

Effects of reduced hydrological connectivity on the nursery use of shallow estuarine habitats within a river delta

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ABSTRACT: We examined the effects of a hydrologically restrictive transportation corridor on the nursery use of various habitats in the Mobile–Tensaw River delta (MTD). We compared nekton assemblage structure in fall 2009 and spring 2010 among 3 locations and 3 major habitat types (marsh, submerged aquatic vegetation [SAV] dominated by *Vallisneria americana*, and shallow non-vegetated bottom [SNB]) commonly found throughout the MTD using 1 m² drop samplers. Sample locations (Tensaw River [TR], Chocolatta Bay [CB], and Below Causeway [BC]) were selected based on their degree of tidal connectivity with the wider estuary (BC > TR > CB). Nekton assemblages varied among locations and habitat types. Recruitment by the young of transient fishery species appeared to drive the nekton assemblage structure at the least hydrologically restricted locations (BC and TR) in the delta, whereas estuarine-resident species dominated the nekton assemblage at CB. Species richness was greater at BC than at CB. Within locations, mean densities of abundant species were concentrated in SAV and marsh. Delta locations directly connected to Mobile Bay, therefore, likely provide an important nursery for fishery species such as white shrimp, blue crab, gulf menhaden, and southern flounder. Additional studies will be needed, however, to determine whether these fishery species represent strong conduits for cross ecosystem transfer of energy and nutrients between the delta and northern Gulf of Mexico.

KEY WORDS: Habitat comparison · Tidal freshwater wetlands · Oligohaline marsh · *Vallisneria americana* · Mobile–Tensaw River delta · Gulf of Mexico

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INTRODUCTION

River deltas of the northern Gulf of Mexico (GoM) are among the most productive ecosystems on Earth (Chaplin & Valentine 2009). In part, this extraordinary productivity is hypothesized to be the result of the strong ecological links among these deltas, upstream watersheds, and the nearshore waters of the northern GoM. The availability of high-quality nursery habitat within these delta systems is essential for sustaining the productive coastal fisheries in

the region, because most fishery species in the GoM are estuarine dependent (Gunter 1967, Beck et al. 2001, Heck et al. 2003). The vast wetlands and estuaries of the Mississippi River delta complex, for example, are known to support some of the most important estuarine-dependent commercial fisheries in North America (Viosca 1928, Gunter 1967, Chesney et al. 2000).

The nursery function of estuarine wetlands is dependent on the strength of the hydrological connection between potential nursery areas and spawn-

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ing sites in the GoM. Any obstruction of this link between deltas and nearshore marine waters (i.e. reducing hydrological connectivity) can potentially diminish the value of nursery areas by disrupting migration and recruitment patterns of estuarine-dependent species, thereby weakening life-history connectivity (Secor & Rooker 2005, Sheaves 2009). This relationship between hydrological and life-history connectivity, however, is complex and not easily quantified. Therefore, the threshold where restrictions in flow begin to affect life-history connectivity and recruitment of fishery species is generally not known.

Most river deltas in the northern GoM today are being gradually reduced in size by subsiding deltaic sediments and the loss of wetlands (Smith 1988, Roberts 1997). Many are further impacted by human activities that degrade and reduce nursery areas, which may have important cascading consequences for fishery populations (Thomas 1999, Chaplin & Valentine 2009, Martin & Valentine 2012). River deltas with little human development are uncommon (Syvitski et al. 2009), but examining such deltas would lessen the risk of human activity confounding research results.

Despite its close proximity to the city of Mobile, Alabama, the Mobile–Tensaw delta (MTD) is relatively undeveloped. Development in the delta is mainly limited to the Mobile River and the US Highway 90-98 Causeway, which was constructed across the delta circa 1925 (Smith 1988). The Causeway reduces the hydrologic connectivity of the delta by decreasing freshwater discharge to Mobile Bay in dry years and restricting most tidal exchange with Mobile Bay to 4 river channels (Goecker et al. 2009, Martin & Valentine 2012). The presence of the Causeway has also altered biological production and nutrient exchange between Mobile Bay and some areas north of the Causeway (Goecker et al. 2009). Although Goecker et al. (2009) showed there is little mixing of consumers between the delta and Mobile Bay, they did not examine the effect of this restricted movement on the use of delta nursery areas by fishery species.

The objective of our study was to examine the effect of the Causeway on the nekton composition and use of potential delta nursery areas. We examined habitat-specific density patterns of juvenile fishery species and other nekton among 3 locations that varied in tidal connectivity to investigate the effect of this factor on nekton assemblage structure. If the Causeway restricts hydrological exchange enough to weaken life-history connectivity between the delta

and Mobile Bay, this weakened connectivity should be reflected by differences in the composition of fishery populations and nekton assemblages north and south of the Causeway. Densities of newly settled individuals and juveniles of fishery species should be relatively low in enclosed embayments north of the Causeway. Transient species, which reproduce outside the delta and recruit to delta nursery areas as young, should also be less abundant than resident nekton at hydrologically restricted locations, and the loss of some of these migratory species should reduce species richness north of the Causeway.

MATERIALS AND METHODS

Study area and sampling design

The MTD is located within the Mobile Basin, which is the sixth largest drainage area, and fourth largest basin in terms of flow volume, in the USA (Sturm et al. 2007). Located at the head of Mobile Bay, the MTD is approximately 72 km long by 16 km wide (Crance 1971). Bottomland hardwood forests and bald cypress swamps occupy the northern part of the delta, but these forested wetlands are gradually replaced near Mobile Bay by tidal freshwater and oligohaline marshes interspersed by numerous shallow open-water bodies. In years of average rainfall, seasonally high river flows occur in late winter and spring, and freshwater conditions prevail throughout the delta; oligohaline conditions may exist in the delta during the low inflow period of late summer and fall (Valentine et al. 2013). The mean tide range is approximately 0.45 m based on data from the nearest tide gauge (NOAA Tide Gauge 8736897; Fig. 1).

