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Sung-Ryong Kang

Louisiana State University and Agricultural and Mechanical College

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AQUATIC MACROINVERTEBRATE AND NEKTON COMMUNITY STRUCTURE
IN A CHENIER MARSH ECOSYSTEM:
IMPLICATIONS FOR WHOOPING CRANE PREY AVAILABILITY

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Renewable Natural Resources

by

Sung-Ryong Kang
B.S., Dong-A University, 2003
M.S., Dong-A University, 2005
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ABSTRACT

A suitable foraging habitat model based on prey density, biomass, and energy values in varying hydrologic conditions can provide an objective quantifiable method to assess habitat conditions for the Whooping Crane (*Grus americana*). Nekton and macroinvertebrates are considered the important prey sources in Whooping Crane's diet at different times. This study focuses on the understanding of habitat relationships of nekton and macroinvertebrate assemblage in the Chenier Plain to provide a foundation for the development for foraging suitability models for the reintroduced Whooping Crane. In this dissertation, in a laboratory study I experimentally examined the effect of salinity on the survival of dominant macroinvertebrates in freshwater marsh (i.e., *Procambarus clarkii* Girard, *Cambarellus puer* Hobbs, Libellulidae, Dytiscidae). In addition, I compared nekton and aquatic macroinvertebrate assemblages in freshwater, brackish and saline marshes of the Chenier Plain. In the laboratory experiment, to determine survival rate, a series of 45 cm x 30 cm x 15 cm plastic trays were filled with water of six salinities (i.e., 0.6, 7.2, 13.5, 19.4, 25.1, and 30.7 gL⁻¹ TDS) both with and without prey for 28 days. At the lower threshold, low salinities (i.e., ≤ 0.6 gL⁻¹TDS) allowed species to survive even without food. Above the upper threshold, however, high salinities (i.e., ≥ 25.1 gL⁻¹TDS) killed species whether they had food or not. Survival of all species was affected by salinity but upper and lower thresholds existed for each species. In the field studies, I measured the effects of hydrologic connectivity on several environmental variables and their combined effect on several nekton community metrics. I collected 31,011 nekton of 42 taxa from 540 seasonal samples with a throw trap and minnow traps. Nekton density of brackish ponds was higher than saline ponds but freshwater ponds did not statistically differ from brackish and saline ponds. However, nekton biomass of brackish and saline ponds was greater than freshwater ponds. Nekton community diversity of freshwater ponds had the highest diversity. Nekton community

composition appeared to be structured by individual species responses to the salinity gradient as well as pond habitat attributes (submerged aquatic vegetation coverage, dissolved oxygen, hydrologic connectivity). To determine the effects of hydrologic connectivity and environmental variables on aquatic macroinvertebrate community metrics, I collected 32,130 aquatic macroinvertebrates from 52 taxa from 252 monthly sweep net samples. A total of 50 taxa were identified in freshwater marsh, 20 in brackish marsh, and 12 in saline marsh. Freshwater marsh had 32 exclusive taxa but brackish and saline did not have any exclusive taxa. Furthermore, density, biomass, and diversity of aquatic macroinvertebrates in freshwater ponds were higher than in brackish and saline ponds. Variation in life history traits of macroinvertebrates and responses to environmental conditions (water depth, salinity) seem to be influenced macroinvertebrate assemblages across multiple marsh types.

CHAPTER 1
GENERAL INTRODUCTION
BACKGROUND

Understanding the relationships between animals and their prey resources is of central importance in ecology (Watson 1970; Morse 1980; Tilman 1982). Birds may derive fitness-related benefits from foraging in habitats where they can most efficiently obtain required prey resources (Stephens and Krebs 1986; Lemon and Barth 1992). Differences among habitats in the abundance of these prey resources can influence habitat selection of foraging waterbirds (Murkin and Kadlec 1986; Colwell and Landrum 1993), although water depth is an important constraint on availability even when prey resources are abundant (Baker 1979; Poysa 1983; Safran et al. 1997). Thus, Gawlik (2002) defined prey availability as a compound variable consisting of prey density and the vulnerability of prey to capture. Prey availability plays a key role in theories of optimal foraging (Emlen 1966; MacArthur and Pianka 1966) and can support decision models of suitable foraging habitat. Ultimately, a decision model of suitable foraging habitat based on prey density, biomass, and energy values in different hydrologic conditions can provide an objective quantifiable method to assess habitat conditions for specific birds within a focused area by measuring how well each habitat variable meets the habitat requirements. This study focuses on the understanding of the effects of habitat characteristics affecting prey assemblages and availability in the Chenier Plain to provide a foundation for the development of a Whooping Crane foraging suitability model for coastal marshes.

Whooping Cranes feed on a wide variety of plant and animal matter such as crustaceans (e.g., red swamp crawfish *Procambarus clarkii* and blue crab *Callinectes sapidus*), large invertebrates, fish, frogs, and snakes (Allen 1952; Novakowski 1966; Bergeson et al. 2001). In

Wood Buffalo National Park, the breeding area of the wild flock of Whooping Cranes, immediately after young cranes have hatched in the spring, large invertebrates, such as dragonfly larvae (sub-order: *Anisoptera*), are the predominant prey fed to chicks (Bergeson et al. 2001). When young cranes are mobile and able to feed on their own, however, family groups are often observed feeding in ponds that consistently contain fish (Sotiropoulos 2002). Thus, both nekton (i.e., fish and decapod crustaceans) and macroinvertebrates appear to be important prey in the Whooping Crane's diet at different times (Classen 2008).

Assemblages of nekton and aquatic macroinvertebrate strongly depend on the characteristics of environmental variables. In nekton assemblages, several studies indicate that salinity strongly affects nekton assemblage structure in coastal marshes (Thorman 1986; Peterson and Ross 1991; Thiel et al. 1995; Martino and Able 2003). For example, brackish marsh tends to support a greater number of nekton than freshwater or saline marshes however, brackish marshes support fewer species because of high salinity fluctuations (Elliott and Whitfield 2011). Also, the presence and depth of water can positively or negatively impact nekton movement (Whoriskey and Fitzgerald 1989; Szedlmayer and Able 1993; Lake 2003; Humphries and Baldwin 2003) and foraging habitat quality (Kneib and Wagner 1994; Balcombe et al. 2005). In addition, spatially variable oxygen level may be important in structuring nekton diversity (Mckinsey 1998). High temperatures in infrequently flooded ponds may contribute to population changes through increased emigration rates (McMahon and Tash 1998). Furthermore, nekton abundance and diversity have generally been shown to be higher along submerged aquatic vegetation beds (Rozas and Odum 1987; Castellanos and Rozas 2001) than within non-vegetated habitats.

For aquatic macroinvertebrates, salinity plays a major role in shaping community structure (Boix et al. 2008). High lateral connectivity among individual water bodies may facilitate movement, thus resulting in high similarity of aquatic macroinvertebrate assemblages (Karaus 2004). Also, macroinvertebrates possess a diverse array of structural and behavioral respiratory adaptations (Eriksen et al. 1984), suggesting that different taxa differ in their oxygen requirements and tolerance to hypoxia (Connolly et al. 2004). Furthermore, macrophyte coverage appears to affect macroinvertebrate distribution by providing refuge from predators (Mittlebach 1988), increasing the availability of food resources (Campeau et al. 1994), and furnishing attachment sites or building materials (Lodge 1985; Dudley 1988).

RESEARCH OBJECTIVE

I studied the linkages among hydrologic connectivity, environmental variables, and nekton and aquatic macroinvertebrate assemblages. To do this, I evaluated macroinvertebrates survival with increasing salinity in the laboratory and local nekton and aquatic macroinvertebrate community response to salinity, hydrologic connectivity, dissolved oxygen, temperature, and submerged aquatic vegetation within multiple marsh and pond types in the Chenier Plain marshes of Louisiana. Eventually, the results of this study can help to the development of prey availability and suitable foraging habitat models for Whooping Cranes (Fig.1.1).

STUDY AREA

State lands in the Chenier Plain of southwestern Louisiana include the White Lake Wetlands Conservation Area (WLWCA) with approximately 20,800 ha of freshwater marsh, and Rockefeller Wildlife Refuge (RWR) with a total area of 42,400 ha, approximately one-third of

which is freshwater marsh and rest is brackish and saline (Fig.1.2). WLWCA is located along the western boundary of Vermilion Parish and is bounded on the south by White Lake. RWR is located in eastern Cameron and western Vermilion Parishes. Both of these conservation areas are managed by the Louisiana Department of Wildlife and Fisheries (LDWF) and using current released site (i.e., WLWCA) of captive Whooping Cranes and considering potential supplementary foraging habitat (i.e., RWR).

DISSERTATION OVERVIEW

In Chapter 2, I experimentally examine two questions regarding aquatic macroinvertebrate survival. I tested whether: 1) increased salinity, absence of prey, and increased duration of exposure would decrease survival of aquatic macroinvertebrates; and 2) crustaceans and large-body taxa (i.e., *Procambarus clarkii*, Dytiscidae) would have higher survival than aquatic insects and small-body taxa (i.e., *Cambarellus puer*, Libellulidae). In Chapter 3 (nekton) and 4 (aquatic macroinvertebrate), I used marsh survey data to 1) examine the effects of hydrologic connectivity on environmental variables and the density, biomass, diversity, and similarity of nekton and aquatic macroinvertebrate communities and 2) compare spatial and temporal patterns of nekton and aquatic macroinvertebrate assemblages in temporarily and permanently connected ponds within freshwater, brackish, and saline marshes. Finally, in Chapter 5, I summarized the conclusions of the previous chapters and synthesized the results with regard to the overall goal of providing baseline data for future research as a development of decision model of suitable foraging habitat of Whooping Crane.

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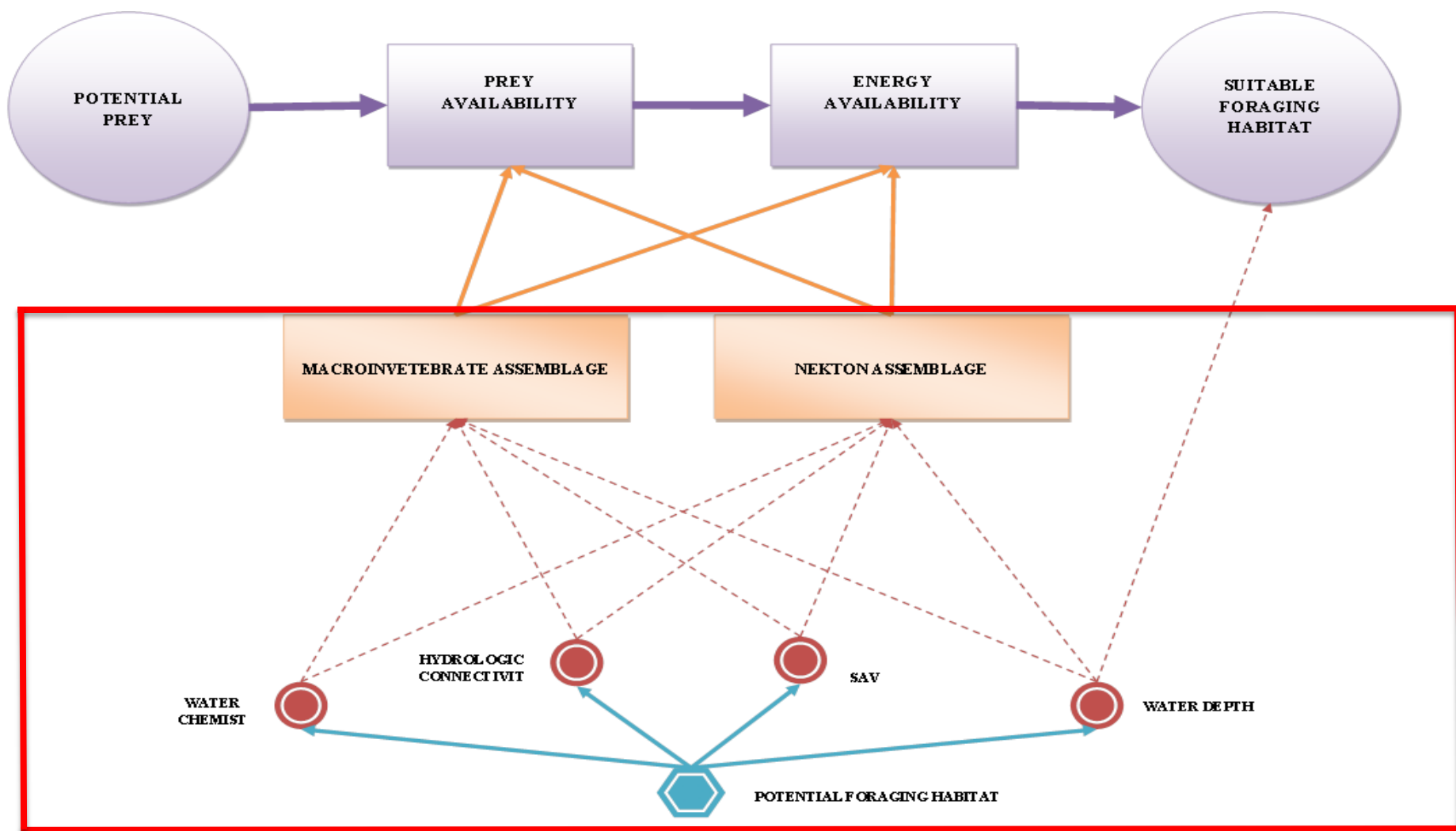


Fig.1.1. Conceptual model illustrating factors affecting suitable foraging habitat. Items in the red box are addressed in this dissertation.

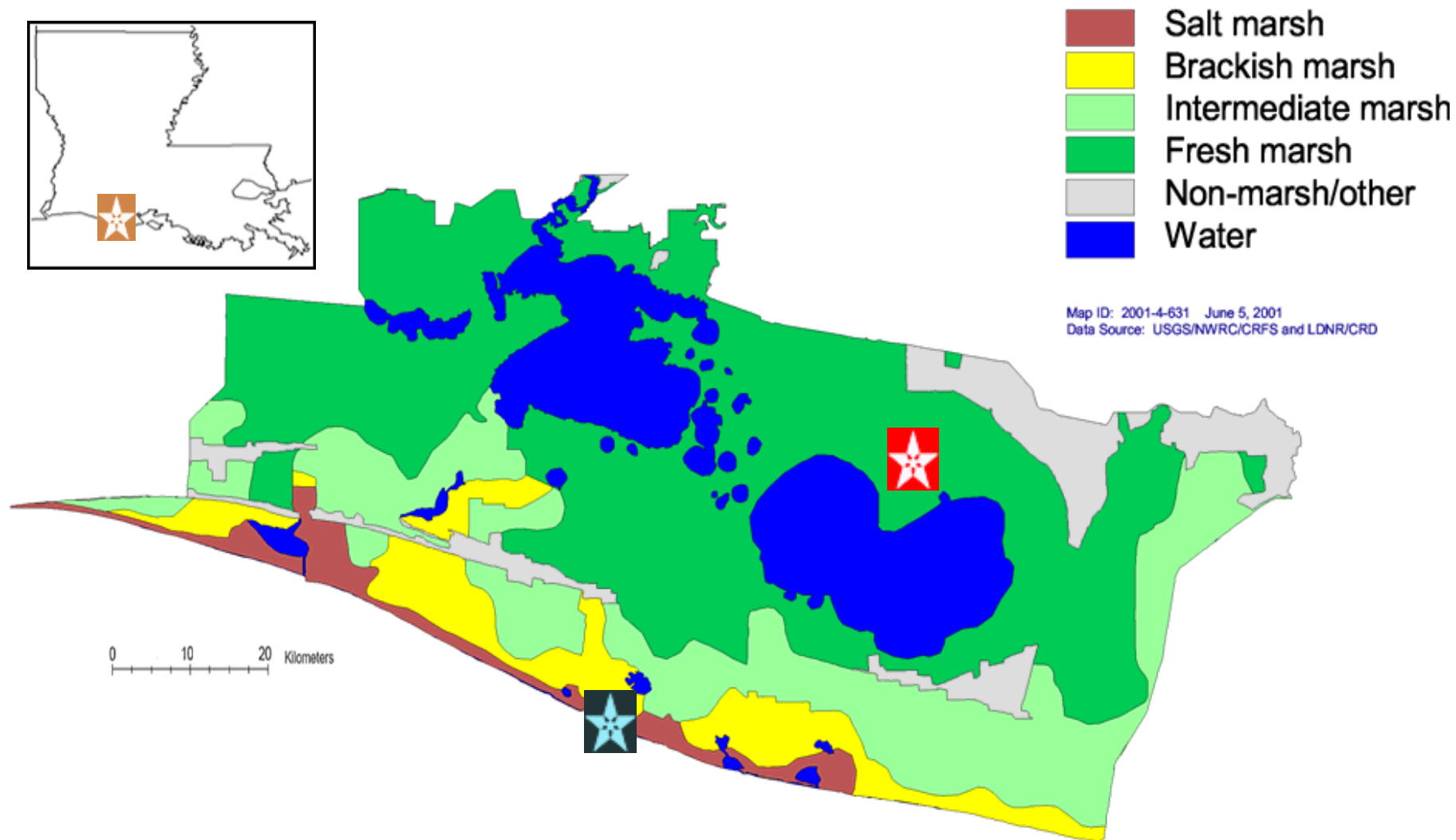


Fig. 1.2. White Lake Wetlands Conservation Area (WLWCA, red star) and Rockefeller Wildlife Refuge (RWR, blue star) in Louisiana Chenier Plain (Chabreck and Linscombe 1997).

CHAPTER 2

EFFECTS OF SALINITY, PREY, AND BODY SIZE ON THE SURVIVAL OF AQUATIC MACROINVERTEBRATES OF A CHENIER FRESHWATER MARSH

INTRODUCTION

Tidal freshwater wetlands are found worldwide at the outlets of coastal rivers with low gradient and low topographic relief at or near sea level (Doyle et al. 2007). They commonly occur in the lower Coastal Plain eco-region along the Atlantic and Gulf of Mexico coasts stretching from Maryland to Texas in the United States (Odum 1988; Mitsch and Gosselink 2000). In southwestern Louisiana, freshwater marshes of the Chenier Plain are located between beach ridges and stranded beach ridges that limit tidal exchange to a few narrow inlets at the mouths of the rivers (Visser et al. 2000).

Extreme natural events like hurricanes can result in sudden, acute exposure of freshwater marshes to high salinity levels due to storm surge (Gardner et al. 1991; Gresham 1993; Rybczyk et al. 1995). Also, sea level rise and/or subsidence can lead to chronic exposure of freshwater marshes to increased salinities resulting in substantial ecological effects (Reed 1995; Engle et al. 2009). Increased salinity is a common problem in coastal freshwater marsh ecosystems (Chabreck and Palmisano 1973; Frazer et al. 2006) and can cause local extinctions of aquatic macroinvertebrates (Halse et al. 2003). Aquatic macroinvertebrates are fundamental components of most aquatic ecosystems (Paradise 2009) and are important for nutrient cycling (Mitsch and Gosselink 2000), food resources for higher vertebrates (Batzer and Wissinger 1996), and biological diversity (Sharitz and Batzer 1999). Thus, altered community structure due to environmental disturbance (e.g., increasing salinity) has the potential to impact ecosystem function and cause extensive environmental damage (Kefford et al. 2003b; Jardine et al. 2007).

Although there are some studies of the effects of salinity on freshwater macroinvertebrates (Mills and Geddes 1980; Kefford et al. 2003a; Horrigan et al. 2007), these studies have been conducted in river and creek habitats but the impacts of increased salinity on aquatic macroinvertebrates of coastal freshwater marshes remain relatively unstudied.

Decreased survival of individual species is at least partially responsible for alterations in community structure of aquatic macroinvertebrates following increases in salinity, extended duration of exposure to higher salinities, and prey absence during salinity exposure. For example, a recent laboratory study (Hassell et al. 2006) observed that increased salinity from 0.6 to 1.6 gl^{-1} total dissolved solids (TDS) reduced survival rate of mayflies (i.e., *Cloeon* spp.) to about 50%; survival dropped to 33% when exposed to salinities of 5.4 gl^{-1} TDS for 21 days. Moreover, Nielsen et al. (2003) noted long-term exposure to salinity may lead to reduction in reproduction and recruitment. Prey availability may also influence the salinity tolerance of aquatic invertebrates. For instance, the copepod *Sulcanus conflictus* Nicholls had lower survival rates at increased salinities when food was limited (Rippingale and Hodgkin 1977). Furthermore, taxa group and body size may affect salinity tolerance as crustaceans may be more tolerant than insects (Clemens and Jones 1954) and small freshwater macroinvertebrates (e.g., Odonata) may have lower salinity tolerance than large macroinvertebrate (Dytiscidae *Cybister*, Shirgur and Kewalramani 1973).

A clear understanding of the linkages among abiotic disturbances (e.g., increased salinity, extended duration of exposure, prey availability) and biological characteristics (e.g., body size) and survival would enhance our understanding of aquatic macroinvertebrates in coastal freshwater systems and facilitate conservation strategies for these organisms. In this study, microcosm experiments were used to assess the effects of increased salinity and prey availability

at different exposure durations on the relative survival rates of four aquatic macroinvertebrates of varying body size groups that are dominant in coastal freshwater marshes of southwestern Louisiana. I hypothesized that 1) increased salinity, absence of prey, and increased duration of exposure would decrease survival of aquatic macroinvertebrates and 2) crustaceans and large body taxa would have higher survival than aquatic insects and small body taxa.

METHODS

Study Area

Field collections occurred in the White Lake Wetlands Conservation Area (WLWCA, 29°52'50" N, 92°31'11" W) in the Chenier Plain of southwestern Louisiana (Fig. 1). This area is owned and operated by the Louisiana Department of Wildlife and Fisheries. WLWCA is located along the western boundary of Vermilion Parish and is bounded on the south by White Lake (28.2 km north of the Gulf of Mexico). The 28,719 ha area includes managed (8,972 ha) and unmanaged (12,106 ha) tidal freshwater marsh.

I sampled two habitat types: pond edge (i.e., within 1-m of pond border) and flooded emergent marsh. Dominant vegetation in the pond edge and in the emergent marsh was emergent non-woody vegetation that included maidencane (*Panicum hemitomon* Schultes) and bulltongue arrowhead (*Sagittaria lancifolia* Linnaeus). Common floating and submerged plants were American white waterlily (*Nymphaea odorata* Aiton) and coontail (*Ceratophyllum demersum* Linnaeus); the most common emergent woody plant was buttonbush (*Cephalanthus occidentalis* Linnaeus). Dominant vegetation height was ≤ 50 cm in the pond edge but 51-100 cm in the emergent marsh.

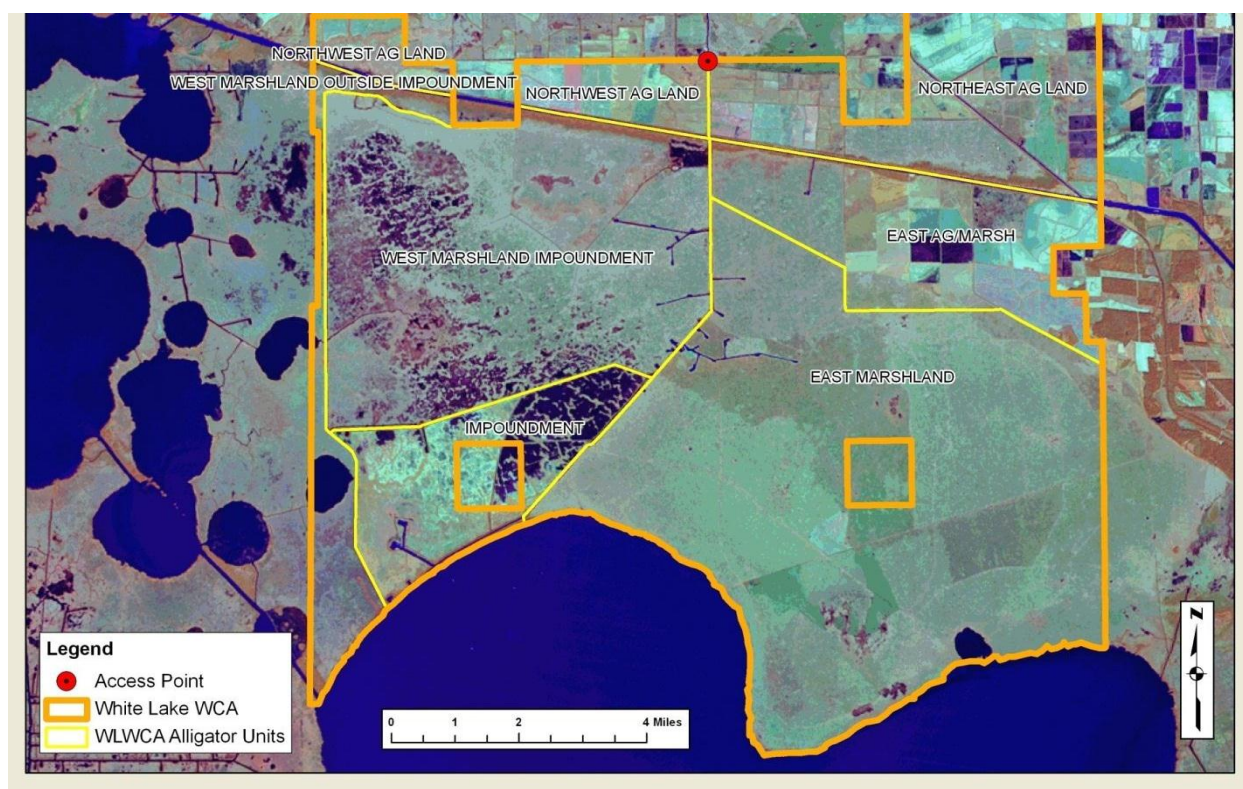


Fig. 2.1. Map of White Lake Wetlands Conservation Area (WLWCA) in Vermilion Parish, Louisiana. Samples collected in west marshland impoundment and east marshland.

Aquatic Macroinvertebrates Collection

As part of a broader study of macroinvertebrate communities at White Lake Wetlands Conservation Area, I sampled aquatic macroinvertebrates from March to May 2010 at random points in eight ponds and four emergent marsh sites using three methods: 1) a D-shaped sweep net along the water surface (Bulduc and Afton 2003), 2) a 1-m² aluminum-sided throw trap (1x1x1 m, with a 3-mm mesh) similar to that described in Kushlan (1981), and 3) Gee minnow traps (42x23 cm, with a 6-mm mesh; Dorn et al. 2005). Aquatic macroinvertebrates were placed in a tank filled with collection site water (i.e., ranges between 0.5 and 0.7 g l⁻¹ TDS). Oxygen was pumped into the tank and temperature was not allowed to rise above 22 °C during transport to the laboratory (2 h).

Aquatic macroinvertebrates were identified in the laboratory under a dissecting microscope. Dominant aquatic macroinvertebrates in pond and emergent marsh were *Procambarus clarkii* (Decapoda: Cambaridae), *Cambarellus puer* (Decapoda: Cambaridae), Libellulidae (Insecta: Odonata), and Dytiscidae (Insecta: Coleoptera). I treated family level of aquatic insects (Libellulidae and Dytiscidae) as a single taxon because I was unable to identify individuals without harm. These four taxa were collected on at least one occasion in sufficient numbers to be exposed to a full range of test salinities.

Salinity and Prey Availability Experiments

To determine survival rate, a series of 45 cm x 30 cm x 15 cm plastic trays were filled with water of six salinities both with and without prey for 28 days. Test salinities were 0.6, 7.2, 13.5, 19.4, 25.1, and 30.7 g l^{-1} TDS. Water temperature was maintained at 22 °C, which is the preferred temperature for feeding activity in crayfish (Cambaridae) (Huner and Barr 1991). Water salinity in each treatment was prepared by dissolving ocean salt with collection site water. Aquatic macroinvertebrates were transferred without previous acclimatization from collection site water (i.e., 0.6 g l^{-1} TDS) to treatment cells. Aquatic insects and crustaceans in feeding groups were fed daily with aquatic vegetation, macroinvertebrates, and small fishes. Individual taxa were housed in separate trays. Survival was checked daily; individuals were considered dead if they were not moving and failed to respond to probing. Dead aquatic macroinvertebrates were removed at the time of observation.

Statistical Analyses

Logistic regression was used to examine the effects of salinity, exposure duration, and prey availability on aquatic macroinvertebrate survival (Proc Glimmix, Version 9.2, SAS Institute, North Carolina). Tukey's Honestly Significant Difference Multiple Comparisons Test

was used to determine differences among treatments for each taxon. ANOVA (Proc Mixed, Version 9.2, SAS Institute, North Carolina) was used to test for statistical differences between large and small body size groups.

RESULTS

Survivorship in the controls (i.e., 0.6 gl^{-1} TDS) was 100%, however, there were clear differences in survival among salinity treatments within the same prey treatment (Fig. 2.2 and 2.3). Also, I found that interactions between salinity and prey availability in most species occurred above and below certain thresholds. At the lower threshold, low salinities (i.e., $\leq 0.6 \text{ gl}^{-1}$ TDS) allowed species to survive even without food. Above the upper threshold, however, high salinities (i.e., $\geq 25.1 \text{ gl}^{-1}$ TDS) killed species whether they had food or not (Fig. 2.4 and Fig. 2.5).

Procambarus clarkii had similar survival patterns up to 13.5 gl^{-1} TDS in both prey treatments. In with- and without-prey treatment, survival decreased at 7.2 gl^{-1} TDS after 9-10 days and at 13.5 gl^{-1} TDS after 8-10 days to 80%, then dropped to 60% at 13.5 gl^{-1} TDS over 28 days (only without prey treatment). Survival at 19.4 gl^{-1} TDS, however, was affected by prey availability. With prey provided, survival at 19.4 gl^{-1} TDS was 80% survival until 21 days (Fig. 2.2), and then dropped to 40% over 28 days. Without prey provided, however, survival declined to 80% after only 4 days and 40% after 11 days. Complete mortality was observed at 12 days (Fig. 2.3).

Cambarellus puer also had 100% survival in salinities $\leq 7.2 \text{ gl}^{-1}$ TDS over 28 days in both prey treatments and survival was 0% in the 30.7 gl^{-1} TDS treatment with or without prey provided on day 1. However, survival at 13.5 ($t = 8.43, p < 0.01$), 19.4 ($t = -10.10, p < 0.01$), and 25.1 ($t = -9.11, p < 0.01$) gl^{-1} TDS was obviously different in both treatments with extended

exposure duration. For example, in the 13.5 gl^{-1} TDS, survival declined to 80% on day 17 and 40% on day 23 to day 28 with prey available, but similar values were achieved on days 8 (80%) and 12-28 (20%) without food available. Also, in 25.1 gl^{-1} TDS, *Cambarellus puer* survival in with-prey decreased after two days to 60%, and then dropped to 20% at 10 days but in without-food, survival declined at first day to 10%, then all died on the second day.

Libellulidae had comparable survival patterns up to 13.5 gl^{-1} TDS during 14 days in with- and without-prey treatment. In both prey treatments, survival decreased at 7.2 gl^{-1} TDS after 9-10 days and at 13.5 gl^{-1} TDS after 12-13 days to 50-60%, then dropped to 30% at 13.5 gl^{-1} TDS over 28 days in with-prey treatment but no survival was observed after 26 days without prey. Libellulidae had no survival between 13.5 and 30.7 gl^{-1} TDS over 28 days in both prey treatments.

There were no surviving Dytiscidae in any salinity and prey treatment. Survival declined at 7.2 gl^{-1} TDS after 6 days to 40% in both prey treatments, then fell to 20% at 20 days in with-prey and 13 days in without-prey. Both aquatic insects (i.e., Libellulidae and Dytiscidae) exposed to the high salinities (19.4-30.7 gl^{-1} TDS) in without-prey experiment died faster than all other treatments.

