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ARTICLE

Effects of Hydrologic Connectivity and Environmental Variables on Nekton Assemblage in a Coastal Marsh System

Sung-Ryong Kang · Sammy L. King

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Abstract Hydrologic connectivity and environmental variation can influence nekton assemblages in coastal ecosystems. We evaluated the effects of hydrologic connectivity (permanently connected pond: PCP; temporary connected pond: TCP), salinity, vegetation coverage, water depth and other environmental variables on seasonal nekton assemblages in freshwater, brackish, and saline marshes of the Chenier Plain, Louisiana, USA. We hypothesize that 1) nekton assemblages in PCPs have higher metrics (density, biomass, assemblage similarity) than TCPs within all marsh types and 2) no nekton species would be dominant across all marsh types. In throw traps, freshwater PCPs in Fall (36.0±1.90) and Winter 2009 (43.2±22.36) supported greater biomass than freshwater TCPs (Fall 2009: 9.1±4.65; Winter 2009: 8.3±3.42). In minnow traps, saline TCPs (5.9±0.85) in Spring 2009 had higher catch per unit effort than saline PCPs (0.7±0.67). Our data only partially support our first hypothesis as freshwater marsh PCPs had greater assemblage similarity than TCPs. As predicted by our second hypothesis, no nekton species dominated across all marsh types. Nekton assemblages were structured by individual species responses to the salinity gradient as well as pond habitat attributes (submerged aquatic vegetation coverage, dissolved oxygen, hydrologic connectivity).

Keywords Chenier Plain marsh · Nekton assemblage · Hydrologic connectivity · Pond characteristics

S.-R. Kang (✉)
School of Renewable Natural Resources, Louisiana State University AgCenter, Rm. 315, RNR Building, Baton Rouge, LA 70803, USA
e-mail: skang1@tigers.lsu.edu

S. L. King
U.S. Geological Survey, Louisiana Fish and Wildlife Cooperative Research Unit, School of Renewable Natural Resources, Louisiana State University AgCenter, Baton Rouge, LA 70803, USA

Introduction

Hydrologic connectivity in coastal ecosystems influences many environmental variables and the assemblage of aquatic organisms (Fernandes et al. 2009; Rozas and Minello 2010). Hydrologic connectivity refers to the spatiotemporal exchange pathways of water and energy along longitudinal and lateral dimensions (Roach et al. 2009). Lateral patterns within coastal marshes are affected by dry and wet phases due to seasonal variations in the relative extent of the flooded area. Longitudinal patterns are affected by regionally varied tidal flooding and freshwater flow based on the connected channel from coast to upstream (Doyle et al. 2007). Thus, coastal brackish and saline marsh areas are often tidally connected to the estuary by one or more channels (Rozas and Minello 2010) but freshwater marshes do not have regular pulses of flooding and drying (Mitsch and Gosselink 2000) because their greater distance from the ocean dampens the influence of the tidal cycle (Day et al. 2007). These connectivity patterns are important drivers of environmental variables, such as salinity, temperature, and oxygen in coastal marsh systems (Chabreck 1988; Hunter et al. 2009). Also, marsh flooding controls the accessibility of the marsh surface by aquatic organisms (Minello et al. 2012).

Regional-scale patterns in the distribution of organisms result primarily from species responses to their physical environment because dominant abiotic variables are thought to act like a physiological sieve (Remmert 1983; Martino and Able 2003). Several studies have indicated that salinity strongly affects nekton assemblages in coastal marshes (Thorman 1986; Peterson and Ross 1991; Thiel et al. 1995; Martino and Able 2003), although most of these studies did not sample across the full salinity gradient. In addition, the presence and depth of water can positively or negatively impact nekton movement (Whoriskey and Fitzgerald 1989; Szedlmayer and Able 1993; Humphries and Baldwin 2003; Lake 2003) and foraging habitat quality

(Kneib and Wagner 1994; Balcombe et al. 2005). Nekton is also affected by variation in oxygen, temperature, and vegetation structure in coastal marshes. McKinsey and Chapman (1998) noted habitat patches of varying oxygen levels across spatial scales may be important in structuring nekton diversity. McMahon and Tash (1988) documented that high temperatures in infrequently flooded ponds may contribute to population changes through increased emigration rates. Moreover, nekton abundance and diversity have generally been shown to be higher along vegetated marsh pond edges (Baltz et al. 1993; Peterson and Turner 1994), within seagrass beds (Connolly 1994), and within freshwater submerged aquatic vegetation (SAV) beds (Rozas and Odum 1987; Castellanos and Rozas 2001) than within non-vegetated habitats. Higher nekton densities in vegetated than unvegetated areas are often ascribed to greater protection and more prey provided by vegetated habitats (Gilinsky 1984; Bell and Westoby 1986; Rozas and Odum 1988; Fredette et al. 1990; Lubbers et al. 1990; Minello 1993). Finally, increased duration of connectivity among habitat types may increase the similarity of nekton assemblages.

A clear understanding of the linkages among hydrologic connectivity, environmental variables, and nekton assemblages would enhance our understanding of nekton habitat characteristics in coastal systems and of the effects of anthropogenic activities, such as marsh management and pond characteristic alteration (e.g., mosquito control ditches: hydrological isolated pond converted to a pond connected to other waterways), on nekton assemblage patterns. The principal objectives of this study are to: 1) examine the effects of hydrologic connectivity (i.e., permanently connected pond [PCP: permanently connected channel during all seasons], temporarily connected pond [TCP: temporarily connected by surface water to the surrounding marsh but not permanently connected to a channel]) on the density, biomass, and similarity of nekton assemblages and 2) compare seasonal patterns of nekton assemblages in different marsh types (i.e., freshwater, brackish, saline). We hypothesize that 1) nekton assemblages in PCPs have higher metrics (density, biomass, and assemblage similarity) than TCPs over all marsh types and 2) no nekton species would be dominant across all marsh types.

Methods

Study Areas

This study was conducted in White Lake Wetlands Conservation Area (WLWCA, 29°52′50″ N, 92°31′11″ W) and Rockefeller State Wildlife Refuge (RSWR, 29°40′93″ N, 92°48′45″ W) in the Chenier Plain of southwestern Louisiana (Fig. 1). The area extended north to south across three (freshwater, brackish, saline) vegetation-salinity areas defined and mapped by Chabreck and Linscombe (1997).

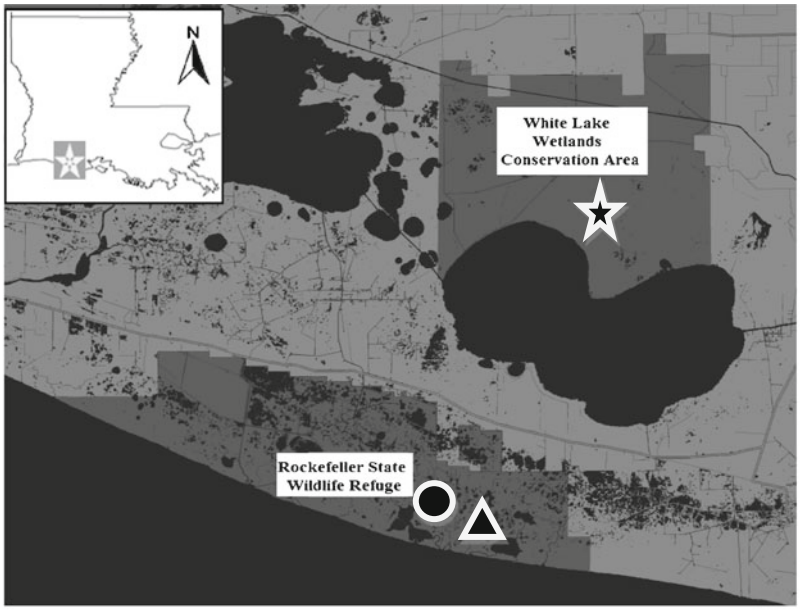
We used marsh vegetation (i.e., freshwater marsh: *Panicum hemitomon*; brackish marsh: *Spartina patens*; saline marsh: *Spartina alterniflora*, Chabreck and Nyman 2005) to define our marsh types because vegetation does not respond to daily salinity fluctuations (Visser et al. 1998; Rozas and Minello 2010). Salinity fluctuation (i.e., freshwater marsh: 0.1–3.4 ppt; brackish marsh: 1.0–8.4 ppt; saline marsh: 8.1–29.4 ppt) was also a major consideration of our decision to select marsh types.

WLWCA is a 28,719 ha freshwater marsh (0.2–1.7 ppt) that is dominated by *Panicum hemitomon* and *Sagittaria lancifolia*. The 42,400 ha RSWR consists of 17 impoundments that allow for control of both water level and salinity of the enclosed marsh through flap gates, weirs, and gated culverts (Wicker et al. 1983). The Unit Six management unit (7,200 ha, 0.9–8.1 ppt) of RSWR was selected as tidal brackish marsh habitat; it was dominated by *Spartina patens* and *Typha latifolia*. In addition, an unmanaged area (2.2–27.7 ppt) of similar size and dominated by *Spartina alterniflora* was selected as tidal saline marsh habitat. The average daily tidal range in Unit Six and unmanaged area next to Unit Six during the sampling period was 3.6 cm and 5.5 cm, respectively (Coastwide Reference Monitoring System: http://www.lacoast.gov/crms2/ Home. aspx, 2009–2010).

