6.93 (0.22)
Depth (cm)	38.1 (1.3)	32.0 (2.6)	28.7 (2.9)	22.9 (3.9)	53.7 (2.0)	36.7 (3.0)
Stem density (# m^{-2})	184.5 (35.7)	83.7 (24.6)	117.7 (30.7)	92.5 (20.8)	144.2 (11.8)	104.8 (19.4)
Percent soil organic content	1.38 (0.11)	0.54 (0.13)	1.35 (0.11)	0.53 (0.15)	1.33 (0.11)	0.53 (0.15)
Percent of samples containing live oyster substrate	33.3	0.0	50.0	0.0	16.7	0.0
Percent of samples containing sea grass	50.0	0.0	83.3	83.3	33.3	33.3

were performed using CANOCO (Version 4, Microcomputer Power) and MRPP was performed using PC-ORD (Version 4; MJM Software).

3. Results

3.1. Habitat

Temperature and salinity were similar for both natural and created marshes. Dissolved oxygen was significantly higher in the created marsh ($t = 2.95$, $P = 0.006$) and depth ($t = 2.50$, $P = 0.017$), *Spartina alterniflora* stem density ($t = 2.46$, $P = 0.019$) and soil organic content ($t = 8.23$, $P < 0.001$) was significantly greater in the natural marsh. Salinity was greater in created marsh samples collected in spring due to a large rain event that occurred during the collection of samples from the natural marsh. Live oyster substrate was present in six samples collected from the natural marsh but was never encountered in created marsh samples (Table 1). *Ruppia maritima* was common in both marshes during summer and fall; however, its areal distribution was sparse but equivalent at both sites.

3.2. Species richness, abundance and biomass

Drop sampling yielded 36 species across marsh types and seasons with 28 species of fish representing 19 families, and eight crustacean species (five shrimp species, three crab species) representing five families. Rozas and Minello (1998) collected 38 species in *Spartina* marsh, sea grass beds and nonvegetated habitats in ANWR from 100 1-m^2 drop samples and our sample size (18 per marsh) appeared adequate to capture the species that could be expected with the gear type. A total of 28 species was collected from the natural marsh, and 22 species were collected from the created marsh, with only 14 species shared among sites (Table 2). Fourteen species (38.9% of the cumulative richness) were collected only from the natural marsh and eight species (22.2% of the cumulative richness) were collected only from the created marsh (Table 2). Mean richness in replicate samples was also greater in the natural marsh (9.8 vs. 6.6 species m^{-2}) and rmANOVA found that differences in richness among marsh type were significant (Table 2).

Estimates produced from rarefaction suggested that the number of samples collected were sufficient to characterize richness and assemblage structure in both marshes during each season. Predicted richness reached an asymptote before all individuals were collected concomitant with a decline in predicted richness variance. Richness was greater in the natural marsh during spring and summer but greater in the created marsh during fall (Fig. 2).

Total nekton density in the created marsh was less than half that in the natural marsh (62.3 vs. 167.8 individuals m^{-2}, $F_{1,35} = 29.42$, $P < 0.001$), and total biomass was more than three times greater in the natural marsh (67.7 g vs. 22.2 g m^{-2}, $F_{1,35} = 26.06$, $P < 0.001$). In both marsh types, daggerblade grass shrimp (*Palaemonetes pugio*) and naked goby (*Gobiosoma bosc*) were the dominant crustacean and fish species, respectively. Both species were over three times more abundant in the natural marsh. No significant difference was detected for aggregate crab biomass, white shrimp density and biomass, and brown shrimp density; however, low statistical power due to small sample size and the adjusted alpha used in rmANOVA made these results unreliable (Table 3). Nevertheless, there was a significant difference in shrimp and fish biomass with samples in the natural marsh yielding greater values (Table 3).

