2002

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Recommended Citation

Bolduc, Francois, "Effects of structural marsh management and salinity on sediments, hydrology, invertebrates, and waterbirds in marsh ponds during winter on the Gulf Coast Chenier Plain" (2002). *LSU Doctoral Dissertations*. 3866.
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EFFECTS OF STRUCTURAL MARSH MANAGEMENT AND SALINITY ON SEDIMENTS, HYDROLOGY, INVERTEBRATES, AND WATERBIRDS IN MARSH PONDS DURING WINTER ON THE GULF COAST CHENIER PLAIN

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 in Philosophy

in

The School of Renewable Natural Resources

by
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M.S., McGill University, 1998
August 2002

TABLE OF CONTENTS

ABSTRACT

Compositions of wintering waterbird communities are dependent upon food accessibility (via water depth), biomasses and sizes of their invertebrate prey, which in turn are influenced by the hydrology and sediments of wetland habitats. The hydrology and sediments of marsh ponds on the Gulf Coast Chenier Plain probably are affected by structural marsh management (levees, water control structures and impoundments; SMM) and salinity; therefore, SMM and salinity ultimately may affect wintering waterbird communities.

Accordingly, I measured sediment and hydrologic variables, biomasses and sizes of common aquatic invertebrates, and densities of common wintering waterbird species in ponds of impounded freshwater (IF), impounded oligohaline (IO), impounded mesohaline (IM), and unimpounded mesohaline (UM) marshes during winters 1997-1998 to 1999-2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana.

SMM affected sediment and hydrologic variables, which negatively affected biomasses of Nematoda and secondarily increased those of Ostracoda. However, few waterbird species possess the capacity to capture these small prey; consequently, I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities between ponds of IM and UM marshes. Comparisons of waterbird densities provided inconsistent results with this prediction because some shorebird and waterfowl species that feed heavily on invertebrates were those that primarily differentiated waterbird communities between ponds of IM and UM marshes.

My comparison of IF, IO, and IM marsh ponds indicated that, except for salinity, they differed little in sediment and hydrologic variables. Accordingly, these marshes only differed in biomass of Oligochaeta; consequently, I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities among ponds of IF, IO, and IM marshes. Accordingly, their waterbird communities primarily differed in densities of waterbird species that feed on vegetation.

In conclusion, some waterbird species exclusively used ponds of UM marshes rather than ponds of IM marshes, and most species had highest densities in IF marshes when water depth favored those that maximized their densities. Consequently, My results suggest that marsh managers should focus on the preservation of UM and IF marshes for the conservation of wintering waterbird populations on the Gulf Coast Chenier Plain.

CHAPTER 1

INTRODUCTION

Louisiana encloses 41 % of all coastal marshes of the United States, and is composed of the Deltaic Plain in the southeast and the Chenier Plain in the southwest (Turner 1990). The Gulf Coast Chenier Plain always has been regarded as prime habitat for wintering waterfowl. However, wintering waterfowl populations declined during the early 20th Century, which coincided with many changes that occurred in Gulf Coast Chenier Plain marshes: dredging of north-south waterways, occurrence of large-scale muskrat eat-outs, and a severe drought that occurred in the early 1950s. These events apparently facilitated saltwater intrusion and caused a large marsh vegetation die-off at the junction of freshwater and oligohaline marshes (Wicker et al. 1983). These simultaneous changes in marshes and waterfowl populations convinced wildlife managers that active management was necessary to retain and improve remaining waterfowl habitats. Consequently, starting during the mid-1950s, structural marsh management (levees, water control structures and impoundments; SMM) was implemented in numerous marshes with objectives of revegetating open water areas that had formed, stopping saltwater intrusion, and increasing productivity of waterfowl food plants (Wicker et al. 1983). SSM now commonly is practiced throughout the Gulf Coast Chenier Plain (Day et al. 1990).

Wildlife managers considered that saltwater intrusion was the primary threat to the integrity of marshes on the Gulf Coast Chenier Plain, because freshwater marshes seemingly were the preferred habitat of wintering waterfowl (Palmisano 1972, Chabreck et al. 1974). However, researchers recently demonstrated that saltwater intrusion was not the primary agent of marsh loss in coastal Louisiana (Turner 1997), and oligohaline marshes apparently have expanded at the expense of freshwater and mesohaline marshes during the last 60 years on the Chenier Plain (Visser et al. 2000). Marshes on the Gulf Coast Chenier Plain are divided into 3 categories of salinity based on the Venice system of estuarine classification (Bulger et al. 1993, Visser et al. 2000): (1)

freshwater (salinity <0.5 ‰), (2) oligohaline (salinity between 0.5 ‰ and 5.0 ‰), and (3) mesohaline (salinity between 5.0 ‰ and 18.0 ‰). These 3 marsh types have distinctive plant communities (Visser et al. 2000).

Management objectives of SMM that initially were to improve habitats for wintering waterfowl through control of water levels and salinities to influence plant communities, and subsequently shifted toward stopping marsh loss and protecting marsh functions (Cowan et al. 1988). An important function of Gulf Coast Chenier Plain marshes is to provide habitats for many nesting, wintering, and migrating shorebird and wading bird species (Helmers 1992, Mikuska et al. 1998). However, little information is available on the influence of SMM and salinity on wintering waterbirds other than waterfowl.

Studies that compared waterbirds among various wetlands often provided equivocal results because of the confounding effect of variation in water depths (Chabreck et al. 1974, Spiller and Chabreck 1975, Epstein and Joyner 1988, Weber and Haig 1996). Water depth greatly influences waterbirds because they have specific morphological adaptations to exploit specific water depths and foods (Nudds and Bowlby 1984, Zwarts and Wanink 1984). Thus, researchers that compare waterbirds between impounded and reference marshes or among marshes differing in salinity must adjust their results for variation in water depth to ensure that results present factual differences among marsh types.

Food availability is an important factor influencing bird communities during winter. Accordingly, objectives of SMM were to increase the growth of plants that waterfowl consume (Jemison and Chabreck 1962). However, recent research on waterfowl food habits indicates that aquatic invertebrates sometimes composed a large share of the diet of wintering waterfowl (e.g., Afton et al. 1991, Euliss et al. 1991, Thompson et al. 1992, Batzer et al. 1993). Moreover, other waterbirds also forage largely on aquatic invertebrates (Skagen and Oman 1996). There is little information available on effects of SMM and salinity on aquatic invertebrates inhabiting marsh ponds of the Gulf Coast Chenier Plain, which may influence compositions of wintering waterbirds communities.

Compositions of aquatic invertebrate communities highly depend on the characteristics of hydrology and sediments (Little 2000). Little information is available on effects of SMM and salinity on marsh hydrology and sediments, although they ultimately may affect wintering waterbird communities by affecting aquatic invertebrate communities.

I examined effects of SMM and salinity on sediments, hydrology, invertebrates, and waterbirds in marsh ponds during winter on the Gulf Coast Chenier Plain. Specifically, I compared (1) sediment variables, (2) hydrologic variables, (3) biomasses and sizes of aquatic invertebrates, and (4) densities of wintering waterbirds between ponds of impounded and unimpounded mesohaline marshes, and among ponds of impounded freshwater, oligohaline and mesohaline marshes during winters 1997-1998 to 1999-2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. Finally, I developed a methodology to correct waterbird densities for variation in water depth that provides unbiased comparisons of wetlands of varying water depths.

CHAPTER 2

SEDIMENTS IN MARSH PONDS ON THE GULF COAST CHENIER PLAIN: EFFECTS OF STRUCTURAL MARSH MANAGEMENT AND SALINITY

INTRODUCTION

Sediments of coastal marshes consist of decaying organic matter and fine-grained mineral particles (Mitsch and Gosselink 1993). Physical characteristics of marsh sediments affect the environment of plant and animal communities, especially benthic invertebrates. For example, abundant interstitial space among sediment particles provides habitat for meiofauna (0.063 - 0.5 mm) (Rhoads 1974). Also, physical support for large epifaunal invertebrates (living on the sediment surface) is limited on soft sediments (Rhoads 1974). Low penetration of oxygen in sediments decreases the abundance of infaunal (living in the sediments) invertebrates (Rhoads 1974). The organic content of sediments affects the production of bacteria and algae that invertebrates consume (Benke 1984, Batzer and Wissinger 1996). The amount of undecomposed vegetation in sediments also affects the structural complexity of invertebrate habitats (Minshall 1984). Thus, physical characteristics of marsh sediments are important factors influencing compositions of benthic invertebrate communities.

Benthic invertebrate communities of ponds (flooded zone of marsh associated with little emergent vegetation) have important functions in the marsh ecosystem during winter. Ponds are the principal area used by many wintering waterbirds, which feed to varying degrees on benthic invertebrates. For example, shorebirds feed almost exclusively on invertebrates (Skagen and Oman 1996), whereas consumption of invertebrates varies widely among waterfowl species (Afton et al. 1991, Euliss et al. 1991, Thompson et al. 1992, Batzer et al. 1993), and generally increases at the end of winter (Krapu and Reinecke 1992). Large wading birds also forage on aquatic invertebrates during winter (Martin and Hamilton 1985). Most waterbirds are adapted for capturing prey of a specific size range or minimal size, and feed at different depths in the water or sediments (Baker 1979, Poysa 1983, Nudds and Bowlby 1984, Zwarts and Wanink 1984); therefore, compositions of the waterbird communities probably are related to compositions of the benthic invertebrate communities in marsh ponds. Thus, physical characteristics of pond sediments during winter ultimately influence waterbird communities of coastal marshes.

Sediments in marsh ponds on the Gulf Coast Chenier Plain probably have changed considerably during last century. Dredging of north-south waterways, occurrence of large-scale muskrat eat-outs, and a severe drought that occurred in the early 1950s, apparently facilitated saltwater intrusion and caused a large marsh vegetation die-off at the junction of the freshwater and oligohaline marshes (Wicker et al. 1983). Consequently, starting during the mid-1950s, numerous marshes were managed using structural marsh management (levees, water control structure and impoundments; SMM) with objectives of revegetating open water areas that had formed, stopping saltwater intrusion, and increasing productivity of waterfowl food plants (Wicker et al. 1983). Drawdowns sometimes occur in marsh impoundments during spring or early summer, which produce oxidation and decomposition of organic matter and encourage growth of seedlings and perennials (Kadlec 1962). Impoundments are reflooded during fall and winter to attract waterfowl (Kadlec 1962). SSM now commonly is practiced throughout the Gulf Coast Chenier Plain (Day et al. 1990). Thus, sediments of marsh ponds of the Gulf Coast Chenier Plain potentially have been affected physically and biologically by SMM during last century.

Comparisons of sediments between impounded and unimpounded marshes indicate that SMM prevents the export and import of sediments between the marsh and the surrounding canals because levees restrict tidal flows (Boumans and Day 1994). Also, SMM decreases sediment deposition (Reed and Foote 1997), belowground plant biomass (Gabrey and Afton 2001), marsh accretion (Cahoon 1994), and soil bulk density (Cahoon 1994), whereas it increases organic matter in sediments (Cahoon 1994). Drawdowns in impounded marshes are believed to consolidate marsh sediments (Kadlec 1962); oxidized organic matter and drying mineral soil together produce sediments without capillary fringes that have hydrophobic behavior (Richardson et al. 2001). However, studies of effects of drawdowns on sediments have not provided strong evidence of consolidation (Kadlec 1986).

Those previous studies that examined effects of SMM on sediments generally have focused on the emergent plant zone (zone of marsh occasionally flooded and associated with dense emergent vegetation), whereas effects of SMM on marsh ponds have not been studied specifically. Ponds and the emergent plant zone within a marsh may differ in sediment characteristics because of lower amounts of decaying vegetation and greater anaerobic conditions produced by regular flooding in ponds. Assuming that effects of SMM on sediments in marsh ponds generally are similar to that reported for the emergent plant zone, I predicted that, due to SMM with drawdowns, (1) the carbon content of pond sediments increases because impoundments prevent the export of organic matter; (2) the C:N ratio of pond sediments increases because of the greater primary production; (3) the hardness of pond sediments increases because drawdowns promote cementing of drying minerals with the organic matter; (4) particle size increases due to consolidation of pond sediments; and (5) oxygen penetration in pond sediments decreases due to their consolidation.

Marshes of the Gulf Coast Chenier Plain are divided into 3 categories of salinity based on the Venice system of estuarine classification (Bulger et al. 1993, Visser et al. 2000): (1) freshwater (salinity <0.5 ‰), (2) oligohaline (salinity between 0.5 ‰ and 5.0 ‰), and (3) mesohaline (salinity between 5.0 ‰ and 18.0 ‰). Oligohaline marshes apparently have expanded at the expense of freshwater and mesohaline marshes during the last 60 years (Visser et al. 2000). Characteristics of pond sediments have not been studied within these 3 marsh categories. Most of these marshes have a similar hydrology (except for mesohaline marshes that still are connected directly to tidal bayous) because the drainage of all marshes was altered intentionally or unintentionally due to the numerous roads, irrigation canals, levees, and waterways that have been built in this area during last century (Turner 1990); thus, most of these marshes are impounded to a certain degree. Primary productivity in freshwater marshes is believed to be higher than in the other 2 marsh types (Mitsch and Gosselink 1993), and freshwater marshes have the lowest inter-annual variability in productivity (Whigham and Simpson 1992). The latter suggests that freshwater marshes generate a greater amount of decaying vegetation that accumulates into the sediments than do oligohaline and mesohaline marshes. Accordingly, I predicted that pond sediments of impounded freshwater marshes should have higher carbon content than those of impounded oligohaline and mesohaline marshes, whereas sediment hardness, particle size, oxygen penetration in sediments, and C:N ratio (assuming similar decomposition processes among marsh types) in ponds should be similar among these marsh types.

I tested the above predictions by comparing sediment variables (carbon content, C:N ratio, hardness, particle size, and oxygen penetration in sediments) of ponds (1) between impounded and unimpounded mesohaline marshes, and (2) among impounded freshwater, oligohaline and mesohaline marshes on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana.

METHODS

STUDY AREA

The Gulf Coast Chenier Plain is bounded by East Bay in Texas and Vermillion Bay in Louisiana (Gosselink et al. 1979). The Chenier Plain was formed by sediments from the Mississippi River that were transported by the westward current in the Gulf of Mexico (Byrne et al. 1959). Periods of low sediment deposition, that occurred when the Mississippi Delta changed location, formed a series of stranded beach ridges composed of sand and shells separated by mud flats where marshes developed (Byrne et al. 1959). Chenier refers to the French word *cheniѐre*, which characterizes a forest or area where oaks (*Quercus* spp.) represent the dominant tree species.

I chose Rockefeller State Wildlife Refuge (RSWR; headquarters coordinates: 29˚ 40’ 30” N, 92˚ 48’ 45” W), near Grand Chenier, in southwestern Louisiana as a representative area of the Gulf Coast Chenier Plain. RSWR comprises 30,700 ha, and contains 17 impoundments (200 to >4,000 ha each, Wicker et al. 1983). Most impoundments on RSWR were constructed during the late 1950s, and are separated by a network of canals that surround the levees (Wicker et al. 1983). Impoundments on RSWR comprise marsh types of various salinities characteristic of the Gulf Coast Chenier Plain, i.e., freshwater, oligohaline, and mesohaline marshes (Visser et al. 2000). RSWR also encloses a large area of unimpounded mesohaline marshes (11,700 ha).

SAMPLING DESIGN

From January through March 2000, I sampled the 4 marsh types of RSWR: (1) 3 freshwater impoundments (IF) (units 8,10, and 13), (2) 3 oligohaline impoundments (IO) (units 3, 4, and 15), (3) 2 mesohaline impoundments (IM) (units 5 and Price Lake), and (4) 2 hydrographic basins of unimpounded mesohaline marshes (UM) (East Little Constance Bayou basin and Rollover Lake/Flat Lake basin). In each impoundment and hydrographic basin, I initially selected 4 to 8 ponds from those that were accessible directly from levees or with a small flat boat when necessary (impounded marshes), or that access would not be prevented at low tides using a small flat boat (UM marshes). I made this initial selection to minimize time spent commuting among sites and disturbance to waterbirds, and to ensure access to study ponds at all times. The number of ponds selected depended on those available accordingly to the above selection criteria. Subsequently, I randomly selected 3 ponds from those initially identified in each impoundment or hydrographic basin. Because of the presence of numerous small ponds (<2 ha), but also a few very large ones (>20 ha) in IM and UM marshes, I chose 1 large pond and 2 small ponds in each of these marsh types. I randomly selected 3 sampling stations in each pond. I determined locations of sampling stations using a table of random numbers to select distances and angles from an observation blind that fell within the pond area, up to a distance of 200 meters from the blind (this maximum distance was important for a concurrent waterbird study).

Between January and March 2000, I measured sediment hardness within each pond with a S-170 pocket soil penetrometer (Boart Longyear, Co., Stone Mountain, Georgia) that was adapted for measurements of soft sediments by attaching a 10 cm diameter vinyl disk at its end. This measurement was an index of the amount of pressure the soil could absorb when the penetrometer was pushed down by 2 cm.

I determined the silt-clay fraction (to describe particle size) by sampling pond sediments with a 5-cm corer sunk to a depth of 10 cm. Sediments were homogenized with a kitchen blender (model 4142, Sunbeam Products, Inc, Boca Raton, Florida), oven-dried at 100 °C for 24 hours, and then weighed (±0.01 g). Following this procedure, I re-hydrated sediments, homogenized them again, and sieved them through a 63 µm mesh sieve to remove the silt-clay fraction. Sediments left in the sieve were oven-dried, and weighed again. The difference in sediment dry-weight before and after sieving divided by the total sediment dry-weight used (* 100) corresponded to the silt-clay fraction in sediments (Buchanan 1984).

I sampled carbon and nitrogen contents of sediments by taking a few grams from homogenized sediments used for the determination of the silt-clay fraction. I preserved samples by freezing and used a CHN analyzer to determine their carbon and nitrogen content and their ratio (C:N) (Buchanan 1984). Finally, I placed metal rods in sediments for a month at random stations within each pond to estimate O_2 penetration. O_2 penetration corresponded to depths where rust stopped along the metal rods (J. W. Fleeger, pers. comm.).

STATISTICAL ANALYSIS

I compared sediment variables between IM and UM marsh ponds and among IF, IM and IO marsh ponds within a single multivariate analysis of variance (MANOVA). Response variables for this analysis were hardness, C:N ratio, carbon content, silt-clay fraction, and O_2 penetration. Explanatory variables included in the model were (1) marsh type (fixed), (2) impoundment within marsh type (random), and (3) pond within impoundment and marsh type (random). I performed separate contrasts to test my 2 *a priori* comparisons (UM vs. IM, and IF vs. IO and IM), with respective contrast equations (0, 1, 0, –1), and (1, –0.5, –0.5, 0) for the corresponding marsh types equation order (IF, IM, IO, UM). For these *a priori* comparisons, I used an error matrix based on the impoundment within marsh type random effect.

I used Wilk's lambda statistic to compute *F*-ratios of MANOVA contrasts (PROC GLM, SAS Institute, Inc. 1999). I considered *P*-values less than 0.05 as significant and estimated effect size (proportion of the variance in response variables attributable to the variance existing in explanatory variables) to avoid declaring significant trivial differences in variable mean responses (effect size = Wilk's lambda – 1, Tabachnick and Fidell 1989). Finally, I computed canonical correlations and standardized canonical coefficients from MANOVA contrasts to investigate the contribution of the various sediment variables to differences among ponds of various marsh types. Because *r* values ≤0.3 correspond to <10% variance overlap between variables (Tabachnick and Fidell 1989), I only interpreted *r* values >0.3. I assessed normality of response variables by computing skewness and kurtosis values (Tabachnick and Fidell 1989), and accordingly transformed O_2 penetration (inverse [x+1]). Note that transformed O_2 penetration data were correlated negatively with the untransformed data (e.g., the inverse (x+1) of a O_2 penetration of 5 is 0.17, 10 is 0.09, etc.). I assessed multivariate normality and homoscedasticity by examining whether model residuals were distributed randomly (Tabachnick and Fidell 1989). I present results as least-square means ± 95% confidence intervals (backtransformed for O_2 penetration) unless notified otherwise. I performed all statistical analyses using SAS 8.2 (SAS Institute, Inc. 1999).

RESULTS

COMPARISON OF IM AND UM MARSH PONDS

My *a priori* MANOVA contrast indicated that the 5 sediment response variables differed between ponds of UM and IM marshes and produced a large effect size between marsh types (Table 2.1). All sediment variables had high standardized canonical coefficients, indicating that they all were important in differentiating between ponds of these 2 marsh types; carbon content and silt-clay fraction were the most important differentiating variables (Table 2.2). There was twice as much carbon in IM than in UM marsh ponds, and almost all sediment particles in UM marsh ponds were of silt-clay size, compared to only half of them in IM marsh ponds (Fig. 2.1). C:N ratios did not vary greatly between UM and IM marsh ponds (C:N = 10.6 in UM marsh ponds and 11.9 in IM marsh ponds), but sediment hardness in IM was 2 times greater than that in UM marsh ponds. Oxygen barely infiltrated sediments further than the sediment-water interface in IM marsh ponds (low O_2 penetration), whereas oxygen penetrated several centimeters down in sediments of UM marsh ponds (Fig. 2.1). Sediment hardness, C:N ratio and carbon content were correlated positively with the first canonical variate, whereas silt-clay fraction and O_2 penetration were negatively correlated with the first canonical variate (Table 2.2). These results indicate that the silt-clay fraction and O_2 penetration were highest and carbon content, C:N ratio and sediment hardness were lowest in UM marsh ponds (Fig. 2.1).

Table 2.1. Summary of *a priori* MANOVA contrasts testing for differences in sediment variables (carbon content, C:N ratio, hardness, oxygen penetration, silt-clay fraction) between ponds of impounded and unimpounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline, and mesohaline marshes (IF vs. IO and IM) on the Gulf Coast Chenier Plain.

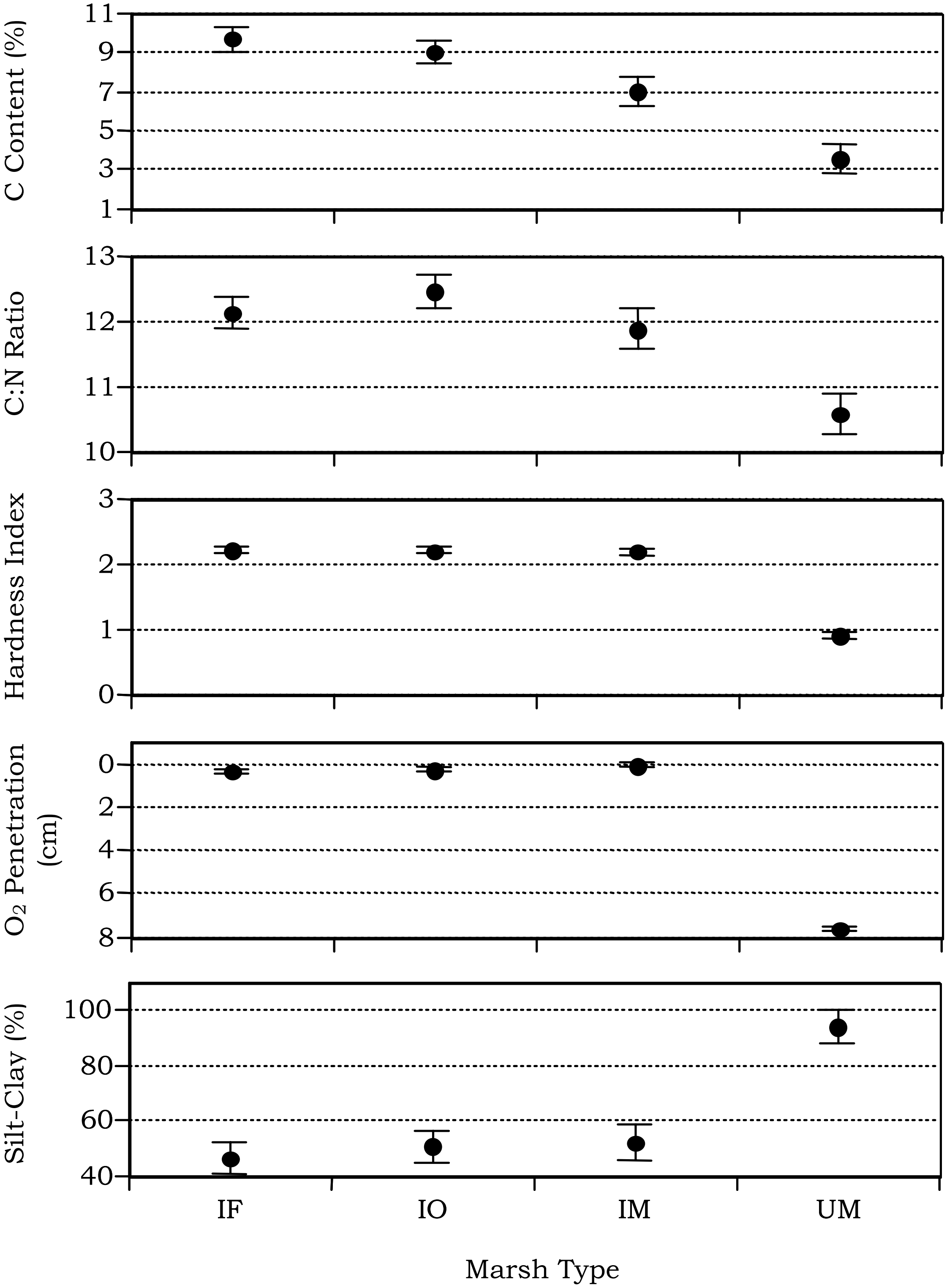
Contrast	Wilk's lambda	*F*	Num df	Den df	Pr. > *F*	Effect size (η^2)
UM vs. IM	0.0012	324.75	5	2	0.0031	0.999
IF vs. IO and IM	0.0100	39.62	5	2	0.0248	0.990

Table 2.2. Canonical correlations (CC) and standardized canonical coefficients (SCC) from MANOVA contrasts testing for a difference in sediment variables (carbon content, C:N ratio, hardness, oxygen penetration, silt-clay fraction) between ponds of impounded and unimpounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline, and mesohaline marshes (IF vs. IO and IM) on the Gulf Coast Chenier Plain.

Variable	UM vs. IM		IF vs. IO and IM	
	CC	SCC	CC	SCC
Hardness	0.737	10.26	0.729	10.25
Carbon/nitrogen	0.440	- 11.53	0.430	- 11.85
Carbon content	0.699	22.53	0.699	22.86
Silt-clay fraction	- 0.409	15.00	- 0.403	15.17
O_2 penetration	(-) 0.662 [a]	9.83	(-) 0.651 [a]	9.67

[a] Transformed (inverse [x+1]) O_2 penetration was correlated negatively with untransformed data (see Methods).

Figure 2.1. Mean values (least square means ± 95% confidence intervals) of sediment variables (carbon content, C:N ratio, hardness, oxygen penetration [O_2 penetration], silt-clay fraction) in ponds of impounded freshwater (IF), oligohaline (IO), and mesohaline (IM) marshes, and of unimpounded mesohaline marshes (UM) on the Gulf Coast Chenier Plain. Note that C = carbon; N = nitrogen; sediment hardness increases with the hardness index.


C Content (%)
11
9
7
5
3
1
C:N Ratio
13
12
11
10
Hardness Index
3
2
1
0
O$_2$ Penetration (cm)
0
2
4
6
8
Silt-Clay (%)
100
80
60
40
IF
IO
IM
UM
Marsh Type

COMPARISON OF IF WITH IO AND IM MARSH PONDS

My *a priori* MANOVA contrast indicated that the 5 sediment response variables differed between ponds of IF marshes and those of the other 2 marsh types, and produced a large effect size between marsh types (Table 2.1). All variables had high standardized canonical coefficients, indicating that all of them contributed in differentiating IF from IO and IM marsh ponds (Table 2.2). Carbon content and silt-clay fraction variables had highest canonical coefficients (Table 2.2). Mean differences in carbon content were 2.7% and 0.7% between IF and IM, and between IF and IO marsh ponds, respectively (Fig. 2.1). Mean differences were small among these marsh types for all other response variables (Fig. 2.1), but large enough to observe a significant difference within the multivariate space defined by these variables (Table 2.1). Sediment hardness, C:N ratio and carbon content were positively correlated with the first canonical variate, whereas silt-clay fraction and O_2 penetration were negatively correlated to this first canonical variate (Table 2.2). These results indicate that the silt-clay fraction and O_2 penetration were lowest and carbon content, C:N ratio, and sediment hardness were highest in ponds of IF marshes compared to ponds of the other 2 marsh types.

DISCUSSION

COMPARISON OF IM AND UM MARSH PONDS

My results indicated that SMM, with spring-summer drawdowns, generally affected pond sediments similarly to that previously described for sediments of the emergent plant zone. Carbon content increased in IM marsh ponds (Fig. 2.1), probably because SMM inhibited exportation of the organic matter (Boumans and Day 1994, Cahoon 1994). Also, drawdowns probably increased the rate of oxidation and decomposition of organic matter (Kadlec 1962), which results in the consolidation of organic matter with the drying mineral soil particles. Consequently, sediments became harder, oxygen penetrated less deeply in sediments, and particle size increased due to the cementing of the organic matter with the drying mineral soil particles. Drawdowns periods sometimes last for several weeks at RSWR because of the rareness of rainfall during the summer (Tom Hess, pers. comm.). Such long dry periods probably affect greatly physical characteristics of pond sediments. Also, pond sediments probably have greater consolidation during summer than during winter because of intentional reflooding of impoundments and more frequent rainfall during fall and winter (Keim et al. 1995).

Although my results indicated that sediments of ponds and those of the emergent plant zone generally are affected similarly by SMM, there were large differences in levels of certain sediment variables measured between ponds and the emergent plant zone. I estimated a percent carbon content of 7.04% ± 0.8 in IM marsh ponds, and 3.56% ± 0.8 in UM marsh ponds (Fig. 2.1), whereas Foret (1997) reported percent carbon content >20% in the first 10 cm of sediments in the emergent plant zone of impounded and unimpounded marshes on RSWR. Furthermore, in both IM and UM marsh ponds, carbon content of sediments was 2 times lower than those under the root zone of emergent plants (>20 cm); about 15% in impounded marshes, and 8% in unimpounded marshes (Foret 1997). C:N ratios of pond sediments were slightly higher than those of microbial fauna decomposing the decaying vegetation (about 6, Swift et al. 1979), which indicates that organic matter is being decomposed. Also, organic matter in pond sediments seemingly is more decomposed than that in the emergent plant zone of marshes at RSWR, where Foret (2001) measured C:N ratios between 17 and 32 in the top 10 cm of sediments. In conclusion, my results in conjunction with those of Foret (1997, 2001) indicate that sediments of ponds and the emergent plant zone differ greatly in their organic composition.

COMPARISON OF IF WITH IO AND IM MARSH PONDS

I found that all sediment variables differed statistically among IF, IO, and IM marsh ponds. However, mean values of individual sediment variables generally were comparable among these marsh types (Fig. 2.1), which suggests that pond sediments of all impounded marshes were affected similarly by SMM. Mean values of individual sediment variables also had small 95% confidence intervals, which suggests that the response of sediments to SMM also was very similar within a marsh type. Thus, I conclude that differences in sediments were small among ponds of these marsh types, but differences detected were very consistent. Carbon content was the primary variable differentiating pond sediments of IF, IO, and IM marshes, and as predicted, was highest in IF marsh ponds. IF marsh ponds probably exhibited greater carbon content than did IO and IM marsh ponds because of the greater production of freshwater marshes than that of saline marshes (Mitsch and Gosselink 1993).

MANAGEMENT IMPLICATIONS

Changes in physical properties of pond sediments, due to SMM and spring-summer drawdowns, probably affect faunal communities of the marsh. Sediment hardness, O_2 penetration, and particle size particularly affect benthic epifaunal (living on the sediment surface) and infaunal (living in the sediments) invertebrates. Hard sediments provide physical support to epifaunal invertebrates (Rhoads 1974). Invertebrates that live in the oxygen-depleted zone of sediments must respire using anaerobic processes or provide their own oxygen through blood pigments or ventilated burrows (Rhoads 1974). Particle size determines how water and oxygen penetrate sediments and the interstitial space available to meiofauna (0.063 – 0.5 mm) (Little 2000). These 3 sediment variables together determine sediment porosity; soft unconsolidated sediments behave like fluids, provide little support and water and oxygen penetrate them easily, whereas compacted sediments behave like solids and provide support but little oxygen and space under the surface (Little 2000).

Ponds of impounded marshes have (1) harder sediments, (2) larger particle size, (3) lower oxygen levels, and (4) higher carbon content and C:N ratio than do ponds of unimpounded marshes. These changes should (1) promote populations of epifaunal macroinvertebrates (Rhoads 1974), and (2) negatively affect infaunal abundance (Rhoads 1974). I am unaware of any studies that compared invertebrate communities between impounded and unimpounded marshes.

