

Hydrologic aspects of marsh ponds during winter on the Gulf Coast Chenier Plain, USA: effects of structural marsh management

François Bolduc^{1,3,*}, Alan D. Afton²

¹School of Renewable Natural Resources, and ²USGS-Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, Louisiana 70803-6202, USA

³Present address: TecSult, 4700 Wilfrid-Hamel, Quebec City, Quebec G1P 2J9, Canada

ABSTRACT: The hydrology of marsh ponds influences aquatic invertebrate and waterbird communities. Hydrologic variables in marsh ponds of the Gulf Coast Chenier Plain are potentially affected by structural marsh management (SMM: levees, water control structures and impoundments) that has been implemented since the 1950s. Assuming that SMM restricts tidal flows and drainage of rainwater, we predicted that SMM would increase water depth, and concomitantly decrease salinity and transparency in impounded marsh ponds. We also predicted that SMM would increase seasonal variability in water depth in impounded marsh ponds because of the potential incapacity of water control structures to cope with large flooding events. In addition, we predicted that SMM would decrease spatial variability in water depth. Finally, we predicted that ponds of impounded freshwater (IF), oligohaline (IO), and mesohaline (IM) marshes would be similar in water depth, temperature, dissolved oxygen (O₂), and transparency. Using a *a priori* multivariate analysis of variance (MANOVA) contrast, we tested these predictions by comparing hydrologic variables within ponds of impounded and unimpounded marshes during winters 1997–1998 to 1999–2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. Specifically, we compared hydrologic variables (1) between IM and unimpounded mesohaline marsh ponds (UM); and (2) among IF, IO, and IM marshes ponds. As predicted, water depth was higher and salinity and O₂ were lower in IM than in UM marsh ponds. However, temperature and transparency did not differ between IM and UM marsh ponds. Water depth varied more among months in IM marsh ponds than within those of UM marshes, and variances among and within ponds were lower in IM than UM marshes. Finally, all hydrologic variables, except salinity, were similar among IF, IO, and IM marsh ponds. Hydrologic changes within marsh ponds due to SMM should (1) promote benthic invertebrate taxa that tolerate low levels of O₂ and salinity; (2) deter waterbird species that cannot cope with increased water levels; and (3) reduce waterbird species diversity by decreasing spatial variability in water depth among and within marsh ponds.

KEY WORDS: Coastal wetlands · Gulf of Mexico · Wintering waterbirds · Ponds

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INTRODUCTION

The hydrology of coastal marshes is characterized by wide fluctuations in water levels, dissolved oxygen, salinity, temperature, and transparency (Oertel & Dunstan 1981, Mitsch & Gosselink 1993). Accordingly, aquatic invertebrate prey of waterbirds (Anseriformes, Charadriiformes, Ciconiiformes, Gaviiformes, Gruiformes,

Pelecaniformes, Phoenicopteriformes, Podicipediformes, and Procellariiformes) in coastal marsh ponds (flooded zones of marsh associated with little emergent vegetation) have a wide array of physiological and morphological adaptations to fluctuating oxygen availability (Rhoads 1974) and salinity (Willmer et al. 2000). Non-diving waterbirds also have morphological adaptations that allow them to feed at different depths and

*Email: f.bolduc@tecsult.com

on different foods (Baker 1979, Pöysä 1983, Nudds & Bowlby 1984, Zwarts & Wanink 1984). Thus, the hydrology of coastal marshes ultimately influences compositions of invertebrate and waterbird communities.

