



Habitat Relations

Breeding Bird Use and Wetland Characteristics of Diked and Undiked Coastal Marshes in Michigan

MICHAEL J. MONFILS,¹ Michigan Natural Features Inventory, Michigan State University Extension, P.O. Box 13036, Lansing, MI 48901-3036, USA

PATRICK W. BROWN,² Michigan Natural Features Inventory, Michigan State University Extension, P.O. Box 13036, Lansing, MI 48901-3036, USA

DANIEL B. HAYES, Department of Fisheries and Wildlife, Michigan State University, 334C Natural Resources Building, East Lansing, MI 48824-1222, USA

GREGORY J. SOULLIERE, U.S. Fish and Wildlife Service, Upper Mississippi River and Great Lakes Region Joint Venture, 2651 Coolidge Road, East Lansing, MI 48823, USA

ERNEST N. KAFCAS, Michigan Department of Natural Resources, Wildlife Division, 33135 S. River Road, Harrison Township, MI 48045, USA

ABSTRACT Dikes were built on Great Lakes coastal wetlands to enable water level management for wetland wildlife, particularly waterfowl, but few studies have compared bird use of these areas to undiked sites. During 2005–2007, we evaluated 9 diked and 7 undiked coastal wetlands at the St. Clair Flats (Lake St. Clair) and Saginaw Bay (Lake Huron) of Michigan, USA. We compared bird use of diked and undiked wetlands via 605 10-minute point counts at randomly selected locations of emergent marsh and 287 45-minute surveys of randomly selected open water areas. We also measured wetland characteristics in 1,521 randomly selected 0.25-m² quadrats to compare vegetation and physical conditions between diked and undiked wetlands. Diked wetlands had greater coverage and density of cattail (*Typha* spp.), coverage of floating-leaved plants, water depth, and organic sediment depth compared to nearby undiked sites, whereas undiked wetlands had greater coverage and density of common reed (*Phragmites australis*) and bulrush (*Schoenoplectus* spp.) than diked wetlands. Bird species richness and similarity indices indicated comparable breeding bird communities. We observed greater abundances of Canada goose (*Branta canadensis*), wood duck (*Aix sponsa*), American bittern (*Botaurus lentiginosus*), least bittern (*Ixobrychus exilis*), and common gallinule (*Gallinula galeata*) in diked wetlands. These species likely responded to the deep-water cattail marsh and aquatic bed dominating most diked sites. American coot (*Fulica americana*), Forster's tern (*Sterna forsteri*), ring-billed gull (*Larus delawarensis*), and herring gull (*Larus argentatus*) abundance indices were greater in undiked wetlands, likely related to nesting and foraging habitat provided by the shallower, more open wetlands and connecting lakes. Diked wetlands did not benefit the bird community to the degree expected and conditions in diked areas were indicative of deep marshes with stabilized water levels. Periodic late-summer drawdowns could encourage growth of plants we found associated with greater abundance of some priority bird species and reduction of floating vegetation negatively associated with abundance of several species. However, effective control of invasive common reed is needed to reduce risk of expansion during impoundment dewatering. © 2013 The Wildlife Society.

KEY WORDS breeding, diked wetlands, Great Lakes coastal wetlands, marsh birds, Michigan.

Impoundments and water control structures have long been used by wildlife managers to manipulate wetlands for wildlife (Kadlec 1962, Harris and Marshall 1963, Whitman 1976, Mitchell et al. 2006), especially breeding and migrating waterfowl. An estimated 7.9% of Michigan's Great Lakes

coastal wetlands are currently impounded (B. Kahler, U.S. Fish and Wildlife Service, unpublished data); many of these wetlands were diked in the mid to late 1960s during periods of below-average lake levels. These marshes were intended to be managed as hemi-marshes, or mosaics with approximately 50:50 emergent plant cover to open water ratios, which researchers in the Prairie Pothole region found to support the greatest densities and diversity of wetland birds (Weller and Spatcher 1965; Weller and Fredrickson 1973; Kaminski and Prince 1981a, b; Murkin et al. 1982).