Analysis of blue crab density and size structure revealed that the created marsh had numerous small crabs whereas the natural marsh had fewer yet larger crabs (Fig. 3). Brown shrimp biomass was significantly greater in the natural marsh and seasonal differences in brown shrimp biomass were significant in both marshes with greater values in spring. The size structure of blue crab ($D = 0.29$, $P < 0.001$) and brown shrimp ($D = 0.23$, $P < 0.001$) populations were significantly different among marshes, with larger individuals collected in the natural marsh. No significant difference was detected for white shrimp ($D = 0.23$, $P = 0.413$) (Fig. 3).

Significant and positive correlations were detected between soil organic content and species richness ($r = 0.50$, $P = 0.002$), shrimp biomass ($r = 0.59$, $P < 0.001$), fish biomass ($r = 0.52$, $P = 0.001$), total nekton biomass ($r = 0.63$, $P < 0.001$) and total nekton density ($r = 0.52$, $P = 0.001$). Oyster was significantly correlated with crab biomass ($r = 0.48$, $P = 0.003$) and nekton density was correlated with depth ($r = 0.47$, $P = 0.003$).

Table 2
Mean density (number m^{-2}) and standard error of all species collected during spring, summer and fall 2004, and species codes for Fig. 5

Species	Code	Total	Natural	Created
Fish				
Gobiosoma bosc (naked goby)	Gob bos	6.17 (1.65)	9.44 (2.87)	2.89 (1.28)
Opsanus beta (gulf toadfish)	Ops bet	1.17 (0.49)	3.33 (0.80)	0
Lagodon rhomboides (pinfish)	Lag rho	0.81 (0.17)	1.28 (0.28)	0.33 (0.16)
Mugil cephalus (striped mullet)	Mug cep	0.23 (0.25)	0.55 (0.50)	0
Lucania parva (rainwater killifish)	Luc par	0.22 (0.20)	0.39 (0.39)	0.06 (0.06)
Menidia beryllina (inland silverside)	Men ber	0.19 (0.09)	0.06 (0.06)	0.33 (0.16)
Gobionellus shufeldti (freshwater goby)	Gob shu	0.17 (0.17)	0	0.33 (0.16)
Sciaenops ocellatus (red drum)	Sci oce	0.17 (0.09)	0.06 (0.06)	0.28 (0.23)
Cynoscion nebulosus (speckled seatrout)	Cyn neb	0.14 (0.11)	0	0.28 (0.23)
Symphurus plagiusa (blackcheek tonguefish)	Sym pla	0.14 (0.10)	0	0.28 (0.23)
Myrophis punctatus (speckled worm eel)	Myr pun	0.13 (0.07)	0.28 (0.13)	0
Anchoa mitchilli (bay anchovy)	Anc mit	0.06 (0.06)	0.11 (0.11)	0
Strongylura marina (Atlantic needlefish)	Str mar	0.06 (0.06)	0.06 (0.06)	0
Poecilia latipinna (sailfin molly)	Poe lat	0.06 (0.06)	0.11 (0.11)	0
Microgobius thalassinus (green goby)	Mic tha	0.06 (0.06)	0.11 (0.11)	0
Gobiesox strumosus (skilletfish)	Gob str	0.06 (0.04)	0.06 (0.06)	0.06 (0.06)
Syngnathus scovelli (gulf pipefish)	Syn sco	0.06 (0.04)	0.06 (0.06)	0.06 (0.06)
Adinia xenica (diamond killifish)	Adi xen	0.03 (0.03)	0.06 (0.06)	0
Fundulus grandis (gulf killifish)	Fun gra	0.03 (0.03)	0	0.06 (0.06)
Syngnathus louisianae (chain pipefish)	Syn lou	0.03 (0.03)	0	0.06 (0.06)
Lutjanus griseus (gray snapper)	Lut gri	0.03 (0.03)	0	0.06 (0.06)
Bairdiella chrysoura (silver perch)	Bai chr	0.03 (0.03)	0	0.06 (0.06)
Chasmodes bosquianus (striped blenny)	Cha bos	0.03 (0.03)	0.06 (0.06)	0
Microgobius gulosus (clown goby)	Mic gul	0.03 (0.03)	0.06 (0.06)	0
Paralichthys lethostigma (southern flounder)	Par let	0.03 (0.03)	0.06 (0.06)	0
Citharichthys spilopterus (bay whiff)	Cit spi	0.03 (0.03)	0	0.06 (0.06)
Achirus lineatus (lined sole)	Ach lin	0.03 (0.03)	0.06 (0.06)	0
Sphoeroides parvus (least puffer)	Sph par	0.03 (0.03)	0.06 (0.06)	0
Crustaceans				
Palaemonetes pugio (daggerblade grass shrimp)	Pal pug	60.97 (10.56)	100.00 (14.02)	21.94 (9.17)
Callinectes sapidus (blue crab)	Cal sap	12.25 (4.34)	3.00 (0.82)	21.5 (7.47)
Eurypanopeus depressus (flatback mud crab)	Eur dep	7.83 (4.55)	15.67 (8.83)	0
Palaemonetes intermedius (brackish grass shrimp)	Pal int	5.53 (1.31)	8.33 (1.91)	2.72 (1.58)
Litopenaeus setiferus (white shrimp)	Lit set	5.42 (1.14)	6.22 (1.97)	4.61 (1.17)
Rithropanopeus harrisii (harris mud crab)	Rit har	5.08 (1.09)	7.55 (1.81)	2.61 (0.93)
Farfantepenaeus aztecus (brown shrimp)	Far azt	3.86 (0.77)	4.67 (1.08)	3.06 (1.09)
Alpheus heterochaelis (snapping shrimp)	Alp het	3.44 (0.93)	6.89 (1.53)	0.72 (0.61)