Hydrologic variability of coastal marshes also has important consequences on other ecological functions. For example, waterlogging and overdrying may cause marsh vegetation die-offs (Turner 1997). Also, wet–dry cycles of marshes affect habitats of invertebrates (Murkin & Ross 2000). Predictability of water depth within a season (seasonal variability) is probably related to predictability of foraging conditions of waterbirds wintering in coastal marshes, and therefore their survival (Lima 1986). Finally, hydrologic variability among and within marsh ponds in a given area and 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 along the Gulf Coast Chenier Plain during the last century. Dredging of north–south waterways, large-scale muskrat *Ondatra zibethica* eat-outs (where they strip the vegetation), and a severe drought that occurred in the early 1950s apparently facilitated saltwater intrusion and caused the loss of a large vegetated area at the junction of freshwater and oligohaline marshes (Wicker et al. 1983). Consequently, from the mid-1950s on, numerous marshes were impounded using structural marsh management (SMM), i.e. construction of a levee to isolate a marsh, which connects with the outside water bodies only through water-control structures (weirs, stop-log, flap- or lift-gate culvert, or pumping units) (Cowan et al. 1988). Primary objectives of SMM were to revegetate open water areas that had formed, stop saltwater intrusion, and increase productivity of waterfowl foods (Wicker et al. 1983).

The primary effect of SMM on marsh hydrology is to restrict the export and import of water between marshes and the surrounding area because levees restrict tidal flows and drainage of rainwater (Boumans & Day 1994). Little is known concerning the effects of SMM on other hydrologic variables of coastal marshes; however, water depth seemingly increases and salinity decreases after implementation of weirs (Chabreck 1960). We predicted that SMM (1) increases water levels; and (2) decreases salinity and transparency in impounded marsh ponds because of the restriction on water exchange.

Water levels in impounded marsh ponds are affected primarily by amounts and frequency of rainfall, and drainage capacities of water control structures. As precipitation is greater than evapotranspiration during fall and winter on the Gulf Coast Chenier Plain (Wicker et al. 1983), managers often leave water control structures open during these periods to evacuate water sur-

plus and maximize fisheries migration into and out of impoundments, depending on yearly climatic events. On the Gulf Coast Chenier Plain, rainfall generally originates from tropical storms, hurricanes, and cold fronts during the fall–winter seasons, which often discharge large amounts of precipitation in a short time (Keim et al. 1995). Marsh impoundments must cope with these flooding events through a limited number of water control structures (Wicker et al. 1983). Consequently, marsh impoundments probably experience large seasonal variability in water levels.

In contrast, unimpounded coastal marshes are characterized by a network of tidal channels of various sizes that allow direct 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 relatively small seasonal variation in water levels. Consequently, we predicted that seasonal variability in water depths is greater in ponds of impounded marshes than in those of unimpounded marshes.

Water levels in ponds of unimpounded marshes depend on ranges of tides at given times, sizes of channels connecting ponds to the Gulf, sizes of ponds, and positions of ponds in hydrographic basins (network of channels connecting all ponds together); thus, all ponds are affected differently by tides. Therefore, tidal regimes of unimpounded marshes should produce a wide spatial variability in water levels among ponds. Conversely, tides should have little influence on water levels of ponds within impoundments because of the hydrologic isolation. Consequently, we predicted that spatial variability in water levels would be greater among ponds of unimpounded marshes than among those of impounded marshes.

Coastal marshes often are classified into 3 categories of salinity based on the Venice system of estuarine classification (Anon 1959, Cowardin et al. 1979): (1) freshwater (salinity < 0.5‰); (2) oligohaline (salinity between 0.5 and 5.0‰); and (3) mesohaline (salinity between 5.0 and 18.0‰). This salinity classification is also based on observed salinity and plant communities on the Gulf Coast Chenier Plain (Chabreck 1972, Visser et al. 2000). Oligohaline marshes have apparently expanded at the expense of freshwater and mesohaline marshes during the last 60 yr (Visser et al. 2000). Information on more recent salinity levels is not available for marshes of the Gulf Coast Chenier Plain. Furthermore, variations in water depth, temperature, dissolved oxygen, and transparency have not been studied in ponds of these altered marshes.

On the Gulf Coast Chenier Plain, most marshes can be considered to be impounded to a certain degree as they have an altered hydrology (except for mesohaline

marshes that are still connected directly to a tidal bayou) because of numerous roads, irrigation canals, levees, and waterways that have been built during the last century (Turner 1990). Consequently, we predicted that ponds of impounded freshwater, oligohaline and mesohaline marshes would be similar in water depth, temperature, near-bottom dissolved oxygen, and transparency because of their expected similar hydrology.

