Chapter 4

INTERACTIONS OF STRUCTURAL MARSH MANAGEMENT, SALINITY, AND WATER DEPTH ON WINTERING WATERBIRD COMMUNITIES

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ABSTRACT

Substantial hydrologic changes occurred during the last century in coastal marshes of southwestern Louisiana, which provide vital habitats for wintering waterbirds of North America. As a result, structural marsh management (levees, water control structures and impoundment; SMM) has been widely implemented for conservation purposes. Our previous research on marsh ponds in this area indicated that SMM mostly decreased biomass of small nematoda and secondarily increased that of ostracoda. We also found that invertebrate communities of impounded freshwater (IF), oligohaline (IO), and mesohaline (IM) marshes differed primarily in biomass of oligochaeta. However, the above invertebrate taxa are not likely major prey of waterbirds. Consequently, we predicted that waterbird species that differentiate communities (1) of IM and unimpounded mesohaline (UM) marshes, and (2) of IF, IO, and IM marshes would not be invertebrate-feeding species. We tested these two predictions by comparing waterbird densities among marsh types using multivariate analysis of variance (MANOVA). We computed standardized canonical coefficients from MANOVA to evaluate contributions of waterbird species to differences in communities among marsh types. We used corrected bird densities (Bolduc and Afton 2008) to remove the confounding effects of water level variation among sampling periods and sites on our comparisons. In contrast to our first prediction, several waterbird species that consume invertebrates contributed most to differences in waterbird communities between ponds of IM and UM marshes.

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(American avocets *Recurvirostra americana*, northern shovelers *Anas clypeata*, and willets *Catoptrophorus semiplamatus*). However, consistent with our second prediction, species that consume vegetation contributed most to differences in waterbird communities among ponds of IF, IO, and IM marsh ponds (common moorhens *Gallinula chloropus*, American coots *Fulica americana*, gadwalls *A. strepera*). Most waterbird species had highest observed densities in IF marshes when water depth was lower than on average, whereas American avocets, northern shovelers, and willets mainly used ponds of UM marshes. We conclude that (1) maintenance of water depths preferred by various waterbirds, (2) promoting hydrological diversity at the landscape level, and (3) the preservation of UM and IF marshes would be most beneficial for the conservation of wintering waterbird populations.

**INTRODUCTION**

Wetlands provide essential habitats to waterbirds (Anseriformes, Charadriiformes, Ciconiiformes, Gaviiformes, Gruiiformes, Pelecaniformes, Phoenicopteriformes, Podicipediformes, and Procellariformes) throughout their life cycle (Weller 1999). Marshes on the northern coast of the Gulf of Mexico are vital habitats for wintering waterbirds of North America. For example, 19% of the waterfowl wintering in the U.S. are observed on marshes of the Louisiana Gulf coast (Michot 1996). This region also is a significant area for wintering wading birds (Mikuska et al. 1998) and migrating shorebirds (Helmers 1992).

Wetlands are disappearing at a rapid pace worldwide, mostly where human density is highest (Mitsch 2005). Various wetland functions also are being altered that are vital to waterbirds and their required resources (Lagos et al. 2008; Anteau and Afton 2011). The Deltaic and Chenier Plains of Louisiana contain 41% of all coastal wetlands in the U.S., and these marshes are receding at significant rates (Turner 1990). Landings of hurricanes Katrina and Rita on the coast of Louisiana in 2005 exacerbated wetland loss in the area, but also increased national exposure, which resulted in numerous wetland restoration initiatives (Day et al. 2007). More specifically, wetlands of southwestern Louisiana have been impacted beginning in the last century; dredging of north-south waterways, occurrence of large-scale muskrat *Ondatra zibethica* eat-outs, and a severe drought that occurred in the early 1950s apparently facilitated saltwater intrusion and caused a large marsh vegetation die-off in the area (Wicker et al. 1983). Starting during the mid-1950s, numerous marshes were managed using structural marsh management (levees, water control structures and impoundments; hereafter SMM) to revegetate open water areas that had formed, stop saltwater intrusion, and increase the productivity of waterfowl food plants (Wicker et al. 1983; Day et al. 1990).