Our 3 study locations in the lower delta varied in their degree of tidal connectivity with the estuary and GoM (Fig. 1). The Below Causeway (BC) location is completely free of any impediments to tidal exchange. An elevated segment of highway minimally restricts water exchange between the bay and the Tensaw River (TR) location. Tidal exchange at the Chocolatta Bay (CB) location is restricted to 2 road culverts similar to those known to impede nekton movement in salt marsh creeks (Eberhardt et al. 2011) and 4 relatively small channels that do not connect directly to Mobile Bay.

The Causeway effectively forms a physical barrier that separates CB from Mobile Bay (Martin & Valentine 2012). Using stable isotope analysis, Goecker et al. (2009) showed that by restricting hydrological connectivity, the Causeway has fundamentally al-

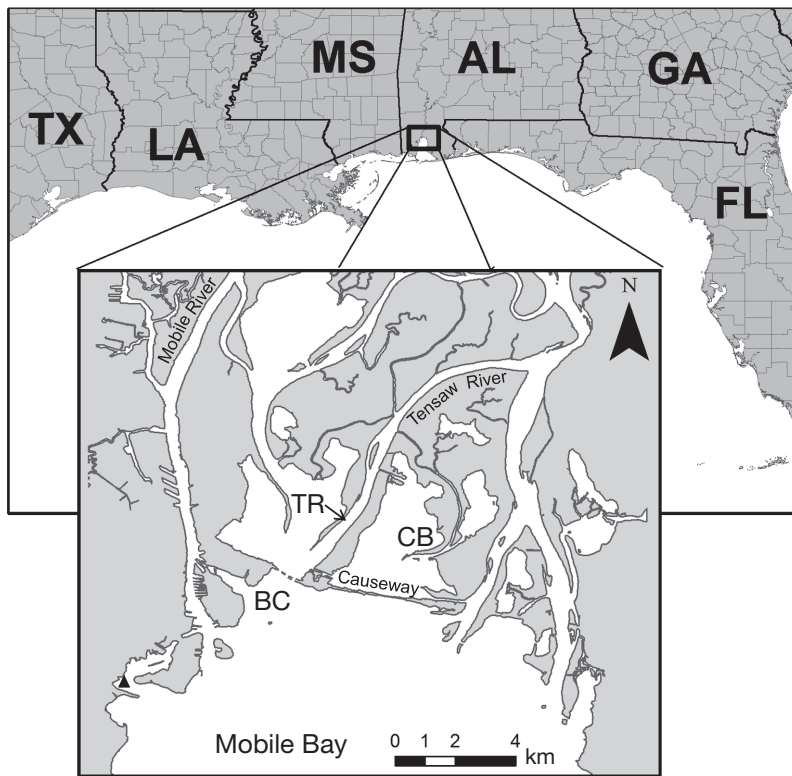


Fig. 1. The study area within the Mobile–Tensaw River delta and its location in the northern Gulf of Mexico. Nekton sampling locations are labeled as—TR: Tensaw River; CB: Chocolatta Bay; BC: Below Causeway (US Highway 90-98). Elevated highway over the Tensaw River is depicted as a broken line. The NOAA Tide Gauge 8736897 (solid triangle) is at latitude $30^{\circ} 38.9' N$ and longitude $88^{\circ} 3.5' W$

tered nutrient and energy exchange between CB and Mobile Bay. The fine-grain sediments, high water retention time, and occasional hypoxic events documented at this location are also consistent with restricted tidal exchange (Valentine & Sklenar 2006).

Within each location, our study focused on 3 major habitat types (submerged aquatic vegetation [SAV] dominated by *Vallisneria americana*, marsh, and shallow non-vegetated bottom [SNB]). *V. americana* is a dominant native freshwater species of delta SAV beds (Chaplin & Valentine 2009, Martin & Valentine 2011), and extensive *V. americana* beds occur both north and south of the Causeway (Martin & Valentine 2012). The SAV beds we sampled also contained *Myriophyllum spicatum* and *Ruppia maritima*, but the percent coverage of these species was observed to be low at our sampling sites.

The marsh vegetation at the 3 locations varied in species composition. The marsh at TR was botanically the most species-rich, composed primarily of *Phragmites australis*, *Typha latifolia*, *Sagittaria lancifolia*, *Shoenopectus maritimus*, and *Zizaniopsis mili-*

acea. The vegetation at CB was dominated by *T. latifolia*, *S. lancifolia*, and *Shoenopectus validus*, whereas the marsh vegetation at the BC location consisted almost exclusively of *T. latifolia*. All nekton samples in the marsh were collected within ~1 m of the marsh edge (marsh–open-water interface).

At each location, we collected 8 replicate nekton samples during daylight and at high tide from each habitat type in fall (13 to 15 October) 2009 and in spring (11 and 12 May) 2010 for a total of 144 samples. We focused our sampling effort in spring and fall when the abundance of most fishery species peaks in estuaries of the northern GoM (Rakocinski et al. 1992, Livingston 1997, Akin et al. 2003, Rozas et al. 2007). Sampling sites within habitat types were randomly selected from a 9 ha area at BC, a 14 ha area at CB, and within a 4 km stretch of the lower TR using random numbers and a grid placed over an aerial photograph of the study area.

Nekton was quantitatively sampled using 1 m^2 drop samplers (cf. Zimmerman et al. 1984). Immediately after the drop sampler was deployed at a sampling site, we measured water temperature,

dissolved oxygen (DO), water depth, and distance to the marsh edge (from the center of the sampler to the nearest marsh shoreline); we also collected a water sample, from which turbidity and salinity were determined later in the laboratory, and removed vegetation at SAV and marsh sites as described by Rozas et al. (2012). The data from these samples were used to characterize and compare the aquatic environment at the sampling sites.

After measuring the environmental variables and removing vegetation, we removed the enclosed animals by using dip nets and filtering the water pumped out of the sampler through a 1 mm mesh net. When the sampler was completely drained, we removed by hand animals remaining in the sampler. Samples were preserved in formalin and returned to the laboratory for processing.