An increase in epifaunal invertebrates may attract larger populations of waterbirds that pick their prey on the sediment surface, whereas a reduction in infaunal invertebrates may negatively affect waterbirds that filter or probe sediments to obtain their food (Nudds and bowlby 1984, Zwarts and Wanink 1984, Skogen and Oman 1996). Results of previous studies examining effects of SMM on waterbirds suggest that food accessibility (via water depth) also is an important factor influencing their abundance (Chabreck et al. 1974, Spiller and Chabreck

1975, Epstein and Joyner 1988, Weber and Haig 1996), probably because waterbirds have morphological adaptations to exploit specific water depth ranges (Baker 1979, Poysa 1983). Thus, further research is needed to investigate effects of SMM on marsh hydrology and communities of benthic invertebrates and wintering waterbirds to fully understand the ecological implications of SMM.

CHAPTER 3

HYDROLOGIC VARIABLES IN MARSH PONDS DURING WINTER ON THE GULF COAST CHENIER PLAIN: EFFECTS OF STRUCTURAL MARSH MANAGEMENT AND SALINITY

INTRODUCTION

The hydrology of coastal marshes is characterized by wide fluctuations in water levels, dissolved oxygen, salinity, and temperature (Mitsch and Gosselink 1993). Turbidity also varies greatly in marshes due to hydraulic turbulences caused by wind and tides (Oertel and Dunstan 1981, Robinson et al. 2000). Accordingly, waterbirds and their aquatic invertebrate prey that inhabit coastal marsh ponds (flooded zone of marsh associated with little emergent vegetation) have a wide array of physiological and morphological adaptations to fluctuating hydrologic conditions. For example, some benthic invertebrates possess blood pigments to overcome periods of low oxygen availability (Rhoads 1974). Mosquito larvae (*Culex* spp.) have a differential growth of papillae depending on the salinity of their environment (Willmer et al. 2000). Many marsh invertebrates feed on algae (Murkin and Ross 2000), and turbidity reduces light penetration in the water column and consequently algal and invertebrate production (Murkin and Ross 2000, Robinson et al. 2000). Non-diving waterbirds have a variety of morphological differences in bill length, bill lamellae distance, neck length, leg length, and body size that allow them to feed at different depths and on different foods (Baker 1979, Poysa 1983, Nudds and Bowlby 1984, Zwarts and Wanink 1984). Thus, the hydrology of coastal marshes influences compositions of invertebrate and waterbird communities.

The hydrologic variability of coastal marshes also has important consequences on other ecological functions. The amplitude and regularity of water level variation through time (temporal variability) define degrees of desiccation and flooding in a marsh. For example, waterloging and overdrying may cause marsh vegetation die-offs (Turner 1997). Aquatic invertebrates vary in their abilities to survive dry periods, and the wet-dry cycle of marshes affects their habitat and therefore compositions of invertebrate communities (Murkin and Ross 2000). Also, the predictability of temporal variability in water depths probably is important to waterbirds because: (1) they are adapted morphologically to feed under specific ranges of water depths, and (2) the predictability of foraging conditions influences survival of wintering birds (Lima 1986). The hydrologic variability among marshes, and more specifically among and within marsh ponds at a given time (spatial variability) defines the habitat diversity available to invertebrates and mobile organisms such as waterbirds.

Considerable changes have occurred in marshes on the Gulf Coast Chenier Plain during the last century. Dredging of north-south waterways, occurrence of large-scale muskrat eat-outs, and a severe drought that occurred in the early 1950s, apparently facilitated saltwater intrusion and caused a large marsh vegetation die-off at the junction of the freshwater and oligohaline marshes (Wicker et al. 1983). Consequently, starting during the mid-1950s, numerous marshes were managed using structural marsh management (levees, water control structures and impoundments; SMM) with objectives of revegetating open water areas that had formed, stopping saltwater intrusion, and increasing productivity of waterfowl food plants (Wicker et al. 1983). SSM now commonly is practiced throughout the Gulf Coast Chenier Plain (Day et al. 1990).

The primary effect of SMM on marsh hydrology is to restrict the export and import of water between the marsh and the surrounding canals because levees restrict tidal flows and drainage of rainwater (Boumans and Day 1994). Little is known concerning effects of SMM on other hydrologic variables of coastal marshes; however, water depth seemingly increases and salinity decreases after the implementation of weirs (Chabreck 1960). Because water flow and drainage of rainwater are reduced between impounded marshes and their surrounding environments, I predicted that SMM (1) increases water levels and (2) decreases salinity and turbidity. I also examined water temperature and near-bottom dissolved oxygen because of their importance to the wetland fauna (Mitsh and Gosselink 1993).

SMM strongly reduces effects of tides on water levels within impoundments, resulting in a low daily temporal variability in water levels (Boumans and Day 1994). Water levels in impoundments depend primarily on amounts and frequency of rainfall and drainage capacities of water control structures. On the Gulf Coast Chenier Plain, rainfall generally comes through sudden tropical storms, hurricanes, and cold fronts during the fall-winter seasons that often discharge large amounts of precipitations in a short time period (Keim et al. 1995). Marsh impoundments must handle these flooding events generally through a limited number of water control structures (Wicker et al. 1983), and thus SMM probably extends the duration of large flooding events. Consequently, marsh impoundments probably have a large temporal variability (on a seasonal basis) in water levels as they pass from periods of heavy rainfall to dryer periods. In contrast to impounded marshes, unimpounded coastal marshes are characterized by a network of tide canals of various sizes that allow exchange of water with the Gulf of Mexico (Wicker et al. 1983). Unimpounded marshes probably have the capacity to handle most flooding events because of their great flushing capacity, and therefore have a relatively small temporal variation in water levels on a seasonal basis. Similarly, partial impounding produced by spoil banks creates fewer but longer flooding events compared to marshes connected to tidal bayous (Swenson and Turner 1987). Also, flooding events were longer inside than outside marshes managed with weirs (Bourgeois and Webb 1998). Consequently, I predicted that the temporal variability (on a seasonal basis) in water depths would be greater in ponds of impounded marshes than in those of unimpounded marshes.

Water levels in ponds of unimpounded marshes depend on the range of the tide at a given time, the size of canals connecting ponds to the Gulf, the size of ponds, and the position of ponds in the hydrographic basin; thus, all ponds are affected differently by tides. Therefore, the tidal regime of unimpounded marshes should produce a wide spatial variability in water levels among ponds. Conversely, ponds within an impoundment may not connect together, or only partially, and water levels of surrounding canals generally have limited influences on water levels of ponds. Also, water trapped inside impounded marshes apparently moves primarily underground (Swenson and Turner 1987). Accordingly, ponds of impounded marshes probably have a relatively low spatial variability in water levels. Consequently, I predicted that spatial variability in water levels would be greater among ponds of unimpounded marshes than among those of impounded marshes.

Marshes of the Gulf Coast Chenier Plain are divided into 3 categories of salinity based on the Venice system of estuarine classification (Bulger et al. 1993, Visser et al. 2000): (1)

freshwater (salinity <0.5 ‰), (2) oligohaline (salinity between 0.5 ‰ and 5.0 ‰), and (3) mesohaline (salinity between 5.0 ‰ and 18.0 ‰). Oligohaline marshes apparently have expanded at the expense of freshwater and mesohaline marshes during the last 60 years (Visser et al. 2000). This salinity classification is based on the occurrence of plants specifically adapted to certain ranges of salinity (Visser et al. 2000), and salinity levels measured along transects during summer 1968 throughout Louisiana coastal marshes (Chabreck 1972). Knowledge is lacking about recent salinity levels in marshes of the Gulf Coast Chenier Plain. Furthermore, variations in water depth, temperature, dissolved oxygen, and turbidity have not been studied in ponds of these 3 marsh types. These marshes have an altered hydrology (except for mesohaline marshes that still are connected directly to a tidal bayou) because of the numerous roads, irrigation canals, levees, and waterways that have been built in this area during last century (Turner 1990). Thus, most marshes are impounded to a certain degree. Consequently, I predicted that ponds of impounded freshwater, oligohaline and mesohaline marshes would be similar in water depth, temperature, near-bottom dissolved oxygen, and turbidity.

I tested the above predictions by comparing hydrologic variables (salinity, water depth, temperature, dissolved oxygen, and turbidity) of ponds (1) between impounded and unimpounded mesohaline marshes, and (2) among impounded freshwater, oligohaline and mesohaline marshes during winters of 1997-1998 to 1999-2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. My results are discussed in terms of implications of SMM and salinity on compositions of invertebrate and waterbird communities.

METHODS

STUDY AREA

The Gulf Coast Chenier Plain is bounded by East Bay in Texas and Vermillion Bay in Louisiana (Gosselink et al. 1979). The Chenier Plain was formed by sediments from the Mississippi River that were transported by the westward current in the Gulf of Mexico (Byrne et al. 1959). Periods of low sediment deposition, that occurred when the Mississippi Delta changed location, formed a series of stranded beach ridges composed of sand and shells separated by mud flats where marshes developed (Byrne et al. 1959). Chenier refers to the French word *chenière*, which characterizes a forest or area where oaks (*Quercus* spp.) represent the dominant tree species.

I chose Rockefeller State Wildlife Refuge (RSWR; headquarters coordinates: 29˚ 40’ 30” N, 92˚ 48’ 45” W), near Grand Chenier, in southwestern Louisiana as a representative area of the Gulf Coast Chenier Plain. RSWR comprises 30,700 ha, and contains 17 impoundments (200 to >4,000 ha each, Wicker et al. 1983). Most impoundments on RSWR were constructed during the late 1950s, and are separated by a network of canals that surround the levees (Wicker et al. 1983). Impoundments on RSWR comprise marsh types of various salinities characteristic of the Gulf Coast Chenier Plain, i.e., freshwater, oligohaline, and mesohaline marshes (Visser et al. 2000). RSWR also contains a large area of unimpounded mesohaline marshes (11,700 ha).

SAMPLING DESIGN

I sampled the 4 marsh types of RSWR: (1) 3 freshwater impoundments (IF) (units 8,10, and 13), (2) 3 oligohaline impoundments (IO) (units 3, 4, and 15 [the latter replaced unit 3 in winter 1999-2000]), (3) 2 mesohaline impoundments (IM) (units 5 and Price Lake), and (4) 2 hydrographic basins of unimpounded mesohaline marshes (UM) (East Little Constance Bayou basin and Rollover Lake/Flat Lake basin). In each impoundment and hydrographic basin, I initially selected 4 to 8 ponds from those that were accessible directly from levees or with a small flat boat when necessary (impounded marshes), or that access would not be prevented at low tides using a small flat boat (UM marshes). I made this initial selection to minimize time spent commuting among sites and disturbance to waterbirds, and to ensure access to study ponds at all times. The number of ponds selected depended on those available accordingly to the above selection criteria. Subsequently, I randomly selected 3 ponds from those initially identified in each impoundment or hydrographic basin. Because of the presence of numerous small ponds (<2 ha), but also a few very large ones (>20 ha) in IM and UM marshes, I chose 1 large pond and 2 small ponds in each of these marsh types. During each visit, I randomly selected 3 sampling stations in each pond. I determined locations of sampling stations using a table of random numbers to select distances and angles from an observation blind that fell within the pond area, up to a distance of 200 meters from the blind (this maximum distance was important for a concurrent waterbird study). I visited ponds monthly, from December to March in 1997-98, and from November to March in 1998-99 and 1999-2000 (14 months total).

At sampling stations, I used a graduated stick (± 1 cm) to measure water depth, a YSI-55 dissolved oxygen meter (Yellow Springs Instrument, Co., Yellow Springs, Ohio) to measure dissolved oxygen (± 0.01 mg/l) (O_2), and a YSI-30 salinity meter (Yellow Springs Instrument, Co., Yellow Springs, Ohio) to measure salinity (± 0.1 ‰) and temperature (± 0.1 °C). I measured these variables 2-3 cm above sediments and during daytime (7:00 – 14:00 PM). To measure water turbidity, I submerged a 10-cm diameter white disk at a 10 cm depth, and categorized turbidity using the following classes: none, little, moderate, and considerable, which were coded 0, 1, 2, and 3, respectively.

STATISTICAL ANALYSIS

I compared hydrologic variables between IM and UM marshes and among IF, IM and IO marshes within a single multivariate analysis of variance (MANOVA). Response variables for this analysis were water depth, O_2, salinity, temperature, and turbidity. Fixed explanatory variables in the model were marsh type, time (months), and their interaction. Time was not considered a repeated measure variable *per se* because I did not measure the same water repeatedly, and therefore this variable was included as another fixed main effect. Random explanatory variables were (1) impoundment within marsh type × time, and (2) pond within impoundment and marsh type × time. I performed separate *a priori* MANOVA contrasts to test my 2 comparisons of interest (UM vs. IM, and IF vs. IO and IM), with respective contrast equations (0, 1, 0, –1) and (1, –0.5, –0.5, 0) for the corresponding marsh types equation order (IF, IM, IO, UM). For these *a priori* comparisons, I used an error matrix based on the impoundment within marsh type × time random effect.

I excluded from analysis those sampling stations (n=66 of 1134 total stations sampled over 14 months) where water was not present at sampling time because it produced missing data for salinity, O_2, turbidity, and temperature. These dry conditions occurred primarily in

UM marshes (95% of occurrences), and never in more than 1 pond within basin at a given month, except during December 1997. Accordingly, the December 1997 time period was excluded from analysis because of the absence of water within all ponds of UM marshes, which prevented estimation of contrasts. The removal of this time period caused a reduction of 5 degrees of freedom for the error term used to test my *a priori* comparisons (i.e., impoundment within marsh type × time). However, 61 degrees of freedom remained for this error term after removal of this time period. Moreover, other missing data scattered throughout the other 13 months of sampling did not affect degrees of freedom on the above error term.

I used Wilk's lambda statistic to compute *F*-ratios of my 2 *a priori* MANOVA contrasts (PROC GLM, SAS Institute, Inc. 1999). I considered *P*-values less than 0.05 as significant and estimated effect size (proportion of the variance in response variables attributable to the variance existing in explanatory variables) to avoid declaring significant trivial differences in variable mean responses (effect size = Wilk's lambda – 1, Tabachnick and Fidell 1989). Finally, I computed canonical correlations and standardized canonical coefficients from MANOVA contrasts to investigate the contribution of the various hydrologic variables to differences among ponds of various marsh types. Because r values ≤ 0.3 correspond to $<10\%$ variance overlap between variables (Tabachnick and Fidell 1989), I only interpreted $r > 0.3$. I assessed normality and homoscedasticity of response variables by computing skewness and kurtosis values, and by examining whether model residuals were distributed randomly (Tabachnick and Fidell 1989). Accordingly, I transformed salinity data (log [x+1]) prior to final analysis. I present results as least-square means ± 95% confidence intervals (backtransformed for salinity) unless noted otherwise.

I compared temporal and spatial variabilities in water depths between ponds of IM and UM marshes using variance components analysis. I estimated variances in water depths for IM and UM marsh ponds among: (1) time periods (n=14), (2) impoundments (or hydrographic basins for UM) within months (n=56), (3) ponds within impoundments and months (n=168), and (4) sampling stations within ponds, impoundments and months (residuals, n=504) using a univariate mixed model (PROC MIXED [SAS Institute, Inc.1999]). I then tested for equality of variances between IM and UM for each effect using a *F*-max test (*F*-ratio of the greater variance over the lesser one, Sokal and Rohlf 1995). Absence of water at some sampling stations within UM marsh ponds did not produce missing data in this analysis as 0 water depths were valid data. I performed all statistical analyses using SAS 8.2 (SAS Institute, Inc. 1999).

RESULTS

COMPARISON OF HYDROLOGIC VARIABLES BETWEEN IM AND UM MARSH PONDS

My *a priori* MANOVA contrast indicated that the 5 hydrologic response variables differed significantly and produced a large effect size between UM and IM marsh ponds (Table 3.1). Standardized canonical coefficients of hydrologic variables indicated that salinity was the primary variable contributing to the difference between ponds of these marsh types (Table 3.2). Salinity was 2 times greater in ponds of UM marshes as compared to those of IM marshes (Fig. 3.1). Water depth and O_2 secondarily contributed to the difference between ponds of these marsh types (Table 3.2). Water depth was 2 times lower and contained 3.3 mg/l more O_2 in ponds of UM marshes than in those of IM marshes (Fig. 3.1). O_2, salinity, and temperature were positively correlated and water depth was negatively correlated, whereas turbidity was not correlated with the first canonical variate (Table 3.2). These results indicated that salinity and O_2 were highest and water depth was lowest in UM marsh ponds. Furthermore, an increase in water depth was correlated with decreases in salinity, O_2, and temperature.

Table 3.1. Summary of *a priori* MANOVA contrasts testing for differences in hydrologic variables (dissolved oxygen, salinity, temperature, turbidity, water depth) between ponds of impounded and unimpounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline, and mesohaline marshes (IF vs. IO and IM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Contrast	Wilk's lambda	*F*	Num df	Den df	Pr. > *F*	Effect size (η^2)
UM vs. IM	0.1224	87.48	5	61	< 0.0001	0.878
IF vs. IO and IM	0.0752	150.04	5	61	< 0.0001	0.925

Table 3.2. Canonical correlations (CC) and standardized canonical coefficients (SCC) from *a priori* MANOVA contrasts testing for a difference in hydrologic variables (dissolved oxygen, salinity, temperature, turbidity, water depth) between ponds of impounded and unimpounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline, and mesohaline marshes (IF vs. IO and IM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Variable	UM vs. IM		IF vs. IO and IM	
	CC	SCC	CC	SCC
Dissolved Oxygen	0.794	1.23	0.747	0.82
Salinity	0.949	3.47	0.976	4.33
Temperature	0.386	0.53	0.351	0.33
Turbidity	0.064	0.24	0.064	0.31
Water depth	- 0.870	- 1.50	-0.837	- 1.05

COMPARISON OF WATER DEPTH VARIANCES BETWEEN IM AND UM MARSH PONDS

Variance components analysis indicated that water depth varied more among months in ponds of IM marshes than in those of UM marshes (Table 3.3). Water depths in ponds of IM marshes sometimes were very low, especially during winter 1999-2000 (Fig. 3.2). However, water depth in IM marsh ponds varied by 30 cm in winters 1997-1998 and 1998-1999 with a maximum of 54 cm (Fig. 3.2). Water depth in UM marsh ponds generally was below 20 cm, and never exceeded 38 cm (Fig. 3.2). Variance in water depth between impoundments (or hydrographic basins for UM) also was greater in IM than in UM marsh ponds (Table 3.3). However, variance in water depth among ponds (within impoundments or hydrographic basins) and within ponds (residual variance) was greater in UM than in IM marshes (Table 3.3). The range of water depths generally was smaller within impoundments than within UM marsh basins in a given month, whereas the range of water depths differed more between impoundments than between basins of UM marshes within months (Fig. 3.2).

Figure 3.1. Mean values (least square means ± 95% confidence intervals) of hydrologic variables (dissolved oxygen, salinity, temperature, turbidity, water depth) in ponds of impounded freshwater (IF), oligohaline (IO), mesohaline (IM) marshes, and of unimpounded mesohaline marshes (UM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Note that turbidity increases with the index (see Methods).

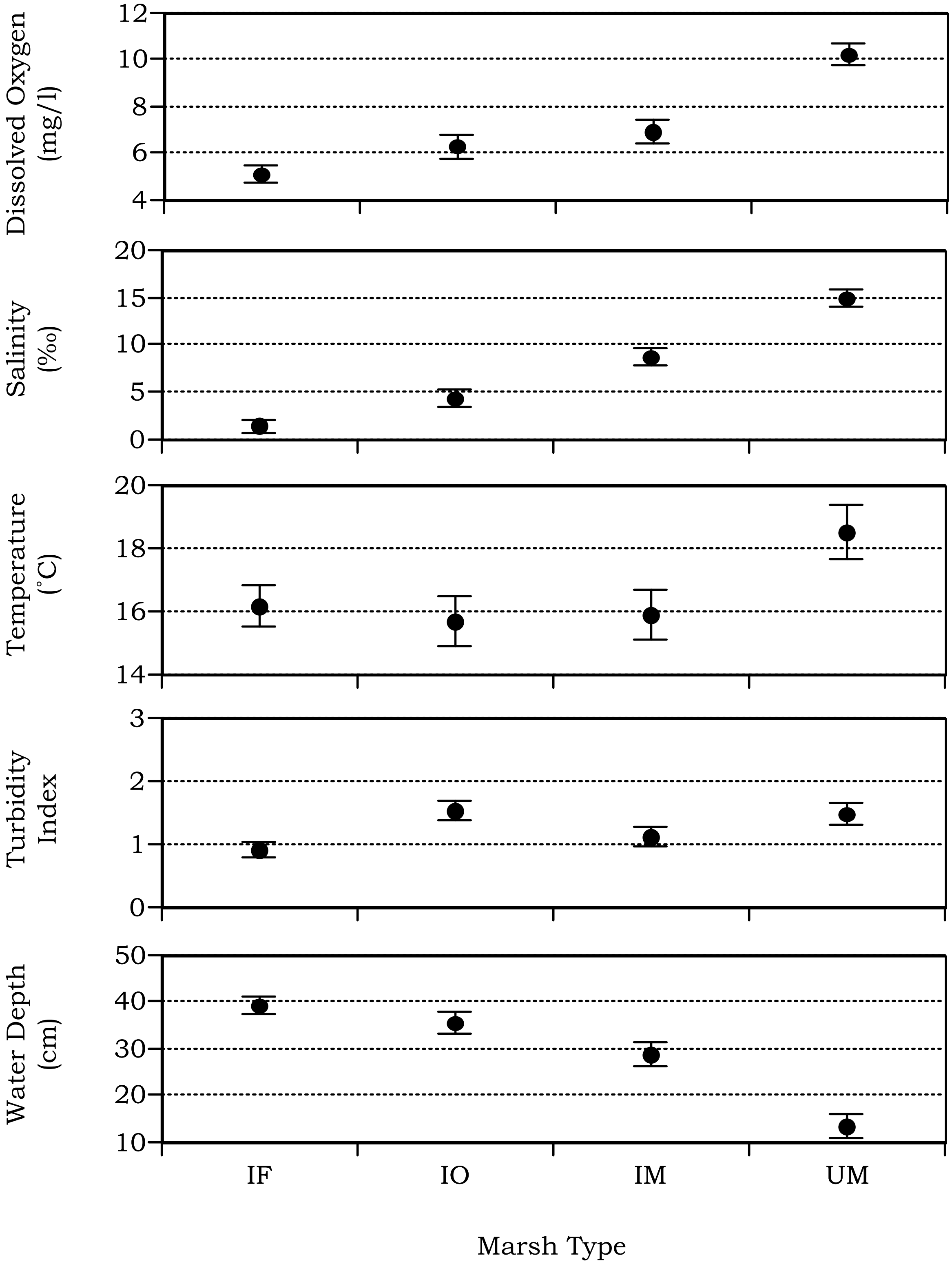

Dissolved Oxygen (mg/l)
12
10
8
6
4
Salinity (‰)
20
15
10
5
0
Temperature (˚C)
20
18
16
14
Turbidity Index
3
2
1
0
Water Depth (cm)
50
40
30
20
10
IF
IO
IM
UM
Marsh Type

Table 3.3. Estimates of water depth variance (σ^2) in ponds of impounded mesohaline marshes (IM) and unimpounded mesohaline marshes (UM) among: (1) months, (2) impoundments (or hydrographic basins for UM) within months, (3) ponds within impoundments and months, and among (4) sampling stations within ponds, impoundments and months (residuals), during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. *F*-ratios test for difference in variance estimates between marsh types for each effect (see Methods).

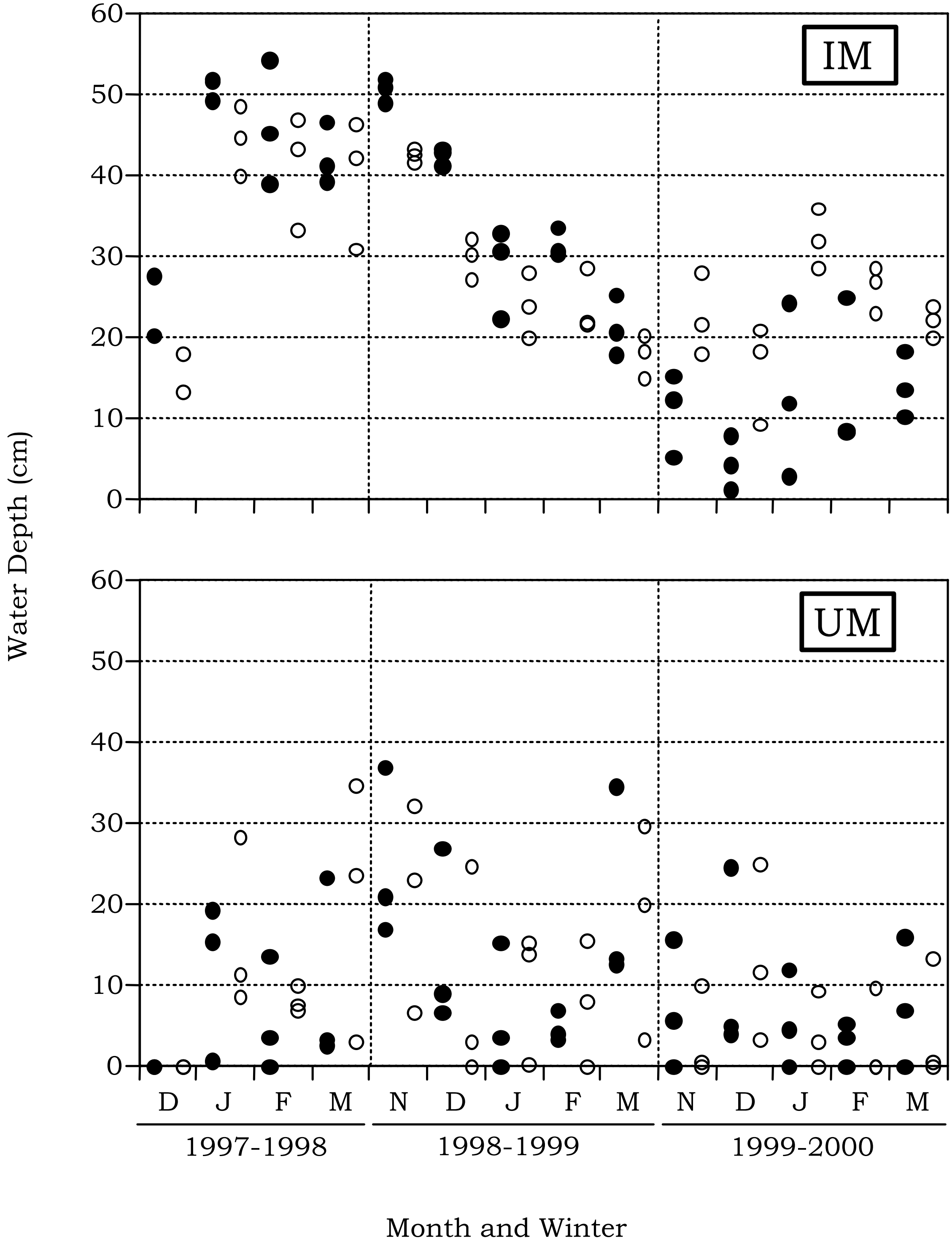
	Months	Impoundments/ hydrographic basins	Ponds	Residuals
σ^2_{IM}	152.98	38.20	22.20	6.66
σ^2_{UM}	23.84	0	78.15	19.77
F-ratio	6.43	- [a]	3.52	2.97
Pr. > *F*	0.0014	- [a]	< 0.0001	< 0.0001

[a] Test not possible due 0 estimated variance.

COMPARISON OF HYDROLOGIC VARIABLES OF IF WITH IO AND IM MARSH PONDS

My *a priori* MANOVA contrast indicated that the 5 hydrologic response variables differed significantly and produced a large effect size between ponds of IF and those of the other 2 marsh types (Table 3.1). Standardized canonical coefficients of hydrologic variables indicated that salinity was the primary variable contributing to the difference between ponds of these marsh types (Table 3.2). Standardized canonical coefficients of other variables were less than 1.1 (Table 3.2), reflecting their small contribution to differences among marsh types. O_2, salinity, and temperature were positively correlated and water depth was negatively correlated, whereas turbidity was not correlated with the first canonical variate (Table 3.2). These results indicate that salinity was lowest in IF marsh ponds, and that salinity was correlated positively with O_2 and temperature but negatively with water depth.

Figure 3.2. Mean water depth in ponds of impounded mesohaline (IM) (● = Price Lake; ○ = unit 5), and unimpounded mesohaline marshes (UM) (● = Rollover Lake/Flat Lake basin; ○ = East Little Constance Bayou basin) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Note that several data points are superposed on each other.



Water Depth (cm)
60
50
40
30
20
10
0
IM
UM
D
J
F
M
N
D
J
F
M
N
D
J
F
M
1997-1998
1998-1999
1999-2000
Month and Winter

DISCUSSION

COMPARISON OF HYDROLOGIC VARIABLES BETWEEN IM AND UM MARSH PONDS

Ponds of IM and UM marshes differed primarily in salinity and secondarily in water depth and O_2. These results are consistent with my predictions that, because SMM decreases tidal influences and drainage of rainwater, water depth increases and concomitantly salinity decreases in ponds of impounded marshes. SMM probably affected salinity because of the multiplicative effects of the decrease in drainage of rainwater and saltwater inputs. The pattern of correlation among variables indicated that temperature, salinity, and O_2 decrease with increasing water depths. Contrary to my predictions, I did not detect absolute decreases in turbidity in ponds of IM marshes compared to those of UM marshes. I did not find that SMM reduced turbidity, possibly because hydraulic turbulences caused by wind on deeper water in ponds of IM marshes were equivalent to those from tides in UM marsh ponds.

I measured O_2 during daytime (7:00 – 14:00 PM), which may have influenced the relationship among water depth, salinity, temperature and O_2. For example, average O_2 readings in ponds of UM marshes (10.5 mg/l) also corresponded to an average of 110% O_2 saturation in the water. Supersaturation, as in this case, is related to an intense photosynthesis by the algae within the water-column (Wetzel 1975). Algae release pure O_2, compared to the atmosphere that contains only 21% of O_2 at sea level (Wetzel 1975). Thus, O_2 gas pressure may be higher in the water than in the atmosphere when intense photosynthesis occurs in aquatic habitats. However, an abundant algae population in the water also may cause an important decrease in O_2 at night when respiration is intense (Wetzel 1975).

COMPARISON OF WATER DEPTH VARIANCES BETWEEN IM AND UM MARSH PONDS

My results were consistent with the prediction that temporal variability (on a seasonal basis) in water depths was greater in ponds of impounded marshes than in those of unimpounded marshes. This finding probably was due to the relatively slow drainage of large rainfall events that occurred during winter 1997-1998 and 1998-1999, and that extended over several months in IM marsh ponds (Fig. 3.2). Ponds of UM marshes were not affected as much as those of IM marshes by these large flooding events, probably because of the greater flushing capacity of tide canals compared to a limited number of water control structures. Thus, my results indicated that flooding events lasted longer in ponds of impounded marshes than in those of unimpounded marshes. Similarly, flooding events last longer within marshes partially impounded by spoil banks than within marshes connected to tidal bayous (Swenson and Turner 1987). Also, flooding events were longer inside than outside marshes managed with weirs (Bourgeois and Webb 1998).

As predicted, I found that spatial variability in water depth was greater among ponds of UM marshes than among those of IM marshes. This difference probably occurred because the tidal flow in UM marshes did not affect water depths simultaneously in ponds distributed throughout a hydrographic basin, whereas the lack of intermittent ebb and flood tides produced stable water levels throughout an impoundment. My results also indicated that variance in water depth within a pond was greater in UM marshes than in IM marshes. The presence of tide canals crossing ponds of UM marshes probably produced a flow of water that reworks sediments differentially throughout a pond, whereas this phenomenon was absent in IM marsh ponds. Thus, water depths probably varied more within ponds of UM marshes than in IM marshes because the sediment elevation varies more in the former.

Interestingly, my results indicated that water depth variance was greater between impoundments than between hydrographic basins of UM marshes. The 2 hydrographic basins of unimpounded marshes were adjacent to each other, and therefore water depths in marsh ponds of these 2 hydrographic basins probably were affected equally by tides on average. However, the impoundments each had 2-3 water control structures, but apparently did not drain equally following flooding events. This difference may have resulted because locations of water control structures differed between the 2 impoundments (Wicker et al. 1983), and/or water flowed more easily in one impoundment than in the other.