3.3. Community structure

Differences in species relative abundances among marsh type were significant both among and within seasons (Table 4). CA produced two axes that explained 35.9% of the variation in species relative abundance. Samples from the natural marsh generally had low scores on CA axis one associated with more gulf toadfish (*Opsanus beta*), snapping shrimp (*Alpheus heterochaelis*), speckled worm eel (*Myrophis punctatus*) and flatback mud crab (*Eurypanopeus depressus*) (Fig. 4). Created marsh samples had high scores on axis one associated with more blue crab, white shrimp, inland silverside (*Menidia beryllina*) and speckled seatrout (*Cynoscion nebulosus*) (Fig. 4). Although all pairwise comparisons were significant, effect size from MRPP declined from spring to fall due to increased within-marsh sample variability.

Tests of seasonal differences in assemblage structure within each marsh type were also significant (Table 4). Pairwise seasonal comparisons in the natural marsh found that nonadjacent seasons (spring and fall) were significantly different, whereas pairwise comparisons in the created marsh were not significant when Bonferroni corrected P values were applied (Table 4). CA sample scores for both marshes became more positive on axis one from spring to fall associated with more blue crab and white shrimp. Natural marsh sample scores were more negative on axis two over time associated with more grass shrimps (*Palaemonetes pugio* and *Palaemonetes intermedius*) and brown shrimp, whereas created marsh sample scores were more positive on axis two over time associated with more juveniles of several transient species that were rare or absent in the spring survey [speckled sea trout, red drum (*Sciaenops ocellatus*), and blackcheek tonguefish (*Symphurus plagiusa*)].

The presence of oyster substrate and soil organic content were the only habitat variables significantly correlated with species relative abundances in CCA. Species that were strongly correlated with the presence of oyster and soil organic content on axis one (eigenvalue 0.200) were also associated with natural sites in the CA ordination (Figs. 4 and 5). Five species (*Anchoa mitchilli, Chasmodes bosquianus, Microgobius thalassinus, Myrophis punctatus, Sphoeroides parvus)*