In the laboratory, nekton was removed from each sample and identified to the lowest possible taxon. Grass shrimps *Palaemonetes* spp. (total = 237; 14 and 8% of grass shrimp collected in the fall and spring, respectively) that could not be identified, because

they lacked the body parts necessary for identification, were classified based on the proportion of identified species in each sample (Rozas et al. 2012). Total length of fishes and shrimps and carapace width (CW) of crabs were measured (± 1 mm), and all individuals of a species in each sample were blotted dry and pooled to determine biomass (± 0.1 g wet weight).

Data analyses

We examined variation in environmental variables among locations and habitat types with a principal component analysis (PCA) based on the correlation matrix and using the factor procedure in SAS (Version 9.3, SAS Institute). The first 3 principal components were rotated using the Varimax option. This approach was used to resolve 5 environmental variables (water temperature, DO, turbidity, water depth, and distance to marsh edge) without missing values into 3 orthogonal variables, which made comparisons easier to interpret. Salinity was not included in the PCA because this variable was measureable only in May when salinity was 1 at 1 CB and 9 BC sites. We also removed 4 outliers (3 CB and 1 BC SNB October samples) from the analysis to avoid masking patterns among other sites. The 5 environmental variables in 137 samples were used to calculate variable loadings and generate principal component scores. These principal component scores were then used to calculate centroids for locations and habitat types. Confidence intervals (± 1 SE) around these centroids were estimated as the mean standard errors on the 3 component axes for each location and habitat type.

PRIMER software was used to examine the extent to which the Causeway has changed the assemblage structure of nekton by weakening the hydrological and biological connectivity between the GoM and the delta (Clarke & Gorley 2006). Only species that occurred in $\geq 10\%$ of the samples collected in either October 2009 or May 2010 were included in these analyses, and we did not include outlier samples (October = 2, May = 7), which contained no animals.

Prior to analyses, the density data (individuals m^{-2}) were $\log(x + 1)$ transformed to preclude dominant species from masking important patterns of less abundant species. We compared nekton density among locations and habitat types using the non-parametric analysis of similarity (ANOSIM, Bray-Curtis similarity) technique. The results of an initial 1-way ANOSIM indicated that significant seasonal differences in the assemblage structure of nekton existed among the 3 locations. Therefore, we con-

ducted separate 2-way ANOSIMs on the density data we collected in October 2009 and May 2010. A non-metric multidimensional scaling (MDS) plot was constructed for each season to graphically display the data using the Bray-Curtis similarity values for each sample (note: outlier samples, October = 2 and May = 7, in which no organisms were captured were not plotted). The contribution of individual species to assemblage structure was calculated using the similarity percentages (SIMPER) routine. We predicted that if delta life-history connectivity were affected by the presence of the Causeway, then the results from these analyses would show significant differences among locations.

We used separate (for each season) 2-way analyses of variance (ANOVA) to test the null hypothesis that species richness, densities of total transients, and sizes of abundant fishery species among locations and habitat types were statistically indistinguishable from each other (JMP, Version 9.0.0, SAS Institute, 2010). Mean transient densities were positively related to the standard deviation, so the raw data were $\ln(x + 1)$ transformed prior to analyses (Quinn & Keough 2005). The species considered transients for this analysis are shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/m492p009_supp.pdf

When the main effect of location was determined to be significant, we used Tukey's honestly significant difference (HSD) post hoc tests to identify significant differences among the 3 locations (Quinn & Keough 2005). If the main effect of habitat type was significant, we used *a priori* contrasts to make the following comparisons: (1) marsh versus SAV and (2) marsh and SAV versus SNB. These comparisons contrasted means between the 2 vegetated habitat types and between vegetated and unvegetated habitat types, respectively.

RESULTS

The PCA identified several environmental patterns, which are illustrated by the centroids of locations and habitat types plotted in 3-dimensional principal component space (Fig. 2). The first 3 principal components (PC) each had an eigenvalue > 1 , and combined explained about 79% of the variation in the environmental data (Table 1). PC 1 indicated a separation of locations and habitat types along a depth gradient, with CB SNB sites tending to be deeper than CB SAV and marsh sites and all BC and TR sites (Fig. 2, Table 1, Table S2 in the Supplement).

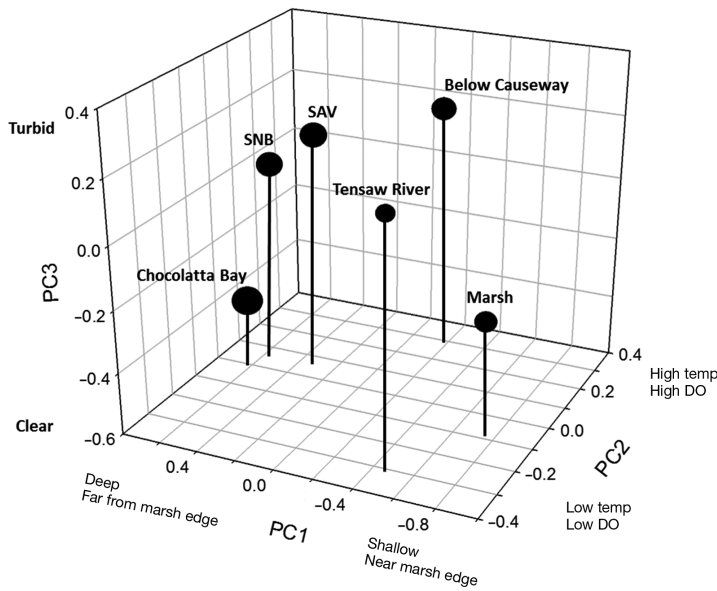


Fig. 2. Comparison of the aquatic environment among locations (Below Causeway, Tensaw River, Chocolatta Bay) and habitat types (submerged aquatic vegetation [SAV] dominated by *Vallisneria americana*, marsh, and shallow non-vegetated bottom [SNB]) in the Mobile-Tensaw River delta. The centroids of each location and habitat type are plotted in 3-dimensional principal components space. Balloon radii represent 1 SE around the means. Each principal component (PC1, PC2, PC3) represents the weighted linear combination of the original 5 environmental variables

Table 1. Rotated principal component (PC) loadings for the environmental variables measured at nekton sample sites in the study area. The influence (strength and direction) of each variable on the principal components is related to the magnitude and sign of the loadings. The loadings shown in **bold** were most important in characterizing the components. The absolute, proportional, and cumulative values of the variance explained by the eigenvalue of each principal component are also given

Environmental variables	Rotated principal component loadings		
	PC 1	PC 2	PC 3
Water temperature	0.101	0.808	-0.091
Water depth	0.865	-0.004	-0.183
Turbidity	-0.084	-0.082	0.986
Dissolved oxygen	0.001	0.838	-0.011
Distance to marsh edge	0.885	0.112	0.054
Variance explained			
Absolute	1.549	1.374	1.016
Proportional	0.310	0.275	0.203
Cumulative	0.310	0.585	0.788

Shallow sites that lacked vegetation were difficult to find in CB, as the depth limit for SAV appeared to be greater there than at the other locations. As a result, SNB sites at CB occurred in deeper water (Table S2).