Comparison of relative survival between aquatic insects and crustaceans showed that crustaceans were substantially more tolerant to salinity and duration exposure than aquatic insects (Fig. 2.4 and 2.5). No survival of aquatic insects was observed after 24 days of exposure to 13.5 gl^{-1} TDS and 7 days to 19.4 gl^{-1} TDS in with-prey treatment. In contrast, crustacean survival remained 40-80% at 13.5 gl^{-1} TDS, but when exposed to 25.1 gl^{-1} TDS for 21 days survival was 0%. For both groups survival decreased after day 1 at salinities 25.1 gl^{-1} TDS in both prey treatments. Aquatic insects reached 100% mortality within 5 days but crustaceans

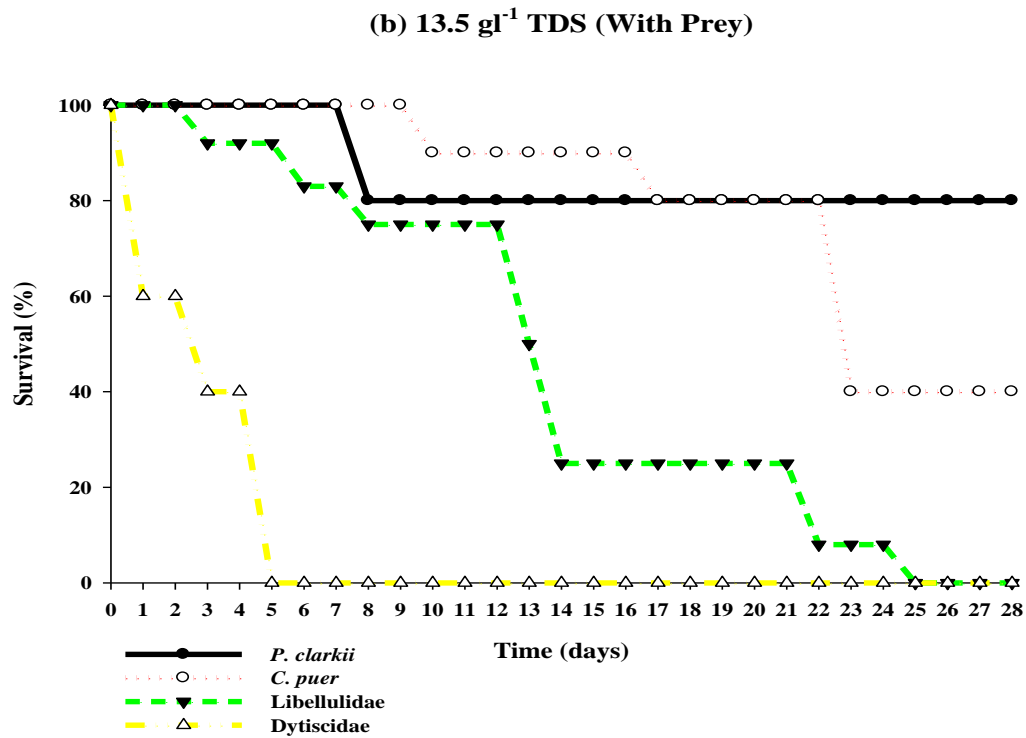
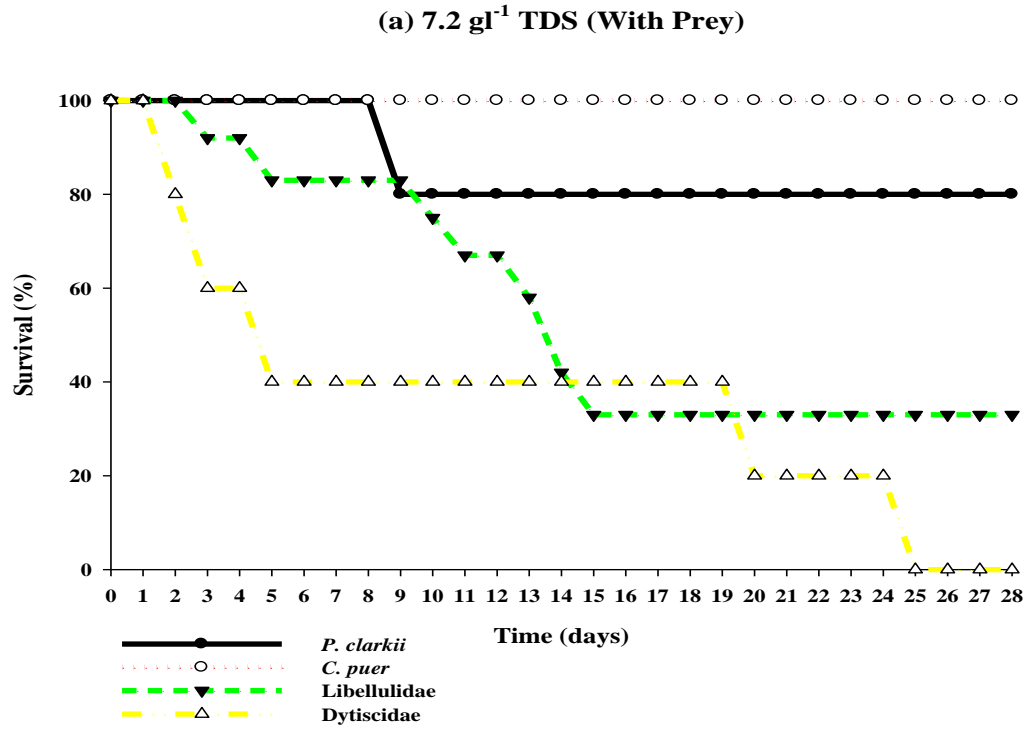
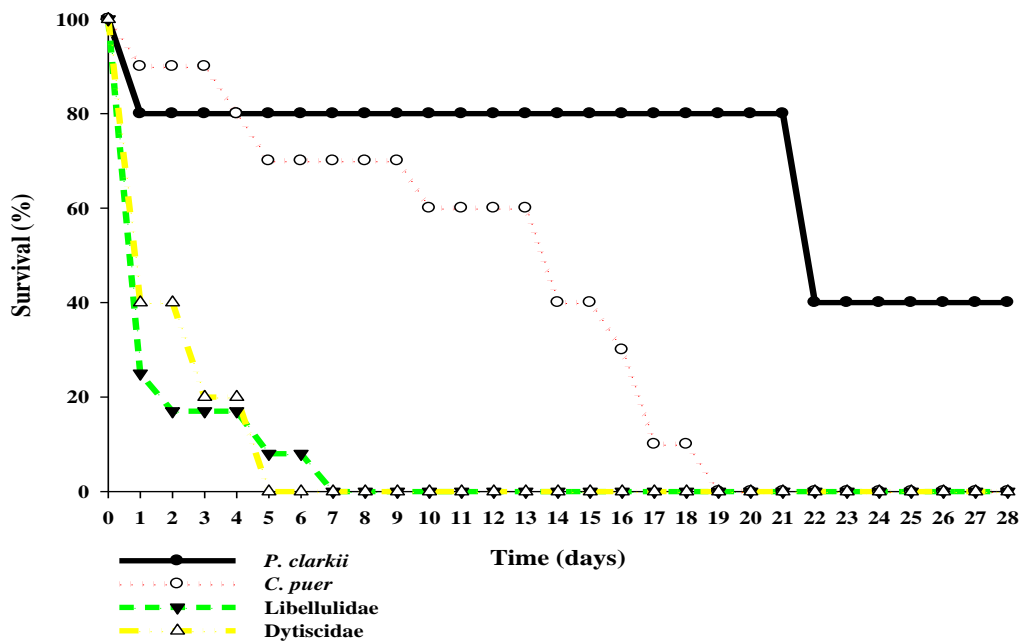


Fig. 2.2. Mean survival rate of aquatic insects and crustaceans by 7.2 and 13.5 (gl^{-1}) with-prey over 28 days.

(c) 19.4 gl^{-1} TDS (With Prey)



(d) 25.1 gl^{-1} TDS (With Prey)

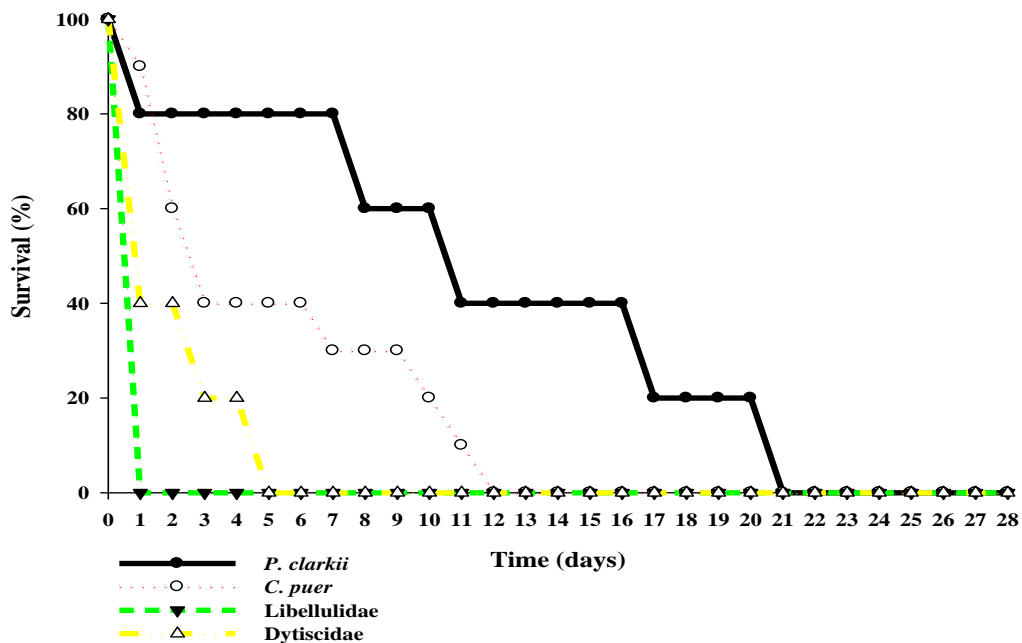


Fig. 2.3. Mean survival rate of aquatic insects and crustaceans by 19.4 and 25.1 (gl^{-1}) with-prey over 28 days.

(e) 30.7 gl^{-1} TDS (With Prey)

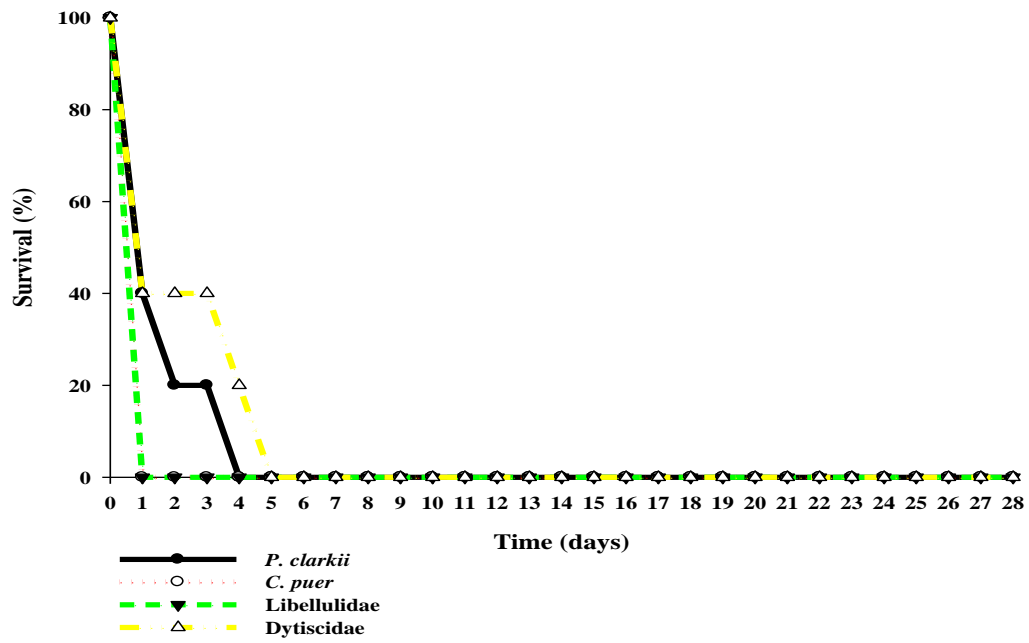


Fig. 2.4. Mean survival rate of aquatic insects and crustaceans by 30.7 (gl^{-1}) with-prey over 28 days.

(a) 7.2 gl^{-1} TDS (Without Prey)

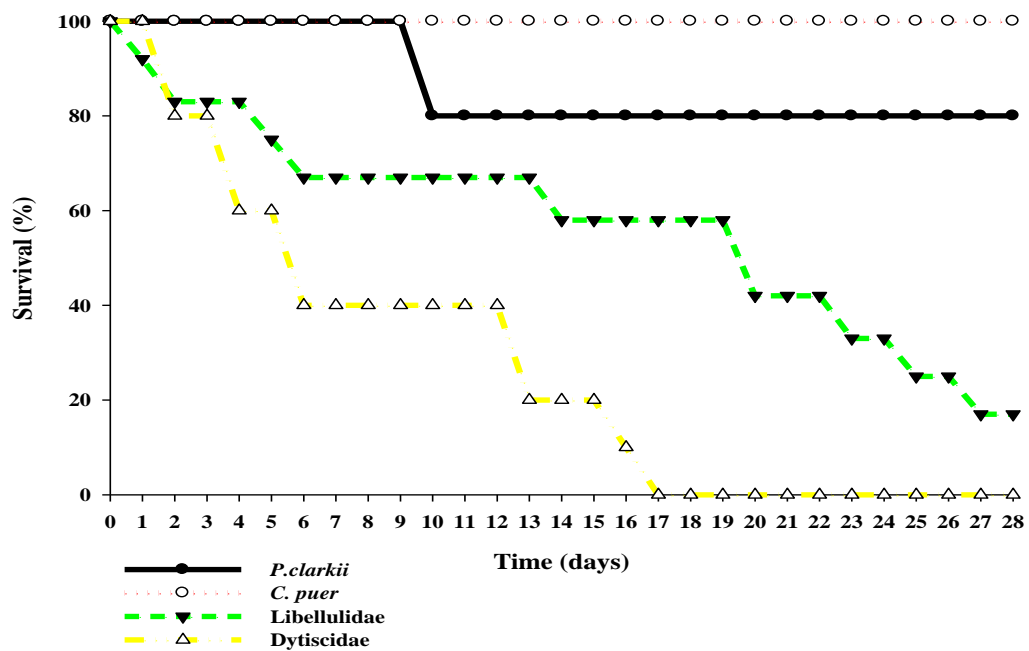
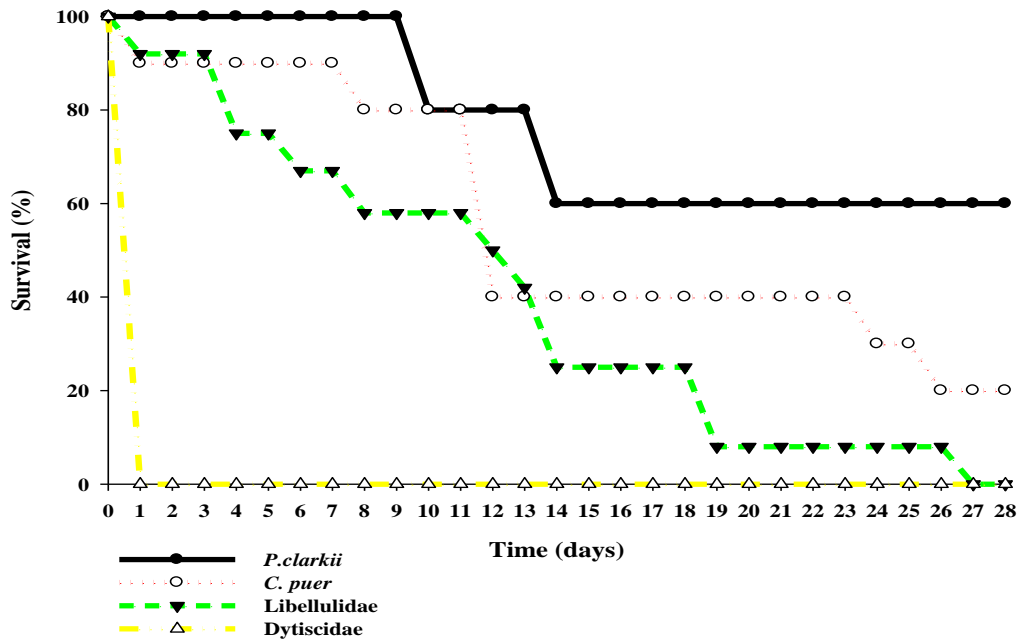


Fig. 2.5. Mean survival rate of aquatic insects and crustaceans by 7.2 (gl^{-1}) without-prey over 28 days.

(b) 13.5 gl^{-1} TDS (Without Prey)



(c) 19.4 gl^{-1} TDS (Without Prey)

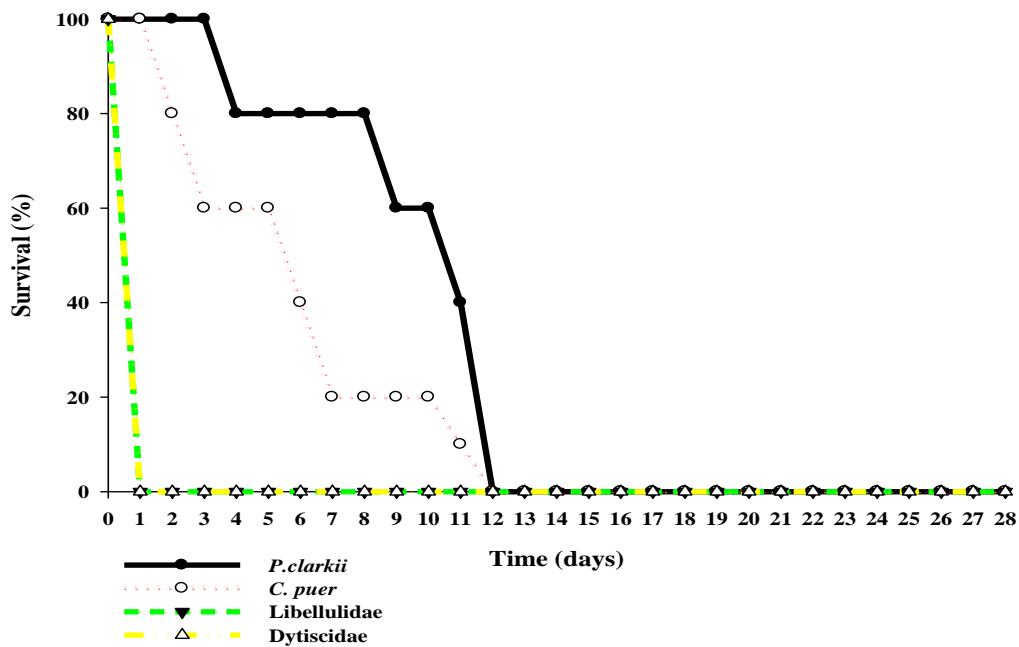
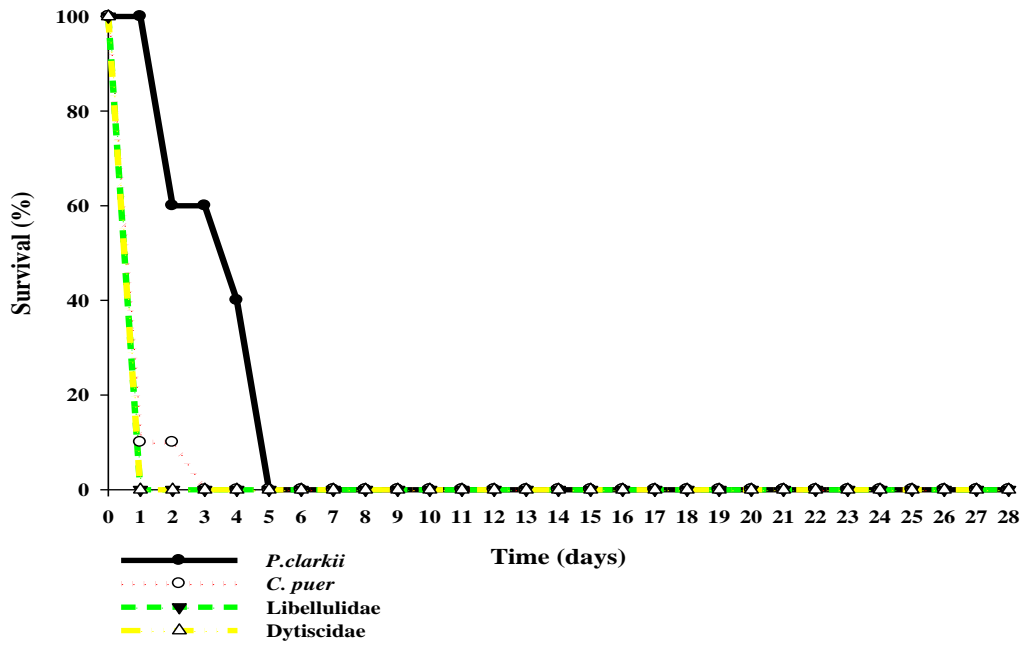


Fig. 2.6. Mean survival rate of aquatic insects and crustaceans by 13.5 and 19.4 (gl^{-1}) without-prey over 28 days.

(d) 25.1 gl^{-1} TDS (Without Prey)



(e) 30.7 gl^{-1} TDS (Without Prey)

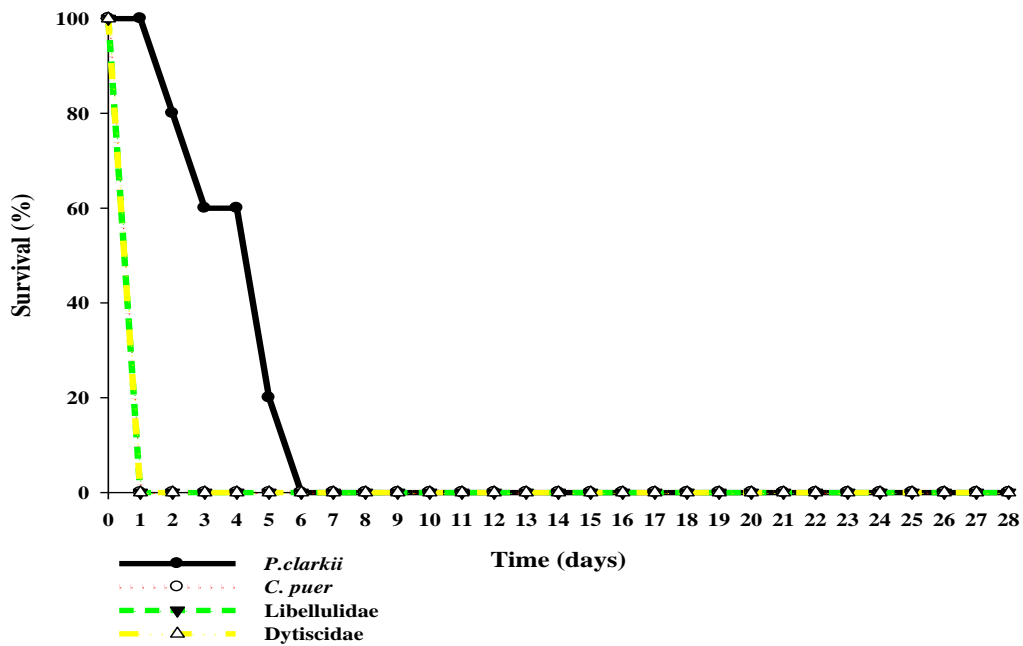


Fig. 2.7. Mean survival rate of aquatic insects and crustaceans by 25.1 and 30.7 (gl^{-1}) without-prey over 28 days.

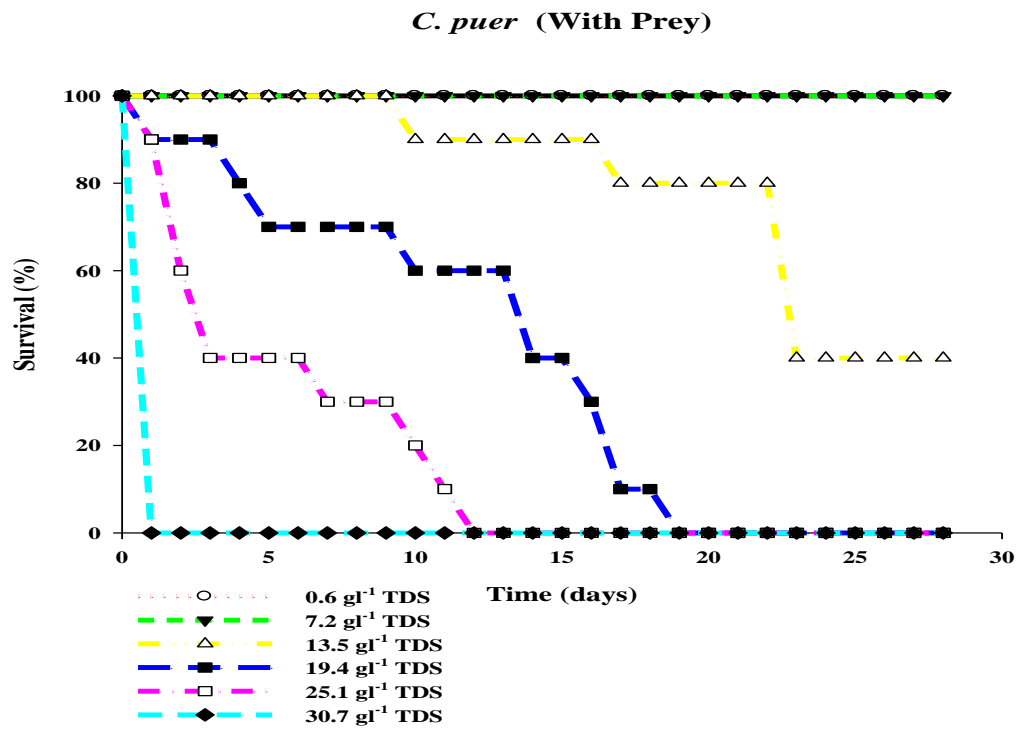
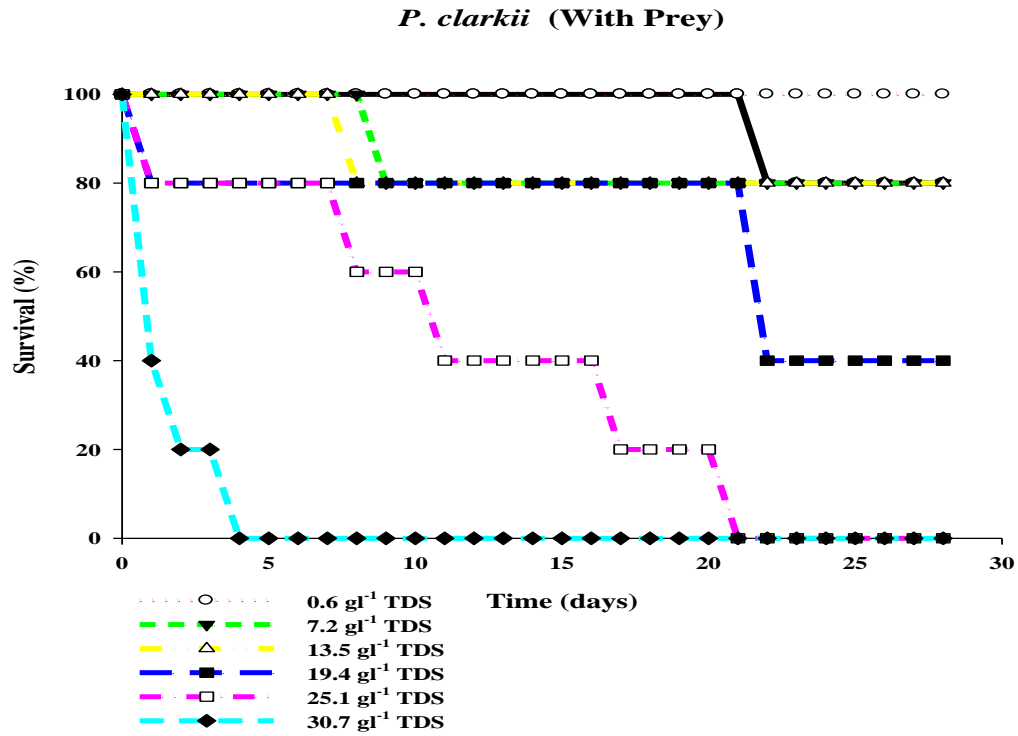


Fig. 2.8. Survivorship curves for crustaceans exposed to a range of salinities (g l^{-1}) with- prey over 28 days.

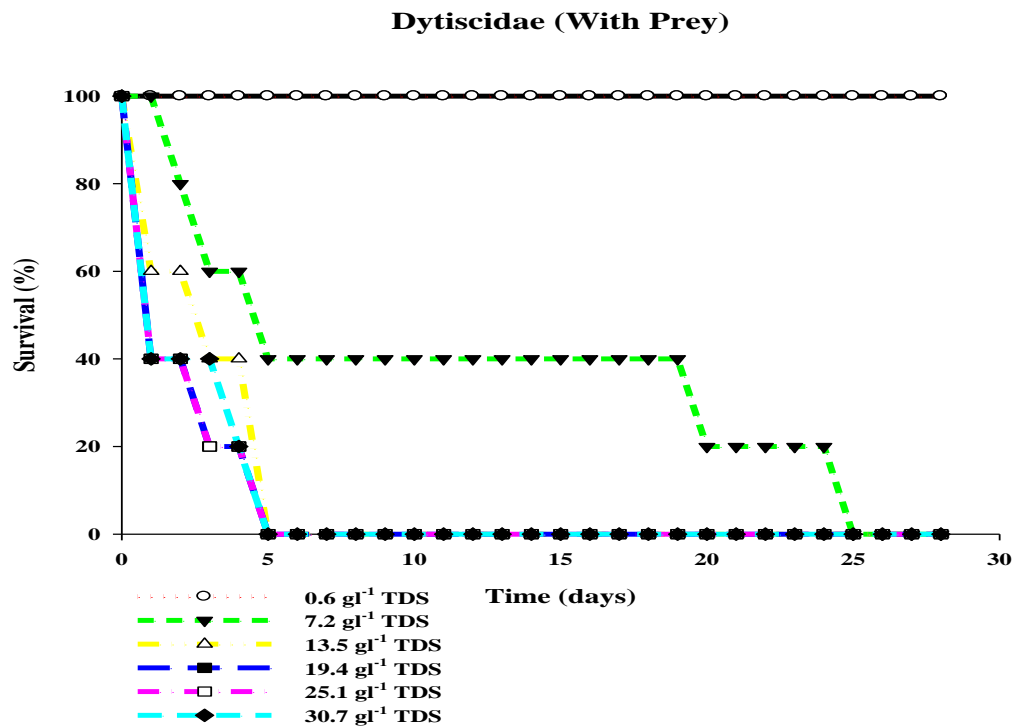
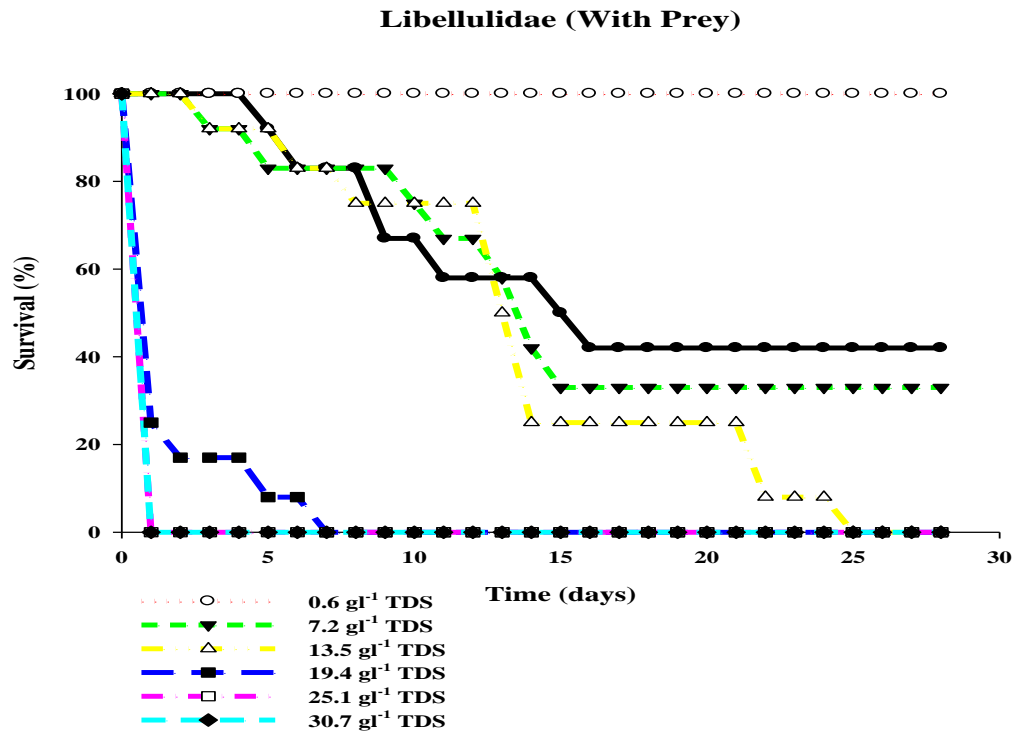


Fig. 2.9. Survivorship curves for aquatic insects exposed to a range of salinities (gl^{-1}) with- prey over 28 days.

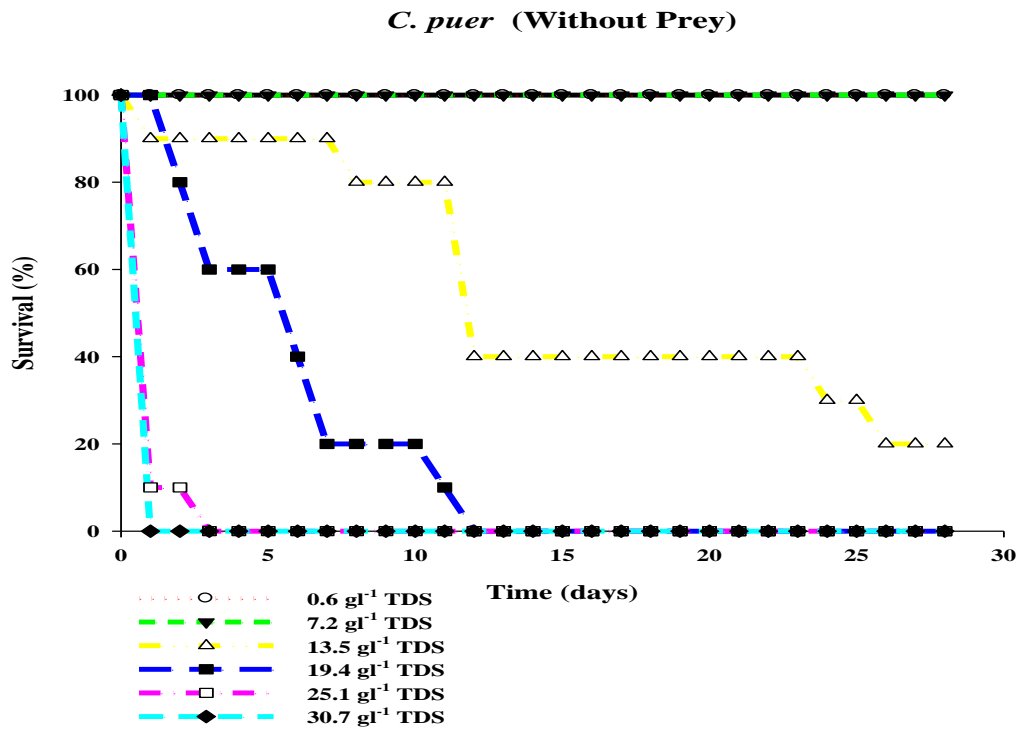
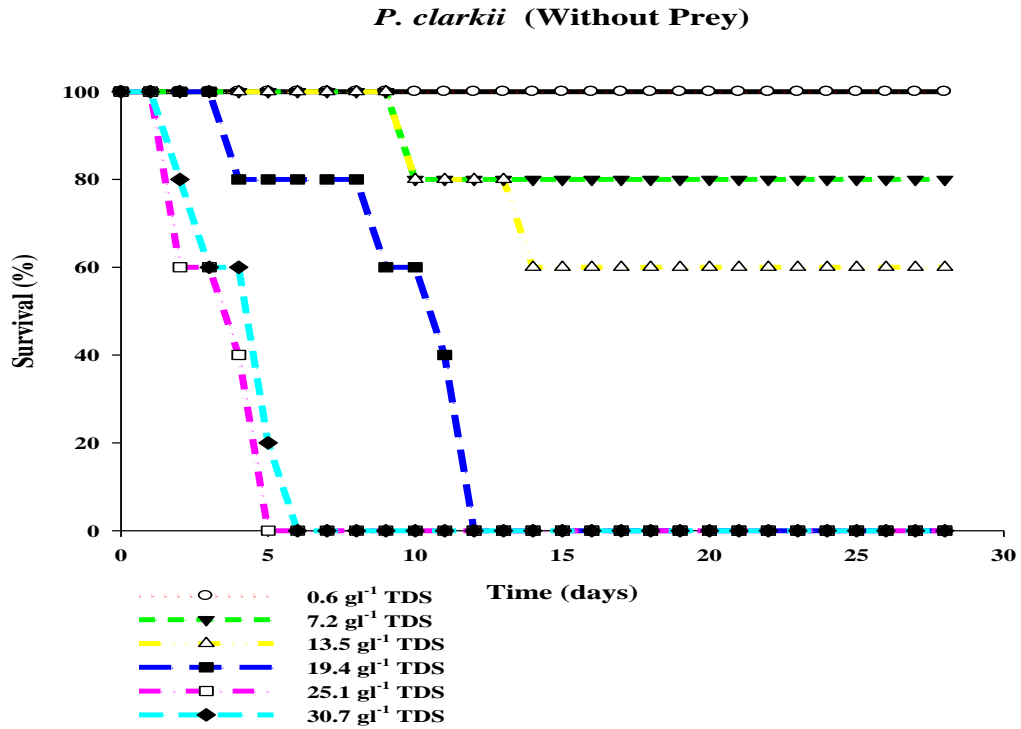


Fig. 2.10. Survivorship curves for crustaceans exposed to a range of salinities (gl^{-1}) without-prey over 28 days.