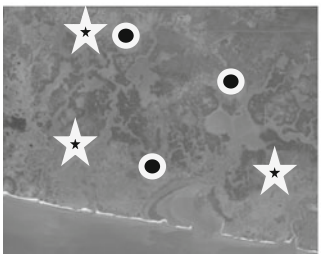
Pond Characteristics

In each marsh type, we randomly selected three PCPs and three TCPs (total 18 ponds) for more intensive study. All ponds in the study sites were identified from aerial photography, field visits, and long-term observations (Jeb Linscombe, Louisiana Department of Wildlife and Fisheries, personal communication) and were then classified as either a PCP (i.e., permanently connected to a channel during all seasons) or a TCP (i.e., temporarily connected by surface water to the surrounding marsh and channel). TCPs did not have an obvious connecting channel.

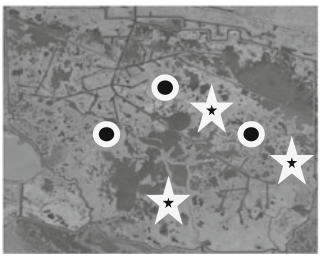
We deployed a water-level recorder in the interior of each pond in November 2008 to measure water depth 6 times per day until the end of the study. Also, a staff gage was established at the border between the pond and emergent marsh to measure disconnection of surface water and connected water depth (CWD). CWD was the water depth at the border between the pond and the emergent marsh when the pond is connected with surface water to the channel or surrounding marsh (marginal zone of the pond). CWD was determined by comparing water depths obtained at the staff gage on several occasions during the study. In the marshes, PCPs typically had a gradually sloped bank whereas TCPs had a more vertical bank. These edge shapes may affect CWD. A second hydrologic metric was the seasonal



(a) White Lake Wetlands Conservation Area and Rockefeller State Wildlife Refuge



(b) Salinemarsh



(c) Brackish marsh

(d) Freshwater marsh

Fig. 1 Rockefeller State Wildlife Refuge and White Lake Wetlands Conservation Area are located in southwestern Louisiana, USA (**a** Modified Google Map, https://maps.google.com, Accessed date: November 16th 2012). Saline (**b** Rockefeller State Wildlife Refuge: *triangle*), brackish (**c** Rockefeller State Wildlife Refuge: *circle*), and freshwater (**d** White Lake Wetlands Conservation Area: *star*) marshes used in our study. In **b**, **c**, and **d**, *circles* (PCPs) and *stars* (TCPs) are our sampling points. **a** White Lake Wetlands Conservation Area and Rockefeller State Wildlife Refuge. **b** Saline marsh. **c** Brackish marsh. **d** Freshwater marsh

duration of isolation (SDI). SDI is the seasonal duration of disconnection among the pond, channel, and emergent marsh. This is the number of days that water was 0 cm deep at the marsh edge.

To assess variation in other environmental parameters, we measured salinity, dissolved oxygen (DO), and temperature with a YSI Model 85 Water Quality Monitor. We used 1-m stick to check sampling point water depth. Percent cover of submerged aquatic vegetation (SAV) in 1×1 m frame was also determined at three points in each pond and the mean coverage was determined.

Nekton Sampling

To determine nekton characteristics, we sampled each pond seasonally from April 2009 to May 2010. For purpose of this study, seasons were defined as: 1) Spring 2009 (March–May); 2) Summer 2009 (June–August); 3) Fall 2009 (September–November); 4) Winter 2009 (December–February); and 5) Spring 2010 (March–May). Once per season, we used a throw trap and minnow traps to sample nekton (Classen 2008) at each pond edge. A 1-m^2 aluminum-sided throw trap similar to that described by Kushlan (1981) was tossed at three random points in each sampling pond. Sweeps with a 1-m wide bar seine (3-mm mesh size) were used to remove the nekton from the trap. Five consecutive sweeps without collecting organisms were completed before the trap was considered free of nekton. Five minnow traps (42×23 cm with a 6-mm mesh, baited with a piece of chicken gizzard) were set at each of 3 random points in each sampling pond for approximately 2 h. Fish and decapod crustaceans were frozen and returned to the laboratory where they were sorted and identified to species or to the lowest possible taxon. Total lengths were measured to the nearest millimeter for fishes. All nekton was weighed to the nearest 0.001 g wet-weight to determine biomass (g/m^2 for throw trap, g/2-hour soak for minnow traps).

Nekton Residence Status

To determine the effect of the marsh and pond types on nekton communities, each species was assigned a residence status based on literature of natural history characteristics

and a search of fishbase (Froese and Pauly 2008; http://www.fishbase.org). Tidal freshwater resident (TFR) species were defined as those that spend their entire life cycle within the estuary and are abundant in the tidal freshwater portion of the estuary (e.g., *Lepomis macrochirus*; *Poecilia latipinna*); brackish migrant (BM) species spent at least a portion or all of their life cycle in the estuary, but typically in more saline water than tidal freshwater species (e.g. *Anchoa mitchilli*; *Gobiosoma bosc*, Piazza and La Peyre 2009a).

Statistical Analyses

All data were analyzed separately by gear type. For ANOVA analyses listed below, data were tested for normality with the Shapiro–Wilks test. In the event that the residuals were not normally distributed, the data were log-transformed. Data are reported as mean ± SE, and significance level was chosen at α=0.05 or less. ANOVA (Proc Mixed, Version 9.2, SAS Institute, North Carolina) was used to test for statistical differences in environmental variables, nekton density and biomass by season, marshes, and pond types. Significant ANOVA effects were tested using post-hoc comparisons of Tukey adjusted least squared means. Linear regression (Proc Mixed, Version 9.2, SAS Institute, North Carolina) was used to examine the potential relationship between nekton assemblage characteristics (i.e., density, biomass) and environmental factors.

Multivariate analyses of nekton communities were also performed for each gear type on a full species abundance matrix. PRIMER software (Clarke and Gorley 2006) was used to test the effect of hydrologic connectivity on assemblage similarity within the same pond types during all sampling periods. ANOSIM was performed on a Bray-Curtis dissimilarity matrix that was computed on the fourth-root transformed abundance data. We compared differences of assemblage similarity for pond types with the one-way SIMPER (p=0.05). This transformation was used to down-weight the contribution of common species so that the presence of rare species could also play a role in determining assemblage structure (Clarke and Warwick 2001). Canonical Correspondence Analysis (CCA, ter Braak and Smilauer 2002) was used to investigate potential associations between taxa and environmental variables at all sites. Species were included in the CCA if they were represented by more than three individuals (Gauch 1982; Piazza and La Peyre 2009b).

Results

Pond Characteristics

The mean diameter of randomly selected PCPs and TCPs were 99.0±14.6 m and 75.4±17.7 m, respectively (Kang 2011). Comparisons of water chemistry (salinity, DO, temperature), physical hydrology (CWD, SPWD, SDI), and SAV coverage by season, within a pond type across marshes (e.g., comparison of PCPs value among freshwater, brackish, saline marsh), and between pond types within a marsh (e.g., PCPs vs. TCPs value in freshwater marsh) are summarized in Table 1; see also Kang (2011).

Nekton Metrics (Density, Biomass, Assemblage Similarity)

We collected 31,011 nekton of 42 taxa from 540 samples that include throw (41 taxa, 24,603 individuals, Table 2) and minnow (33 taxa, 6,408 individuals, Table 3) trap samples. We identified a total of 23 nekton taxa in freshwater marsh (PCPs: 23 taxa, 3,820 individuals; TCPs: 17 taxa, 3,824 individuals), 18 nekton taxa in brackish marsh (PCPs: 16 taxa, 11,214 individuals; TCPs: 14 taxa, 7,845 individuals), and 24 nekton taxa in saline marsh (PCPs: 22 taxa, 951 individuals; TCPs: 18 taxa, 3,357 individuals). In throw trap samples, species richness within a pond type across marshes was greater in freshwater PCPs than in saline PCPs ($F_{2,132}$= 8.71, p<0.01) while species richness in TCPs in all marshes did not differ. Species richness calculated from minnow trap samples also did not differ.