COMPARISON OF HYDROLOGIC VARIABLES OF IF WITH IO AND IM MARSH PONDS

Except for the expected marked differences in salinity, my results indicated that ponds of IF marshes generally had similar values of hydrologic variables as compared to those of IO and IM marshes. Mean salinity levels recorded in ponds of each marsh type (Fig. 3.1) fell within ranges of their actual salinity classifications (Visser et al. 2000). Salinities that I recorded also were consistent with those reported by Chabreck (1972) for these marsh types. Given correlations among hydrologic variables, subsequent changes in water levels within ponds of impounded marshes may bring changes in other hydrologic variables; deeper ponds have lower temperature, salinity, and near-bottom O_2. Finally, based on my results, levels of salinity, O_2, and temperature clearly were dependent on water depth.

MANAGEMENT IMPLICATIONS

One important goal of SMM is to prevent saltwater intrusion (Wicker et al. 1983). My results indicated that this goal was accomplished because average salinity was greater in ponds of UM than in those of IM marshes. Based on my results, several predictions can be made concerning compositions of invertebrates and waterbird communities inhabiting these marsh ponds: (1) reductions of near-bottom O_2 should promote populations of certain Oligochaeta, Chironomidae, and Cladocera that tolerate anoxia (Murkin and Ross 2000); (2) reductions in salinity should promote populations of Oligochaeta, certain insect larvae, and other freshwater oriented invertebrates (Murkin and Ross 2000); and (3) increases in water depth should promote the usage of these marshes by large ducks, divers, and large wading birds, but deter shorebirds (White and James 1978, Baker 1979, Poysa 1983, Ntiamoa-Baidu 1998).

The observed greater temporal variability (on a seasonal basis) in water depths within ponds of IM as compared to those of UM marshes indicated that control of water levels in ponds of IM marshes may be more difficult to obtain than expected, probably because of the water regime on the Gulf Coast Chenier Plain. During the fall-winter seasons in this area, rainfall generally comes from sudden tropical storms, hurricanes, and cold fronts that often discharge large amounts of precipitations in a short time period (Keim et al. 1995). Typically, a limited number of water control structures have difficulties handling large flooding events in marsh impoundments as compared to more numerous natural tide canals in unimpounded marshes. Control of water levels probably would be more efficient within impoundments of smaller size or with better drainage capability.

The greater temporal variability (on a seasonal basis) in water depth in ponds of impounded marshes probably has several important consequences: (1) lower marsh accretion due to waterlogging and overdrying (Turner 1997); and (2) the promotion of plant and invertebrate species that are adapted to large fluctuations in hydrologic variables (water depth was correlated with O_2, salinity, and temperature). Also, the lower temporal variability in water levels in ponds UM marshes indicates that hydrologic conditions are more predictable for a variety of organisms in these habitats. The predictability of the environment is believed to be important to wintering birds because habitats of highest predictability are associated with best avian survival rates (Lima 1986).

The observed lower spatial variability in water depths in ponds of IM marshes compared to those of UM marshes indicated that SMM may have important consequences on plant and animal species diversity. A lower spatial variability in water depths in IM marsh ponds may result in fewer plant and animal species using these ponds at a given time compared to ponds of UM marshes. This is especially important for waterbirds because several species have morphological features that enable them to feed most efficiently under specific water depths (Baker 1979, Poysa 1983, Nudds and bowlby 1984, Zwarts and Wanink 1984). Also, because temporal water depth variability (on a seasonal scale) is large and spatial variability is small in IM marsh ponds, plant and invertebrate communities probably vary little within a whole impoundment, and may be composed primarily of generalist species. In contrast, temporal variability in water depths is small and spatial variability is large in UM marsh ponds, which should promote species diversity in space and produce hydrologic conditions predictable for a variety of organisms in these ponds.

Interestingly, I found that water depth varied more between impoundments than between hydrographic basins; consequently, impoundments do not necessarily provide similar water depths at a given time. This suggests that, although spatial water depth variability is lower within impoundments than within unimpounded marshes, allowing adjacent impoundments to vary in water depth would provide habitat diversity at the landscape level and thus would be a good way to counteract potential negative effects of SMM on animal species diversity. However, any selected water depth necessarily will benefit some species and negatively affect others because of the low spatial variability in water depth within impoundments.

In conclusion, changes in hydrologic variables due to SMM and salinity have several implications for compositions of animal communities in marsh ponds of the Gulf Coast Chenier Plain. Furthermore, SMM and salinity also affect sediments in ponds of the Gulf Coast Chenier Plain marshes, which have their own implications for compositions of animal communities (Chapter 2). Finally, further research is essential to fully understand all the ecological consequences of SMM and changes in salinity in marsh ponds of the Gulf Coast Chenier Plain.

CHAPTER 4

EFFECTS OF STRUCTURAL MARSH MANAGEMENT AND SALINITY ON INVERTEBRATE PREY OF WINTERING WATERBIRDS ON THE GULF COAST CHENIER PLAIN

INTRODUCTION

Marshes along the northern Gulf coast are important habitats for wintering wading birds (Mikuska et al. 1998) and migrating shorebirds (Helmers 1992). Moreover, 19% of the waterfowl wintering in the U.S. use marshes of the Louisiana Gulf Coast (Michot 1996). Aquatic invertebrates represent primary food resources for many wintering waterbirds (anseriformes, charadriiformes, ciconiiformes, gaviiformes, gruiformes, pelecaniformes, phoenicopteriformes, podicipediformes, and procellariformes). For example, shorebirds feed almost exclusively on invertebrates (Skagen and Oman 1996), whereas the usage of invertebrates varies widely among waterfowl (Afton et al. 1991, Euliss et al. 1991, Thompson et al. 1992, Batzer et al. 1993) and generally increases at the end of winter (Krapu and Reinecke 1992). Large wading birds also consume aquatic invertebrates during winter (Martin and Hamilton 1985). Non-diving waterbirds are adapted to capture prey of different sizes or minimal sizes and forage at different depths in the water or sediments (Baker 1979, Poysa 1983, Nudds and Bowlby 1984, Zwarts and Wanink 1984).

Aquatic invertebrate communities inhabiting marsh sediments are influenced greatly by sediment and hydrologic variables. Sediment organic content and water turbidity affect the production of bacteria and algae that many invertebrates consume (Benke 1984, Batzer and Wissinger 1996, Robinson et al. 2000). The amount of undecomposed vegetation in sediments affects the structural complexity of invertebrate habitats (Minshall 1984). Levels of salinity, dissolved oxygen (O_2), and temperature greatly affect the level of stress, osmoregulation and metabolism in aquatic invertebrates; therefore, invertebrates exhibit various ranges of tolerance to variations in these variables (Perkins 1974).

Sediment hardness, penetration depth of oxygen (O_2 penetration), and particle size particularly affect benthic epifaunal (living on the sediment surface) and infaunal (living in the sediments) invertebrates. Hard sediments provide physical support to epifaunal invertebrates (Rhoads 1974). Invertebrates that live in the oxygen-depleted zone of sediments must respire using anaerobic processes or provide their own oxygen through blood pigments or ventilated burrows (Rhoads 1974). Particle size determines how water and oxygen penetrate sediments and the interstitial space available to meiofauna (0.063 – 0.5 mm) (Little 2000). These 3 sediment variables together determine sediment porosity; soft unconsolidated sediments behave like fluids, provide little support and water and oxygen penetrate them easily, whereas compacted sediments behave like solids and provide support but minimal oxygen penetration and interstitial space under the surface (Little 2000).

Marshes of the Gulf Coast Chenier Plain have changed greatly during the last century. Dredging of north-south waterways, occurrence of large-scale muskrat eat-outs, and a severe drought that occurred in the early 1950s, apparently facilitated saltwater intrusion and caused a large marsh vegetation die-off at the junction of the freshwater and oligohaline marshes (Wicker et al. 1983). Consequently, starting during the mid-1950s, numerous marshes were managed using structural marsh management (levees, water control structures and impoundments; SMM) with objectives of revegetating open water areas that had formed, stopping saltwater intrusion, and increasing productivity of waterfowl food plants (Wicker et al. 1983). Drawdowns sometimes occur in marsh impoundments during spring or early summer to allow oxidation of organic matter and encourage growth of seedlings and perennials (Kadlec 1962). Impoundments then are reflooded during fall and winter to attract waterfowl (Kadlec 1962). SSM now commonly is practiced throughout the Gulf Coast Chenier Plain (Day et al. 1990).

Little information is available on effects of SMM on aquatic invertebrates. Previous research indicates that SMM consolidates sediments, decreases O_2

penetration, and increases particle size and carbon content of sediments during winter in this area (Chapter 2). Consequently, SMM was predicted to promote populations of epifaunal invertebrates and negatively affect those of infaunal invertebrates (Chapter 2). SMM also reduces salinity and O_2 close to sediments in marsh ponds during winter in this area (Chapter 3). Accordingly, SMM was predicted to promote populations of invertebrates that tolerate low levels of O_2 and salinity, and negatively affect those that do not tolerate low salinity (Chapter 3).

Marshes of the Gulf Coast Chenier Plain are divided into 3 categories of salinity based on the Venice system of estuarine classification (Bulger et al. 1993, Visser et al. 2000): (1) freshwater (salinity <0.5 ‰), (2) oligohaline (salinity between 0.5 ‰ and 5.0 ‰), and (3) mesohaline (salinity between 5.0 ‰ and 18.0 ‰). Oligohaline marshes apparently have expanded at the expense of freshwater and mesohaline marshes during the last 60 years (Visser et al. 2000). Little information is available concerning potential differences in invertebrate communities among these marsh types. I previously found little differences in pond sediments among freshwater, oligohaline, and mesohaline marshes, and predicted that communities of benthic invertebrates should be similar among these marshes (Chapter 3). Furthermore, I found that salinity was the only hydrologic variable that differentiated ponds of impounded freshwater, oligohaline, and mesohaline marshes (Chapter 3). Consequently, I predicted that invertebrate biomasses would be similar among these marsh types, except for those adapted to specific ranges of salinity (Chapter 3).

I examined biomasses of common invertebrates available as prey for wintering waterbirds on marsh ponds of the Gulf Coast Chenier Plain. Specifically, I tested the above general predictions concerning effects of SMM and salinity on invertebrates by comparing their biomasses and sizes (1) between ponds of impounded and unimpounded mesohaline marshes, and (2) among ponds of impounded freshwater, oligohaline and mesohaline marshes during winters 1997-1998 to 1999-2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. I also investigated relationships among sediment variables (carbon content, C:N ratio, hardness, particle size, and O_2 penetration), hydrologic variables (salinity, water depth, temperature, O_2, and turbidity), biomasses and sizes of common invertebrate classes, and marsh types.

METHODS

STUDY AREA

The Gulf Coast Chenier Plain is bounded by East Bay in Texas and Vermillion Bay in Louisiana (Gosselink et al. 1979). The Chenier Plain was formed by sediments from the Mississippi River that were transported by the westward current in the Gulf of Mexico (Byrne et al. 1959). Periods of low sediment deposition, that occurred when the Mississippi Delta changed location, formed a series of stranded beach ridges composed of sand and shells separated by mud flats where marshes developed (Byrne et al. 1959). Chenier refers to the French word *chenière*, which characterizes a forest or area where oaks (*Quercus* spp.) represent the dominant tree species.

I chose Rockefeller State Wildlife Refuge (RSWR; headquarters coordinates: 29˚ 40’ 30” N, 92˚ 48’ 45” W), near Grand Chenier, in southwestern Louisiana as a representative area of the Gulf Coast Chenier Plain. RSWR comprises 30,700 ha, and contains 17 impoundments (200 to >4,000 ha each, Wicker et al. 1983). Most impoundments on RSWR were constructed during the late 1950s, and are separated by a network of canals that surround the levees (Wicker et al. 1983). Impoundments on RSWR comprise marsh types of various salinities characteristic of the Gulf Coast Chenier Plain, i.e., freshwater, oligohaline, and mesohaline marshes (Visser et al. 2000). RSWR also contains a large area of unimpounded mesohaline marshes (11,700 ha).

SAMPLING DESIGN

I sampled the 4 marsh types of RSWR: (1) 3 freshwater impoundments (IF) (units 8,10, and 13), (2) 3 oligohaline impoundments (IO) (units 3, 4, and 15 [the latter replaced unit 3 in winter 1999-2000]), (3) 2 mesohaline impoundments (IM) (units 5 and Price Lake), and (4) 2 hydrographic basins of unimpounded mesohaline marshes (UM) (East Little Constance Bayou basin and Rollover Lake/Flat Lake basin). In each impoundment and hydrographic basin, I initially selected 4 to 8 ponds from those that were accessible directly from levees or with a small flat boat when necessary (impounded marshes), or that access would not be prevented at low tides using a small flat boat (UM marshes). I made this initial selection to minimize time spent commuting among sites and disturbance to waterbirds (important for a concurrent waterbird study), and to ensure access to study ponds at all times. The number of ponds selected depended on those available accordingly to the above selection criteria. Subsequently, I randomly selected 3 ponds from those initially identified in each impoundment or hydrographic basin. Because of the presence of numerous small ponds (<2 ha), but also a few very large ones (>20 ha) in IM and UM marshes, I randomly chose 2 small ponds and 1 large pond in each of these marsh types. During each visit, I randomly selected 3 sampling stations in each pond. I determined locations of sampling stations using a table of random numbers to select distances and angles from an observation blind that fell within the pond area, up to a distance of 200 meters from the blind (this maximum distance was important for a concurrent waterbird study). I visited ponds monthly, from December to March in 1997-98 and from November to March in 1998-99 and 1999-2000 (14 months total).

COLLECTION OF INVERTEBRATE SAMPLES

I used 3 different techniques to sample aquatic invertebrates to ensure adequate representation of benthic meiofauna (0.063 – 0.5 mm), macrofauna (> 0.5 mm), and water-column (epiphytic and nektonic) macrofauna (>0.5 mm) in my overall estimates of invertebrate biomasses. At each sampling station, I used a sediment corer (12-cm diameter) sunk to 10-cm depth in the pond bottom to collect benthic macrofauna. I subsequently sieved samples through a 500 µm mesh at sampling sites. I sampled meiofauna with a smaller corer (2.5-cm diameter) sunk to 2-cm depth, and sieved samples through a 63 µm mesh. I sampled water-column invertebrates using a D-shaped sweep net (opening 30 cm large, mesh 500 µm) filtering a volume of water of approximately 0.7 m^3, which is equivalent to a net movement through a distance of 20 meters (e.g., 10 sweeps of 2 m long, surface covered = 6 m^2) along the water surface. All material retained by sieves was preserved in 10% buffered formaldehyde mixed with rose bengal protein stain (Hartley et al. 1988).

ESTIMATES OF INVERTEBRATE BIOMASSES

Diets and foods available to waterbirds frequently are described using dry-weights (Afton et al. 1991, Euliss et al. 1991, Weber and Haig 1996, Safran et al. 1997), ash-free dry-weights (Zwarts and Wanink 1991), or caloric contents (Nudds and Bowlby 1984) because these estimators are believed to provide a realistic estimate of invertebrate energetic payoffs to waterbirds. Accordingly, I used ash-free dry-weight to quantify invertebrate biomass.

Most studies of waterbird food resources have classified aquatic invertebrates into families, orders, classes or phyla (Euliss et al 1991, Thompson et al. 1992) probably because (1) of the large variety and numbers of invertebrates, and (2) feeding apparatuses of waterbirds principally are adapted to pick or filter prey of a certain size or minimal dimensions (Nudds and Bowlby 1984, Zwarts and Wanink 1984). Therefore, shapes and sizes of invertebrates probably are more important to waterbirds than are taxonomic classifications of food items. Consequently, I arbitrarily determined classes that discriminated shapes and sizes of invertebrates to reduce time spent in lab identifying invertebrates.

In the lab, I filtered samples through a series of sieves of declining mesh size to assess invertebrate body size (5000, 2000, 1000, and 500 µm for macrofauna and water-column invertebrates; 500, 200, 100, and 63 µm for meiofauna). Following this, I identified (1) Diptera, Mollusca, and Decapoda to the family level, (2) other Insecta and Arthropoda to order, (3) Annelida, and Granuloreticulosa to class, and (4) Nematoda to phylum. I counted individuals of each taxon present by the above size classes.

I calculated biomasses of invertebrates by multiplying the number of individuals counted for each taxon and size class by individual ash-free dry-weights obtained from fresh (unpreserved) individuals collected during winter 1999-2000 (35 benthic macrofauna and 37 water-column macrofauna samples). I dried invertebrates from the latter samples by size class and taxon at 60°C for 12 hours in a drying oven in samples of 1 to 50 individuals (depending on size and numbers), weighed them, and then burned them in a muffle furnace at 550°C for 4 hours (Widbom 1984). Subsequently, I placed samples in a desiccator and re-weighed them. The ash-weight was subtracted from the dry-weight to obtain the ash-free dry-weight. I used estimates from the literature for meiofauna and uncommon size classes of macrofauna identified, but not found in my samples used to measure individual ash-free dry-weight (Reger 1982, Widbom 1984, Edgar 1990).

MEASUREMENTS OF HYDROLOGIC VARIABLES

At sampling stations, I used a graduated stick (± 1 cm) to measure water depth, a YSI-55 dissolved oxygen meter (Yellow Springs Instrument, Co., Yellow Springs, Ohio) to measure dissolved oxygen (± 0.01 mg/l) (O_2), and a YSI-30 salinity meter (Yellow Springs Instrument, Co., Yellow Springs, Ohio) to measure salinity (± 0.1 ‰) and temperature (± 0.1 °C). I measured these variables 2-3 cm above sediments and during daytime (8:00 – 12:00). To measure water turbidity, I submerged a 10-cm diameter white disk at a 10 cm depth, and categorized turbidity using the following classes: none, little, moderate, and considerable, which were coded 0, 1, 2, and 3, respectively.

MEASUREMENTS OF SEDIMENT VARIABLES

Between January and March 2000, I measured sediment hardness within each pond with a S-170 pocket soil penetrometer (Boart Longyear, Co., Stone Mountain, Georgia) that was adapted for measurements of soft sediments by attaching a 10-cm diameter vinyl disk at its end. This measurement was an index of the amount of pressure the soil could absorb when the penetrometer was pushed down by 2 cm.

I determined the silt-clay fraction (to estimate particle size) by sampling pond sediments with a 5-cm corer sunk to a depth of 10 cm. Sediments were homogenized with a kitchen blender (model 4142, Sunbeam Products, Inc, Boca Raton, Florida), oven-dried at 100 °C for 24 hours, and then weighed (±0.01 g). Following this procedure, I re-hydrated sediments, homogenized them again, and sieved them through a 63 µm mesh sieve to remove the silt-clay fraction. Sediments left in the sieve were oven-dried, and re-weighed. The difference in sediment dry-weight before and after sieving divided by the total sediment dry-weight used (* 100) corresponded to the silt-clay fraction in sediments (Buchanan 1984).

I sampled carbon and nitrogen contents of sediments by taking a few grams from homogenized sediments used for the determination of the silt-clay fraction. I preserved samples by freezing and used a CHN analyzer to determine their carbon and nitrogen content and their ratio (C:N) (Buchanan 1984). Finally, I placed metal rods in sediments for 1 month at random stations within each pond to estimate O_2 penetration. O_2 penetration corresponded to depths where rust stopped along the metal rods (J. W. Fleeger, pers. comm.).

STATISTICAL ANALYSES

Effects of SMM and salinity on invertebrate biomasses: I limited my analysis to common invertebrate classes collected on RSWR. I defined common invertebrate classes based on taxonomic and size differences. First, I grouped invertebrates identified to family into their respective orders to reduce the number of taxa with little representation. Secondly, I grouped the 7 size classes into 3 larger classes (63 – 199 µm, 200 – 999 µm, ≥1000 µm) within invertebrate taxa (1) to reduce the number of classes, and (2) to reflect known food sizes consumed by waterbirds. For waterfowl, the smallest potential food sizes begin within 200 to 999 µm and all species can capture prey ≥1000 µm (Nudds and Bowlby 1984, Tremblay and Couture 1986, Kooloos et al. 1989). Finally, I defined common invertebrate classes as those with a percent frequency ≥25 % in at least one of the marsh types. I used biomasses of common invertebrate classes as response variables in subsequent analyses.

I compared biomasses of common invertebrate classes between ponds of IM and UM marshes and among ponds of IF, IM and IO marshes within a single multivariate analysis of variance (MANOVA). Fixed explanatory variables in the model were marsh type, time (months), and their interaction. Time was not considered a repeated measure variable *per se* because I did not sample the same sediments repeatedly; therefore this variable was included as a fixed main effect. Random explanatory variables were (1) impoundment within marsh type × time, and (2) pond within impoundment and marsh type × time. I performed separate *a priori* MANOVA contrasts to test my 2 comparisons of interest (UM vs. IM, and IF vs. IO and IM), with respective contrast equations (0, 1, 0, –1) and (1, –0.5, –0.5, 0) for the corresponding marsh types equation order (IF, IM, IO, UM). For these *a priori* comparisons, I used an error matrix based on the impoundment within marsh type × time random effect.

I used Wilk's lambda statistic to compute *F*-ratios of my 2 *a priori* MANOVA contrasts (PROC GLM, SAS Institute, Inc. 1999). I considered *P*-values less than 0.05 as significant and estimated effect size (proportion of the variance in response variables attributable to the variance existing in explanatory variables) to avoid declaring significant but trivial differences in variable mean responses (effect size = Wilk's lambda – 1, Tabachnick and Fidell 1989). Finally, I computed canonical correlations and standardized canonical coefficients from MANOVA contrasts to investigate the contribution of the various common invertebrate classes to differences among ponds of various marsh types. Because *r* values ≤0.3 correspond to <10% variance overlap between variables (Tabachnick and Fidell 1989), I only interpreted *r* values >0.3. I estimated skewness and kurtosis values and examined whether model residuals were distributed randomly to assess normality and homoscedasticity of response variables (Tabachnick and Fidell 1989). Accordingly, I transformed all response variables (natural log +1) to meet normality assumptions of parametric tests. I present results as backtransformed least-square means ± standard errors unless noted otherwise. I performed all statistical analyses using SAS 8.2 (SAS Institute, Inc. 1999).

Relationships with environmental variables**:** I used canonical correspondence analysis (CCA) and CANOCO statistical software (ter Braak and Verdonschot 1995) to examine relationships among environmental variables (sediment and hydrologic variables; EVs), biomasses of common invertebrate classes, and marsh types. This multivariate technique extracts uncorrelated ordination axes that maximize distance among invertebrate class centroids from measured EVs. Each invertebrate class centroid corresponds to mean axis scores of sites where the invertebrate class occurred. Distance among invertebrate class centroids explained by the CCA axes corresponds to the proportion of inertia (total weighted variance in the dataset) explained by their eigenvalues (weighted variance of species centroids due to the axes), expressed in percentage. I used a Monte Carlo permutation test to evaluate the significance ($P < 0.05$) of the CCA solution and the first axis eigenvalues (ter Braak and Verdonschot 1995).

In the CCA, I included 4 qualitative variables with the EVs that represent the 4 marsh types surveyed (IF, IO, IM, and UM) to estimate their average axis scores and compare them to invertebrate class centroids on the CCA ordination biplot. These qualitative variables were coded “1” when they corresponded to the marsh type where the sampling occurred, and “0” otherwise. I also introduced a covariable matrix in the model to account for sampling replication through time, i.e., 14 binary variables that included one for each month that I collected data.

Following CCA, I used forward selection to rank EVs in the order that maximizes the cumulative eigenvalue (λ_a) (ter Braak and Verdonschot 1995). The forward selection first computed each EV eigenvalue (λ) (as if they were the only variable included in the model) and then selected the variable with the highest eigenvalue. Following this, the other variables were reordered by their eigenvalues computed in conjunction with the eigenvalue of the variables (s) already selected, and again the variable with the highest eigenvalue was selected. This process continued until all variables were considered. I tested the significance ($P < 0.05$) of the effect of each variable on the CCA eigenvalue with a Monte Carlo permutation test (ter Braak and Verdonschot 1995).

RESULTS

COMMON INVERTEBRATE CLASSES

The classification of invertebrates based on taxonomy and size yielded a total of 53 invertebrate classes from my samples. Among these classes, I identified 19 invertebrate classes as common (Appendix A). Common invertebrate classes were composed of Amphipoda between 200 to 999 µm and ≥1000 µm; Cladocera between 200 to 999 µm; Copepoda between 63 to 199 µm and 200 to 999 µm; Diptera between 200 to 999 µm and ≥1000 µm; Foraminifera between 63 to 199 µm and 200 to 999 µm; Hemiptera between 200 to 999 µm and ≥1000 µm; Nematoda between 63 to 199 µm and 200 to 999 µm; Oligochaeta and Polychaeta of size classes 200 to 999 µm and ≥1000 µm; and Ostracoda between 63 to 199 µm and 200 to 999 µm (Appendix A). Total biomasses of benthic meiofauna, benthic macrofauna, water column macrofauna, and total invertebrate biomasses are presented by marsh types and months in Appendix B and C.

COMPARISON OF IM AND UM MARSH PONDS

My *a priori* MANOVA contrast indicated that biomasses of the 19 common invertebrate classes differed significantly between IM and UM marsh ponds and produced a large effect size (Table 4.1). Standard canonical coefficients of invertebrate classes indicated that biomasses of Foraminifera between 63 to 199 µm, Nematoda between 63 to 199 µm, Ostracoda between 200 to 999 µm, and Foraminifera between 200 to 999 µm were the classes that differed most between ponds of these 2 marsh types (Table 4.2). Biomasses of Ostracoda (200 to 999 µm) were highest in ponds of IM marshes, whereas Foraminifera (63 to 199 µm and 200 to 999 µm) and Nematoda (63 to 199 µm) were highest in ponds of UM marshes (Fig. 4.1 and 4.2).

Biomasses of Copepoda (63 to 199 µm and 200 to 999 µm), Foraminifera (63 to 199 µm and 200 to 999 µm), Nematoda (63 to 199 µm and 200 to 999 µm), and Polychaeta (200 to 999 µm and ≥1000 µm) were positively correlated, whereas those of Ostracoda (200 to 999 µm) were negatively correlated with the first canonical variate (Table 4.2). Invertebrate classes with greatest biomasses in ponds of UM marshes were Nematoda (200 to 999 µm and 63 to 199 µm) and Copepoda (200 to 999 µm and 63 to 199 µm), whereas Nematoda (200 to 999 µm), Copepoda (200 to 999 µm), Ostracoda (200 to 999 µm), Nematoda (63 to 199 µm) and Copepoda (63 to 199 µm) had greatest biomasses in ponds of IM marshes (Fig. 4.1, 4.2, and 4.3).

COMPARISON OF IF WITH IO AND IM MARSH PONDS

My *a priori* MANOVA contrast indicated that biomasses of the 19 common invertebrate classes differed significantly among IF, IO, and IM marsh ponds and produced a large effect size (Table 4.1). Standardized canonical coefficients indicated that Amphipoda (200 to 999 µm), Cladocera (200 to 999 µm), Oligochaeta (200 to 999 µm), and Foraminifera (63 to 199 µm and 200 to 999 µm) were the primary classes that contributed to the difference between ponds of these marsh types (Table 4.2). Biomasses of Cladocera (200 to 999 µm) and Oligochaeta (200 to 999 µm) were greatest in ponds of IF marshes, whereas those of Amphipoda (200 to 999 µm) and Foraminifera (63 to 199 µm and 200 to 999 µm) were greatest in ponds of IO marshes (Fig. 4.1 and 4.2).

Biomasses of Copepoda (63 to 199 µm), Foraminifera (63 to 199 µm and 200 to 999 µm), Nematoda (63 to 199 µm and 200 to 999 µm), and Polychaeta (200 to 999 µm and ≥1000 µm) were positively correlated, whereas those of Cladocera (63 to 199 µm), Hemiptera (≥1000 µm), Oligochaeta (200 to 999 µm and ≥1000 µm) were negatively correlated to the first canonical variate (Table 4.2). Invertebrate classes with greatest biomasses in ponds of IF marshes were Copepoda (200 to 999 µm), Oligochaeta (200 to 999 µm), Nematoda (200 to 999 µm), Ostracoda (200 to 999 µm), and Diptera (≥1000 µm), whereas Diptera (≥1000 µm), Nematoda (200 to 999 µm), Copepoda (200 to 999 µm), Nematoda (63 to 199 µm), Ostracoda (200 to 999 µm), and Diptera (200 to 999 µm) had greatest biomasses in ponds of IO marshes (Fig. 4.1, 4.2, and 4.3).

Table 4.1. Summary of *a priori* MANOVA contrasts that tested for differences in biomasses of common invertebrate classes between ponds of unimpounded and impounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline and mesohaline marshes (IF vs. IO and IM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Contrast	Wilk's lambda	*F*	Num df	Den df	Pr. > *F*	Effect size (η^2)
UM vs. IM	0.13	15.91	19	52	<0.0001	0.87
IF vs. IO and IM	0.04	53.61	19	52	<0.0001	0.96

RELATIONSHIPS WITH ENVIRONMENTAL VARIABLES

The CCA solution on common invertebrate classes explained a significant amount of the weighted variance in invertebrate biomass, or distance among invertebrate class centroids (Monte Carlo test, $F = 9.3$, $P = 0.005$). The first axis also explained significant distance among invertebrate class centroids (Monte Carlo test, $F = 69.3$, $P = 0.005$). This first axis explained 14.3 % of the distance among invertebrate class centroids, and 70.6 % of the CCA solution. The second axis explained 3.3 % of the distance among invertebrate class centroids, and 16.4 % of the CCA solution. Eigenvalues of the first and second axis were 0.374 and 0.087 respectively, and inertia was 2.615. The first axis was correlated with all EVs (r >0.33), except turbidity (r <0.05). EVs that best correlated with axis 1 were salinity ($r = 0.86$), silt-clay fraction ($r = 0.80$), and O_2 penetration ($r = 0.80$). Environmental conditions (i.e., the combination of EVs that defines mean axis scores) in ponds of IF and UM marshes also were correlated with the first axis ($r = -0.41$ and 0.96, respectively). Few EVs correlated with axis 2 (Fig. 4.4); only carbon content and turbidity exhibited correlation coefficients >0.3. Environmental conditions in ponds of IF, IO and IM marshes also were correlated with the second axis ($r = –0.80$, 0.55, and 0.47, respectively).

Table 4.2. Canonical correlations (CC) and standardized canonical coefficients (SCC) from *a priori* MANOVA contrasts that tested for differences in biomasses of common invertebrate classes between ponds of unimpounded and impounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline and mesohaline marshes (IF vs. IO and IM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Taxon	Size	UM vs. IM		IF vs. IO and IM	
	(µm)	CC	SCC	CC	SCC
Amphipoda	200 - 999	-0.001	0.201	0.181	0.693
Amphipoda	≥1000	-0.142	-0.056	-0.148	-0.422
Cladocera	200 - 999	-0.267	-0.121	-0.521	-0.640
Copepoda	63 - 199	0.483	0.272	0.363	0.265
Copepoda	200 - 999	0.301	-0.030	0.184	-0.217
Diptera	200 - 999	-0.204	-0.429	0.100	0.372
Diptera	≥1000	-0.021	0.426	-0.151	-0.162
Foraminifera	63 - 199	0.622	0.923	0.723	0.508
Foraminifera	200 - 999	0.433	-0.607	0.723	0.535
Hemiptera	200 - 999	-0.205	-0.014	-0.250	0.092
Hemiptera	≥1000	-0.290	0.026	-0.360	-0.110
Nematoda	63 - 199	0.767	0.772	0.417	-0.109
Nematoda	200 - 999	0.514	-0.031	0.355	0.262
Oligochaeta	200 - 999	-0.222	-0.161	-0.439	-0.583
Oligochaeta	≥1000	-0.091	0.033	-0.327	0.066
Ostracoda	63 - 199	-0.193	0.185	-0.052	0.325
Ostracoda	200 - 999	-0.477	-0.616	-0.224	-0.254
Polychaeta	200 - 999	0.452	0.261	0.500	0.266
Polychaeta	≥1000	0.351	0.050	0.456	0.474

Fig. 4.1. Biomasses (backtransformed least-square means of ash-free dry-weight ± SE, µg / m^2) of the 4 common aquatic invertebrate taxa (x-axis) of size between 63 and 199 µm by marsh type (● = impounded freshwater, ♦ = impounded oligohaline, ■ = impounded mesohaline, and □ = unimpounded mesohaline) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Note that Y-axis is in log scale.