We tested our predictions by comparing salinity, water depth, transparency, water temperature and near-bottom dissolved oxygen of ponds (1) between impounded and unimpounded mesohaline marshes; and (2) among impounded freshwater, oligohaline and mesohaline marshes from the winters of 1997–1998 to 1999–2000 on Rockefeller State Wildlife Refuge, near Grand Chenier, Louisiana. We discuss our results in terms of implications of SMM and salinity on compositions of waterbird communities and their foods, because these taxa are often focal points of marsh management plans.

MATERIALS AND METHODS

Study area. The Gulf Coast Chenier Plain is bounded by East Bay in Texas and Vermilion Bay in Louisiana (Gosselink et al. 1979, Gabrey et al. 2001). 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, which 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).

We chose Rockefeller State Wildlife Refuge (RSWR; headquarters coordinates: 29° 40' 30" N, 92° 48' 45" W), near Grand Chenier, in SW Louisiana as a representative area of the Gulf Coast Chenier Plain. RSWR comprises 30 700 ha, and contains 17 impoundments (200 to >4000 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 consist of marshes 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 (11700 ha).

Sampling design. We sampled the 4 marsh types of RSWR: (1) 3 freshwater impoundments (IF) (Units 8, 10, and 13); (2) 2 oligohaline impoundments (IO) (Units 3, 4, and 15 [the latter replaced Unit 3 in winter 1999–2000]); (3) 2 mesohaline impoundments (IM) (Unit 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 (impounded marshes) or with a small boat (UM marshes). We chose these ponds to minimize both time spent commuting among sites and disturbance to waterbirds (important for a concurrent study). Subsequently, we randomly selected 3 ponds from those initially identified in each impoundment or hydrographic basin for a total of 27 ponds. 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.

During each visit, we randomly selected 3 sampling stations within each selected pond. We determined locations of sampling stations using a table of random numbers to select distances and angles from an observation blind (concealed enclosure) that fell within the pond area, up to a distance of 200 m from the blind (this maximum distance was important for the concurrent waterbird study). We visited ponds monthly, from December to March in 1997–1998, and from November to March in 1998–1999 and 1999–2000 (14 mo total).

At all sampling stations, we measured water depth (± 1 cm) with a graduated stick, dissolved oxygen (± 0.01 mg l⁻¹) (O₂) with a YSI-55 dissolved oxygen meter (Yellow Springs Instrument), and salinity (± 0.1 ‰) and temperature (± 0.1 °C) with a YSI-30 salinity meter (Yellow Springs Instrument). We sampled O₂, salinity and temperature 2 to 3 cm above sediments and all variables between 08:00 and 10:00 h. To measure water transparency, we submerged a 10 cm diameter white disk to 10 cm below the surface, and categorized transparency using the following classes: none, little, moderate, and considerable, which were coded 0, 1, 2, and 3, respectively.

Statistical analysis. We compared hydrologic variables between IM and UM ponds and among IF, IM and IO ponds within a single multivariate analysis of variance (MANOVA). For this analysis, response variables were water depth, O₂, salinity, temperature, and transparency. Fixed explanatory variables in the model were marsh type, time (month), and their interaction term. Time was not considered a repeated measure variable *per se* because we 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 \times time; and (2) pond within impoundment and marsh type \times time. We performed separate *a priori* MANOVA contrasts to test our 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-type equation order (IF, IM, IO, UM). For these *a priori* comparisons, we used an error matrix based on the impoundment within marsh type \times time random effect.

We excluded from analysis sampling stations ($n = 66$ of 1134 total stations sampled over 14 mo) where water was not present during sampling periods, because it produced missing data for salinity, O_2 , transparency, and temperature. These dry conditions occurred primarily in UM marshes (95% of occurrences), and never in more than 1 pond within a 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 df for the error term used to test our *a priori* comparisons (i.e. impoundment within marsh type \times time). However, 61 df remained for this error term after removal of this time period. Moreover, other missing data scattered throughout the other 13 mo sampling did not affect degrees of freedom on the above error term.