Throw Trap Sampling

Seasonal nekton density ranged from 3.6±2.23 organisms/m^2 (mean ± SE; saline PCPs-Winter 2009) to 423.9± 89.11 organisms/m^2 (brackish PCPs-Fall 2009) (Table 4). Nekton density within a pond type across marshes indicated that freshwater and brackish PCPs in Summer 2009 were higher than saline PCPs ($F_{2,24}$=5.73, p=0.04). Brackish TCPs in Spring 2009 was higher than in freshwater and saline ($F_{2,24}$=8.16, p=0.02) TCPs. Between pond types within a marsh, nekton densities did not differ for any marsh type. Nekton biomass ranged from 0.3±0.26 g wet wt/m^2 (saline PCPs-Winter 2009) to 46.5±25.74 g wet wt/m^2 (brackish PCPs-Spring 2010). Similar to nekton density, nekton biomass also showed several seasonal differences within a pond type across marshes. Nekton biomass in freshwater and brackish PCPs in Winter 2009 was greater than that of saline PCPs ($F_{2,24}$=40.90, p<0.01). Brackish TCPs in Fall 2009 supported higher biomass than freshwater TCPs but biomass in saline TCPs did not differ ($F_{2,24}$= 13.71, p<0.01). Between pond types within a marsh, freshwater PCPs in Fall and Winter 2009 supported greater biomass than freshwater TCPs (Table 4). Linear regression analysis revealed nekton density and biomass in freshwater ponds were negatively related with CWD (density: R^2= 0.50, p<0.01) and SPWD (density: R^2=0.61, p<0.01; biomass: R^2=0.63, p<0.01). However, no statistically significant relationships were observed between environmental

Table 1 Comparison of means (±SE) of connectivity factors (n=7,668), water chemistry (n=252), and SAV coverage (n=90) within a pond type across marshes (letters). Means sharing a capital (among PCPs) or lower case (among TCPs) letter on a row do not differ (p>0.05)

	Freshwater		Brackish		Saline	
	PCP	TCP	PCP	TCP	PCP	TCP
Spring 2009						
Salinity (ppt)	1.2 (0.15)A	0.4 (0.07)a	6.9 (0.53)A	5.6 (0.35)ab	16.4 (2.18)B	13.6 (3.10)b
Dissolved oxygen (mg/l)	2.8 (0.24)A	3.3 (0.59)a	4.5 (0.13)A	4.4 (0.08)a	3.2 (0.84)A	3.1 (0.77)a
Temperature (°C)	30.1 (2.05)A	27.2 (1.95)a	25.7 (3.35)A	25.8 (3.00)a	25.8 (1.20)A	25.4 (1.35)a
SAV coverage (%)	34.4 (5.47)A	32.2 (4.75)a	14.2 (4.17)B	12.1 (7.23)ab	0.0 (0.00)B	0.0 (0.00)b
Sampling point water depth (cm)	34.4 (4.03)A	36.4 (1.04)a	39.6 (1.45)A	42.0 (2.66)a	10.8 (2.84)B	22.2 (1.07)b
Connected water depth (cm)	14.2 (0.38)A	18.1 (0.42)a	35.9 (1.56)B	38.9 (1.91)b	11.6 (0.23)A	25.0 (1.82)a
Seasonal duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)a	0.0 (0.00)A	0.0 (0.00)a	0.0 (0.00)A	0.0 (0.00)a
Summer 2009						
Salinity (ppt)	1.6 (0.08)A	0.5 (0.07)a	7.0 (0.56)B	7.0 (0.75)a	18.4 (0.79)C	19.4 (4.14)b
Dissolved oxygen (mg/l)	1.4 (0.33)A	1.1 (0.46)a	3.7 (0.06)B	3.8 (0.90)b	4.1 (0.85)B	3.6 (0.49)b
Temperature (°C)	31.4 (0.85)A	30.8 (0.58)a	32.4 (2.26)A	33.4 (2.59)a	31.4 (1.49)A	32.5 (2.08)a
SAV coverage (%)	49.4 (20.69)A	34.4 (12.03)a	19.4 (2.00)A	8.9 (8.89)a	0.0 (0.00)A	0.0 (0.00)a
Sampling point water depth (cm)	30.8 (3.15)A	16.0 (0.80)a	22.1 (0.67)A	21.9 (1.58)b	10.7 (2.73)B	17.0 (1.44)ab
Connected water depth (cm)	2.9 (1.02)A	3.6 (1.86)a	12.4 (2.33)B	14.9 (2.29)b	7.9 (2.43)AB	12.1 (1.72)ab
Seasonal duration of isolation (days)	0.0 (0.00)A	74.1 (5.84)a	0.0 (0.00)A	15.0 (2.52)b	0.0 (0.00)A	15.0 (2.52)b
Fall 2009						
Salinity (ppt)	0.5 (0.01)A	0.3 (0.05)a	2.7 (0.44)AB	2.6 (0.34)ab	9.9 (3.12)B	8.8 (1.66)b
Dissolved oxygen (mg/l)	2.4 (0.64)A	1.2 (0.45)a	3.1 (0.10)AB	3.5 (0.48)b	4.4 (0.39)B	3.2 (0.42)b
Temperature (°C)	23.1 (3.33)A	22.0 (2.21)a	21.3 (2.43)A	20.8 (2.40)a	22.1 (0.87)A	22.5 (0.64)a
SAV coverage (%)	37.2 (16.17)A	36.7 (18.95)a	28.3 (14.37)A	27.2 (15.88)a	0.0 (0.00)A	0.0 (0.00)a
Sampling point water depth (cm)	40.9 (1.67)AB	47.9 (3.50)a	48.3 (3.06)A	53.6 (2.30)a	24.6 (6.89)B	30.7 (2.10)b
Connected water depth (cm)	26.4 (9.43)A	24.6 (8.91)a	42.7 (6.98)A	45.6 (7.25)a	25.2 (1.57)A	29.0 (2.50)a
Seasonal duration of isolation (days)	0.0 (0.00)A	12.9 (4.33)a	0.0 (0.00)A	0.0 (0.00)a	0.0 (0.00)A	0.0 (0.00)a
Winter 2009						
Salinity (ppt)	0.3 (0.02)A	0.2 (0.00)a	1.1 (0.06)AB	1.0 (0.04)a	6.7 (2.34)B	4.9 (1.57)b
Dissolved oxygen (mg/l)	5.6 (0.14)A	4.6 (1.03)a	6.6 (0.67)A	5.7 (1.51)a	6.7 (0.75)A	6.0 (1.29)a
Temperature (°C)	11.9 (1.69)A	11.8 (0.79)a	12.9 (1.15)A	13.1 (1.09)a	15.0 (2.36)A	14.2 (2.92)a
SAV coverage (%)	27.2 (2.00)A	11.7 (2.55)a	0.0 (0.00)B	2.8 (1.47)b	0.0 (0.00)B	0.0 (0.00)b
Sampling point water depth (cm)	27.2 (0.76)A	33.9 (3.78)a	31.1 (0.86)A	35.2 (1.66)a	17.0 (2.07)B	23.3 (0.47)b
Connected water depth (cm)	40.2 (2.14)A	34.6 (3.45)a	41.5 (6.19)A	45.1 (5.93)a	15.3 (4.43)B	25.3 (3.92)a
Seasonal duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)a	0.0 (0.00)A	0.0 (0.00)a	0.0 (0.00)A	1.0 (1.00)a
Spring 2010						
Salinity (ppt)	0.7 (0.08)A	0.2 (0.02)a	2.7 (1.16)A	3.7 (2.22)ab	14.1 (4.75)A	15.0 (2.50)b
Dissolved oxygen (mg/l)	2.0 (0.49)A	2.3 (0.21)a	3.9 (0.84)A	5.4 (0.27)b	4.3 (0.07)A	4.3 (0.46)b
Temperature (°C)	24.8 (3.33)A	25.1 (5.17)a	23.6 (3.45)A	25.4 (3.91)a	29.8 (3.50)A	31.7 (4.00)a
SAV coverage (%)	24.4 (7.35)A	45.0 (7.26)a	8.9 (5.89)AB	9.4 (5.30)b	0.0 (0.00)B	0.0 (0.00)b
Sampling point water depth (cm)	25.2 (3.11)A	24.6 (1.05)a	15.4 (0.80)B	20.1 (0.00)ab	12.4 (3.20)B	17.2 (1.48)b
Connected water depth (cm)	13.3 (7.04)A	10.0 (5.57)a	8.1 (5.62)A	11.4 (7.37)a	9.0 (3.09)A	13.3 (1.73)a
Seasonal duration of isolation (days)	0.0 (0.00)A	41.1 (7.80)a	0.0 (0.00)A	42.0 (9.07)a	0.0 (0.00)A	3.0 (1.00)a

variables and nekton density/biomass in brackish and saline marshes.