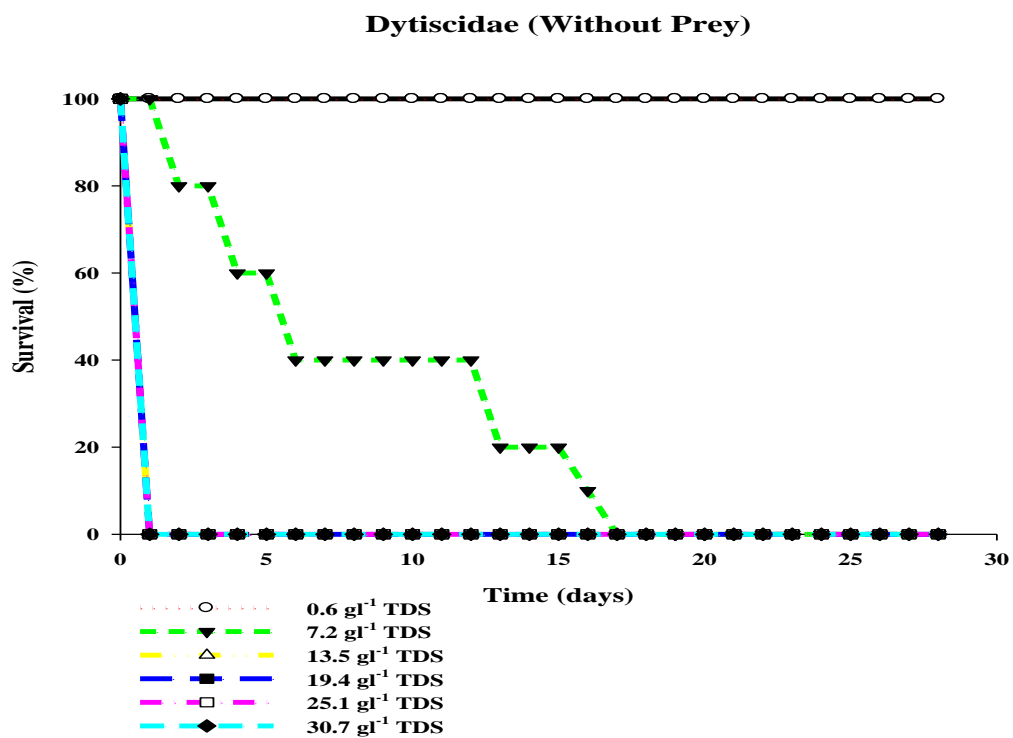
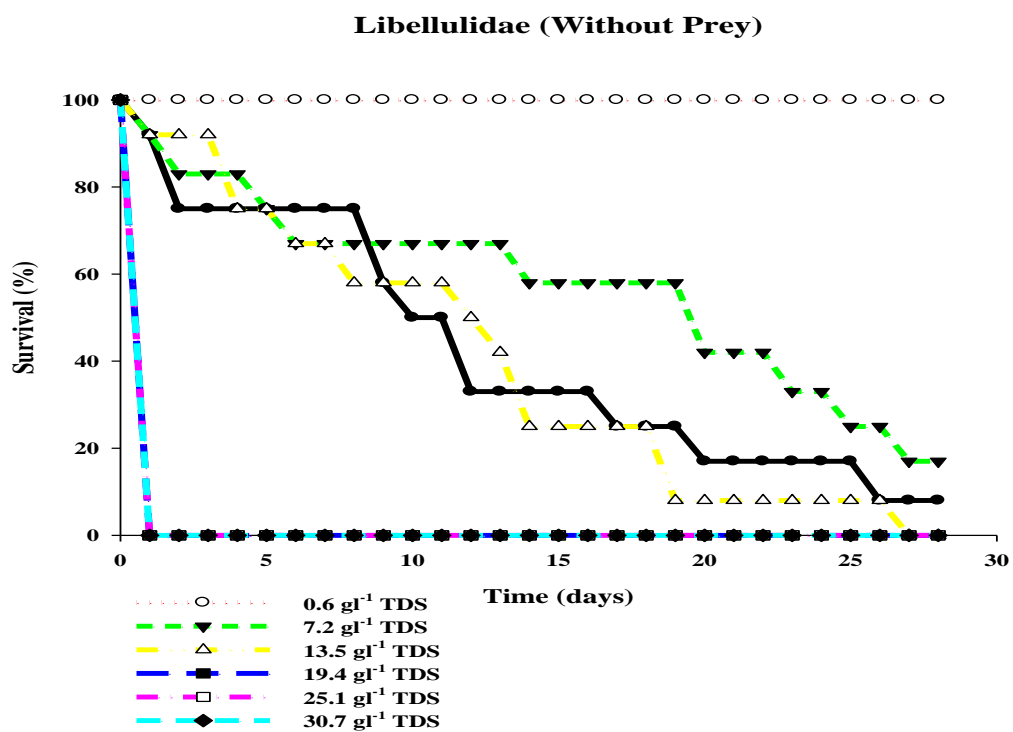


Fig. 2.11. Survivorship curves for aquatic insects exposed to a range of salinities (g l^{-1}) without-prey over 28 days.

survived until 20 days. Logistic regression analysis of salinity, prey, and exposure duration by taxon were similar as taxa group comparison. Relative survival by taxa group varied due to salinity (d.f =5, $F=3.5$, $p \leq 0.01$) but prey (d.f =1, $F=0.0$, $p=0.95$) and interaction between salinity and prey (d.f =4, $F=0.5$, $p=0.76$) did not indicate differences. Relative survival between different body sizes in each crustacean and aquatic insect group (i.e., Large: *Procambarus clarkii*, Dytiscidae; Small: *Cambarellus puer*, Libellulidae) did not differ. *Procambarus clarkii* and *Cambarellus puer* had similar tolerance (i.e., moderate salinities, 7.2 g l^{-1} TDS) for prolonged periods (i.e., > 80% survival for 4 weeks) and exhibited > 60% survival of 13.5 and 19.4 g l^{-1} TDS for 3 days. In addition, Dytiscidae and Libellulidae did not survive salinities > 7.2 g l^{-1} TDS.

DISCUSSION

Salinity stress may cause mortality particularly when acting together with other stressful conditions. A species that can easily withstand large variation of salinity in the laboratory may not survive much smaller changes in the field if these changes are associated with other factors, such as food shortages, which may themselves constitute a stress (Gilles and Pequeux 1983). The results of this study partially support my first hypothesis and suggest that increases in salinity could cause differential survival of aquatic macroinvertebrates in coastal freshwater marshes of southwestern Louisiana, particularly if prey is limited. While survival of all species was affected by increased salinity, upper and lower species-specific thresholds existed for each species. All aquatic macroinvertebrates recorded high survival rates at low salinity (i.e., 7.2 g l^{-1} TDS) in with-prey treatment but no survival was observed when salinities exceeded 19.4 g l^{-1} TDS in without-prey treatment. In addition, survival of macroinvertebrates in both prey treatments obviously declined when exposure duration was increased. For example, *Cambarellus puer*

survival in both prey treatments declined to 80% on day 17 and 40% on day 23 at 13.5 gl^{-1} TDS. Hassell et al. (2006) observed comparable survival pattern of aquatic invertebrates in a without-prey treatment. Consequently, effects of increased salinity, extended duration of exposure, and the interaction between salinity and prey availability on survival was clear by taxon, but the effect of prey availability was not obviously different. Paradise (2009) also found no differences in survival of freshwater invertebrates due to prey presence or absence. This finding suggests that prey availability may not affect survival of macroinvertebrates exposed to continuous salinity stress.

Previous studies reported several crustaceans (e.g., crayfish-*Pacifastacus leniusculus*, *Cherax destructor*, *Procambarus zonangulus*) survived up to 19 gl^{-1} TDS in the field and in laboratory experiments (Miller 1960; Mills and Geddes 1980; Newsome and Davis 1994) but aquatic insects (e.g., Odonata-Gomphidae, Hemicorduliidae) survived only up to 8 to 10 gl^{-1} TDS (Horrigan et al. 2007). I observed similar results and different taxa group hypothesis received support in this study. However, body size hypothesis received little support. Although *Procambarus clarkii* (i.e., relatively large, 9cm) and *Cambarellus puer* (i.e., relatively small, 3.5cm) had different body sizes, the effects of increased salinity, extended duration of exposure, and prey absence revealed similar survival. Aquatic insects (i.e., Dytiscidae (relatively large, 3cm); Libellulidae (relatively small, 1.5cm)) also had similar survival patterns.

Coastal marshes of the Gulf of Mexico regularly encounter hurricanes and tropical storms that are subject to repeating surge effects. For instance, salinity data from 15 coastwide reference monitoring system (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2008) stations in Louisiana coastal freshwater marshes before and after Hurricanes Gustav and Ike indicate that salinity increased over pre-storm values for one or more days, reaching up to 24.3 gl^{-1} TDS (e.g.,

range: 2.4 – 24.3 gl^{-1} TDS, median: 13.5 gl^{-1} TDS) for one day to several days. According to the results, Libellulidae and Dytiscidae may not survive for one day if hurricanes alter the salinity level up to 24.3 gl^{-1} TDS without prey. *Procambarus clarkii* and *Cambarellus puer*, however, may survive about 10 days in the same condition. However, all four species tested may survive at least 14 days without food when storm surge increase the salinity level up to 7.2 gl^{-1} TDS. At the median salinity (i.e., 13.5 gl^{-1} TDS), exposure duration of 7 days and one day with prey available would begin to impact crayfish and aquatic insect survival, respectively. At the higher salinity ranges (i.e., 24.3 gl^{-1} TDS) mortality of all species would be expected after one day with or without food. Actual gage data suggest, however, that the average number of days that salinity exceeded 13.5 gl^{-1} TDS following hurricanes Gustav and Ike was 1.22 ± 0.15 days.

Our study results may be less applicable to the effects of gradual sea level rise and different life stage. Sea level has been rising over the last century by as much as 1-2 mm/year (Douglas 1991; Gornitz 1995) and a much greater rate of 3.1 mm per year from 1993 to 2003 (IPCC 2007). Increased rates of rise in the future can lead to saltwater intrusion into freshwater marshes but salinity changes resulting from this intrusion are likely to be gradual outside of storm surges. As a result, aquatic macroinvertebrate survival may be greater than those observed here as acclimation may enhance survival (Kay et al. 2001, Kefford et al. 2004). In addition, if macroinvertebrate eggs or larvae suffered high salinity, they may have different salinity tolerance. Nevertheless, our findings provide novel information about salinity tolerances of macroinvertebrates subjected to acute salinity increases in coastal freshwater marsh ecosystems and may help managers better understand the impacts of these events on aquatic invertebrate communities.

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CHAPTER 3

EFFECTS OF HYDROLOGIC CONNECTIVITY AND ENVIRONMENTAL VARIABLES ON NEKTON ASSEMBLAGE IN A COASTAL MARSH SYSTEM

INTRODUCTION

Hydrologic connectivity in coastal ecosystems influences many environmental variables and the community 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). Longitudinal hydrologic connectivity patterns in coastal wetlands 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 the inundation pattern of freshwater marshes is not a regular pulse of flooding and drying (Mithsch and Gosselink 2000) because their greater distance from the ocean dampens the influence of the tidal cycle (Day et al. 2007). Lateral pond-channel-emergent marsh hydrologic connectivity patterns within coastal marshes are affected by dry and wet phases due to seasonal variations in the relative extent of the flooded area. These connectivity patterns are important drivers of environmental variables in coastal marsh systems. For example, decreasing salinity from the coast (i.e., saline marsh) towards inland (i.e., freshwater marsh) due to reduced hydrologic connectivity (i.e., channels) of the marsh to the sea is typical for coastal marsh systems (Chabreck 1988). Also, tidally flooded ponds that are hydrologically connected with other ponds, channels, and emergent marshes may have cooler temperatures and higher oxygen concentrations than infrequently flooded ponds in coastal marshes (Hunter et al. 2009).

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). Thus, variation in environmental variables as a result of varying hydrologic connectivity can potentially affect nekton assemblages. Several studies have indicated that salinity strongly affects nekton community structure 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; Lake 2003; Humphries and Baldwin 2003) and foraging habitat quality (Kneib and Wagner 1994; Balcombe et al. 2005). Nekton are also affected by variation in oxygen, temperature, and vegetation structure in coastal marshes. McKinsey (1998) noted habitat patches of varying oxygen level across spatial scales may be important in structuring nekton diversity, and 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 community assemblages.

A clear understanding of the linkages among hydrologic connectivity, environmental variables, and nekton community assemblages would enhance our understanding of nekton habitat characteristics in coastal systems and facilitate conservation strategies for these organisms. The principal objectives of this study are to: 1) examine the effects of hydrologic connectivity on environmental variables and the density, biomass, diversity, and similarity of nekton communities and 2) compare spatial and temporal patterns of nekton assemblages in different marsh (i.e., freshwater, brackish, saline) and pond (i.e., permanently connected pond, temporarily connected pond) types. I hypothesize that 1) permanently connected ponds (PCPs) have greater flood duration, water depth, SAV coverage, and dissolved oxygen (DO) and lower temperatures than temporarily connected ponds (TCPs); 2) nekton communities in PCPs have higher density, biomass, diversity, and community similarity than TCPs over all marsh types, and 3) dominant nekton species distributions vary across the salinity gradient.

METHODS

Study Area

This study was conducted in White Lake Wetlands Conservation Area (WLWCA, 29°52'50" N, 92°31'11" W) and Rockefeller State Wildlife Refuge (RWR, 29°40'93" N, 92°48'45" W) in the Chenier Plain of southwestern Louisiana (Fig. 3.1). Both areas are owned and operated by the Louisiana Department of Wildlife and Fisheries. White Lake Wetlands Conservation Area is located along the western boundary of Vermilion Parish and is bounded on the south by White Lake (28.2 km north of the Gulf of Mexico). The 28,719 ha area includes managed (8,972 ha) and unmanaged (12,106 ha) freshwater marsh. Dominant vegetation is maidencane (*Panicum hemitomon*) and bulltongue arrowhead (*Sagittaria lancifolia*). Rockefeller

State Wildlife Refuge is a 42,400 ha refuge located in eastern Cameron and western Vermilion Parishes, wedged between Grand Chenier Highway 82 and the Gulf of Mexico. This area borders the Gulf of Mexico for 41.8 km and extends inland toward the Grand Chenier ridge. This refuge consists of 17 impoundments, which allow for control of both water level and salinity (Wicker et al. 1983). The Unit Six management area was selected as tidal brackish marsh habitat. Unit Six is a 7,200 ha brackish impoundment dominated by *Spartina patens*. In addition, an unmanaged area of similar size was selected as tidal saline marsh habitat. The saline marsh is dominated by *Spartina alterniflora*.

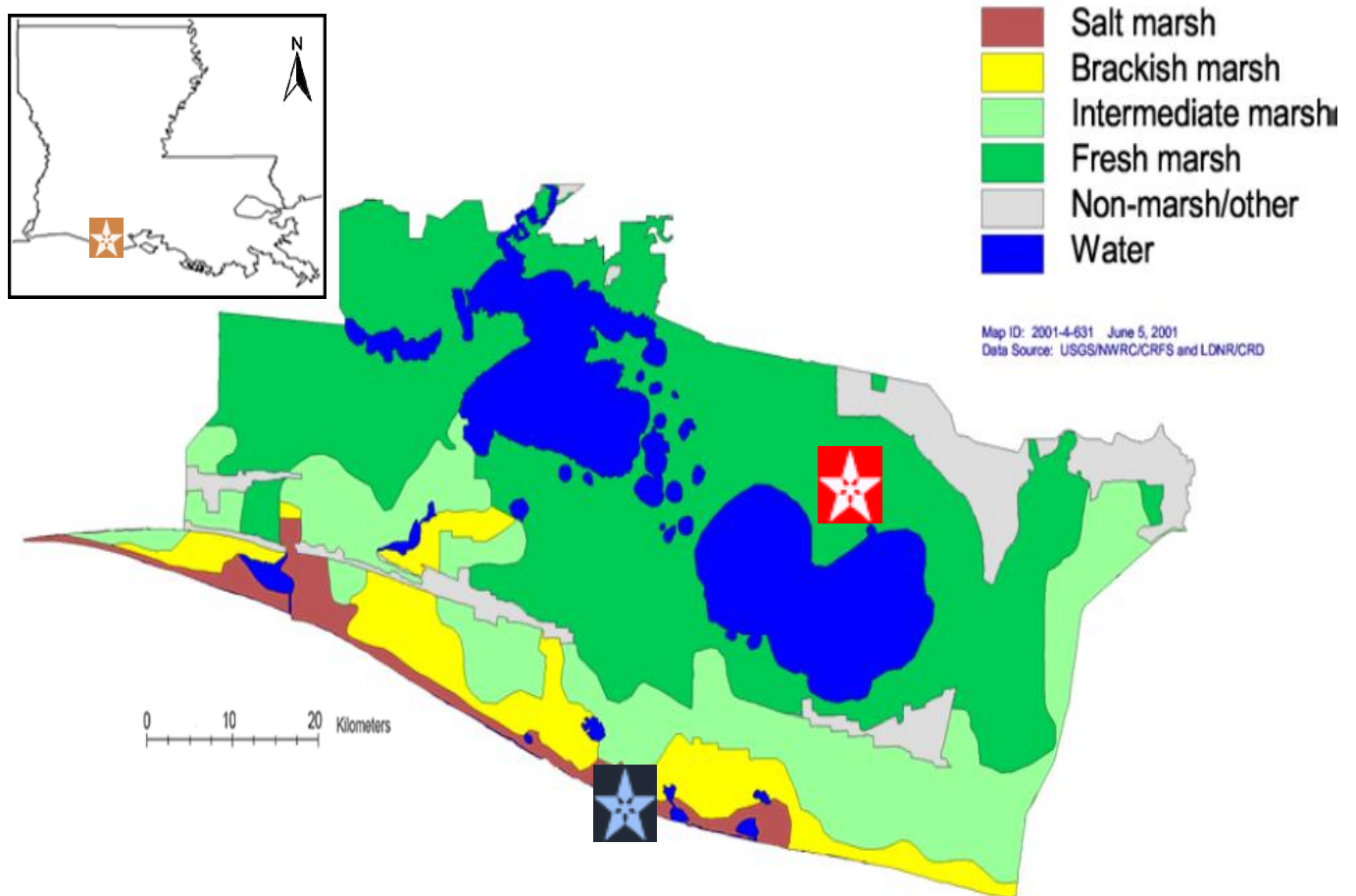


Fig. 3.1. White Lake Wetlands Conservation Area (red star) and Rockefeller Wildlife Refuge (blue star) are located in Vermilion Parish, Louisiana (Chabreck and Linscombe 1997).

Table 3.1. The types of ponds and environmental variables measured in this study as well as variable names, sampling units and abbreviations.

	Variable name	Units	Abbreviation
Pond types	Permanently Connected Pond	number	PCP
	Temporarily Connected Pond	number	TCP
	Pond Total (PCP+TCP)		PT
Environmental variables	Salinity	ppt	Salinity
	Dissolved Oxygen	mg/L	DO
	Temperature	°C	Temp
	Sampling Point Water Depth	cm	SPWD
	Connected Water Depth	cm	CWD
	Duration of Isolation	days	DI
	Frequency of Isolation	times	FI
	Vegetation Coverage	%	VC

Hydrologic and Environmental Data

In each of the three marsh types, I identified all ponds from aerial photography and field visits and classified them each as either a PCP (i.e., permanently connected to a man-made [some in freshwater marsh] or natural [all marshes] channel during all seasons) or a TCP (i.e., temporarily connected by surface water to the surrounding marsh but not permanently connected to a channel). I randomly selected three PCPs and three TCPs in each marsh type for more intensive study and deployed a continuous water level recorder in the interior of each pond (Fig. 3.2) in November 2008. Also, a staff gage was set at the border between the pond and emergent marsh to measure connected water depth (CWD; i.e., water depth at border between pond and emergent marsh when the pond is connected with surface water to the channel or surrounding marsh). CWD was determined by comparing water depths obtained at the meter stick on several occasions prior to the study and once per month during the study with those of the continuous

water level recorder. The difference between water levels at the continuous water level recorder and the staff gage was calculated and a basic arithmetic equation was used to predict water depth measurements at the staff gage. Monthly water depth measurements at the meter stick were always within 1 cm of the predicted values. I then determined lateral connectivity based on the criteria that $CWD > 0$, and calculated duration of isolation (DI; i.e., duration of disconnection among the pond, channel, and emergent marsh), frequency of isolation (FI; i.e., frequency of disconnection between the pond and channel/emergent marsh), and CWD.

To assess variation in environmental variables across pond types, I measured salinity (ppt), water temperature ($^{\circ}\text{C}$), and DO (mg L^{-1}) with a YSI Model 85 Water Quality Monitor. Also, sampling point water depth (SPWD; cm) within each throw and minnow trap was estimated by calculating the mean of three depth measurements taken inside the throw trap and next to the minnow trap. Following each nekton sample, these variables were measured 2-3 cm above the sediment between 08:00 and 17:00. Percent cover of SAV in a 1x1-m frame was also determined at three points in each pond and the mean coverage was calculated.

Nekton Sampling

To determine nekton characteristics, I 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); 5) Spring 2010 (March-May). Once per season, I sampled nekton by throw trap and minnow traps (Classen 2008) at each pond. 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 x 23 cm with a 6-mm mesh, baited with a piece of chicken gizzard) were set for approximately 2 hours at three random points in each sampling pond. Five minnow traps could cover 1 m² at each sampling point. 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 were weighed to the nearest 0.001 g wet-weight to determine biomass (g/m²).

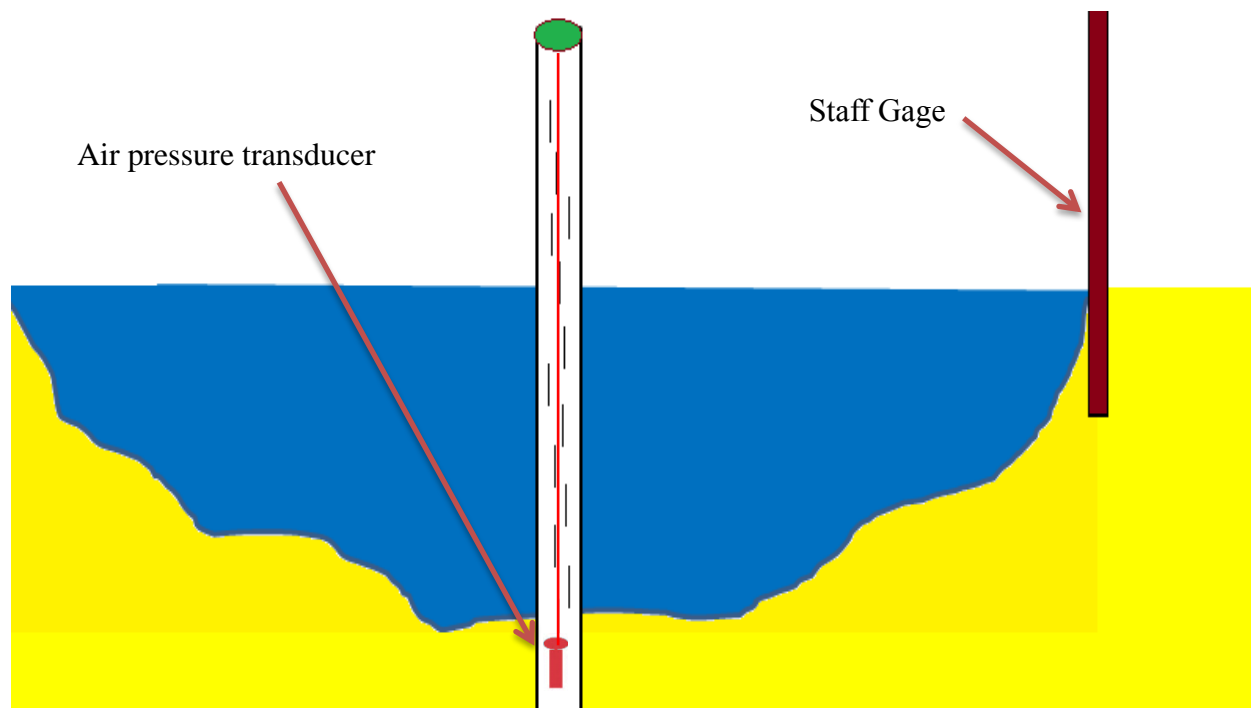


Fig. 3.2. Schematic of water-level recording devices in each pond. A continuous water level recorder (pressure transducer) was placed in the center or interior of each pond. A meter stick was placed on the edge of the pond at the border between the pond and the emergent marsh.

Statistical Analyses

Environmental variables and nekton density and biomass were natural log ($x+1$) transformed to achieve normality. Data were tested for normality with the Shapiro-Wilks test. Significance level was chosen at 0.05.

Environmental Variables: Multivariate analysis of variance (MANOVA: Proc Mixed, Version 9.2, SAS Institute, North Carolina) was used to compare environmental variables (Table 3.1) by seasons, marshes, and pond types. Following significant MANOVA results, individual one-way analysis of variance (ANOVA: Proc Mixed) tests were performed. Significant ANOVA effects were tested using post-hoc comparisons of Tukey adjusted least squared means.

Nekton Density, Biomass, Diversity, and Community Similarity: ANOVA (Proc Mixed) was used to test for statistical differences in density, biomass and diversity by seasons, marshes, and pond types. Multiple linear regression (Proc Mixed) was used to examine the potential relationship between nekton community characteristics (i.e., density, biomass, diversity) and environmental factors (Table 3.1). PRIMER software (Clarke and Gorley 2006) was used to test the effect of hydrologic connectivity on community similarity that compared the overlapped species in same pond types during all sampling periods. ANOSIM was performed on a Bray-Curtis dissimilarity matrix that computed on the fourth-root transformed abundance data. I compared differences of community similarity for pond types with the one-way SIMPER ($p=0.05$) test on standardized fourth-root transformed abundance data. 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 community structure (Clarke and Warwick 2001).

Nekton Community Distribution: 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 I caught more than three individuals in the samples (Gauch 1982; Piazza and La Peyre 2009).

RESULTS

Environmental Variables

The mean diameter of randomly selected PCPs and TCPs were 99.0 ± 14.6 m and 75.4 ± 17.7 m, respectively. Water depths in freshwater and brackish PCPs and TCPs fluctuated with rainfall patterns but saline PCPs and TCPs had a weaker relationship with rainfall. PCPs and TCPs always contained some water with the exception of one saline TCP but all pond edges dried seasonally (Fig. 3.3-3.14). The timing of drying in freshwater and saline TCPs was July 2009 and in brackish TCPs was May 2010. TCPs in all marshes disconnected and reconnected to the surrounding emergent marsh in June 2009. Thereafter, TCPs in brackish and saline marshes were continuously reconnected to surrounding areas in August 2009; freshwater TCPs were reconnected in September 2009.

Seasonal salinity in freshwater ($F_{2,57}=39.15$, $p<0.01$) and brackish ($F_{2,57}=7.80$, $p=0.01$) marsh ponds was higher in Summer 2009 than Winter 2009; salinity did not differ seasonally in the saline marsh ($p=0.1261$). Salinity differed among marsh types with the highest in saline marsh and the lowest in freshwater marsh ($F_{2,177}=17.61$, $p=0.01$). Between pond types among marshes, saline PCPs and TCPs had greater salinity than brackish and freshwater PCPs and TCPs, respectively (PCPs: $F_{2,87}=26.97$, $p < 0.01$; TCPs: $F_{2,87}=34.54$, $p<0.01$). Within freshwater marshes (t value=2.42, $p=0.04$), salinity was higher in PCPs (0.9 ± 0.23) than in TCPs (0.3 ± 0.07); salinity did not differ between PCPs and TCPs in brackish ($p=0.98$) and saline marshes ($p=0.77$).

Seasonal DO in freshwater marsh ponds was greater in Winter 2009 than in Summer 2009 ($F_{2,57}=15.47$, $p=0.01$); no difference was observed in brackish ($p=0.09$) and saline ($p=0.05$) marshes. Comparison of DO among marsh types indicated that brackish and saline PT in Summer 2009 was higher than freshwater PT ($F_{2,57}=74.40$, $p<0.01$, Table 3.2). Between pond

types across marshes, DO was higher in brackish (4.5 ± 0.43) than in fresh (2.5 ± 0.67) TCPs ($F_{2,87}=4.49$, $p=0.04$) but did not differ in PCPs. There were no differences in DO between pond types within a marsh.

Temperature in freshwater ($F_{2,57}=8.28$, $p<0.01$) and brackish ($F_{2,57}=8.07$, $p<0.01$) marshes were higher in Summer 2009 than Winter 2009; no seasonal difference was recorded in saline marshes ($p=0.17$). Comparison of temperature among marsh types indicated that saline PT in Winter 2009 ($F_{2,57}=33.17$, $p<0.01$) and Spring 2010 ($F_{2,57}=21.01$, $p=0.02$) was higher than brackish and freshwater PT (Table 3.2). However, temperature did not differ between pond types across marshes or between pond types within a marsh.

Seasonal SAV coverage within each marsh did not differ. However, SAV coverage differed among marsh types with the highest in freshwater marsh and no SAV in saline marsh ($F_{2,177}=25.95$, $p<0.01$). Between pond types among marshes, freshwater PCPs and TCPs had greater SAV coverage than brackish and saline PCPs and TCPs, respectively (PCPs: $F_{2,87}=9.88$, $p=0.01$; TCPs: $F_{2,87}=8.43$, $p=0.02$). Comparison of between pond types within a marsh showed that SAV coverage in Winter 2009 in freshwater PCPs was higher than in TCPs (Table 3.3, $p=0.01$); SAV coverage did not differ between pond types in brackish and saline marshes.

SPWD in freshwater ($F_{2,57}=8.32$, $p=0.04$), brackish ($F_{2,57}=7.20$, $p<0.01$), and saline marshes ($F_{2,57}=6.78$, $p<0.01$) was greater in Fall and Winter 2009 than Summer 2009 and Spring 2010. Among marsh types, saline PT in Spring 2009 was lower than brackish PT ($F_{2,57}=13.98$, $p=0.03$). Comparisons between pond types among marshes indicated that SPWD in saline PCPs (15.1 ± 2.62) was lower than fresh (31.7 ± 2.78) and brackish (31.3 ± 5.90) PCPs ($F_{2,87}=5.44$, $p=0.02$) but TCPs did not differ. Within a marsh, saline TCPs had higher SPWD than PCPs in Spring 2009 ($p=0.02$) and Winter 2009 ($p=0.04$) (Table 3.3).

Seasonal comparisons of CWD in freshwater ($F_{2,57}=5.80, p=0.01$), brackish ($F_{2,57}=9.02, p<0.01$), and saline marshes ($F_{2,57}=7.20, p<0.01$) indicated that CWD was higher in Fall and Winter 2009 than Summer 2009 and Spring 2010. Among marsh types, CWD in brackish PT was greater than freshwater PT in Summer 2009 ($F_{2,57}=13.70, p=0.03$) and Fall 2009 ($F_{2,57}=13.70, p=0.03$). Between pond types across marshes, CWD in saline PCPs in Winter 2009 was lower than brackish and freshwater PCPs ($F_{2,57}=10.49, p=0.01$). Within a marsh, freshwater ($p=0.02$) and saline ($p=0.02$) TCP had higher CWD than PCPs.

Seasonal DI of TCPs in freshwater marsh was greater in Summer 2009 than in Winter 2009 ($F_{2,57}=4.20, p=0.03$). DI of TCPs did not differ among marsh types. Within a marsh, DI of TCPs in Summer 2009 was greater than PCPs ($p=0.04$).

Seasonal FI in each marsh type did not differ (freshwater marsh: $F_{2,57}=1.31, p=0.34$; brackish marsh: $F_{2,57}=1.85, p=0.20$; saline marsh: $F_{2,57}=1.27, p=0.35$). Also, FI did not differ among marsh types, between pond types across marshes, and between pond types within a marsh.

Nekton Density, Biomass, Diversity, and Community Similarity

I collected 31,011 nekton of 42 taxa from 540 samples. I 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) (Table 3.4). Freshwater PCPs had 6 exclusive taxa but TCPs did not have any exclusive taxa within a marsh. PCPs and TCPs in brackish marsh had 4 and 2 exclusive taxa, respectively. Within a saline marsh, PCPs (6 taxa) had greater exclusive taxa than TCPs (2 taxa).

Table 3.2. Comparison of means (\pm SE) of environmental variables (salinity, dissolved oxygen, temperature, sampling point water depth, SAV coverage; n=180) and connectivity factors (connected water depth, TCPs duration of isolation, TCPs frequency of isolation; n=456) among marsh types. Means sharing a letter on a row do not differ ($p > 0.05$).

