Seasonal nekton assemblages in a flooded coastal freshwater marsh, Southwest Louisiana, USA

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ABSTRACT
Marsh flooding and drying may be key factors affecting seasonal nekton distribution and density because habitat connectivity and water depth can impact nekton accessibility to the marsh surface. Recent studies have characterized freshwater nekton assemblages in marsh ponds; however, a paucity of information exists on the nekton assemblages in freshwater emergent marshes. The principal objectives of this study are to characterize the seasonal nekton assemblage in a freshwater emergent marsh and compare nekton species composition, density, and biomass to that of freshwater marsh ponds. We hypothesize that 1) freshwater emergent marsh has lower taxa richness than freshwater marsh ponds; and 2) freshwater emergent marsh has a lower seasonal density and biomass than freshwater marsh ponds. Mosquito-fish Gambusia affinis and least killifish Heterandria formosa were abundant species in both habitats while some abundant species (e.g., banded pygmy sunfish Elassoma zonatum) in freshwater ponds were absent in freshwater emergent marsh. Our data did not support our first and second hypotheses because taxa richness, seasonal density and biomass between freshwater emergent marsh and ponds did not statistically differ. However, freshwater emergent marsh was dry during the summer months and thus supports no fish species during this period. Additional long-term research on the effects of flow regime in the freshwater marsh on nekton assemblages would potentially improve our understanding of nekton habitat requirements.

Keywords: Freshwater Emergent Marsh; Freshwater Pond; Nekton Assemblage; Hydrologic Connection

1. INTRODUCTION
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 [1,2]. Marsh flooding and drying are likely to be key factors affecting seasonal nekton distribution and density because habitat connectivity and water depth can determine nekton accessibility to the marsh surface [3-7]. Moreover, flow regime plays a profound role in the lives of fish through its effect on critical life events (e.g., reproduction, spawning, larval survival, recruitment) [8-13]. In this sense, lateral hydrologic connectivity between coastal freshwater emergent-herbaceous marsh (adjacent to ponds and channels; hereafter termed “freshwater emergent marsh, FEM”) and ponds during flooding may increase nekton density in the freshwater emergent marsh while nekton density in ponds may decrease due to nekton movement from ponds to the freshwater emergent marsh. However, shallow water depths may not provide equal access for all nekton (e.g., larger species) thereby restricting some nekton taxa from the freshwater ponds. Also, ponds that have a relatively longer hydroperiod and longer hydrologic connectivity to permanent water bodies may have relatively higher nekton density and biomass than the freshwater emergent marsh. For example, several studies suggest that a low degree of connection with adjacent waterways support relatively few organisms due to limited recruitment [14] and severe envi-
ronmental conditions (e.g., salinization, drying [15-17]).

In freshwater habitats, low dissolved oxygen (DO) also creates stressful conditions for many species [18]. However, relatively abundant species (e.g., mosquitofish) in freshwater marsh are adapted to low DO. [19] documented that mosquitofish reached the greatest abundance in habitats with relatively low DO (e.g., 2 mg/L), high submerged aquatic vegetation (SAV) cover, and low salinity (e.g., <0.5 ppt). Thus, nekton assemblages in freshwater emergent marshes and ponds may have similar dominant species even though freshwater emergent marshes exhibit severe environmental conditions (e.g., drying).

The extent of coastal marsh loss in many parts of the world has intensified efforts to develop marsh management and conservation strategies that include habitat value assessment for nekton [20-23]. [24] characterized freshwater nekton assemblages in marsh ponds, however, a paucity of information exists on nekton assemblages in freshwater emergent marshes compared to assemblages in freshwater marsh ponds. A clear understanding of the similarity and differences between freshwater emergent marsh and marsh ponds would enhance our understanding of nekton habitat requirements in freshwater marshes as well as the effects of anthropogenic activities, such as habitat conversion (e.g., freshwater emergent marsh to pond), on their distribution. The principal objectives of this study are to characterize the seasonal nekton assemblage in a freshwater emergent marsh and compare nekton species composition, density, and biomass to that of freshwater marsh ponds. We hypothesize that 1) freshwater emergent marsh has lower taxa richness than marsh ponds; and 2) freshwater emergent marsh has a lower seasonal density and biomass than marsh ponds.