We used Wilk's lambda statistic to compute *F*-ratios of our 2 *a priori* MANOVA contrasts (PROC GLM, SAS Institute 1999). We 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 & Fidell 1989). Finally, we computed canonical correlations and standardized canonical coefficients from MANOVA contrasts to investigate contribution of various hydrologic variables to differences among ponds of various marsh types. Because *r*-values ≤ 0.3 correspond to $<10\%$ variance overlap between variables (Tabachnick & Fidell 1989), we only interpreted *r*-values >0.3 . We assessed normality and homoscedasticity of response variables by computing skewness and kurtosis values, and by examining whether model residuals were distributed randomly (Tabachnick & Fidell 1989). Accordingly, we transformed salinity data ($\log[x+1]$) prior to final analysis. We present results as least-square means $\pm 95\%$ CIs (backtransformed for salinity), unless stated otherwise.

We compared seasonal and spatial variability in water depths between ponds of IM and UM marshes using variance components analysis. We estimated variances in water depth for IM and UM marsh ponds among (1) time periods ($n = 14$); (2) impoundments (or hydrographic basins for UM) within months ($n = 56$);

Table 1. Summary of *a priori* MANOVA contrasts testing for differences in hydrologic response variables (dissolved oxygen, salinity, temperature, transparency, water depth) between impounded and unimpounded mesohaline marsh ponds (UM vs IM), and among impounded freshwater, oligohaline, and mesohaline marsh ponds (IF vs IO and IM) during winters of 1997–98 to 1999–2000 on the Gulf Coast Chenier Plain, USA. Num: numerator; Den: denominator

Contrast	Wilk's lambda	<i>F</i>	Num df	Den df	<i>p</i> -value	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

(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 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 & 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 for this analysis. We performed all statistical analyses using SAS 8.2 (SAS Institute 1999).

RESULTS

Comparison of hydrologic variables between IM and UM marsh ponds

The 5 hydrologic response variables differed significantly and produced a large effect size between UM and IM marsh ponds (Table 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 2). Salinity was 2 times greater in UM ponds than in IM ponds (Fig. 1). Water depth and O_2 second-

Table 2. Canonical correlations (CC) and standardized canonical coefficients (SCC) from *a priori* MANOVA contrasts testing for a difference in hydrologic response variables between impounded and unimpounded mesohaline marsh ponds (UM vs IM), and among impounded freshwater, oligohaline, and mesohaline marsh ponds (IF vs IO and IM) during winters 1997–1998 to 1999–2000 on the Gulf Coast Chenier Plain, USA

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
Transparency	0.064	0.24	0.064	0.31
Water depth	-0.870	-1.50	-0.837	-1.05

arily contributed to the difference between ponds of these 2 marsh types (Table 2). Water depth was 2 times lower and contained 3.3 mg l⁻¹ more O₂ in UM ponds than in IM ponds (Fig. 1). O₂, salinity, and temperature were positively correlated, water depth was negatively correlated, and transparency was not correlated with the first canonical variate (Table 2). These results indicated that an increase in water depth was correlated with decreases in salinity, O₂, and temperature.

Comparison of water depth variances between IM and UM marsh ponds

Our variance components analysis indicated that water depth varied more among months in IM ponds