	Freshwater marsh	Brackish marsh	Saline marsh	<i>p</i> value
Spring 2009				
Salinity (ppt)	0.8 (0.11)A	6.3 (0.44)B	15.0 (2.64)C	<0.01
Dissolved oxygen (mg/l)	3.1 (0.42)A	4.5 (0.11)B	3.2 (0.81)A	<0.01
Temperature (°C)	28.7 (2.00)A	25.8 (3.18)A	25.6 (1.28)A	0.13
Sampling point water depth (cm)	35.4 (2.54)AB	40.8 (2.06)A	16.5 (1.96)B	0.03
SAV coverage (%)	33.3 (5.11)A	13.2 (5.70)B	0.0 (0.00)C	<0.01
Connected water depth (cm)	16.2 (0.40)A	37.4 (1.74)A	18.3 (1.03)A	0.06
Duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)A	0.0 (0.00)A	n.s
Frequency of isolation (times)	0.0 (0.00)A	0.0 (0.00)A	0.0 (0.00)A	n.s
Summer 2009				
Salinity (ppt)	1.1 (0.08)A	7.0 (0.66)B	18.9 (2.47)C	<0.01
Dissolved oxygen (mg/l)	1.3 (0.40)A	3.8 (0.48)B	3.9 (0.67)B	<0.01
Temperature (°C)	31.1 (0.72)A	32.9 (2.43)A	32.0 (1.79)A	0.15
Sampling point water depth (cm)	23.4 (1.98)A	22.0 (1.13)A	13.9 (2.09)A	0.41
SAV coverage (%)	41.9 (16.36)A	14.2 (5.45)AB	0.0 (0.00)B	0.02
Connected water depth (cm)	3.3 (1.44)A	13.7 (2.31)B	10.0 (2.08)AB	0.03
Duration of isolation (days)	17.4 (2.92)A	2.5 (1.26)A	2.5 (1.26)A	0.56
Frequency of isolation (times)	0.0 (0.00)A	0.5 (0.29)A	0.5 (0.29)A	0.65
Fall 2009				
Salinity (ppt)	0.4 (0.03)A	2.7 (0.39)B	9.4 (2.39)C	<0.01
Dissolved oxygen (mg/l)	1.8 (0.55)A	3.3 (0.29)A	3.8 (0.41)A	0.13
Temperature (°C)	22.6 (2.77)A	21.1 (2.42)A	22.3 (0.76)A	0.12
Sampling point water depth (cm)	44.4 (2.59)AB	51.0 (2.68)A	27.7 (4.50)B	0.03
SAV coverage (%)	37.0 (17.56)A	27.8 (15.13)B	0.0 (0.00)C	<0.01
Connected water depth (cm)	25.5 (9.17)A	44.2 (7.12)B	27.1 (2.04)A	<0.01
Duration of isolation (days)	2.2 (2.17)A	0.0 (0.00)A	0.0 (0.00)A	0.46
Frequency of isolation (times)	0.2 (0.17)A	0.0 (0.00)A	0.0 (0.00)A	0.46

Table 3.2. Continued.

	Freshwater marsh	Brackish marsh	Saline marsh	<i>p</i> value
Winter 2009				
Salinity (ppt)	0.3 (0.01)A	1.1 (0.05)A	5.8 (1.96)B	<0.01
Dissolved oxygen (mg/l)	5.1 (0.59)A	6.2 (1.09)A	6.4 (1.02)A	0.24
Temperature (°C)	11.9 (1.24)A	13.0 (1.12)A	14.6 (2.64)B	<0.01
Sampling point water depth (cm)	30.6 (2.27)A	33.2 (1.26)A	20.2 (1.27)A	0.09
SAV coverage (%)	19.5 (2.28)A	1.4 (0.74)A	0.0 (0.00)A	0.09
Connected water depth (cm)	37.4 (2.80)AB	43.3 (6.06)A	20.3 (4.18)B	0.04
Duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)A	0.5 (0.50)A	0.46
Frequency of isolation (times)	0.0 (0.00)A	0.0 (0.00)A	0.2 (0.17)A	0.46
Spring 2010				
Salinity (ppt)	0.5 (0.05)A	3.2 (1.69)B	14.6 (3.36)C	<0.01
Dissolved oxygen (mg/l)	2.2 (0.35)A	4.7 (0.56)A	4.3 (0.27)A	0.05
Temperature (°C)	25.0 (4.25)A	24.5 (3.68)A	30.8 (3.75)B	0.02
Sampling point water depth (cm)	24.9 (2.08)A	17.8 (0.40)A	14.8 (2.34)A	0.07
SAV coverage (%)	34.9 (7.31)A	9.2 (5.60)AB	0.0 (0.00)B	0.05
Connected water depth (cm)	11.7 (6.31)A	9.8 (6.50)A	11.2 (2.41)A	0.77
Duration of isolation (days)	6.9 (3.90)A	7.0 (4.54)A	0.5 (0.50)A	0.69
Frequency of isolation (times)	0.7 (0.44)A	0.2 (0.17)A	0.2 (0.17)A	0.63
Winter 2009				
Salinity (ppt)	0.3 (0.01)A	1.1 (0.05)A	5.8 (1.96)B	<0.01
Dissolved oxygen (mg/l)	5.1 (0.59)A	6.2 (1.09)A	6.4 (1.02)A	0.24
Temperature (°C)	11.9 (1.24)A	13.0 (1.12)A	14.6 (2.64)B	<0.01
Sampling point water depth (cm)	30.6 (2.27)A	33.2 (1.26)A	20.2 (1.27)A	0.09
SAV coverage (%)	19.5 (2.28)A	1.4 (0.74)A	0.0 (0.00)A	0.09
Connected water depth (cm)	37.4 (2.80)AB	43.3 (6.06)A	20.3 (4.18)B	0.04
Duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)A	0.5 (0.50)A	0.46
Frequency of isolation (times)	0.0 (0.00)A	0.0 (0.00)A	0.2 (0.17)A	0.46

Table 3.3. Comparison of means (\pm SE) of environmental variables (salinity, dissolved oxygen, temperature, sampling point water depth, SAV coverage; n=180) and connectivity factors (connected water depth, duration of isolation, frequency of isolation; n=456) between pond types across marshes (letters) and within a marsh (*: $p < 0.05$ and n.s.: $p > 0.05$). 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	<i>p</i> -value	PCP	TCP	<i>p</i> -value	PCP	TCP	<i>p</i> -value
Spring 2009									
Salinity (ppt)	1.2 (0.15)A	0.4 (0.07)a	*	6.9 (0.53)A	5.6 (0.35)ab	n.s	16.4 (2.18)B	13.6 (3.10)b	n.s
Dissolved oxygen (mg/l)	2.8 (0.24)A	3.3 (0.59)a	n.s	4.5 (0.13)A	4.4 (0.08)a	n.s	3.2 (0.84)A	3.1 (0.77)a	n.s
Temperature (°C)	30.1 (2.05)A	27.2 (1.95)a	n.s	25.7 (3.35)A	25.8 (3.00)a	n.s	25.8 (1.20)A	25.4 (1.35)a	n.s
Sampling point water depth (cm)	34.4 (4.03)A	36.4 (1.04)a	n.s	39.6 (1.45)A	42.0 (2.66)a	n.s	10.8 (2.84)B	22.2 (1.07)b	*
SAV coverage (%)	34.4 (5.47)A	32.2 (4.75)a	n.s	14.2 (4.17)B	12.1 (7.23)ab	n.s	0.0 (0.00)B	0.0 (0.00)b	n.s
Connected water depth (cm)	14.2 (0.38)A	18.1 (0.42)a	*	35.9 (1.56)B	38.9 (1.91)b	n.s	11.6 (0.23)A	25.0 (1.82)a	*
Duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s
Frequency of isolation (times)	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s
Summer 2009									
Salinity (ppt)	1.6 (0.08)A	0.5 (0.07)a	*	7.0 (0.56)B	7.0 (0.75)a	n.s	18.4 (0.79)C	19.4 (4.14)b	n.s
Dissolved oxygen (mg/l)	1.4 (0.33)A	1.1 (0.46)a	n.s	3.7 (0.06)B	3.8 (0.90)b	n.s	4.1 (0.85)B	3.6 (0.49)b	n.s
Temperature (°C)	31.4 (0.85)A	30.8 (0.58)a	n.s	32.4 (2.26)A	33.4 (2.59)a	n.s	31.4 (1.49)A	32.5 (2.08)a	n.s
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	n.s	10.7 (2.73)B	17.0 (1.44)ab	n.s
SAV coverage (%)	49.4 (20.69)A	34.4 (12.03)a	n.s	19.4 (2.00)A	8.9 (8.89)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s
Connected water depth (cm)	2.9 (1.02)A	3.6 (1.86)a	n.s	12.4 (2.33)B	14.9 (2.29)b	n.s	7.9 (2.43)AB	12.1 (1.72)ab	n.s
Duration of isolation (days)	0.0 (0.00)A	24.7 (5.84)a	*	0.0 (0.00)A	5.0 (2.52)b	n.s	0.0 (0.00)A	5.0 (2.52)b	n.s
Frequency of isolation (times)	0.0 (0.00)A	0.7 (0.33)a	n.s	0.0 (0.00)A	1.0 (0.58)a	n.s	0.0 (0.00)A	1.0 (0.58)a	n.s
Fall 2009									
Salinity (ppt)	0.5 (0.01)A	0.3 (0.05)a	n.s	2.7 (0.44)AB	2.6 (0.34)ab	n.s	9.9 (3.12)B	8.8 (1.66)b	n.s
Dissolved oxygen (mg/l)	2.4 (0.64)A	1.2 (0.45)a	n.s	3.1 (0.10)AB	3.5 (0.48)b	n.s	4.4 (0.39)B	3.2 (0.42)b	n.s
Temperature (°C)	23.1 (3.33)A	22.0 (2.21)a	n.s	21.3 (2.43)A	20.8 (2.40)a	n.s	22.1 (0.87)A	22.5 (0.64)a	n.s
Sampling point water depth (cm)	40.9 (1.67)AB	47.9 (3.50)a	n.s	48.3 (3.06)A	53.6 (2.30)a	n.s	24.6 (6.89)B	30.7 (2.10)b	n.s
SAV coverage (%)	37.2 (16.17)A	36.7 (18.95)a	n.s	28.3 (14.37)A	27.2 (15.88)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s
Connected water depth (cm)	26.4 (9.43)A	24.6 (8.91)a	n.s	42.7 (6.98)A	45.6 (7.25)a	n.s	25.2 (1.57)A	29.0 (2.50)a	n.s
Duration of isolation (days)	0.0 (0.00)A	4.3 (4.33)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s
Frequency of isolation (times)	0.0 (0.00)A	0.3 (0.33)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s

Table 3.3. Continued.

	Freshwater			Brackish			Saline		
	PCP	TCP	<i>p</i> -value	PCP	TCP	<i>p</i> -value	PCP	TCP	<i>p</i> -value
Winter 2009									
Salinity (ppt)	0.3 (0.02)A	0.2 (0.00)a	*	1.1 (0.06)AB	1.0 (0.04)a	n.s	6.7 (2.34)B	4.9 (1.57)b	n.s
Dissolved oxygen (mg/l)	5.6 (0.14)A	4.6 (1.03)a	n.s	6.6 (0.67)A	5.7 (1.51)a	n.s	6.7 (0.75)A	6.0 (1.29)a	n.s
Temperature (°C)	11.9 (1.69)A	11.8 (0.79)a	n.s	12.9 (1.15)A	13.1 (1.09)a	n.s	15.0 (2.36)A	14.2 (2.92)a	n.s
Sampling point water depth (cm)	27.2 (0.76)A	33.9 (3.78)a	n.s	31.1 (0.86)A	35.2 (1.66)a	n.s	17.0 (2.07)B	23.3 (0.47)b	*
SAV coverage (%)	27.2 (2.00)A	11.7 (2.55)a	**	0.0 (0.00)B	2.8 (1.47)b	n.s	0.0 (0.00)B	0.0 (0.00)b	n.s
Connected water depth (cm)	40.2 (2.14)A	34.6 (3.45)a	n.s	41.5 (6.19)A	45.1 (5.93)a	n.s	15.3 (4.43)B	25.3 (3.92)a	n.s
Duration of isolation (days)	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	1.0 (1.00)a	n.s
Frequency of isolation (times)	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.0 (0.00)a	n.s	0.0 (0.00)A	0.3 (0.33)a	n.s
Spring 2010									
Salinity (ppt)	0.7 (0.08)A	0.2 (0.02)a	*	2.7 (1.16)A	3.7 (2.22)ab	n.s	14.1 (4.75)A	15.0 (2.50)b	n.s
Dissolved oxygen (mg/l)	2.0 (0.49)A	2.3 (0.21)a	n.s	3.9 (0.84)A	5.4 (0.27)b	n.s	4.3 (0.07)A	4.3 (0.46)b	n.s
Temperature (°C)	24.8 (3.33)A	25.1 (5.17)a	n.s	23.6 (3.45)A	25.4 (3.91)a	n.s	29.8 (3.50)A	31.7 (4.00)a	n.s
Sampling point water depth (cm)	25.2 (3.11)A	24.6 (1.05)a	n.s	15.4 (0.80)B	20.1 (0.00)ab	n.s	12.4 (3.20)B	17.2 (1.48)b	n.s
SAV coverage (%)	24.4 (7.35)A	45.0 (7.26)a	n.s	8.9 (5.89)AB	9.4 (5.30)b	n.s	0.0 (0.00)B	0.0 (0.00)b	n.s
Connected water depth (cm)	13.3 (7.04)A	10.0 (5.57)a	n.s	8.1 (5.62)A	11.4 (7.37)a	n.s	9.0 (3.09)A	13.3 (1.73)a	n.s
Duration of isolation (days)	0.0 (0.00)A	13.7 (7.80)a	n.s	0.0 (0.00)A	14.0 (9.07)a	n.s	0.0 (0.00)A	1.0 (1.00)a	n.s
Frequency of isolation (times)	0.0 (0.00)A	1.3 (0.88)a	n.s	0.0 (0.00)A	0.3 (0.33)a	n.s	0.0 (0.00)A	0.3 (0.33)a	n.s
Total mean									
Salinity (ppt)	0.9 (0.14)A	0.3 (0.04)a	*	3.9 (0.71)B	3.9 (0.74)b	n.s	12.8 (1.97)C	12.3 (1.88)c	n.s
Dissolved oxygen (mg/l)	2.8 (0.45)A	2.42 (0.44)a	n.s	4.3 (0.40)A	4.55 (0.41)b	n.s	4.3 (0.51)A	4.18 (0.40)b	n.s
Temperature (°C)	23.8 (2.15)A	23.1 (2.12)a	n.s	23.0 (2.05)A	23.5 (2.16)a	n.s	21.8 (2.31)A	24.2 (2.10)a	n.s
Sampling point water depth (cm)	31.7 (2.78)A	31.8 (5.42)a	n.s	31.3 (5.90)A	34.6 (6.72)a	n.s	15.1 (2.62)B	22.1 (2.51)a	n.s
SAV coverage (%)	34.5 (4.37)A	32.0 (5.52)a	n.s	14.2 (4.77)B	12.1 (4.07)ab	n.s	0.0 (0.00)B	0.0 (0.00)b	n.s
Connected water depth (cm)	19.8 (4.25)A	18.2 (3.73)a	n.s	27.6 (4.68)A	30.6 (4.79)a	n.s	14.0 (2.10)A	20.7 (2.18)a	n.s
Duration of isolation (days)	0.0 (0.00)A	25.6 (14.23)a	n.s	0.0 (0.00)A	11.4 (8.18)a	n.s	0.0 (0.00)A	4.2 (2.78)a	n.s
Frequency of isolation (times)	0.0 (0.00)A	1.4 (0.75)a	n.s	0.0 (0.00)A	0.8 (0.58)a	n.s	0.0 (0.00)A	1.0 (0.55)a	n.s

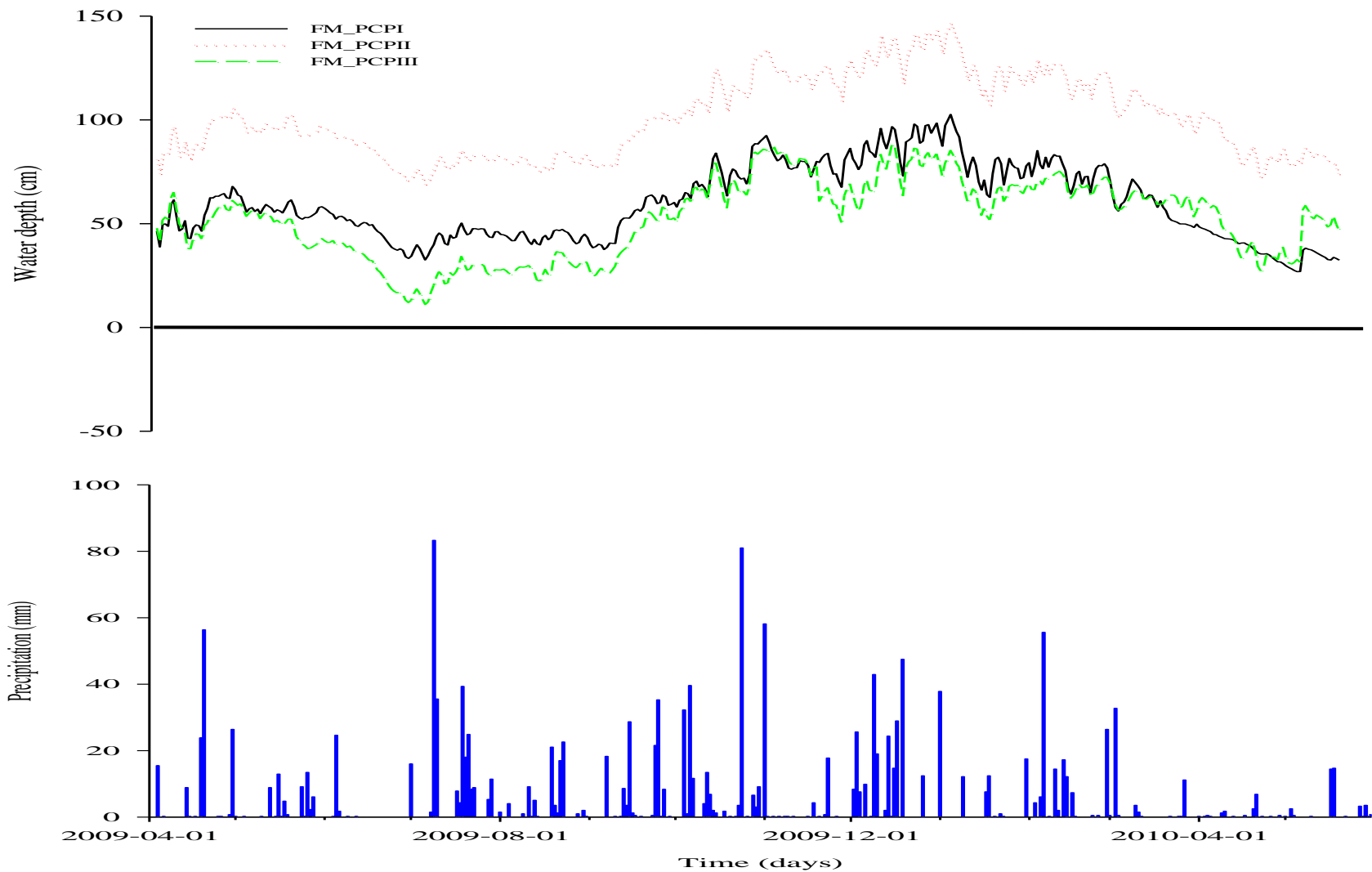


Fig. 3.3. Water depths of interior points in freshwater marsh PCPs (White Lake Wetlands Conservation Area) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: [http://www.lacoast.gov/crms2/ Home.aspx](http://www.lacoast.gov/crms2/Home.aspx), 2009-2010).

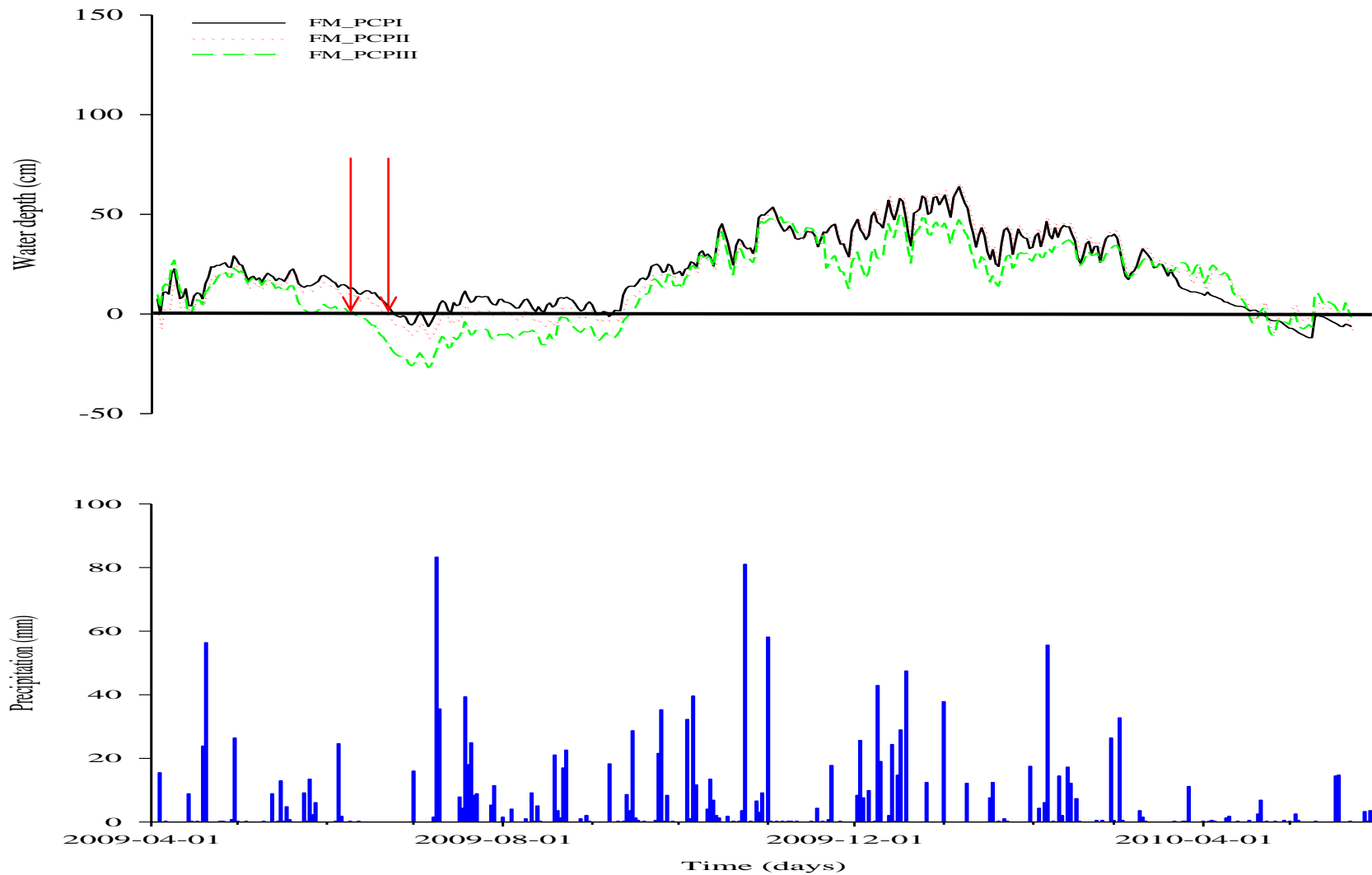


Fig. 3.4. Water depths at the pond edge in freshwater marsh PCPs (White Lake Wetlands Conservation Area) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: [http://www.lacoast.gov/crms2/ Home.aspx](http://www.lacoast.gov/crms2/Home.aspx), 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.

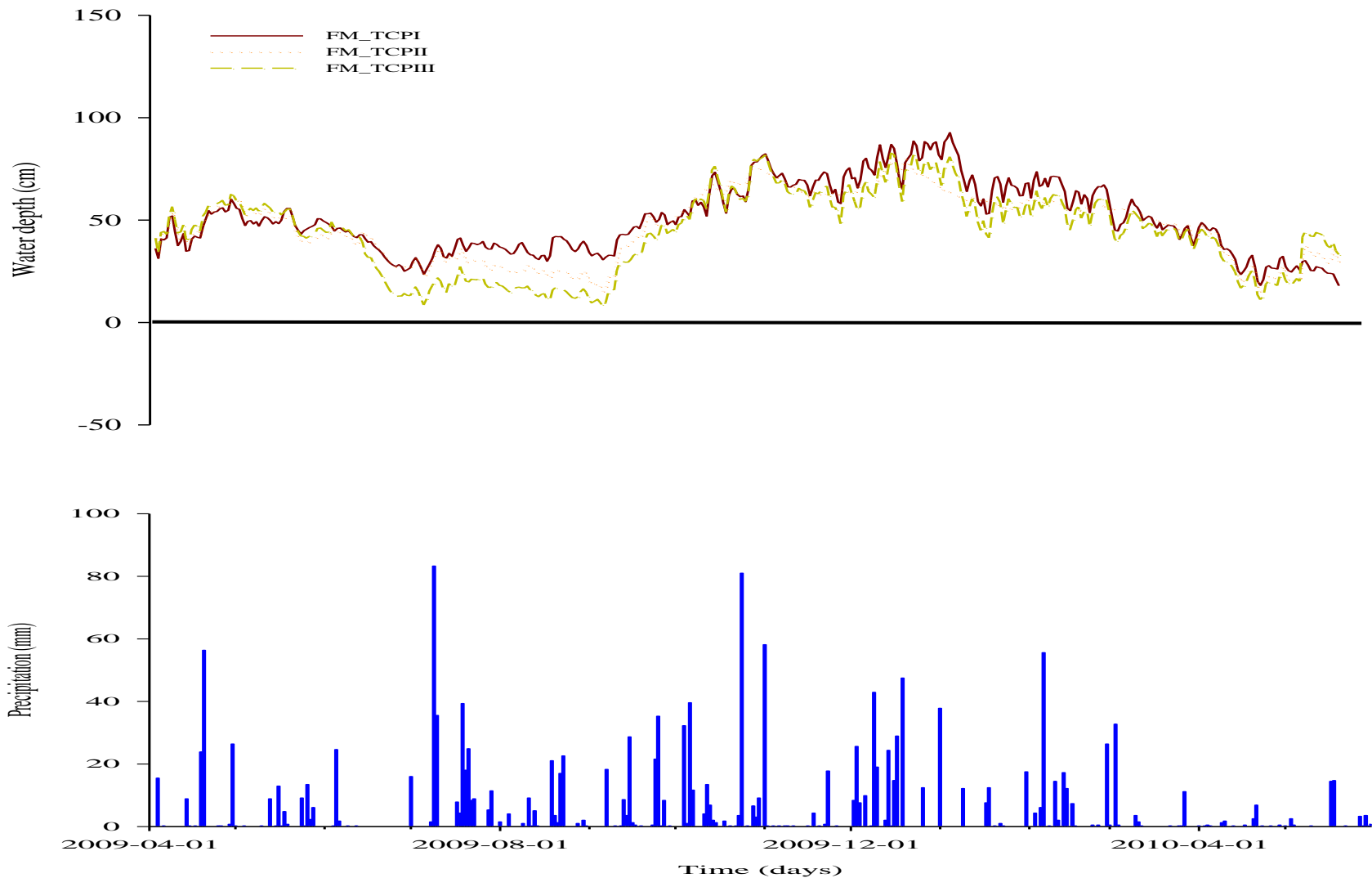


Fig. 3.5. Water depths of interior points in freshwater marsh TCPs (White Lake Wetlands Conservation Area) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: [http://www.lacoast.gov/crms2/ Home.aspx](http://www.lacoast.gov/crms2/Home.aspx), 2009-2010).

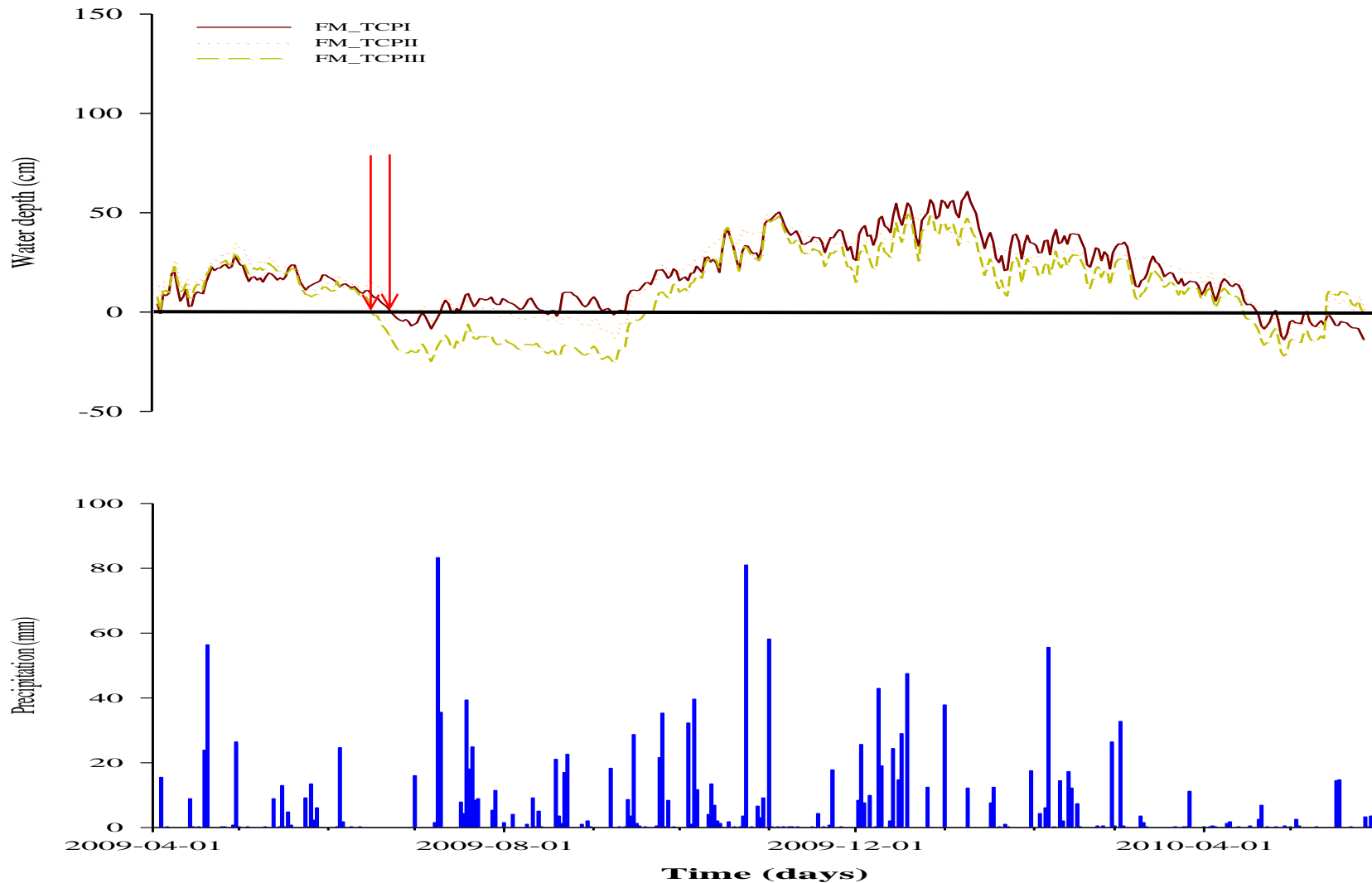


Fig. 3.6. Water depths at the pond edge in freshwater marsh TCPs (White Lake Wetlands Conservation Area) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: [http://www.lacoast.gov/crms2/ Home.aspx](http://www.lacoast.gov/crms2/Home.aspx), 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.

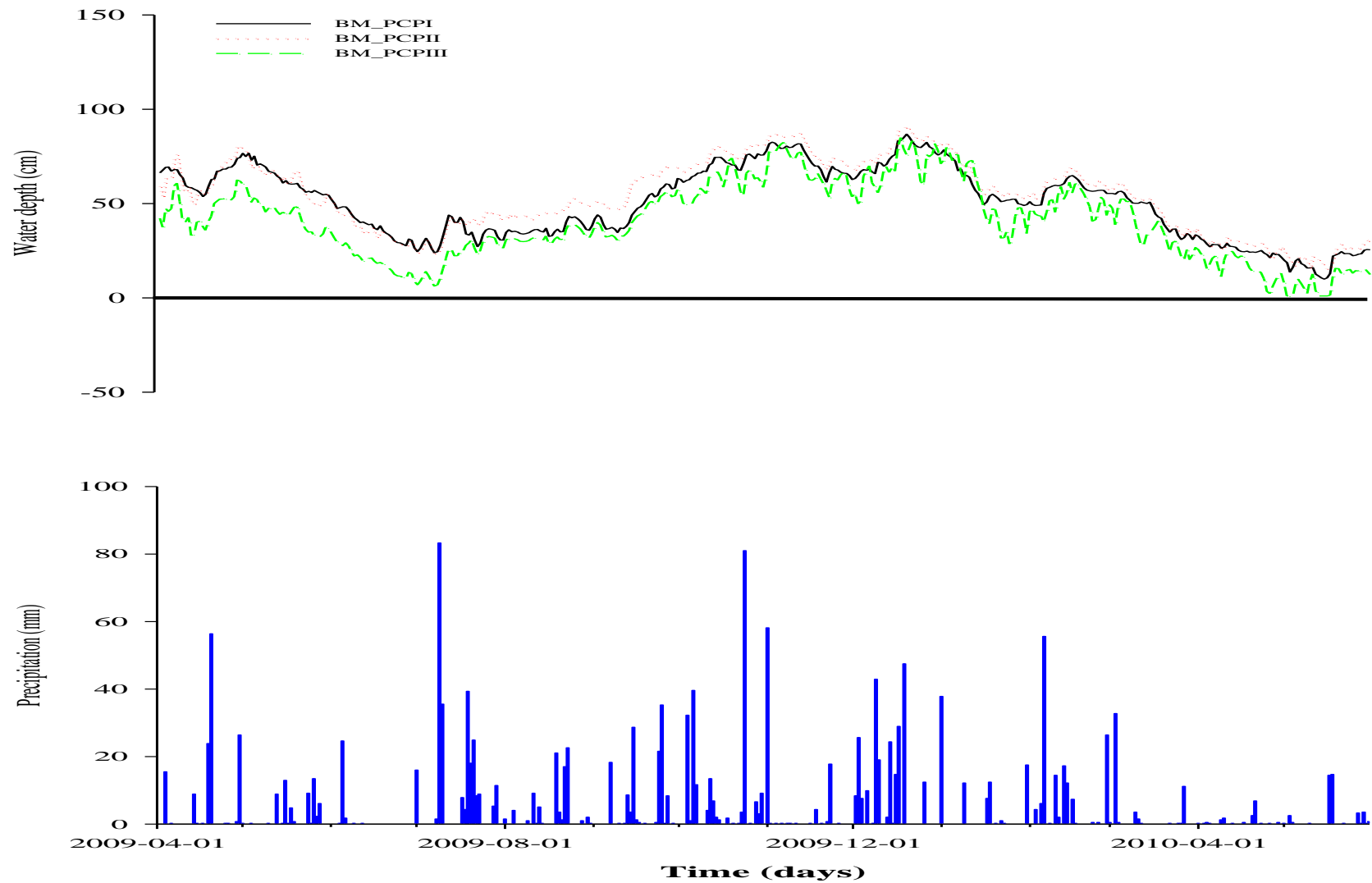


Fig. 3.7. Water depths of interior points in brackish marsh PCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: [http://www.lacoast.gov/crms2/ Home.aspx](http://www.lacoast.gov/crms2/Home.aspx), 2009-2010).