The ANOSIM results in freshwater (Global R: 0.21, p< 0.01) and saline (Global R: 0.13, p<0.01) marsh demonstrated that assemblage similarity between pond types within a marsh was affected by hydrologic connectivity (i.e., SDI), but no relationship was observed between assemblage similarity and SDI in brackish ponds (Global R: 0.07, p=0.06). In all cases, SIMPER (p=0.05) detected differences in average similarity between pond types

Table 2 Mean nekton density (organisms/m^2 (±SE)) in throw trap samples by pond type in three marsh types. Residence status classification is as follows: TFR, tidal freshwater resident; BM, brackish migrant. Definitions for both categories are from Piazza and La Peyre (2009a) and are described in the text. Abbreviations are as follows: Abb = abbreviation, RS = residence status, and % TC = total catch percentage

	Abb	RS	Freshwater			Brackish			Saline		
			PCP	TCP	% TC	PCP	TCP	% TC	PCP	TCP	% TC
Banded pygmy sunfish	BPS	TFR	4.1 (1.42)	3.3 (2.37)	5.1						
Bantam sunfish	BS	TFR	1.5 (0.38)	0.2 (0.13)	1.2						
Bayou killifish	BK	TFR	0.0 (0.04)	0.0 (0.00)	0.0	0.5 (0.21)	0.3 (0.89)	0.2	0.1 (0.07)	0.6 (0.28)	1.4
Bluegill	BG	TFR	0.5 (0.51)	0.0 (0.04)	0.3						
Creek chubsucker	CCS	TFR	0.0 (0.02)	0.0 (0.04)	0.0						
Diamond killifish	DK	TFR							0.0 (0.02)	0.2 (0.11)	0.4
Golden topminnow	GT	TFR	2.6 (1.25)	1.0 (0.76)	2.5						
Grass pickerel	GP	TFR	0.1 (0.08)	0.1 (0.13)	0.1						
Grass shrimp	GS	TFR	9.0 (3.64)	2.2 (0.71)	7.7	174.6 (61.09)	85.4 (41.43)	74.1	5.0 (2.49)	24.1 (8.19)	58.7
Gulf killifish	GK	TFR				0.2 (0.08)	0.2 (0.10)	0.1	0.2 (0.08)	0.2 (0.12)	0.8
Gulf pipefish	GPF	TFR				0.0 (0.02)	0.0 (0.00)	0.0			
Least killifish	LK	TFR	23.8 (10.83)	17.5 (11.83)	28.6	0.0 (0.00)	12.8 (6.73)	3.6			
Mosquitofish	MF	TFR	14.4 (7.77)	57.1 (52.35)	49.4	4.1 (1.43)	0.0 (0.00)	1.2	0.2 (0.15)	1.7 (1.59)	3.8
Northern starhead topminnow	NST	TFR	0.1 (0.09)	0.0 (0.04)	0.1						
Pirate perch	PP	TFR	0.0 (0.02)	0.0 (0.02)	0.0						
Rainwater killifish	RK	TFR	1.3 (1.07)	0.0 (0.00)	0.9	6.4 (1.14)	3.1 (1.02)	2.7	0.0 (0.04)	0.1 (0.11)	0.2
Redspotted sunfish	RS	TFR	0.1 (0.06)	0.0 (0.04)	0.1						
Red swamp crawfish	RSC	TFR	0.0 (0.04)	0.0 (0.00)	0.0	0.1 (0.13)	0.2 (0.19)	0.1			
Sailfin molly	SM	TFR	3.2 (2.18)	0.3 (0.19)	2.4	16.3 (6.53)	12.9 (2.91)	8.3	0.0 (0.04)	5.2 (2.7)	10.5
Sheepshead minnow	SHM	TFR	0.6 (0.44)	0.0 (0.00)	0.4	10.5 (2.31)	7.9 (1.50)	5.2	0.4 (0.27)	1.0 (0.26)	2.8
Spotted bass	SB	TFR	0.0 (0.04)	0.0 (0.00)	0.0						
Swamp darter	SD	TFR	0.0 (0.02)	0.0 (0.04)	0.0						
Swamp dwarf crawfish	SDC	TFR	1.2 (0.57)	0.4 (0.18)	1.1	0.2 (0.19)	0.9 (0.52)	0.3			
Warmouth	WM	TFR	0.0 (0.02)	0.0 (0.07)	0.0						
Yellow bullhead	YB	TFR	0.0 (0.02)	0.0 (0.02)	0.0						
Atlantic croaker	AC	BM									
Bay anchovy	BA	BM							1.3 (1.27)	0.0 (0.00)	2.6
Bay whiff	BW	BM							0.1 (0.04)	0.0 (0.00)	0.2
Black drum	BD	BM							0.0 (0.04)	0.1 (0.07)	0.2
Blue crab	BC	BM				0.5 (0.22)	0.3 (0.16)	0.2	1.0 (0.21)	1.7 (0.40)	5.4
Brown shrimp	BS	BM							0.6 (0.43)	1.0 (0.95)	3.2
Clown goby	CG	BM				0.1 (0.09)	0.0 (0.00)	0.0			

Table 2 (continued)

	Abb	RS	Freshwater			Brackish			Saline		
			PCP	TCP	% TC	PCP	TCP	% TC	PCP	TCP	% TC
Darter goby	DG	BM				0.1 (0.11)	0.0 (0.00)	0.0	0.0 (0.00)	0.0 (0.04)	0.0
Fat sleeper	FS	BM							0.0 (0.03)	0.3 (0.29)	0.6
Fiddler crab	FC	BM							0.0 (0.03)	0.0 (0.00)	0.0
Gulf menhaden	GM	BM							0.0 (0.02)	0.0 (0.00)	0.0
Inland silverside	IS	BM				9.8 (4.65)	0.8 (0.37)	3.0	0.1 (0.09)	0.2 (0.11)	0.5
Naked goby	NG	BM				2.5 (1.67)	0.1 (0.09)	0.7	0.0 (0.00)	0.0 (0.04)	0.0
Speckled worm eel	SWE	BM							0.1 (0.11)	0.0 (0.00)	0.2
Spot croaker	SC	BM							0.3 (0.31)	0.0 (0.00)	0.6
Striped mullet	STM	BM				0.1 (0.04)	0.0 (0.00)	0.0	0.5 (0.21)	0.1 (0.08)	1.2
White shrimp	WS	BM							2.1 (2.13)	1.1 (1.07)	6.5

(Table 5). Assemblage similarity of PCPs in freshwater marsh was greater than in TCPs, however, saline TCPs had higher similarity than PCPs.

Minnow Trap Sampling

Seasonal nekton catch per unit effort (CPUE, organisms/-minnow trap during 2 h) ranged from 0 (freshwater TCPs-Summer 2009) to 29.3±10.88 organisms/2 h (brackish TCPs-Summer 2009) in all marsh types (Table 4). Within a pond type across marshes, brackish and saline TCPs in Summer 2009 had a higher CPUE than freshwater TCPs ($F_{2,24}$=12.09, p<0.01) while PCPs in all marshes did not differ. Between pond types within a marsh, freshwater PCPs in Summer 2009 supported greater CPUE than freshwater TCPs (p=0.03) but saline TCPs in Spring 2009 had higher CPUE than saline PCPs (p=0.04). Nekton biomass ranged from 0 g wet wt/minnow trap during 2 h (freshwater TCPs-Summer 2009) to 37.2±26.64 g wet wt/minnow trap during 2 h (saline TCPs-Spring 2010). Seasonal nekton biomass within a pond type across marshes and between pond types within a marsh showed similar patterns in the throw trap data (Table 4). However, environmental variables in all marshes and nekton metrics did not reveal any relationship in linear regression analysis. The ANOSIM results in all marshes revealed the same patterns as in the throw trap data (Table 5).

Nekton Assemblage Distribution

For both gear types, CCA indicated significant relationships between the measured environmental variables and nekton assemblage during all sampling periods (1st axis: p<0.01, All axes: p<0.01). Furthermore, the results had similar patterns between the gear types (Figs. 2 and 3). Analysis of the species–environment relationships indicated that a number of relatively abundant species in freshwater ponds (e.g., least killifish *Heterandria formosa*, mosquitofish *Gambusia affinis*, golden topminnow *Fundulus chrysotus*, bantam sunfish *Lepomis symmetricus*, Table 2) were positively associated with SAV and negatively with salinity. Conversely, relatively abundant species in saline ponds (e.g., gulf killifish *Fundulus grandis*, blue crab *Callinectes sapidus*, brown shrimp *Farfantepenaeus aztecus*) were positively associated with salinity and CWD. Relatively abundant species in brackish marsh such as inland silverside *Menidia beryllina*, sheepshead minnow *Cyprinodon variegatus*, sailfin molly *Poecilia latipinna*, and grass shrimp *Palaemonetes* spp. were located between the dominant groups of fresh and saline ponds and were positively associated with DO and SDI (Figs. 2 and 3). Although grass shrimp was the most abundant species (40.1 %) in saline marsh, it was grouped with the brackish marsh group and

Table 3 Mean nekton density (organisms/minnow trap during 2 h (±SE)) in minnow trap samples by pond type in three marsh types. Residence status classification is as follows: TFR, tidal freshwater resident; BM, brackish migrant. Definitions for both categories are from Piazza and La Peyre (2009a) and are described in the text. Abbreviations are as follows: Abb = abbreviation, RS = residence status, and % TC = total catch percentage