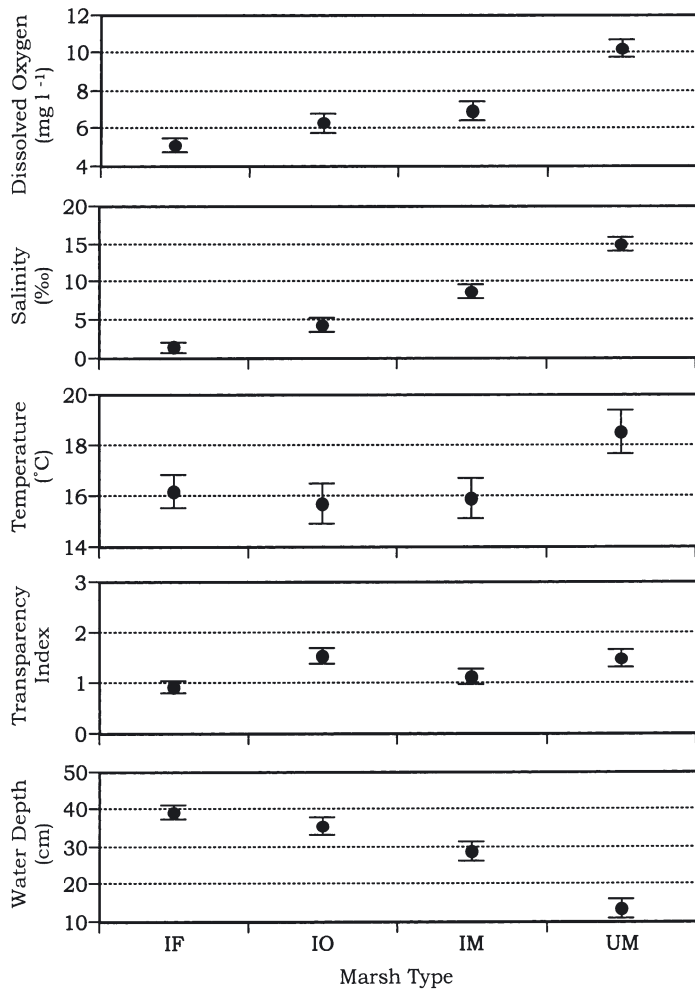


Fig. 1. Mean values (least square means ± 95% CIs) of hydrologic response variables in impounded freshwater (IF), oligohaline (IO), and mesohaline (IM) marsh ponds, and unimpounded mesohaline (UM) marsh ponds during winters 1997–1998 to 1999–2000 on the Gulf Coast Chenier Plain, USA

Table 3. Estimates of variance (σ^2) in water depth in impounded mesohaline (IM) and unimpounded mesohaline (UM) marsh ponds among months, impoundments (or hydrographic basins for UM) within months, ponds within impoundments and months, and sampling stations within ponds, impoundments and months (residuals), during winters 1997–1998 to 1999–2000 on the Gulf Coast Chenier Plain, USA. –: test not possible due to 0 estimated variance

	Months	Impoundments/ hydrogr. 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	–	3.52	2.97
p-value	0.0014	–	<0.0001	<0.0001

than in UM ponds (Table 3). Water depths in IM ponds sometimes were very low, especially during winter 1999–2000 (Fig. 2). However, water depth in IM marsh ponds varied by 30 cm in 1997–1998 and 1998–1999 winters, with a maximum of 54 cm (Fig. 2). Water depth in UM marsh ponds generally was <20 cm, and never exceeded 38 cm (Fig. 2). Variance in water depth between impoundments was greater than between hydrographic basins (Table 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). The range of water depths generally was smaller within impoundments than within UM hydrographic basins in a given month, whereas the range of water depths differed more between impoundments than between basins of UM marshes within months (Fig. 2).

Comparison of hydrologic variables of IF with IO and IM marsh ponds

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 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 2). Salinity generally was lowest in IF marsh ponds (Fig. 1). Standardized canonical coefficients of other variables were less than 1.1 (Table 2), reflecting their relatively small contribution to differences among marsh types. Examination of canonical correlations (CC) indicated that O₂, salinity, and temperature were positively correlated and water depth was negatively correlated, whereas transparency was not correlated with the first canonical variate (Table 2).