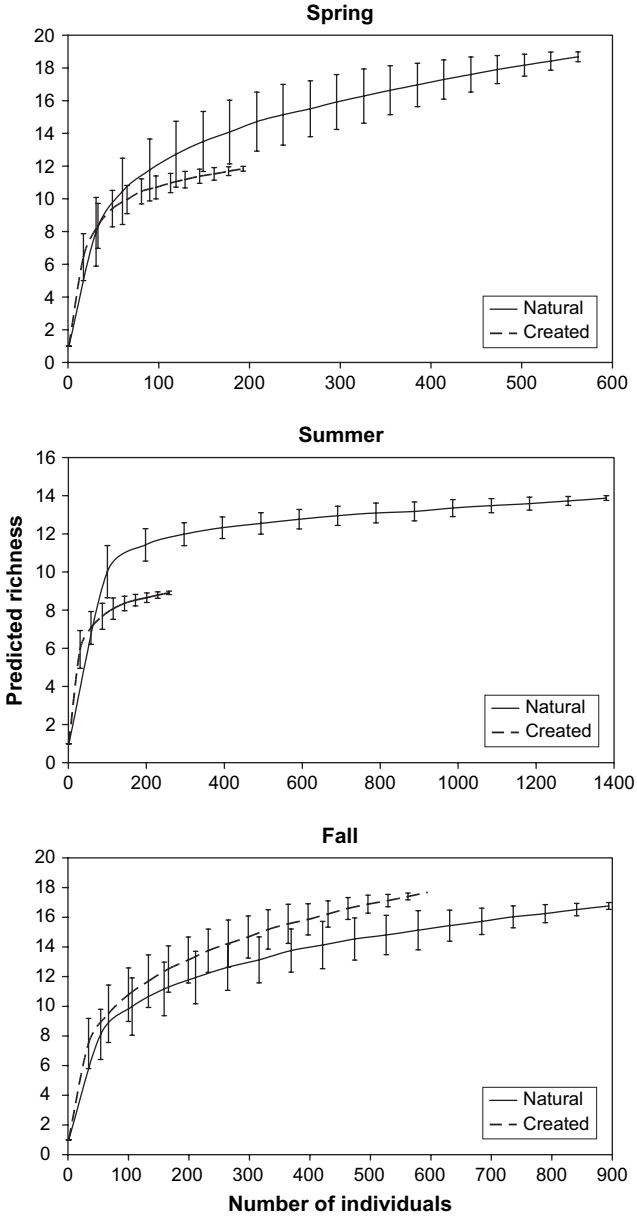

Fig. 2. Rarefaction curves for the natural and created marshes in each season.

were collected only in samples containing oyster substrate and several species (gulf toadfish, flatback mudcrab, snapping shrimp) had strong correlations with oyster despite being collected over other substrates (Fig. 5). The explanatory power of CCA axis two was low (eigenvalue of 0.066) and species correlations with this axis were therefore not interpreted.

4. Discussion

The natural and created marshes in our study supported nekton assemblages that were significantly different across all seasons despite similarity in the density and/or biomass of some species and taxonomic groups. Several species that had positive correlations with oyster in CCA (gulf toadfish, flatback mudcrab, snapping shrimp) were abundant in the natural marsh but rare or absent in the created marsh where this substrate was not encountered. Other structural components such as *Ruppia maritima* and *Spartina alterniflora* were encountered in both marsh types and appeared to serve similar functions as species correlations with these features in CCA were weak or not significant. This suggests that oyster was an important habitat feature that limited the ability of the created marsh to support species that were dominant in the natural assemblage.

Glancy et al. (2003) found that oyster reef supported different assemblages of decapod crustaceans than marsh edge, and several studies have reported species associations with oyster (snapping shrimp, flatback mud crab) similar to those found in the current study (Zimmerman et al., 1989; Meyer and Townsend, 2000; Glancy et al., 2003). Oyster reef is widely recognized as an important estuarine habitat that can enhance species diversity (Lehnert and Allen, 2002), growth, and survival (Minello et al., 2003), and reefs located adjacent to salt marsh may have greater functional value than either habitat in isolation (Micheli and Peterson, 1999; Grabowski et al., 2005). Structural components such as vegetation can rapidly become established in created marshes (Streever, 2000; Edwards and Proffitt, 2003); whereas oyster reef may require long time periods to develop and reach equivalence with natural reference sites if marsh designs do not specifically address this component. The created site was over 30 years old