	Abb	RS	Freshwater			Brackish			Saline		
			PCP	TCP	% TC	PCP	TCP	% TC	PCP	TCP	% TC
Banded pygmy sunfish	BPS	TFR	0.0 (0.01)	0.0 (0.01)	0.4						
Bantam sunfish	BS	TFR	0.8 (0.30)	0.0 (0.01)	15.9						
Bayou killifish	BK	TFR	0.0 (0.02)		0.4	0.1 (0.06)	0.4 (0.31)	3.0	0.1 (0.03)	0.3 (0.11)	3.4
Bluegill	BG	TFR	0.0 (0.02)		0.6						
Creek chubsucker	CCS	TFR									
Diamond killifish	DK	TFR					0.0 (0.01)	0.1	0.0 (0.01)	0.0 (0.02)	0.5
Golden topminnow	GT	TFR	0.5 (0.33)	0.3 (0.27)	16.4						
Grass pickerel	GP	TFR		0.0 (0.01)	0.4						
Grass shrimp	GS	TFR	0.3 (0.16)	0.0 (0.01)	6.9	2.8 (1.04)	4.9 (2.31)	53.9	0.5 (0.12)	1.4 (0.52)	20.3
Gulf killifish	GK	TFR				0.3 (0.09)	0.2 (0.08)	3.2	0.7 (0.47)	2.7 (1.80)	36.6
Gulf pipefish	GPF	TFR									
Least killifish	LK	TFR	0.0 (0.01)	0.0 (0.01)	0.6						
Mosquitofish	MF	TFR	2.3 (2.05)	0.1 (0.05)	49.2	0.1 (0.05)	0.3 (0.24)	2.5		0.1 (0.03)	0.9
Northern starhead topminnow	NST	TFR	0.0 (0.01)		0.4						
Pirate perch	PP	TFR									
Rainwater killifish	RK	TFR	0.1 (0.03)		1.1	0.2 (0.14)	0.3 (0.13)	3.4	0.0 (0.01)	0.1 (0.10)	1.6
Redspotted sunfish	RS	TFR	0.0 (0.03)		0.9						
Red swamp crawfish	RSC	TFR									
Sailfin molly	SM	TFR	0.3 (0.13)		5.3	0.3 (0.24)	0.9 (0.63)	8.8		1.3 (1.01)	13.6
Sheepshead minnow	SHM	TFR	0.0 (0.01)		0.3	0.7 (0.34)	2.2 (2.10)	20.7	0.0 (0.02)	1.1 (1.02)	12.8
Spotted bass	SB	TFR	0.0 (0.02)		0.4						
Swamp darter	SD	TFR									
Swamp dwarf crawfish	SDC	TFR		0.0 (0.02)	0.4						
Warmouth	WM	TFR		0.0 (0.02)	0.4						
Yellow bullhead	YB	TFR									
Atlantic croaker	AC	BM									
Bay anchovy	BA	BM									
Bay whiff	BW	BM									
Black drum	BD	BM									
Blue crab	BC	BM				0.0 (0.01)		0.1	0.1 (0.02)	0.1 (0.06)	1.8
Brown shrimp	BS	BM					0.0 (0.01)	0.1	0.4 (0.17)	0.2 (0.14)	7.3
Clown goby	CG	BM									
Darter goby	DG	BM									
Fat sleeper	FS	BM								0.0 (0.03)	0.3
Fiddler crab	FC	BM									
Gulf menhaden	GM	BM									
Inland silverside	IS	BM				0.1 (0.08)	0.5 (0.36)	4.2	0.0 (0.02)	0.0 (0.01)	0.3
Naked goby	NG	BM				0.0 (0.02)		0.1			
Speckled worm eel	SWE	BM									
Spot croaker	SC	BM									
Striped mullet	STM	BM								0.0 (0.01)	0.3
White shrimp	WS	BM									

Table 4 Seasonal nekton density (throw trap, organisms/m^2 (±SE)), catch per unit effort (minnow trap, organisms/minnow trap during 2 h (±SE)) and biomass (throw trap: g wet wt/m^2; minnow trap: g wet wt/minnow trap during 2 h) by pond type in three marsh types. Means sharing a capital (among PCPs) or lower case (among TCPs) letter on a row do not differ ($p>0.05$)

	Freshwater		Brackish		Saline	
	PCP	TCP	PCP	TCP	PCP	TCP
Throw trap (density)						
Spring 2009	9.0 (4.63)A	7.8 (3.68)a	78.7 (33.05)B	111.8 (23.36)b	6.6 (5.90)A	45.0 (16.51)ab
Summer 2009	139.2 (62.28)A	341.1 (149.63)a	94.4 (37.89)A	48.3 (27.02)a	5.3 (3.08)B	18.7 (12.22)a
Fall 2009	36.0 (1.90)A	9.1 (4.65)a	423.9 (89.11)A	307.0 (145.73)b	27.2 (15.78)A	40.6 (29.05)ab
Winter 2009	43.2 (22.36)AB	8.3 (3.42)a	184.6 (54.12)A	80.2 (29.73)b	3.6 (2.23)B	7.8 (3.82)a
Spring 2010	86.8 (49.76)A	45.2 (18.66)a	348.3 (230.62)A	81.9 (52.59)a	17.9 (16.09)A	76.2 (38.45)a
Throw trap (biomass)						
Spring 2009	4.1 (1.17)A	1.8 (0.84)a	33.0 (15.42)A	37.4 (12.62)b	11.6 (11.55)A	44.8 (22.27)b
Summer 2009	14.6 (5.90)A	19.3 (6.82)a	37.4 (14.49)A	42.6 (12.26)a	13.4 (9.13)A	31.8 (16.89)a
Fall 2009	4.2 (1.23)A	0.8 (0.58)a	37.5 (11.19)A	34.3 (16.73)b	20.7 (12.15)A	6.8 (1.05)b
Winter 2009	10.1 (3.07)A	1.2 (0.36)a	16.4 (3.00)A	8.6 (2.80)a	0.3 (0.26)B	1.8 (1.34)a
Spring 2010	27.8 (12.28)A	16.8 (4.12)a	46.5 (25.74)A	43.4 (22.35)a	20.4 (20.00)A	15.8 (7.52)a
Minnow trap (CPUE)						
Spring 2009	2.2 (1.54)A	0.4 (0.15)a	3.5 (1.75)A	10.7 (3.73)b	0.7 (0.67)A	5.9 (0.85)b
Summer 2009	3.6 (1.71)A	0.0 (0.00)a	11.2 (0.56)A	29.3 (10.88)b	2.1 (2.07)A	15.1 (6.72)b
Fall 2009	0.1 (0.04)A	0.1 (0.06)a	3.7 (0.78)A	7.7 (3.80)a	3.9 (3.53)A	2.3 (1.12)a
Winter 2009	0.6 (0.31)A	0.1 (0.06)a	3.2 (1.41)A	0.8 (0.35)ab	0.7 (0.52)A	1.4 (0.06)b
Spring 2010	15.4 (11.16)A	2.1 (0.70)a	1.7 (0.85)A	0.0 (0.00)b	1.7 (1.69)A	12.2 (7.25)a
Minnow trap (biomass)						
Spring 2009	2.6 (1.14)A	0.4 (0.30)a	1.5 (0.91)A	4.5 (1.50)b	0.8 (0.75)A	5.5 (0.83)b
Summer 2009	3.8 (2.28)A	0.0 (0.00)a	5.6 (2.80)A	13.8 (7.36)b	1.5 (1.47)A	11.5 (3.98)b
Fall 2009	0.1 (0.06)A	0.1 (0.03)a	2.0 (0.43)A	3.0 (1.71)a	3.7 (3.33)A	2.4 (1.16)a
Winter 2009	0.4 (0.18)A	0.2 (0.07)a	4.6 (4.43)A	0.8 (0.62)a	0.4 (0.24)A	0.9 (0.12)a
Spring 2010	10.6 (4.19)A	4.1 (2.12)a	5.1 (2.62)A	0.0 (0.00)a	3.1 (3.13)A	37.2 (26.64)a

was influenced by DO and SDI. In addition, the relatively abundant taxa in both freshwater and brackish marsh types in both the throw and minnow trap samples were tidal freshwater residents (freshwater PCPs, TCPs: 100 %; brackish PCPs: 63 %, TCPs: 71 %) whereas the relatively greater density and CPUE taxa in saline ponds were brackish migrants (PCPs: 64 %, TCPs: 56 %).