PC 2 indicated a gradient in DO and water temperature, with BC sites having higher values for these variables than CB and TR sites (Table 1, Fig. 2). PC 3 indicated a gradient in water clarity, with CB sites being less turbid than TR and BC sites (Table 1, Fig. 2). The habitat types were separated most in the analysis by depth and water clarity. Marsh sites were shallower and less turbid than SAV and SNB sites (Fig. 2).

We collected totals of 2431 individuals, 11 species, and 0.9 kg total biomass of crustaceans and 10 032 individuals, 40 species, and 2.1 kg total biomass of fishes during our study (Table S1). The range and mean size (± 1 SE) of crustaceans were 2 to 135 mm and 18 ± 0.27 mm, respectively. Overall, the most abundant crustaceans included daggerblade grass shrimp *Palaemonetes pugio*, blue crab *Callinectes sapidus*, riverine grass shrimp *P. paludosus*, marsh grass shrimp *P. vulgaris*, brackish grass shrimp *P. intermedius*, estuarine mud crab *Rhithropanopeus harrisi*, and white shrimp *Litopenaeus setiferus* (Table S1). Fishes ranged in size from 8 to 198 mm (mean ± 1 SE = 32 ± 0.44 mm).

Gulf menhaden *Brevoortia patronus*, rain-water killifish *Lucania parva*, darter goby *Ctenogobius boleosoma*, naked goby *Gobiosoma bosc*, bay anchovy *Anchoa mitchilli*, gulf pipefish *Syngnathus scovelli*, freshwater goby *Ctenogobius shufeldti*, and clown goby *Microgobius gulosus* were the most abundant fishes (Table S1).

Nekton density and composition varied across the delta study area (Table 2). Based on ANOSIM, differences in nekton assemblage structure within the delta were statistically significant among locations, regardless of season (fall: $p = 0.001$, global $R = 0.464$; spring: $p = 0.001$, global $R = 0.569$) and habitat types (fall: $p = 0.001$, global $R = 0.344$; spring: $p = 0.004$, global $R = 0.153$). Subsequent pairwise comparisons detected significant differences among all locations and habitat types (fall: $p = 0.001$, global $R \geq 0.233$; spring: $p = 0.008$, global $R \geq 0.229$) except between marsh and SAV in spring ($p = 0.121$, $R = 0.06$).

MDS plots of Bray-Curtis similarity values of nekton samples showed clear differentiation between BC and CB in both seasons, with TR overlapping these locations (Fig. 3). The BC sites had higher densities of blue crab, darter goby, and white shrimp during October 2009 and blue crab, darter goby, and daggerblade grass shrimp during May 2010. Higher densities of the same 2 species, riverine grass shrimp

Table 2. Comparison of SIMPER (similarity percentage) analysis results on density data. The percent contribution to similarity and density (mean individuals m⁻² ± 1 SE) are given for each species that contributed to the nekton assemblage structure of each location (Below Causeway, Tensaw River, and Chocolata Bay) and habitat type (submerged aquatic vegetation [SAV] dominated by *Vallisneria spiralis*, marsh, and shallow non-vegetated bottom [SNB]) in October 2009 and May 2010. Each mean density is estimated from 24 samples (except for October 2009 [23 Tensaw River/SNB] and May 2010 [23 Below Causeway/SNB and 23 Tensaw River/SAV]). For taxonomic names see Table S1 in the Supplement at www.int-res.com/articles/suppl/m492p009_supp.pdf. -: No/minimal contribution to similarity