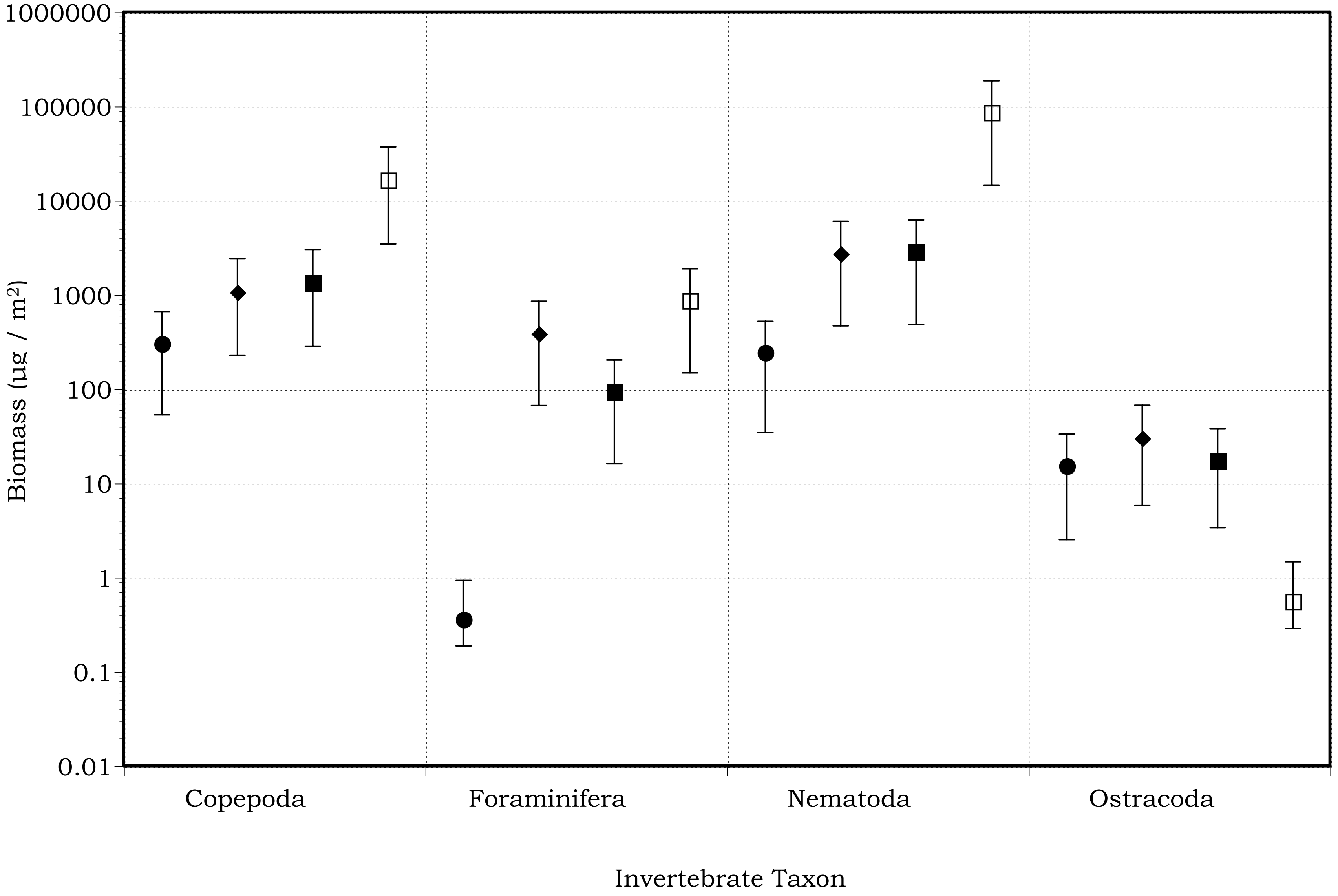

Biomass (µg / m²)
1000000
100000
10000
1000
100
10
1
0.1
0.01
Copepoda
Foraminifera
Nematoda
Ostracoda
Invertebrate Taxon

Fig. 4.2. Biomasses (backtransformed least-square means of ash-free dry-weight ± SE, µg / m^2) of the 10 common aquatic invertebrate taxa (x-axis) of size between 200 and 999 µm by marsh type (● = impounded freshwater, ♦ = impounded oligohaline, ■ = impounded mesohaline, and □ = unimpounded mesohaline) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Note that Y-axis is in log scale.

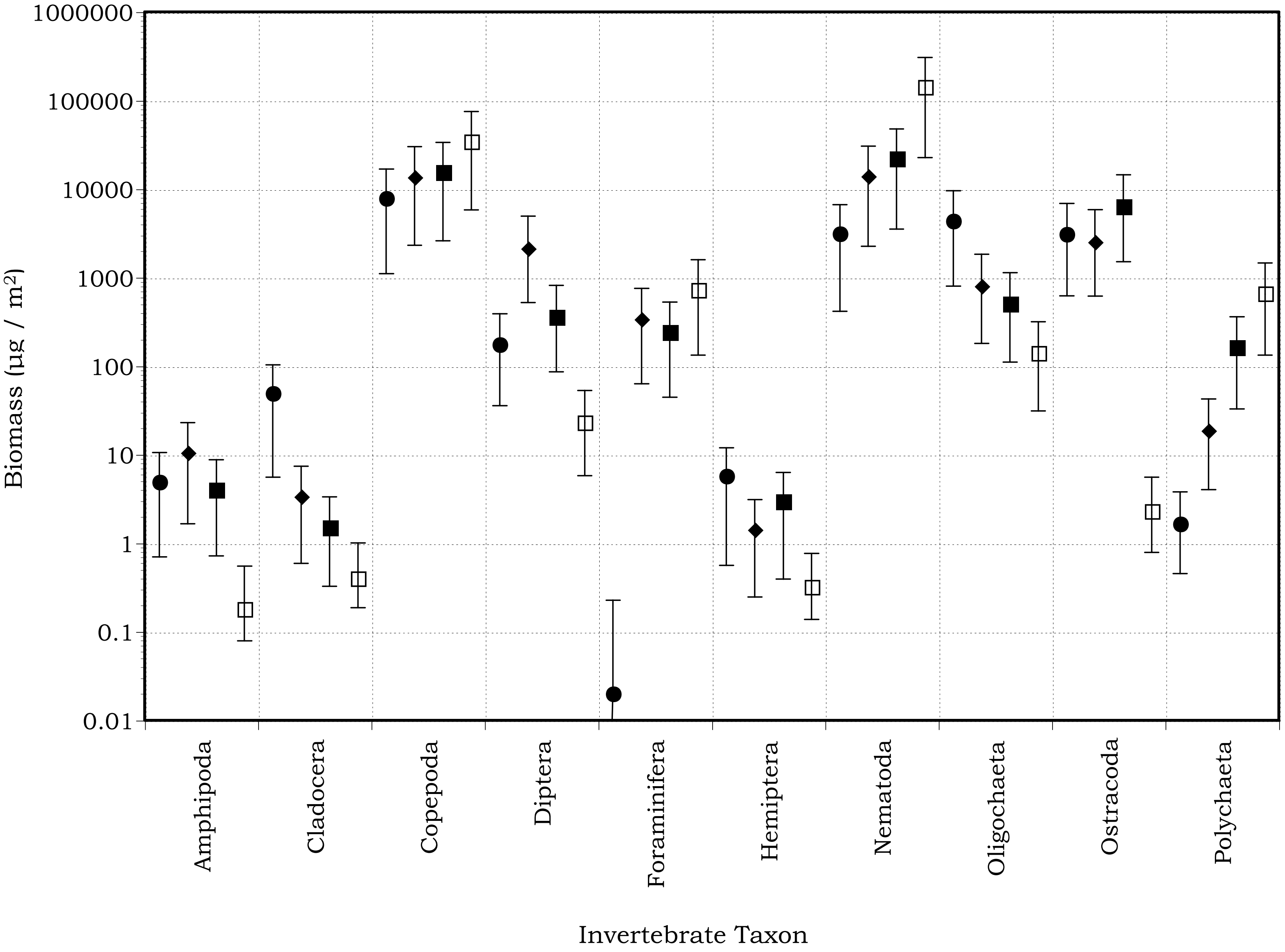

1000000
100000
10000
1000
100
10
1
0.1
0.01
Biomass (µg / m²)
Amphipoda
Cladocera
Copepoda
Diptera
Foraminifera
Hemiptera
Nematoda
Oligochaeta
Ostracoda
Polychaeta
Invertebrate Taxon

Fig. 4.3. Biomasses (backtransformed least-square means of ash-free dry-weight ± SE, μg / m^2) of the 5 common aquatic invertebrate taxa (x-axis) of size ≥1000 μm by marsh type (● = impounded freshwater, ♦ = impounded oligohaline, ■ = impounded mesohaline, and □ = unimpounded mesohaline) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Note that Y-axis is in log scale.

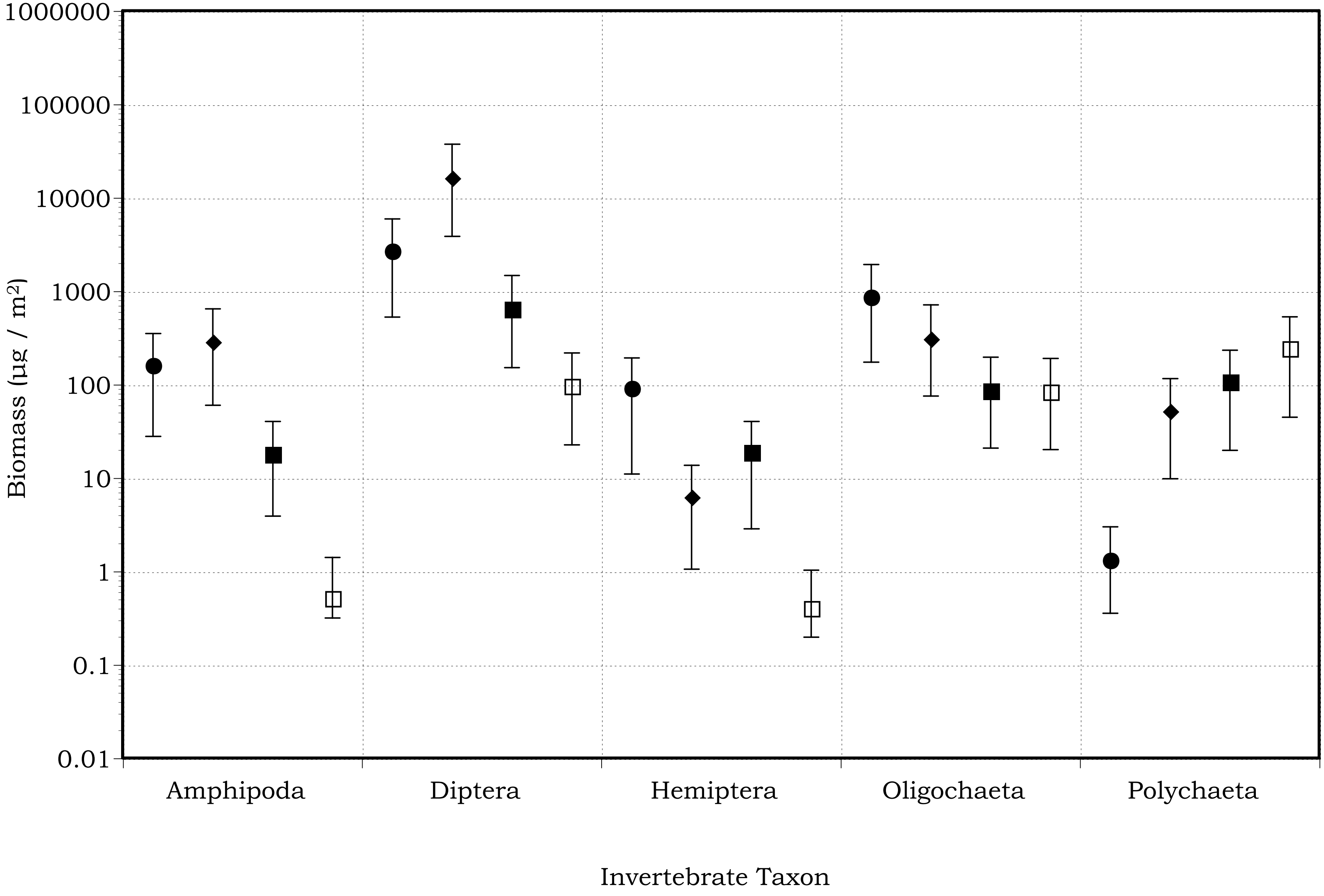

1000000
100000
10000
1000
100
10
1
0.1
0.01
Biomass (µg / m²)
Amphipoda
Diptera
Hemiptera
Oligochaeta
Polychaeta
Invertebrate Taxon

Fig. 4.4. Ordination biplot from canonical correspondence analysis displaying correlations among axes and environmental variables (arrows), and mean axis score of common invertebrate classes (●) and marsh types (■) (IF: impounded freshwater; IO: impounded oligohaline; IM: impounded mesohaline; UM: unimpounded mesohaline) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain, near Grand Chenier, Louisiana. Invertebrate class labels are composed of the first 2 letters of their associated taxon (AM = Amphipoda, CL = Cladocera, CO = Copepoda, DI = Diptera, FO = Foraminifera, HE = Hemiptera, NE = Nematoda, OL = Oligochaeta, OS = Ostracoda, and PO = Polychaeta) and 3 figures describing their size class (006 = size between 63 and 199 µm, 020 = size between 200 and 999 µm, and 100 = size ≥1000 µm). Note that clay designates the variable silt-clay fraction, and O_2 penetration designates depth penetration of dissolved oxygen in sediments.

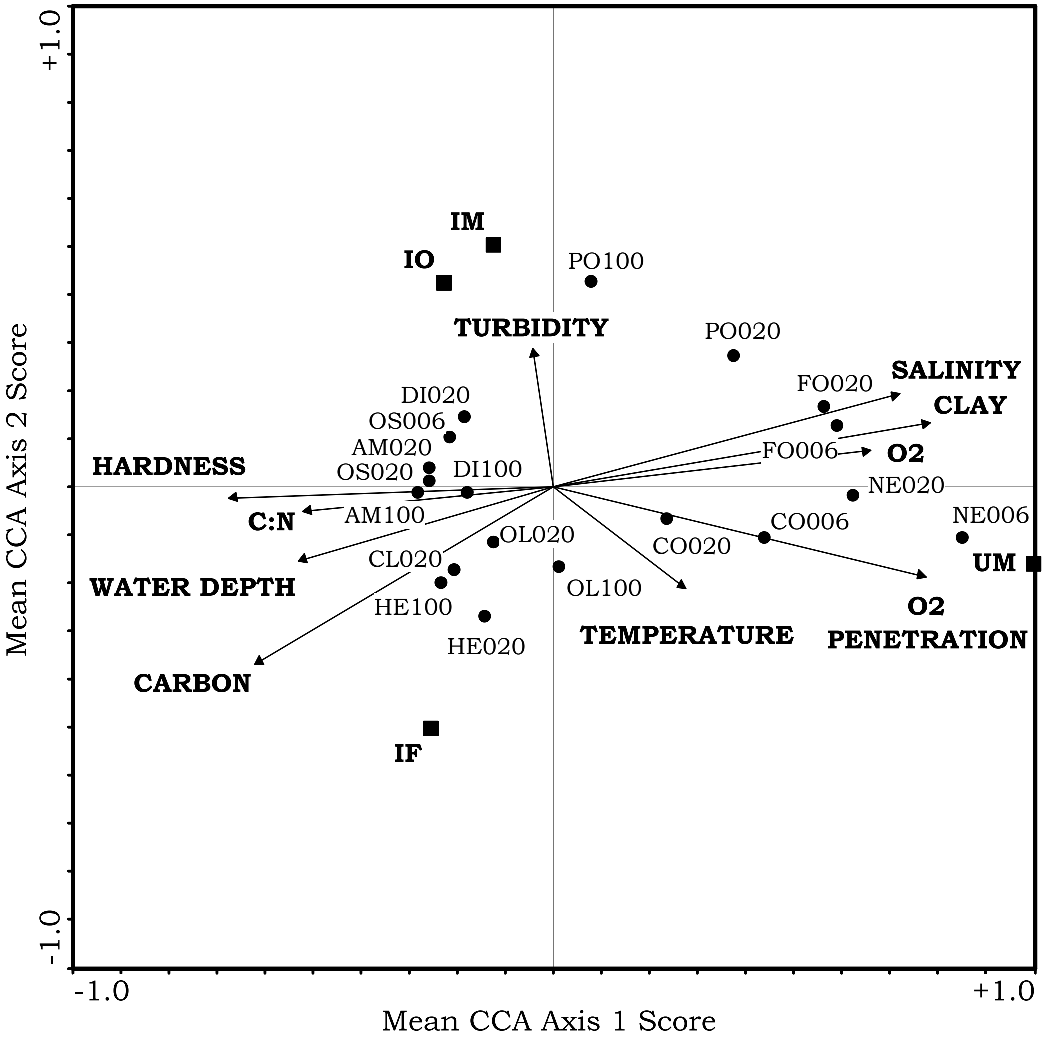

+1.0
-1.0
Mean CCA Axis 2 Score
-1.0
+1.0
Mean CCA Axis 1 Score
IM
IO
PO100
TURBIDITY
PO020
SALINITY
FO020
CLAY
DI020
OS006
FO006
O2
AM020
HARDNESS
OS020
DI100
NE020
NE006
C:N
AM100
OL020
CO006
CO020
UM
CL020
WATER DEPTH
OL100
HE100
O2
TEMPERATURE
PENETRATION
HE020
CARBON
IF

Table 4.3. Cumulative conditional effects (λ_a = cumulative eigenvalues) and marginal effects (λ = eigenvalues of each variable) of environmental variables on common invertebrate biomasses in marsh ponds during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain as computed by forward selection (see Methods). *F* ratios and *P* values associated with marginal effects were computed by Monte Carlo permutations. Seasonal variation is partialled out using month class variables as covariables.

Variable	λ_a	λ	*F*	*P*
Salinity	0.29	0.29	52.50	0.005
Oxygen Penetration Depth in Sediments	0.36	0.24	14.49	0.005
Silt-Clay Fraction	0.39	0.25	6.15	0.005
Water Depth	0.42	0.20	5.13	0.005
Turbidity	0.44	0.02	3.53	0.005
Sediment Hardness	0.45	0.21	2.73	0.010
Carbon	0.47	0.17	2.85	0.005
C:N	0.49	0.11	5.09	0.005
Dissolved Oxygen	0.51	0.19	2.68	0.010
Temperature	0.52	0.05	2.09	0.025
Impounded Freshwater		0.12		
Impounded Oligohaline		0.07		
Impounded Mesohaline		0.04		
Unimpounded Mesohaline		0.35		

Based on the results of forward model selection, salinity and O_2 penetration best explained distance among invertebrate class centroids (Table 4.3). All EVs had a significant effect on invertebrate class biomasses, but each one added little to the effect of salinity and O_2 penetration (λ_a, Table 4.3). Environmental conditions in ponds of UM marshes also explained a relatively large amount of distance among classes centroids (λ = 0.35).

The CCA biplot indicated that Foraminifera (63 to 199 µm and 200 to 999 µm), Nematoda (63 to 199 µm and 200 to 999 µm), Copepoda (63 to 199 µm), and ponds of UM marshes were associated with relatively high values of salinity, silt-clay fraction, O_2, O_2 penetration, and with low values of hardness, C:N, water depth, and carbon (Fig. 4.4). Polychaeta and Copepoda (200 to 999 µm) were associated with values of EVs closer to those of impounded marsh ponds as compared to the above invertebrate classes (Fig. 4.4). All other invertebrate classes were associated with relatively high values of hardness, C:N, water depth, carbon, and low values of salinity, silt-clay fraction, O_2, and O_2 penetration (Fig. 4.4). Ponds of IF, IO, and IM marshes were associated with similar values of EVs (Fig. 4.4). Within invertebrate classes generally associated with ponds of impounded marshes, large Polychaeta (≥1000 µm) were associated with ponds of IM and IO marshes, whereas all size classes of Hemiptera, Oligochaeta, and Cladocera were associated with ponds of IF marshes (Fig. 4.4).

DISCUSSION

COMPARISON OF IM AND UM MARSH PONDS

My results indicated that SMM reduces the biomass of Nematoda (63 to 199 µm) and Foraminifera (63 to 199 µm and 200 to 999 µm) in marsh ponds, whereas it increases that of Ostracoda (200 to 999 µm). However, all size classes of Foraminifera generally were collected in small quantities in ponds of all marsh types (Fig. 4.1 and 4.2); therefore, differences in biomass of Foraminifera among ponds of UM and IM marshes probably are of little biological importance as prey of waterbirds. Nematoda are considered to be infaunal invertebrates because most live among particle interstices (Little 2000), whereas Ostracoda are considered to be epifaunal invertebrates because their locomotion generally is limited to crawling on the sediment-water interface (Delorme 1989). These changes in biomasses of Nematoda and Ostracoda probably occurred because SMM produces more compacted sediments and reduces O_2 penetration in sediments (Chapter 2), whereas the sediment-water interface is largely unconsolidated in UM marsh ponds (Chapter 2). Greater O_2 penetration in sediments may sustain greater populations of infaunal invertebrates (Rhoads 1974, Coull 1985), whereas greater consolidation of sediments probably provides better support to epifaunal invertebrates (Rhoads 1974). My results are consistent with the predictions that SMM increases biomasses of epifaunal invertebrates and decreases that of the infaunal invertebrates. However, I found no differences in biomasses of epifaunal and infaunal invertebrate classes ≥1000 um in size. I am unaware of other studies that have examined effects of SMM or consolidation of soft-sediment on aquatic invertebrate communities.

Although biomasses of Ostracoda (200 to 999 µm) differed significantly between IM and UM marshes, Nematoda was the most important invertebrate class in ponds of UM and IM marshes, followed by Copepoda (Fig. 4.1, 4.2, and 4.3). Ostracoda (200 to 999 µm) had the third highest biomass among common invertebrate classes in ponds of IM marshes, but I collected only 6305 $\mu g/m^2$ of Ostracoda in these ponds on average (Fig. 4.2). Based on my results, meiofaunal invertebrates are the most important components of the invertebrate communities of mesohaline marshes on the Gulf Coast Chenier Plain. Nematoda and Copepoda also are important taxa in salt marshes along the southeastern U.S. coast (Kneib 1984). Finally, I found that Nematoda (63 to 199 µm) were present in greater biomasses in ponds of UM marshes than in those of IM marshes. Finally, my results suggest that SMM negatively affects the most important invertebrate taxon (Nematoda), whereas only secondary classes, such as Ostracoda, benefit from SMM. Thus, SMM affects biomasses of infaunal invertebrate more so than those of epifaunal invertebrates.

I predicted that SMM would positively affect invertebrates that are adapted to lower levels of O_2 and salinity, whereas SMM would negatively affect invertebrates that cannot tolerate low levels of salinity. Ostracoda species can be found at various levels of salinities (Aladin and Potts 1996). However, certain brackish Nematoda species increase O_2 consumption as salinity decreases, and they become inactive at salinities below 5 ‰ (Moens and Vincx 2000). Moreover, other studies documented decreasing quantities of

Nematoda with a decreasing salinity (Montagna and Kalke 1992). However, certain Nematoda species sometimes flourish in freshwater marshes (Yozzo and Smith 1995). Also, Nematoda are very sensitive to changes in sediment variables (Heip et al. 1985), which were correlated with salinity in my study. Thus, it is unclear whether a decrease in Nematoda biomasses was caused by salinity or by changes in sediment variables, or both. Oligochaeta and Diptera sometimes have specific adaptations to low levels of O_2, and are most often found at low salinities (Murkin and Ross 2000). These 2 classes had tendencies for greater biomasses in ponds of IM marshes than in those of UM marshes, but variations in their respective biomasses probably were too large to result in large standardized canonical coefficients in my analysis. Thus, as predicted, my results suggest that reduction in O_2 and salinity caused by SMM affected the most important meiofaunal taxon (Nematoda) of UM marsh ponds.

COMPARISON OF IF WITH IO AND IM MARSH PONDS

My results indicated that biomasses of Foraminifera (63 to 199 µm and 200 to 999 µm) and Amphipoda (200 to 999 µm) were highest in ponds of IM and/or IO marshes, whereas these of Oligochaeta (200 to 999 µm) and Cladocera (200 to 999 µm) were highest in ponds of IF marshes. However, except for Oligochaeta, these invertebrate classes did not have average biomasses greater than 400 $\mu g/m^2$ in ponds of any marsh type (Fig. 4.1 and 4.2); therefore, these invertebrate classes probably were of little biological importance in the diet of waterbirds. Oligochaeta are affected greatly by high levels of salinities but tolerate variation in O_2 because of their blood pigments (Murkin and Ross 2000). Thus, except for the effects of differences in salinities, my results, as predicted, indicated that invertebrate biomasses of IF marsh ponds do not differ greatly from those of IO and IM marsh ponds. These results probably are the consequences of similar hydrologic and sediment variables among ponds of these marsh types as argued previously (Chapters 2 and 3).

RELATIONSHIPS WITH ENVIRONMENTAL VARIABLES

My CCA results indicated that salinity and O_2 penetration were the primary variables explaining distance among centroids of common invertebrate classes in ponds of Gulf Coast Chenier Plain marshes. However, most EVs were correlated with the first CCA axis (Fig. 4.2). Therefore, the effects of many EVs probably were confounded within the effects of salinity and O_2 penetration on distance among invertebrate class centroids. Accordingly, marginal effects (λ) of several sediment and hydrologic variables were close to marginal effects of salinity and O_2 penetration, but did not add much to the cumulative conditional effect (λ_a) of these 2 variables (Table 4.4). Also, UM marsh ponds obtained a higher marginal effect (0.35) than any EVs, which probably corresponds to the cumulative effect of differences in many EVs between unimpounded and impounded marsh ponds. Strong correlations among most EVs correspond to effects of SMM on marsh pond sediments and hydrology because SMM (1) consolidates sediments and increases sediment carbon content, and decreases silt-clay fraction and O_2 penetration (Chapter 2), (2) decreases salinity, O_2, and (3) increases water depth (Chapter 3). Consequently, centroids of IF, IO, and IM marsh ponds were located on 1 side of the CCA biplot, and the centroid of UM marsh ponds on the other side. Thus, my CCA integrated well the effects of SMM on sediments and the hydrology of marsh ponds of the Gulf Coast Chenier Plain.

The strong effect of salinity on invertebrate communities has been reported previously; salinity influences the composition of invertebrate communities because many organisms of soft sediments are adapted to specific ranges of salinity (Kneib 1984, Coull 1985, Flint and Kalke 1986, Ingole and Parulekar 1998, Murkin and Ross 2000). O_2 penetration also affects invertebrates by restricting potential vertical distribution within sediments for non-burrowing organisms (Rhoads 1974, Coull 1985, Flint and Kalke 1986, Moodley et al. 2000). However, contrary to my results, it was observed that O_2 penetration usually increases with particle size because larger particles allow water to move deeper in sediments (Rhoads 1974). I found an inverse relationship between particle size and O_2 penetration probably because: (1) drawdowns in impounded marshes probably result in formation of larger particles due to the cementing of mineral particles with the organic matter, which also consolidates sediments and prevents oxygen from penetrating them (Chapter 2), and (2) frequent reworking of sediments in ponds of UM marshes due to tidal flows probably result in formation of sediments that comprise a large clay-silt fraction but that also are softer and therefore allow deeper penetration of oxygen (Chapters 2 and 3). Thus, sediment hardness and turbulence due to tides seemingly are more important than is particle size in determining O_2 penetration in marsh ponds of the Gulf Coast Chenier Plain. Finally, invertebrate communities of soft sediments are affected strongly by simultaneous changes in both salinity and O_2 penetration (Coull 1985, Flint and Kalke 1986).

MANAGEMENT IMPLICATIONS

My results indicated that SMM reduces biomasses of the most important infaunal invertebrates in ponds of UM marshes (Nematoda 63 to 199 µm). Previous studies suggest that meiofauna may be important foods for certain species of wintering waterfowl such as Green-winged Teal (*Anas crecca*) (Gaston 1992), Northern Shovelers (*Anas clypeata*) (Gaston 1992), and shorebirds such as Western Sandpipers (*Caladris mauri*) (Sutherland et al. 2000). However, the above waterfowl species probably cannot filter prey smaller than 200 µm (Nudds and Bowlby 1984, Tremblay and Couture 1986, Kooloos et al. 1989). Moreover, other waterfowl species probably do not use meiofauna as a food resource because of their incapacity to sieve food items of a minimal size between 0.8 and 1.3 mm (Nudds and Bowlby 1984, Tremblay and Couture 1986, Kooloos et al. 1989). The minimum prey size of shorebirds is unknown (Sutherland et al. 2000). Therefore, reduction in biomasses of small Nematoda following implementation of SMM in UM marshes on the Gulf Coast Chenier Plain probably does not greatly affect biomasses of invertebrate foods available to wintering waterbirds and concomitantly densities of wintering waterbirds. However, diet studies of wintering waterbirds rarely document the ingestion of meiofauna because stomach contents generally are inspected macroscopically to identify food items (Afton et al. 1991, Euliss et al. 1991, Thompson et al. 1992, Sutherland et al. 2000); therefore, very small prey could be missed. Accordingly, I recommend that meiofauna and their importance as foods to waterbirds be given more attention in future research on wetlands of the Gulf Coast Chenier Plain.

My results indicated that SMM increases biomasses of Ostracoda (200 to 999 µm). Waterbird species that are capable of capturing prey of the size of Ostracoda include Green-winged Teal (Gaston 1992), Northern Shovelers (Gaston 1992), and Sandpipers (Sutherland et al. 2000). However, the above waterfowl species consume prey of a variety of sizes (Nudds and Bowlby 1984) and Green-winged Teal consume seeds and invertebrates during winter (Euliss and Harris 1987). Therefore, it is unlikely that the observed increase in Ostracoda (200 to 999 µm) due to SMM have major effects on biomasses of invertebrate prey available to waterbirds and consequently on densities of waterbirds in impounded marsh ponds.

My results suggest that the primary effect of the conversion of IF marshes to marsh types of higher salinity levels relative to invertebrate communities would be a reduction in the biomass of Oligochaeta (200 to 999 µm). Previous studies suggest that Oligochaeta may complement diets of certain shorebirds (Skagen and Oman 1996) and waterfowl (Safran et al. 1997) that use Gulf Coast marshes during winter. However, there is little evidence that changes in biomasses of Oligochaeta would greatly affect the biomasses of invertebrate prey available to waterbirds because vertebrate predators seemingly do not affect quantities of Oligochaeta in freshwater marshes (Thorp and Bergey 1981). Based on these results, I predict that densities of invertebrate-feeding waterbirds should be similar between ponds of IF marshes and those of IO and IM marshes. Further research on the importance of Oligochaeta as prey for waterbirds of coastal marshes of the Chenier Plain is needed to clarify whether conversion of IF marshes to marsh types of higher salinity may affect invertebrate prey available to wintering waterbirds.

My CCA integrated well the variation in sediments and salinities that differentiate ponds of the various marsh types on the Gulf Coast Chenier Plain. Moreover, my results indicated that environmental conditions maximizing invertebrate biomasses probably lie somewhere between those in ponds of IF, IO, IM, and UM marshes because only few invertebrate class centroids were associated closely with centroids of any of these marsh types (Fig. 4.4). Thus, marsh management with objectives of maximizing biomasses of various invertebrate classes should diversify sediments and salinity within and among ponds. Management objectives for increasing aquatic invertebrates in order to maximize the use of marshes by waterbirds are common (Euliss and Grodhaus 1987, Twedt et al 1998). However, little information is available on effects of sediments, hydrology, and invertebrate biomasses on wintering waterbirds using marsh ponds of the Gulf Coast Chenier Plain. Research clearly is needed to increase our knowledge of consequences of SMM and variations in salinity on marsh ponds of the Gulf Coast Chenier Plain.

CHAPTER 5

COMPARING WATERBIRD ABUNDANCES AMONG WETLANDS: A QUANTITATIVE METHOD TO CONTROL FOR VARIATION IN WATER DEPTH

INTRODUCTION

Waterbirds (i.e., anseriformes, charadriiformes, ciconiiformes, gaviiformes, gruiformes, pelecaniformes, podicipediformes, and procellariformes) have a variety of adaptations for exploiting wetland habitats. In non-diving waterbirds, variation in morphological features, such as bill length and shape, bill lamellae distance, neck length, leg length, and body size allow species to forage at different depths and on different foods (Baker 1979, Poysa 1983, Nudds and Bowlby 1984, Zwarts and Wanink 1984). Morphological differences among species apparently produce foraging niche differentiation that reduces interspecific competition and increases species persistence (Jefferies and Lawton 1984).