Discussion

Each of the three marsh types provides productive but potentially stressful environments. For instance, low DO creates stressful conditions for many species in freshwater habitats (Mckinsey and Chapman 1998). Although brackish and saline marshes have higher DO, fluctuating salinities in the brackish marsh (Elliott and Whitfield 2011) and high salinity in the saline marsh provide the dominant stressors to freshwater nekton species in those habitats. In this sense, relatively abundant species in each marsh seem to be well adapted to the stressful conditions within that particular marsh type but no species possessed adaptations to allow dominance across all marsh types. For example, in the freshwater marshes, three abundant species (i.e., mosquitofish, golden topminnow,

Table 5 ANOSIM and SIMPER results for hydrologic connectivity (PCP vs. TCP) comparison of assemblage similarity in three marsh types. All reported results were significant at $p=0.05$. Presented are the Global R (* $p<0.01$) for significant ANOSIM tests and the SIMPER results for percentage similarity within same pond type

	Freshwater		Brackish		Saline	
	PCP	TCP	PCP	TCP	PCP	TCP
Throw trap						
Global R	0.21*		0.07		0.13*	
Similarity (%)	55.0	36.5	58.3	55.2	15.0	42.0
Minnow trap						
Global R	0.17*		0.02		0.24*	
Similarity (%)	23.4	15.0	36.8	26.0	14.5	51.9

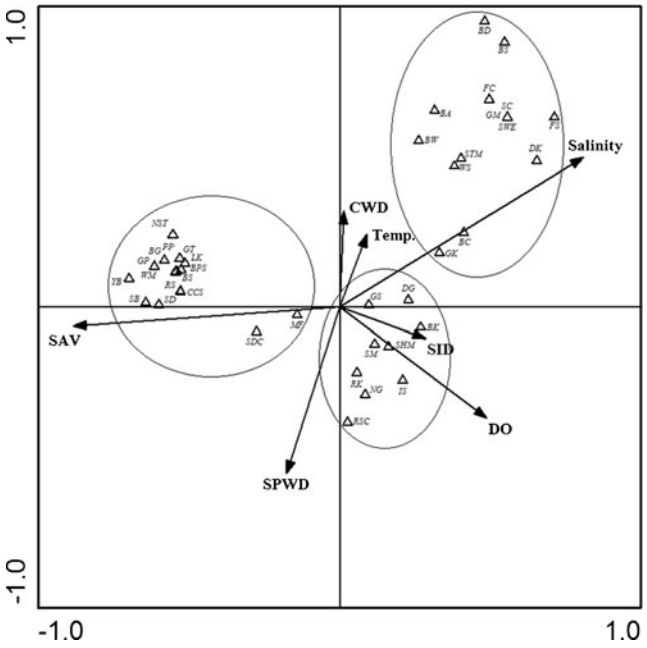


Fig. 2 Association of environmental variables and nekton assemblage characteristics in throw trap samples based on canonical correspondence analysis for all ponds in freshwater, brackish, and saline marshes from April 2009 to May 2010. Full names and abbreviations of taxa are listed in Table 2. Abbreviations of environmental variable names are as follows: Salinity (*Salinity*), Dissolved Oxygen (*DO*), Temperature (*Temp*), Sampling Point Water Depth (*SPWD*), Connected Water Depth (*CWD*), Seasonal Duration of Isolation (*SDI*), Submerged Aquatic Vegetation coverage (*SAV*)

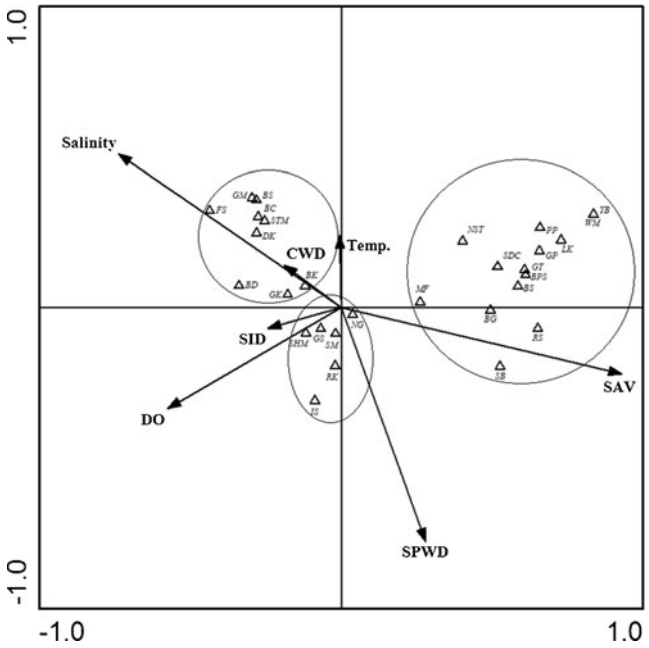


Fig. 3 Association of environmental variables and nekton assemblage characteristics in minnow trap samples based on canonical correspondence analysis for all ponds in freshwater, brackish, and saline marshes from April 2009 to May 2010. Full names and abbreviations of taxa are listed in Table 2. Abbreviations of environmental variable names are as follows: Salinity (*Salinity*), Dissolved Oxygen (*DO*), Temperature (*Temp*), Sampling Point Water Depth (*SPWD*), Connected Water Depth (*CWD*), Seasonal Duration of Isolation (*SDI*), Submerged Aquatic Vegetation coverage (*SAV*)

bantam sunfish) are structurally and/or physiologically able to tolerate low DO conditions (Cech et al. 1985; Killgore and Hoover 2001). Although they are also able to tolerate higher salinities (Chipman 1959; Griffith 1974; Chervinski 1983), they were found at lower densities in the more saline habitats. These species reach their greatest abundance in habitats with relatively high SAV coverage, low salinity, and low DO (Hubbs 1971; Burr 1977; Shute 1980). The sailfin molly can tolerate a broad salinity range (i.e., freshwater to 87 ppt; Sublette et al. 1990), but its abundance pattern revealed clear differences across the salinity gradient that was related to covarying habitat factors. This species peaked in the brackish marsh with moderate salinities, high DO, and high SAV coverage, and was found at lower densities in the freshwater marsh (low salinity and DO, high SAV coverage) and in the saline marsh (higher salinity and DO, no SAV). These findings suggest that the habitat requirements of nekton change across marsh types.

One of the more abundant species in saline marsh, brown shrimp, has been captured in salinities from freshwater (Swingle 1971) to 69 ppt (Simmons 1957), but few have been captured in waters of less than 5 ppt (Christmas and Langley 1973; Loesch 1976) and brown shrimp cannot survive water of 0.5 ppt or less (Venkataramaiah et al. 1972). In the present study, the absence of brown shrimp in the brackish and freshwater marsh is not surprising because the brackish and freshwater marsh areas are passively managed to minimize salinity increases; salinity values in brackish ponds during peak spawning seasons (Fall 2009, Spring 2010) were lower than 5 ppt. In this study, we identified grass shrimp only to genus. The grass shrimp in the freshwater marsh was likely mostly *P. paludosus*. The saline area likely was dominated by *P. pugio*, but *P. intermedius* and *P. vulgaris* were likely also present (Anderson 1985). Thus, comparing the density of the genus *Palaemonetes* across marsh types does not reveal the distributional patterns of individual species.

Individual species responses to salinity and pond habitat attributes (i.e., SAV coverage, DO, salinity, temperature) may be predicted in the context of their life history–environment relationships (Olden et al. 2006). The results of the direct gradient analysis revealed that three environmental factor groups (i.e., freshwater marsh: SAV coverage; brackish marsh: DO; saline marsh: salinity, temperature) drove most of the observed variation in assemblage structure among marshes. For instance, fish abundance in freshwater marsh ponds had a positive relationship with SAV coverage, whereas crustacean abundance showed a negative relationship. Overall nekton abundance in freshwater marsh showed a positive relationship with SAV coverage due to the

relatively high fish density. The negative relationship between crustacean density and SAV coverage is possibly related to the crawfish eating most or all of the SAV during the growing season. In addition, ANOSIM analysis data indicated that hydrologic connectivity (i.e., SDI) affected assemblage similarity between pond types.

CWD and SDI, both measures of hydrologic connectivity, were also important. Several studies suggest ponds that have a low degree of connectivity with adjacent waterways support relatively few organisms due to limited recruitment (Rozas and Minello 1999), severe environmental conditions (Dunson et al. 1993; Rowe and Dunson 1995; Gascon et al. 2008), and predation and food competition (Loftus and Eklund 1994; Layman et al. 2000). Rozas and Minello (2010) also noted that constantly and tidally connected brackish and saline marsh ponds support more species and greater densities than infrequently connected ponds. The data in our study partially agree with those other studies as CWD and SDI were negatively or positively associated with nekton density and assemblage similarity, respectively. In freshwater marsh, nekton density was negatively correlated with CWD in PCPs and TCPs. This negative relationship between nekton density and CWD seems to be related to flooding of the adjacent emergent marsh. When emergent marsh is flooded (i.e., lateral connectivity), nekton will move from ponds into the marsh, resulting in decreased nekton density in ponds (Minello 1999; Baker and Minello 2010). In addition, the greater volume of water associated with increased CWD may also result in a decline of nekton density. Nekton assemblage data in flooded emergent marsh during Fall and Winter 2009 indicated no unique species in the flooded marsh and common pond inhabitants were also common in the flooded marsh (Kang and King, unpublished manuscript). This finding suggests that the hydrologic connectivity between different habitats may affect nekton density of ponds when the emergent marsh is flooded.

The relationship between SDI and assemblage similarity within PCPs and TCPs varied according to marsh types. Freshwater PCPs had higher assemblage similarity than TCPs but saline marsh ponds showed an opposite pattern. As expected, low similarity among TCPs in freshwater marsh was associated with long annual duration of isolation (128.1± 3.3 / 456 days). However, relatively high similarity in saline TCP type may result from the relatively short annual duration of isolation (21±0.7 / 456 days) caused by the tidal exchange. The lack of a difference detected between assemblage similarity of nekton assemblages in brackish PCPs and TCPs may be influenced by broader scale hydrologic alterations.