SMM generally increases food abundance because it promotes the growth of vegetation that waterfowl consume (Jemison and Chabreck 1962). However, aquatic invertebrates also comprise a primary food resource for many wintering waterbirds (Martin and Hamilton 1985; Krapu and Reinecke 1992; Gaston 1992; Skagen and Oman 1996). SMM mostly decreases biomass of small nematoda and secondarily increases that of ostracoda (Bolduc and Afton 2003). However, few waterbird species possess the capacity to capture these small prey (Nudds and Bowlby 1984; Zwarts and Wanink 1984); consequently, we predicted that waterbird species that differentiate communities of impounded and unimpounded marshes would not be invertebrate-feeding species.
Salinity has a large effect on winter habitats of waterbirds because it influences compositions of plant and invertebrate communities (Chabreck 1972; Ma et al. 2010). Marshes of southwestern Louisiana are divided into 3 categories of salinity based on the Venice system (Bulger et al. 1993; Visser et al. 2000): (1) freshwater (salinity < 0.5‰), (2) oligohaline (salinity 0.5 - 5.0‰), and (3) mesohaline (salinity 5.0 - 18.0‰). Little information is available concerning habitat use of waterbirds in southwestern Louisiana marshes in relation to salinity, except that densities of wintering dabbling ducks increase with decreasing salinity on the Louisiana coast (Palmsano 1972; Link and Afton In Press). Such information is needed because oligohaline marshes have expanded at the expense of freshwater and mesohaline marshes in the area before landings of hurricanes Katrina and Rita in 2005, and freshwater and intermediate wetlands loss generally was twice that of higher salinity marsh during the 2005 hurricane season (Visser et al. 2000, Howes et al. 2010). Ponds of impounded freshwater, oligohaline, and mesohaline marshes have similar hydrologic characteristics (Bolduc and Afton 2004b), sediment characteristics (Bolduc and Afton 2005), and their invertebrate communities differ mostly in biomass of oligochaeta (Bolduc and Afton 2003). Oligochaeta prey are of minor importance to shorebirds (Skagen and Oman 1996) and waterfowl (Safran et al. 1997); therefore, changes in biomass of oligochaeta would not be expected to greatly affect waterbird communities (Krapu and Reineke 1992; Skagen and Oman 1996). Consequently, we predicted that waterbird species that differentiate communities of impounded freshwater, oligohaline, and mesohaline marshes would not be invertebrate-feeding species.

Water depth limits food accessibility to most waterbirds, and, thus, bird density often varies with this metric during winter (Bolduc and Afton 2004a, Ma et al. 2010). Non-diving waterbirds have particular physical attributes that allow them to feed at specific water depths (Pöysä 1983; Zwarts and Wanink 1984). On the other hand, diving waterbirds probably are limited by a minimum water depth that prevents diving and foraging efficiently. Therefore, a fluctuating hydrology within the landscape largely dictates where and when waterbird species are observed. Changes in food accessibility potentially occur when SMM is implemented because it controls water inflows and outflows at the local scale. Yet, previous studies examining effects of SMM on waterbird densities have provided equivocal results because data analysis did not account for water level variability among sampling periods and sites in both impounded and reference marshes (Chabreck et al. 1974; Epstein and Joyner 1988; Weber and Haig 1996). Clearly, waterbird densities need to be adjusted for variation in water depth to obtain reliable estimates for habitat comparisons (Bolduc and Afton 2008).

Assessment of management procedures is critical within an adaptive management process, whereby managers adapt practices as they acquire knowledge on wetlands. Changes in hydrology via wetland management should produce predictable changes in plant and animal communities allowing managers to determine how waterbirds respond to changes in their resources and accessibility. Using waterbird survey data, we first describe differences in water levels among marsh types, and the relationship between bird density and water levels. We subsequently test our two predictions above concerning effects of SMM and salinity using corrected bird densities (Bolduc and Afton 2008), to control for the confounding effect of water level variation among marsh types and sampling periods.
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 westward currents 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 (i.e., Cheniers) composed of sand and shells separated by mud flats where marshes developed (Byrne et al.1959).

We chose Rockefeller State Wildlife Refuge (RSWR; 29˚40’30” N, 92˚48’45” W), located on the Gulf Coast Chenier Plain, as a representative area of southwestern Louisiana. 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 were separated by a network of canals that surround the levees (Wicker et al.1983). Impoundments on RSWR contain marsh types of various salinities characteristic of southwestern Louisiana, i.e., freshwater, oligohaline, and mesohaline marshes (Visser et al. 2000). RSWR also contains a large area of unimpounded mesohaline marshes (11,700 ha). No hunting is allowed on RSWR and therefore disturbance affecting waterbird distribution is negligible in this area.

Sampling Design

We sampled 4 marsh types of RSWR: (1) 3 impounded freshwater marshes (IF) (units 8, 10, and 13), (2) 3 impounded oligohaline marshes (IO) (units 3, 4, and 15 [the latter replaced unit 3 in winter 1999-2000]), (3) 2 impounded mesohaline marshes (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, we initially identified 4 to 8 ponds that were accessible directly from levees or with a small boat. We chose these ponds to minimize both time spent commuting among sites and disturbance to waterbirds, and to ensure access to study ponds at all times. Subsequently, we 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, we randomly selected 1 large pond and 2 small ponds in each of these marsh types.

We visited all 27 ponds monthly, from December to March in 1997-98, and from November to March in 1998-99 and 1999-2000 (14 months total). During each visit to a pond, 2 observers entered a permanent blind at sunrise, waited 90 minutes, and then counted birds present on the pond within a 200 m 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 for each species in the 2 scans comprised the final count. After bird counts, observers randomly selected 3 sampling stations to measure water depth within each selected pond. Observers 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 m.
from the blind. Three sampling stations within a pond were sufficient to estimate water depth because it generally varied little within ponds (Bolduc and Afton 2004b). At all sampling stations, observers used a graduated stick (± 1 cm) to measure water depth.