Researchers that have examined the influence of water depth on the abundance of non-diving waterbirds generally report the average water depth used by each species (Weber and Haig 1996, Safran et al. 1997, Isola et al. 2000) or the range of water depths used (Davis and Smith 1998, Ntiamoa-Baidu 1998). Some researchers have reported negative correlations between water depth and bird abundance (Epstein and Joyner 1988, Colwell and Taft 2000), although the end result of this is biologically unrealistic because it implies that maximum waterbird abundance is found where there is no water. In general, there should be a water depth that maximizes a species abundance and a range of water depths that a species uses, which depend on the interaction between feeding strategy and morphological features of the species. The relationship between water depth and bird abundance probably is nonlinear for most species, with low abundance at water depth 0, followed by an increase afterward until a maximum is reached, and then a decrease to abundance 0 when water depth is too deep for a species to forage. However, the mathematical functions of such non-linear relationships are unknown, and probably vary among species depending on the flexibility in water depths that each species can exploit.

Scientific studies comparing animal abundances among habitats require replication in space (e.g., blocks, plots, subplots) and time (repeated measurements) so that conclusions can be generalized to the greatest extent possible (Sokal and Rohlf 1995). Statistical comparisons of waterbird abundances among wetlands are difficult because water depths generally cannot be controlled, and therefore are likely to vary among replicated areas and time periods. Therefore, both wetland and water depth effects are confounded, and one cannot easily ascertain the extent to which of the 2 factors affect bird abundance. Several researchers that compared bird abundances among wetlands admitted a confounding effect of the variation in water depth on wetland comparisons, but did not include water depth in their predictive models (Hands et al. 1991, Frederick and McGehee 1994). I believe that such confounded analyses provide equivocal results and may lead to incorrect conclusions. Because the relationship between waterbird abundance and water depth probably is not linear and varies among species, it is difficult to control for the effect of water depth on bird abundance directly in statistical models used to compare bird abundances among wetlands. Accordingly, there is a need for a methodological framework that estimates bird abundance corrected for water depth, which allows unbiased comparisons of various wetlands.

I described a method to correct bird abundance for variation in observed water depth that can be used for comparisons among wetlands; I initially used nonparametric regressions to estimate how bird abundance varies with water depth. I then computed differences between observed abundances and those predicted by the nonparametric regression at recorded water depths (analogous to residuals in parametric models), and corrected differences for their relative levels of observed and corrected abundances. Finally, I compared wetlands using both observed and corrected abundances within an analysis of variance to illustrate differences between these 2 estimates.

METHODS

To illustrate my methodology, I created hypothetical survey data for 2 waterbird species that differed in their water depth and wetland selection. Species *G* (i.e., a generalist species) uses a large range of water depths and its abundance is maximized at water depth of 15 cm. Species *S* (i.e., a specialist species) uses a narrow range of water depths and its abundance is maximized at a water depth of 5 cm. I built a curve of maximum abundance by 1-cm water depth classes for depths between 0 and 40 cm for each species to compute hypothetical bird counts using the following equations:

for *G* species in water depths 0-15 cm, $\mathrm{MAX} = \log(\mathrm{WD})$,

for *G* species in water depths 16-40 cm, $\mathrm{MAX} = \log(\mathrm{PWD} - [\log(\mathrm{PWD})])$,

for *S* species in water depths 0-5 cm, $\mathrm{MAX} = (\mathrm{WD})^3$,

for *S* species in water depths 6-40 cm, $\mathrm{MAX} = ((\mathrm{PWD}) - 0.2)^3$,

where MAX is the maximum abundance, WD is water depth, PWD is the water depth of the previous water depth class after transformation (e.g., for the *S* species at WD 6, PWD = 4.8; at WD 7, PWD = 4.6; etc.), and log corresponds to the natural logarithm. I subtracted 0.2 or log(PWD) from the previous water class to obtain asymmetric curves to obtain a decrease in maximum abundance after a peak in maximum abundance is reached.

I produced the above maximum abundance curves for 4 hypothetical wetlands that differed in their range of water depths through replicated bird counts (Table 1). I used a total of 125 hypothetical bird counts in each wetland (both species counted), where the average water depth was measured after the bird counts. Bird counts were classified by their average water depth (by 1-cm classes), and occurred 3 times for each 1-cm water depth classes in wetland A and D, and 5 times each for wetland B and C. I computed bird counts using the following equation:

bird abundance = MAX * habitat preference factor * random number,

where I used MAX associated with the water depth at which the bird count occurred, the habitat preference factor was expressed by a multiplicative factor that varied among wetlands (Table 5.1), and the random number was selected between 0 and 1, using the function RAND in the program Excel 2000 (Microsoft Corporation 1999). Habitat preference factors and ranges in water depths for each species were distributed in such way that I obtained wetlands similarly preferred but with different ranges of water depths, and wetlands differently preferred with similar ranges of water depths (Table 5.1). I created such hypothetical distributions to separate the effect of water depth from the effect of wetland preference on waterbird abundance.

Table 5.1. Preferred water depth and habitat preference factor used to compute hypothetical abundances of a specialist (*S* species) and generalist waterbird species (*G* species) during 125 surveys in 4 wetlands of varying water depth (WD range).

	Wetland			
	A	B	C	D
S species				
Preferred water depth	5	5	5	5
Habitat preference factor	2	0.1	0.1	0.1
G species				
Preferred water depth	15	15	15	15
Wetland preference factor	10	100	100	100
Observed WD range (cm)	0-40	16-40	0-24	0-40

RELATIONSHIP BETWEEN WATER DEPTH AND BIRD ABUNDANCE

For each species, I quantified the relationship between bird abundance and water depth using nonparametric regressions (Schimek 2000). For each species, I classified bird counts by their average water depth, and averaged bird abundance for all bird counts and wetlands by 1-cm depth class; I assumed that the relationship between water depth and bird abundance generally was equivalent throughout all wetlands because it is primarily related to the species morphologic features, such as leg length and body size. Also, I assumed that water depth varied little within water bodies where bird counts occurred, and therefore that the average water depth represents a good estimate of the water depth to which bird species are adapted. Nonparametric regression is considered as a compromise between a linear regression of 2 variables, and a series of linear regressions for each pair of consecutive points of these 2 variables (i.e., local regressions) (Schimek 2000). Nonparametric regressions use a smoothing parameter (λ) that penalizes slopes of consecutive local regressions that vary too rapidly (Schimek 2000). If $\lambda = \infty$, then the nonparametric regression produces a constant linear regression fit, whereas at $\lambda = 0$ the nonparametric regression retains all original local regressions (Schimek 2000). The generalized cross-validation criterion (GCV) is used to estimate λ that minimizes the mean square error; the lowest GCV value is associated with the lowest mean square error (Schimek 2000).

I used PROC LOESS in SAS 8.2 (Institute 1999) to compute nonparametric regressions between mean bird abundance (by 1-cm depth classes) and water depth. I computed nonparametric regressions for smoothing parameter values at each decimal between 0.1 and 1.0, and chose the smoothing parameter associated with the lowest GCV (SAS Institute, Inc. 1999). In PROC LOESS, I requested that 2 degrees of local polynomials be used for each local regression (option DEGREE=2, SAS Institute 1999) because of my model assumption that bird abundance increases until a maximum is reached, and decreases afterward (i.e., quadratic function).

CORRECTION OF OBSERVED ABUNDANCES FOR VARYING WATER DEPTH

I compared observed abundances with predicted mean bird abundances from nonparametric regressions at corresponding 1-cm water depth classes and computed differences (i.e., analogous to residuals of parametric models). These differences represent water depth corrected abundances, where there is a common water depth (the fit), and therefore can be used as estimates of the variation in bird abundance unexplained by water depth.

I encountered some problems with negative predicted values; a negative predicted abundance coupled with an absence of birds provides a positive difference. To avoid this problem, I replaced negative predicted abundances with 0. Furthermore, I found that negative differences were limited to differences between the fit and 0 birds, which may lead to biased mean differences between a wetlands differing in average water depth. For example, at a model prediction of 0.1 birds, the difference with an observed value cannot be lower than –0.1, whereas at a prediction of 2 birds, the maximum negative difference was -2. Therefore, I transformed differences in observed-predicted abundances by a relative measure of their corresponding observed and predicted abundances:

relative corrected abundance = $([(OBS - PRED) / (OBS + PRED)] * 100)$,

where OBS is the observed abundance, and PRED is the predicted abundance. In cases when both observed and predicted abundances were 0, I set relative corrected abundances to –100% to ensure that I always obtain average abundances of –100% when no birds were present. These calculations allowed me to obtain: (1) relative differences of 0 when predicted and observed abundances were equal at any level of abundances (except when predicted and observed abundances were 0), (2) negative values when predicted abundances exceeded observed abundances (always ≥-100%), and (3) positive values when observed abundances exceeded predicted abundances (always ≤100%) (Table 5.2).

Table 5.2. Relative corrected abundance ([observed – predicted abundance] /[observed + predicted abundance] X 100) at various levels of abundances observed and predicted from nonparametric regression of water depth with mean observed abundance by 1-cm water depth classes.

Predicted	Observed abundance														
abundance	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1	2	5	10	100
0	-100[a]	100	100	100	100	100	100	100	100	100	100	100	100	100	100
0.1	-100	0	33	50	60	67	71	75	78	80	82	90	96	98	100
0.2	-100	-33	0	20	33	43	50	56	60	64	67	82	92	96	100
0.3	-100	-50	-20	0	14	25	33	40	45	50	54	74	89	94	99
0.4	-100	-60	-33	-14	0	11	20	27	33	38	43	67	85	92	99
0.5	-100	-67	-43	-25	-11	0	9	17	23	29	33	60	82	90	99
0.6	-100	-71	-50	-33	-20	-9	0	8	14	20	25	54	79	89	99
0.7	-100	-75	-56	-40	-27	-17	-8	0	7	13	18	48	75	87	99
0.8	-100	-78	-60	-45	-33	-23	-14	-7	0	6	11	43	72	85	98
0.9	-100	-80	-64	-50	-38	-29	-20	-13	-6	0	5	38	69	83	98
1	-100	-82	-67	-54	-43	-33	-25	-18	-11	-5	0	33	67	82	98
2	-100	-90	-82	-74	-67	-60	-54	-48	-43	-38	-33	0	43	67	96
5	-100	-96	-92	-89	-85	-82	-79	-75	-72	-69	-67	-43	0	33	90
10	-100	-98	-96	-94	-92	-90	-89	-87	-85	-83	-82	-67	-33	0	82
100	-100	-100	-100	-99	-99	-99	-99	-99	-98	-98	-98	-96	-90	-82	0

[a] Relative corrected abundance was set to - 100 when both predicted and observed abundances were 0 (see Methods).

Relative corrected abundance estimates are related to the observed:predicted abundance ratio. For example, at observed abundance 0.1 and predicted abundance 0.4, the relative corrected abundance is –60% (Table 5.2), and therefore the ratio observed: predicted abundance is 0.25 (0.1/0.4). At observed abundance 0.5 and predicted abundance 2.0, the relative corrected abundance also is –60% (Table 5.2), and the observed:predicted abundance ratio also is 0.25 (0.5/2.0). Thus, for each relative corrected abundance, there is a corresponding observed:predicted abundance ratio. One could argue that the use of this ratio rather than the relative corrected abundance would be more straightforward. However, when 0 birds are predicted, the observed: predicted abundance ratio is problematic because of the insolvability of the ratio when the denominator is 0.

In summarizing these calculations, the observed abundance describes how many birds were using the wetland surveyed, whereas the relative corrected abundance describes the extent at which bird abundances followed predictions from recorded water depths. Thus, the comparison of observed abundances among wetlands indicates whether more birds were using one wetland than another. In contrast, comparison of relative corrected abundances among wetlands indicates whether wetlands differ in bird abundances with respect to that expected based upon the average use at recorded water depths.

STATISTICAL ANALYSIS OF OBSERVED AND RELATIVE CORRECTED ABUNDANCES

I used separate analysis of variance (ANOVA) to compare wetlands for both relative corrected abundances and observed abundances of my 2 hypothetical waterbird species among wetlands using PROC MIXED (SAS Institute 1999). Pairwise comparisons of abundances among wetlands were conducted using the pdiff option in PROC MIXED. In the results, I present least-square means with their corresponding standard errors. I used $P < 0.05$ as the critical value in all statistical tests.

RESULTS

NONPARAMETRIC REGRESSIONS OF BIRD ABUNDANCE ON WATER DEPTH

As desired, the nonparametric regression fit of *G* species abundance with water depth (GCV = 0.91, smoothing parameter = 0.5) indicated that this species used a wide range of water depths (Fig. 5.1). The regression model predicted >10 birds at water depths between 1 and 31 cm, and a maximum abundance of about 50 birds at a water depth of 17 cm (Fig. 5.1).

The nonparametric regression fit of *S* species abundance with water depth (GCV = 0.67, smoothing parameter = 0.2) indicated that this species generally was associated with low water depth (maximum predicted abundance of 53 birds at 5 cm of water) and was more restricted by water depth than was the *G* species (Fig. 5.2). The regression model for this species predicted more than 10 birds between 3 and 15 cm of water only, and less than 1 birds for water depths greater than 22 cm (Fig. 5.2).

COMPARISONS OF OBSERVED AND RELATIVE CORRECTED ABUNDANCES AMONG WETLANDS

The mean observed abundance of the *G* species varied greatly among wetlands (3.2 to 42.0 birds) (Table 5.3). ANOVA and subsequent pairwise comparisons indicated that observed abundances differed among all wetlands (Table 5.3). In contrast, mean relative corrected abundances for the *G* species in wetlands B, C, and D, were close to 0, which indicates that bird abundances generally were close to abundances expected based on recorded water depth in those wetlands (Table 5.3). Mean relative corrected abundance of the *G* species in wetland A was –71.8, which indicates that approximately 6 times fewer birds were counted there than that expected based on recorded water depth (associated ratio observed:predicted abundance = 0.16). ANOVA and subsequent pairwise comparisons indicated that relative corrected abundance on wetland A differed from the other wetlands, whereas estimates for wetlands B, C, and D did not differ (Table 5.3).

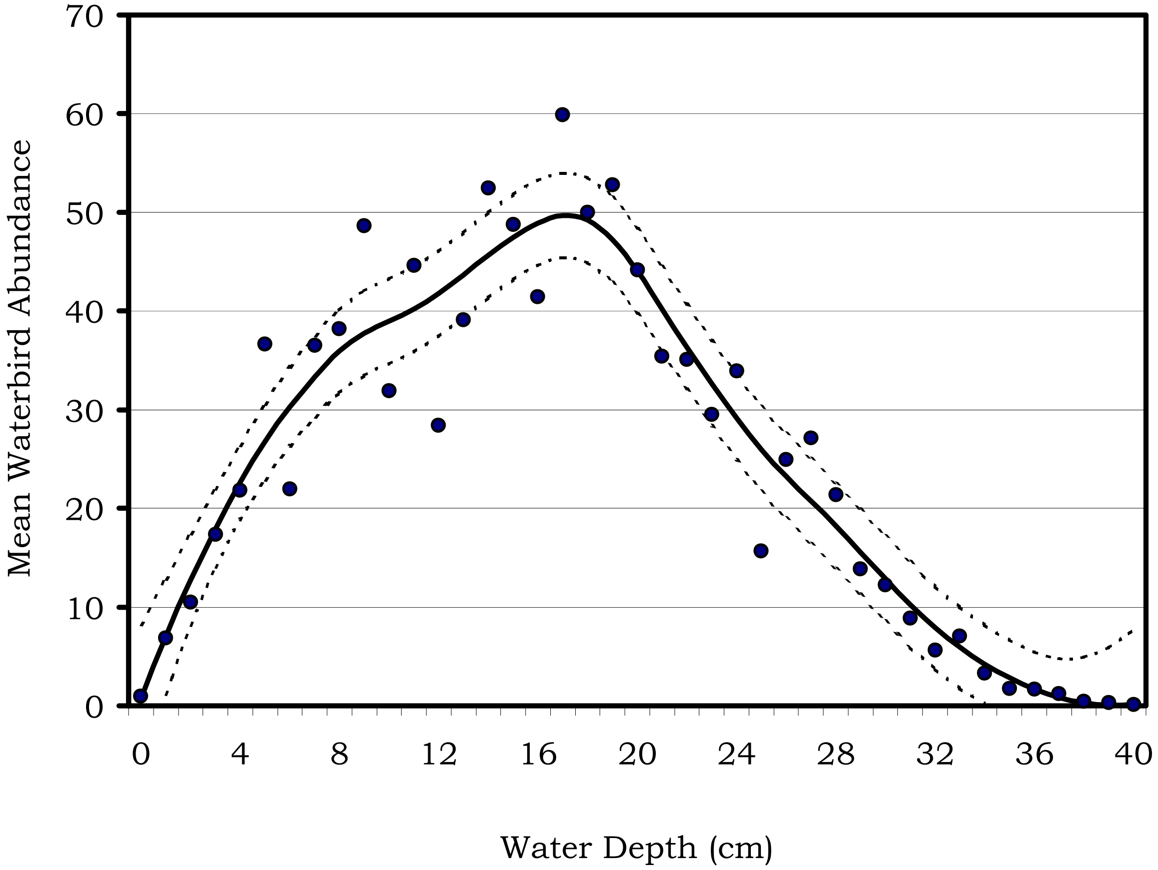


Fig. 5.1: Mean observed abundance of a hypothetical generalist waterbird (*G* species) by 1-cm water depth classes (dots) and nonparametric fit between these 2 variables (solid line) with associated 95% confidence intervals (dotted lines) as computed from hypothetical surveys in 4 wetlands (see Methods for calculations).

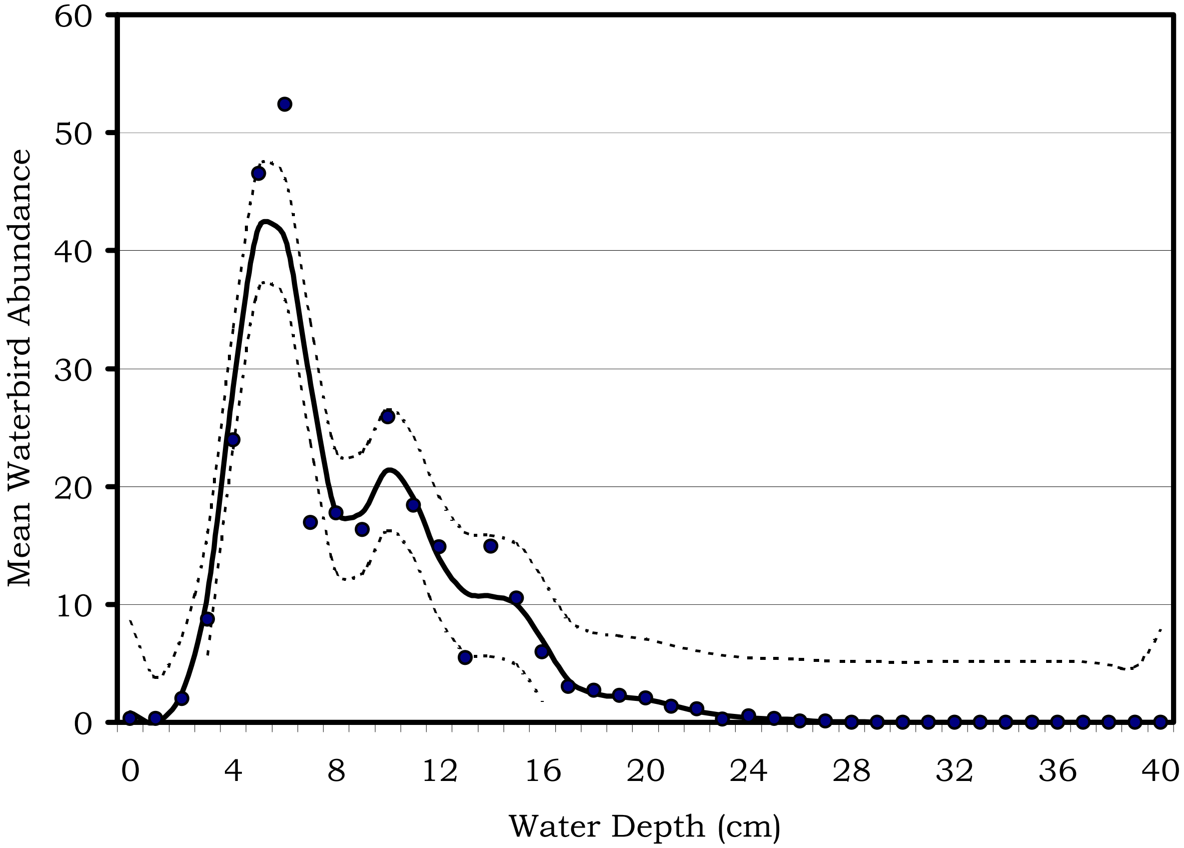


Fig. 5.2: Mean observed abundance of a hypothetical specialist waterbird (*S* species) by 1-cm water depth classes (dots) with the nonparametric fit between these 2 variables (solid line) with associated 95% confidence intervals (dotted lines) as computed from hypothetical surveys in 4 wetlands (see Methods for calculations).

Table 5.3: Mean (least-square means ± SE) observed abundances (OA) and relative corrected abundances (MRCA) of hypothetical generalist (G species) and specialist (*S* species) species of waterbirds, and mean water depth (MWD) in 4 hypothetical wetlands.

Wetland	MWD	*G* species		*S* species	
	(cm)	OA	MRCA	OA	MRCA
A	20	3.2 ± 2.4 ^{a}	-71.8 ± 3.3 ^{a}	23.3 ± 1.9 ^{a}	0.6 ± 4.0 ^{a}
B	28	26.2 ± 2.4 ^{b}	1.0 ± 3.3 ^{b}	0.2 ± 1.9 ^{b}	-84.3 ± 4.0 ^{b}
C	12	42.0 ± 2.4 ^{c}	0.6 ± 3.3 ^{b}	2.2 ± 1.9 ^{b}	-60.6 ± 4.0 ^{c}
D	20	33.0 ± 2.4 ^{d}	2.2 ± 3.3 ^{b}	1.1 ± 1.9 ^{b}	-75.3 ± 4.0 ^{b}

^{abcd} Similar letters denote means that did not differ (P >0.05) within a column.

The mean observed abundance of the *S* species varied between 0.2 and 23.3 birds (Table 5.3), and ANOVA and subsequent pairwise comparisons indicated a significant difference among all wetlands. Mean relative corrected abundances of Wetland A approached 0, indicating that bird abundance in this wetland closely followed that expected based solely on recorded water depth. ANOVA and subsequent pairwise comparisons indicated that mean relative corrected abundances of *S* species differed among wetlands, with wetland A supporting higher bird abundances than the 3 other wetlands (Table 5.3). Mean relative corrected abundance of wetlands B, C, and D ranged between – 60.6 to –84.3, indicating that these wetlands supported between 4 and 13 times fewer birds than those expected based on recorded water depth (associated observed:predicted abundance ratios between 0.25 and 0.08). Finally, mean relative corrected abundance was greater in wetland C than in wetlands B and D (Table 5.3).

DISCUSSION

Waterbird species generally are adapted to exploit different ranges in water depth (Baker 1979, Poysa 1983, Nudds and Bowlby 1984, Zwarts and Wanink 1984). This causes problems when comparing waterbird abundances among wetlands because it is difficult to separate effects of wetlands from effects of water depth. Accordingly, I developed a methodology to correct waterbird abundance for variation in water depth based on the nonparametric regression of these 2 variables, which can be used in subsequent comparisons of wetland habitats.

My analysis of observed and relative corrected abundances of the *G* species provided contrasting results. Three hypothetical wetlands of similar preference factor (wetlands B, C, and D) differed in observed abundances just by manipulating water depths at which birds were recorded, whereas their relative corrected abundances did not differ. Consequently, my proposed methodology using relative corrected abundance adequately removed effects of variation in water depth from effects of wetlands on variation in bird abundance for the *G* species.

My analysis also indicated that relative corrected abundances of the *S* species differed among hypothetical wetlands of similar preference factor in some cases. This is because the *S* species used a narrow range of water depths that corresponded best to those recorded in wetland C, whereas the other 2 wetlands of similar preference (B and C) comprised many counts associated with water depths that the specialist bird avoided. Thus, my methodology may yield differences in relative corrected densities of waterbirds among wetlands of similar preferences, but these results are biologically insignificant because of the very low usage of such wetlands. Comparisons of observed and relative corrected abundances of the *S* species indicated that both estimates of abundance provide similar results when differences among wetlands are very large.

In conclusion, my proposed methodology, using relative corrected abundances, adequately separates the effect of water depth from the effect of the wetlands, and therefore provides unbiased estimates that can be used for comparisons of wetlands of varying water depths. Accordingly, I recommend that users of my methodology present both relative corrected abundances and observed abundances to ensure an adequate interpretation of results. Also, because there is no equation associated with nonparametric regressions, I suggest that users include their predicted abundances by water depth classes in their publications. These data could be useful to researchers that want to compare results among studies, or do not have sufficient data to compute their own predicted abundances.

CHAPTER 6

EFFECTS OF WATER DEPTH, SALINITY, AND STRUCTURAL MARSH MANAGEMENT ON WINTERING WATERBIRD DENSITIES OF MARSH PONDS ON THE GULF COAST CHENIER PLAIN

INTRODUCTION

Waterbird (anseriformes, charadriiformes, ciconiiformes, gaviiformes, gruiformes, pelecaniformes, phoenicopteriformes, podicipediformes, and procellariformes) communities are influenced greatly by food accessibility within wetlands, which often is limited by water depth. Non-diving waterbirds have specific bill lengths and shapes, neck lengths, leg lengths, and body sizes that allow them to feed at specific water depths and on certain foods (Baker 1979, Poysa 1983, Zwarts and Wanink 1984). Diving waterbirds probably are limited by a minimum water depth that allows them to forage. Therefore, fluctuating hydrologies within and among wetlands dictate where and when waterbird species can access their foods.

Waterbird communities also are influenced by types and quantities of foods available within wetlands. Aquatic invertebrates represent a primary food resource for many wintering waterbirds. For example, shorebirds feed almost exclusively on invertebrates (Skagen and Oman 1996), whereas consumption of invertebrates varies widely among waterfowl (Afton et al. 1991, Euliss et al. 1991, Thompson et al. 1992, Batzer et al. 1993), and generally increases at the end of winter (Krapu and Reinecke 1992). Large wading birds also consume aquatic invertebrates during winter (Martin and Hamilton 1985). Non-diving waterbirds are adapted to capture prey of different sizes or minimal sizes in the water or sediments (Nudds and Bowlby 1984, Zwarts and Wanink 1984). Prey selection by dabbling ducks in relation to food item size is related to bill lamellae distance, which varies between 0.43 and 1.06 mm in most species, except for Mallards (*Anas platyrhynchos*) (Nudds and Bowlby 1984, Tremblay and Couture 1986, Kooloos et al. 1989). Thus, compositions of waterbird communities probably are influenced by compositions of aquatic invertebrate communities present in wetlands.

Aquatic invertebrate communities primarily are affected by hydrologic and sediment variables that determine the presence of specific taxa, their abundances, and sizes. Sediment organic content and water turbidity affect the production of bacteria and algae upon which invertebrates feed (Benke 1984, Batzer and Wissinger 1996, Robinson et al. 2000). The amount of undecomposed vegetation in sediments affects the structural complexity of invertebrate habitats (Minshall 1984). Levels of salinity, dissolved oxygen (O_2), and temperature greatly affect osmoregulation and respiration in aquatic invertebrates; consequently, invertebrates generally adapted to specific ranges of these variables (Perkins 1974). Sediment hardness, penetration of oxygen, and particle size particularly affect benthic epifaunal (living on the sediment surface) and infaunal (living in the sediments) invertebrates. Hard sediments provide physical support to large epifaunal invertebrates (Rhoads 1974). Invertebrates that live in the oxygen-depleted zone of sediments must respire using anaerobic processes or provide their own oxygen (Little 2000). Particle size determines how water and oxygen penetrate sediments and the interstitial space available to meiofauna (0.063 – 0.5 mm) (Little 2000). Thus, sediment and hydrologic characteristics of wetlands may affect waterbird communities because of their effects on invertebrate communities.

Marshes along the northern coast of the Gulf of Mexico are important to wintering waterbirds because 19% of the waterfowl wintering in the U.S. use marshes of the Louisiana Gulf coast (Michot 1996); this region also is a key area for wintering wading birds (Mikuska et al. 1998) and migrating shorebirds (Helmers 1992). However, considerable changes have occurred in marshes of the Gulf Coast Chenier Plain during the last century. Dredging of north-south waterways, occurrence of large-scale muskrat eat-outs, and a severe drought that occurred in the early 1950s apparently facilitated saltwater intrusion and caused a large marsh vegetation die-off at the junction of freshwater and oligohaline marshes (Wicker et al. 1983). Consequently, starting during the mid-1950s, numerous marshes were managed using structural marsh management (levees, water control structures and impoundments; SMM) with objectives of revegetating open water areas that had formed, stopping saltwater intrusion, and increasing the productivity of waterfowl food plants (Wicker et al. 1983). SSM now commonly is practiced throughout the Gulf Coast Chenier Plain (Day et al. 1990).

Studies of effects of SMM on plant foods preferred by waterfowl suggest that impoundments on the Gulf Coast Chenier Plain should be used more heavily by waterfowl than are their unimpounded counterparts (Chabreck 1960, Jemison and Chabreck 1972). However, there is little evidence that SMM within the Gulf Coast Chenier Plain effectively attracts wintering waterfowl (Chabreck et al. 1974) despite the increasing proliferation of impoundments during the last 60 years. Previous research indicated that SMM decreases biomasses of small Nematoda and secondarily increases those of Ostracoda (Chapter 4). However, few waterbird species possess the capacity to capture these small prey (Nudds and Bowlby 1984, Skagen and Oman 1996, Sutherland et al. 2000); consequently, I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities between ponds of impounded and unimpounded marshes.

Studies examining effects of SMM on waterbird densities have provided equivocal results because of the variability in water levels in both impounded and reference unimpounded marshes (Chabreck et al. 1974, Spiller and Chabreck 1975, Epstein and Joyner 1988, Weber and Haig 1996). Previous studies generally concluded that SMM increases waterfowl and/or waterbird density, but most admit inconsistent results due to tides (Weber and Haig 1996), flooding events (Chabreck et al. 1974), or drying events (Spiller and Chabreck 1975). Waterbird densities should be corrected for variation in water depth to obtain unbiased estimates for habitat comparisons (Chapter 5). Also, previous studies compared the total number of birds counted, or birds grouped by foraging guilds (shorebirds, waterfowl, etc.). However, comparison of waterbird guilds may hide differences in species compositions among wetlands because of interspecific differences in diets and adaptations to water levels within a guild (Baker 1979, Poysa 1983, Nudds and Bowlby 1984, Zwarts and Wanink 1984).

Marshes of the Gulf Coast Chenier Plain are divided into 3 categories of salinity based on the Venice system of estuarine classification (Bulger et al. 1993, Visser et al. 2000): (1) freshwater (salinity <0.5 ‰), (2) oligohaline (salinity between 0.5 ‰ and 5.0 ‰), and (3) mesohaline (salinity between 5.0 ‰ and 18.0 ‰). Oligohaline marshes apparently have expanded at the expense of freshwater and mesohaline marshes during the last 60 years (Visser et al. 2000). Little information is available concerning waterbird use of Gulf Coast Chenier Plain marshes in relation to salinity, except that densities of dabbling ducks may increase with decreasing salinity on the Louisiana Coast (Palmisano 1972). Ponds of these marsh types have little hydrologic differences (Chapter 3) and only small differences in sediment characteristics (Chapter 2); their invertebrate communities differ only in biomasses of Oligochaeta (Chapter 4). Previous studies suggest that Oligochaeta may complement diets of certain shorebirds (Skagen and Oman 1996) and waterfowl (Safran et al. 1997) that use the Gulf Coast marshes during winter. However, it is unlikely that changes in biomasses of Oligochaeta would affect greatly waterbirds because vertebrate predators seemingly do not affect numbers of Oligochaeta in freshwater marshes (Thorp and Bergey 1981). Consequently, I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities among ponds of IF, IO, and IM marshes.

I estimated densities of common wintering waterbirds on marsh ponds of the Gulf Coast Chenier Plain. I included all species of waterbirds to complement the available information on waterbird communities in this area. More specifically, I tested the above general predictions concerning effects of SMM and salinity on wintering waterbird communities by comparing waterbird densities (1) between ponds of impounded and unimpounded mesohaline marshes, and (2) among ponds of impounded freshwater, oligohaline and mesohaline marshes during winters 1997-1998 to 1999-2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. Secondarily, I investigated relationships between water depth and densities of common wintering waterbirds to remove effects of water depth on comparisons of waterbird communities among marsh types. I also examined maximum densities of common waterbirds within marsh types and their relationships with water depth. Finally, I investigated relationships among sediment variables (carbon content, C:N ratio, hardness, particle size, and oxygen penetration), hydrologic variables (salinity, water depth, temperature, dissolved oxygen, and turbidity), sizes and biomasses of common invertebrate taxa, densities of common waterbird species, and marsh types using canonical correspondence analysis.