Although diked wetlands allow manipulation of water levels and associated emergent vegetation for target bird

Received: 29 June 2012; Accepted: 2 September 2013;
Published: 19 November 2013

¹E-mail: monfilms@msu.edu

²Present address: Biology Department, Northern Michigan University, 1401 Presque Isle Avenue, Marquette, MI 49855, USA

species, hydrologic alteration can negatively affect flood storage, sediment movement (Wilcox 1993), nutrient cycling (Wilcox and Whillans 1999), plant diversity (Keddy and Reznicek 1986, Wilcox et al. 1993, Keough et al. 1999, Herrick and Wolf 2005), and habitat for invertebrates, fish, and other wildlife (Jude and Pappas 1992, Wilcox 1995). Despite birds being the focus of management, few studies have compared bird use of diked and undiked Great Lakes coastal wetlands. Galloway et al. (2006) conducted a 1-year evaluation of breeding bird use at diked and undiked coastal wetlands on the Canadian shores of Lakes Ontario, Erie, and St. Clair and observed greater abundance and species richness of several bird groups in diked compared to undiked wetlands. They indicated long-term research is needed to account for variation in bird and vegetation communities associated with water-level fluctuations and management activities. Prince (1985) compared bird use of diked and undiked sites, but focused on wetlands associated with rivers located inland from Michigan's coasts. Differences in invertebrates (McLaughlin and Harris 1990, Provence 2008), fish (Johnson et al. 1997, Markham et al. 1997), plant foods for waterfowl (Brasher et al. 2007), and plant communities (Thiet 2002, Herrick and Wolf 2005, Herrick et al. 2007) have been investigated, but we found no other studies evaluating bird use of diked Great Lakes coastal wetlands. Our goal was to compare breeding bird use, vegetation composition and structure, and physical attributes of diked and undiked coastal marshes to evaluate current management for wetland birds.

STUDY AREA

We studied 16 coastal wetlands (9 diked, 7 undiked) at St. Clair Flats of Lake St. Clair and Saginaw Bay of Lake Huron (Fig. 1). We selected St. Clair Flats and Saginaw Bay because they are 2 of Michigan's largest and most intact wetland complexes (Bookhout et al. 1989, Krieger et al. 1992), contain preferred breeding sites for several bird species of management importance, and possess both diked and undiked wetlands. Sites were located on flat lake plains of Lake Huron or Lake St. Clair, with the 3 northernmost sites occurring in Northern Lacustrine-influenced Lower Michigan and the remaining sites in the Southern Lower Michigan regional landscape ecosystem (Albert 1995). Average annual precipitation ranges from 71 to 91 cm and the climate is moderated by the presence of the Great Lakes, resulting in warmer winters and cooler summers compared to other areas of similar latitude (Albert 1995). Dike construction in Michigan during the 1960s was perceived as a means to restore coastal marsh lost during a low-water period. Diked units in these areas were typically placed landward at slightly higher elevations than adjacent lakeward coastal wetlands left undiked. We acknowledge that the diked and undiked sites investigated may have differed (e.g., hydrology, vegetation, etc.) prior to dike construction, which could have lasting influence on present-day functioning and our results. Albert and Brown (2008) examined historical aerial photographs of diked wetlands on Saginaw Bay and St. Clair Flats and noted the sites appeared to be wet meadows

mixed with dense emergent marsh prior to diking. After 40 years of impoundment, our diked study wetlands were dominated by emergent marsh, which we compared to proximate undiked emergent marshes. We only sampled undiked wetlands within 400 m of open water to focus surveys in emergent wetlands most similar to the diked marshes.

Diked wetlands represented a range of management capabilities, from impoundments with high-volume water pumps to sites managed with only simple water control structures. St. Clair Flats is a freshwater estuary occurring at the confluence of the St. Clair River and Lake St. Clair. The 2 diked wetlands sampled at St. Clair Flats were located on Harsens Island and had the capability of being managed with water pumps, whereas 2 undiked sampling locations included bays of Harsens Island and neighboring Dickinson Island. Three diked Saginaw Bay wetlands were managed with water control structures only and 4 were capable of being managed with pumps as Lake Huron water levels permitted. We sampled 5 undiked Saginaw Bay sites representing the geomorphic settings in which they occur, including fringing shoreline marshes, river mouth wetlands, and protected marshes associated with islands or other land features.

METHODS

Avian Surveys

We used 2 survey methods to compare bird abundance indices (detections/ha) and community composition between diked and undiked coastal wetlands. We conducted point counts to assess secretive marsh bird and passerine use of emergent vegetation zones. We used timed-area surveys to evaluate bird use of open water-aquatic bed zones (hereafter open water zone), which allowed us to detect species potentially missed during point counts, such as waterfowl, herons, and shorebirds.