Table 3
Means with standard errors and results from repeated measures ANOVA comparing species richness (species m^{-2}), biomass of aggregate taxonomic groupings (g m^{-2}), and the density (number m^{-2}) and biomass (g m^{-2}) of three commercially important crustaceans. Significance was assessed at $\alpha_{adjusted} = 0.017$ and power for *F*-tests was calculated with Geisser–Greenhouse adjustments

Parameter	Natural	Created	*F*	*P*	Power
Richness	9.9 (0.54)	6.6 (0.62)	17.05	<0.001	0.94
Shrimp biomass	40.0 (5.0)	9.7 (2.6)	41.96	<0.001	0.99
Crab biomass	11.8 (4.6)	4.7 (1.4)	1.46	0.237	0.11
Fish biomass	15.7 (3.5)	7.7 (4.3)	8.88	0.005	0.67
Brown shrimp density	4.6 (1.1)	3.1 (1.1)	2.79	0.105	0.21
Brown shrimp biomass	5.2 (1.1)	1.8 (0.5)	9.26	0.004	0.70
White shrimp density	6.2 (2.0)	4.6 (1.2)	0.07	0.900	0.02
White shrimp biomass	1.9 (0.7)	1.4 (0.4)	0.01	0.919	0.02
Blue crab density	3.0 (0.8)	21.5 (8.2)	31.13	<0.001	0.99
Blue crab biomass	4.7 (1.5)	4.6 (1.4)	0.17	0.684	0.02

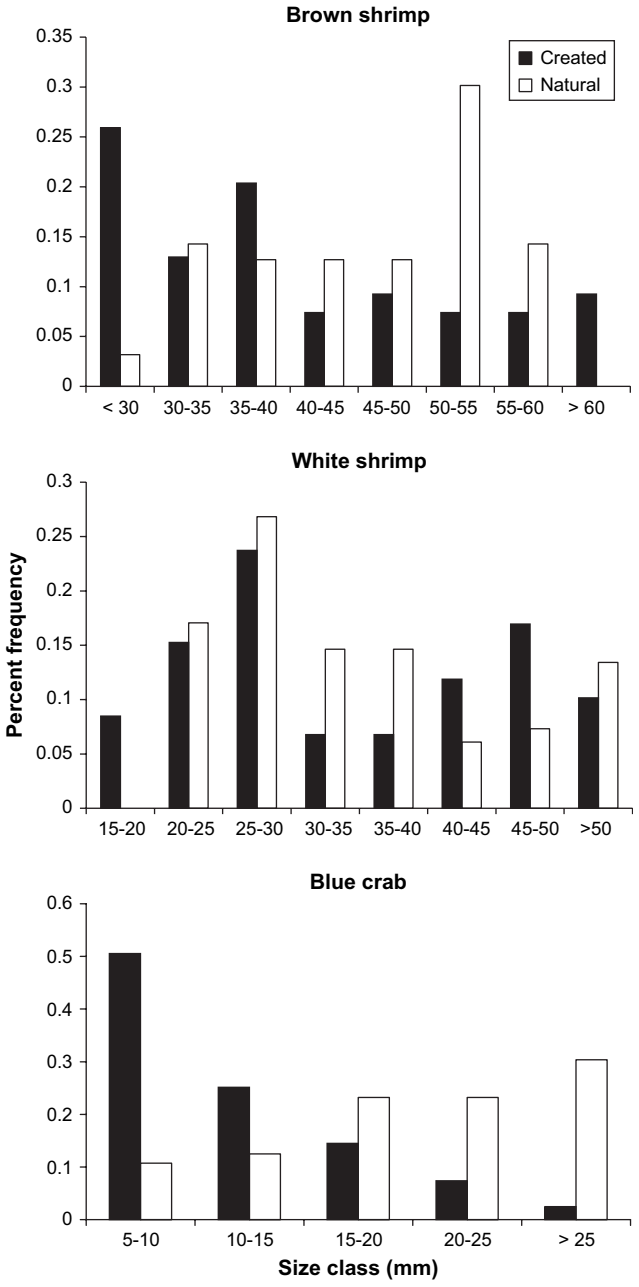

Fig. 3. Length-frequency histograms for white shrimp, brown shrimp and blue crab collected in the created and natural marsh during spring, summer and fall surveys.