METHODS

STUDY AREA

The Gulf Coast Chenier Plain is bounded by East Bay in Texas and Vermillion Bay in Louisiana (Gosselink et al. 1979). The Chenier Plain was formed by sediments from the Mississippi River that were transported by the westward current in the Gulf of Mexico (Byrne et al. 1959). Periods of low sediment deposition, that occurred when the Mississippi Delta changed location, formed a series of stranded beach ridges composed of sand and shells separated by mud flats where marshes developed (Byrne et al. 1959). Chenier refers to the French word *chenière*, which characterizes a forest or area where oaks (*Quercus* spp.) represent the dominant tree species.

I chose Rockefeller State Wildlife Refuge (RSWR; headquarters coordinates: 29˚ 40’ 30” N, 92˚ 48’ 45” W), near Grand Chenier, in southwestern Louisiana as a representative area of the Gulf Coast Chenier Plain. RSWR comprises 30,700 ha, and contains 17 impoundments (200 to >4,000 ha each, Wicker et al. 1983). Most impoundments on RSWR were constructed during the late 1950s, and are separated by a network of canals that surround the levees (Wicker et al. 1983). Impoundments on RSWR comprise marsh types of various salinities characteristic of the Gulf Coast Chenier Plain, i.e., freshwater, oligohaline, and mesohaline marshes (Visser et al. 2000). RSWR also contains a large area of unimpounded mesohaline marshes (11,700 ha).

SAMPLING DESIGN

I sampled the 4 marsh types of RSWR: (1) 3 freshwater impoundments (IF) (units 8,10, and 13), (2) 3 oligohaline impoundments (IO) (units 3, 4, and 15 [the latter replaced unit 3 in winter 1999-2000]), (3) 2 mesohaline impoundments (IM) (units 5 and Price Lake), and (4) 2 hydrographic basins of unimpounded mesohaline marshes (UM) (East Little Constance Bayou basin and Rollover Lake/Flat Lake basin). In each impoundment and hydrographic basin, I initially selected 4 to 8 ponds from those that were accessible directly from levees or with a small flat boat when necessary (impounded marshes), or that access would not be prevented at low tides using a small flat boat (UM marshes). I made this initial selection to minimize time spent commuting among sites and disturbance to waterbirds, and to ensure access to study ponds at all times. The number of ponds selected depended on those available accordingly to the above selection criteria. Subsequently, I randomly selected 3 ponds from those initially identified in each impoundment or hydrographic basin. Because of the presence of numerous small ponds (<2 ha), but also a few very large ones (>20 ha) in IM and UM marshes, I randomly chose 1 large pond and 2 small ponds in each of these marsh types. During each visit, I randomly selected 3 sampling stations in each pond. I determined locations of sampling stations using a table of random numbers to select distances and angles from an observation blind that fell within the pond area, up to a distance of 200 meters from the blind. I visited ponds monthly, from December to March in 1997-98, and from November to March in 1998-99 and 1999-2000 (14 months total).

ESTIMATES OF WATERBIRD DENSITIES

During a visit to a pond, two observers entered a permanent blind at sunrise, waited 90 minutes, and then counted birds present on the pond within a 200-meter radius of the blind. Distances between birds and the blind were estimated using a Yardage Pro 500 laser rangefinder (Bushnell®, Overland Park, Kansas). Each observer scanned birds independently, and the maximum number by species in the two scans comprised the final count. I computed the area (m^2) surveyed on each pond using aerial photograph (1:12,000) taken during winter 1998 for RSWR and ArcView GIS 3.2 software (Environmental Systems Research Institute, Inc., Redlands, California), and transformed bird counts into densities (birds/ha surveyed).

COLLECTION OF INVERTEBRATE SAMPLES

I used 3 different techniques to sample aquatic invertebrates to ensure adequate representation of benthic meiofauna (0.063 – 0.5 mm), macrofauna (>0.5 mm), and water-column (epiphytic and nektonic) macrofauna (>0.5 mm) in my overall estimates of invertebrate biomasses. At each sampling station, I used a sediment corer (12-cm diameter) sunk to 10-cm depth in the pond bottom to collect benthic macrofauna. I subsequently sieved samples through a 500 µm mesh at sampling sites. I sampled meiofauna with a smaller corer (2.5-cm diameter) sunk to 2 cm depth, and sieved samples through a 63 µm mesh. I sampled water-column invertebrates using a D-shaped sweep net (opening 30 cm large, mesh 500 µm) filtering a volume of water of approximately 0.7 m^3, which is equivalent to a net movement through a distance of 20 meters (e.g., 10 sweeps of 2 m long, surface covered = 6 m^2) along the water surface. All material retained by sieves was preserved in 10% buffered formaldehyde mixed with rose bengal protein stain (Hartley et al. 1988).

ESTIMATES OF INVERTEBRATE BIOMASSES

Diets and foods available to waterbirds most often are described using dry-weights (Afton et al. 1991, Euliss et al. 1991, Weber and Haig 1996, Safran et al. 1997), ash-free dry-weights (Zwarts and Wanink 1991), or caloric contents (Nudds and Bowlby 1984) because these estimators are believed to provide a realistic estimate of invertebrate energetic payoffs to waterbirds. Accordingly, I used ash-free dry-weight to quantify invertebrate biomass.

Most studies of waterbird food resources have classified aquatic invertebrates into families, orders, classes or phyla (Euliss et al 1991, Thompson et al. 1992) probably because (1) of the large variety and numbers of invertebrates, and (2) feeding apparatuses of waterbirds principally are adapted to pick or filter prey of a certain size or minimal dimensions (Nudds and Bowlby 1984, Zwarts and Wanink 1984). Therefore, shapes and sizes of invertebrates probably are more important to waterbirds than are taxonomic specifications of food items. Consequently, I arbitrarily determined classes that discriminated shapes and sizes of invertebrates to reduce time spent in lab identifying invertebrates (Chapter 4).

In the lab, I filtered samples through a series of sieves of declining mesh size to assess invertebrate size (5000, 2000, 1000, and 500 µm for macrofauna and water-column invertebrates; 500, 200, 100, and 63 µm for meiofauna). Following this, I identified (1) Diptera, Mollusca, and Decapoda to the family level, (2) other Insecta and Arthropoda to order, (3) Annelida, and Granuloreticulosa to class, and (4) Nematoda to phylum. I counted individuals of each taxon present by the above size classes.

I calculated biomasses of invertebrates by multiplying the number of individuals counted for each taxon and size class by individual ash-free dry-weights obtained from fresh (unpreserved) individuals collected during winter 1999-2000 (35 benthic macrofauna and 37 water-column macrofauna samples). I dried invertebrates from the latter samples by size class and taxon at 60°C for 12 hours in a drying oven in samples of 1 to 50 individuals (depending on size and numbers), weighed them, and then burned them in a muffle furnace at 550°C for 4 hours (Widbom 1984). Subsequently, I placed samples in a desiccator and re-weighed them. The ash-weight was subtracted from the dry-weight to obtain the ash-free dry-weight. I used estimates from the literature for meiofauna and uncommon size classes of macrofauna identified, but not found in my samples used to measure individual ash-free dry-weight (Reger 1982, Widbom 1984, Edgar 1990).

I limited my analysis to common invertebrate classes collected on RSWR. I defined common invertebrate classes based on taxonomic and size differences. First, I grouped invertebrates identified to family into their respective orders to reduce the number of taxa with little representation. Secondly, I grouped the 7 size classes into 3 larger classes (63 – 199 µm, 200 – 999 µm, ≥1000 µm) within invertebrate taxa (1) to reduce the number of classes, and (2) because waterbirds (at least waterfowl) cannot capture foods smaller than 200 µm, whereas smallest potential food sizes begin within 200 to 999 µm and all species can capture prey ≥1000 µm (Nudds and Bowlby 1984, Tremblay and Couture 1986, Kooloos et al. 1989). Finally, I defined common invertebrate classes as those with a percent frequency ≥25 % in at least one of the marsh types (Chapter 4).

MEASUREMENTS OF HYDROLOGIC VARIABLES

At sampling stations, I used a graduated stick (± 1 cm) to measure water depth, a YSI-55 dissolved oxygen meter (Yellow Springs Instrument, Co., Yellow Springs, Ohio) to measure dissolved oxygen (± 0.1 %) (O_2), and a YSI-30 salinity meter (Yellow Springs Instrument, Co., Yellow Springs, Ohio) to measure salinity (± 0.1 ‰) and temperature (± 0.1 °C). I measured these variables 2-3 cm above sediments and during daytime (7:00 – 14:00). To measure water turbidity, I submerged a 10-cm diameter white disk at a 10 cm depth, and categorized turbidity using the following classes: none, little, moderate, and considerable, which were coded 0, 1, 2, and 3, respectively.

MEASUREMENTS OF SEDIMENT VARIABLES

Between January and March 2000, I measured sediment hardness within each pond with a S-170 pocket soil penetrometer (Boart Longyear, Co., Stone Mountain, Georgia) that was adapted for measurements of soft sediments by attaching a 10 cm diameter vinyl disk at its end. This measurement was an index of the amount of pressure the soil could absorb when the penetrometer was pushed down by 2 cm.

I determined the silt-clay fraction (to estimate particle size) by sampling pond sediments with a 5-cm corer sunk to a depth of 10 cm. Sediments were homogenized with a kitchen blender (model 4142, Sunbeam Products, Inc, Boca Raton, Florida), oven-dried at 100 °C for 24 hours, and then weighed (±0.01 g). Following this procedure, I re-hydrated sediments, homogenized them again, and sieved them through a 63 µm mesh sieve to remove the silt-clay fraction. Sediments left in the sieve were oven-dried, and weighed again. The difference in sediment dry-weight before and after sieving divided by the total sediment dry-weight used (* 100) corresponded to the silt-clay fraction in sediments (Buchanan 1984).

I sampled carbon and nitrogen contents of sediments by taking a few grams from homogenized sediments used for the determination of the silt-clay fraction. I preserved samples by freezing and used a CHN analyzer to determine their carbon and nitrogen content and ratio (C:N) (Buchanan 1984). Finally, I placed metal rods in sediments for a month at random stations within each pond to estimate O_2 penetration. O_2 penetration corresponded to depths where rust stopped along the metal rods (J. W. Fleeger, pers. comm.).

STATISTICAL ANALYSES

Effects of SMM and salinity on waterbird densities: I limited my analyses to common waterbird species of RSWR. I defined common waterbirds based on the following 2 arbitrary rules: (1) a species had a percent frequency ≥10% in at least one of the marsh types surveyed; and (2) a species had an absolute frequency of occurrence ≥20 over all marsh types. I analyzed the relationship between water depth and mean density of common waterbirds by 2-cm water depth classes using nonparametric regressions (PROC LOESS, SAS Institute, Inc. 1999). I averaged water depth for each pond to obtain similar sampling units for both water depth and bird density. Based on this analysis, I computed relative corrected densities of common wintering waterbird species ([observed – predicted density from non parametric regression] / [observed + predicted density] * 100) to remove effects of variation in water depth on comparisons of waterbird densities among wetlands (Chapter 5). I used relative corrected densities of common waterbird species as response variables in subsequent analyses.

I compared relative corrected densities of common waterbird species between ponds of IM and UM marshes and among ponds of IF, IM and IO marshes within a single multivariate analysis of variance (MANOVA). Fixed explanatory variables in the model were marsh type, time (months), and their interaction. The random explanatory variable was impoundment within marsh type × time. I performed separate *a priori* MANOVA contrasts to test my 2 comparisons of interest (UM vs. IM, and IF vs. IO and IM), with respective contrast equations (0, 1, 0, –1), and (1, –0.5, –0.5, 0) for the corresponding marsh types equation order (IF, IM, IO, UM). For these *a priori* comparisons, I used an error matrix based on the random effect of impoundment within marsh type × time.

I used Wilk's lambda statistic to compute *F*-ratios of my 2 *a priori* MANOVA contrasts (PROC GLM, SAS Institute, Inc. 1999). I considered *P*-values less than 0.05 as significant and estimated effect size (proportion of the variance in response variables attributable to the variance existing in explanatory variables) to avoid declaring significant but trivial differences in variable mean responses (effect size = Wilk's lambda – 1, Tabachnick and Fidell 1989). Finally, I computed canonical correlations and standardized canonical coefficients from MANOVA contrasts to investigate the contribution of the various common waterbird species to differences among ponds of various marsh types. Because r values ≤ 0.3 correspond to $<10\%$ variance overlap between variables (Tabachnick and Fidell 1989), I only interpreted r values >0.3.

Normality of response variables frequently could not be achieved because of the high frequency of zero counts, which produced data distributions that were highly skewed to the left. Nevertheless, I used parametric statistics because transformation of variables of similar distribution provides only marginal improvements in analysis, and a sample size that produces 20 degrees of freedom or more for the error term ensures robustness of multivariate tests (Tabachnick and Fidell 1989). My sampling design provided 56 degrees of freedom for the error term associated with the fixed effects. I present results as least-square means ± standard errors unless noted otherwise. To help interpret least-square means of relative corrected densities, I provided the corresponding ratio of observed: predicted density from nonparametric regressions between water depth and mean density. For example, a ratio of observed: predicted density of 0.67 indicates that 1.5 time fewer birds were recorded than that predicted from observed water depth, the ratio 0.33 corresponds to 3 times fewer birds, 0.10 to 10 times fewer birds, etc (Chapter 5). The above statistical analyses were performed using SAS 8.2 (SAS Institute, Inc. 1999).

Relationships with environmental variables: I used canonical correspondence analysis (CCA) and CANOCO statistical software (ter Braak and Verdonschot 1995) to examine relationships among environmental variables (sediment and hydrologic variables, biomasses of common invertebrate classes; EVs), densities of common waterbirds, and marsh types. This multivariate technique extracts uncorrelated ordination axes that maximize distance among waterbird centroids from measured EVs. Each waterbird centroid corresponds to mean axis scores of sites where the species occurred. Distance among waterbird centroids explained by the CCA axes corresponds to the proportion of inertia (total weighted variance in the dataset) explained by their eigenvalues (weighted variance of species centroids due to the axes), expressed in percentage. I used a Monte Carlo permutation test to evaluate the significance ($P < 0.05$) of the CCA solution and the first axis eigenvalues (ter Braak and Verdonschot 1995).

In the CCA, I included 4 qualitative variables with the EVs that represent the 4 marsh types surveyed (IF, IO, IM, and UM) to estimate their average axis scores and compare them to waterbird centroids on the CCA ordination biplot. These qualitative variables were coded “1” when they corresponded to the marsh type where the sampling occurred and “0” otherwise. I also introduced a covariable matrix in the model to account for sampling replication through time, i.e., 14 binary variables that included one for each month that I collected data. I averaged EVs for each pond to obtain the same sampling unit as for densities of common waterbirds.

Following CCA, I used forward selection to rank EVs in the order that maximizes the cumulative eigenvalue (λ_a) (ter Braak and Verdonschot 1995). The forward selection first computed each EV eigenvalue (λ) (as if they were the only variable included in the model) and then selected the variable with the highest eigenvalue. Following this, the other variables were reordered by their eigenvalues computed in conjunction with the eigenvalue of the variables(s) already selected, and again the variable with the highest eigenvalue was selected. This process continued until all variables were considered. I tested the significance ($P < 0.05$) of the effect of each variable on the CCA eigenvalue with a Monte Carlo permutation test (ter Braak and Verdonschot 1995).

RESULTS

COMMON WATERBIRDS

I recorded a minimum of 55 species of waterbirds during the study (Appendix D). I recorded 15 common waterbird species that had a percent frequency ≥10% in at least one marsh type and an absolute frequency of occurrence ≥20 for all marsh types combined. Common waterbirds included 5 species of anseriformes: Blue-winged Teal (*Anas discors*), Gadwall (*A. strepera*), Green-winged Teal (*A. crecca*), Mottled Duck (*A. fulvigula*), and Northern Shoveler (*A. clypeata*); 3 species of charadriiformes: American Avocet (*Recurvirostra Americana*), Black-necked Stilt (*Himantopus mexicanus*), and Willet (*Catoptrophorus semipalmatus*); 3 species of ciconiiformes: Great Egret (*Casmerodius albus*), Great Blue Heron (*Ardea herodias*), and Snowy Egret (*Egretta thula*); 2 species of gruiformes: American Coot (*Fulica Americana*) and Common Moorhen (*Gallinula chloropus*); 1 species of pelecaniformes: Double-crested Cormorant (*Phalacrocorax auritus*); and 1 species of podicipediformes: Pied-billed Grebe (*Podilymbus podiceps*).

MAXIMUM WATERBIRD DENSITIES BY MARSH TYPE

Except for charadriiformes and pelecaniformes, most common waterbirds had maximum observed densities in ponds of IF marshes (Table 6.1). Only Gadwalls and Double-crested Cormorants obtained their maximum densities in ponds of IO marshes; however, Blue-winged Teal, Green-winged Teal, American Coots, and Common Moorhens also had maximum densities greater than 20 birds/ha in those ponds (Table 6.1). Only Black-necked Stilts had a maximum observed density in ponds of IM marshes, with Gadwalls and Green-winged Teal reaching maximum densities of 24 and 161 birds/ha respectively in those ponds (Table 6.1). Northern

Shovelers, American Avocets, and Willets had maximum observed densities in ponds of UM marshes, with Green-winged Teal reaching 56 birds/ha in those ponds (Table 6.1).

RELATIONSHIP BETWEEN WATER DEPTH AND WATERBIRD DENSITIES

Anseriformes generally had highest mean densities at water depths under 26 cm (Fig. 6.1, panel A). Green-winged Teal had highest mean density by water depth classes among this order (at 13 cm), followed by Northern Shovelers at 5 cm, Gadwalls at 25 cm, Blue-winged Teal at 23 cm, and Mottled Ducks at 25 cm (Fig. 6.1, panel A). All anseriformes had small increases in density as depth increased after reaching low densities around 35-45 cm (Fig. 6.1, panel A).

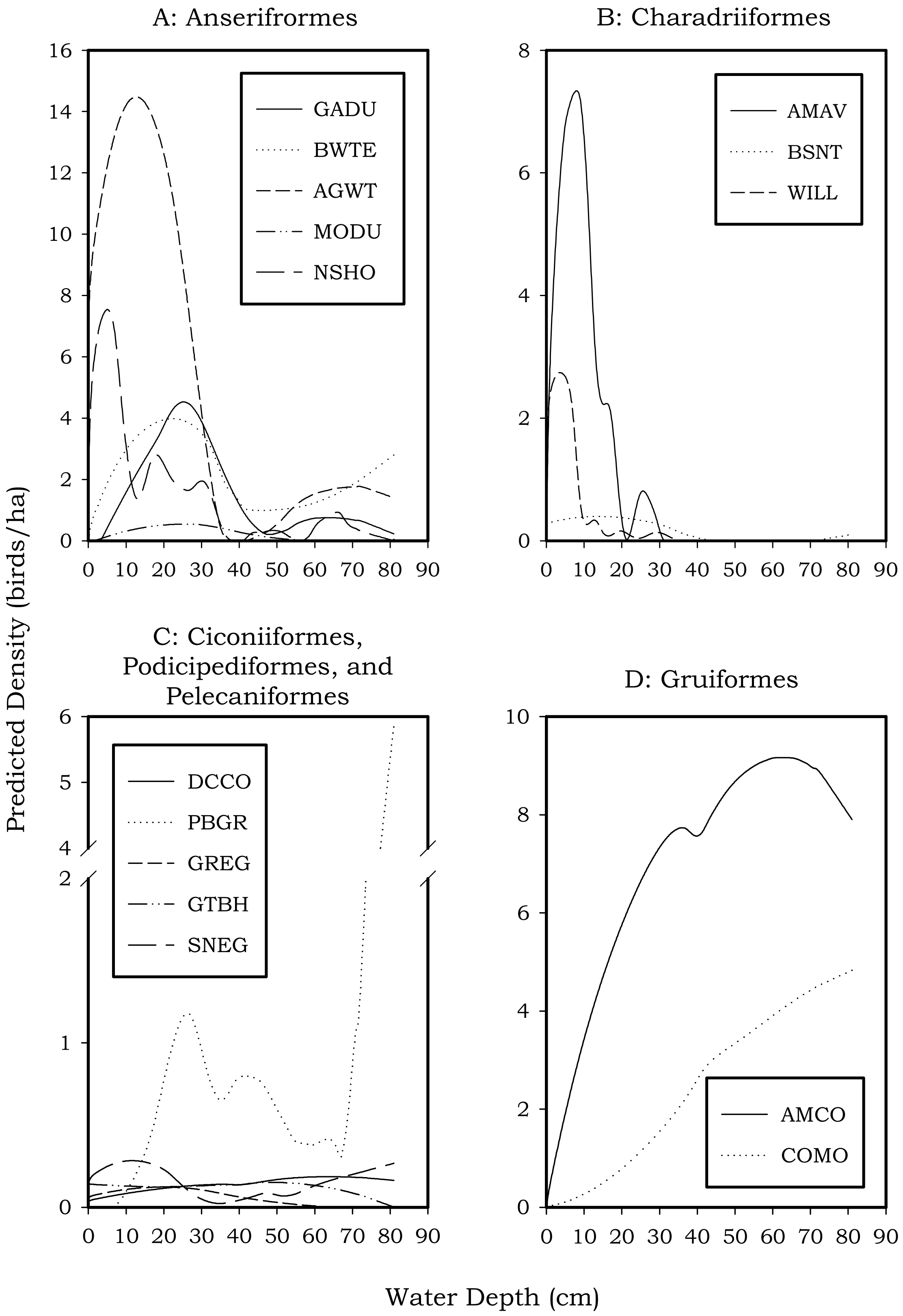
Among charadriiformes, American Avocets had highest mean densities by water depth classes at 7 cm, followed by Willets at 3 cm, and Black-necked Stilts at 13 cm (Fig. 6.1, panel B). Ciconiiformes showed little variation in mean densities among water depth classes (range of predicted densities: 0 – 0.28 birds/ha; Fig. 6.1, panel C). Snowy Egrets obtained the highest mean predicted density in this group (Fig. 6.1, panel C). Pied-billed Grebes reached highest mean predicted density at deep water depths (Fig. 6.1, panel C), but this observed increase was influenced greatly by a single observation at 81 cm. Double-crested Cormorants had only a small increase in mean predicted density with water depth (Fig. 6.1, panel C). Gruiformes had highest predicted mean densities at deeper water depth than did species of other bird orders (Fig. 6.1, panel D). Common Moorhens did not have any tendency toward a water depth that maximized densities (Fig. 6.1, panel D), whereas American Coots did so at 61 cm. Appendices E and F summarize data used to construct Figure 6.1.

Table 6.1: Maximum (Max) density (birds/ha) of common waterbirds and associated water depth (cm) recorded in ponds of unimpounded mesohaline marshes (UM) and impounded freshwater (IF), oligohaline (IO) and mesohaline (IM) marshes during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

<u>Order</u> and Species [a]	IF		IO		IM		UM	
	Max	Depth	Max	Depth	Max	Depth	Max	Depth
<u>Anseriformes</u>								
Blue-winged Teal	345	17	20	27	4	22	0	-
Gadwall	50	29	71	24	24	20	5	8
Green-winged Teal	460	17	62	18	161	4	56	5
Mottled Duck	12	28	6	33	7	7	2	8
Northern Shoveler	25	29	11	31	14	8	34	5
<u>Charadriiformes</u>								
American Avocet	0	-	0	-	1	5	142	7
Black-necked Stilt	2	9	3	24	33	22	3	7
Willet	0	-	6	19	3	2	70	3
<u>Ciconiiformes</u>								
Great Egret	2	11	1	16	1	18	2	4
Great Heron	4	17	1	32	1	20	2	0
Snowy Egret	10	15	2	27	3	20	2	1
<u>Gruiformes</u>								
American Coot	314	17	50	28	12	28	0	-
Common Moorhen	44	56	27	33	2	39	0	-
<u>Pelecaniformes</u>								
Double-crested Cormorant	2	21	8	45	3	31	1	25
<u>Podicipediformes</u>								
Pied-billed Grebe	10	24	5	28	6	22	< 1	25

[a] Scientific names of waterbird species are given in Appendix D.

Fig. 6.1. Mean densities (birds/ha) (least-square means ± SE) of common waterbirds by 2-cm water depth classes during winters 1997-1998 to 1999-2000 on the Chenier Plain Gulf Coast as predicted by nonparametric regressions. Anseriformes were Green-winged Teal (AGWT), Blue-winged Teal (BWTE), Gadwall (GADU), Mottled Duck (MODU), and Northern Shoveler (NSHO), charadriiformes were American Avocet (AMAV), Black-necked Stilt (BNST), and Willet (WILL), ciconiiformes were Great Blue Heron (GTBH), Great Egret (GREG), and Snowy Egret (SNEG), gruiformes were American Coot (AMCO), and Common Moorhen (COMO), pelecaniforme was Double-crested Cormorant (DCCO), and podicipediforme was Pied-billed Grebe (PBGR). Scientific names of waterbird species are given in Appendix D.


A: Anserifrormes
16
14
12
10
8
6
4
2
0
GADU
BWTE
AGWT
MODU
NSHO
B: Charadriiformes
8
6
4
2
0
AMAV
BSNT
WILL
C: Ciconiiformes, Podicipediformes, and Pelecaniformes
6
5
4
2
1
0
DCCO
PBGR
GREG
GTBH
SNEG
D: Gruiformes
10
8
6
4
2
0
AMCO
COMO
0 10 20 30 40 50 60 70 80 90
Predicted Density (birds/ha)
Water Depth (cm)

COMPARISON OF IM AND UM MARSH PONDS

My *a priori* MANOVA contrast indicated that relative corrected densities of the 15 common waterbird species differed significantly between UM and IM marsh ponds and produced a large effect size (Table 6.2). Standardized canonical coefficients of common waterbird species indicated that relative corrected densities of Pied-billed Grebes, Northern Shovelers, Willets, American Avocets, and Gadwalls differed most between IM and UM marsh ponds (largest standardized coefficients, Table 6.3). Relative corrected densities of Pied-billed Grebes and Gadwalls were higher in ponds of IM marshes, whereas those of Northern Shovelers, Willets, and American Avocets were higher in ponds of UM marshes (Fig. 6.2). All common waterbirds of IM and UM marshes exhibited negative mean relative corrected densities (ratio observed: predicted density <1, Fig. 6.2).

Relative corrected densities of Willets, American Avocets, and Northern Shovelers were correlated positively, whereas those of Pied-billed Grebes were correlated negatively with the first canonical variate (Table 6.3). Common waterbirds with highest relative corrected densities in ponds of UM marshes were Northern Shovelers, Green-winged Teal, Willets, American Avocets, and Snowy Egrets (Fig. 6.2). Other common waterbirds rarely used ponds of UM marshes (ratio observed: predicted density <0.1, Fig. 6.2). In ponds of IM marshes, Pied-billed Grebes had the highest relative corrected density, whereas all other species exhibited mean relative corrected densities of approximately –70% (ratio observed: predicted density <0.17, Fig. 6.2), or rarely were observed (American Avocets, American Coots, Blue-winged Teal, Common Moorhens, and Willets [ratio observed: predicted density <0.05], Fig. 6.2).

Table 6.2. Summary of *a priori* MANOVA contrasts testing for differences in relative corrected densities of common waterbirds between ponds of impounded and unimpounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline and mesohaline marshes (IF vs. IO and IM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Contrast	Wilk's lambda	*F*	Num df	Den df	Pr. > *F*	Effect size (η^2)
UM vs. IM	0.15	19.45	15	56	<0.0001	0.85
IF vs. IO and IM	0.11	27.79	15	56	<0.0001	0.89

COMPARISON OF IF WITH IO AND IM MARSH PONDS

My *a priori* MANOVA contrast indicated that relative corrected densities of the 15 common waterbird species differed significantly among ponds of IF, IO, and IM marshes and produced a large effect size (Table 6.2). Standardized canonical coefficients of common waterbird species indicated that relative corrected densities of Common Moorhens, American Coots, and Gadwalls differed most among these marsh types (largest standardized coefficients, Table 6.3). Common Moorhen and American Coots obtained greatest relative corrected densities in ponds of IF marshes (Table 6.3), whereas Gadwalls obtained greatest relative corrected densities in the other marsh types (Table 6.3). Relative corrected densities of Common Moorhens and American Coots were correlated positively, whereas those of Gadwalls were correlated negatively with the first canonical variate (Table 6.3). Species that had highest relative corrected densities in ponds of IF marshes were American Coot, Common Moorhen, and Blue-winged Teal (ratio observed: predicted density >0.25, Fig. 6.2). Other common waterbirds rarely used ponds of IF marshes (relative corrected density <-70%, ratio observed: predicted density <0.17, Fig. 6.2). In IO marsh ponds, Pied-billed Grebes had the highest relative corrected density, whereas all other species obtained mean relative corrected densities <–60% (ratio observed: predicted density <0.25), or were not observed (American Avocets and Willets [ratio observed: predicted density = 0], Fig. 6.2).

All common waterbirds of IF, IO, and IM marsh ponds had negative mean relative corrected densities (Fig. 6.2).

RELATIONSHIPS WITH ENVIRONMENTAL VARIABLES

The CCA solution on waterbirds explained a significant amount of distance among species centroids (Monte Carlo test, $F = 4.7$, $P = 0.005$). The first axis also explained significant amount of distance among species centroids (Monte Carlo test, $F = 41.2$, $P = 0.005$), corresponding to 12.1 % of distance among species centroids, and 49.3 % of the CCA solution. The second axis explained 5.4 % of distance among species centroids, and 21.9 % of the CCA solution. Eigenvalues of axis 1 and 2 were 0.561 and 0.249 respectively, and inertia was 4.631. Temperature and turbidity were the only EVs describing the hydrology or sediments that were not correlated with axis 1, other EVs each had $r > 0.65$. Eight EVs describing invertebrate biomasses were correlated with axis 1 ($r > 0.30$). Primary EVs that correlated with axis 1 were water depth ($r = -0.87$), clay ($r = 0.77$), and salinity ($r = 0.76$). Only O_2 penetration was correlated with the second axis ($r > 0.35$).

Based on results of forward model selection, water depth was the primary EV explaining distance among waterbird centroids, followed by O_2 penetration (Table 6.4). All other EVs describing hydrology or sediments also had a significant effect on distance among waterbird centroids (except temperature), but added little to the cumulative effects the 2 principal EVs (Table 6.4). Many EVs describing invertebrate biomasses also had a significant effect on distance among waterbird centroids, especially Nematoda and Copepoda (63 to 199 µm) that had high marginal effects ($\lambda = 0.22$ and 0.12, respectively). Although not included in the forward selection process, variables UM and IF also were important in explaining the distance among waterbird centroids ($\lambda = 0.46$ and 0.33 respectively, Table 6.4).

Table 6.3. Canonical correlations (CC) and standardized canonical coefficients (SCC) from *a priori* MANOVA contrasts that tested for differences in relative corrected densities of common waterbirds between ponds of unimpounded and impounded mesohaline marshes (UM vs. IM), and among ponds of impounded freshwater, oligohaline and mesohaline marshes (IF vs. IO and IM) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Species	UM vs. IM		IF vs. IO and IM	
	CC	SCC	CC	SCC
American Avocet [a]	0.523	0.59	- 0.089	0.05
American Coot	- 0.177	0.40	0.591	0.92
Black-necked Stilt	- 0.124	- 0.34	- 0.050	0.13
Blue-winged Teal	- 0.205	- 0.34	0.299	- 0.24
Common Moorhen	- 0.089	0.22	0.862	1.49
Double-crested Cormorant	0.023	0.13	- 0.023	0.04
Gadwall	- 0.320	- 0.54	- 0.315	- 0.77
Great Egret	- 0.106	0.11	- 0.103	0.17
Great Heron	- 0.125	- 0.19	0.146	0.20
Green-winged Teal	0.195	- 0.11	- 0.141	- 0.09
Mottled Duck	- 0.192	0.07	- 0.168	- 0.39
Northern Shoveler	0.382	0.92	- 0.049	0.34
Pied-billed Grebe	- 0.564	- 1.04	0.031	- 0.36
Snowy Egret	0.072	- 0.01	- 0.045	- 0.05
Willet	0.662	0.82	- 0.133	- 0.17

[a] Scientific names of waterbird species are given in Appendix D.

Fig. 6.2. Mean relative corrected densities (least-square means ± SE) and corresponding ratio of observed:predicted densities (see Methods) of common waterbirds by marsh type (● = impounded freshwater, ♦ = impounded oligohaline, ■ = impounded mesohaline, and □ = unimpounded mesohaline) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain marshes. Species were Green-winged Teal (AGWT), American Avocet (AMAV), American Coot (AMCO), Black-necked Stilt (BNST), Blue-winged Teal (BWTE), Common Moorhen (COMO), Double-crested Cormorant (DCCO), Gadwall (GADU), Great Blue Heron (GTBH), Great Egret (GREG), Mottled Duck (MODU), Northern Shoveler (NSHO), Pied-billed Grebe (PBGR), Snowy Egret (SNEG), and Willet (WILL). Scientific names of waterbird species are given in Appendix D.