Species	Below Causeway			Location			Chocolata Bay			SAV			Marsh			SNB		
	SIMPER	Density		SIMPER	Density		SIMPER	Density		SIMPER	Density		SIMPER	Density		SIMPER	Density	
October 2009																		
Blue crab	26.4	9.8 ± 1.86	38.6	4.8 ± 0.81	17.5	2.3 ± 0.49	24.6	9.3 ± 1.37	25.5	5.0 ± 1.56	36.0	2.4 ± 0.54						
Darter goby	22.3	3.2 ± 0.45	10.4	1.3 ± 0.38	-	0.0 ± 0.04	6.2	1.5 ± 0.31	8.8	1.1 ± 0.34	32.0	2.0 ± 0.59						
White shrimp	14.3	7.2 ± 1.71	-	0.0 ± 0.00	-	0.0 ± 0.04	3.2	1.9 ± 0.87	11.9	4.2 ± 1.74	4.8	1.3 ± 0.68						
Daggerblade grass shrimp	11.3	29.7 ± 13.03	-	0.2 ± 0.22	-	1.2 ± 0.64	10.1	12.0 ± 4.20	-	19.0 ± 13.00	-	0.0 ± 0.04						
Marsh grass shrimp	10.7	7.9 ± 2.41	-	1.8 ± 1.31	-	0.2 ± 0.17	10.3	8.7 ± 2.53	-	1.1 ± 0.72	-	0.0 ± 0.04						
Estuarine mud crab	5.5	1.5 ± 0.35	17.3	3.7 ± 1.00	-	0.6 ± 0.21	13.2	4.0 ± 0.81	5.3	1.3 ± 0.50	-	0.4 ± 0.15						
Naked goby	-	1.2 ± 0.28	8.0	1.0 ± 0.29	15.5	2.8 ± 0.89	11.2	2.8 ± 0.58	7.2	1.0 ± 0.23	5.0	1.2 ± 0.78						
Gulf pipefish	-	1.3 ± 0.65	6.3	0.8 ± 0.19	-	0.6 ± 0.24	-	0.8 ± 0.20	6.3	1.7 ± 0.65	-	0.3 ± 0.16						
Clown goby	-	0.4 ± 0.17	3.9	0.8 ± 0.29	11.7	1.0 ± 0.34	-	0.6 ± 0.21	-	0.6 ± 0.22	14.8	1.1 ± 0.38						
Rainwater killifish	-	0.2 ± 0.13	3.6	1.3 ± 0.64	15.3	6.3 ± 2.89	-	1.1 ± 0.43	12.5	6.1 ± 2.91	-	0.5 ± 0.44						
Riverine grass shrimp	-	0.2 ± 0.17	-	1.3 ± 0.49	21.9	6.6 ± 2.49	5.4	2.6 ± 0.86	13.7	5.3 ± 2.47	-	0.1 ± 0.06						
Brackish grass shrimp	-	0.5 ± 0.32	3.4	2.3 ± 1.18	7.4	4.0 ± 2.17	6.5	6.1 ± 2.29	-	0.4 ± 0.26	-	0.3 ± 0.19						
Redear sunfish	-	0.0 ± 0.04	-	0.3 ± 0.13	3.3	0.5 ± 0.19	-	0.3 ± 0.12	-	0.5 ± 0.20	-	0.0 ± 0.00						
May 2010																		
Blue crab	25.3	2.3 ± 0.52	-	0.6 ± 0.18	9.5	0.4 ± 0.12	11.4	1.6 ± 0.54	9.9	0.8 ± 0.21	9.6	0.9 ± 0.25						
Gulf menhaden	22.6	48.5 ± 20.1	70.9	341.1 ± 108.20	-	0.1 ± 0.07	35.7	105.1 ± 41.82	29.0	125.5 ± 94.36	64.0	153.6 ± 60.99						
Daggerblade grass shrimp	17.2	3.8 ± 1.22	-	0.0 ± 0.00	-	0.1 ± 0.13	-	1.3 ± 0.83	12.1	2.3 ± 1.00	-	0.3 ± 0.26						
Spot	9.2	1.0 ± 0.38	-	0.0 ± 0.04	-	0.0 ± 0.00	-	0.1 ± 0.06	-	0.1 ± 0.07	7.1	0.9 ± 0.39						
Speckled worm eel	8.8	0.9 ± 0.29	-	0.1 ± 0.10	-	0.1 ± 0.07	-	0.3 ± 0.18	-	0.2 ± 0.10	7.2	0.6 ± 0.27						
Darter goby	5.3	1.2 ± 0.49	-	0.0 ± 0.00	-	0.0 ± 0.00	-	0.7 ± 0.44	-	0.1 ± 0.09	-	0.4 ± 0.27						
Pinfish	4.6	0.7 ± 0.21	-	0.0 ± 0.00	-	0.0 ± 0.00	-	0.1 ± 0.07	-	0.3 ± 0.13	-	0.2 ± 0.18						
Freshwater goby	-	0.3 ± 0.15	14.1	2.0 ± 0.34	-	0.0 ± 0.00	9.4	1.1 ± 0.35	9.9	0.6 ± 0.22	-	0.5 ± 0.22						
Estuarine mud crab	-	0.2 ± 0.11	7.3	1.8 ± 0.54	-	0.0 ± 0.04	5.9	1.4 ± 0.56	4.6	0.4 ± 0.16	-	0.2 ± 0.13						
Rainwater killifish	-	0.7 ± 0.56	-	0.4 ± 0.22	61.8	1.5 ± 0.37	14.0	1.6 ± 0.63	26.0	1.0 ± 0.28	-	0.0 ± 0.04						
Riverine grass shrimp	-	0.3 ± 0.27	-	0.2 ± 0.11	24.8	2.8 ± 1.14	15.4	3.2 ± 1.18	-	0.3 ± 0.19	-	0.0 ± 0.00						
Bay whiff	-	0.2 ± 0.13	-	0.6 ± 0.19	-	0.0 ± 0.00	-	0.1 ± 0.07	-	0.1 ± 0.09	5.6	0.6 ± 0.20						

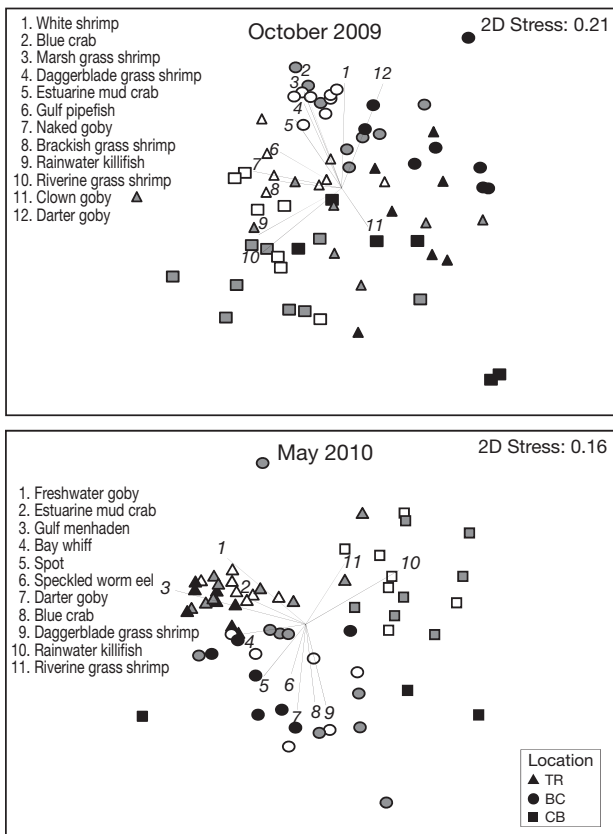


Fig. 3. Comparisons of nekton assemblage structure in the Mobile-Tensaw River delta (MTD) during fall 2009 and spring 2010 in multidimensional space. These non-metric multidimensional scaling plots display data from the Bray-Curtis similarity values for each sample in which organisms were collected. The symbols are shaded to represent habitat types — white: submerged aquatic vegetation; grey: marsh; black: shallow non-vegetated bottom. Species vectors indicate the direction of increasing density. Vector lengths are proportional to the magnitude of correlation with the ordination space and represent each species contribution to the community structure of locations (TR: Tensaw River; BC: Below Causeway; CB: Chocolatta Bay) and habitat types. For taxonomic names see Table S1 in the Supplement

and rainwater killifish, characterized CB during both sampling periods. In contrast, TR sites were quite variable during October 2009, many with higher densities of clown goby and most with relatively low densities of daggerblade grass shrimp and marsh grass shrimp. Assemblage composition shifted substantially at TR in May, when higher densities of gulf menhaden and freshwater goby were present.