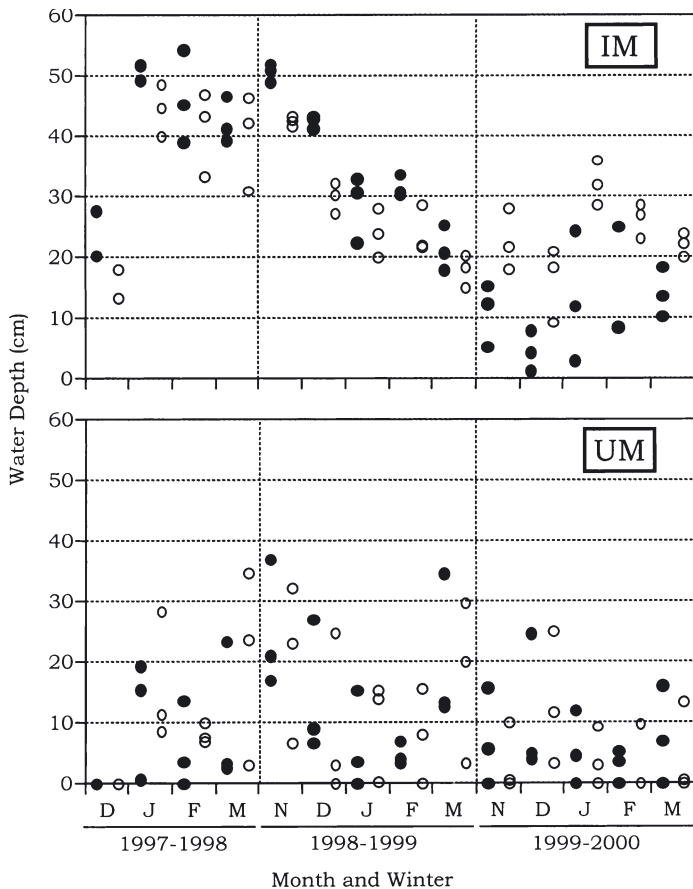


Fig. 2. Mean water depths in impounded mesohaline (IM) (● = Price Lake; ○ = Unit 5), and unimpounded mesohaline (UM) (● = Rollover Lake/Flat Lake basin; ○ = East Little Constance Bayou basin) marsh ponds during winters 1997–1998 to 1999–2000 on the Gulf Coast Chenier Plain, USA. Note that several data points are superposed on each other

DISCUSSION

Comparison of hydrologic variables between IM and UM marsh ponds

We found that IM and UM marsh ponds differed primarily in salinity and secondarily in water depth and O_2 . These results are consistent with our predictions that, because SMM decreases tidal influences and drainage of rainwater, water depth increases and concomitantly salinity decreases in ponds of impounded marshes. Contrary to our predictions, we did not find that SMM reduced transparency, possibly because hydraulic turbulences caused by wind on deeper water in IM marsh ponds were equivalent to those from tides in UM marsh ponds. Differences in density of phytoplankton and water color also may have influenced our results, but no obvious differences in those parameters were noticed during sampling.

Measuring O_2 during the daytime may have influenced the relationship among water depth, salinity, temperature, and O_2 . For example, average O_2 readings in UM marsh ponds (10.5 mg l^{-1}) were 110% of O_2 saturation in water. This supersaturation is related to an intense photosynthesis by algae (Wetzel 1975). Algae release pure O_2 , and thus, O_2 gas pressure may be higher in the water than in the atmosphere when intense photosynthesis occurs in aquatic habitats (Wetzel 1975). However, an abundant algae population in the water may also 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

Our results were consistent with our prediction that seasonal variability in water depth would be greater in impounded marsh ponds than in unimpounded marsh ponds. This finding was probably due to the relatively slow drainage of water following large rainfall events that occurred during 1997–1998 and 1998–1999 winters (Fig. 2). Accordingly, the presence of spoil banks creates fewer but longer flooding events compared to marshes directly connected to tidal bayous (Swenson & Turner 1987). Flooding events are also longer inside than outside marshes managed with weirs (Bourgeois & Webb 1998).

As predicted, we 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. We also documented that variance in water depth was greater within UM ponds than in IM ponds, which probably occurred because sediment elevations vary more in the former. The presence of tidal channels crossing ponds of UM marshes probably produced a flow of water that reworked sediments differentially throughout a pond, whereas this phenomenon was absent in IM marsh ponds.

Interestingly, our results indicated that water depth variance was greater between impoundments than between UM hydrographic basins. The 2 UM hydrographic basins that we studied were adjacent to each other, and therefore water depths in marsh ponds of these 2 hydrographic basins probably were affected equally by tides. Each impoundment had 2 to 3 water control structures, but apparently these impounded areas did not drain equally following flooding events.

This difference may have resulted because the efficiency and locations of water control structures may have differed between impoundments (Wicker et al. 1983), and/or water flowed more easily out of one impoundment than the other.