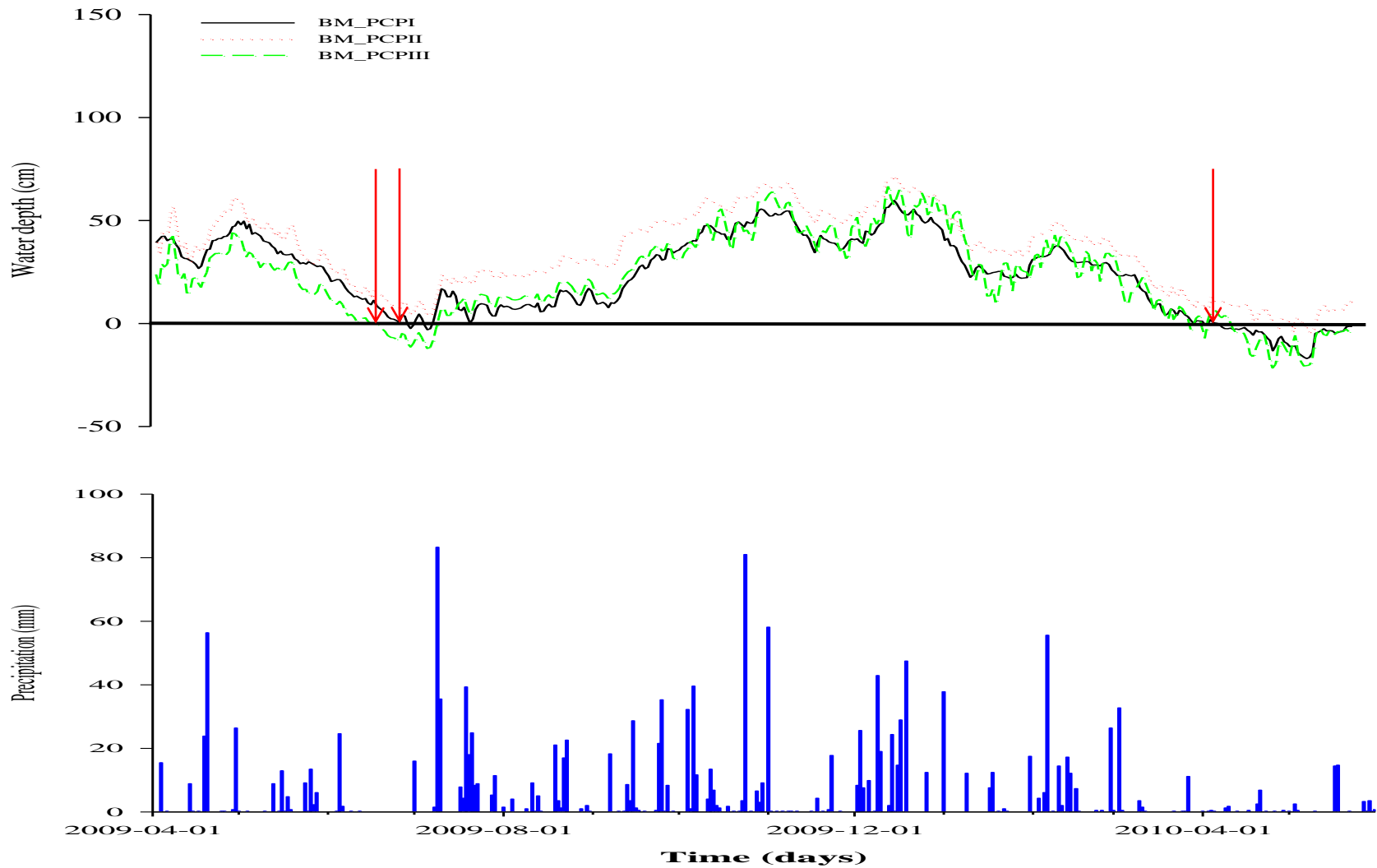


Fig. 3.8. Water depths at the pond edge in brackish marsh PCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.

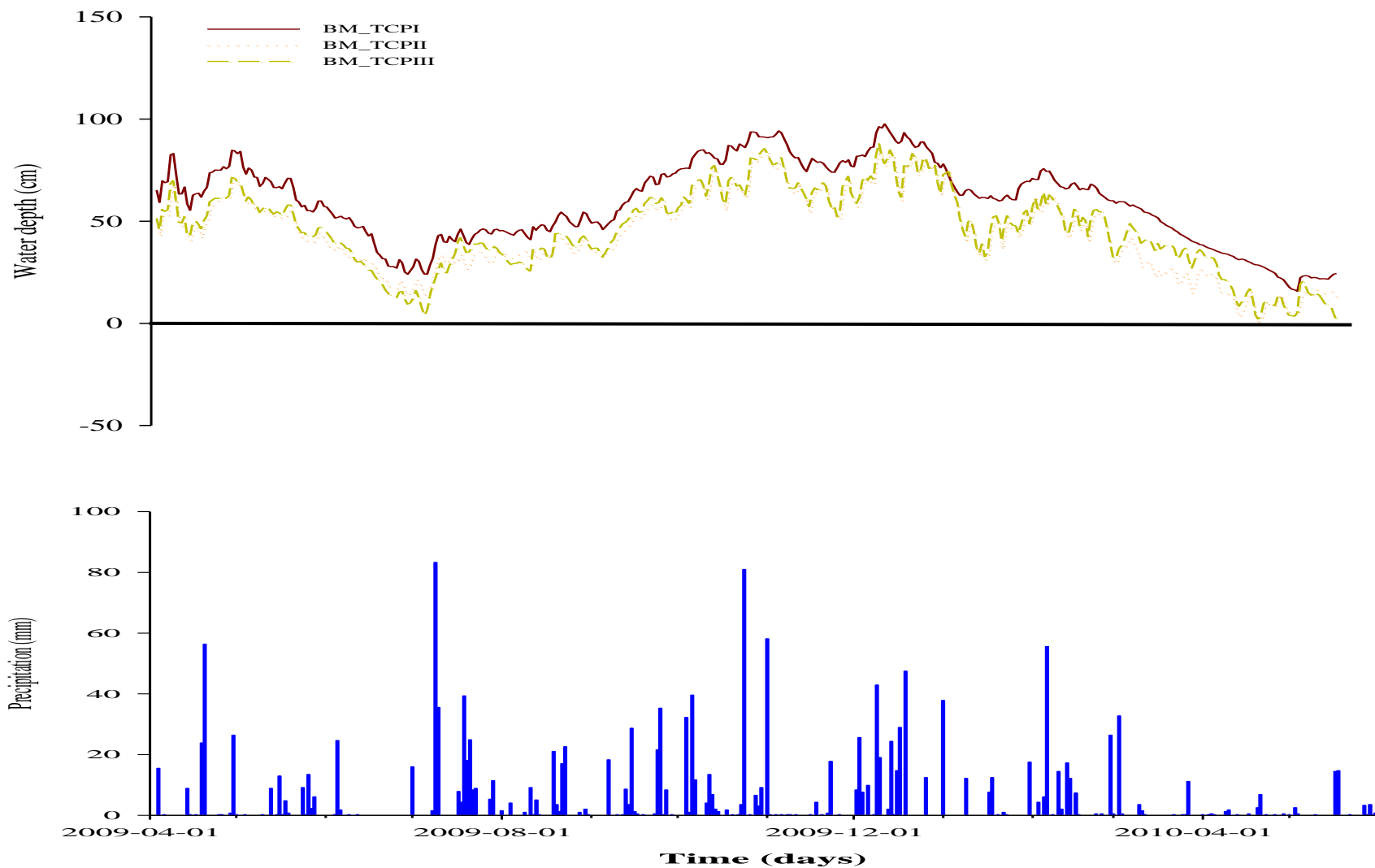


Fig. 3.9. Water depths of interior points in brackish marsh TCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010).

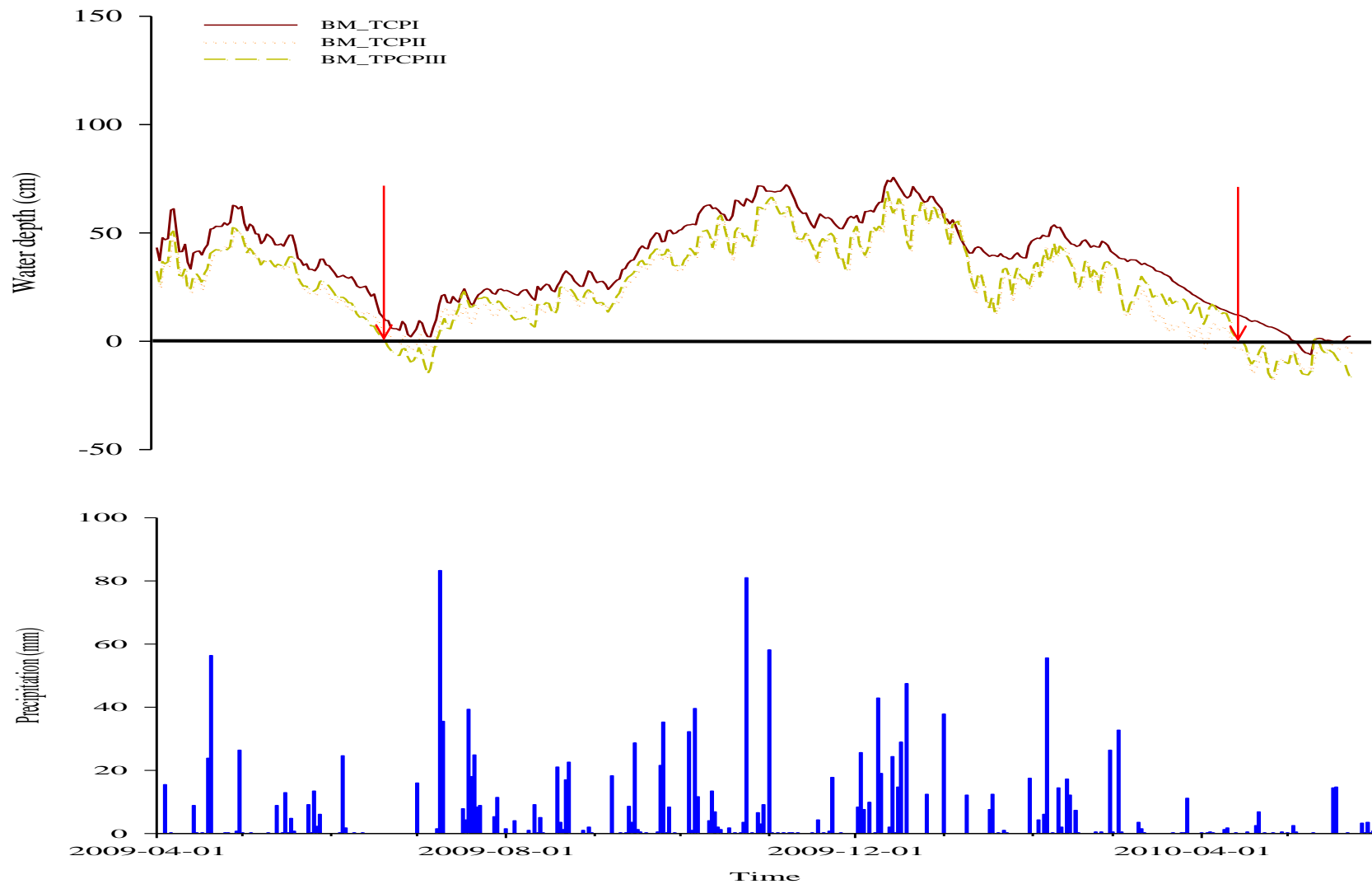


Fig. 3.10. Water depths at the pond edge in brackish marsh TCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.



Fig. 3.11. Water depths of interior points in saline marsh PCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010).

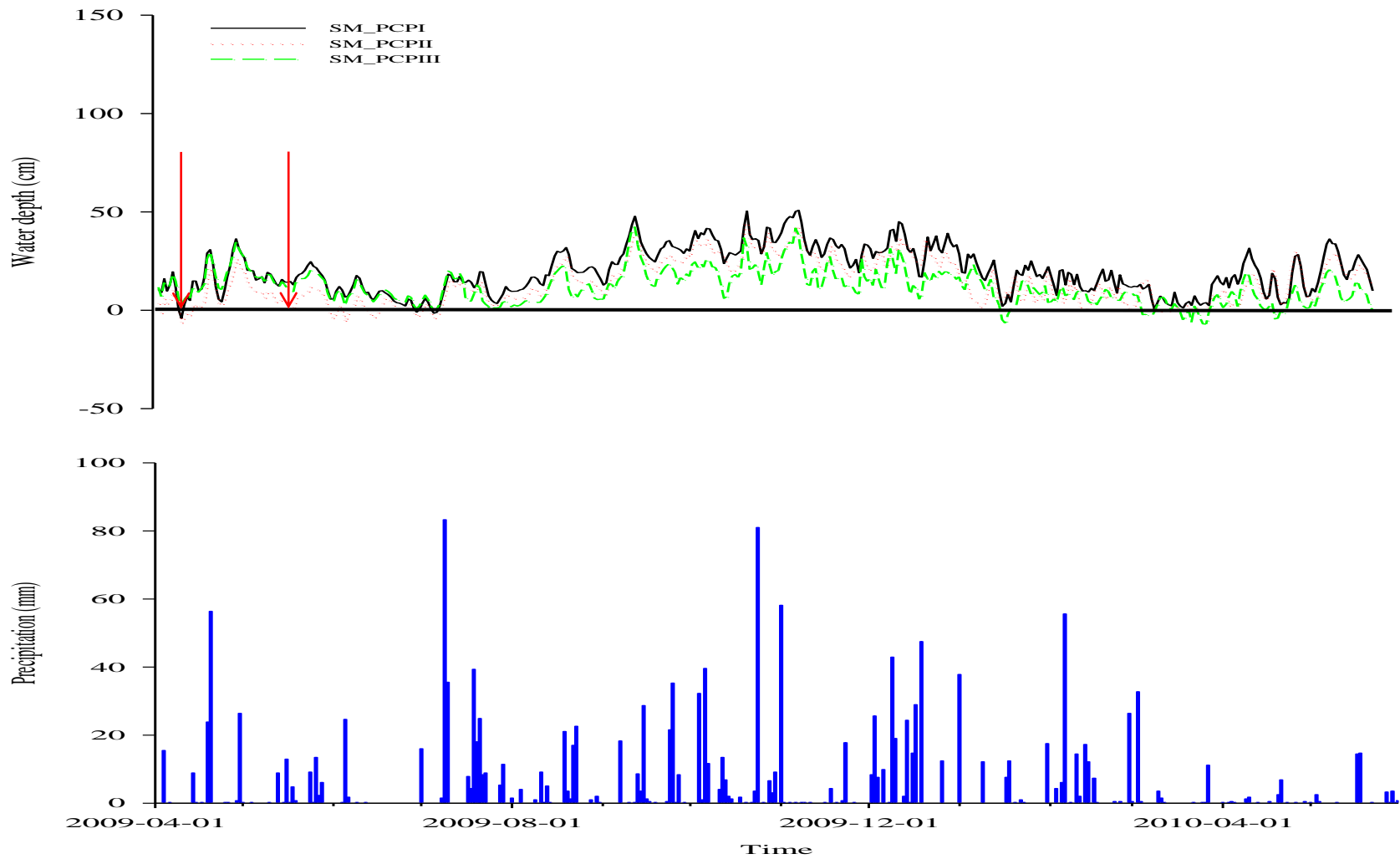


Fig. 3.12. Water depths at the pond edge in saline marsh PCPIs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.

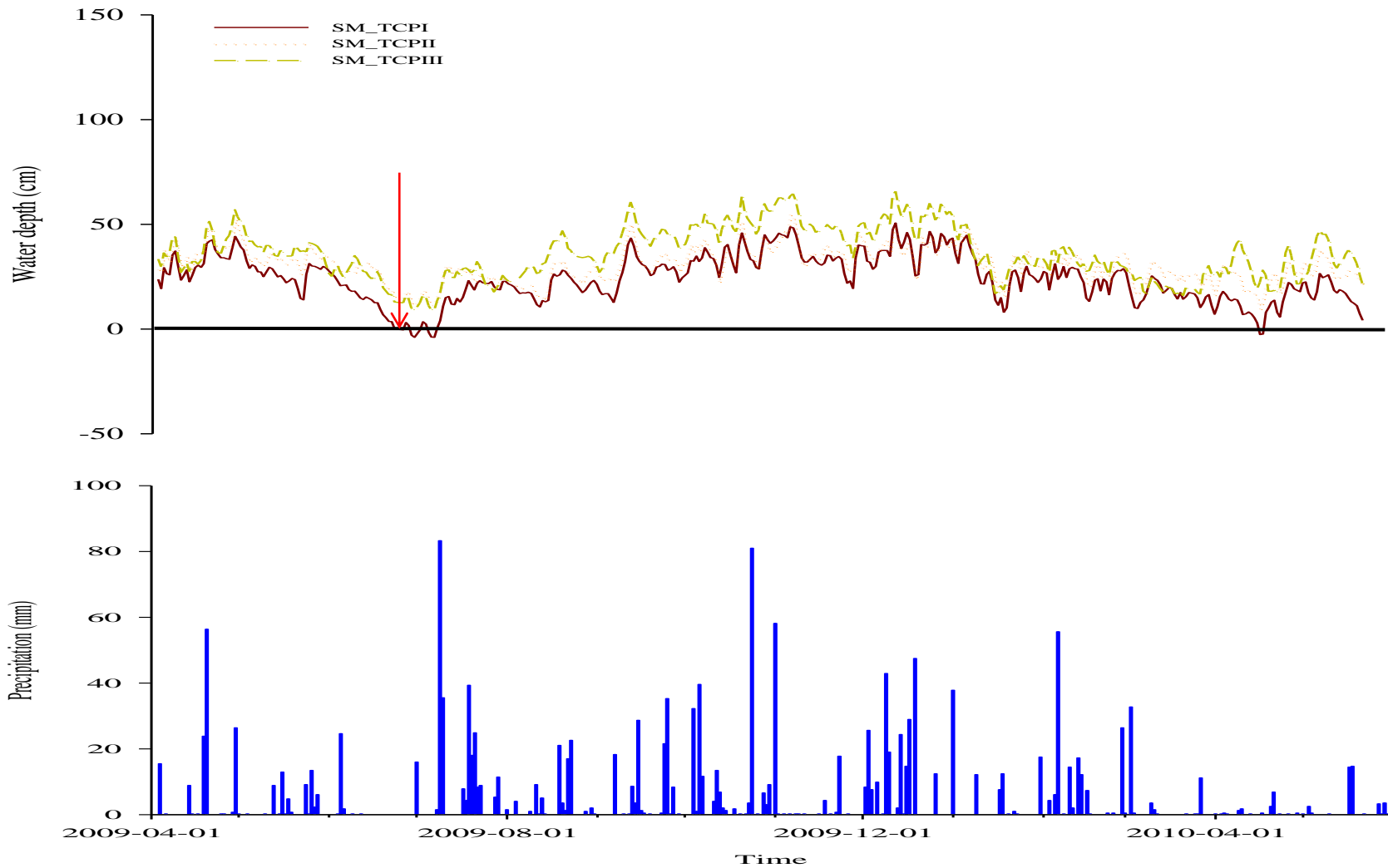


Fig. 3.13. Water depths of interior points in saline marsh TCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.

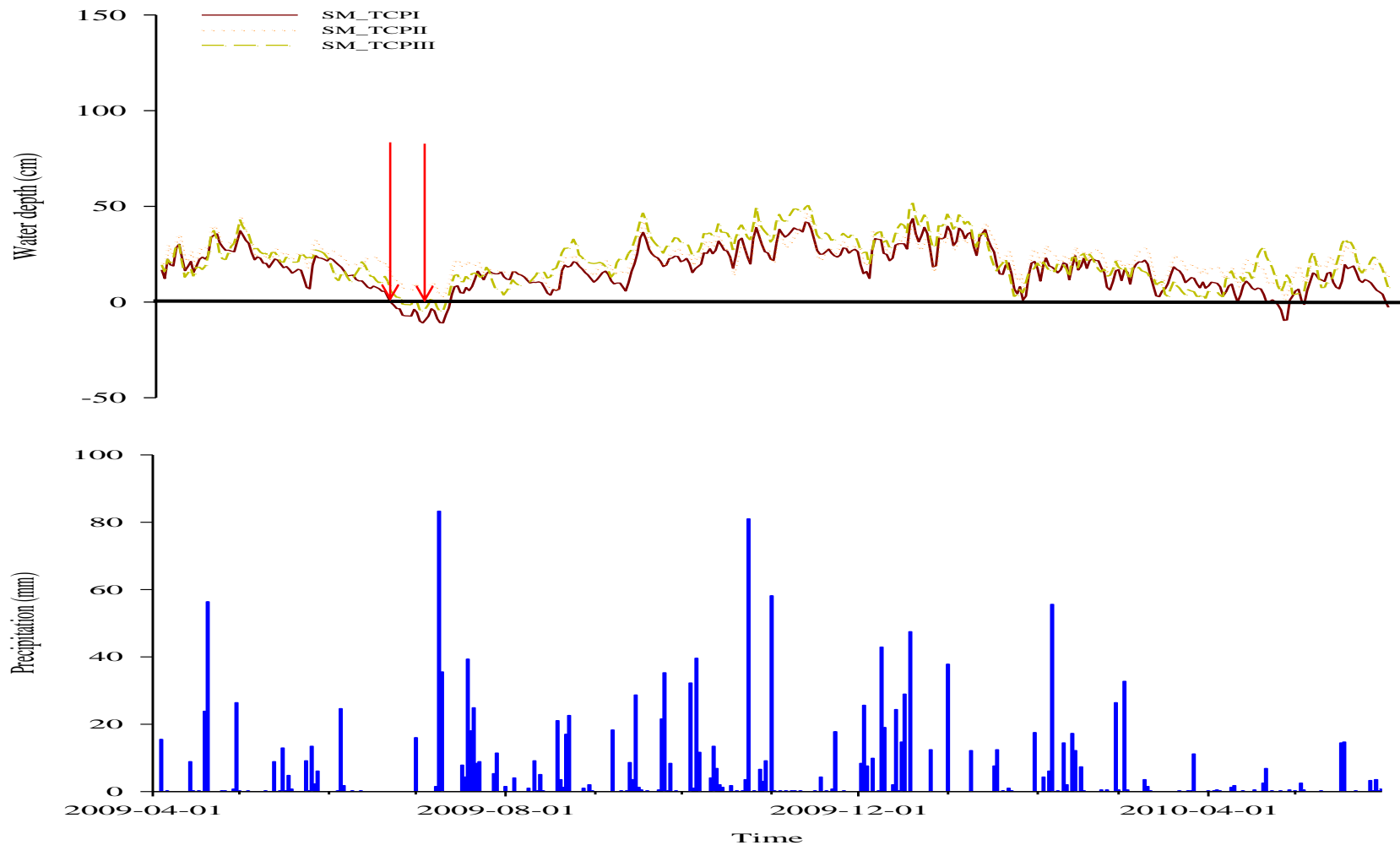


Fig. 3.14. Water depths at the pond edge in saline marsh TCPs (Rockefeller State Wildlife Refuge) from April 2009 through May 2010. The bottom graph represents rainfall variation; rainfall data were obtained from the Coastwide Reference Monitoring System (CRMS: <http://www.lacoast.gov/crms2/Home.aspx>, 2009-2010). The red arrow represents the disconnection point between the pond and emergent marsh.

Seasonal PT nekton density (CPUE, organisms/m²) ranged from 2.3 ± 1.51 (saline marsh-Winter 2009) to 85.6 ± 65.82 (brackish marsh-Fall 2009) in all marsh types. However, nekton densities did not differ seasonally within a marsh type. Comparison of nekton density among marsh types indicated that brackish PT (105.9 ± 24.04) was greater than saline PT (23.9 ± 5.70) ($F_{2,537}=5.11, p=0.02$). Between pond types across marshes, PCPs (124.6 ± 35.52) in brackish marsh was higher than saline PCPs (10.6 ± 3.59) but freshwater PCPs (42.4 ± 15.63) did not differ ($F_{2,267}=13.39, p<0.01$). In addition, nekton density in TCPs did not differ (freshwater: 42.5 ± 32.33 ; brackish: 87.2 ± 24.11 ; saline: 37.3 ± 10.25) (Fig. 3.15). Within a marsh, TCPs nekton density in saline marsh was higher than PCPs (t value=2.47, $p=0.03$) but nekton density did not differ in freshwater and brackish marshes (Fig. 3.16). In addition, multiple regression analysis revealed nekton density of all freshwater marsh ponds was negatively related with connected water depth ($R^2=0.38, p=0.03$) and sampling point water depth ($R^2=0.60, p=0.03$) (Fig. 3.17). However, no statistically significant relationships were observed between environmental variables and nekton density in brackish and saline marshes.

Seasonal PT nekton biomass (g wet wt/m²) during five seasons ranged from 1.4 ± 0.90 (freshwater marsh, Fall 2009) to 80.1 ± 20.70 (saline marsh, Spring 2010). Nekton biomass did not differ seasonally within a marsh type. Comparison of nekton biomass among marsh types showed that brackish (27.1 ± 5.03) and saline (25.1 ± 9.57) PT was greater than freshwater PT (10.6 ± 5.15) ($F_{2,537}=4.50, p=0.02$). However, between pond types across marshes, nekton biomass in PCPs and TCPs did not differ (Fig. 18). Within a marsh, nekton biomass between PCPs and TCPs did not differ in all marshes (Fig. 3.19). No statistically significant relationships were observed between environmental variables and nekton biomass in all marsh types.

Seasonal comparisons of nekton diversity did not indicate any difference within a marsh type. However, mean values of Shannon-Wiener diversity differed among marsh types with the highest in freshwater marsh ($F_{2,537}=5.46$, $p=0.01$, Fig. 3.20). Between pond types across marshes, freshwater PCPs were higher diversity than in brackish PCPs ($F_{2,267}=11.99$, $p=0.01$). Within a marsh, freshwater PCPs was higher diversity than TCPs ($p=0.05$) but PCPs and TCPs did not differ in brackish and saline marshes (Fig. 3.21).

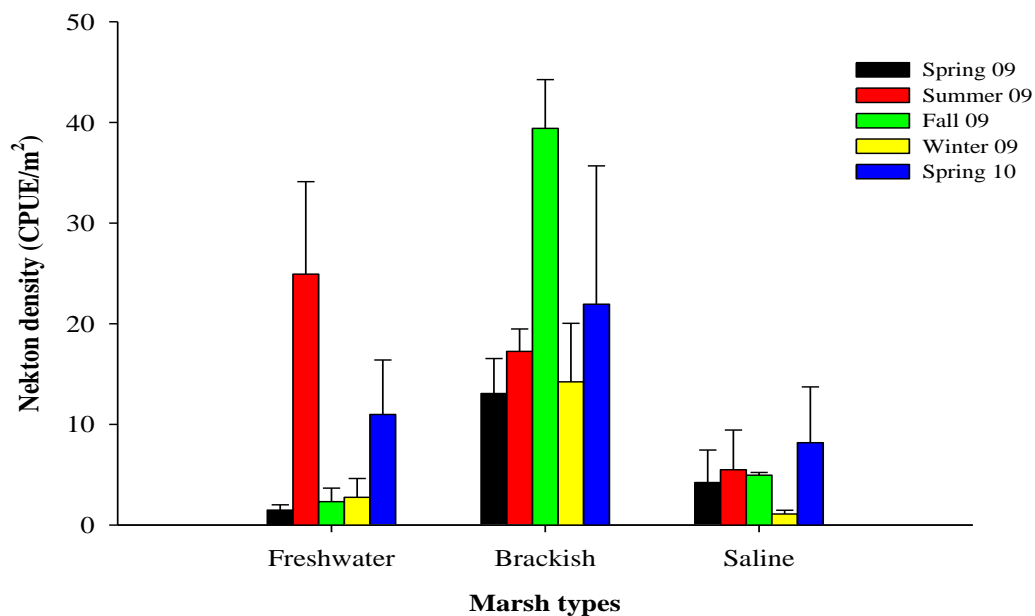


Fig. 3.15. Comparison of seasonal nekton density (CPUE, organisms/m²) in different marsh types from April 2009 to May 2010.

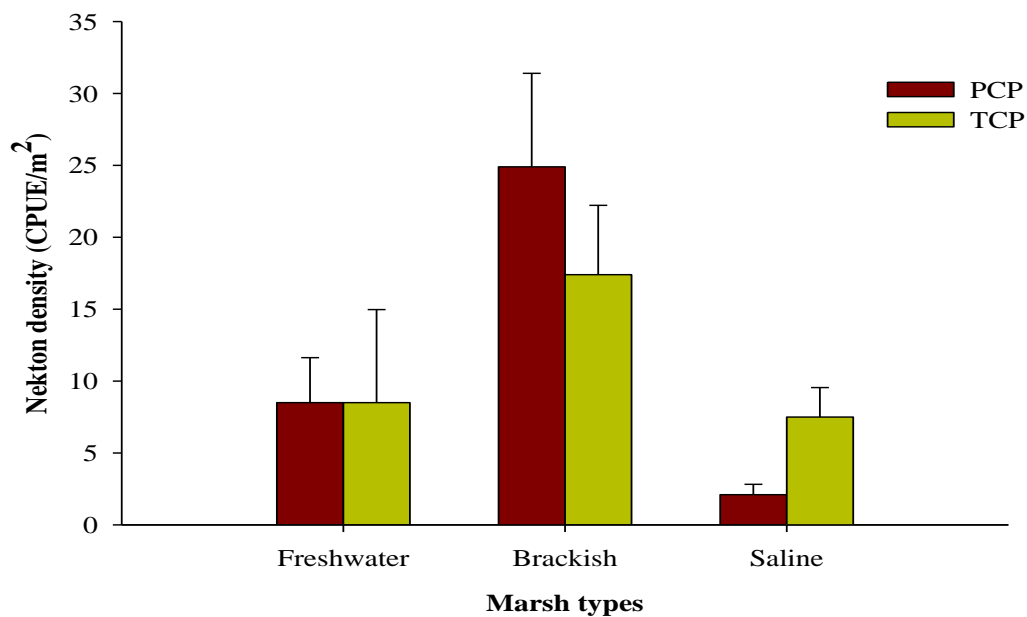


Fig. 3.16. Comparison of nekton density (CPUE, organisms/m²) between different pond types in multiple marshes from April 2009 to May 2010.

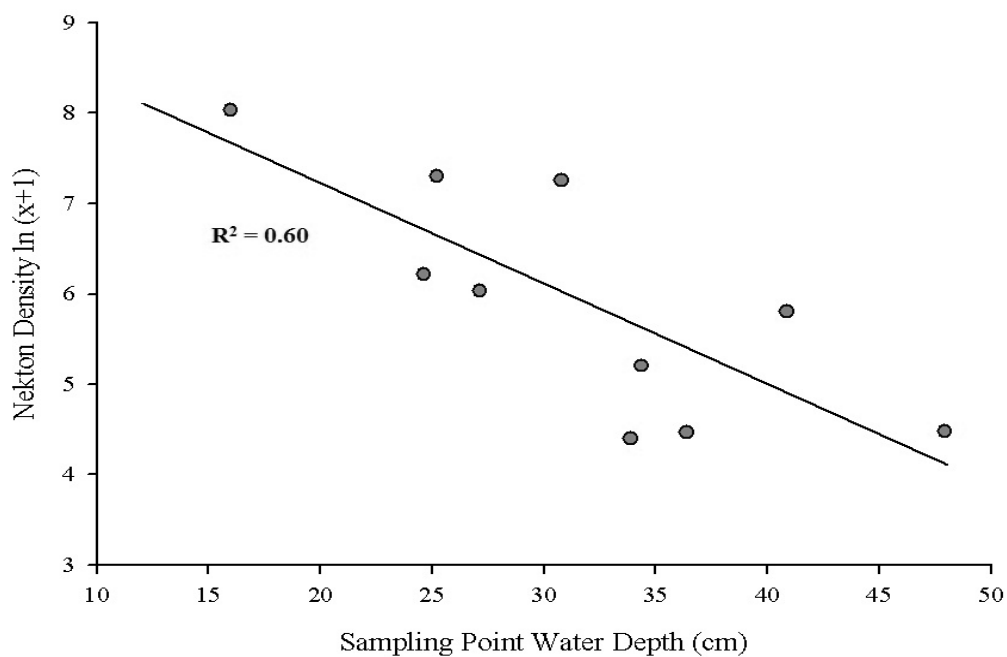


Fig. 3.17. Relationship between Ln (x+1) transformed nekton density and sampling point water depth (cm) in PCPs and TCPs in freshwater marsh.