Emergent zone.—We located point count stations at undiked sites within 400 m of open water, because undiked wetlands at comparable elevations to diked sites were dry because of low Great Lakes water levels. We identified potential survey points using a geographic information system (GIS), aerial photographs, and 200-m by 200-m grids overlaid on the study sites. We randomly selected points from the grid so they were ≥ 400 m apart. We surveyed only points having standing water or saturated soils and $\geq 50\%$ emergent vegetation cover within 200 m. We surveyed 2–15 points per site each year depending on wetland size (mean = 7.6 points per site per year). We surveyed points during 2005–2007 within 3 periods: 1–20 May, 21 May–10 June, and 11–30 June; however, we only surveyed some points once or twice because of weather or time constraints. Each survey at a given point was separated by ≥ 7 days and we started surveys at St. Clair Flats 1 week earlier than at Saginaw Bay to account for latitudinal differences in breeding phenology (Brewer et al. 1991). Previous experience at these sites helped establish appropriate timing to survey breeding birds and avoid migrants. Because wind could potentially decrease detection of birds, we recorded wind

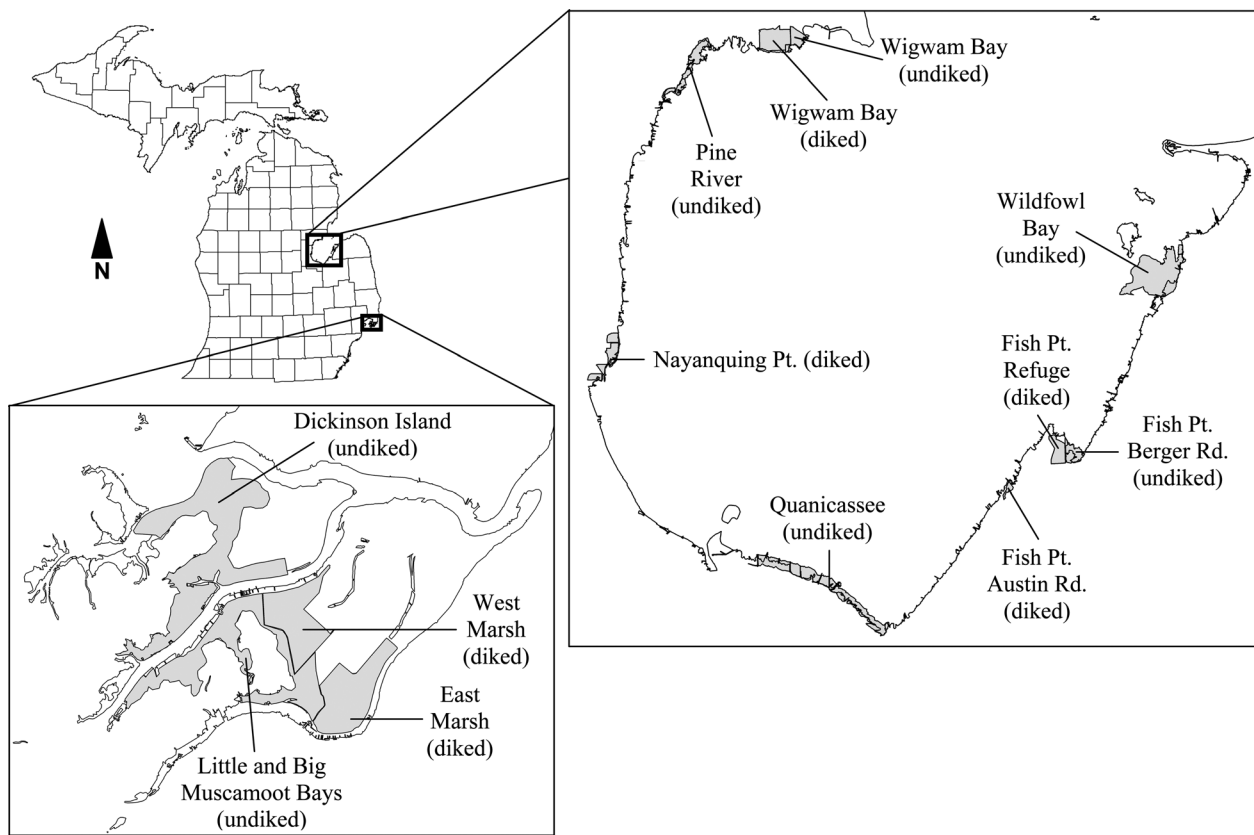


Figure 1. Locations of St. Clair Flats (bottom frame; Lake St. Clair) and Saginaw Bay (right frame; Lake Huron) coastal wetland study sites surveyed for birds during 2005–2007 in Michigan, USA.