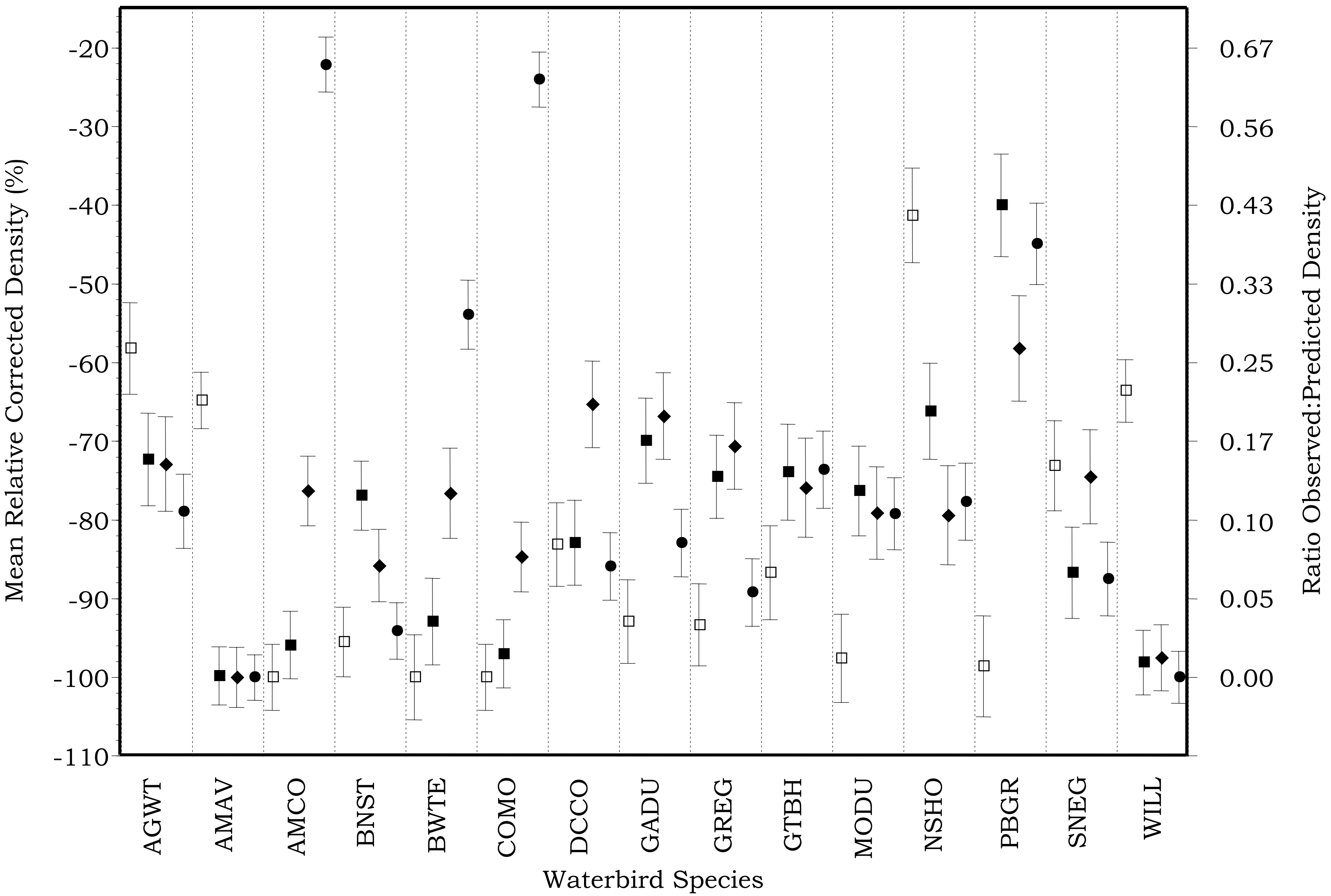

Mean Relative Corrected Density (%)
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110
Ratio Observed:Predicted Density
0.67
0.56
0.43
0.33
0.25
0.17
0.10
0.05
0.00
AGWT
AMAV
AMCO
BNST
BWTE
COMO
DCCO
GADU
GREG
GTBH
MODU
NSHO
PBGR
SNEG
WILL
Waterbird Species

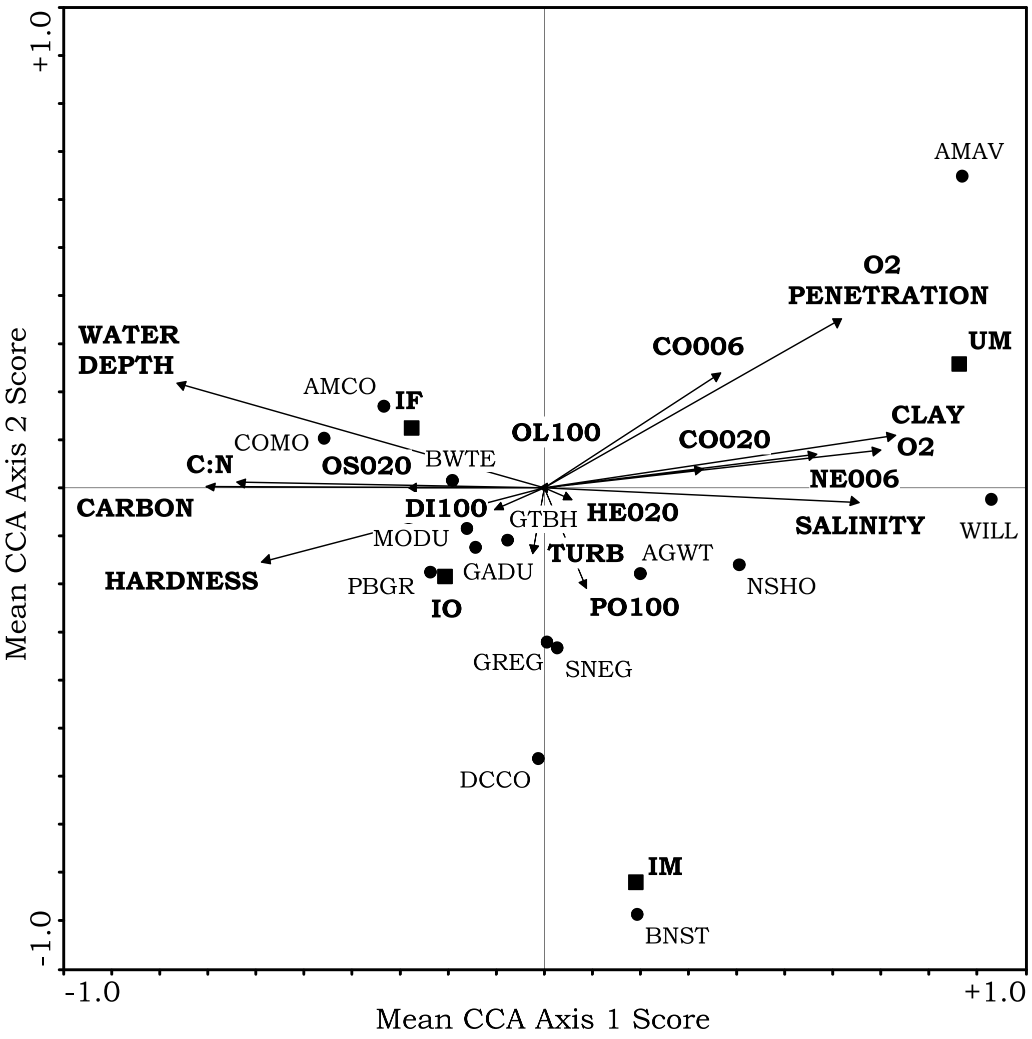
Table 6.4: Cumulative conditional effects (λ_a = cumulative eigenvalues), and marginal effects (λ, eigenvalues of each variable) of environmental variables on densities of common waterbirds during winters 1997-1998 to 1999-2000 in ponds of Gulf Coast Chenier Plain marshes as computed by forward selection (see Methods). *F* ratios and *P* values are associated with marginal effects.

Variable	λ_a	λ	*F*	*P*
Water Depth	0.41	0.44	35.4	0.005
Oxygen Penetration Depth in Sediments	0.57	0.28	10.3	0.005
Polychaeta (≥ 1000 µm)	0.64	0.07	5.6	0.010
Dissolved Oxygen	0.70	0.32	5.3	0.005
Nematoda (63 to 199 µm)	0.75	0.22	4.7	0.015
Salinity	0.81	0.34	4.8	0.005
Copepoda (63 to 199 µm)	0.86	0.12	4.6	0.020
Hemiptera (200 to 999 µm)	0.91	0.04	4.0	0.010
Sediment Hardness	0.95	0.30	3.7	0.005
Ostracoda (200 to 999 µm)	0.98	0.10	3.3	0.020
Carbon	1.02	0.33	3.1	0.010
Silt-clay faction	1.06	0.35	3.8	0.005
Carbon:Nitrogen	1.09	0.26	3.2	0.010
Oligochaeta (≥ 1000 µm)	1.12	0.01	2.5	0.030
Turbidity	1.15	0.03	2.3	0.010
Amphipoda (200 to 999 µm)	1.17	0.07	2.2	0.055
Copepoda (200 to 999 µm)	1.19	0.08	1.9	0.045
Diptera (200 to 999 µm)	1.21	0.06	1.8	0.055
Diptera (≥ 1000 µm)	1.23	0.03	2.3	0.035
Temperature	1.25	0.07	1.8	0.065
Foraminifera (200 to 999 µm)	1.27	0.07	1.5	0.130

Table 6.4. Continued.

Variables	λ_a	λ	F	P
Foraminifera (63 to 199 µm)	1.28	0.08	1.5	0.150
Nematoda (200 to 999 µm)	1.30	0.29	1.4	0.160
Ostracoda (63 to 199 µm)	1.31	0.04	1.3	0.175
Cladocera (200 to 999 µm)	1.32	0.03	1.3	0.235
Oligochaeta (200 to 999 µm)	1.34	0.04	1.3	0.185
Hemiptera (≥ 1000 µm)	1.35	0.02	0.9	0.455
Polychaeta (200 to 999 µm)	1.35	0.08	0.8	0.555
Amphipoda (≥ 1000 µm)	1.36	0.08	0.6	0.700
Impounded Freshwater		0.33		
Impounded Oligohaline		0.09		
Impounded Mesohaline		0.13		
Unimpounded Mesohaline		0.46		

Fig. 6.3. Ordination biplot from canonical correspondence analysis displaying correlations among axes and environmental variables (arrows), and mean axis score of common waterbird species (●) and marsh types (■) (IF: impounded freshwater; IO: impounded oligohaline; IM: impounded mesohaline; UM: unimpounded mesohaline) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain, near Grand Chenier, Louisiana. Waterbird species were Green-winged Teal (AGWT), American Avocet (AMAV), American Coot (AMCO), Black-necked Stilt (BNST), Blue-winged Teal (BWTE), Common Moorhen (COMO), Double-crested Cormorant (DCCO), Gadwall, (GADU), Great Egret (GREG), Great Blue Heron (GTBH), Mottled Duck (MODU), Northern Shoveler (NSHO), Snowy Egret (SNEG), and Willet (WILL). Invertebrate classes within environmental variables were Copepoda between 63 and 199 µm (CO006), Copepoda between 200 and 999 µm (CO020), Diptera ≥1000 µm (DI100), Hemiptera between 200 and 999 µm (HE020), nematoda between 63 and 199 µm (NE006), Ostracoda between 200 and 999 µm (OS020), Oligochaeta ≥1000 µm (OL100), and Polychaeta ≥1000 µm (PO100). Environmental variables with insignificant effects on distance among waterbird species centroids were not displayed to keep the figure as simple as possible. Scientific names of waterbird species are given in Appendix D.


+1.0
-1.0
Mean CCA Axis 2 Score
-1.0
+1.0
Mean CCA Axis 1 Score
AMAV
O2
PENETRATION
UM
WATER
DEPTH
CO006
AMCO
IF
COMO
OL100
CLAY
CO020
O2
C:N
OS020
BWTE
NE006
CARBON
DI100
GTBH
HE020
SALINITY
WILL
MODU
TURB
AGWT
HARDNESS
GADU
NSHO
PBGR
IO
PO100
GREG
SNEG
DCCO
IM
BNST

Environmental conditions (i.e., the combination of EVs that defines mean axis scores) that maximized densities of Common Moorhens (COMO), American Coots (AMCO), and Blue-winged Teal (BWTE) corresponded closely to environmental conditions in ponds of IF marshes (species and marsh type centroids close together, Fig. 6.3). Similarly, environmental conditions that maximized densities of Gadwalls (GADU), Pied-billed Grebes (PBGR), Mottled Ducks, Great Herons (GTBH), Snowy Egrets (SNEG), Great Egrets (GREG), (MODU) corresponded to those of IO marsh ponds. Environmental conditions that maximized densities of Double-crested Cormorants (DCCO) and Black-necked Stilts corresponded to those in ponds of IM marshes. Environmental conditions that maximized densities of American Avocets (AMAV) and Willets (WILL) corresponded to those of UM marsh ponds (Fig. 6.3). Environmental conditions that maximized densities of Northern Shovelers (NSHO) and Green-winged Teal (AGWT) were not associated closely to those of any specific marsh type (Fig. 6.3).

DISCUSSION

COMMON WATERBIRDS

I recorded 15 common waterbird species under survey and environmental conditions encountered on marsh ponds during the 3 winters of my study. Some waterbirds probably were underrepresented in my results because of their more discrete habits, such as rails, small herons (Least Bittern [*Ixobrychus exilis*], Green Heron [*Butorides striatus*]), or night herons (*Nycticorax* spp.). Some avian species may have had low frequencies during my study, but may be representative of other wetland types of the Chenier Plain, such as agricultural lands and crawfish ponds. For example, Northern Pintails (*Anas acuta*) seemingly prefer fallow and pasture lands to marsh, permanent open water, rice fields, and other agricultural lands in southwestern Louisiana (Cox and Afton 1997). Also, wading birds such as White Ibis (*Eudocimus albus*), sometimes intensely use crawfish ponds during winter (Martin and Hamilton 1985). Finally, some of the species that had low frequencies (Appendix D) might have been more important if low water depths had occurred more frequently during my study (Chapter 3) (e.g., shorebirds).

RELATIONSHIPS BETWEEN WATER DEPTH AND WATERBIRD DENSITIES

Water depths associated with highest mean bird densities of common waterbirds generally corresponded to those recorded for the same species in other studies (Thomas 1982, Weber and Haig 1996, Safran et al. 1997). Based on nonparametric regressions, I did not detect any obvious trends between bird density and water depth for ciconiiformes, gruiformes and divers (podicipediformes and pelecaniformes). The large size of herons probably allows them to use a wide range of water depths. Gruiformes seemingly were associated with deep water depths because (1) they primarily were associated with IF marshes where water depth generally was high (Table 6.1); and (2) they probably were not limited by high water depths as their diets are composed primarily of emergent and submerged plants (Thomas 1982). The relationship between bird density and water depth for divers probably is driven principally by minimum water depths required for diving.

COMPARISON OF IM AND UM MARSH PONDS

I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities of impounded and unimpounded marshes ponds. I developed this prediction because ponds of impounded and unimpounded mesohaline marshes differed only in biomasses of invertebrates of very small size (Nematoda 63 to 199 µm) that probably are not consumed by waterbirds during winter (Chapter 4). However, in contrast to my prediction, 3 of the 4 species (Northern Shovelers, Willets, and American Avocets) that differed most between ponds of IM and UM marshes do feed heavily on invertebrates during winter (Euliss et al. 1991, Gaston 1992, Batzer et al. 1993, Skagen and Oman 1996, Tietje and Teer 1996). These 3 species also had greatest relative corrected densities in ponds of UM marshes as compared to those of IM marshes.

Most plants growing in UM marshes are not consumed by waterfowl (Chabreck 1960); therefore, the composition of the seed bank in pond sediments of UM marshes probably did not influence waterbird densities. Thus, differences between the above prediction and my results suggest that: (1) some common waterbirds in ponds of UM marshes can capture very small invertebrates that pass through sieves of a mesh size below their minimal prey size, and/or (2) slight differences in biomasses of most important invertebrate classes of UM and IM marsh ponds, although statistically insignificant, may be biologically important enough to allow birds to meet their daily energetic requirements by feeding on these invertebrates. Some avian species may have avoided ponds of UM marshes because they could not meet their daily energy budget in those marshes by filtering meiofaunal invertebrates.

Larger relative corrected densities of Gadwalls in IM than in UM marsh ponds probably are due to their preference for consumption of submerged aquatic vegetation during winter (Paulus 1982), which was absent in ponds of UM marshes (Chabreck 1960, F. Bolduc, pers. obs.). Grebes may have had greater relative corrected densities in ponds of IM than UM marshes because of higher water levels in the former marsh type and they forage primarily on fish (Wetmore 1924). Shorebirds probably had low relative corrected densities in ponds of IM marshes because water depths in these ponds often were outside the range of water depths that these birds can use (Chapter 3).

COMPARISON OF IF WITH IO AND IM MARSH PONDS

I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities of IF, IO, and IM marsh ponds. I developed this prediction because ponds of IF, IO, and IM marshes differed only in biomasses of Oligochaeta (Chapter 4), which probably are not important prey of waterbirds during winter. My results indicated that waterbird communities in ponds of IF, IO and IM marshes primarily differed in relative corrected densities of Common Moorhens, American Coots, and Gadwalls. These species feed mainly on emergent or submerged aquatic vegetation (Paulus 1982, Thomas 1982). Species that potentially feed on invertebrates (American Avocet, Black-necked Stilt, Blue-winged Teal, Green-winged Teal, Mottled Duck, Northern Shoveler, and Willet) had standardized canonical coefficients at least 2 times lower than those of Common Moorhens, American Coots, and Gadwalls, which indicate their relative low importance in differentiating waterbird communities in ponds of IF, IO, and IM marshes. Consequently, my results were consistent with my prediction with regards to differences among waterbird communities of IF, IO, and IM marsh ponds.

All common waterbirds had negative mean relative corrected densities in all marsh types, which means that recorded bird densities generally were lower than that expected based on recorded water depth (Chapter 5). These low relative corrected densities probably resulted from the general low frequency of occurrence of waterbirds during my study (Appendix D). In more than 40% of bird counts, all waterbirds had a relative corrected density of –100% (absence of birds) because all species exhibited percent frequencies of occurrence lower than 60%, except for gruiformes (Appendix D).

An absence of birds during specific counts may be related to 2 different phenomena relative to water depth: (1) the water depth recorded was within the range used by the species, but no birds were counted; or (2) the recorded water depth was outside the range used by the species and accordingly no birds were counted. An absence of birds when water depth was within the range that a species use may be related to timing of migration and weather patterns on northern areas prior to arrival on my study area. Low frequencies of occurrence that I recorded probably also were related to high water depths frequently recorded in my study ponds (Chapter 3), which often were greater than those that maximized densities of many species (Fig. 6.1).

DIFFERENCES BETWEEN MAXIMUM AND RELATIVE CORRECTED DENSITIES

My MANOVA contrast testing differences in relative corrected densities among IF, IO, and IM marsh ponds generally indicated that only a few species differed among ponds of these marsh types (i.e., Common Moorhen, American Coot, and Gadwalls). However, most species had maximum densities in ponds of IF marshes, even species such as Green-winged Teal, Mottled duck, Great Blue Heron, and Snowy Egret, which differed little on average among IF, IO, and IM marsh ponds. The disparity between results of the MANOVA contrast and the distribution of maximum densities among marsh types may be explained by the variation in water depths during my study. Water depths associated with maximum densities of all waterbird species always were lower than the average water depth in ponds of the corresponding marsh type (39.1 ± 1.0 cm in IF marsh ponds, 35.5 ± 1.3 cm in IO marsh ponds, and 28.7 ± 1.2 cm in IM marsh ponds, and 13.4 ± 1.4 cm in UM marsh ponds, Chapter 3), except for gruiformes and divers.

The observed distribution of waterbird maximum densities among marsh types suggests that IF marshes are the most productive marshes of the 4 types because most species maximized their densities in ponds of IF marshes when water depth corresponded to their preferred water depth. Waterbirds for which mean relative corrected densities and maximum densities occurred in ponds of different marsh types (e. g., Green-winged Teal) probably are generalist species that prefer ponds of a specific marsh type, but also can use ponds of other marsh types accordingly to their water depth preferences. Waterbirds for which maximum and mean corrected densities occurred in ponds of the same marsh type, but for which water depth associated with their maximum densities was lower than the average one (e. g., Blue-winged Teal, Gadwalls) probably are habitat specific species. These species probably had no choice but to cope with more inferior water depths than those preferred, or leave my study area.

It is difficult to compare my results with those of previous studies that examined waterbird usage of similar habitats because of important differences in response variables used for comparisons. In previous studies, results are presented in numbers of birds (Palmisano 1972, Weber and Haig 1996), or densities per acre over the entire marsh area (Chabreck et al. 1974), whereas I used observed densities of waterbirds per ha of surveyed areas of ponds or relative corrected densities. Also, previous studies often grouped waterbirds into guilds (Chabreck et al. 1974, Spiller and Chabreck 1975, Epstein and Joyner 1988), whereas I used densities computed by species. Finally, other studies did not correct their results for variation in water depth (Chabreck et al. 1974, Spiller and Chabreck 1975, Epstein and Joyner 1988, Weber and Haig 1996).

RELATIONSHIPS WITH ENVIRONMENTAL VARIABLES

My CCA results indicated that water depth and secondarily O_2 penetration were the primary EVs explaining distance among waterbird centroids. The importance of water depth in differentiating habitat preferences of various waterbird species is consistent with several previous studies that segregated waterbirds in guilds that exploit different ranges of water depth (White and James 1978, Helmers 1992, Ntiamoa-Baidu 1998). The exploitation of different water depth ranges probably has evolved to decrease competition among species (Jefferies and Lawton 1984).

The primary importance of water depth, as compared to the lesser importance of any invertebrate classes in determining waterbird presence and densities, suggests that food accessibility is more important for birds than are the types of food present, at least for species that feed on invertebrates. The importance of water depth may be explained by: (1) neck length, leg length, and body size limitations on water depths that non-diving waterbirds can access (Baker 1979, Poysa 1983), and (2) feeding apparatuses of these birds limit their prey sizes (Nudds and Bowlby 1984, Zwarts and Wanink 1984) and food gathering techniques (Skagen and Oman 1996). Therefore, waterbirds probably are very opportunistic predators within the range of prey that their morphology allows them to capture.

O_2 penetration probably affects waterbirds through its effect on invertebrate biomasses. O_2 penetration affects infaunal invertebrates by limiting depths at which most invertebrates can sustain life in sediments, unless they have evolved alternative means for respiration (Rhoads 1974). Accordingly, biomasses of Copepoda and Nematoda were correlated with O_2 penetration (Fig. 6.3). Few waterbird species (i.e., Green-winged Teal, Northern Shovelers, Sandpipers) potentially feed on these small invertebrates (Gaston 1992, Nudds and Bowlby 1984, Sutherland et al. 2000). It is unknown whether meiofauna are ingested by other important waterbirds (e.g., American Avocet, Willet) in ponds of UM marshes, where O_2 penetration also was greatest (Fig. 6.3). Thus, changes in O_2 penetration especially affect meiofauna biomasses, and ultimately densities of a few waterbird species.

Although species such Green-winged Teal and Northern Shovelers can feed on small invertebrates, their centroids were not associated with ponds of UM marshes (Fig. 6.3), where biomasses of these invertebrates were greatest (Chapter 4). These 2 waterbird species have diets composed of a wide variety of prey during winter (Euliss et al. 1991, Batzer et al. 1993, Tietje and Teer 1996). Therefore, foraging sites that provide the best energetic payoff for these birds may change from ponds of one marsh type to another depending on prey accessibility (via water depth), type, and quantity.

Interestingly, 2 species with different water depth requirements (i.e., Black-necked Stilt and Double-crested Cormorant) were associated with ponds of IM marshes (Fig. 6.3). Associations between these waterbird species and IM marsh ponds probably are related to the high variation in water depths that occurred in those ponds (Chapter 3) and demonstrate the potential effects of changes in water depths on compositions of waterbird communities.

MANAGEMENT IMPLICATIONS WITHIN MARSH TYPES

Several authors have suggested that shallow water (<20 cm) is associated with highest waterbird diversity because most species use a wide range of water depths, which generally includes shallow water (Reid 1993, Colwell and Taft 2000). For wetlands of the California's Central Valley, Colwell and Taft (2000) recommended that wetland managers seek for diversity in land elevation, shallow water, and maximization of wetland size. Accordingly, my results on relationships among hydrologic and sediment variables, invertebrate biomasses and sizes, wintering waterbird densities, and marsh types (in conjunction with results of Chapter 2, 3, and 4) indicate that (1) spatial diversity in water depths, (2) range of water depths, and (3) sediment characteristics are the most important factors determining densities and species of waterbirds that use ponds of a given marsh type on the Gulf Coast Chenier Plain.

Based on these results, I recommend that managers of coastal marshes on the Gulf Coast Chenier Plain seek diversity in water depths by maintaining impoundments at different levels, if the conservation of wintering waterbird habitats is a high priority. Such management would promote spatial diversity in water depths at the landscape level and may prevent droughts from affecting large SMM areas with similar water levels. Also, spring-summer drawdowns should occur in different years on different SMM areas to maximize habitat diversity for waterbirds at this time of the year.

Managers of coastal marshes also should consider implementing SMM techniques that allow better control on water depth to maintain shallow water within impoundments. However, selection of water levels to be maintained would need careful consideration in order to best meet management objectives. Managers targeting specific water depths necessarily will favor certain bird species to the detriment of others. Little information is available on particular water levels that maximize waterbird diversity, however, my results indicated that most common species had maximum densities at water depths between 3 and 25 cm (Fig. 6.1). SMM techniques that might increase water level control would include the construction of more water control structures within impoundments, smaller impoundments, more pumping units to allow faster drainage of impoundments, and better canalization within impoundments that allow a better water flow among water bodies and toward water control structures.

Finally, my results suggest that sediment characteristics should be diverse among marsh ponds of the Gulf Coast Chenier Plain to provide habitats for various invertebrate prey of waterbirds, but also to allow diverse levels of sediment consolidation for the encroachment of submerged aquatic plants (Kadlec 1962). Submerged aquatic plants are consumed by some waterbird species such as Gadwalls (Paulus 1982), or provide habitats for many aquatic invertebrates that are consumed by waterbirds (Teels et al. 1976). My results (in conjunction with those from Chapter 2 and

3) suggest that water flow, the amount of organic matter in sediments, and drawdowns are most important factors affecting sediment characteristics of marsh ponds on the Gulf Coast Chenier Plain. Managers of coastal marshes should consider allowing increased connections between impoundments and sources of water of equal or lesser salinity to improve the water flow within impoundments without increasing salinities. Increased water flow within impoundments would positively also to affect sediments throughout the impoundment. Drawdowns primarily affect sediments because the oxidized organic matter is the “cement” that binds drying mineral particles together (Richardson et al. 2001, Chapter 2); therefore, drawdowns produce stronger consolidation of pond sediments within impoundments than in those of unimpounded marshes because of the presence of greater amounts of organic matter within impoundments (Chapter 2). Thus, my results suggest that intentional drawdowns should be limited to prevent very strong consolidation of sediments that affect infaunal invertebrate prey of certain waterbirds (Chapter 4). Also, drawdowns that last a few days are sufficient to promote the germination of seeds of emergent marsh plants (Kadlec 1962). However, unintentional extended drawdowns often occur within impoundments on the Gulf coast Chenier Plain during summers of low rainfall (Tom Hess, pers. comm.). Water flow within impoundments could be increased by using greater number of pumping units and connections between impoundments and sources of water of equal or lesser salinity to prevent unintentional drawdowns.

In conclusion, my results suggest that current SMM practices on my study area do not control adequately the hydrology within impoundments (as compared to unimpounded marshes), and this has important consequences on sediments, invertebrates, and wintering waterbirds. The large temporal variation in water levels that I observed within impounded marshes (Chapter 3) also may reduce accretion rates and increase marsh land loss (Swenson and Turner 1983, Turner 1997). SMM areas, as currently managed, may preserve historical isohaline boundaries within coastal marshes and support certain populations of resident and transient fisheries when water control structures allow water exchange between impoundments and the surrounding canals (Rogers et al. 1994). However, my results suggest that managers of coastal marshes need better control of the hydrology of impounded marshes to maintain coastal marsh functions.

MANAGEMENT IMPLICATIONS AMONG MARSH TYPES

Daily tides in ponds of UM marshes seemingly produce greater spatial variability in water depth and maintain shallow water as compared to the hydrology of IM marshes ponds (Chapter 3). Hydrologic conditions in ponds of UM marshes associated with sediments composed of fine silt and clay with low carbon content seemingly produce soft sediments with deep dissolved oxygen penetration (Chapter 2) where aquatic invertebrate communities primarily are composed of meiofaunal taxa (Chapter 4). Low spatial variability and high temporal variability in water depths within IM marsh ponds (Chapter 3), concurrently with the high carbon content within their sediments produce large consolidated sediment particles with low penetration of dissolved oxygen into the sediments (Chapter 2); consequently, Nematoda biomasses are reduced and biomasses of Ostracoda secondarily increase slightly within IM marsh ponds (Chapter 4).

My results suggest that differences in hydrology, sediments, and invertebrate communities between ponds of UM and IM marshes produce differences in waterbird communities. American Avocets, Northern Shovelers, and Willets had greater relative corrected densities in ponds of UM marshes, whereas Pied-billed Grebes and Gadwalls had greater relative corrected densities in ponds of IM marshes. Relatively small differences between invertebrate communities of UM and IM marsh ponds apparently affected waterbird communities because species with higher densities in ponds of UM, as compared to IM marsh ponds, primarily consume invertebrates (Euliss et al. 1991, Batzer et al. 1993, Skagen and Oman 1996, Tietje and Teer 1996).

My results suggest that further implementation of SMM in mesohaline marshes may affect populations of wintering American Avocets, Northern Shovelers, and Willets, whereas transforming IM marshes ponds back into UM marsh ponds may affect wintering populations of Pied-billed Grebes and Gadwalls. However, common waterbirds characteristic of UM marsh ponds (American Avocets, Northern Shovelers, Willets) generally were not observed in ponds of IM, IO, or IF marshes, but common waterbirds characteristic of IM marsh ponds (Pied-billed Grebes and Gadwalls) had similar or differed little in relative corrected densities among ponds of IO and IF marsh ponds. Thus, in a context where oligohaline marshes potentially expand at the expense of freshwater and mesohaline marshes (Visser et al. 2000), marsh managers concerned with objectives of conserving functions of coastal marshes of the Chenier Plain including their inherent wintering waterbird populations should consider focusing on the preservation of UM marshes.

Ponds of IF, IO, and IM marshes generally differed little in hydrologic and sediment variables, except for salinities (Chapter 2 and 3). Invertebrate communities of these ponds differed only in biomasses of Oligochaeta, which were greatest within ponds of IF marshes (Chapter 4). Consistent with my predictions, waterbird species that most differed in relative corrected densities among ponds of IF, IO, and IM marshes were not those that feed on invertebrates, but rather those that primarily feed on vegetation (American Coots, Common Moorhens, and Gadwalls); IF and IO marshes produce several plant species that many waterbird species consume (Chabreck 1960, Jemison and Chabreck 1972, Chabreck et al. 1974). However, my results also indicated that ponds of IF marshes were used extensively by many waterbird species when water depth fell within their preferred ranges. Finally, my results suggest that ponds of freshwater marshes are of primary importance for wintering waterbirds in general, and most importantly, maintenance of preferred water depths within ponds of IF marshes is high priority for waterbird conservation.

Freshwater marshes seemingly have declined to the benefit of IO marshes on the Gulf Coast Chenier Plain (Visser et al. 2000). Recent wetland conservation actions on the Louisiana coast targeted the maintenance or creation of vegetated marsh areas (i.e., all marsh types) rather than for the conservation of specific marsh habitats (Cowan et al. 1988). Therefore, I believe that the creation and conservation of freshwater marshes with management of preferred water depth should be given higher priority within the context of wintering waterbird habitat conservation.

CHAPTER 7

SUMMARY AND CONCLUSIONS

Compositions of wintering waterbird communities are dependent upon food accessibility (via water depth), biomasses and sizes of their invertebrate prey, which in turn are influenced by the hydrology and sediments of wetland habitats. The hydrology and sediments of Gulf Coast Chenier Plain marshes may be affected by structural marsh management (levees, water control structures and impoundments; SMM) and salinity; therefore, SMM and salinity ultimately may affect compositions of wintering waterbird communities.