The SIMPER results confirmed these differences in nekton assemblage structure and revealed the importance of transient fishery species in driving the differentiation among locations. For example, blue crab and white shrimp in fall (41%) and gulf menhaden and blue crab in spring (48%) contributed

much more to the assemblage structure of nekton at BC than CB (Table 2). Other transient species (spot: 9%; speckled worm eel: 9%; pinfish: 5%) also contributed to the assemblage structure of nekton at BC in spring (Table 2), but were absent from CB. Transients (all species combined) were much more abundant at BC (ANOVA: fall: $MS = 15.7756$, $F_{2,62} = 24.7406$, $p = 0.0001$; spring: $MS = 100.9165$, $F_{2,61} = 47.4363$, $p = 0.0001$) than CB. Transient fishery species also contributed substantially (e.g. blue crab in fall: 39%; gulf menhaden in spring: 71%) to the assemblage structure of nekton at TR (Table 2). In each season, resident species such as riverine grass shrimp and rainwater killifish dominated CB, and these 2 species contributed substantially to nekton assemblage structure (fall: 37%; spring: 87%) (Table 2).

The absence of some transient species at CB also reduced species richness at this location. Species richness was significantly greater at BC than CB in fall (ANOVA: $MS = 26.0461$, $F_{2,62} = 6.9918$, $p = 0.0018$) and greater at both BC and TR than CB in spring (ANOVA: $MS = 73.4400$, $F_{2,61} = 18.3815$, $p = 0.0001$).

Densities of most abundant taxa were concentrated in SAV beds and emergent marsh vegetation (Table 2, Fig. 4). Species richness was higher at vegetated (SAV, marsh) habitat types than SNB (ANOVA: fall: $MS = 109.6182$, $F_{2,62} = 29.4259$, $p = 0.0001$; contrast: $p = 0.0001$; spring: $MS = 23.1125$, $F_{2,61} = 5.7849$, $p = 0.0050$; contrast: $p = 0.0071$) and in fall, higher in SAV than marsh (ANOVA contrast: $p = 0.0021$). In fall, densities of transients were significantly higher at vegetated than non-vegetated sites (ANOVA: $MS = 5.0092$, $F_{2,62} = 7.8558$, $p = 0.0009$; contrast: $p = 0.0013$) and higher in SAV than marsh (contrast: $p = 0.0400$). Blue crab dominated the nekton assemblages of both vegetated habitat types (marsh: 26%; SAV: 25%) (Table 2). Estuarine mud crab (13%), naked goby (11%), daggerblade grass shrimp (10%), and marsh grass shrimp (10%) also contributed most to the assemblage structure of nekton in SAV, whereas riverine grass shrimp (14%), rainwater killifish (13%), and white shrimp (12%) were most important at marsh sites (Table 2). Densities of most species were relatively low over SNB (Fig. 4), and, in fall, blue crab (36%), darter goby (32%), and clown goby (15%) contributed most to the assemblage structure of nekton in this habitat type (Table 2). In spring, gulf menhaden (SAV: 36%; marsh: 29%), rainwater killifish (SAV: 14%; marsh: 26%), and blue crab (SAV: 11%; marsh: 10%) contributed to the assemblage structure of nekton in both vegetated habitat types; riverine grass shrimp