**Statistical Analyses**

We limited our analyses to common waterbird species observed on RSWR. We defined common waterbirds based on 2 arbitrary rules: (1) a species that had a percent frequency ≥10% in at least 1 of the marsh types surveyed; and (2) a species that had an absolute frequency of occurrence ≥20 over all marsh types (Bolduc and Afton 2004a). We computed bird densities using bird counts and the area (m²) surveyed on each pond within 200 m using aerial photographs (1:12,000) taken during winter 1998 for RSWR and ArcView GIS 3.2 software. We analyzed the relationship between water depth and mean density of common waterbirds by 2-cm water depth classes overall all habitats using nonparametric regressions (PROC LOESS, SAS Institute, Inc. 1999) because of the nonlinear relationship between these variables (Bolduc and Afton 2008). We used the generalized cross-validation criterion to estimate the smoothing parameter that minimizes the mean square error in the nonparametric regressions (Schimek 2000).

For each pond visit, we averaged the 3 water depths to obtain similar sampling units for both water depth and bird density. Ponds were flat-bottomed, displaying little variation in water depth within ponds (Bolduc and Afton 2004b). Based on this analysis, we computed corrected densities of common wintering waterbird species ([observed – predicted density from nonparametric regression] / [observed + predicted density] * 100; Bolduc and Afton 2008). A negative corrected density implies that we observed a lower density than predicted by the parametric regression at the observed water depth. We used corrected densities of common waterbird species as the response variable in tests of our predictions. We also compared tests of predictions using observed and corrected densities to assess the benefits of using corrected densities, as suggested in Bolduc and Afton (2008). We used the 95th percentile of observed bird densities to explore the association among highest densities, marsh types and water depth. To help interpret results from corrected densities, we provided the corresponding ratio of observed: predicted waterbird density from nonparametric regressions between water depth and mean waterbird density. For example, a ratio of observed: predicted density of - 67 indicated that 1.5 times fewer birds were recorded than that predicted from observed water depth (Bolduc and Afton 2008).

We compared densities of common waterbird species between ponds of IM and UM marshes and among ponds of IF, IM and IO marshes using multivariate analyses of variance (MANOVA). Fixed explanatory variables were marsh type, time (months), and their interaction. The random explanatory variable was impoundment within marsh type × time. We did not include a year effect and only include a time (month) variable in our model to reduce the model complexity and provide more robust results because (1) our sampling scheme was based on a monthly schedule of pond visitation, and (2) a priori analyses showed no correlation between consecutive monthly counts within pond among years (pers. comm., D.C. Blouin, LSU Experimental Statistics Department). We did not consider a repeated measures model because different birds within ponds probably were counted in consecutive months. We performed separate a priori MANOVA contrasts to test our two predictions of
interest (UM vs. IM, and IF vs. IO and IM). For these a priori comparisons, we used an error matrix based on the random effect of impoundment within marsh type × time.

We used Wilk’s λ statistic to compute F-ratios of our 2 a priori MANOVA contrasts (PROC GLM, SAS Institute, Inc. 1999). We considered P-values < 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 λ – 1, Tabachnick and Fidell 1989). Finally, we computed canonical correlations and standardized canonical coefficients from MANOVA contrasts to evaluate the contribution of various common waterbird species to differences among marsh types. Our sampling design provided 56 degrees of freedom for the error term associated with the fixed effects, which is more than the minimum of 20 needed to ensure robustness of multivariate tests (Tabachnick and Fidell 1989).

We compared water depth between ponds of IM and UM marshes and among ponds of IF, IM and IO marshes using an analysis of variance, following a similar design as for comparisons of bird densities, but where water depth was the only response variable (PROC MIXED, SAS Institute, Inc. 1999, see also Bolduc and Afton 2004b). We compared seasonal and spatial variabilities in water depths between ponds of IM and UM marshes using variance components analysis. We 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). We 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). We present results as least-square means ± standard errors unless noted otherwise. We performed all statistical analyses using SAS 8.2 (SAS Institute, Inc. 1999).

**RESULTS**

**Differences in Water Depth among Marsh Types**

Water depth differed between IM and UM marsh ponds ($F_{1, 70} = 114.3, P < 0.0001$), where mean water depth was 18.7 ± 1.7 cm higher in IM marsh ponds than in UM marsh ponds on average (Figure 1). Water depth also differed among IF, IO and IM marsh ponds ($F_{1, 70} = 25.6, P < 0.0001$). Mean water depth was higher in IF than in IO or IM marsh ponds by 6.8 ± 1.3 cm on average (Figure 1). Our variance components analysis indicated that water depth varied more among months in ponds of IM marshes than in those of UM marshes (Table 1). Variance in water depth between impoundments (or hydrographic basins for UM) also was greater in IM than in UM marsh ponds (Table 1). 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 1).
From Bolduc and Afton 2004b.