My comparisons of aquatic invertebrate biomasses between ponds of impounded (IM) and unimpounded mesohaline (UM) marshes indicated that SMM decreases biomasses of small Nematoda and secondarily increases those of Ostracoda. However, few waterbird species possess the capacity to capture these small prey; consequently, I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities between ponds of IM and UM marshes.

My comparisons of aquatic invertebrate biomasses among ponds of impounded freshwater (IF), impounded oligohaline (IO), and IM marshes indicated that their invertebrate communities differed only in biomasses of Oligochaeta. Previous studies suggest that it is unlikely that changes in biomasses of Oligochaeta would affect greatly waterbird densities; consequently, I predicted that avian species that consume invertebrates would not be among those differentiating waterbird communities among ponds of IF, IO, and IM marshes.

Accordingly, I estimated densities of waterbird species in ponds of IF, IO, IM, and UM marshes during winters 1997-1998 to 1999-2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. Secondarily, I investigated relationships among sediment and hydrologic variables, invertebrate biomasses and sizes, densities of waterbirds, and marsh types.

I found that most common waterbird species had maximum densities in ponds of IF marshes (as compared to ponds of IO, IM, and UM marshes) at times when water depth was lower than average in this marsh type.

I found that waterbird communities in ponds of IM and UM marshes primarily differed in densities of American Avocets (*Recurvirostra americana*), Gadwalls (*Anas strepera*), Northern Shovelers (*Anas clypeata*), Pied-billed Grebes (*Podilymbus podiceps*), and Willets (*Catoptrophorus semipalmatus*). These results contradicted my prediction with regards to differences between waterbird communities of IM and UM marsh ponds because American Avocets, Northern Shovelers, and Willets primarily consume invertebrates.

I found that waterbird communities in ponds of IF, IO and IM marshes primarily differed in relative corrected densities of American Coots (*Fulica Americana*), Common Moorhens (*Gallinula chloropus*), and Gadwalls. These results were consistent with my prediction with regards to differences among waterbird communities of IF, IO, and IM marsh ponds because these avian species primarily consume emergent or submerged aquatic vegetation.

I found that water depth and penetration of dissolved oxygen into sediments (O_2 penetration) were the primary variables explaining the distribution of common waterbird species on my study area. The primary importance of water depth, as compared to the lesser importance of any invertebrate classes in determining waterbird presence and densities, suggests that food accessibility is more important for birds than are the types of food present, at least for species that feed on invertebrates. O_2 penetration probably affects waterbirds through its effect on biomasses of meiofauna. Accordingly, biomasses of Copepoda and Nematoda were correlated with O_2 penetration.

My results suggest that managers of coastal marshes on the Gulf Coast Chenier Plain should consider improving SMM techniques to (1) increase spatial diversity in water depths at the landscape level, (2) maintain shallow water within impoundments, and (3) limit the length of intentional drawdowns to prevent strong consolidation of sediments. Finally, my results also suggest that marsh managers concerned with objectives of conserving functions of coastal marshes of the Chenier Plain, including their inherent wintering waterbird populations, should consider focusing on the preservation of UM and IF marshes.

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APPENDIX A

FREQUENCIES AND BIOMASSES OF INVERTEBRATE TAXA

Appendix A. Percent frequencies of occurrence (Freq) and medians of biomass (µg / m^2) of invertebrate taxa, by size class, in ponds of impounded freshwater (IF), impounded oligohaline (IO) impounded mesohaline (IM), and unimpounded mesohaline (UM) marshes during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Phylum / Subphylum	Class	Order / Family	Size (µm)	IF Freq	IF Median	IM Freq	IM Median	IO Freq	IO Median	UM Freq	UM Median
Annelida											
	Hirudinea		63 - 199								
			200 - 999	0.5	11876.5	0.4	4750.6	1.7	4750.6		
			≥1000	9.2	323028.7	2.0	12084.0	1.3	59334.0	0.4	853980.9
	Oligochaeta		63 - 199	4.9	2043.5	8.9	2724.6	5.8	2043.5	11.7	5344.5
			200 – 999[a]	82.4	36370.7	61.8	25529.6	67.9	19341.7	49.2	24177.2
			≥1000[a]	63.7	40864.85	42.7	27243.2	55.8	27243.2	40.0	91255.2
	Polychaeta		63 - 199	0.8	1362.3	4.1	2724.6	1.3	2724.6	12.9	4052.0
			200 – 999[a]	11.7	6811.6	49.2	23340.9	30.8	13623.1	62.1	28527.8
			≥1000[a]	9.2	22116.9	40.7	79021.1	35.4	64593.6	47.1	125963.6
Arthropoda / Arachnida											
			63 - 199	5.4	3161.3	4.1	2357.9	2.5	2375.3	1.3	3143.8

Appendix A. Continued

Phylum /	Class	Order /		IF		IM		IO		UM	
Subphylum		Family	Size (µm)	Freq	Median	Freq	Median	Freq	Median	Freq	Median
Arthropoda / Arachnida											
			200 - 999	2.7	2270.5	1.6	3405.8			0.8	2270.5
			≥1000								
Arthropoda / Crustacea											
	Branchiopoda	Cladocera	63 - 199	7.6	1711.6	6.1	3423.3	4.6	5134.9		
			200 – 999[a]	42.8	24427.4	15.0	111.6	21.7	860.4	5.4	81.1
			≥1000								
	Copepoda		63 - 199[a]	58.8	12575.2	74.0	18775.5	71.7	15719.0	85.8	62876.0
			200 – 999[a]	87.8	30685.1	90.7	40869.4	90.0	38598.9	89.2	108985.1
			≥1000								
	Malacostraca	Amphipoda	63 - 199	0.3	2584.9						
			200 – 999[a]	26.6	955.0	20.7	3819.9	34.2	1909.9	2.5	955.0
			≥1000[a]	47.4	60589.2	26.8	92103.5	48.3	133401.9	4.2	29794.3

Appendix A. Continued

Phylum / Subphylum	Class	Order / Family	Size (µm)	IF Freq	IF Median	IM Freq	IM Median	IO Freq	IO Median	UM Freq	UM Median
		Decapoda /									
		Astacidea	63 - 199								
			200 - 999								
			≥1000	0.3	1393670.9	0.4	1405242.3				
		Brachyura	63 - 199								
			200 - 999			0.4	10.1	0.8	45.6		
			≥1000					0.8	407509.3	4.2	8357.1
		Penaeidae	63 - 199								
			200 - 999	0.3	4374.9	2.4	4374.9	3.8	8749.8	0.4	257.9
			≥1000	5.7	3104359.5	11.4	5328931.0	21.7	3104359.5	7.1	3104359.5
		Isopoda	63 - 199								
			200 - 999	2.4	773.6	0.8	4374.9	0.4	4374.9		
			≥1000	7.3	895.6	1.2	2319.7	0.8	94036.4	0.4	22419.9
		Mysidacea	63 - 199								

Appendix A. Continued

Phylum / Subphylum	Class	Order / Family	Size (µm)	IF		IM		IO		UM	
				Freq	Median	Freq	Median	Freq	Median	Freq	Median
		Mysidacea	200 - 999	0.5	5930.7	7.3	103.1	8.3	180.5	2.5	51.6
			≥ 1000	1.9	2089.0	14.2	7940.4	14.2	5565.2	5.0	1044.5
	Ostracoda		63 - 199[a]	33.6	5134.9	32.9	6846.5	37.9	10269.8	5.4	3423.3
			200 – 999[a]	66.4	222685.9	72.4	183388.4	62.9	366776.8	10.8	39297.5
			≥1000								
Arthropoda / Uniramia											
	Insecta	Coleoptera	63 - 199								
			200 - 999			2.0	7077.4	3.3	8846.8		
			≥1000	22.2	677699.7	21.1	371255.7	20.0	645293.9	0.4	32405.9
		Diptera	63 - 199	5.1	7684.8	11.0	7684.8	7.5	7684.8	5.8	8531.9
			200 – 999[a]	54.7	25849.0	57.3	47323.7	70.8	48317.9	31.7	14515.3
			≥1000[a]	67.2	358452.2	54.9	174222.1	75.4	535096.9	38.8	103265.0
		Ephemeroptera	63 - 199								
			200 - 999	6.5	295.4	1.6	110.8	5.4	147.7		

Appendix A. Continued

Phylum / Subphylum	Class	Order / Family	Size (µm)	IF		IM		IO		UM	
				Freq	Median	Freq	Median	Freq	Median	Freq	Median
		Ephemeroptera	≥1000	19.5	5605.3	4.9	5920.3	13.8	26347.9	0.4	46306.2
		Hemiptera	63 - 199								
			200 – 999[a]	33.9	368.0	25.2	157.7	17.1	105.1	4.2	762.3
			≥1000[a]	50.7	14335.3	31.7	16373.1	22.5	4123.1	3.8	5345.1
		Lepidoptera	63 - 199								
			200 - 999			0.4	63.3				
			≥1000	0.8	146.6	0.4	440.3	0.4	440.3		
		Megaloptera	63 - 199								
			200 - 999								
			≥1000	0.8	37350.4	2.0	37350.4				
		Odonata	63 - 199								
			200 - 999	1.1	3206.6						
			≥1000	20.1	249248.9	7.3	551736.4	11.7	269851.0	0.4	2938.1
		Trichoptera	63 - 199								

Appendix A. Continued

Phylum / Subphylum	Class	Order / Family	Size (µm)	IF		IM		IO		UM	
				Freq	Median	Freq	Median	Freq	Median	Freq	Median
		Trichoptera	200 - 999								
			≥1000	0.8	12434.0			1.7	12434.0		
Mollusca											
	Bivalvia		63 - 199	0.3	751.0	0.4	1502.0				
			200 - 999	0.3	12118.9	0.8	112390.9	1.7	12118.9	3.8	12118.9
			≥1000	1.4	24237.7	0.8	10101.1	3.8	20202.2	14.6	113117.6
	Gastropoda		63 - 199	1.4	4506.1	2.8	8261.2	2.1	2253.1	5.8	8261.2
			200 - 999	8.7	217.3	10.2	27944.9	20.4	36865.6	6.3	48903.6
			≥1000	18.7	1049.1	2.8	174.9	17.5	224102.3	1.7	9743.6
Nematoda											
			63 - 199[a]	68.6	2934.2	89.4	8173.9	86.7	6287.6	92.5	203613.5
			200 – 999[a]	84.0	14671.1	95.5	39122.9	92.5	29342.2	93.8	322763.6
			≥1000								

Appendix A. Continued

Phylum / Subphylum	Class	Order / Family	Size (µm)	IF		IM		IO		UM	
				Freq	Median	Freq	Median	Freq	Median	Freq	Median
Granuloreticulosa											
	Foraminifera		63 - 199[a]	4.9	1070.9	56.5	2105.3	63.8	9968.9	66.7	21820.8
			200 – 999[a]	0.3	4191.7	56.5	10605.1	56.7	28692.4	59.6	41917.4
			≥1000								

[a] Defined as common invertebrate class and included in analyses (see Methods).

APPENDIX B

BIOMASSES OF INVERTEBRATE TAXA BY MONTH IN IF AND IO MARSH PONDS

Appendix B. Medians of biomass (mg / m^2) of benthic meiofauna (0.063 - 0.5 mm), benthic macrofauna (>0.5 mm), water-column (epiphytic and nektonic) macrofauna (>0.5 mm), and all invertebrates confounded (Total) by winter and month in ponds of impounded freshwater (IF) and impounded oligohaline (IO) marshes on the Gulf Coast Chenier Plain.

Winter	Month	IF				IO			
		Meiofauna	Macrofauna	Water-column	Total	Meiofauna	Macrofauna	Water-column	Total
1997-1998	December	604.82	3246.92	1081.58	5243.66	3347.16	148.80	0.00	3705.46
	January	269.81	4048.03	32.90	4416.22	492.35	3448.91	5.00	4278.87
	February	295.92	2429.47	14.08	3486.34	422.69	1197.62	3.11	1945.55
	March	222.48	3716.44	15.74	4438.20	409.48	1855.80	2.25	2162.75
1998-1999	November	104.79	48.32	0.00	238.64	174.57	4.36	0.00	396.47
	December	148.35	90.49	0.00	685.56	143.62	0.00	0.00	389.27
	January	266.42	395.68	0.00	793.41	218.16	458.11	0.00	755.05
	February	206.84	656.79	0.00	1021.48	314.53	687.83	0.00	1034.94
	March	191.49	696.97	3.30	1210.25	261.06	690.75	0.48	1348.24
1999-2000	November	262.12	42.08	12.44	769.44	300.46	287.71	2.48	2989.25
	December	385.57	29.38	0.00	605.99	921.94	742.56	0.55	4469.09
	January	392.00	305.20	21.76	896.34	889.84	737.10	0.00	2915.67
	February	653.95	104.80	69.11	1641.95	1139.96	1357.81	0.00	2113.77
	March	848.83	157.34	1.48	1613.05	1379.74	619.25	2.17	4355.33

APPENDIX C

BIOMASSES OF INVERTEBRATE TAXA BY MONTH IN IM AND UM MARSH PONDS

Appendix C. Medians of biomass (µg / m²) of benthic meiofauna (0.063 - 0.5 mm), benthic macrofauna (>0.5 mm), water-column (epiphytic and nektonic) macrofauna (>0.5 mm), and all invertebrates confounded (Total) by winter and month in ponds of impounded mesohaline and unimpounded mesohaline marshes on the Gulf Coast Chenier Plain.

Winter	Month	IM				UM			
		Meiofauna	Macrofauna	Water-column	Total	Meiofauna	Macrofauna	Water-column	Total
1997-1998	December	549.36	675.45	1.57	2098.69	0.00	249.80	0.00	273.01
	January	302.09	1942.71	3.05	2916.68	740.54	482.99	0.95	2014.84
	February	482.46	1195.95	2.88	1779.77	939.82	657.91	0.00	2078.47
	March	241.67	3280.39	0.15	3474.58	717.63	1301.54	0.00	2321.25
1998-1999	November	567.28	32.49	0.00	650.85	262.15	0.00	0.00	383.73
	December	130.68	223.11	0.00	561.97	235.21	19.62	0.00	378.08
	January	284.28	560.67	0.00	933.52	941.53	0.00	0.00	1139.58
	February	448.03	539.18	0.00	1334.81	1854.82	199.99	0.00	2239.71
	March	527.45	128.17	4806.68	7747.26	1459.75	60.56	0.00	2202.90
1999-2000	November	519.54	106.65	38.45	970.83	422.05	11.85	0.00	578.70
	December	350.99	85.87	0.00	683.44	1007.87	133.30	0.00	1429.38
	January	1345.79	261.48	0.00	1634.68	1014.36	115.32	0.00	1181.94
	February	424.88	243.30	2.03	1154.68	1091.81	173.90	0.00	1650.02
	March	258.54	48.53	0.00	378.57	1408.23	180.67	0.00	1801.93

APPENDIX D

FREQUENCIES AND DENSITIES OF WATERBIRDS

Appendix D. Percent frequencies of occurrence (PFO), mean observed densities (MOD) (birds/ha) of waterbird in ponds of impounded freshwater (IF), oligohaline (IO) mesohaline (IM), and unimpounded mesohaline (UM) marshes and their absolute frequencies of occurrence (AFO) for all marsh types combined (TOTAL) during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain.

Order and Species	IF		IO		IM		UM		TOTAL
	PFO	MOD	PFO	MOD	PFO	MOD	PFO	MOD	AFO
<u>Anseriformes</u>									
Green-winged Teal (*Anas crecca*) [a]	30.1	7.3 ± 3.9	24.7	4.0 ± 1.2	34.6	6.4 ± 2.4	50.0	6.6 ± 1.4	123
Northern Shoveler (*Anas clypeata*) [a]	21.1	1.4 ± 0.4	16.9	0.6 ± 0.2	35.9	1.5 ± 0.4	60.0	4.8 ± 0.9	115
Blue-winged Teal (*Anas discors*) [a]	47.2	5.8 ± 2.9	23.4	1.4 ± 0.5	11.5	0.2 ± 0.1	0.0	0.0 ± 0.0	85
Gadwall (*Anas strepera*) [a]	17.1	1.9 ± 0.7	31.2	4.2 ± 1.5	30.8	1.2 ± 0.4	7.5	0.2 ± 0.1	75
Mottled Duck (*Anas fulvigula*) [a]	12.2	0.5 ± 0.2	16.9	0.3 ± 0.1	15.4	0.3 ± 0.1	1.3	<0.1 ± 0.0	41
Lesser Scaup (*Aythya affinis*)	6.5	0.2 ± 0.1	9.1	<0.1 ± 0.0	1.3	0.1 ± 0.1	1.3	<0.1 ± 0.0	17
Mallard (*Anas platyrhynchos*)	4.9	0.3 ± 0.2	6.5	<0.1 ± 0.0	2.6	<0.1 ± 0.0	0.0	0.0 ± 0.0	13
Northern Pintails (*Anas acuta*)	2.4	0.3 ± 0.2	2.6	0.1 ± 0.1	9.0	0.9 ± 0.5	0.0	0.0 ± 0.0	12
Hooded Merganser (*Aix sponsa*)	0.0	0.0 ± 0.0	3.9	<0.1 ± 0.0	7.7	0.1 ± 0.1	1.3	<0.1 ± 0.0	10
Ring-necked Duck (*Aythya collaris*)	7.3	0.4 ± 0.2	1.3	<0.1 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	10
American Widgeon (*Anas americana*)	1.6	<0.1 ± 0.0	1.3	<0.1 ± 0.0	2.6	0.1 ± 0.1	0.0	0.0 ± 0.0	5

Appendix D. Continued.

Order and Species	IF		IO		IM		UM		TOTAL
	PFO	MOD	PFO	MOD	PFO	MOD	PFO	MOD	AFO
Bufflehead (*Bucephala albeola*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	3.8	<0.1 ± 0.0	0.0	0.0 ± 0.0	3
Ruddy Duck (*Oxyura jamaicensis*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	3.8	0.5 ± 0.5	0.0	0.0 ± 0.0	3
Fulvious Whistling Duck (*Dendrocygna bicolor*)	1.6	0.6 ± 0.6	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	2
Redhead (*Aythya americana*)	0.8	<0.1 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1
<u>Charadriiformes</u>									
Willet (*Catoptrophorus semipalmatus*) [a]	0.0	0.0 ± 0.0	1.3	0.1 ± 0.1	2.6	<0.1 ± 0.0	32.5	2.0 ± 0.9	29
American Avocet (*Recurvirostra americana*) [a]	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	30.0	6.1 ± 2.1	25
Black-necked Stilt (*Himantopus mexicanus*) [a]	4.1	<0.1 ± 0.0	9.1	0.1 ± 0.1	12.8	0.8 ± 0.4	2.5	0.1 ± 0.1	24
Ring-billed Gull (*Larus delawarensis*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	22.5	0.4 ± 0.1	19
Laughing Gull (*Larus atricilla*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	21.3	0.5 ± 0.2	18
Dowitcher sp. (*Limnodromus sp.*)	0.0	0.0 ± 0.0	1.3	0.3 ± 0.3	6.4	1.3 ± 0.8	8.8	1.4 ± 0.9	13
Yellowleg sp. (*Tringa sp.*)	0.8	0.1 ± 0.1	1.3	<0.1 ± 0.0	5.1	0.3 ± 0.2	5.0	0.2 ± 0.1	10
Sanderling (*Calidris alba*)	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	3.8	0.3 ± 0.3	6.3	1.1 ± 0.8	9
Foster's Tern (*Sterna fosteri*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	10.0	0.3 ± 0.2	8

Appendix D. Continued.

Order and Species	IF		IO		IM		UM		TOTAL
	PFO	MOD	PFO	MOD	PFO	MOD	PFO	MOD	AFO
Killdeer (*Charadrius vociferus*)	1.6	0.1 ± 0.1	1.3	<0.1 ± 0.0	5.1	0.1 ± 0.1	1.3	<0.1 ±0.0	8
Black-billed Plover (*Pluvialis squatarola*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	6.3	0.1 ± 0.1	5
Marbled Godwit (*Limosa fedoa*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	3.8	0.1 ± 0.1	3
Herring Gull (*Larus argentatus*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	3.8	<0.1 ± 0.0	3
Royal Tern (*Sterna maxima*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	3.8	<0.1 ±0.0	3
Dunlin (*Calidris alpina*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	2.5	0.2 ±0.2	2
Common Snipe (*Gallinago gallinago*)	0.8	0.1 ± 0.1	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1
Caspian Tern (*Sterna caspia*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ±0.0	1
Long-billed Curlew (*Numenius americanus*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ±0.0	1
Semiplamated Sandpiper (*Calidris pusilla*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	1.4 ± 1.4	1
Stilt Sandpiper (*Calidris himantopus*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3		1
Ciconiiformes									
Great Blue Heron (*Ardea herodias*) [a]	16.3	0.2 ± 0.1	15.6	0.1 ± 0.1	17.9	0.1 ± 0.1	10.0	0.1 ± 0.1	54
Snowy Egret (*Egretta thula*) [a]	8.1	0.2 ± 0.1	16.9	0.1 ± 0.1	9.0	0.1 ± 0.1	20.0	0.1 ± 0.1	46

Appendix D. Continued.

Order and Species	IF		IO		IM		UM		TOTAL
	PFO	MOD	PFO	MOD	PFO	MOD	PFO	MOD	AFO
Great Egret (*Casmerodius albus*) [a]	10.6	0.1 ± 0.1	20.8	0.1 ± 0.1	15.4	0.1 ± 0.1	3.8	<0.1 ± 0.0	44
Tricolored Heron (*Egretta tricolor*)	5.7	<0.1 ± 0.0	10.4	<0.1 ± 0.0	7.7	0.1 ± 0.1	7.5	0.1 ± 0.1	27
Little Blue Heron (*Egretta caerulea*)	7.3	0.2 ± 0.1	6.5	<0.1 ±0.0	7.7	0.1 ± 0.1	2.5	<0.1 ± 0.0	22
Roseate Spoonbill (*Ajaja ajaja*)	1.6	0.1 ± 0.1	7.8	0.1 ± 0.1	7.7	0.1 ± 0.1	5.0	0.1 ± 0.1	18
White Ibis (*Eudocimus albus*)	5.7	0.2 ± 0.1	5.2	0.2 ± 0.2	0.0	0.0 ± 0.0	2.5	<0.1 ± 0.0	13
Glossy Ibis (*Plegadis falcinellus*)	4.1	0.2 ± 0.1	2.6	<0.1 ± 0.0	1.3	<0.1 ± 0.0	0.0	0.0 ± 0.0	8
Black-crowned Night Heron (*Nycticorax nycticorax*)	3.3	0.1 ± 0.1	0.0	0.0 ± 0.0	2.6	<0.1 ± 0.0	0.0	0.0 ± 0.0	6
American Bittern (*Botaurus lentiginosus*)	0.8	<0.1 ± 0.0	1.3	<0.1 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	2
Green Heron (*Butorides striatus*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	0.0	0.0 ± 0.0	1
Reddish Egret (*Egretta rufescens*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	1
Gruiformes									
American Coot (*Fulica americana*) [a]	85.4	16.0 ± 3.1	41.6	3.4 ± 1.1	9.0	0.3 ± 0.2	0.0	0.0 ± 0.0	144
Common Moorhen (*Gallinula chloropus*) [a]	69.9	4.2 ± 0.6	19.5	0.6 ± 0.4	3.8	0.1 ± 0.1	0.0	0.0 ± 0.0	104
Virginia Rail (*Rallus limilcola*)	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	2

Appendix D. Continued.

Order and Species	IF		IO		IM		UM		TOTAL
	PFO	MOD	PFO	MOD	PFO	MOD	PFO	MOD	AFO
Clapper Rail (*allus longirostris*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	1
King Rail (*Rallus elegans*)	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	1.3	<0.1 ± 0.0	1
<u>Pelecaniformes</u>									
Double-crested Cormorant (*Phalacrocorax auritus*) [a]	8.1	0.1 ± 0.1	22.1	0.3 ± 0.1	12.8	0.1 ± 0.1	11.3	0.1 ± 0.1	46
American White Pelican (*Pelecanus erythrorhynchos*)	0.0	0.0 ± 0.0	2.6	<0.1 ± 0.0	0.0	0.0 ± 0.0	17.5	0.2 ± 0.1	16
<u>Podicipediforme</u>									
Pied-billed Grebe (*Podilymbus podiceps*) [a]	39.0	7.3 ± 3.9	45.5	0.5 ± 0.1	53.8	0.9 ± 0.2	2.5	<0.1 ± 0.0	127

[a] Defined as common wintering waterbirds and included in analyses (see Methods).

APPENDIX E

PREDICTED DENSITIES OF CHARADRIIFORMES, CICONIIFORMES, PELECANIFORMES, AND PODICIPEDIFORMES BY 2-CM WATER DEPTH CLASS

Appendix E. Predicted densities (birds/ha) of charadriiformes, ciconiiformes, pelecaniformes, and podicipediformes by 2-cm water depth class in marsh ponds during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Predicted densities were computed using nonparametric regressions (See Methods). Waterbird species are American Avocets (AMAV), Black-necked Stilts (BNST), Willets (WILL), Great Egrets (GREG), Great Blue Herons (GTBH), Snowy Egrets (SNEG), Double-crested Cormorants (DCCO), and Pied-billed Grebe (PBGR).

Depth (cm)	AMAV	BNST	WILL	GREG	GTBH	SNEG	DCCO	PBGR
0	0.00	0.26	1.49	0.06	0.14	0.15	0.03	0.02
1	2.90	0.30	2.37	0.07	0.14	0.19	0.04	0.00
3	5.36	0.33	2.73	0.08	0.14	0.22	0.05	0.00
5	6.79	0.35	2.68	0.09	0.13	0.25	0.06	0.00
7	7.27	0.37	2.11	0.10	0.13	0.27	0.07	0.01
9	7.19	0.38	0.63	0.11	0.13	0.28	0.08	0.06
11	5.54	0.39	0.27	0.11	0.13	0.28	0.09	0.13
13	3.05	0.40	0.33	0.12	0.13	0.28	0.09	0.22
15	2.23	0.40	0.13	0.12	0.13	0.27	0.10	0.33
17	2.10	0.39	0.09	0.12	0.12	0.26	0.11	0.47
19	0.89	0.38	0.16	0.12	0.12	0.24	0.11	0.67
21	0.04	0.37	0.13	0.12	0.12	0.21	0.12	0.87
23	0.32	0.35	0.06	0.12	0.13	0.17	0.12	1.04
25	0.78	0.34	0.04	0.12	0.13	0.13	0.13	1.16
27	0.71	0.31	0.10	0.11	0.13	0.09	0.13	1.17
29	0.39	0.28	0.14	0.11	0.13	0.06	0.13	1.05
31	0.02	0.25	0.11	0.10	0.13	0.04	0.14	0.87

Appendix E. Continued.

Depth (cm)	AMAV	BNST	WILL	GREG	GTBH	SNEG	DCCO	PBGR
33	0.00	0.20	0.05	0.09	0.13	0.03	0.14	0.72
35	0.00	0.15	0.00	0.08	0.13	0.02	0.14	0.65
37	0.00	0.10	0.00	0.08	0.14	0.03	0.14	0.69
39	0.00	0.07	0.00	0.07	0.14	0.04	0.14	0.77
41	0.00	0.03	0.00	0.06	0.14	0.05	0.14	0.80
43	0.00	0.01	0.00	0.05	0.15	0.06	0.14	0.79
45	0.00	0.00	0.00	0.04	0.15	0.08	0.15	0.78
47	0.00	0.00	0.00	0.04	0.15	0.09	0.16	0.72
49	0.00	0.00	0.00	0.03	0.15	0.08	0.17	0.64
51	0.00	0.00	0.00	0.03	0.15	0.07	0.17	0.55
53	0.00	0.00	0.00	0.02	0.15	0.07	0.18	0.47
55	0.00	0.00	0.00	0.02	0.14	0.08	0.18	0.40
57	0.00	0.00	0.00	0.01	0.14	0.10	0.18	0.39
59	0.00	0.00	0.00	0.01	0.14	0.12	0.18	0.38
61	0.00	0.00	0.00	0.01	0.13	0.14	0.18	0.39
65	0.00	0.00	0.00	0.00	0.11	0.17	0.19	0.40
67	0.00	0.00	0.00	0.00	0.10	0.18	0.18	0.31
69	0.00	0.00	0.00	0.00	0.09	0.19	0.18	0.59
71	0.00	0.01	0.00	0.00	0.08	0.21	0.18	1.08
73	0.00	0.02	0.00	0.00	0.07	0.22	0.18	1.72
81	0.00	0.10	0.00	0.00	0.00	0.27	0.16	5.88

APPENDIX F

PREDICTED DENSITIES OF GRUIFORMES ANSERIFORMES BY 2-CM WATER DEPTH CLASS

Appendix F. Predicted densities (birds/ha) of gruiformes and anseriformes by 2-cm water depth class in marsh ponds during winters 1997-1998 to 1999-2000 on the Gulf Coast Chenier Plain. Predicted densities were computed using nonparametric regressions (See Methods). Waterbird species are American Coots (AMCO), Common Moorhens (COMO), Gadwalls (GADU), Blue-winged Teal (BWTE), Green-winged Teal (AGWT), Mottled Ducks (MODU), and Northern Shovelers (NSHO).

Depth (cm)	AMCO	COMO	GADU	BWTE	AGWT	MODU	NSHO
0	0.00	0.01	0.00	0.00	7.09	0.00	1.87
1	0.47	0.03	0.00	0.65	9.14	0.00	5.16
3	1.21	0.06	0.00	1.30	10.84	0.06	7.01
5	1.90	0.11	0.42	1.87	12.20	0.14	7.55
7	2.55	0.16	0.89	2.37	13.24	0.22	6.82
9	3.14	0.23	1.36	2.79	13.97	0.28	4.29
11	3.70	0.31	1.81	3.14	14.37	0.34	2.20
13	4.22	0.40	2.24	3.42	14.48	0.40	1.36
15	4.70	0.50	2.66	3.64	14.29	0.44	1.90
17	5.14	0.60	3.07	3.80	13.83	0.48	2.70
19	5.56	0.72	3.50	3.91	13.10	0.50	2.72
21	5.95	0.85	4.01	3.97	12.10	0.52	2.26
23	6.31	0.99	4.38	3.98	10.77	0.54	1.88
25	6.64	1.14	4.53	3.93	9.02	0.54	1.70
27	6.94	1.29	4.44	3.82	7.08	0.54	1.66
29	7.21	1.46	4.12	3.63	5.15	0.53	1.90
31	7.44	1.63	3.63	3.34	3.30	0.50	1.89
33	7.62	1.81	3.06	2.90	1.66	0.46	1.32

Appendix F. Continued.

Depth (cm)	AMCO	COMO	GADU	BWTE	AGWT	MODU	NSHO
35	7.72	2.01	2.47	2.25	0.45	0.42	0.56
37	7.71	2.23	1.92	1.70	0.00	0.37	0.08
39	7.58	2.47	1.41	1.46	0.00	0.31	0.00
41	7.61	2.73	0.97	1.09	0.00	0.26	0.00
43	7.88	2.93	0.62	1.01	0.23	0.21	0.05
45	8.15	3.07	0.37	0.99	0.27	0.17	0.18
47	8.39	3.18	0.22	0.99	0.28	0.13	0.30
49	8.59	3.29	0.22	1.01	0.44	0.10	0.34
51	8.75	3.39	0.29	1.03	0.65	0.07	0.30
53	8.88	3.50	0.38	1.05	0.93	0.05	0.15
55	8.99	3.61	0.54	1.09	1.17	0.03	0.02
57	9.07	3.73	0.65	1.14	1.35	0.01	0.01
59	9.13	3.84	0.71	1.20	1.48	0.00	0.24
61	9.16	3.96	0.75	1.28	1.57	0.00	0.60
65	9.16	4.18	0.75	1.49	1.69	0.00	0.90
67	9.12	4.28	0.74	1.61	1.73	0.00	0.87
69	9.05	4.37	0.71	1.75	1.75	0.00	0.52
71	8.94	4.46	0.67	1.90	1.76	0.00	0.40
73	8.81	4.54	0.62	2.07	1.74	0.00	0.28
81	7.90	4.83	0.22	2.80	1.40	0.05	0.00

VITA

François Bolduc, the last of 5 sons of Micheline Marceau and Gerard Bolduc, was born 17 November 1965, in Québec City, Québec, Canada. He graduated from St-Jean Eudes High School in Québec City, in 1983. Prior to his bachelor degree, he obtained a collegial degree in wildlife techniques from College St-Felicien in 1986. He earned his bachelor's degree in biology with a specialization in ecology from Université du Québec à Rimouski in 1993. He received his master's degree in science from McGill University in 1998, where he studied the effects of human disturbance on the nesting success of Common Eiders. In August 2002, he will receive the degree of Doctor of Philosophy.