Comparison of hydrologic variables of IF with IO and IM marsh ponds

Hydrologic response variables other than salinity generally were similar among IF, IO, and IM ponds. Mean salinity levels recorded in ponds of each marsh type (Fig. 1) were within the range for each salinity classification, except for freshwater marsh ponds that had an average salinity of 1.4 ± 0.7 during our study (Chaberck 1972, Visser et al. 2000). Given correlations among hydrologic variables, events that change water levels within impounded marsh ponds may also lead to changes in other hydrologic variables. For example, rainfall events that deepen ponds may also lower temperature, salinity, and near-bottom O_2 .

Management implications

Differences in hydrologic variables between IM and UM ponds have many implications for managing Gulf Coast Chenier Plain marshes as habitats for wintering waterbirds and their invertebrate prey. Our finding of lower salinity in IM ponds compared to UM ponds suggests that SMM prevents saltwater intrusion, as intended (Wicker et al. 1983). Our results also suggest that (1) reductions in salinity should enhance populations of freshwater Oligochaeta, insect larvae, and other freshwater invertebrates (Murkin & Ross 2000); (2) reductions of near-bottom O_2 should promote populations of Oligochaeta, Chironomidae, and Cladocera that tolerate low levels of O_2 (Murkin & Ross 2000); and (3) relatively deep water in IM marsh ponds may prevent their use by small ducks and shorebirds (White & James 1978, Baker 1979, Pöysä 1983, Ntiamoa-Baidu et al. 1998).

Our observation of a greater seasonal variability in water depths among IM ponds than UM ponds indicates that control of water levels in IM marshes may be more difficult to obtain than expected. During fall and winter in this area, sudden tropical storms, hurricanes, and cold fronts generate the most rainfall. These rainfall events often discharge large amounts of precipitations in a short time-period (Keim et al. 1995). The limited number of water control structures seemingly do not have the capacity to handle these large flooding events. Control of water levels would be more efficient within impoundments of smaller size or with better

drainage capability. Alternative methods of marsh management should also be explored (Weinstein et al. 1997, Turner & Streever 2002).

The greater seasonal variability in water depth in IM ponds than in UM ponds may have several important consequences for impounded marshes: (1) lower accretion due to waterlogging and overdrying (Turner 1997); and (2) 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). The lower seasonal variability in water levels in UM marsh ponds indicates that hydrologic conditions are more predictable in those ponds. The predictability of the environment is believed to be important to wintering birds because habitats of highest predictability are associated with the best avian survival rates (Lima 1986).

The observed lower spatial variability in water depths in IM marsh ponds than in UM marsh ponds indicates that SMM may have important consequences for 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 UM marsh ponds. For example, waterbirds have morphological features that enable them to feed most efficiently under specific water depths (Baker 1979, Poysa 1983, Nudds & Bowlby 1984, Zwarts & Wanink 1984), and therefore fewer species would be found at a given time in IM ponds than UM ponds. Also, because seasonal variability in water depth is large and spatial variability is small in IM marsh ponds, plant and invertebrate communities probably vary little within an impoundment, and may be composed primarily of generalist species. In contrast, seasonal 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, we 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 variability in water depth 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 the 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.

Acknowledgements. Financial support for our research was provided by the Rockefeller State Wildlife Refuge through the Fur and Refuge Division of the Louisiana Department of Wildlife and Fisheries and by the Louisiana Cooperative Fish and Wildlife Research Unit, School of Renewable Natural Resources, and Graduate School at Louisiana State University. We thank Amy Bleckinger, Martina Kallenberger, Francis Roy, and Anik Wagner for assistance with the fieldwork. We also are grateful to Barry Wilson for his help in initiating the project. Finally, we would like to thank Robert S. Carney, John W. Fleeger, Robert B. Hamilton, Jeb Linscombe, J. Andy Nyman, R. Eugene Turner, Barry Wilson, and 3 anonymous reviewers for their helpful comments on the manuscript.

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Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA

*Submitted: August 30, 2002; Accepted: October 22, 2003
Proofs received from author(s): January 22, 2004*