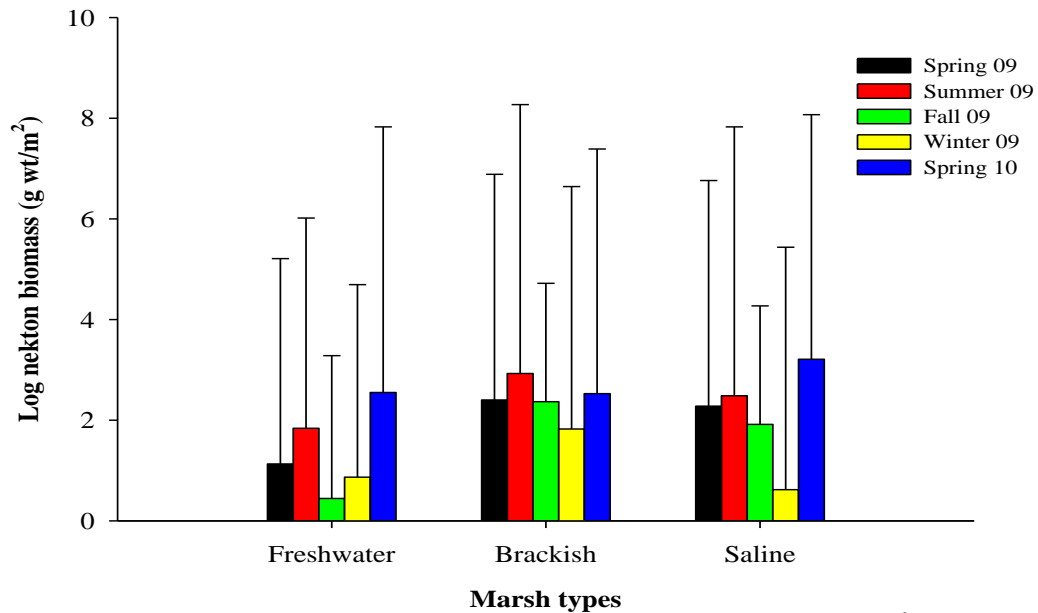


Figure 3.18. Comparison of seasonal log nekton biomass (CPUE, g wet wt/m²) (log (x +1) transformed) in different marsh types from April 2009 to May 2010.

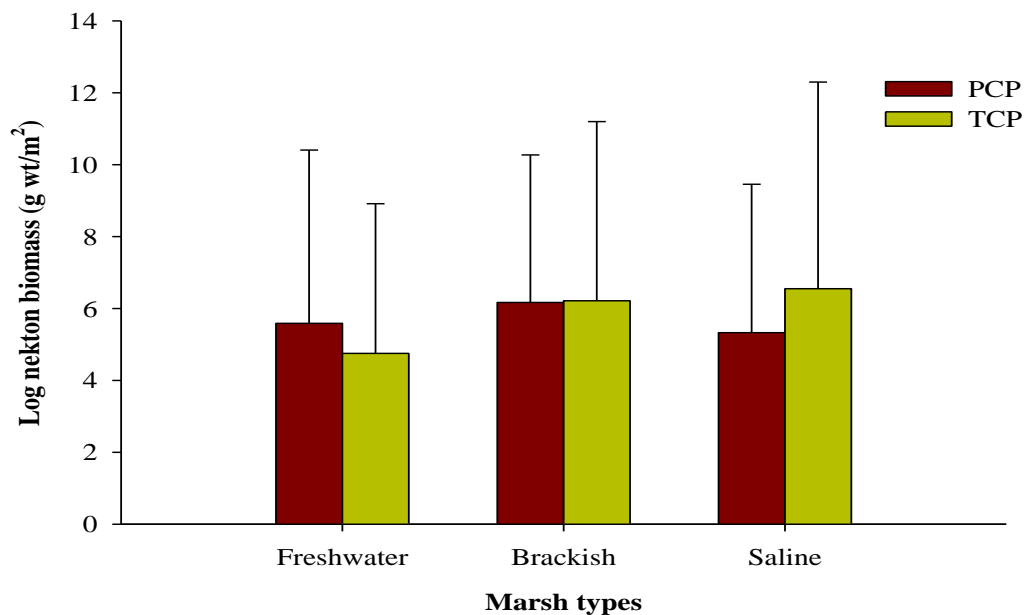


Figure 3.19. Comparison of log nekton biomass (CPUE, g wet wt/m²) (log (x +1) transformed) between different pond types in multiple marshes from April 2009 to May 2010.

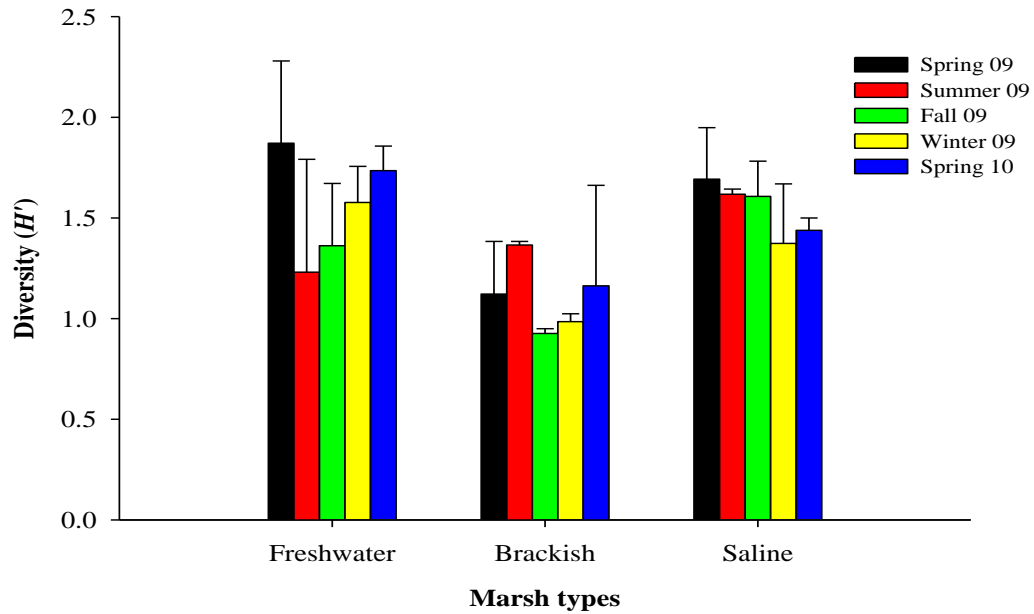


Fig. 3.20. Comparison of seasonal nekton diversity (Shannon-Wiener diversity index H') in different marsh types from April 2009 to May 2010.

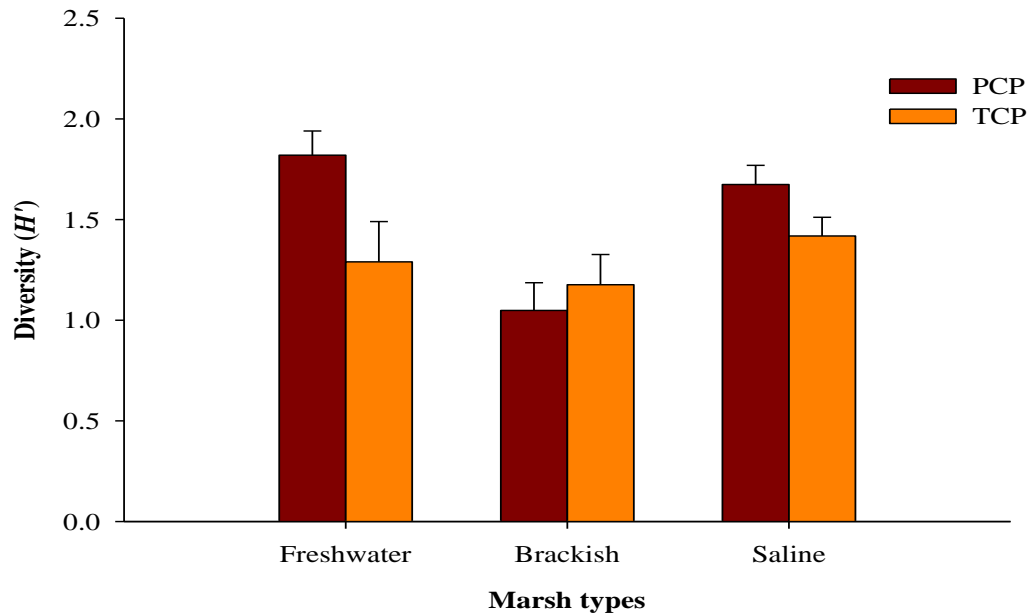


Fig. 3.21. Comparison of nekton diversity (Shannon-Wiener diversity index H') between pond types in multiple marsh types from April 2009 to May 2010.

The ANOSIM results in fresh (Global R: 0.159, $p=0.005$) and saline (Global R: 0.273, $p=0.003$) marsh demonstrated that community similarity within pond types was affected by hydrologic connectivity (i.e., DI), but no relationship was observed between community similarity and DI in brackish ponds (Global R: 0.045, $p=0.098$). In all cases, SIMPER ($p=0.05$) detected differences in average similarity between pond types (Table 3.5). Assemblage similarity of PCPs in freshwater marsh was greater than in TCPs, however, saline TCPs had higher similarity than PCPs.

Nekton Community Distribution

The results of the canonical correspondence analysis (CCA) show significant relationships between the measured environmental variables and nekton assemblage during all sampling periods (1st axis: $p=0.002$, All axes: $p=0.002$). Canonical correspondence analysis eigenvalues of the first four multivariate axes were 0.49 (CCA1), 0.20 (CCA2), 0.09 (CCA3), and 0.06 (CCA4). Species-environment correlation coefficients for the four axes were 0.92, 0.86, 0.71, and 0.77, respectively. Cumulative percentage variance of species for the four axes (CCA 1-4) was 41.0. The first and second axes of species data modeled 23.7% and 9.7%, respectively. Also, the first two axes of the species-environment relationship represented 70.7% of variation. Axis 1 was correlated positively to vegetation coverage (0.84) and Axis 2 correlated most strongly with salinity (0.35). DO was highly correlated with both axes (Axis 1=-0.42, Axis2=-0.36).

Analysis of the species-environment relationships indicated that a number of the dominant species in freshwater ponds (e.g., least killifish *Heterandria formosa*, mosquitofish *Gambusia affinis*, golden topminow *Fundulus chrysotus*, bantam sunfish *Lepomis symmetricus*) were associated positively with vegetation and negatively with salinity. Conversely, dominant

Table 3.4. Mean nekton density (CPUE, organisms (\pm SE)) and % total catch by pond type in three marsh types.

Species	Freshwater			Brackish			Saline		
	PCP	TCP	% TC*	PCP	TCP	% TC	PCP	TCP	% TC
<i>Myrophis punctatus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	1 (1.00)	0 (0.00)	0.1
<i>Menidia beryllina</i>	0 (0.00)	0 (0.00)	0.0	93 (45.05)	29.2 (19.27)	3.2	1.8 (1.80)	2 (1.14)	0.4
<i>Brevoortia patronus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	0.2 (0.20)	0.2 (0.20)	0.0
<i>Anchoa mitchilli</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	11.4 (11.40)	0 (0.00)	1.3
<i>Cyprinodon variegatus</i>	6.2 (4.15)	0 (0.00)	0.4	127 (35.47)	172.6 (96.64)	7.9	5.4 (2.16)	60.4 (46.72)	7.6
<i>Adinia zenica</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0.6 (0.60)	0.0	0.6 (0.24)	3.6 (1.33)	0.5
<i>Fundulus chrysotus</i>	45.2 (22.49)	22.8 (12.47)	4.4	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Fundulus dispar</i>	1.8 (1.11)	0.4 (0.40)	0.1	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Fundulus grandis</i>	0.2 (0.20)	0 (0.00)	0.0	15.2 (4.12)	8.4 (4.15)	0.6	32.6 (21.89)	122 (81.10)	17.9
<i>Fundulus pulvereus</i>	1.2 (1.20)	0 (0.00)	0.1	9.5 (4.59)	27.4 (14.13)	0.9	3 (1.38)	16.6 (6.95)	2.3
<i>Lucania parva</i>	14.2 (9.64)	0 (0.00)	0.9	68 (10.7)	39 (13.17)	2.8	1.25 (0.25)	7.2 (5.25)	1.0
<i>Gambusia affinis</i>	234.2 (130.05)	518.4 (470.02)	49.2	39.6 (14.57)	128.4 (56.44)	4.4	1.6 (1.36)	19.2 (14.77)	2.4
<i>Heterandria formosa</i>	215 (97.97)	158.4 (106.44)	24.4	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Poecilia latipinna</i>	40 (19.67)	2.6 (1.69)	2.8	160.8 (54.47)	158.2 (26.50)	8.4	0.4 (0.40)	103.2 (56.98)	12.0
<i>Erimyzon oblongus</i>	0.2 (0.20)	0.4 (0.40)	0.0	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Esox americanus</i>	1.4 (0.75)	1.8 (1.56)	0.2	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Syngnathus scovelli</i>	0 (0.00)	0 (0.00)	0.0	0.2 (0.20)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Mugil cephalus</i>	0 (0.00)	0 (0.00)	0.0	1 (0.45)	0 (0.00)	0.0	4.4 (2.04)	2.4 (0.68)	0.8
<i>Lepomis symmetricus</i>	48.2 (13.46)	2.2 (1.46)	3.3	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Lepomis miniatus</i>	3.2 (1.56)	0.4 (0.40)	0.2	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Lepomis macrochirus</i>	6.2 (4.50)	0.4 (0.40)	0.4	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0

*. % TC: total catch percentage

Table 3.4. Continued.

Species	Freshwater			Brackish			Saline		
	PCP	TCP	% TC*	PCP	TCP	% TC	PCP	TCP	% TC
<i>Lepomis gulosus</i>	0.2 (0.20)	1.4 (1.40)	0.1	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Micropterus punctulatus</i>	1.2 (0.80)	0 (0.00)	0.1	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Elassoma zonatum</i>	37.4 (13.18)	30.6 (21.45)	4.4	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Dormitator maculatus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	0.6 (0.40)	3.8 (3.80)	0.5
<i>Gobionellus boleosoma</i>	0 (0.00)	0 (0.00)	0.0	1 (1.00)	0 (0.00)	0.0	0 (0.00)	0.4 (0.40)	0.0
<i>Gobiosoma bosc</i>	0 (0.00)	0 (0.00)	0.0	23.6 (14.73)	0.8 (0.80)	0.6	0 (0.00)	0.6 (0.40)	0.1
<i>Microgobius gulosus</i>	0 (0.00)	0 (0.00)	0.0	0.8 (0.80)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Etheostoma fusiforme</i>	0.2 (0.20)	0.4 (0.40)	0.0	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Leiostomus xanthurus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	2.8 (2.80)	0 (0.00)	0.3
<i>Micropogonias undulatus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	0.2 (0.20)	0 (0.00)	0.0
<i>Pogonias cromis</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	0.4 (0.40)	0.8 (0.58)	0.1
<i>Aphredoderus sayanus</i>	0.4 (0.40)	0.4 (0.40)	0.1	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Citharichthys spilopterus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	0.6 (0.40)	0 (0.00)	0.1
<i>Ameiurus natalis</i>	0.2 (0.20)	0.4 (0.40)	0.0	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0
<i>Procambarus clarkii</i>	0.4 (0.40)	0 (0.00)	0.0	1.2 (1.20)	2.2 (1.74)	0.1	0 (0.00)	0 (0.00)	0.0
<i>Cambarellus puer</i>	11.4 (5.14)	4 (2.10)	1.0	2.2 (1.74)	8.2 (4.82)	0.3	0 (0.00)	0 (0.00)	0.0
<i>Palaemonetes</i> spp.	95.4 (30.86)	19.8 (6.18)	7.5	1696.6 (520.98)	991 (387.45)	70.5	66.8 (23.97)	278.8 (75.48)	40.1
<i>Farfantepenaeus aztecus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0.4 (0.40)	0.0	24.2 (8.00)	20 (12.92)	5.1
<i>Litopenaeus setiferus</i>	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	19.2 (19.20)	9.6 (9.60)	3.3
<i>Callinectes sapidus</i>	0 (0.00)	0 (0.00)	0.0	5 (1.90)	2.6 (1.44)	0.2	11.6 (2.48)	20.6 (5.07)	3.7
<i>Uca</i> spp.	0 (0.00)	0 (0.00)	0.0	0 (0.00)	0 (0.00)	0.0	0.4 (0.24)	0 (0.00)	0.0

Table 3.5. ANOSIM and SIMPER results for hydrologic connectivity (PCP vs. TCP) comparison of community similarity in three marsh types. All reported results were significant at $p=0.05$. Presented are the Global R for significant ANOSIM tests and the SIMPER results for percentage similarity within same pond type.

	Freshwater		Brackish		Saline	
	PCP	TCP	PCP	TCP	PCP	TCP
Global R	0.159*		0.045		0.273*	
Similarity (%)	48.2	34.5	59.6	56.7	38.3	55.4

* $p<0.01$

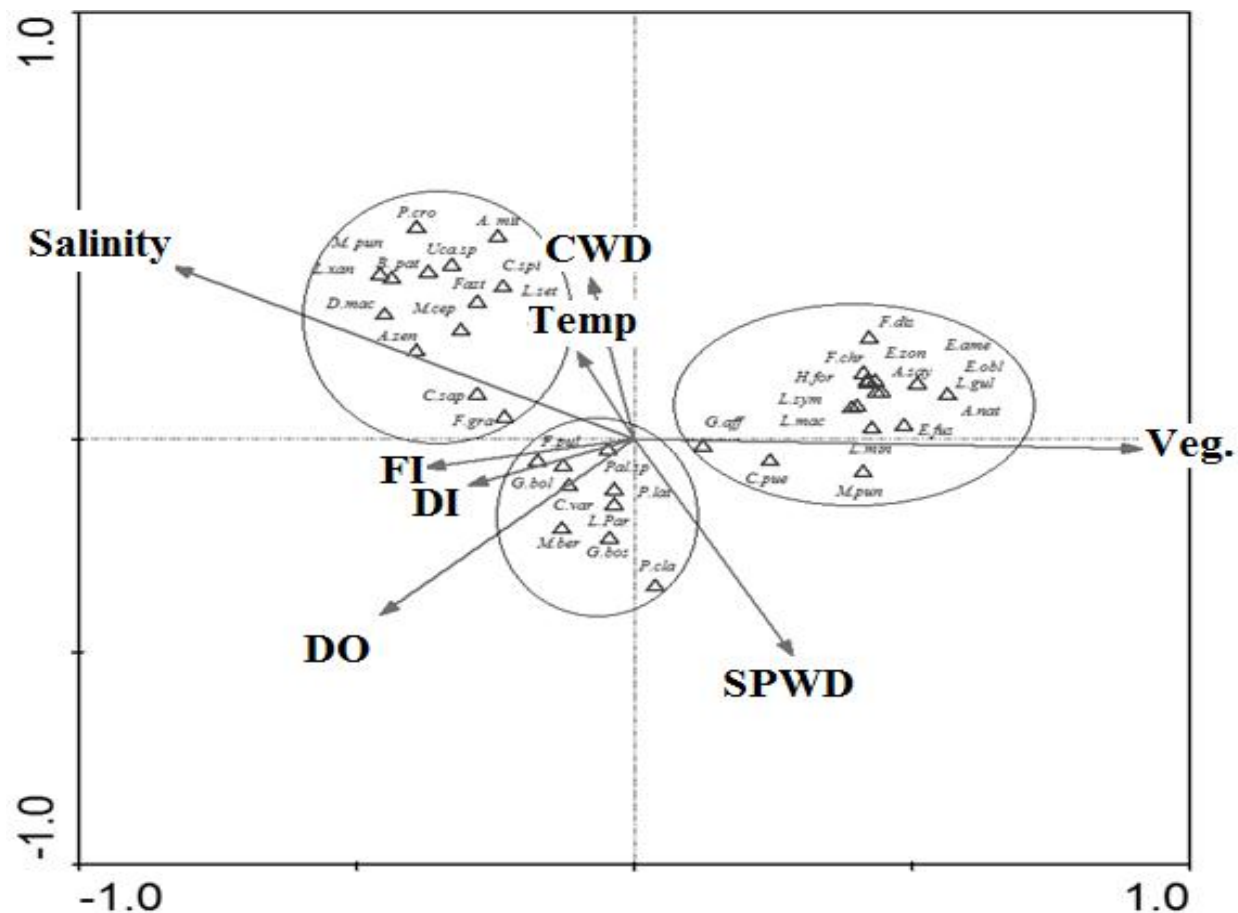


Fig. 3.22. Association of environmental variables and nekton assemblage characteristics based on canonical correspondence analysis for all ponds in freshwater, brackish, and saline marsh from April 2009-May 2010. Environmental variables and taxa full names are listed in Tables 3.1 and 3.3.

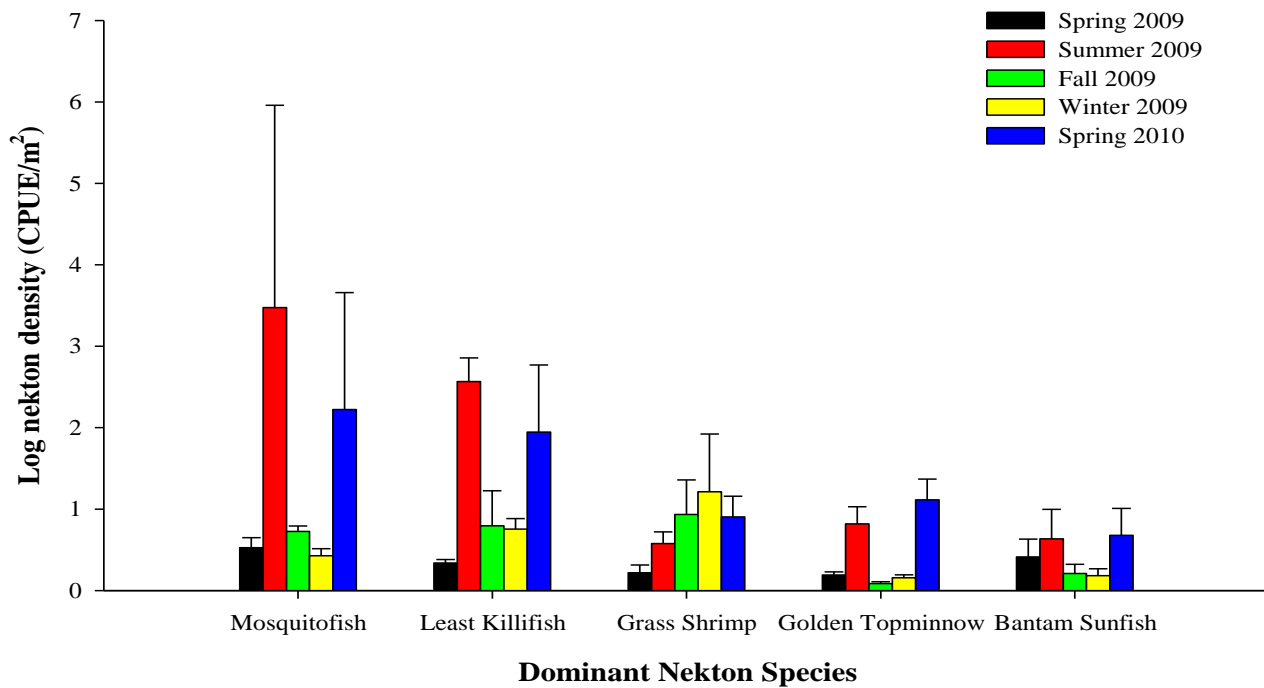


Fig. 3.23. Comparison of dominant nektun density (CPUE, organisms/m²) (log (x + 1) transformed) in freshwater marsh from April 2009 to May 2010.

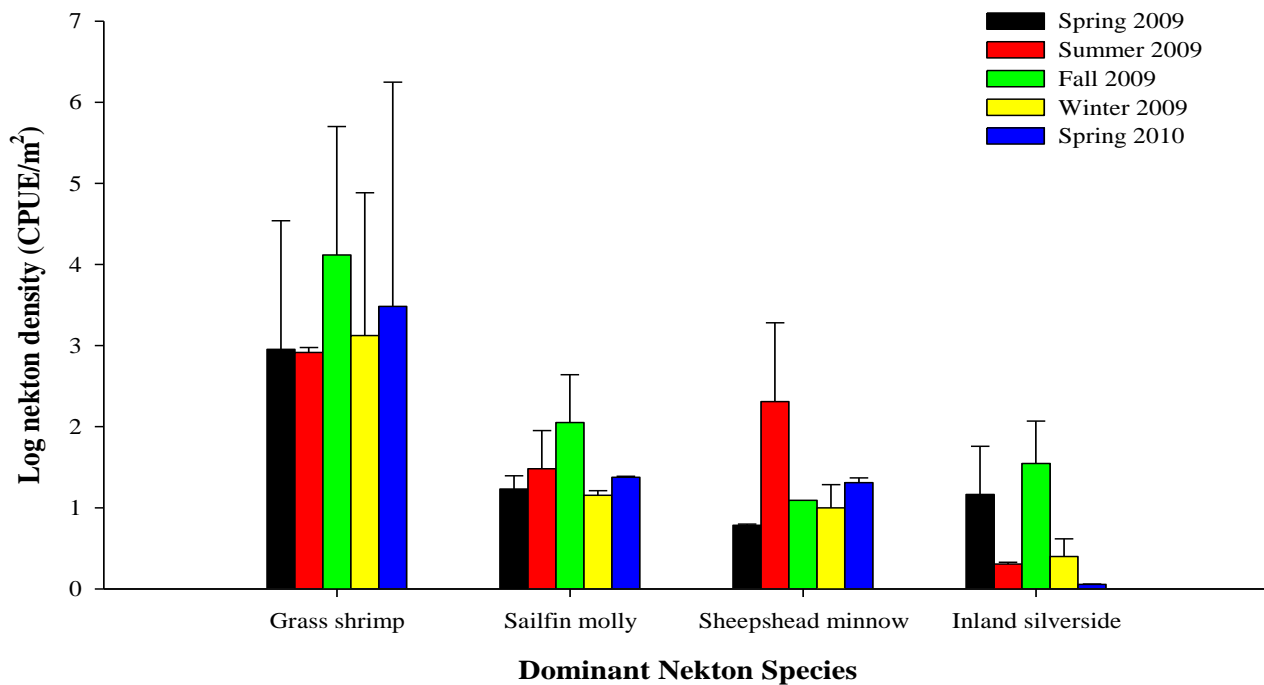


Fig. 3.24. Comparison of dominant nektun density (CPUE, organisms/m²) (log (x + 1) transformed) in brackish marsh from April 2009 to May 2010.

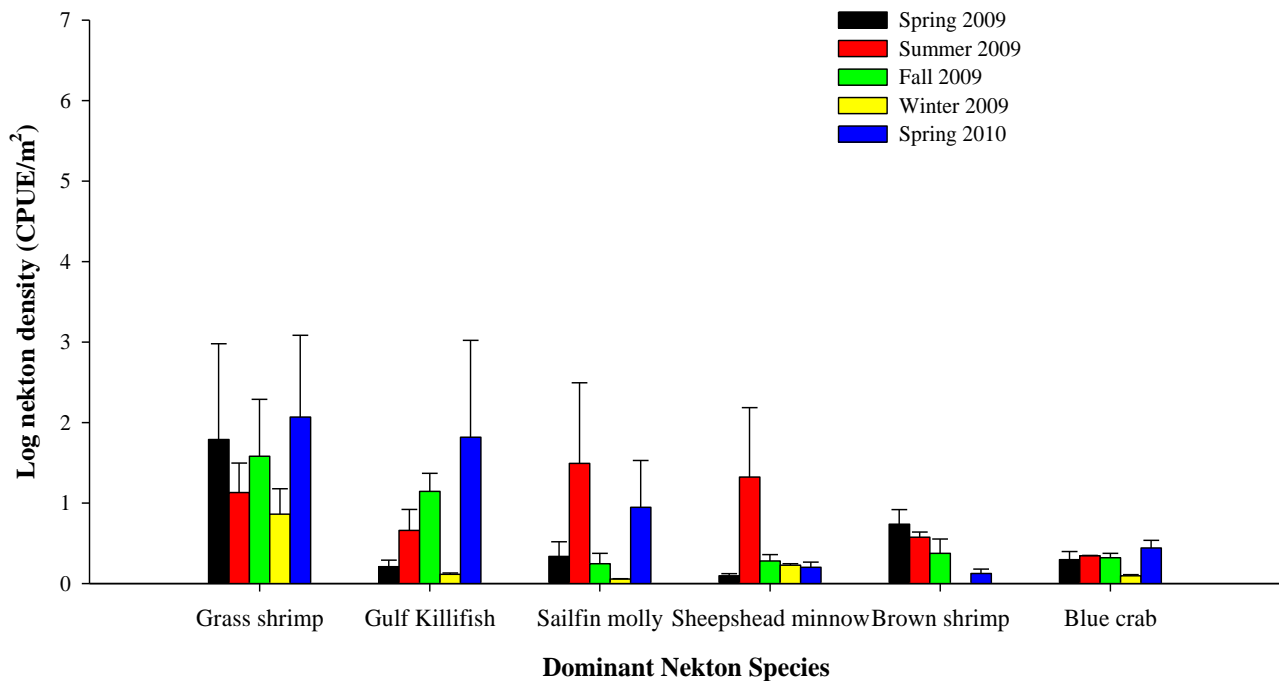


Fig. 3.25. Comparison of dominant nekton density (CPUE, organisms/m²) (log (x + 1) transformed) in saline marsh from April 2009 to May 2010.

species in saline ponds (e.g., gulf killifish *Fundulus grandis*, blue crab *Callinectes sapidus*,

brown shrimp *Farfantepenaeus aztecus*) were associated positively with salinity and CWD.

Dominant species of the 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 DI (Fig. 3.22).

DISCUSSION

Environmental Variables

Environmental variables did not differ between pond types due to hydrologic connectivity, but differences did occur by marsh type, and highlight systemic differences among Chenier plain marshes. The most obvious environmental gradients were increasing salinity from

inland (i.e., freshwater marsh) towards the ocean (i.e., saline marsh) and decreasing SAV and DI in the same direction. These patterns are typical for coastal marsh systems, which are characterized by abiotic gradients resulting from the convergence of the freshwater environment with the adjacent marine environment (Weinstein et al. 1980; Day 1981; Martino and Able 2003). Analysis of the environmental variables in this study illustrated strong variation across marsh types but many of these differences have been reported previously. For instance, seasonal changes in salinity of marsh ponds are a result of varying rainfall and evaporation (Adam 1990). The lack of SAV in saline ponds was also expected. Presence and absence of SAV within Louisiana marsh ponds is generally inversely related to salinity (Chabreck 1971) and SAV only occasionally occurs in saline ponds (Adair et al. 1994; Merino et al. 2009). However, some environmental variables did not vary as expected. For example, it is surprising that the effect of hydrologic connectivity on DO, temperature, and water depth was minimal because of their connection to deeper water sources that were presumably more oxygenated and cooler. However, while connected to these deeper areas, the ponds can be several km from the deeper water and are connected by shallow vegetated ditches with little water flow, thus resulting in higher water temperatures and lower oxygen than would be expected if connected by deeper and less vegetated ditches. Similarly, I expected brackish and saline PCPs that are hydrologically connected with other ponds, channels, and emergent marshes to have cooler temperatures than TCPs. The relatively long flood duration (i.e., short DI) of saline and brackish TCPs, however, may minimize temperature differences between pond types in both marsh types.

Community Metrics and Environmental Variables

Nekton community metrics (i.e., density, biomass, biodiversity, community similarity) appear to be structured by individual species responses to the salinity gradient as well as pond

habitat attributes. The results of the direct gradient analysis (Fig. 3.22) 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. ANOSIM analysis data (Table 3.5) also indicated that hydrologic connectivity (i.e., DI) affected community similarity between pond types.

Variability in SAV coverage among marsh types affected nekton community structure (Castellanos and Rozas 2001; Merino et al. 2005; Kanouse et al. 2006; Hitch 2009). Brackish ponds supported SAV coverage and had higher total nekton densities than saline marsh ponds, which were all unvegetated. In addition, the highest SAV coverage was recorded in brackish ponds in Fall 2009 which coincided with their highest total nekton density. Crustacean and fish densities in the brackish marsh were also positively related to SAV coverage. In contrast, nekton density of vegetated freshwater ponds did not differ from that of unvegetated saline ponds. Furthermore, fish density in freshwater marsh had a positive relationship with SAV coverage, whereas crustacean density showed a negative relationship. Overall nekton density showed a positive relationship due to the relatively high fish density. These findings suggest that the habitat requirements of fish and crustaceans change across marsh (Kanouse et al. 2006).

Even though SAV is a strong predictor of assemblage structure among marsh types, CWD and DI, 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 this study partially agree with those other studies as CWD and DI were negatively or positively associated with nekton density and community similarity, respectively. In freshwater marsh, nekton density was negatively correlated with CWD in PCPs and TCPs. Similarly, Minello (1999) suggested that increased connectivity of temporary ponds due to tides or precipitation can potentially decrease nekton densities. The relationship between DI and community similarity within PCPs and TCPs varied according to marsh types. Freshwater PCPs had higher community similarity than temporally disconnected ponds but saline marsh ponds showed an opposite pattern. As expected, low similarity of TCPs in freshwater marsh was associated with relatively long DI (i.e., 25.6 ± 14.23 days per season). However, relatively high similarity in saline TCP type may result from the high connectivity caused by the tidal exchange.