Figure 1. Mean water depth (least square means ± standard errors) by marsh type (IF = impounded freshwater, IO = impounded oligohaline, IM = impounded mesohaline, and UM = unimpounded mesohaline) during winters 1997-1998 to 1999-2000 in southwestern Louisiana marshes.

Table 1. Estimates of variance ($\sigma^2$) in water depth 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 (4) sampling stations within ponds, impoundments and months (residuals), during winters 1997-1998 to 1999-2000 in southwestern Louisiana

<table>
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<th>Months</th>
<th>Impoundments/</th>
<th>Ponds</th>
<th>Residuals</th>
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<tbody>
<tr>
<td>$\sigma^2_{IM}$</td>
<td>152.98</td>
<td>38.20</td>
<td>22.20</td>
<td>6.66</td>
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<tr>
<td>$\sigma^2_{UM}$</td>
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<td>0</td>
<td>78.15</td>
<td>19.77</td>
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<tr>
<td>p-value</td>
<td>0.0014</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td></td>
</tr>
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</table>

*Test not possible due 0 estimated variance.

$F$-ratios test for difference in variance estimates between marsh types for each effect.

From Bolduc and Afton 2004b.

Relationship between Water Depth and Waterbird Densities

Species-specific nonparametric regressions indicated that Anseriformes generally had highest predicted densities at water depths under 26 cm (Figure 2a). Green-winged teal (Anas crecca) had highest predicted density by water depth classes among this order (at 13 cm), followed by northern shovelers (A. clypeata) at 5 cm, gadwalls (A. strepera) at 25 cm, blue-winged teal (A. discors) at 23 cm, and mottled ducks (A. fulvigula) at 25 cm (Figure 2a).

Among Charadriiformes, American avocets (Recurvirostra Americana) had highest predicted densities by water depth classes at 7 cm, followed by willets at 3 cm, and black-necked stilts (Himantopus mexicanus) at 13 cm (Figure 2b). Ciconiiformes showed little
variation in predicted densities among water depth classes (range: 0 – 0.28 birds/ha; Figure 2c). Pied-billed grebes (Podilymbus podiceps) reached highest predicted density at deep water depths (Figure 2c), but this increase was influenced greatly by a single observation at 81 cm. Double-crested cormorants (Phalacrocorax auritus) had only a small increase in predicted density with water depth (Figure 2c). Gruiformes had highest predicted densities at deeper water depths than did species of other bird orders (Figure 2d). Predicted densities of common moorhens (Gallinula chloropus) apparently increased with water depth (Figure 2d), whereas predicted densities of American coots (Fulica americana) were maximized at 61 cm.

Data used in this figure are provided in Bolduc (2002).

Figure 2. Predicted mean densities (birds/ha) of common waterbirds by 2-cm water depth classes during winters 1997-1998 to 1999-2000 in southwestern Louisiana based on nonparametric regressions (see Methods) for a) Anseriformes; green-winged teal (AGWT), blue-winged teal (BWTE), gadwall (GADW), mottled duck (MODU), and northern shoveler (NSHO), for b) Charadriiformes; American avocet (AMAV), black-necked stilt (BNST), and willet (WILL), for c) Ciconiiformes; great blue heron (GBHE), great egret (GREG), and snowy egret (SNEG), Podicipediformes; pied-billed grebe (PBGR), Pelecaniformes; double-crested cormorant (DCCO), and for d) Gruiformes; American coot (AMCO) and common moorhen (COMO).
Comparison of IM and UM Marsh Ponds Using Corrected Densities

Our *a priori* MANOVA contrast indicated that corrected densities of the 15 common waterbird species differed between UM and IM marsh ponds (Wilk’s λ=0.15, $F_{15, 56} = 19.45$, $P<0.001$, Effect size = 0.85). Standardized canonical coefficients of common waterbird species indicated that corrected densities of pied-billed grebes, northern shovellers, willets (*Tringa semipalmata*), American avocets, and gadwalls differed most between IM and UM marsh ponds (largest standardized coefficients, Table 2).

Common waterbirds with highest corrected densities in ponds of UM marshes were northern shovellers, green-winged teal, willets, American avocets, and snowy egrets (*Egretta thula*) (Figure 3). Other common waterbirds rarely used ponds of UM marshes (ratio observed: predicted density < 0.1, or about a density 20 of what predicted, Figure 3). In ponds of IM marshes, pied-billed grebes had the highest corrected density, whereas all other species had corrected densities of approximately ~70 (ratio observed: predicted density < 0.17, Figure 3), or rarely were observed (American avocets, American coots, blue-winged teal, common moorhens, and willets [ratio observed: predicted density < 0.05], Figure 3).