Like most coastal marshes in the United States, conditions at our study sites partly are the product of almost a century of hydrologic modification and the results of our study may be affected by both broad-scale and local hydrologic conditions. The 187,500 ha Mermentau River Basin of southwestern Louisiana has been affected by a series of major navigation canals, such as Freshwater Bayou, Superior Canal, Calcasieu Ship Channel, and the Gulf Intracoastal Waterway, that allow saltwater intrusion and by water-control structures designed to hold freshwater and decrease salinity pulses to provide stable freshwater irrigation for rice farmers (Gunter and Shell 1958). These broad-scale changes have undoubtedly affected the prevailing environmental conditions in some seasons/years and the movement of organisms among marsh types throughout the vast majority of the Basin. For instance, major navigation canals increase recruitment of marine species into the Basin whereas water control structures in White Lake restrict recruitment of marine species into freshwater marshes. Yozzo and Smith (1998) compared nekton assemblage between tidal freshwater and saline marsh in Virginia and found blue crab and naked goby in both tidal freshwater and saline marsh in their study; we recorded these species only in the saline marsh. However, Piazza and La Peyre (2009a) compared pre- and post-Hurricane Katrina nekton assemblages in a deltaic tidal freshwater marsh in Louisiana and found no marine species in the freshwater marsh. They did find 13 species of brackish migrants in the freshwater marsh but these species were found in only the 2nd year of the 3 year study (the year after Hurricane Katrina) and accounted for only 1.2 % of total density recorded. Thus, while it is possible the broader-scale hydrologic alterations have affected nekton assemblages in our study, the overall contribution of marine and brackish species to non-hydrologically altered freshwater ponds may be minimal.

At a more local level, minor canals, constructed for oil and gas mining, and structural marsh management (SMM), a common management strategy in the Chenier Plain, also affected our results. In addition to being affected by canals, all of our brackish ponds were subjected to SMM which involves placing levees and water-control structures in a marsh to facilitate water-level and/or salinity management but it can restrict direct access of transient species by reducing or blocking water exchange (Morton 1973; Rozas and Minello 1999). Marine crustaceans and fish recruit to coastal wetland habitats throughout the year, but distinct seasonal peaks in recruitment do occur (Rogers and Herke 1985; Hartman et al. 1987). In this sense, canals increase recruitment but SMM reduces recruitment of these organisms when recruits are abundant (McGovern and Wenner 1990). In addition, seasonal access limitations can modify species assemblages, and subsequent modifications may affect fish and nekton density and biomass. In contrast to the negative effect of SMM on fishery species, generally SMM has a positive effect on the standing crops of resident species, although emigration from managed areas may be limited for residents (Rogers et al. 1992, 1994). In our study, density of transient species (i.e., blue crab and brown shrimp) in brackish ponds was lower than saline ponds but management

appeared to benefit estuarine resident species that were dominant in brackish marsh and had significantly higher density in managed than unmanaged (saline) marsh. These findings are congruent with the results of Rozas and Minello (1999). Kanouse et al. (2006) studied natural brackish marsh ponds in Louisiana and noted similar common species but found some rare species (e.g., speckled worm eel, bay whiff, Atlantic croaker) that were not captured in our brackish marsh ponds. Furthermore, in our study, grass shrimp was far more abundant and three of their most common species (i.e., rainwater killifish, sheepshead minnow, sailfin molly) were less abundant in our study.

The relationships we observed between nekton density/-biomass and environmental variables are supported by previously published data and we provide novel information on the effects of hydrologic connectivity on nekton communities in the Chenier Plain. The goal of our study was to determine the effects of hydrologic connectivity on nekton assemblages by comparing nekton density, biomass, and assemblage similarity in ponds of a coastal marsh ecosystem. Our first hypothesis that nekton assemblages in PCPs have higher metrics (density, biomass, and assemblage similarity) than TCPs over all marsh types was only partially supported. Our results indicate that PCPs have lower density and assemblage similarity in saline marshes than TCPs, but PCPs have greater assemblage similarity than TCPs in freshwater marsh ponds. As predicted by our second hypothesis, no nekton species dominated across all marsh types. Thus, anthropogenic activities, such as marsh management (Chabreck 1988) and mosquito control ditches (Balling et al. 1980), that convert TCPs to PCPs can potentially alter nekton assemblage structure in saline marsh. A companion study also indicates that conversion among TCPs and PCPs could also alter macroninvertebrate assemblage structure (Kang and King in press).

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References

Anderson G (1985) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)-grass shrimp. USFWS Biological Report 82 (11.35) USACE TR EL-82-4, pp 19

Baker R, Minello TJ (2010) Growth and mortality of juvenile white shrimp *Litopenaeus setiferus* in a marsh pond. Marine Ecology Progress Series 413:95–104

Balcombe SR, Bunn SE, McKenzie-Smith FJ, Davies PM (2005) Variability of fish diets between dry and flood periods in an arid zone floodplain river. Journal of Fish Biology 67:1552–1567

Balling SS, Stoehr T, Resh VH (1980) The effects of mosquito control recirculation ditches on the fish community of a San Francisco bay salt marsh. California Fish & Game 66:25–34

Baltz DM, Rakocinski C, Fleeger JW (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36:109–126

Bell JD, Westoby M (1986) Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 68:205–209

Burr BM (1977) The bantam sunfish, *Lepomis symmetricus*: systematics and distribution, and life history in Wolf Lake, Illinois. Illinois Natural History Survey Bulletin 31:437–466

Castellanos DL, Rozas LP (2001) Nekton use of submerged aquatic vegetation, marsh, and shallow unvegetated bottom in the Atchafalaya River delta, a Louisiana tidal freshwater ecosystem. Estuaries 24:184–197

Cech JJ Jr, Massingill MJ, Vondracek B, Linden AL (1985) Respiratory metabolism of mosquitofish, *Gambusia affinis*: effects of temperature, dissolved oxygen, and sex difference. Environmental Biology of Fishes 13:297–307

Chabreck RH (1988) Coastal marshes: ecology and wildlife management, 1st edn. University of Minnesota Press, pp 160

Chabreck RH, Linscombe J (1997) Vegetation type map of the Louisiana coastal marshes. Louisiana Department of Wildlife and Fishes, Baton Rouge

Chabreck RH, Nyman JA (2005) Management of coastal wetlands. In: Braun CE (ed) Techniques for wildlife investigations and management, 6th edn. The Wildlife Society, Bethesda, pp 839–860

Chervinski J (1983) Salinity tolerance of the mosquitofish, *Gambusia affinis* (Baird and Girard). Journal of Fish Biology 22:9–11

Chipman RK (1959) Studies of tolerance of certain freshwater fishes to brine water from oil wells. Ecology 40:299–302

Christmas JY, Langley W (1973) Estuarine invertebrates. In: Christmas JY (ed) Cooperative Gulf of Mexico estuarine inventory and study, Mississippi. Gulf Coast Research Laboratory, Ocean Springs, pp 255–317

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and in interpretation, 2nd edn. PRIMER-E, Plymouth

Classen MCM (2008) Monitoring potential prey of the Whooping Crane: valuating gear types and spatial–temporal variation in aquatic fauna. Thesis, University of Alberta, Edmonton, Alberta, Canada

Connolly RM (1994) A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australia estuary. Australian Journal of Marine & Freshwater Research 45:1033–1044

Day RH, Williams TM, Swarzenski CM (2007) Hydrology of tidal freshwater forested wetlands of the southeastern United States. In: Conner WH, Doyle TW, Krauss KW (eds) Ecology of tidal freshwater forested wetlands of the southeastern United States. Springer, pp 29–63

Doyle TW, O'Neil CP, Melder MPV, From AS, Palta MM (2007) Tidal freshwater swamps of the southeastern United States: effects of land use, hurricanes, sea-level rise, and climate change. In: Conner WH, Doyle TW, Krauss KW (eds) Ecology of tidal freshwater forested wetlands of the southeastern United States. Springer, pp 1–28

Dunson WA, Friacano P, Sadinski WJ (1993) Variation in tolerance to abiotic stresses among sympatric salt marsh fish. Wetlands 13:16–24

Elliott M, Whitfield AK (2011) Challenging paradigms in estuarine ecology and management. Estuarine, Coastal and Shelf Science 94:306–314

Fernandes R, Gomes LC, Pelicice FM, Agostinho AA (2009) Temporal organization of fish assemblages in floodplain lagoons: the role of hydrological connectivity. Environmental Biology of Fishes 85:99–108

Fredette TJ, Diaz RJ, van Montfrans J, Orth RJ (1990) Secondary production within a seagrass bed (*Zostera marina* and *Tuppia maritime*) in lower Chesapeake Bay. Estuaries 13:431–440

Froese R, Pauly D (2008) FishBase. World Wide Web electronic publication. http://www.fishbase.org version (09/2008)