Species Response

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). Each of the three marsh types provides productive but potentially stressful environments. In freshwater marshes, low DO creates stressful conditions for many species. 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. The dominant species in each habitat are able to effectively cope or thrive in these otherwise stressful habitats, but because of the uniqueness of the necessary adaptations to thrive in each habitat, no species dominated across all marsh types. For example, in the freshwater marshes, three dominant species (i.e., mosquitofish, golden topminnow, bantam sunfish, Fig. 3.23) 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 reached their greatest abundance in habitats with relatively high SAV coverage, low salinity, and low DO (Hubbs 1971; Burr 1977; Shute 1980). In addition, even though the dominant species (i.e., grass shrimp, Fig. 3.24) in brackish marsh can tolerate a broad salinity range (i.e., 0 to 55 ppt; Kirby and Knowlton 1976; Morgan 1980), its density pattern revealed clear differences across the salinity gradient in this study that were related to co-varying 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 (relatively low DO, high SAV coverage) and in the saline marsh (higher DO, no SAV). Other studies have also related positive relationships among grass shrimp density, DO (Barrett et al. 1978) and SAV (Rozas and Odum 1987). Furthermore, one of the dominant species in saline marsh, brown shrimp (Fig. 3.25), 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 marsh is not surprising because brackish marsh area is passively managed to minimize salinity increases; salinity values during peak spawning seasons (Spring and Fall 2009, Spring 2010) were lower than 5 ppt. Thus, brown shrimp were only found in saline marsh.

The goal of our study was to use hydrologic connectivity to assess habitat value by comparing nekton density, biomass, diversity, and community similarity in a coastal marsh ecosystem. Our results indicate that PCPs have lower density and community similarity in saline

marshes than TCPs, but PCPs have greater diversity and community similarity than TCPs in freshwater marshes ponds. 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 community structure in saline marsh. Furthermore, conversion of PCPs to TCPs could have an even greater impact on aquatic macroinvertebrate communities (Chapter 4).

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CHAPTER 4

EFFECTS OF HYDROLOGIC CONNECTIVITY AND ENVIRONMENTAL VARIABLES ON AQUATIC MACROINVERTEBRATE ASSEMBLAGES IN DIFFERENT MARSH TYPES

INTRODUCTION

Hydrologic connectivity influences environmental variables and the community of aquatic organisms in coastal ecosystems (Fernandes et al. 2009; Rozas and Minello 2010). Connectivity is generally associated with the spatiotemporal exchange pathways of water along longitudinal and lateral dimensions (Roach et al. 2009). Longitudinal hydrologic connectivity is strongly influenced by tidal regimes and freshwater inflows (Doyle et al. 2007). In southwestern Louisiana, coastal Chenier brackish and saline marshes are often tidally connected to the estuary by one or more channels (Rozas and Minello 2010) but the inundation pattern of freshwater marshes is not a typical flooding pulse (Mitsch and Gosselink 2000) because their relatively longer distance from the ocean dampens the effect of the tidal cycle. In addition, seasonal dry and wet phases may affect lateral hydrologic connectivity patterns. All of these connectivity patterns can possibly affect environmental variables in coastal marsh systems. For instance, decreasing salinity from the coast towards inland by channels is typical for the Chenier Plain marsh system (Chabreck 1988).

Abiotic (Poff 1997; Hieber et al. 2005; Zilli and Marchese 2011) and biotic (Hornung and Foote 2006) conditions act as a filter for regional species pools. Thus, because of the effect of hydrology on these processes, it can impact local and regional species composition, including aquatic macroinvertebrate communities. For example, Boix et al. (2008) noted that salinity plays a major role in shaping aquatic macroinvertebrate community structure, although their study did not sample across the full salinity gradient. Water depth also may inhibit or enhance movement

of many aquatic macroinvertebrate species (Jeffries 2005). When low water levels, high elevation disconnected ponds from other water bodies, aquatic organisms become strand in these areas. High lateral connectivity among individual water bodies also may facilitate movement, thus resulting in high similarity of aquatic macroinvertebrate assemblages (Karaus 2004). Furthermore, macrophyte coverage appear to affect macroinvertebrate distribution by providing refuge from predators (Mittlebach 1988), increasing the availability of food resources (Campeau et al. 1994), and furnishing attachment sites or building materials (Lodge 1985; Dudley 1988).

Feeding strategies of macroinvertebrates reflect the adaptation of species to environmental conditions. Thus, the distribution of macroinvertebrate functional feeding groups (FFGs) reflects aquatic ecosystem attributes (Rawer-Jost et al. 2000). During recent decades, the categorization of macroinvertebrates into FFGs has shown considerable promise as a tool for assessing spatial changes of communities based on environmental conditions (Wallace and Webster 1996; Blasius and Merritt 2002). For instance, Barbour et al. (1996) noted that specialized feeders, such as scrapers and shredders, are presumed to be more sensitive to perturbation, while generalists (e.g., gatherer and filter collectors) are more tolerant to pollution that might alter the availability of certain food. However, no studies that have evaluated the effects of environmental variables across the full salinity gradient on FFGs in coastal marsh ecosystems.

A clear understanding of the linkages among hydrologic connectivity, environmental variables, and aquatic macroinvertebrate assemblages would enhance our understanding of aquatic macroinvertebrate habitat characteristics in coastal systems and facilitate conservation strategies for these organisms. The principal objectives of this study are to: 1) examine the effects of hydrologic connectivity and environmental variables on aquatic macroinvertebrate

assemblages (i.e., density, biomass, diversity, and community similarity) and the distribution of FFGs in a coastal marsh system; and 2) compare spatial patterns of aquatic macroinvertebrate community and FFG composition in different marsh and pond types. I hypothesized that 1) aquatic macroinvertebrate communities in PCPs have higher density, biomass, diversity, and community similarity than TCPs and 2) dominant aquatic macroinvertebrate species and FFG distributions vary across the salinity gradient.

METHODS

Study Area

This study was conducted in White Lake Wetlands Conservation Area (WLWCA, 29°52'50" N, 92°31'11" W) and Rockefeller State Wildlife Refuge (RWR, 29°40'93" N, 92°48'45" W) in the Chenier Plain of southwestern Louisiana (Fig. 4.1). Both areas are owned and operated by the Louisiana Department of Wildlife and Fisheries. White Lake Wetlands Conservation Area is located along the western boundary of Vermilion Parish and is bounded on the south by White Lake (28.2 km north of the Gulf of Mexico). The 28,719 ha area includes managed (8,972 ha) and unmanaged (12,106 ha) freshwater marsh. Dominant vegetation is maidencane (*Panicum hemitomon*) and bulltongue arrowhead (*Sagittaria lancifolia*). Rockefeller State Wildlife Refuge is a 42,400 ha refuge located in eastern Cameron and western Vermilion Parishes, wedged between Grand Chenier Highway 82 and the Gulf of Mexico. This area borders the Gulf of Mexico for 41.8 km and extends inland toward the Grand Chenier ridge. This refuge consists of 17 impoundments, which allow for control of both water level and salinity (Wicker et al. 1983). The Unit Six management area was selected as tidal brackish marsh habitat. Unit Six is a 7,200 ha brackish impoundment dominated by *Spartina patens*. In addition, an unmanaged area

of similar size was selected as tidal saline marsh habitat. The saline marsh is dominated by *Spartina alterniflora*.

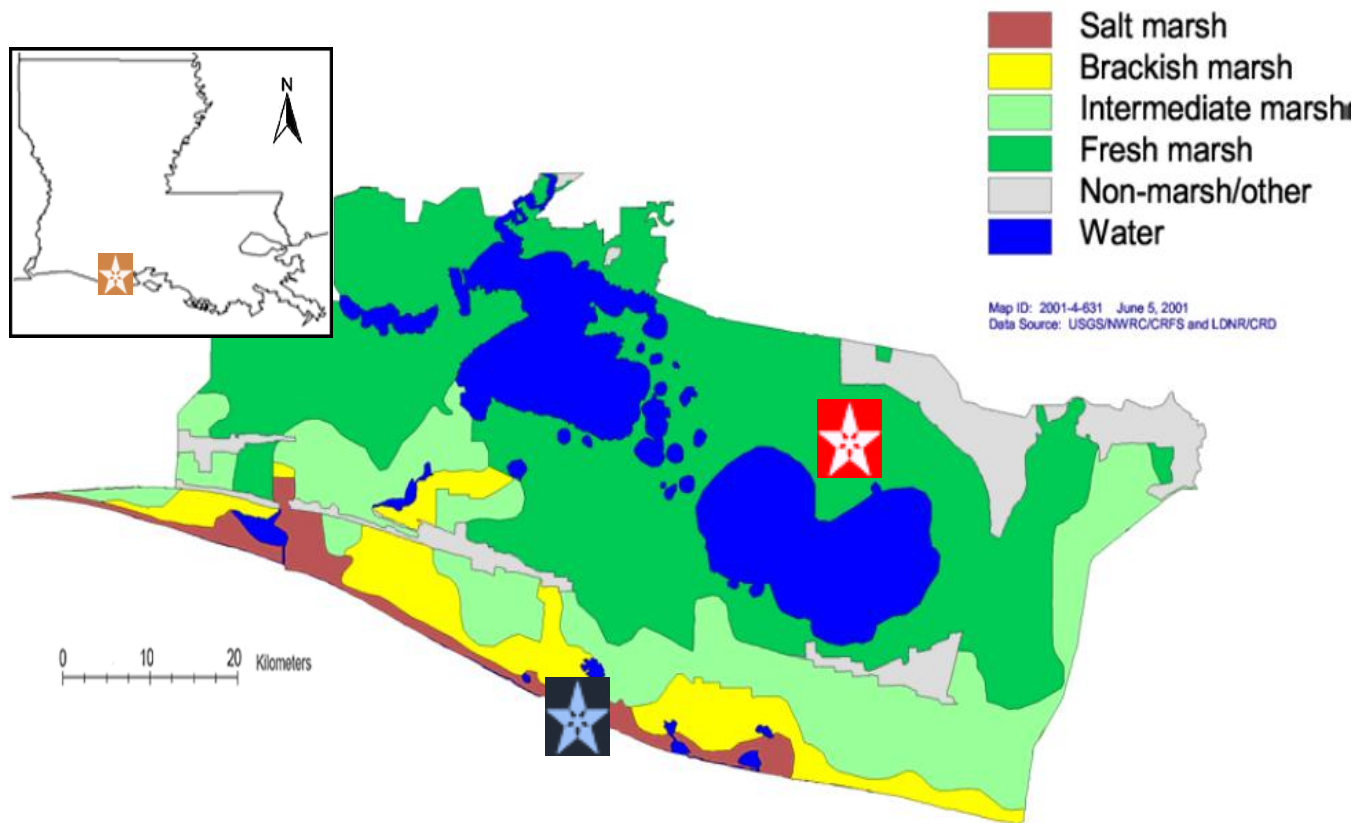


Fig. 4.1. White Lake Wetlands Conservation Area (red star) and Rockefeller Wildlife Refuge (blue star) are located in Vermilion Parish, Louisiana (Chabreck and Linscombe 1997).

Hydrologic and Environmental Data

Methods for classification of ponds (i.e., PCPs, TCPs, Table 4.1) and evaluation of their hydrologic characteristics are described in Chapter III. To assess variation in environmental variables across pond types, I measured salinity (ppt), water temperature ($^{\circ}\text{C}$), dissolved oxygen (DO , mg L^{-1}), and water depth (sampling point water depth; SPWD, cm) with a YSI Model 85 Water Quality Monitor. Also, water depth (sampling point water depth; SPWD, cm) was measured by meter stick at sampling point. Following each macroinvertebrate sample, these variables were measured 2-3 cm above the sediment between 08:00 and 17:00. Percent cover of

submerged aquatic vegetation (SAV) in a 1 x 1m frame was also determined at three points in each pond and the mean coverage was determined. Monthly mean environmental variable data combined together to examine seasonal patterns. 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); 5) Spring 2010 (March-May).

Table 4.1. The types of ponds and environmental variables measured in this study as well as variable names, sampling units and abbreviations.

	Variable Name	Units	Abbreviation
Pond Types	Permanently Connected Pond	number	PCP
	Temporarily Connected Pond	number	TCP
	Pond Total (PCP+TCP)		PT
Environmental Variables	Salinity	ppt	Salinity
	Dissolved Oxygen	mg/L	DO
	Temperature	°C	Temp
	Sampling Point Water Depth	cm	SPWD
	Connected Water Depth	cm	CWD
	Duration of Isolation	days	DI
	Frequency of Isolation	times	FI
	Vegetation Coverage	%	VC

Aquatic Macroinvertebrate Sampling

To determine aquatic macroinvertebrate community characteristics, I sampled each pond monthly from April 2009 to May 2010. Monthly mean environmental variable data combined together to examine seasonal patterns. I sampled water-column macroinvertebrates (i.e., aquatic insects, amphipod, isopod) using a D-shaped sweep net with a 30-cm opening and 1-mm mesh size. I conducted a total of 10 sweeps of 2-m long each (surface covered 6 m²; Bolduc and Afton 2003). All materials were preserved in 95% ethyl alcohol at sampling ponds and in 80% ethyl

alcohol after identification. All aquatic macroinvertebrates were weighed to the nearest 0.001 g wet weight to determine biomass.

Functional Feeding Group Assignments

FFGs are a classification approach that is based on morpho-behavioral mechanisms of food acquisition. In this study, aquatic macroinvertebrates were assigned to FFGs according to the ecological data by Merritt and Cummins (2009) and Cummins and Wilzbach (1985). The major FFGs in this study are 1) scrapers, which consume algae and associated material; 2) shredders, which consume leaf litter or other coarse particulate organic matter (CPOM); 3) collectors, which collect fine particulate organic matter (FPOM) from the water bottom (collector-gatherers) or from the water column with a variety of filters (collector-filterers); and 4) predators, which feed on other consumers.

Statistical Analyses

Environmental variables and nekton density and biomass were natural log ($x+1$) transformed to achieve normality. Data were tested for normality with the Shapiro-Wilks test. Significance level was chosen at 0.05.

Environmental Variables: As noted in Chapter III, multivariate analysis of variance (MANOVA: Proc Mixed, Version 9.2, SAS Institute, North Carolina) was used to compare environmental variables (Table 3.1) by seasons, marshes, and pond types. Following significant MANOVA results, individual one-way analysis of variance (ANOVA: Proc Mixed) tests were performed. Significant ANOVA effects were tested using post-hoc comparisons of Tukey adjusted least squared means.

Aquatic Macroinvertebrate Density, Biomass, Biodiversity, Community Similarity: ANOVA (Proc Mixed) was used to test for statistical differences in density, biomass and diversity by

seasons, marshes, and pond types. Multiple linear regression (Proc Mixed) was used to examine the relationship between nekton community characteristics (i.e., density, biomass, diversity) and environmental factors (Table 4.1). PRIMER software (Clarke and Gorley 2006) was used to test the effect of hydrologic connectivity on community similarity within pond types across all sampling periods. ANOSIM was performed on a Bray-Curtis dissimilarity matrix computed on the fourth-root transformed abundance data. I compared differences of community similarity for pond types with the one-way SIMPER ($p=0.05$) test. 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 community structure (Clarke and Warwick 2001).

Aquatic Macroinvertebrate Assemblage Composition: 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 more than three individuals were present in the samples (Gauch 1982; Piazza and La Peyre 2009).

RESULTS

Environmental Variables

Results of the environmental variables are reported in Chapter III (Table 3.2-3.3) but are also repeated here. Seasonal salinity in freshwater ($F_{2,57}=39.15$, $p<0.01$) and brackish ($F_{2,57}=7.80$, $p=0.01$) marsh ponds was higher in Summer 2009 than Winter 2009; salinity did not differ seasonally in the saline marsh ($p=0.1261$). Salinity differed among marsh types with the highest in saline marsh and the lowest in freshwater marsh ($F_{2,177}=17.61$, $p=0.01$). Between pond types among marshes, saline PCPs and TCPs had greater salinity than brackish and freshwater PCPs and TCPs, respectively (PCPs: $F_{2,87}=26.97$, $p<0.01$; TCPs: $F_{2,87}=34.54$, $p<0.01$). Within

freshwater marshes (t value=2.42, $p=0.04$), salinity was higher in PCPs (0.9 ± 0.23) than in TCPs (0.3 ± 0.07); salinity did not differ between PCPs and TCPs in brackish ($p=0.98$) and saline marshes ($p=0.77$). Seasonal DO in freshwater marsh ponds was greater in Winter 2009 than in Summer 2009 ($F_{2,57}=15.47$, $p=0.01$); no difference was observed in brackish ($p=0.09$) and saline ($p=0.05$) marshes. Comparison of DO among marsh types indicated that brackish and saline PT in Summer 2009 was higher than freshwater PT ($F_{2,57}=74.40$, $p<0.01$, Table 3.2). Between pond types across marshes, DO was higher in brackish (4.5 ± 0.43) than in fresh (2.5 ± 0.67) TCPs ($F_{2,87}=4.49$, $p=0.04$) but did not differ in PCPs. There were no differences in DO between pond types within a marsh. Temperature in freshwater ($F_{2,57}=8.28$, $p<0.01$) and brackish ($F_{2,57}=8.07$, $p<0.01$) marshes were higher in Summer 2009 than Winter 2009; no seasonal difference was recorded in saline marshes ($p=0.17$). Comparison of temperature among marsh types indicated that saline PT in Winter 2009 ($F_{2,57}=33.17$, $p<0.01$) and Spring 2010 ($F_{2,57}=21.01$, $p=0.02$) was higher than brackish and freshwater PT (Table 3.2). However, temperature did not differ between pond types across marshes or between pond types within a marsh. Comparison among seasonal SAV coverage within each marsh did not differ. However, SAV coverage differed among marsh types with the highest in freshwater marsh and no SAV in saline marsh ($F_{2,177}=25.95$, $p<0.01$). Between pond types among marshes, freshwater PCPs and TCPs had greater SAV coverage than brackish and saline PCPs and TCPs, respectively (PCPs: $F_{2,87}=9.88$, $p=0.01$; TCPs: $F_{2,87}=8.43$, $p=0.02$). Comparison of between pond types within a marsh showed that SAV coverage of Winter 2009 in freshwater PCPs had higher than TCPs (Table 3.3, $p=0.01$) but SAV coverage did not differ between pond types in brackish and saline marshes. SPWD in freshwater ($F_{2,57}=8.32$, $p=0.04$), brackish ($F_{2,57}=7.20$, $p<0.01$), and saline marshes ($F_{2,57}=6.78$, $p<0.01$) was greater in Fall and Winter 2009 than Summer 2009 and Spring 2010. Among marsh types, saline

PT SPWD in Spring 2009 was lower than brackish PT ($F_{2,57}=13.98$, $p=0.03$). Comparisons between pond types among marshes indicated that SPWD in saline PCPs (15.1 ± 2.62) was lower than fresh (31.7 ± 2.78) and brackish (31.3 ± 5.90) PCPs ($F_{2,87}= 5.44$, $p=0.02$) but TCPs did not differ. Within a marsh, saline TCPs had higher SPWD than PCPs in Spring 2009 ($p=0.02$) and Winter 2009 ($p=0.04$) (Table 3.3).

Seasonal comparisons of CWD in freshwater ($F_{2,57}=5.80$, $p=0.01$), brackish ($F_{2,57}=9.02$, $p<0.01$), and saline marshes ($F_{2,57}=7.20$, $p<0.01$) indicated that CWD was higher in Fall and Winter 2009 than Summer 2009 and Spring 2010. Among marsh types, CWD in brackish PT was greater than freshwater PT in Summer 2009 ($F_{2,57}=13.70$, $p=0.03$) and Fall 2009 ($F_{2,57}=13.70$, $p=0.03$). Between pond types across marshes, CWD in saline PCPs in Winter 2009 was lower than brackish and freshwater PCPs ($F_{2,57}=10.49$, $p=0.01$). Within a marsh, freshwater ($p=0.02$) and saline ($p=0.02$) TCP had higher CWD than PCPs. Seasonal DI of TCPs in freshwater marsh was greater in Summer 2009 than in Winter 2009 ($F_{2,57}=4.20$, $p=0.03$). DI of TCPs did not differ among marsh types. Within a marsh, DI of TCPs in Summer 2009 was obviously greater than PCPs ($p=0.04$). Seasonal FI in each marsh type did not differ (freshwater marsh: $F_{2,57}=1.31$, $p=0.34$; brackish marsh: $F_{2,57}=1.85$, $p=0.20$; saline marsh: $F_{2,57}=1.27$, $p=0.35$). Also, FI did not differ among marsh types, between pond types across marshes, and between pond types within a marsh.

Aquatic Macroinvertebrate Density and Biomass

In 252 monthly samples, I collected 32,130 aquatic macroinvertebrates from 52 taxa (Table 4.2). Aquatic macroinvertebrate biomass during five seasons ranged from $0.6 \pm 0.03 \text{ \#/m}^2$ (brackish marsh, Fall 2009) to $47.6 \pm 38.53 \text{ \#/m}^2$ (brackish marsh, Spring 2009). Comparison of seasonal density within a marsh indicated that brackish marshes in Spring 2009 (47.6 ± 38.53)

was higher than Fall (0.6 ± 0.03) ($F_{4,79}=4.64$, $p=0.03$) but did not differ seasonally in freshwater and saline ponds (Fig. 4.2). Among marsh types, aquatic macroinvertebrate PT density in freshwater (10.5 ± 0.75) was higher than in brackish (5.9 ± 0.42) and saline (4.8 ± 0.34) PT ($F_{2,249}=13.41$, $p<0.01$). Comparisons of density between pond types and across marshes indicated that freshwater PCPs (15.5 ± 1.11) supported higher densities than brackish (9.7 ± 0.69) and saline (2.4 ± 0.17) PCPs ($F_{2,123}=17.43$, $p<0.01$). Within a marsh type, density in PCPs in freshwater marsh was higher than TCPs ($t=3.34$, $p<0.01$), however, density in saline marsh TCPs was greater than PCPs ($t=3.71$, $p=0.01$, Fig. 4.3).

Aquatic macroinvertebrate biomass during five seasons ranged from 0 g wet wt/m² (brackish marsh, Fall 2009) to 0.2 ± 0.10 g wet wt/m² (brackish marsh, Spring 2009) (Fig. 4.4). In freshwater ($F_{4,79}=6.25$, $p<0.01$) and brackish ($F_{4,79}=6.85$, $p<0.01$) marshes, seasonal biomass (g wet wt/m²) in Spring 2009 (freshwater: 0.1 ± 0.01 ; brackish: 0.2 ± 0.10) was greater than Summer 2009 (freshwater: 0; brackish: 0); no seasonal differences in biomass were observed in saline marshes. Freshwater PT supported the highest biomass among marsh types ($F_{2,249}=14.06$, $p<0.01$). Comparison of biomass between pond types across marshes indicated that freshwater PCPs supported higher biomass than brackish and saline PCPs ($F_{2,123}=20.72$, $p<0.01$) but biomass in TCPs did not differ ($F_{2,123}=0.86$, $p=0.43$). Within a marsh, biomass in PCPs in freshwater marsh was higher than that of freshwater TCPs ($t=3.62$, $p<0.01$), however, saline TCPs was greater than that of saline PCPs (biomass: $t=3.06$, $p<0.01$, Fig. 4.5).

Table 4.2. Mean density (#/m² (SE)) of aquatic macroinvertebrates in different habitat and marsh types.

Feeding Group	Order	Family	Genus/Species	Freshwater		Brackish		Saline	
				PCP	TCP	PCP	TCP	PCP	TCP
Scraper	Lepidoptera	Pyrilidae		0.22 (1.79)	0.19 (1.15)				
Shredder	Coleoptera	Chrysomelidae	<i>Donacia</i>	0.02 (0.29)	0.01 (0.14)				
		Curculionidae	<i>Lissorhoptrus</i>	0.04 (0.32)	0.08 (0.50)				
			<i>Onychylis</i>	0.01 (0.10)			0.01 (0.10)		
			<i>Stenopelmus</i>	0.01 (0.10)					
	Diptera	Scirtidae	<i>Scirtes</i>	0.04 (0.57)	0.11 (0.74)				
		Ephydriidae			0.01 (0.10)				
		Tipulidae		0.02 (0.17)					
Piercer	Coleoptera	Dytiscidae	<i>Copelatus</i>	0.06 (0.60)	0.04 (0.45)				
		Halipilidae	<i>Halipilus</i>	0.02 (0.17)	0.02 (0.17)				
			<i>Peltodytes</i>	0.07 (0.60)	0.05 (0.73)				
		Hydrophilidae	<i>Berosus</i>	0.22 (1.39)	0.13 (0.63)	0.02 (0.22)	0.06 (0.38)		0.01 (0.14)
Collector/gatherer	Coleoptera	Hydrophilidae	<i>Derallus</i>		0.02 (0.20)				
			<i>Enochruss</i>	0.13 (1.23)	0.09 (0.34)	0.04 (0.38)	0.08 (0.88)		0.02 (0.23)
	Ephemeroptera	Baetidae		0.04 (0.37)					
		Caenidae	<i>Caenis</i>	1.48 (9.04)	0.23 (2.23)				
	Trichoptera	Hydroptilidae	<i>Oxyethira</i>	0.02 (0.23)					
	Diptera	Chironomidae		6.90 (20.44)	5.75 (29.33)	3.62 (41.37)	1.04 (4.72)	1.19 (15.86)	1.39 (6.09)
		Culicidae			0.06 (0.59)				
		Stratomyidae			0.01 (0.10)				
	Amphipoda	Corophiidae	<i>Corophium</i>			2.79 (27.48)	0.10 (1.45)	0.12 (0.94)	0.24 (2.97)
		Crangonyctidae	<i>Synurella</i>	2.53 (27.37)	2.37 (16.78)	0.02 (0.36)	0.02 (0.36)	0.01 (0.14)	
		Hyalellidae	<i>Hyalella</i>	23.99 (154.13)	1.21 (5.07)				
		Gammaridae	<i>Gammarus</i>			0.69 (8.40)	1.94 (26.83)	0.60 (3.83)	0.59 (7.70)
	Isopoda	Asellidae	<i>Caecidotea</i>	1.43 (8.15)	2.23 (16.14)				
			<i>Lirceus</i>	1.23 (8.10)	0.22 (1.40)				

Table 4.2. Continued.

Feeding Group	Order	Family	Genus/Species	Freshwater		Brackish		Saline	
				PCP	TCP	PCP	TCP	PCP	TCP
Predator	Odonata	Aeshnidae	<i>Coryphaeschna</i>	0.04 (0.20)	0.05 (0.27)		0.01 (0.10)		
		Coenagrionidae	<i>Enallagma</i>	0.51 (1.91)	0.57 (2.97)	0.65 (3.97)	0.72 (2.69)		0.10 (0.96)
			<i>Ischnura</i>	0.13 (0.79)	0.10 (0.42)	0.12 (0.79)	0.06 (0.38)		0.02 (0.29)
		Libellulidae	<i>Erythemis</i>	0.54 (2.59)	0.23 (1.39)				
	Coleoptera	Dytiscidae	<i>Pachydiplax</i>	1.37 (7.51)	0.41 (1.71)				
			<i>Celina</i>	0.43 (2.57)	0.13 (0.79)				
			<i>Cybister</i>	0.04 (0.43)	0.01 (0.14)				
			<i>Desmopachria</i>		0.01 (0.15)				
			<i>Hydrovatus</i>	0.26 (1.86)	0.11 (0.70)				
		Hydrophilidae	<i>Laccophilus</i>	0.01 (0.10)	0.01 (0.10)				
			<i>Matus</i>	0.02 (0.22)	0.02 (0.36)				
			<i>Thermonectus</i>	0.02 (0.16)	0.02 (0.19)				
			<i>Tropisternus</i>	0.19 (1.73)	0.20 (1.07)	0.23 (1.64)	0.43 (4.30)		0.04 (0.53)
	Hemiptera	Noteridae	<i>Hydrocanthus</i>	0.17 (1.17)	0.37 (2.29)				
		Staphylinae	<i>Euaesthetus</i>		0.01 (0.10)				
		Belostomatidae	<i>Belostoma</i>	0.19 (1.23)	0.06 (0.41)	0.04 (0.32)	0.11 (0.89)		
		Corixidae	<i>Trichocorixa</i>	3.10 (13.74)	1.11 (9.21)	20.74 (353.22)	1.73 (15.85)	5.37 (69.11)	19.24 (159.16)
		Mesoveliidae	<i>Mesovelia</i>	0.14 (1.31)	0.07 (1.06)	0.03 (0.43)			
		Naucoridae	<i>Pelocoris</i>	0.24 (2.21)	0.17 (0.84)				
		Nepidae	<i>Ranatra</i>	0.04 (0.27)	0.03 (0.25)				
		Notonectidae	<i>Notonecta</i>	0.09 (0.89)	0.10 (1.00)		0.02 (0.22)		
	Trichoptera	Leptoceridae	<i>Oecetis</i>	0.02 (0.23)					
	Megaloptera	Corydalidae	<i>Chauliodes</i>		0.01 (0.15)				
Diptera		Ceratopogonidae		0.31 (3.41)	0.06 (0.41)	0.01 (0.11)	0.05 (0.60)		
		Dolichopodidae			0.01 (0.10)				
		Tabanidae		0.13 (1.09)	0.02 (0.20)	0.01 (0.11)	0.02 (0.13)		

*. Feeding Group Reference: Merritt and Cummins, 2008

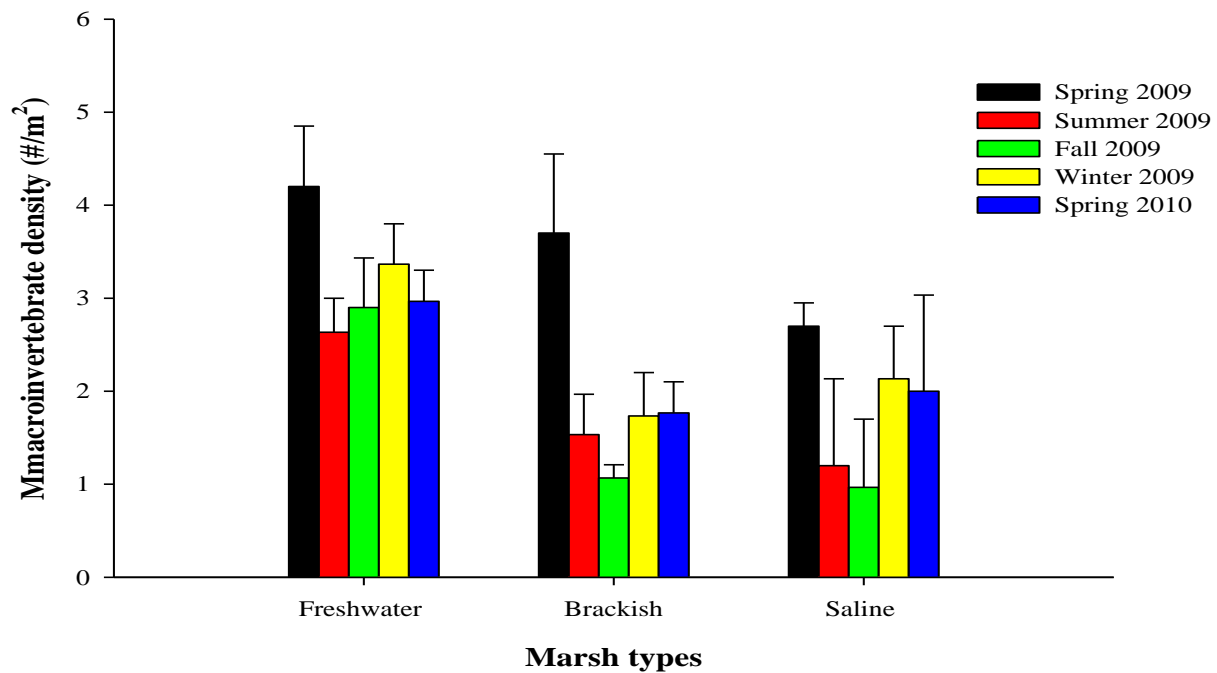


Fig. 4.2. Comparison of seasonal log (x+1) transformed macroinvertebrates density (#/m²) in different marsh types from April 2009 to May 2010.

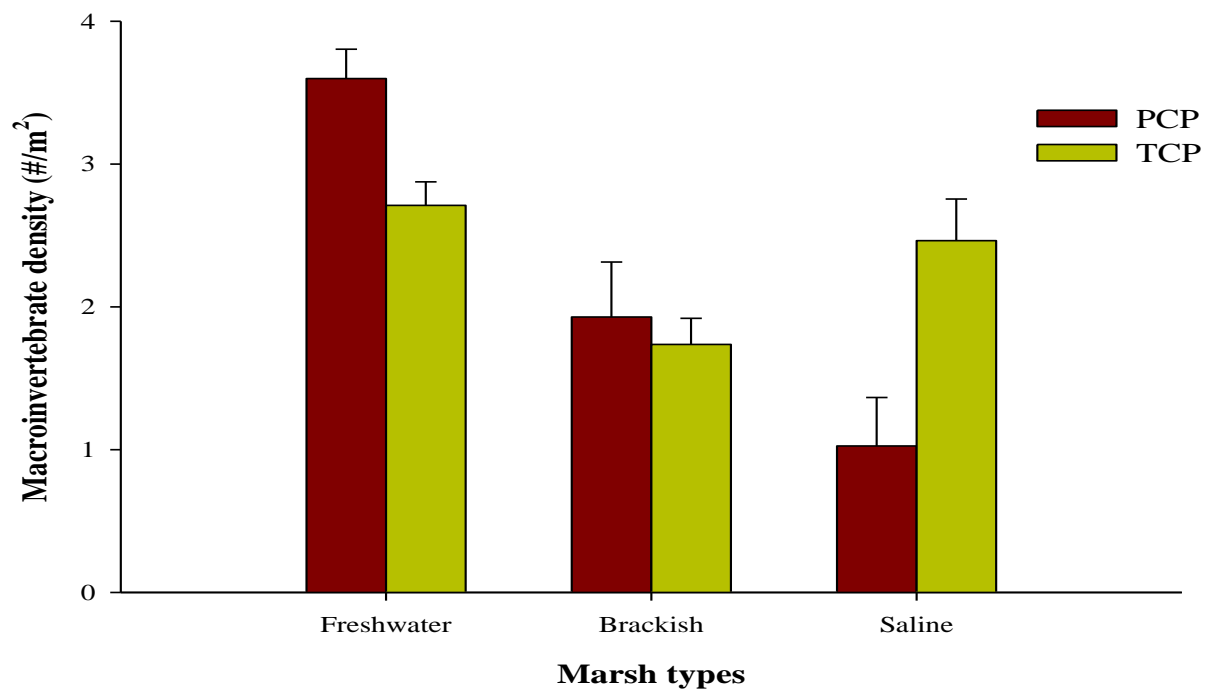


Fig. 4.3. Comparison of log (x+1) transformed macroinvertebrates density (#/m²) between pond types in multiple marshes during five seasons.