Table 2. Canonical correlations (CC) and standardized canonical coefficients (SCC) from *a priori* MANOVA contrasts that tested for differences in corrected densities (and in observed densities in parentheses) 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 in southwestern Louisiana

<table>
<thead>
<tr>
<th>Species</th>
<th>UM vs. IM CC</th>
<th>UM vs. IM SCC</th>
<th>IF vs. IO and IM CC</th>
<th>IF vs. IO and IM SCC</th>
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<tbody>
<tr>
<td>American avocet</td>
<td>0.52 (0.42)</td>
<td>0.59 (0.55)*</td>
<td>-0.09 (-0.04)</td>
<td>0.05 (0.04)</td>
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<tr>
<td>American coot</td>
<td>-0.18 (-0.17)</td>
<td>0.40 (-0.16)</td>
<td>0.59 (0.73)</td>
<td>0.92 (0.88)</td>
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<td>-0.12 (-0.13)</td>
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<td>-0.05 (-0.08)</td>
<td>0.13 (-0.03)</td>
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<tr>
<td>blue-winged teal</td>
<td>-0.21 (-0.06)</td>
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<td>0.30 (0.27)</td>
<td>-0.24 (-0.12)</td>
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<td>common moorhen</td>
<td>-0.09 (-0.16)</td>
<td>0.22 (0.03)</td>
<td>0.86 (0.81)</td>
<td>1.49 (0.69)</td>
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<td>double-crested cormorant</td>
<td>0.02 (-0.04)</td>
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<td>-0.32 (-0.11)</td>
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<td>great egret</td>
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<td>northern shoveler</td>
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<td>snowy egret</td>
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<td>willet</td>
<td>0.66 (0.43)</td>
<td>0.82 (0.56)</td>
<td>-0.13 (-0.12)</td>
<td>-0.17 (-0.08)</td>
</tr>
</tbody>
</table>

*Bolded scores represent species that contributed most to the difference among marsh types. Positive coefficients indicate a difference favorable to the first marsh type included in the comparison.*
Figure 3. 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 in southwestern Louisiana 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 (GADW), great blue heron (GBHE), great egret (GREG), mottled duck (MODU), northern shoveler (NSHO), pied-billed grebe (PBGR), snowy egret (SNEG), and willet (WILL).

**Comparison of IF with IO and IM Marsh Ponds Using Corrected Densities**

Our *a priori* MANOVA contrast indicated that corrected densities of the 15 common waterbird species differed among ponds of IF, IO, and IM marshes (Wilk’s $\lambda = 0.11$, $F_{15, 56} = 27.79$, $P<0.001$, Effect size = 0.89). Standardized canonical coefficients of common waterbird species indicated that corrected densities of common moorhens, American coots, and gadwalls differed most among these marsh types (largest standardized coefficients, Table 2). Species that had highest corrected densities in ponds of IF marshes were American coot, common moorhen, pied-billed grebe, and blue-winged teal (ratio observed: predicted density > 0.25, Figure 3). Other common waterbirds rarely used ponds of IF marshes (corrected density < -70, ratio observed: predicted density < 0.17, Figure 3). In IO marsh ponds, pied-billed grebes had the highest corrected density, whereas all other species obtained corrected densities < -60 (ratio observed: predicted density < 0.25), or were not observed (American avocets and willets [ratio observed: predicted density = 0], Figure 3).
Comparisons of Marsh Types Using Observed Densities

Our *a priori* MANOVA contrast indicated that observed densities of the 15 common waterbird species differed between UM and IM marsh ponds (Wilk’s $\lambda=0.28$, $F_{15, 56} = 8.56$, $P<0.001$, Effect size = 0.72). Standardized canonical coefficients of common waterbird species indicated that observed densities of pied-billed grebes, northern shovellers, willets, American avocets, and green-winged teal differed most between IM and UM marsh ponds (largest standardized coefficients, Table 2). Common waterbirds with highest observed densities in ponds of UM marshes were green-winged teal, American avocets, northern shovellers, and willets (Figure 4). In ponds of IM marshes, green-winged had greatest densities, whereas all other species had low observed densities (Figure 4).

Our *a priori* MANOVA contrast indicated that observed densities of the 15 common waterbird species differed among ponds of IF, IO, and IM marshes (Wilk’s $\lambda=0.31$, $F_{15, 56} = 7.70$, $P<0.001$, Effect size = 0.69). Standardized canonical coefficients of common waterbird species indicated that observed densities of common moorhens and American coots differed most among these marsh types (largest standardized coefficients, Table 2).

![Figure 4](image-url)

Figure 4. Observed densities (least-square means ± SE) of common waterbirds by marsh type (● = impounded freshwater, ♦ = impounded oligohaline, ■ = impounded mesohaline, and □ = unimpounded mesohaline) during winters 1997-1998 to 1999-2000 in southwestern Louisiana 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 (GADW), great blue heron (GBHE), great egret (GREG), mottled duck (MODU), northern shoveler (NSHO), pied-billed grebe (PBGR), snowy egret (SNEG), and willet (WILL).
Common moorhen, American coots, green-winged and blue-winged teal obtained greatest observed densities in ponds of IF marshes, whereas gadwalls, green-winged teal and common moorhen obtained greatest observed densities in IO marshes, and green-winged teal in IM marshes (Figure 4).