2. STUDY AREA AND METHODS

2.1. Study Area

This study was conducted in White Lake Wetlands Conservation Area (WLWCA, 29°52′N, 92°31′W, Figure 1) in the Chenier Plain of southwestern Louisiana. WLWCA, a 28,719 ha freshwater marsh, is bounded on the south by White Lake (28.2 km north of the Gulf of Mexico). Dominant vegetation is maidencane (Panicum hemitomon Schultes) and bulltongue arrowhead (Sagittaria lancifolia Linnaeus). We used marsh vegetation (i.e., freshwater marsh: Panicum hemitomon, [25]) to define our marsh types because vegetation does not respond to daily salinity fluctuations [25,26]. Salinity (i.e., freshwater marsh: 0.1 - 3.4 ppt) was also a major consideration of our decision to select marsh types.

2.2. Data Collection

In November 2008, we deployed continuous water level recorders in freshwater emergent marshes (i.e., 100 m from channel or pond margin) and ponds to measure water depth 6 times per day. Water depths were validated by comparing water level recorder readings to discrete monthly water depths obtained with a meter stick adjacent to the recorder; both water depths were always within 1 cm of each other. We then determined flooding depth and duration based on the criteria that daily water depth (DWD) > 0. We also deployed a staff gage at the border between the pond and freshwater 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 freshwater emergent marsh when the pond is connected with surface water to the channel or surrounding marsh (marginal zone of the pond).

To determine nekton characteristics, we sampled freshwater emergent marshes (i.e., 100 m from channel or pond margin) seasonally from March 2009 to February 2010. Seasons were defined as: 1) Spring (March-May); 2) Summer (June-August); 3) Fall (September-November); 4) Winter (December-February). A 1-m² aluminum-sided throw trap (mesh size: 3 mm), similar to that described by [28], was tossed at three random points in each sampling plot within the freshwater emergent marsh (4 sampling sites) and ponds (i.e., 3 permanently connected ponds [PCP: permanently connected by a channel during all seasons], 3 temporarily connected ponds [TCP: temporarily connected by surface water to the surrounding marsh but not permanently connected to a channel], [24]). 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 organ-
isms were completed before the trap was considered free of nekton. 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. All nekton were weighed to the nearest 0.001 g wet-weight to determine biomass (g m$^{-2}$).

2.3. Statistical Analysis

Data are reported as mean ± standard error (SE), and significance level was chosen at $\alpha = 0.05$. Analyses of variance (ANOVA) and T-test (Proc Mixed, Version 9.3, Cary, SAS Institute, North Carolina) were used to test for statistical differences in environmental variables and nekton density and biomass by season. We used one-way ANOVA for each response variable that included environmental variable and nekton density. We conducted a one-way ANOVA with one fixed effect. Significant one-way ANOVA effects were tested using post-hoc comparisons of Tukey adjusted least squared means. For ANOVA analyses, 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. Linear regression (Proc Mixed, Version 9.3, SAS Institute, North Carolina) was used to examine the potential relationship between nekton assemblage characteristics (i.e., density, biomass) and environmental factors.

3. RESULTS

In the freshwater emergent marshes, summer was the driest period (flooded days: 23/92 days) and winter was the wettest period (flooded days: 90/90 days). DWD ranged from 31.7 ± 0.54 cm (mean ± SE; winter) to 1.3 ± 0.41 cm (summer). DWD differed among all seasons ($F_{3,12} = 190.55$, $p < 0.01$). CWD ranged from 40.2 ± 2.14 cm (winter, PCP) to 2.9 ± 1.02 cm (summer, PCP).

We recorded 439 individuals of 11 taxa in 60 samples in the freshwater emergent marsh. Seasonal nekton density (organisms/m$^2$) ranged from 14.7 ± 5.37 (mean ± SE; winter) to 0 (summer, Figure 2). However, nekton density within freshwater emergent marsh did differ among spring, fall, and winter ($F_{2,9} = 0.52$, $p = 0.61$). Nekton biomass (g wet wt/m$^2$) ranged from 4.9 ± 0.95 (winter) to 0 (summer). Nekton biomass had similar seasonal patterns as nekton density ($F_{2,9} = 2.47$, $p = 0.14$). No statistically significant relationships were observed between environmental variables and nekton density/biomass in the freshwater emergent marsh. Relatively abundant species were mosquitofish (spring: 58%, fall: 29%, winter: 23%), least killifish (spring: 34%, fall: 30%, winter: 24%), and swamp dwarf crawfish (spring: 7%, fall: 30%, winter: 34%).