and had not developed live oyster within the emergent vegetation despite the presence of live oyster less than 25 m from the marsh edge.

Several factors related to geomorphology and hydrology may have influenced the lack of oyster in the created marsh. Wave exposure in the created marsh may be greater due to a longer fetch at this location (Fig. 1); however, the natural marsh is also exposed to frequent wave action from commercial barge traffic through the GIWW (Davis, unpublished data). The natural marsh had greater depth and although inundation period is unlikely to affect these habitats during the seasons we surveyed (Rozas and Minello, 1998), inundation time during winter may be limiting oyster development in the created marsh. Additionally, the created marsh may have a reduced larval supply which could significantly affect the establishment of oyster (Roughgarden et al., 1988), or there maybe insufficient substrate for settlement of oyster spat.

Table 4
Effect size (A) and probability values from MRPP for pairwise comparisons of nekton assemblage structure based on species relative abundance between natural and created marsh, and seasonal comparisons within each marsh type. Significance was assessed at $\alpha_{adjusted} = 0.004$

Comparison	A	P
Natural × created (all seasons)	0.236	<0.001
Natural × created (spring)	0.483	<0.001
Natural × created (summer)	0.351	0.003
Natural × created (fall)	0.262	0.003
Natural spring × summer	0.041	0.205
Natural spring × fall	0.427	0.002
Natural summer × fall	0.145	0.058
Created spring × summer	0.024	0.251
Created spring × fall	0.115	0.033
Created summer × fall	0.068	0.094

The natural marsh supported greater cumulative species richness in spring and summer, and differences in species composition suggested that the created marsh assemblage was not necessarily a nested subset of the natural assemblage (only 14 of 36 species collected in both marshes). Previous evaluations of nekton in created or restored marsh have found richness to be equal or greater than natural reference sites (Minello and Zimmerman, 1992; Ambrose and Meffert, 1999; Talley, 2000). Five rare species (<3 individuals) were only collected over oyster substrate, and this was similar to the difference in cumulative richness among marsh type (6 species). Zimmerman et al. (1989) compared species composition and density in oyster, *Spartina*, and nonvegetated bottom habitats in Texas and found several species were only collected over oyster. The effect of structural complexity on diversity in aquatic ecosystems is well recognized (Charbonnel et al., 2002; Wyda et al., 2002; Gratwicke and Speight, 2005) and lower complexity (specifically the absence of live oyster) in the created marsh may have influenced the difference in cumulative richness among marshes.

Although nekton assemblage structure in both marshes was variable among seasons, none of the environmental characteristics measured were significantly correlated with seasonal assemblage variability in CCA. Although the current study was conducted over three seasons, environmental changes over longer time scales may result in assemblage shifts that could not be detected within this short time period (Levin and Talley, 2002). Changes in dominance patterns and relative abundance among seasons were likely related to recruitment of resident and transient species. Blue crab, white shrimp, and naked goby increased in abundance over time in both marshes. Additionally, juveniles of several larger fish species (speckled seatrout, red drum and blackcheek tonguefish) were collected during fall when juvenile recruitment to vegetated habitats in the Guadalupe Estuary is high (Rooker et al., 1998). Recruitment of transient species has been shown to significantly influence marsh species assemblages (Akin et al., 2003; Able et al., 2004), with the strength of this effect