**Relationship between 95th Percentile of Observed Bird Densities, Marsh Type, and Water Depth**

We used the 95th percentile of observed bird densities to explore the association among highest densities, marsh types and water depth. Nine of the 15 common species in our study area had most of their highest counts in IF marsh ponds (Table 3). Three species comprised most of the highest counts in UM marsh ponds, whereas 2 and 1 species did so in IM and IO marsh ponds respectively (Table 3). Gadwalls, great blue herons (*Ardea Herodias*), and pied-billed grebes, which were species with most of their highest counts in IF marsh ponds, still displayed a proportion between 36 and 43% of their highest counts in other marsh types (Table 3). Mean water depth associated with observed densities > 95th percentile was between 25.2 and 42.5 cm for species with most of their highest counts in IF marsh ponds, between 16.4 and 23.4 cm for species with most of their highest counts in IM marsh ponds, and between 5.2 and 11.3 cm for species with most of their highest counts in UM marsh ponds (Table 3). Only the double-crested cormorant had most of its highest counts in IO marsh ponds (Table 3).

**DISCUSSION**

**Comparison of Waterbird Communities between IM and UM Marshes**

The three species (northern shovelers, willets, and American avocets) that contributed most to differences in waterbird communities between IM and UM marshes mainly feed on invertebrates (Skagen and Oman 1996; Tietje and Teer 1996). This finding contradicts our prediction that invertebrate-feeding waterbird species would not differentiate waterbird communities between ponds of IM and UM. Our prediction was based on results of Bolduc and Afton (2003) who demonstrated that SMM affects only biomass of small nematoda and ostracoda. We also assumed that few waterbird species possess the capacity to capture these small prey (Kooloos et al. 1989; Gaston 1992; Skagen and Oman 1996; Sutherland et al. 2000). However, our results suggest that: (1) several 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) the slight differences in biomass between UM and IM marsh ponds in invertebrate species with highest biomass observed by Bolduc and Afton (2003), although statistically similar, may be biologically important enough to allow birds to meet their daily energetic requirements. 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.
Table 3. 95\textsuperscript{th} Percentile of observed bird densities (birds/ha), mean depth (cm) and standard deviation associated with observed bird densities ≥ the 95\textsuperscript{th} percentile, number of counts with densities ≥ the 95\textsuperscript{th} percentile and percent number of these counts by marsh type for common waterbirds in ponds of unimpounded mesohaline marshes (UM) and impounded freshwater (IF), oligohaline (IO) and mesohaline (IM) marshes during winters 1997-1998 to 1999-2000 in southwestern Louisiana