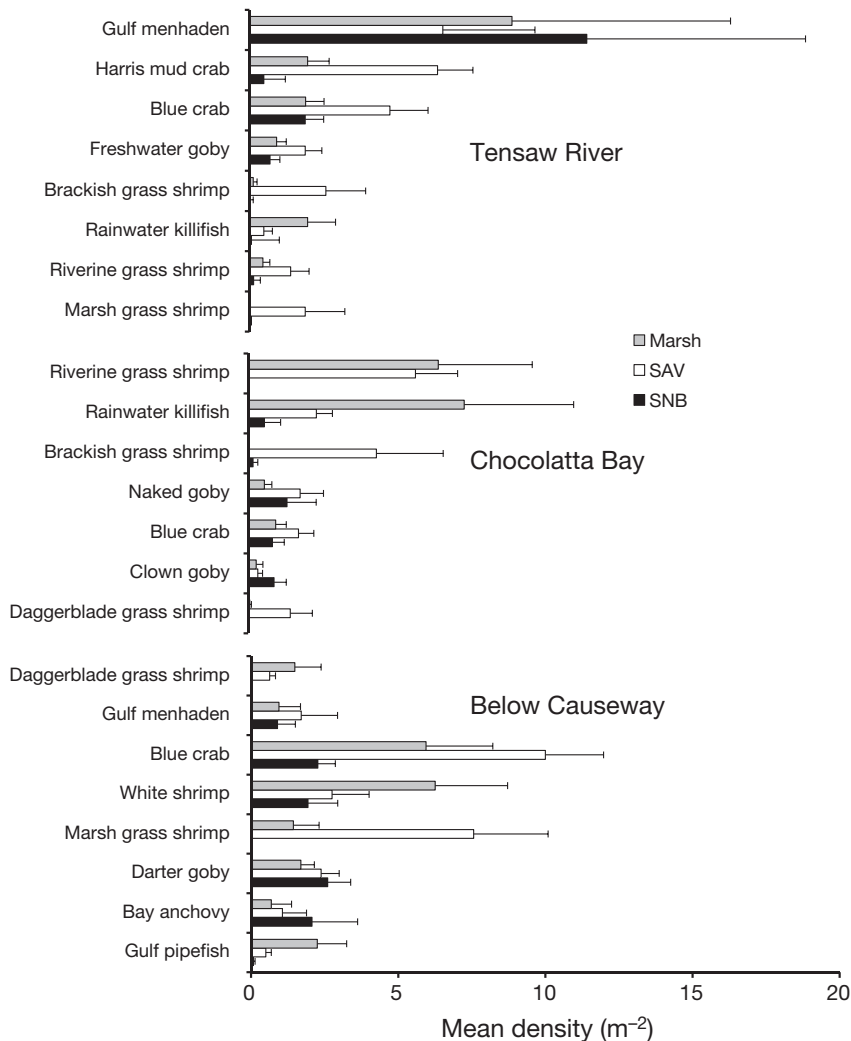


Fig. 4. Comparison of nekton assemblages among locations. Species within each location are listed in descending order of total abundance, and their distribution is shown among habitat types (marsh, SAV: submerged aquatic vegetation, and SNB: shallow non-vegetated bottom). The data shown for gulf menhaden (Tensaw River and Below Causeway) and daggerblade grass shrimp (Below Causeway only) represent only 5% of actual values. Error bars = 1 standard error (SE). Means (individuals m^{-2}) and SEs were calculated from 16 samples per habitat type (except Below Causeway [SNB = 15] and Tensaw River [SNB and SAV = 15 samples each]). For taxonomic names see Table S1 in the Supplement

(15%) and daggerblade grass shrimp (12%) were also important in SAV and marsh, respectively (Table 2). The relative contribution by gulf menhaden to the assemblage structure of nekton was higher in SNB (64%) than in the vegetated habitat types, and spot (7%), speckled worm eel (7%), and bay whiff (6%) also were important in SNB, but not in SAV or marsh.

Mean size differed by location for gulf menhaden and by habitat type for blue crab. We collected the largest gulf menhaden at the BC location (ANOVA:

$MS = 10.7344$, $F_{2,28} = 17.2731$, $p = 0.0001$). Blue crab size did not differ among locations, but we collected significantly larger blue crabs at marsh (18.3 ± 2.88 mm) and SAV (26.2 ± 6.02 mm) sites than SNB (10.7 ± 0.49 mm) sites (ANOVA: $MS = 1207.7400$, $F_{2,51} = 3.7223$, $p = 0.0310$; contrast: SAV + marsh vs. SNB, $p = 0.0275$). All but 1 white shrimp (83 mm total length at CB) were collected at the BC location. Within the BC location, no difference was detected in shrimp size among habitat types (ANOVA: $MS = 28.5595$, $F_{2,13} = 1.6892$, $p = 0.2228$).

DISCUSSION

The seasonal recruitment of transient species, which is possible only with a hydrologically connected migration corridor, appears to drive the assemblage structure of nekton in delta habitats and is necessary to maintain nekton species richness and the integrity of nekton assemblages. In our study, transient fishery species were major contributors to nekton composition at the hydrologically connected locations, and these areas appeared to provide important nursery habitat for several species. The seasonal recruitment of offshore spawning species is also a key factor in maintaining nekton assemblages in estuaries and coastal lagoons of the USA (Murphy & Secor 2006), Bahamian tidal creeks (Valentine-Rose & Layman 2011), and estuarine and floodplain wetlands in Australia (Sheaves et al. 2007, 2010, Sheaves & Johnston

2008). In contrast, hydrologically restricted CB had a significantly different nekton assemblage, presumably because fewer marine-spawned species could recruit there to potential nursery habitats as young. Estuarine residents dominated the assemblage structure of nekton in CB.

This delta–GoM connection enables other essential ecosystem processes such as the accumulation and translocation of nutrients by migrating nekton (Kneib 1997, Sheaves 2009). Estuarine-dependent fishery species may represent important conduits for the

transfer of energy and nutrients from hydrologically connected delta habitat to the lower estuary and nearshore GoM. For example, Deegan (1993) estimated that gulf menhaden migrating from the Atchafalaya delta to the GoM transfer 5 to 10% of total primary production from the estuary to the coastal marine ecosystem. This GoM–delta connectivity is critical both for maintaining this trophic transfer to coastal waters and enabling the juveniles of fishery species to recruit from delta habitats to adult populations. The degree to which this transfer of secondary production from the MTD supports coastal fisheries of the north-central GoM is unknown and warrants further study.

Gulf menhaden *Brevoortia patronus* in our study area appear to initially recruit as larvae and small juveniles to sites in the TR (based on differences in sizes: BC > TR) and gradually move down estuary as they increase in size (Deegan 1993). This fishery species, which dominated the nekton at BC and TR in spring, is one of the most abundant fish within estuaries throughout the northern GoM in late winter and early spring (Deegan & Thompson 1985, Felley 1987). Although adjacent and connected to the TR, and located approximately the same distance from the source of new recruits, we collected only 3 gulf menhaden in CB. Apparently, the lack of an unrestricted connection to upper Mobile Bay limits recruitment into the potential nursery areas of CB.

Juvenile blue crabs *Callinectes sapidus* were also an important component of the nekton in marsh and SAV beds at the 2 locations (BC, TR) directly connected to Mobile Bay. They can also dominate nekton in vegetated habitats of the Atchafalaya River delta, with mean densities in SAV beds of up to 17 m⁻² (Castellanos & Rozas 2001). Rakocinski & McCall (2005) examined blue crab recruitment in a Mississippi estuary and commonly collected juveniles (>6 mm CW) at their farthest up-estuary site within SAV beds of *Vallisneria americana* and *Ruppia maritima*; smaller blue crabs (earlier life stages), however, were rare at this site. Despite being an important component of faunal assemblages in *Myriophyllum spicatum*- and *Heteranthera dubia*-dominated SAV beds in the MTD (Martin & Valentine 2011), densities of early life stages were reported to be relatively low in a nearby location of the delta (Heck et al. 2001). Based on the distribution of megalopae and small juveniles (2 to 8 mm CW) within Mobile Bay, Heck et al. (2001) identified the lower portion of the bay as the primary blue crab nursery area. Because larger juveniles were common at their delta site in the summer and early fall, Heck et al.