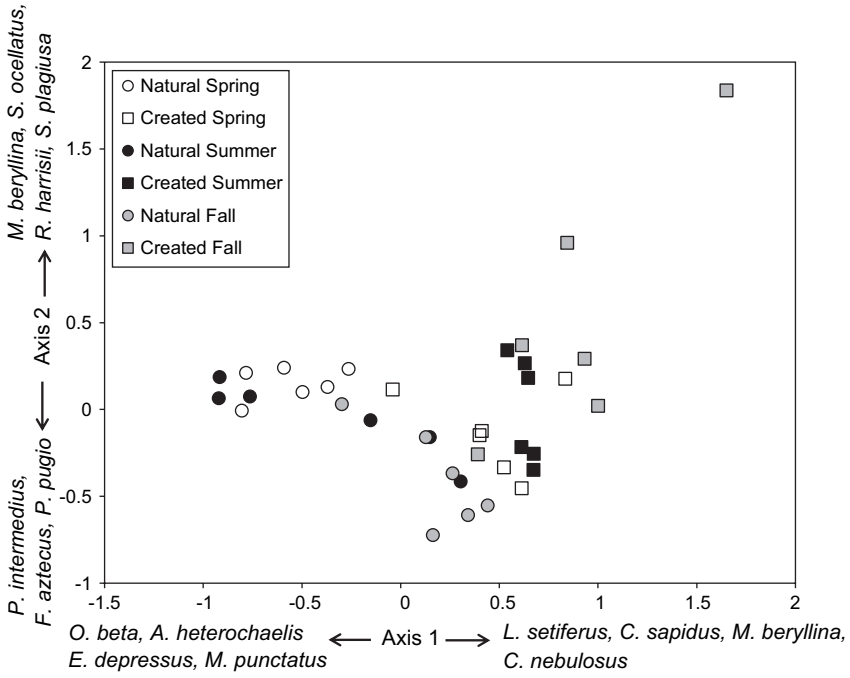

Fig. 4. Plot of sample scores from correspondence analysis. Natural and created sample groupings were significant within and among seasons.

related to distance from source habitats (Akin et al., 2003). The created marsh was located slightly closer to Mesquite Bay (<1 km) which connects to the Gulf of Mexico, and the effect of transient species recruitment may have been stronger in this marsh (Fig. 2).

The created marsh contained greater densities of smaller crabs relative to the natural marsh. Previous studies found created marshes to support blue crab populations similar to natural reference marshes (Minello and Zimmerman, 1992; Jivoff and Able, 2003). Differences in density and size in the present study may be related to the spatial position of the created marsh which was located slightly closer to the Gulf of Mexico (<1 km). Habitats located closer to larval sources act as ''landing strips'' for blue crab larvae entering estuaries (Etherington and Eggleston, 2000), and larval supply has been shown to influence the abundance of other invertebrate species with planktonic dispersal (Roughgarden et al., 1988). Additionally, variation in the abundance of carbon sources supporting crab populations may have influenced observed differences in size distributions among marsh types with larger crabs relying more on *Spartina*-derived carbon which was more abundant in the natural marsh (Hoeinghaus and Davis, in press). The equivalence of blue crab biomass in the created marsh may be particularly beneficial for endangered whooping cranes