<table>
<thead>
<tr>
<th>Species</th>
<th>95\textsuperscript{th} percentile of observed bird densities (birds/ha)</th>
<th>Mean depth (cm) and standard deviation associated with observed bird densities ≥ the 95\textsuperscript{th} percentile</th>
<th>Number of counts with densities ≥ the 95\textsuperscript{th} percentile</th>
<th>Percent counts with densities ≥ the 95\textsuperscript{th} percentile in IF marshes</th>
<th>Percent counts with densities ≥ the 95\textsuperscript{th} percentile in IO marshes</th>
<th>Percent counts with densities ≥ the 95\textsuperscript{th} percentile in IM marshes</th>
<th>Percent counts with densities ≥ the 95\textsuperscript{th} percentile in UM marshes</th>
</tr>
</thead>
<tbody>
<tr>
<td>American avocet</td>
<td>1.3</td>
<td>9.6 ± 7.8</td>
<td>19</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>100.0</td>
</tr>
<tr>
<td>American coot</td>
<td>35.2</td>
<td>41.5 ± 16.7</td>
<td>19</td>
<td>84.2</td>
<td>15.8</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Black-necked stilt</td>
<td>0.8</td>
<td>16.4 ± 10.9</td>
<td>19</td>
<td>15.0</td>
<td>30.0</td>
<td>45.0</td>
<td>10.0</td>
</tr>
<tr>
<td>Blue-winged teal</td>
<td>9.6</td>
<td>34.2 ± 18.2</td>
<td>19</td>
<td>78.9</td>
<td>21.1</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Common moorhen</td>
<td>10.2</td>
<td>42.5 ± 19.1</td>
<td>19</td>
<td>94.7</td>
<td>5.3</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Double-crested cormorant</td>
<td>0.6</td>
<td>31.6 ± 18.8</td>
<td>19</td>
<td>26.3</td>
<td>36.8</td>
<td>21.1</td>
<td>15.8</td>
</tr>
<tr>
<td>Gadwall</td>
<td>8.5</td>
<td>31.4 ± 13.1</td>
<td>19</td>
<td>52.6</td>
<td>36.8</td>
<td>10.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Great egret</td>
<td>0.6</td>
<td>23.7 ± 10.5</td>
<td>19</td>
<td>31.6</td>
<td>21.1</td>
<td>42.1</td>
<td>5.3</td>
</tr>
<tr>
<td>Great blue heron</td>
<td>0.7</td>
<td>30.9 ± 18.4</td>
<td>21</td>
<td>52.4</td>
<td>4.8</td>
<td>38.1</td>
<td>4.8</td>
</tr>
<tr>
<td>Green-winged teal</td>
<td>37.5</td>
<td>16.4 ± 14.9</td>
<td>19</td>
<td>31.6</td>
<td>10.5</td>
<td>31.6</td>
<td>26.3</td>
</tr>
<tr>
<td>Mottled duck</td>
<td>1.8</td>
<td>26.9 ± 10.9</td>
<td>20</td>
<td>55.0</td>
<td>20.0</td>
<td>20.0</td>
<td>5.0</td>
</tr>
<tr>
<td>Northern shoveler</td>
<td>13.4</td>
<td>11.3 ± 11.0</td>
<td>19</td>
<td>31.6</td>
<td>0.0</td>
<td>5.3</td>
<td>63.2</td>
</tr>
<tr>
<td>Pied-billed grebe</td>
<td>3.6</td>
<td>33.8 ± 14.6</td>
<td>19</td>
<td>47.4</td>
<td>10.5</td>
<td>42.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Snowy egret</td>
<td>0.7</td>
<td>25.2 ± 22.6</td>
<td>19</td>
<td>47.4</td>
<td>15.8</td>
<td>10.5</td>
<td>26.3</td>
</tr>
<tr>
<td>Willet</td>
<td>0.8</td>
<td>5.2 ± 5.0</td>
<td>19</td>
<td>0.0</td>
<td>5.3</td>
<td>5.3</td>
<td>89.5</td>
</tr>
</tbody>
</table>
Comparison of Waterbird Communities among IF, IO and IM Marshes

We predicted that invertebrate-feeding waterbird species would not differentiate waterbird communities among ponds of IF, IO, and IM marshes. Accordingly, species that contributed most to differences in waterbird communities among these marsh types (common moorhens, American coots, and gadwalls) feed mainly on aquatic vegetation (Paulus 1982; Thomas 1982). IF and IO marshes produce several plant species that many waterbird species consume (Chabreck 1960; Jemison and Chabreck 1972; Chabreck et al. 1974). Waterbird species that potentially feed on invertebrates (i.e., American avocet, black-necked stilt, blue-winged teal, green-winged teal, mottled duck, northern shoveler, and willet [Euliss, et al. 1991; Skagen and Oman 1996]) had standardized canonical coefficients at least 2 times lower than those of common moorhens, American coots, and gadwalls. Thus, invertebrate-feeding waterbird species contributed little to differences among waterbird communities in ponds of IF, IO, and IM marshes. Consequently, our results were consistent with our prediction regarding differences among waterbird communities of IF, IO, and IM marsh ponds.

Observed vs. Corrected Densities

Use of corrected densities allows comparison of marsh types without the confounding effects of water levels variation. For example, mean observed densities of gadwalls suggested that greatest densities were found in IO marshes (Figure 4) and that this species did not contribute to differences in waterbird communities among marsh types (Table 2). The latter statement might lead to the unjustified conclusion that management for this species would primarily consider conservation or the expansion of IO marshes. However, mean corrected densities of gadwalls suggested otherwise, as both IO and IM marshes were associated with greatest corrected densities (Figure 3), and that this species differentiated waterbird communities of IO and IM marshes as compared to that of UM and IF marshes (Table 2). Remember that corrected densities result from the difference between observed densities and that predicted from nonparametric regression between observed densities and water levels, similar to residuals in a regression. Therefore, the difference between mean observed and corrected densities of gadwalls is related to water depths variation together with that of observed densities in the different marsh types; observed gadwall densities were greater than that predicted by the nonparametric regression in IM marsh ponds as compared to other marsh types on average. Previous research supports the conclusion that IM marshes are important to gadwalls, as they feed heavily on submerged vegetation such as widgeongrass (Ruppia maritima; Paulus 1982). The latter plant species is affected positively by management in mesohaline marshes (Nyman and Chabreck 1996).

Mean corrected densities were always negative, which occurred because birds of a given species frequently were not present at the time of a survey, which resulted in lower mean densities than expected from the observed water depth. Numerous zeros are characteristics of count data and the binomial family of data distributions, and therefore were to be expected.
Comparison of Results Using 95th Percentiles and Corrected Densities

Our comparison of waterbird densities among IF vs. IO, and IM marsh ponds, indicated that densities of only a few species differed among these marsh types, whereas most species had their highest (i.e., above 95th percentile) densities in ponds of IF marshes. The above disparity may be explained by the variation in water depths during our study (Bolduc and Afton 2004b). Water depths associated with highest densities of waterbird species always were lower than the average water depth in the corresponding marsh type, except for species with highest densities in UM marsh ponds (Figure 1, Table 3, Bolduc and Afton 2004b). These results suggest that IF marsh ponds are most attractive to waterbirds when the observed water depth is close to their preferred water depth.