In the freshwater marsh ponds, we recorded 22 nekton taxa in 90 samples. Nekton density and biomass between freshwater emergent marsh and ponds did not differ for any season (Table 1). A total of 22 taxa were found in ponds and 11 taxa in the freshwater emergent marsh; no unique species were observed in the freshwater emergent marsh. Freshwater emergent marsh and ponds shared some abundant species (i.e., mosquitofish, least killifish) but some abundant species (i.e., banded pygmy sunfish, golden topminnow Fundulus chrysotus) in freshwater ponds were absent in the freshwater emergent marsh.

4. DISCUSSION

The present study considered the hypothesis that freshwater emergent marsh would have lower nekton taxa richness than freshwater marsh ponds due to seasonal isolation of surface water from other water bodies, such as ponds/channels, and relatively shallow CWD. As habitats become spatially reduced, the contact among species may intensify and/or harsh abiotic conditions may develop; in either case, some species may go locally extinct [29]. In addition, the relatively shallow flooded water depth (<32 cm) in freshwater emergent marsh may...
restrict accessibility of large predator species (e.g., bantam sunfish, bluegill). Our data did not support our first hypothesis as taxa richness between freshwater emergent marsh and ponds did not statistically differ, although no fish taxa used the emergent marsh in summer because of lack of water. Similarly, [27] noted that nekton taxa in intermediate marsh ponds included most of the nekton taxa in flooded intermediate freshwater emergent marsh (88% same species). This finding suggests that nekton in freshwater emergent marsh is a nested subset of those in freshwater marsh ponds.

[24] noted that nekton density in freshwater marsh ponds was negatively correlated with CWD and this relationship appears to be related to flooding of the adjacent freshwater emergent marsh. When freshwater emergent marsh is flooded (i.e., lateral hydrologic connectivity), some nekton species will migrate from ponds to the marsh, resulting in decreased nekton density in ponds [30]. We hypothesized that freshwater emergent marsh had lower nekton density and biomass to that of freshwater marsh ponds, but our results indicate that they did not statistically differ. High variability in nekton density within the freshwater emergent marsh and ponds suggests that nekton in freshwater emergent marsh are patchily distributed. Despite the high variability and limited temporal availability, the freshwater emergent marsh is still an important and widely distributed habitat for nekton.

Individual species responses to habitat attributes (e.g., vegetation cover) may be predicted in the context of their life history-environment relationships [31]. Our results indicated that common pond inhabitants (i.e., mosquitofish, least killifish) were common in the freshwater emergent marsh. This finding is similar to previous studies that found relatively higher population densities of mosquitofish and least killifish in shallow water with thick vegetation, low DO and salinity [19,32,33]. Some abundant species in freshwater ponds, however, were not caught in freshwater emergent marsh as expected. We expected banded pygmy sunfish and golden topminnow to have relatively higher density in freshwater emergent marsh because they prefer shallow water with macrophytes [34-35]. [36] noted vegetation structural complexity may affect nekton habitat use in SAV (e.g., pond) and the freshwater emergent marsh. Differences in the structural complexity of vegetation between habitat types may have been responsible for the absence of banded pygmy sunfish and the relatively low density of golden topminnow. These findings suggest that some abundant species in freshwater emergent marsh and ponds may be well adapted to low DO with high vegetation cover.

Dry conditions are common in wetlands and are an important part of the hydrological cycle. Variation in life history traits of nekton seems to be correlated with hydrologic condition (i.e., flooding duration). [37] noted that flow regime adaptations range from behaviors that result in the avoidance of individual floods or droughts, to life-history strategies that are synchronized with long-term flow patterns. In addition, [13] noted that many fish species in highly variable flow regimes have evolved life history traits of nekton seems to be correlated with hydrologic condition (i.e., flooding duration). [37] noted that flow regime adaptations range from behaviors that result in the avoidance of individual floods or droughts, to life-history strategies that are synchronized with long-term flow patterns. In addition, [13] noted that many fish species in highly variable flow regimes have evolved life history strategies that ensure strong recruitment. Our results of high variability in nekton density within the freshwater emergent marsh indicate that nekton is patchily distributed. Furthermore, we observed that variability in flooding is common among years during the same season. During spring sampling, the freshwater emergent marsh was flooded, providing ample access to the marsh by nekton. However, during March to May 2010 (spring period), dry conditions prevailed and the marsh remained unflooded (unpublished data, no nekton sample). Strictly from a nekton perspective, our results suggest that anthropogenic activities such as marsh management that