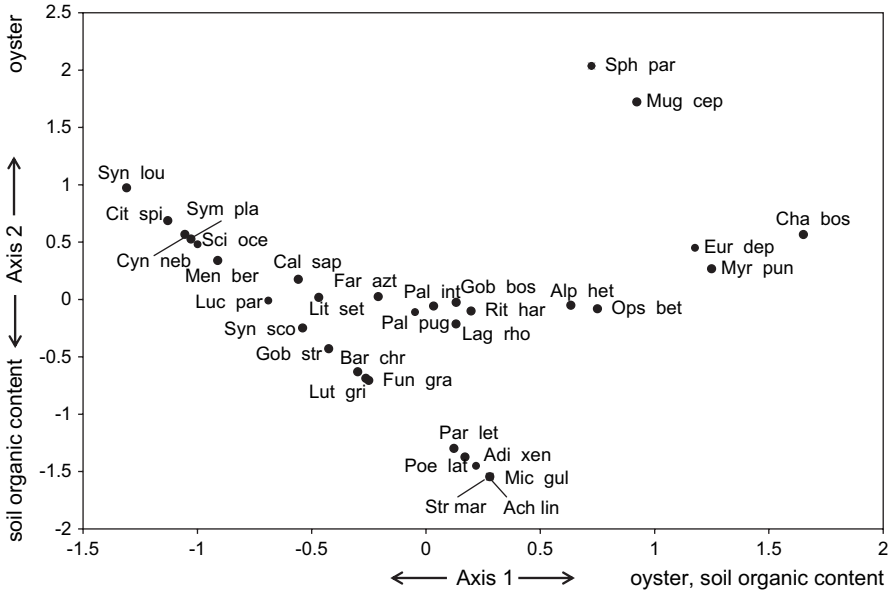

Fig. 5. Plot of species scores from canonical correspondence analysis. Species codes are listed in Table 2.

(*Grus americana*) that over-winter at ANWR and forage for blue crabs in adjacent marsh habitats.

Lower densities of infauna in created marshes may decrease nekton utilization by reducing prey availability (Minello and Zimmerman, 1992; Minello et al., 1994). Although densities of infauna were not estimated in this study, a similar pattern of reduced nekton utilization of created marsh was apparent. For example, biomass of brown shrimp and aggregate fish and shrimp groupings were significantly higher in the natural marsh and strong positive correlations were detected between organic content and measures of nekton density and biomass. Several studies have reported links between infaunal densities and measures of soil organic content in created marshes (Minello and Zimmerman, 1992; Minello and Webb, 1997; Craft et al., 1999; Talley and Levin, 1999; Levin and Talley, 2002). At our sites, percent soil organic content in the created marsh was less than half that in the natural marsh. Statistical power for comparisons of white shrimp density and biomass was insufficient to make meaningful conclusions; however, size structure was similar in both marshes and Rozas and Minello (2001) found no difference in white shrimp density in other created and natural marshes. Establishment of causal relationships between soil organic content, prey abundance and nekton utilization is complicated by predator selectivity (Meng et al., 2004) and future studies would benefit by establishing trophic relationships among marsh fauna.

Marsh habitats bordering old spoil islands can be seen as unintentional restorations that may be used to evaluate created marsh development over long time periods (Callaway, 2005). Our evaluation of spoil island marsh suggests that lower substrate complexity (lack of live oyster) and soil organic content limited the development of equivalent nekton assemblages in comparison with the natural reference marsh. Despite the clear pattern of nekton utilization, these results should be interpreted with caution. The small number of marshes sampled may restrict the extrapolation of these results to created marshes in general. Additionally, although habitat selection (oyster, sea grass, *Spartina*) at small scales was not specifically addressed in the study, this may be an important factor influencing nekton assemblages that could not be elucidated with multivariate analysis (CA, CCA) used to describe trends at the scale of the whole marsh.

Site-specific differences in hydrology and wave exposure that affect deposition may have influenced the development of similar soil organic content in the created marsh; however, estimates of created marsh successional trajectories in other estuaries suggest that soil organic content may require long time periods (>25 years) to reach equivalency with natural marsh soils (Craft et al., 1999; Edwards and Proffitt, 2003). Nekton biomass may not reach levels observed in natural marshes until similar soil characteristics are established; however, future restorations would benefit by incorporating natural levels of substrate complexity into new marsh habitats which would likely increase the similarity of nekton assemblage compared to natural marsh.

Marsh designs that provide habitat heterogeneity similar to natural reference sites are more successful in developing equivalent nekton assemblages (Thom et al., 2004) and species-specific habitat requirements should be considered when new marsh is created (Levin et al., 1996). Creation of new salt marsh habitats on dredge spoil is likely to continue in estuaries along the Gulf Intra-Coastal Waterway (Wagner, 2000) and improvement of marsh designs is essential to increase the similarity of created and natural marsh nekton assemblages.

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