Our results also suggest that opportunist species were those with mean corrected densities and highest observed densities not associated with the same marsh types, and probably used different marsh types depending on conditions (e.g., green-winged teal, gadwalls). Habitat specific species probably were those with mean corrected densities and highest observed densities associated with the same marsh types, but for which water depth associated with their highest observed densities was lower than the average one (e.g., American avocet, blue-winged teal).

CONCLUSION

Birds with highest mean corrected densities in UM marsh ponds (American avocets, northern shovelers, willets) were observed at much lower mean corrected densities in ponds of IM, IO, or IF marshes, but birds with highest mean corrected densities in IM marsh ponds (green-winged teal, pied-billed grebes and gadwalls) generally had similar mean corrected densities among ponds of IO and/or IF marshes. Birds of UM marshes likely have the morphological adaptations and feeding strategies allowing them to exploit the soft sediments of UM marsh ponds and their inherent meiofaunal invertebrate communities (Bolduc and Afton 2003, 2004a, 2005). Birds of IM marsh ponds must be adapted to exploit macroinvertebrates located on the bottom surface (Bolduc and Afton 2003, 2004a, 2005). UM marsh ponds also are characterized by a lower temporal variation and a larger spatial variation in water depth as compared to IM marsh ponds (Table 1; Bolduc and Afton 2004b). These spatio-temporal differences in water depth variation between UM and IM ponds suggest that UM marsh ponds may provide highly predictable and beneficial foraging conditions to several species, whereas water level conditions of IM marsh ponds are suitable only to a few species at a given time, and suitable to others at another time (Bolduc and Afton 2004a, 2004b). Therefore, the average waterbird community of IM marshes represents a variety of species that respond differently to conditions at a given time. Accordingly, our results suggest that preservation of UM marshes is highly beneficial to the conservation wintering waterbird populations of southwestern coastal marshes.

Recent wetland conservation actions on the Louisiana coast targeted the maintenance or creation of vegetated marsh areas rather than conservation of specific marsh habitats (Cowan et al. 1988). Also, the area of freshwater marshes seemingly has declined, whereas that of IO marshes has increased in southwestern Louisiana before landings of hurricanes Katrina and
Rita in 2005 (Visser et al. 2000), and freshwater and intermediate wetlands loss was twice that of higher salinity marsh during the 2005 hurricane season (Howes et al. 2010). Howes et al. (2010) suggested that restoration and creation of freshwater/oligohaline marshes should be reassessed because of their greater susceptibility to degradation. Low salinity coastal marshes provide other functions than just a barrier against hurricanes, as IF marshes were used extensively by many waterbird species when water depth fell within their preferred ranges. Therefore, the conservation of freshwater marshes, with maintenance of preferred water depths, would be desirable for habitat conservation of wintering waterbirds of southwestern Louisiana.

Finally, our results demonstrate that water depth is paramount in influencing waterbird densities and the composition of the waterbird community. Colwell and Taft (2000) suggested that shallow water maximizes waterbird diversity. However, selective management of water levels needs to be carefully considered in order to best meet management objectives in southwestern Louisiana. Our results suggest that specific water depths would favor certain bird species over others (Figure 2). Also, as temporal variability in water depth within SMM is high (Table 1; Bolduc and Afton 2004b) and water depth is the major variable differentiating habitats of waterbirds in our study area (Bolduc and Afton 2004a), implementation of management techniques that allow better control of water depth, maintenance of shallow water within impoundments, and diverse water levels among and within ponds and impoundments would be beneficial to waterbird populations. Because of the diverse needs of the wintering waterbird communities of southern Louisiana, landscape level management is of primary interest. Alternative methods of marsh management also should be explored in an adaptive fashion using regular assessment surveys to optimize future resources and benefits (i.e., Weinstein et al. 1997; O’Connell and Nyman 2010).

ACKNOWLEDGMENTS

Financial support for our research was provided by Rockefeller State Wildlife Refuge through the Fur and Refuge Division of Louisiana Department of Wildlife and Fisheries, and the Louisiana Cooperative Fish and Wildlife Research Unit, School of Renewable Natural Resources, and Graduate School at Louisiana State University. We thank A. Bleckinger, M. Kallenberger, F. Roy, and A. Wagner for assistance with the field work. We also are grateful to B. Wilson for his help in initiating the project. Finally, we thank R. S. Carney, J. W. Fleeger, R. B. Hamilton, J. Linscombe, T. Hess, L. Weber, B. Wilson, and J. A. Nyman for their helpful comments on the initial manuscript.

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