(2001) also surmised that blue crabs move up the estuary toward the delta following megalopae settlement in the lower estuary. We also collected few small juveniles at our delta sample sites during spring. In fall, however, juvenile densities in the delta were much higher than in spring, but even then, most blue crabs (78%) in our samples were larger (>8 mm CW) juveniles. Perhaps a recruitment pulse occurred between our sampling events, and our fall sampling date was too late to document the occurrence of newly settled megalopae and small juveniles from this recruitment event. Nonetheless, we agree with Heck et al. (2001) that the delta may play a significant nursery role in determining the density of adults in this estuary. To provide this nursery function, however, delta habitats must be open to the wider estuary to allow for unfettered life-history migrations to and from these areas (Secor & Rooker 2005, Sheaves 2009). CB contains potential blue crab nursery habitat, but based on the results of our study, its full capacity does not appear to be realized.

Juvenile white shrimp *Litopenaeus setiferus* were also relatively important numerically to the assemblage structure of nekton at delta marsh sites in fall, but only at the BC location. Freshwater conditions prevailed at TR and CB in fall, and some studies show that white shrimp densities are reduced in low-salinity environments (Peterson & Ross 1991, Rozas & Minello 2010). In a 3 yr comparison of white shrimp densities at 5 sites located along a salinity gradient in Mobile Bay, Howe et al. (1999) reported relatively low white shrimp densities of 0.0 to 0.3 m⁻² at their delta sample site (Polecat Bay) when compared to densities of 0.7 to 7.7 m⁻² at high-salinity sites closer to the coast. White shrimp density was also positively correlated with salinity in their study (Howe et al. 1999). The lack of shrimp at TR and CB, however, cannot be explained simply by differences in salinity among locations because freshwater conditions prevailed throughout the delta during our fall sampling trip. Perhaps the slightly longer distance to the upper delta sites is too far for new recruits, but this also seems unlikely. Recruits are capable of reaching locations north of the Causeway as others have shown (Howe et al. 1999, Goecker et al. 2009).

Southern flounder *Paralichthys lethostigma* may use the MTD as a nursery area as well, and perhaps also as a spawning area (Lowe et al. 2011), but densities of this species were low in the delta. We collected only 8 individuals exclusively at hydrologically unrestricted locations in the delta. Peak densities of southern flounder in river systems coincide with early spring floods (Rozas & Hackney 1984, Rogers

et al. 1984, Allen & Baltz 1997), and we likely sampled the delta too late in the spring to observe the peak recruitment period for this species.

Our PCA analyses identified some differences in environmental characteristics (water depth, water temperature, DO, turbidity) that separated habitat types or locations. Habitat types were differentiated most in physical characteristics by water depth. This variable and vegetation structure both influence habitat selection by nekton (Baltz et al. 1993, Ruiz et al. 1993, Minello 1999). Other than gulf menhaden, the young of most fishery species we collected were concentrated in SAV and marsh habitat. Most comparisons of estuarine habitats show this pattern of higher nekton abundance and species richness at shallow vegetated than at non-vegetated sites (Heck et al. 2001, Kanouse et al. 2006, Rozas & Minello 2006). Differences among locations were small in magnitude (except depth), likely biologically unimportant, and not useful in explaining patterns of nekton distribution. We considered the possibility that the deeper SNB sites at CB may partially explain the lower densities of transient species at CB. This explanation seems unlikely, however, because densities of these species in CB also were low at marsh and SAV sites, and these sites at CB were similar in depth to those at the other locations. The Causeway does alter the aquatic environment (reduces salinity and wave energy; Martin & Valentine 2012; increases the likelihood of hypoxia; Valentine & Sklenar 2006) and impairs nutrient and energy exchange (Goecker et al. 2009) in ways that may indirectly affect nekton densities and assemblage structure. The more important effect on nekton populations in the delta, however, is the direct interference the Causeway has on the recruitment processes of marine-spawned species.

Based on comparisons of nekton abundance and assemblage structure in our study area, we conclude that the US Highway 90-98 Causeway has severely reduced the potential nursery function of vegetated habitats in CB and other parts of the delta by physically blocking a direct hydrological connection for recruits from Mobile Bay. This conclusion is similar to other examples of diminished nursery function resulting from hydrological restrictions documented in the literature. In fact, road construction may be the most common activity cited for disrupting ecosystem-wide hydrologic connectivity (Layman et al. 2004, Eberhardt et al. 2011). Other human activities can also reduce hydrological connectivity and limit the nursery function of wetlands: agricultural impoundments (Trepagnier et al. 1995, Tupper & Able 2000,

Navodaru et al. 2005), flood control (Viosca 1928, Miranda 2005), mosquito control (Harrington & Harrington 1982), and structural marsh management for waterfowl and wildlife (Cowan et al. 1988, Rogers et al. 1994, Rozas & Minello 1999). Many of these activities were implemented decades ago before the full effects were known. Yet, storm surge barriers and levees across estuarine basins are currently being planned to control flooding from hurricanes in Louisiana (Coastal Protection & Restoration Authority of Louisiana 2007). Openings for nekton passage through the structures are being considered, but the efficacy of these openings is unknown.

Breeching or completely removing tidal restrictions can often reverse impacts to the nursery function of estuarine wetlands (Roman et al. 2002, Navodaru et al. 2005, Valentine-Rose & Layman 2011), but avoiding future projects altogether would be more prudent. Replacing sections of the US Highway 90-98 Causeway with an elevated highway to restore the hydrological connection between the delta and Mobile Bay should be considered. Such a project would restore environmental conditions (e.g. increase wave energy and mixing) in the delta that may improve water quality and favor *Vallisneria americana* over non-native species such as *Myriophyllum spicatum* (Martin & Valentine 2012). Moreover, breeching the Causeway would increase access north of the Causeway to currently impaired nursery habitat for fishery species.

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