<table>
<thead>
<tr>
<th>Species</th>
<th>FEM</th>
<th>PCP</th>
<th>TCP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Banded pygmy sunfish</td>
<td>4.1 (1.84)</td>
<td>1.0 (0.57)</td>
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<tr>
<td>Bantam sunfish</td>
<td>0.1 (0.06)</td>
<td>1.5 (0.49)</td>
<td>0.0 (0.03)</td>
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<td>Bayou killifish</td>
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<td></td>
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<tr>
<td>Bluegill</td>
<td>0.1 (0.06)</td>
<td>0.7 (0.63)</td>
<td></td>
</tr>
<tr>
<td>Creek chubsucker</td>
<td>0.0 (0.03)</td>
<td>0.1 (0.06)</td>
<td></td>
</tr>
<tr>
<td>Golden topminnow</td>
<td>0.2 (0.16)</td>
<td>2.1 (1.52)</td>
<td>1.1 (0.97)</td>
</tr>
<tr>
<td>Grass pickerel</td>
<td>0.0 (0.04)</td>
<td>0.1 (0.11)</td>
<td></td>
</tr>
<tr>
<td>Grass shrimp</td>
<td>0.0 (0.04)</td>
<td>9.5 (4.65)</td>
<td>1.6 (0.54)</td>
</tr>
<tr>
<td>Least killifish</td>
<td>2.6 (0.88)</td>
<td>19.1 (12.61)</td>
<td>17.7 (15.27)</td>
</tr>
<tr>
<td>Mosquitofish</td>
<td>3.2 (1.23)</td>
<td>12.8 (9.82)</td>
<td>69.5 (65.66)</td>
</tr>
<tr>
<td>Northern starhead topminnow</td>
<td>0.2 (0.11)</td>
<td>0.1 (0.06)</td>
<td></td>
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<tr>
<td>Pirate perch</td>
<td>0.0 (0.00)</td>
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<tr>
<td>Rainwater killifish</td>
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<td>1.4 (1.37)</td>
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<tr>
<td>Redspotted sunfish</td>
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<td></td>
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<td>Red swamp crawfish</td>
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<td>0.1 (0.06)</td>
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</tr>
<tr>
<td>Sailfin molly</td>
<td>0.4 (0.30)</td>
<td>2.9 (2.80)</td>
<td>0.3 (0.24)</td>
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<tr>
<td>Sheepshead minnow</td>
<td>0.6 (0.57)</td>
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<td>Spotted bass</td>
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<tr>
<td>Swamp darter</td>
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<tr>
<td>Swamp dwarf crawfish</td>
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<td>1.2 (0.73)</td>
<td>0.3 (0.21)</td>
</tr>
<tr>
<td>Warmouth</td>
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<td></td>
</tr>
<tr>
<td>Yellow bullhead</td>
<td>0.0 (0.03)</td>
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</tbody>
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increases or decreases duration of lateral hydrologic connection between freshwater emergent marsh and adjacent water bodies can potentially alter nekton habitat value (i.e., non-suitable, less suitable, suitable) in freshwater marsh.

Previous studies [38,39] noted that the natural flow regime has a profound influence on the biodiversity of aquatic ecosystems (e.g., streams, rivers and their floodplain wetlands). Several interrelated flow characteristics influence nekton assemblages in aquatic systems at different temporal and spatial scales; no single flow characteristic is responsible. [13] noted that it is difficult to resolve which attributes of the altered flow regime are directly responsible for observed impacts. Similarly, in our study, it is unclear as to what hydrologic characteristics are most important in structuring nekton communities in freshwater marsh. Additional long-term research on the effects of flow regime in the freshwater marsh on nekton assemblages would potentially improve our understanding of nekton habitat requirements.

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