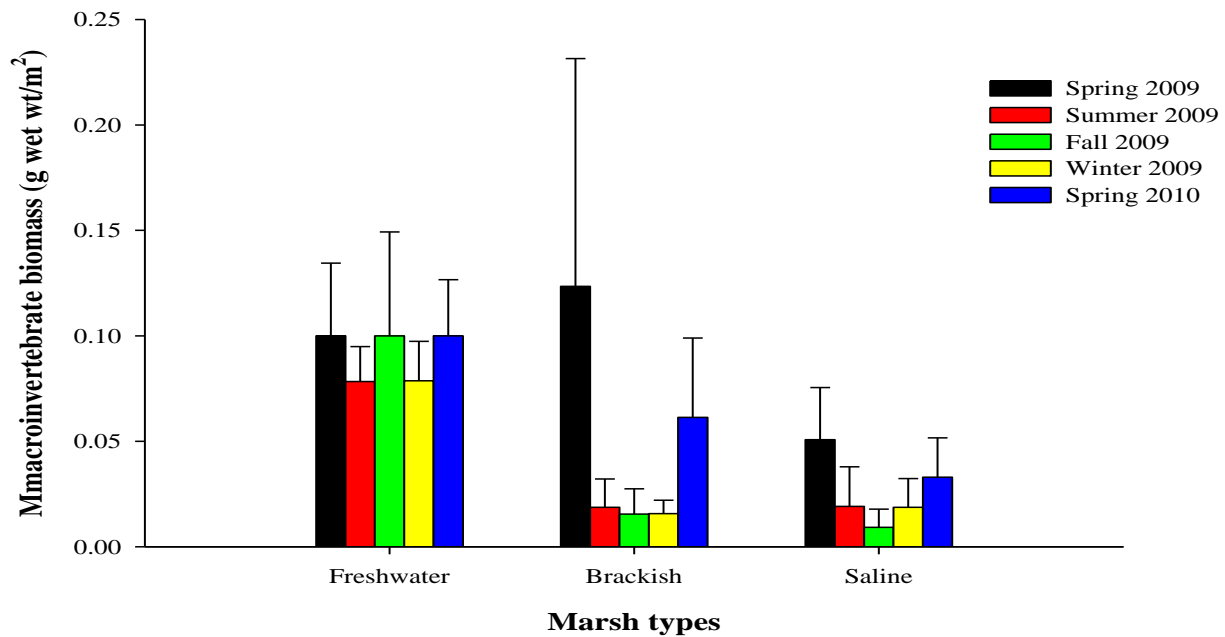


Fig. 4.4. Comparison of seasonal log (x+1) transformed macroinvertebrate biomass (g wet wt/m²) in different marsh types from April 2009 to May 2010.

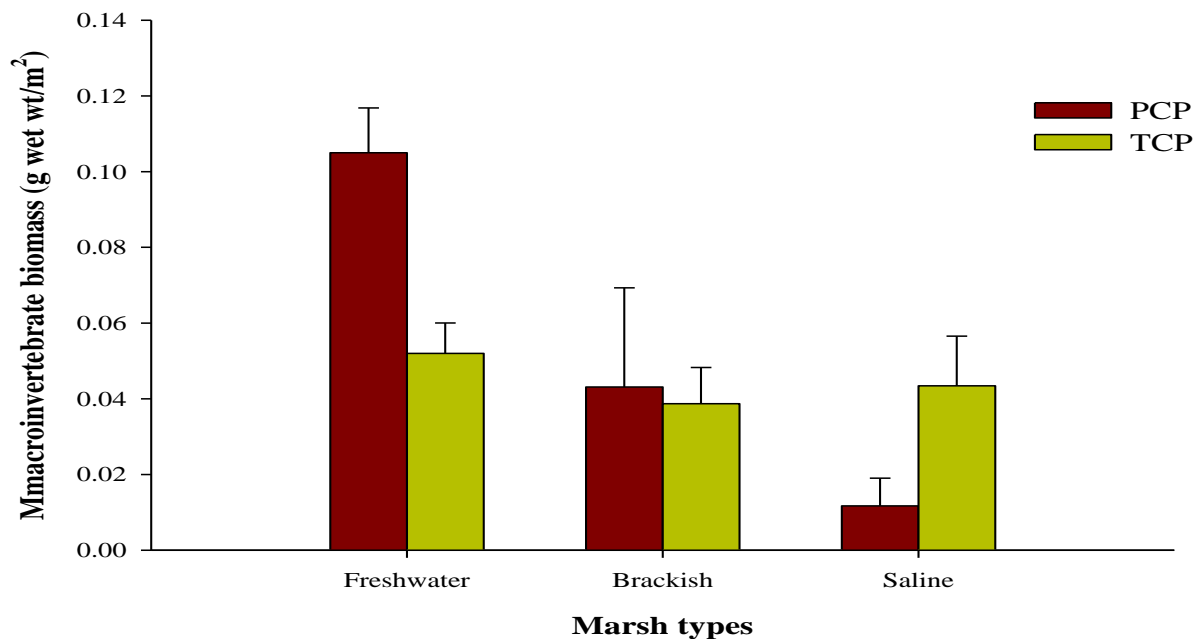


Fig. 4.5. Comparison of log (x+1) transformed macroinvertebrate biomass (g wet wt/m²) between pond types in multiple marshes during five seasons.

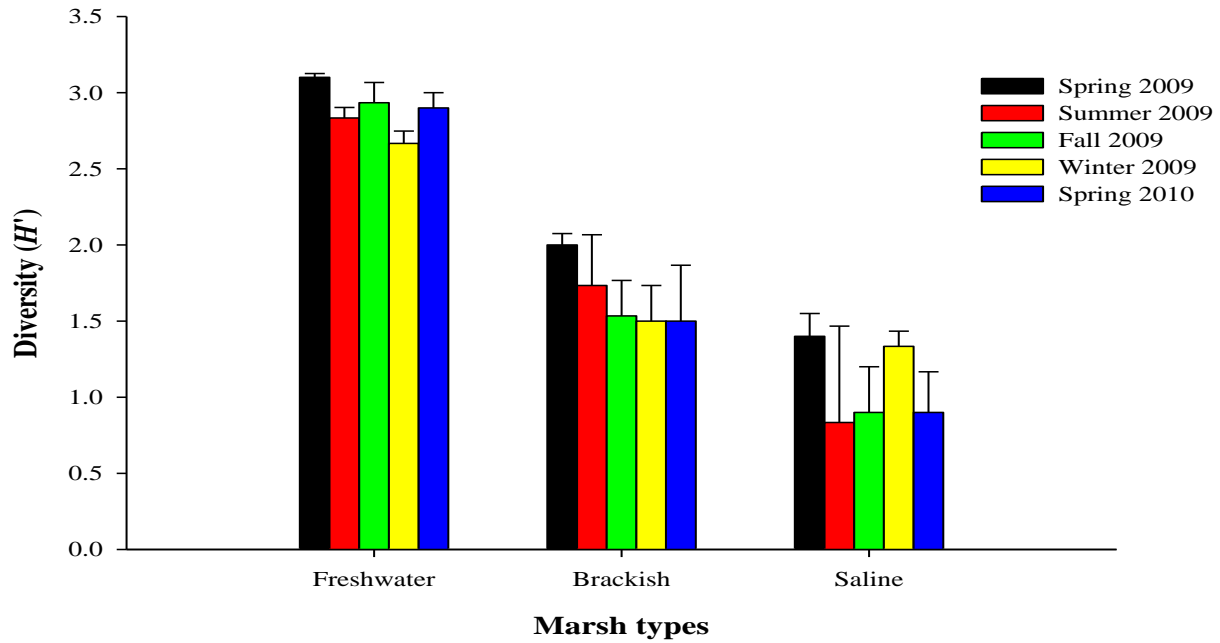


Fig. 4.6. Comparison of monthly macroinvertebrate diversity (Shannon-Wiener diversity index H') in different marsh types from April 2009 to May 2010.

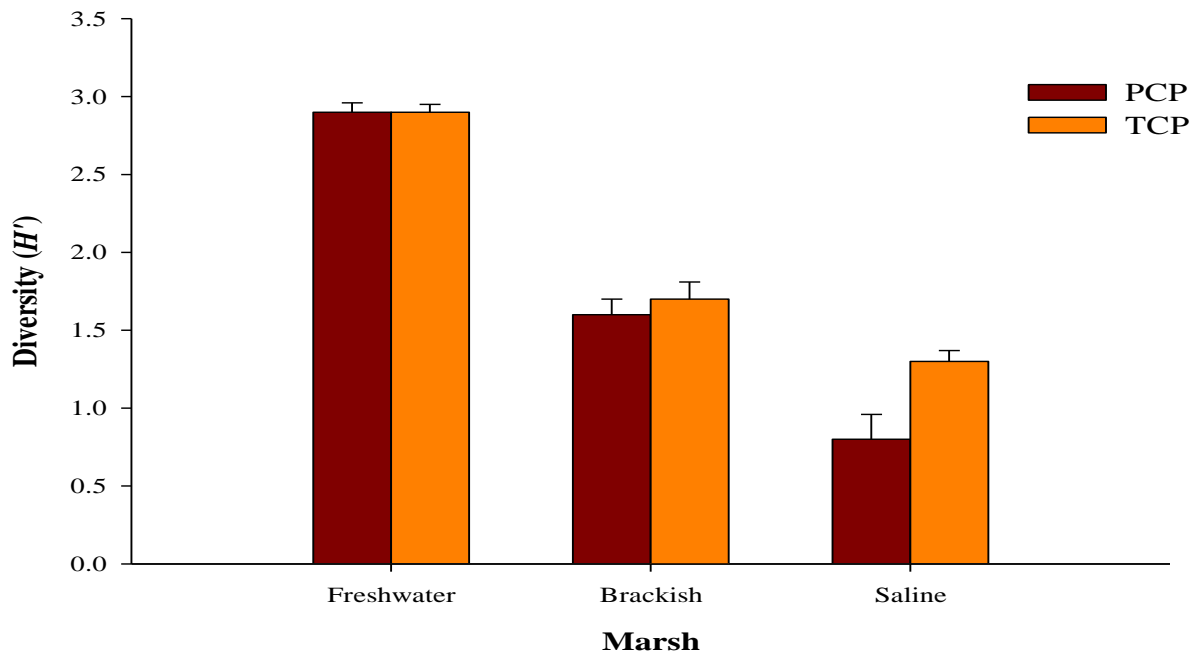


Fig. 4.7. Comparison of macroinvertebrate diversity (Shannon-Wiener diversity index H') between different pond type in multiple marsh types from April 2009 to May 2010.

Aquatic Macroinvertebrate Biodiversity and Community Similarity

I identified a total of 52 aquatic macroinvertebrates taxa including 47 taxa (20,855 individuals) in PCPs and 49 taxa (11,275 individuals) in TCPs. A total of 50 taxa were identified in freshwater marsh (PCPs: 45 taxa, 11,708 individuals; TCPs: 46 taxa, 4,205 individuals), 20 in brackish marsh (PCPs: 15 taxa, 7,311 individuals; TCPs: 18 taxa, 1,609 individuals), and 12 in saline marsh (PCPs: 7 taxa, 1,836 individuals; TCPs: 12 taxa, 5,461 individuals). Freshwater marsh had 32 exclusive taxa but brackish and saline did not have any exclusive taxa.

Mean values of Shannon-Wiener diversity differed among marsh types ($F_{2,81} = 153.62$, $p < 0.01$). Comparisons between pond types across marshes indicated that the highest Shannon-Wiener diversity was in freshwater PCPs and TCPs and the lowest in both saline pond types (PCPs: $F_{2,39} = 84.81$, $p < 0.0001$; TCPs: $F_{2,39} = 97.86$, $p < 0.0001$, Fig. 4.6). Within a marsh, PCPs and TCPs did not differ in fresh and brackish marsh but in the saline marsh TCPs had greater diversity than PCPs ($t = 3.08$, $p < 0.01$) (Fig. 4.7).

Table 4.3. ANOSIM and SIMPER results for hydrologic connectivity (PCP vs TCP) comparison of community similarity in three marsh types. All reported results were significant at $p = 0.05$. Presented are the Global R for significant ANOSIM tests and the SIMPER results for percentage similarity within same habitat type and dissimilarity between different habitat types.

	Freshwater		Brackish		Saline	
	PCP	TCP	PCP	TCP	PCP	TCP
Global R	0.168*		0.061		0.149*	
Similarity	47.2	34.7	27.2	33.5	15.0	40.7

*: $p < 0.01$, **: n.s: no significant

The ANOSIM results in fresh (Global R: 0.168, $p = 0.001$) and saline (Global R: 0.149, $p = 0.001$) marsh demonstrated that community similarity within pond types was affected by hydrologic connectivity, but brackish ponds were not affected (Global R: 0.045, $p > 0.05$). In all

cases, SIMPER ($p=0.05$) detected differences in average similarity between pond types.

Assemblage similarity of PCPs (47.2%) in freshwater marsh was greater than in TCPs (34.7%), however, similarity in saline TCPs (40.7%) was higher than that of PCPs (15.0%) (Table 4.3).

Aquatic Macroinvertebrate Assemblage Composition

The CCA results indicated significant relationships between the measured environmental variables and aquatic macroinvertebrate assemblage characteristics during all sampling periods (1st axis: $p=0.002$, All axes: $p=0.002$). CCA eigenvalues of the first four multivariate axes were 0.34 (CCA1), 0.09 (CCA2), 0.05 (CCA3), and 0.03 (CCA4). Species-environment correlation coefficients for the four axes were 0.84, 0.83, 0.65, and 0.60, respectively. Cumulative percentage variance of species for the four axes (CCA 1-4) was 29.3. The first and second axes of species data accounted for 16.2% and 5.2% of the variation, respectively. Also, the first two axes of the species-environment relationship represented 78.5% of the variance. Axis 1 was correlated positively to salinity (0.75) and Axis 2 related most strongly with water depth (SPWD: 0.60; CWD: 0.64). Also, DO was negatively related to DI and FI (Axis 2=-0.31).

Analysis of the species-environment relationships indicated that a number of the dominant species in brackish and saline (e.g., Gammaridae *Gammarus*, Corophiidae *Coirrophium*, Corixidae *Trichocorixa*, Chironomidae) marshes were associated positively with salinity and DO. Also, dominant species groups in freshwater (e.g., Odonata: Libellulidae *Pachydiplax*; Amphipoda: Hyalellidae *Hyalella*, Crangonyctidae *Synurella*; Isopoda: Asellidae *Caecidotea*, *Asellidae Lirceus*) were associated positively with deep water. Conversely, non-dominant species groups in freshwater ponds such as Coleoptera: Dytiscidae *Copelatus*, Dytiscidae *Cybister*; Hemiptera: Mesoveliidae *Mesovelia*; Diptera: Culicidae were positively associated with DI and temperature (Fig. 4.8).

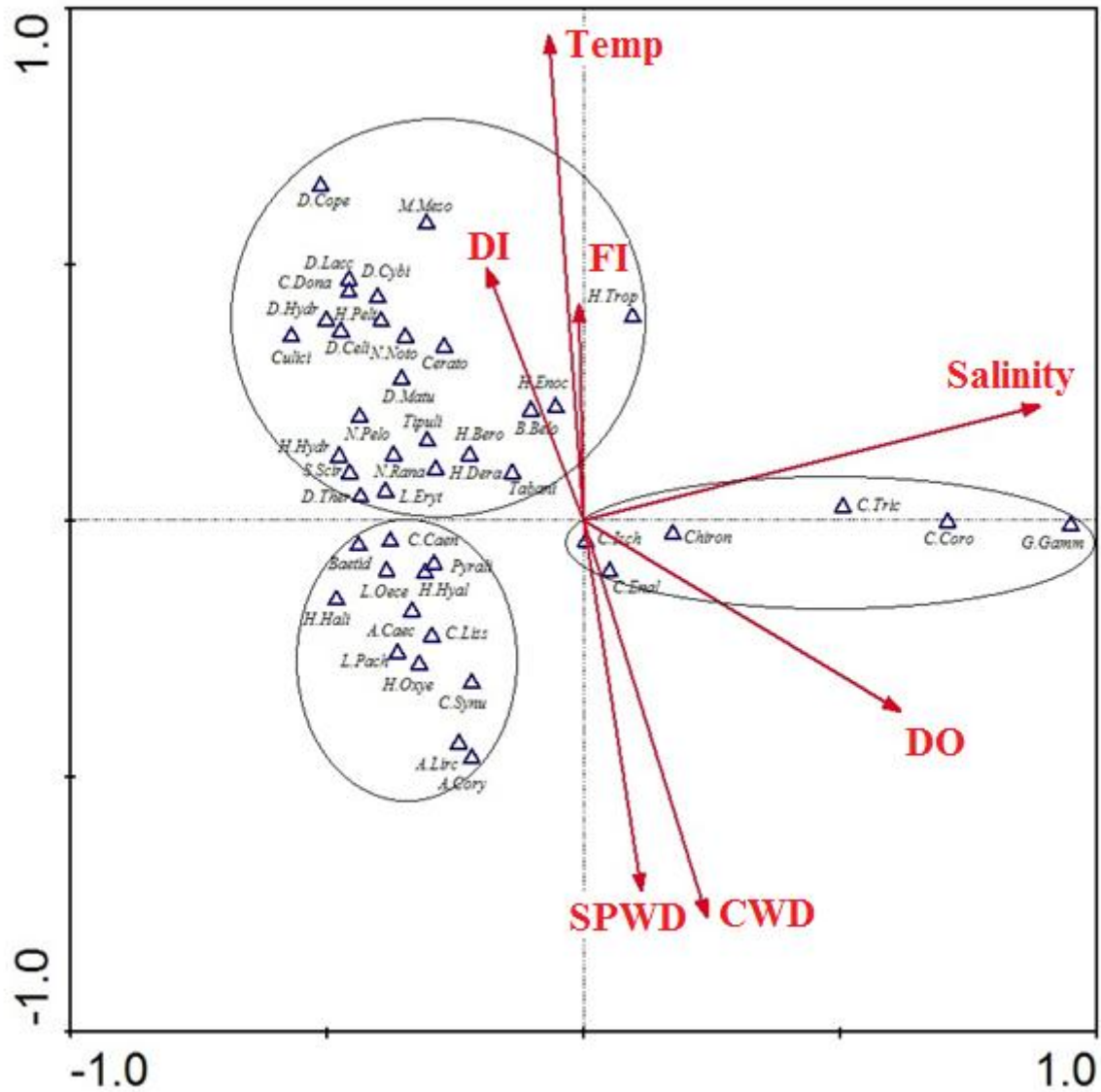


Fig. 4.8. Association of environmental variables and aquatic macroinvertebrate assemblage characteristics based on canonical correspondence analysis for all ponds in freshwater, brackish, and saline marsh from April 2009-May 2010. Environmental variables and taxa full names are listed in Table 4.1 and 4.3.

Functional Feeding Groups

Among marsh types, the density of all FFGs except predators was greater in freshwater PCPs and TCPs than brackish and saline ponds (scrapers: $F_{2,249}=21.78$, $p<0.01$; shredders: $F_{2,249}=37.57$, $p<0.01$; piercers: $F_{2,249}=49.52$, $p<0.01$; collectors: $F_{2,249}=20.37$, $p<0.01$; $F_{2,249}=1.39$, $p=0.26$, Fig. 4.9). Predator density in TCPs was higher in brackish and saline marsh than freshwater marsh (predators: $F_{2,123}=6.38$, $p<0.01$). Within a marsh type, piercers in brackish TCPs were higher than PCPs ($t=2.13$, $p=0.04$) and collectors in freshwater PCPs were greater than TCPs ($t=3.103$, $p<0.01$). Moreover, predator density in freshwater PCPs was higher than that of TCPs ($t=2.65$, $p=0.01$) but saline PCPs supported lower density than TCPs ($t=4.44$, $p<0.01$).

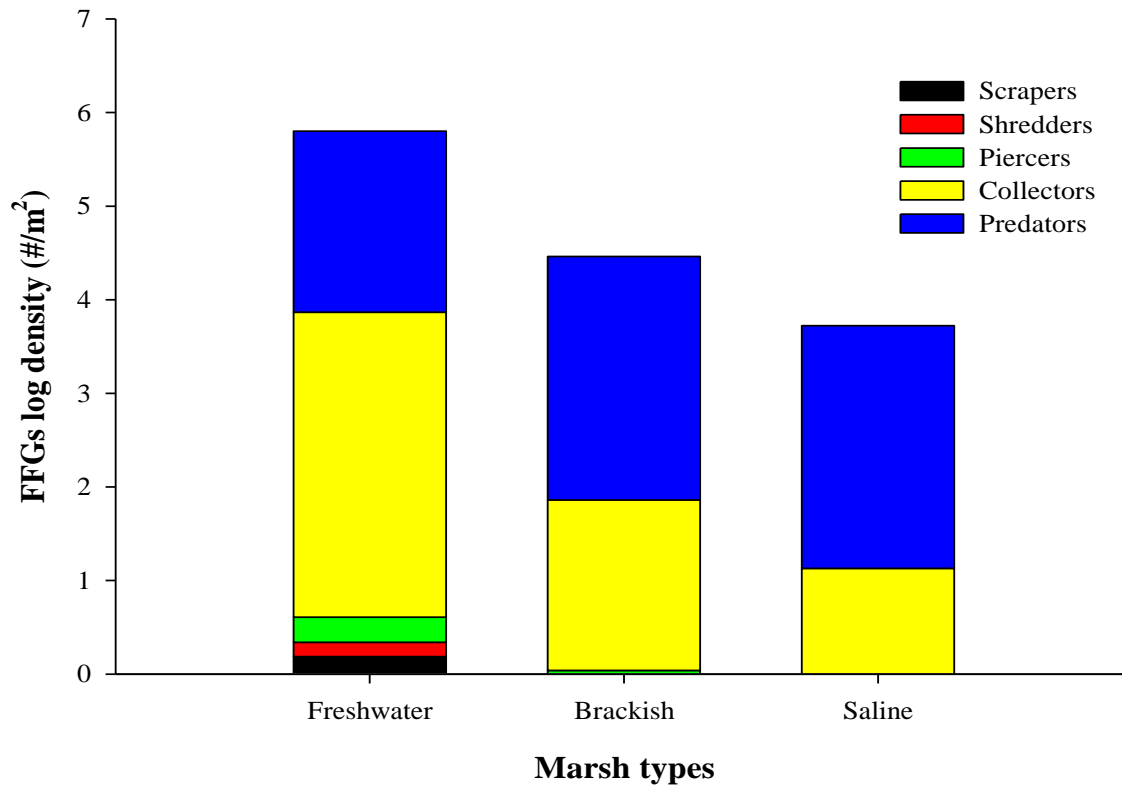


Fig. 4.9. Comparison of functional feeding group density $\ln(x+1)$ in different habitat and marsh types from April 2009 to May 2010.

DISCUSSION

Community Metrics and Environmental Variables

The results of this study indicate that macroinvertebrate assemblages strongly differ across a salinity gradient and may be a result of co-varying environmental variables as has been documented in several other studies (Williams and Williams 1998; Cognetti and Maltagliati 2000; Velasco et al. 2006; Boix et al. 2008). Relatively low salinity ponds in freshwater marsh showed the highest mean density, biomass, species richness, and Shannon-Wiener diversity but relatively high salinity ponds in saline marsh indicated the lowest values and indices. Species number also clearly declined along an increased salinity gradient among marsh types. However, responses to salinity varied among taxa and FFGs. The proportion of aquatic insect taxa positively increased with salinity, whereas the proportion of amphipods declined with salinity increases.

Even though salinity is a strong predictor of assemblage structure among marsh types, variation in CWD and DI, both measures of hydrologic connectivity, across marsh types was also important. Leigh and Sheldon (2009) suggested hydrologic connectivity can be considered the key driver of aquatic macroinvertebrate structural composition in aquatic systems. Other studies also illustrated that the duration of connectivity between ponds in floodplain systems affected aquatic invertebrate community density, species richness, Shannon-Wiener diversity, and community similarity (Ward 1998; Tockner et al. 1999; Amoros and Bornette 2002; Ward et al. 2002; Karaus 2004; Whiles and Goldowitz 2005). The data in this study only partially agree with these studies as the effects of connectivity were inconsistent. Shannon-Wiener diversity did not differ between pond types in any marsh. However, freshwater marsh PCPs had higher density and biomass than TCPs but saline marsh ponds showed an opposite pattern. In addition, the relationship of DI and community similarity within PCPs and TCPs varied according to marsh

type. Freshwater PCPs had higher community similarity than TCPs but saline marsh ponds showed an opposite pattern. Low similarity of TCPs in freshwater marsh was associated with relatively long DI (i.e., 25.6 ± 14.23 days per season) and the relatively high similarity in saline TCP type may be due to the high connectivity resulting from the tidal cycle.

Distribution of FFGs

Previous studies (Heino 2000; Hornung and Foote 2006) suggested that FFGs varied according to the vegetation types because of the effect of vegetation on food availability and predation rates. In this study, the density of scraper, shredders, piercers, and collectors (i.e., herbivorous groups) decreased with increased salinity but predator density increased. Restriction of herbivorous groups to the freshwater marsh seems to be partially a result of the salinity tolerance of individual species. For example, Horrigan et al. (2005; 2007) found that the maximum salinity tolerance of scrapers (e.g., Pyralidae), shredders (Scirtidae), piercers (Hydrophilidae), and collectors (Culicidae) was about 12 ppt. Despite the relatively high salinity tolerance of herbivorous groups, they were mostly observed in the mean salinity range from 0.3 to 0.5 ppt habitats (Horrigan et al. 2005), which is similar to the freshwater marsh (up to 1.7 ppt) in the present study. The distribution of SAVs relative to salinity may have a greater effect on the FFG distribution pattern. Freshwater ponds had greater SAV coverage than brackish and saline marsh ponds thus providing better habitat quality and supporting much greater herbivorous group densities than brackish and saline marsh ponds. Similarly, Diehl and Kornijow (1998) noted aquatic macroinvertebrates used macrophytes as a refuge from predators, a grazing substrate, and a food source. The SAV distribution patterns may have also affected the distribution of some predators. Several dominant predators (Odonata: Aeshnidae, Libellulidae) in freshwater marsh were not observed in brackish and saline ponds although they have a relatively high salinity

tolerance (i.e., between 5 to 14 ppt, Horrigan et al. 2005; Chapter II). Heino (2000) also found that macrophyte beds had a higher abundance of predaceous macroinvertebrates than did open water. However, the effect of SAV on predators was not consistent across marsh types. Overall density of predators had a positive relationship with increased salinity, which is opposite of the distribution pattern of SAV. The reason for this pattern is probably due to the noticeably increased density of one particular species (i.e., Corixidae *Trichocorixa*) in more saline habitats. Total density of Corixidae *Trichocorixa* in freshwater marsh (1069) was obviously lower than brackish (5,661) and saline (6,201) marshes. *Trichocorixa*, the dominant Corixidae in brackish and saline marshes in this study, is known to have high salinity tolerance (Gunter and Christmas 1959, Tones and Hammer 1975; Kelts 1979; Meutter et. al. 2010), but is apparently a poor competitor in freshwater environments. These findings suggest that SAV coverage is an important habitat component for herbivorous groups but also that no single environmental trait is responsible for macroinvertebrate distribution patterns across marsh types.

Individual Taxon Response

Clearly, FFG distribution patterns are a function of individual species responses to the environmental gradients. The variation in environmental variables across marsh types creates potentially stressful abiotic and biotic conditions that are unique to each marsh type. In freshwater marshes, low DO produces stressful conditions for many species. Dramatically fluctuating salinities in the brackish marsh and high salinity in the saline marsh provide the dominant stressors in these habitats. The dominant species in each habitat was able to adequately endure or thrive in these stressful habitats, but due to the uniqueness of the necessary adaptations to thrive in each habitat, no species dominated across all marsh and pond types.

Even among marsh and pond types, variation in life history traits and responses to environmental conditions were observed. For example, one of the non-dominant taxa groups in freshwater marsh (i.e., coleopterans: predaceous diving beetle Dytiscidae *Copelatus*, leaf beetle Chrysomelidae *Donacia*, Marsh Beetle Scirtidae *Scirtes*) was negatively associated with water depth but one of the dominant taxa groups (i.e., odonata: Darner Aeshnidae *Coryphaeschna*, skimmer Libellulidae *Pachydiplax*) was positively related with water depth. Coleopteran are known to possess physiological and behavioral mechanisms to survive desiccation during dry periods (e.g., Dytiscidae, Nilsson 1986) and these traits may allow them to use shallow water and avoid higher predator densities in deeper water. However, odonates may require a relatively longer hydroperiod for the full development of nymphs even though they appear in shallow water (Wissinger 1988; Smiley and Tessier 1998; Zimmer et al. 2001).

Individual species also responded strongly to the salinity gradient. Two species, water boatman Corixidae *Trichocorixa* and non-biting midge Chironomidae, were found in all marsh types and possess broad salinity tolerances (e.g., Corixidae *Trichocorixa*: up to 60 ppt, Stonedahl and Lattin 1986; Chironomidae: over 35 ppt, Velasco et al. 2006), but demonstrated opposite density patterns along the salinity gradients. Corixidae *Trichocorixa* increased with increasing salinity and Chironomidae decreased with increasing salinity. The highest density of Chironomidae (i.e., collector-gather) in freshwater marsh is not surprising because ponds in freshwater marsh provides greater food resources (i.e., SAV, Hornung and Foote 2006) than brackish (lesser SAV) and saline (no SAV) marsh ponds during the entire sampling period. Furthermore, the higher density of Corixidae *Trichocorixa* in brackish and saline ponds may be because it is a relatively small predator and may compete poorly with large and stronger macroinvertebrate predators in freshwater marshes.

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CHAPTER 5

GENERAL CONCLUSIONS

The goal of this dissertation was to determine relationships among hydrologic connectivity, environmental variables, and nekton and macroinvertebrate assemblages in Chenier Plain marshes with an underlying purpose of assessing prey community composition and prey availability for reintroduced Whooping Cranes. Because these systems are threatened by sea-level rise and coastal storm surges, I experimentally examined the salinity tolerance of dominant freshwater macroinvertebrates. I also assessed the effects of hydrologic connectivity on several environmental variables and their combined role in nekton and macroinvertebrate community structure, density, biomass, diversity, and community similarity among freshwater, brackish, and saline marsh ponds.

The experimental salinity study, found in Chapter II, indicated that increases in salinity could cause differential survival of dominant aquatic macroinvertebrates (i.e., *Procambarus clarkii* Girard, *Cambarellus puer* Hobbs, Libellulidae, Dytiscidae). While survival of all species was affected by increased salinity, upper and lower species-specific thresholds existed for each species. Consequently, effects of increased salinity, extended duration of exposure, and the interaction between salinity and prey availability on survival was clear by taxon, but the effect of prey availability was not obviously different. These findings provide information about salinity tolerances of dominant macroinvertebrates and may help managers better understand the impacts of natural events (e.g., storm surge) on potential prey items of Whooping Cranes.

In Chapter III, I assessed the effects of hydrologic connectivity on environmental variables and their combined effects on nekton communities. Environmental variables did not differ between pond types due to hydrologic connectivity, but differences did occur by marsh

type, and highlight systemic differences among Chenier plain marshes. Comparison of nekton community metrics (i.e., density, biomass, biodiversity, community similarity) indicated that assemblage structure seems to be affected by individual species responses to the salinity gradient as well as pond habitat attributes (i.e., SAV coverage, dissolved oxygen, hydrologic connectivity). These results are compatible with current concepts of community composition, whereby physiological thresholds related to environmental variables shape community structure at broad scales. In addition, the results indicate that PCPs have lower density and community similarity in saline marshes than TCPs. Thus, anthropogenic activities, such as marsh management and mosquito control ditches that convert TCPs to PCPs can potentially alter nekton community structure in saline marshes.

In Chapter IV, I evaluated the effects of hydrologic connectivity and environmental variables on macroinvertebrate communities. This study indicated that dominant environmental variables structuring macroinvertebrate communities differed across marsh types. Macroinvertebrate assemblages in brackish and saline ponds were affected by salinity. In freshwater ponds, dominant taxa (e.g., dragonfly) were positively associated with a water depth but non-dominant taxa were negatively related to water depth. Moreover, PCPs supported greater density, biomass, and community similarity than TCPs in freshwater marsh. The results of this study have also contributed to our knowledge of macroinvertebrate distributions. Evans et al. (1999) noted that a paucity of information exists on aquatic macroinvertebrates in freshwater marshes. This study has contributed both to our understanding of macroinvertebrate assemblages in coastal marshes as well as to our understanding of some of the important processes affecting these assemblages.

A clear understanding of the linkages 1) among abiotic disturbances, biological characteristics and survival (Chapter 2) and 2) among hydrologic connectivity, environmental variables, and nekton (Chapter 3) and aquatic macroinvertebrate (Chapter 4) assemblages enhances our understanding of habitat characteristics affecting aquatic organisms in coastal marshes. This information also provides a foundation for the development of foraging suitability models for the reintroduced Whooping Crane and how foraging suitability varies across environmental gradients.

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VITA

Sung-Ryong Kang was born in September 1977, in Busan, South Korea. He is the son of Jong-Hwa Kang and Yeon-Hyo Lee and brother of Min-Sook and Kyung-Hee Kang. He graduated from Busan Jin High School in 1996. Sung-Ryong attended the Dong-A University and graduated in 2003 with majors in biological science.

In 2003, Sung-Ryong entered the graduate program in evolution and environmental ecology at Dong-A University. He studied the habitat selection, foraging strategy, and energy intake of barn swallows. Sung-Ryong graduated with a Master of Science degree in 2005, while working as a researcher at Basic Science Research Institute in Dong-A University. In 2006, Sung-Ryong accepted a position as a project specialist in Natural Ecosystem Management Institute, South Korea.

He entered the doctoral program in the School of Renewable Natural Resources as a full-time student in August 2007 and will graduate in December 2011. Sung-Ryong has studied aquatic macroinvertebrate and nekton assemblage as Whooping Crane prey community in coastal marsh systems. He will get a position with the Louisiana Department of Wildlife and Fisheries, where he will research Whooping Crane breeding and wintering habitats condition for Whooping Crane Reintroduction Program.