Gascon S, Boix D, Sala J, Quintana XD (2008) Relation between macroinvertebrate life strategies and habitat traits in Mediterranean salt marsh ponds (Emporda wetlands, NE Iberian Peninsula). Hydrobiologia 597:71–83

Gauch HG Jr (1982) Multivariate analysis in community ecology. Cambridge University Press, Cambridge

Gilinsky E (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65:455–468

Griffith RW (1974) Environment and salinity tolerances in the genus *Fundulus*. Copeia 2:319–331

Gunter G, Shell WE (1958) A study of an estuarine area with water-level control in the Louisiana marsh. The Proceedings of the Louisiana Academy of Sciences 21:5–34

Hartman RD, Bryan CF, Korth JW (1987) Community structure and dynamics of fishes in a southeast Texas estuary. U.S. Fish and Wildlife Service, Albuquerque, p 116

Hubbs C (1971) Competition and isolation mechanisms in the *Gambusia affinis* X *G. heterochir* hydrid swarm. Texas Memorial Museum Bulletin 19:46

Humphries P, Baldwin DS (2003) Drought and aquatic ecosystem: an introduction. Freshwater Biology 48:1141–1146

Hunter KL, Fox MG, Able KW (2009) Influence of flood frequency, temperature and population density on migration of *Fundulus heteroclitus* in semi-isolated marsh pond habitats. Marine Ecology Progress Series 391:83–96

Kang SR (2011) Aquatic macroinvertebrate and nekton community structure in a Chenier marsh ecosystem: Implications for Whooping Crane prey availability. Dissertation, Louisiana State University, USA

Kang SR, King SL (in press) Effects of hydrologic connectivity on aquatic macroinvertebrate assemblages in different marsh types. Aquatic Biology

Kanouse S, La Peyre MK, Nyman JA (2006) Nekton use of *Ruppia maritime* and non-vegetated bottom habitat types within brackish marsh ponds. Marine Ecology Progress Series 327:61–69

Killgore KJ, Hoover JJ (2001) Effects of hypoxia on fish assemblages in a vegetated water body. Journal of Aquatic Plant Management 39:40–44

Kneib RT, Wagner SL (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. Marine Ecology Progress Series 106:227–238

Kushlan JA (1981) Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110:557–562

Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 46:1161–1172

Layman CA, Smith DE, Herod JD (2000) Seasonally varying importance of abiotic and biotic factors in marsh–pond fish communities. Marine Ecology Progress Series 207:155–169

Loesch HC (1976) Penaeid shrimp distributions in Mobile bay, Alabama including low salinity records. Gulf Research Reports 5:43–45

Loftus WF, Eklund AM (1994) Long-term dynamics of an everglades small-fish assemblage. In: Davis SM, Ogden JC (eds) Everglades: the ecosystem and its restoration, 1st edn. St. Lucie, Delray Beach, pp 461–483

Lubbers LW, Boynton R, Kemp WM (1990) Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecology Progress Series 65:1–14

Martino EJ, Able KW (2003) Fish assemblages across the marine to low salinity transition zone of a temperate estuary. Estuarine, Coastal and Shelf Science 56:969–987

McGovern JC, Wenner CA (1990) Seasonal recruitment of larval and juvenile fishes into impounded and non-impounded marshes. Wetlands 10:203–221

McKinsey DM, Chapman LJ (1998) Dissolved oxygen and fish distribution in a Florida spring. Environmental Biology of Fishes 53:211–223

McMahon TE, Tash JC (1988) Experimental analysis of the role of emigration in population regulation of desert pupfish. Ecology 69:1871–1883

Minello TJ (1993) Chronographic tethering: a technique for measuring prey survival time and testing predation pressure in aquatic habitats. Marine Ecology Progress Series 101:99–104

Minello TJ (1999) Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. American Fisheries Society Symposium 22:43–75

Minello TJ, Rozas LP, Baker R (2012) Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. Estuaries and Coasts 35:501–514

Mitsch WJ, Gosselink JG (2000) Tidal freshwater marshes. In: Mitsch WJ, Gosselink JG (eds) Wetlands, 3rd edn. John Wiley and Sons, New York, pp 307–333

Morton T (1973) The ecological effects of water control structures on an estuarine area, White Lake, Louisiana, 1972–1973. University of Southwestern Louisiana. pp 86

Olden JD, Poff NL, Bestgen KR (2006) Life-history strategies predict fish invasions and extirpations in the Colorado river basin. Ecological Monographs 76:25–40

Peterson MS, Ross ST (1991) Dynamics of littoral fishes and decapods along a coastal river-estuarine gradient. Estuarine, Coastal and Shelf Science 33:467–483

Peterson GW, Turner RE (1994) The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17:235–262

Piazza BP, La Peyre MK (2009a) The effect of Hurricane Katrina on nekton communities in the tidal freshwater marshes of Breton Sound, Louisiana, USA. Estuarine, Coastal and Shelf Science 83:97–104

Piazza BP, La Peyre MK (2009b) Nekton community response to a large-scale Mississippi river discharge: examining spatial and temporal response to river management. Estuarine, Coastal and Shelf Science 91:379–387

Remmert H (1983) Studies and thoughts about the zonation along the rocky shores of the Baltic. Zoologica 22:121–125

Roach KA, Thorp JH, Delong MD (2009) Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the upper Mississippi river. Freshwater Biology 54:607–620

Rogers BD, Herke WH (1985) Estuarine-dependent fish and crustacean movements and weir management. In: Bryan CF, Zwank PJ, Chabreck RH (eds) Proceedings of the fourth coastal marsh and estuary management symposium. Louisiana state university agricultural center, Louisiana cooperative fish and wildlife research unit, Baton Rouge, LA, pp 201–219

Rogers DR, Rogers BD, Herke WH (1992) Effects of a marsh management plan on fishery communities in coastal Louisiana. Wetlands 12:53–62

Rogers DR, Rogers BD, Herke WH (1994) Structural marsh management effects on coastal fishes and crustaceans. Environmental Management 18:351–369

Rowe CL, Dunson WA (1995) Individual and interactive effects of salinity and initial fish density on a salt marsh assemblage. Marine Ecology Progress Series 128:271–278

Rozas LP, Minello TJ (1999) Effects of structural marsh management on fishery species and other nekton before and during a spring drawdown. Wetlands Ecology and Management 7:121–139

Rozas LP, Minello TJ (2010) Nekton density patterns in tidal ponds and adjacent wetlands related to pond size and salinity. Estuaries and Coasts 33:652–667

Rozas LP, Odum WE (1987) Fish and macrocrustacean use of submerged plant beds in tidal freshwater marsh creeks. Marine Ecology Progress Series 38:101–108

Rozas LP, Odum WE (1988) Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77:101–106

Shute JR (1980) *Fundulus chrystotus*, Golden topminnow. In: Lee DS, Gilbert C, Hocutt C, Jenkins R, McAllister (eds) 1st edn, Atlas of North American freshwater fishes. North Carolina Museum of Natural Science, pp 510

Simmons EG (1957) An ecological survey of the upper laguan madre of Texas. Publications of the institute of marine science. The University of Texas Marine Science Institute 4:156–200

Sublette JE, Hatch MD, Sublette M (1990) The fishes of New Mexico. University of New Mexico Press, Albuquerque, p 393

Swingle HA (1971) Biology of Alabama estuarine areas. Cooperative Gulf of Mexico estuarine inventory. Alabama Marine Resources Bulletin 5

Szedlmayer ST, Able KW (1993) Ultrasonic telemetry of age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. Copeia 1993:728–736

ter Braak CJF, Smilauer P (2002) CANOCO Reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5), Microcomputer Power, Ithaca, NY

Thiel R, Sepulveda A, Kafemann R, Nellen W (1995) Environmental factors as forces structuring the fish community of the Elbe Estuary. Journal of Fish Biology 46:47–69

Thorman S (1986) Physical factors affecting the abundance and species richness of fishes in the shallow waters of the southern Bothnian Sea (Sweden). Estuarine, Coastal and Shelf Science 22:357–369

Venkataramaiah A, Lakshmi GJ, Gunter G (1972) The effects of salinity, temperature and feeding levels on the food conversion, growth and survival rates of the shrimp *Penaeus* aztecus. Proceedings of the Food–Drugs from the sea, Marine Technology Society

Visser JM, Sasser CE, Chabreck RH, Linscombe RG (1998) Marsh vegetation types of the Mississippi river deltaic plain. Estuaries 21:818–828

Whoriskey FG, Fitzgerald GJ (1989) Breeding-season habitat use by sticklebacks (Pisces: Gasterosteidae) at Isle Verte, Quebec. Canadian Journal of Zoology 67:2126–2130

Wicker KM, Davis D, Roberts D (1983) Rockefeller state wildlife refuge and game preserve: evaluation of wetlands management techniques: Coastal management section, Louisiana Department of Natural Resource, Baton Rouge, Louisiana

Yozzo DJ, Smith DE (1998) Composition and abundance of resident marsh-surface nekton: comparison between tidal freshwater and salt marshes in Virginia, USA. Hydrobiologia 362:9–19