speed during each point count using an electronic wind meter. We counted all birds seen or heard during 10-minute surveys completed between 0.5 hour before sunrise and 1000 hours. We conducted point counts following Conway (2005), except that we continued surveys until 1000 hours rather than 3 hours after sunrise. During the final 5 minutes of the point count, we broadcasted calls of 5 secretive species in the following order (Conway 2005): least bittern (*Ixobrychus exilis*), sora (*Porzana carolina*), Virginia rail (*Rallus limicola*), king rail (*Rallus elegans*), and American bittern (*Botaurus lentiginosus*). We estimated distances from survey points to birds using aural estimation and a laser rangefinder and recorded observations within 1 of 3 distance categories: ≤ 18 m (consistent with Brown and Dinsmore 1986), 18–50 m, and 50–100 m.

Open water zone.—We conducted timed-area surveys only at St. Clair Flats in 2005, but surveyed sites at both St. Clair Flats and Saginaw Bay in 2006 and 2007. We identified potential survey sites (e.g., embayments, open water areas surrounded by marsh) dominated by shallow open water and/or aquatic vegetation using aerial photographs and on-site visits. We randomly selected survey areas from a pool of potential sites for each round of surveys. We conducted surveys in the morning between 0.5 hour before and 4 hours after sunrise during 4 periods (late May, mid Jun, mid Jul, and early Aug) separated by 2–3 weeks. A minimum of 3 surveys per site is typically recommended when detection probability is >0.5 and more

surveys are needed when detection is lower (MacKenzie and Royle 2005); however, sampling more sites with fewer repeat surveys is recommended for rare species (MacKenzie et al. 2006). Anticipating multiple species with unknown detection and occupancy probabilities, we used 4 survey periods per season to balance the need to maximize detection with the need to maximize the number of sites visited. We selected survey stations that afforded the best view of the area, caused the least disturbance, and offered concealment. We surveyed each area for 45 minutes beginning upon arrival from a stationary boat, canoe, or vehicle. We estimated the size of the survey area using field maps drawn with a laser rangefinder, compass, and aerial photographs to account for changing visibility because of vegetation growth. We digitized field maps in ArcView 3.2 (ESRI, Redlands, CA) to estimate survey area size. We counted all waterfowl, waterbirds, and shorebirds seen or heard within the survey area, including birds flushed upon arrival and aerial foragers (e.g., terns). We noted the time of each observation and excluded possible repeat detections of individual birds.

Wetland Characteristics

We identified vegetation and collected physical data at 3 randomly selected 0.25-m² quadrats surrounding point count stations surveyed in 2006–2007. Quadrat frames were situated randomly between 1 m and 18 m along 3 compass bearings (120°, 240°, and 360°). For each quadrat, we

estimated percent cover of 6 plant taxa (cattail [*Typha* spp.], bulrush [*Schoenoplectus* spp.], sedge [*Carex* spp.], rush [*Juncus* spp.], common reed [*Phragmites australis*], and grass [other than common reed]) and 6 vegetation structural categories (persistent deep-water emergents [e.g., cattail, bulrush], persistent shallow-water emergents [e.g., common reed, sedge], non-persistent deep-water emergents [e.g., *Sagittaria* spp., *Zizania* spp.], non-persistent shallow-water emergents [e.g., *Eleocharis* spp., *Polygonum* spp.], floating-leaved and free-floating vegetation [e.g., *Nuphar* spp., *Lemna* spp.], and submersed aquatic species [e.g., *Potamogeton* spp., *Chara* spp.]). We measured water depth, depth of organic sediments, maximum height of standing live or dead vegetation, and visual obstruction (Robel et al. 1970) at the center of each quadrat, and counted live and dead shrub and tree stems >2 m tall within 2.5 m of the quadrat center (Riffell et al. 2001). We measured maximum vegetation height to the nearest 5 cm using the same pole used to estimate visual obstruction. We measured water depth to the nearest cm using a 1.2-m wooden rod (2-cm diameter, graduated in cm) and estimated depth of organic sediments to the nearest cm by pushing the rod to the bottom of the organic layer and measuring the depth of the sediments minus water depth. We also recorded stem density within the quadrat for cattail, bulrush, and common reed, which were the most frequently observed taxa at our study sites ($\geq 25\%$ of the quadrats).

Analysis

Avian composition.—We estimated total species richness in diked and undiked wetlands using coverage-based rarefaction and extrapolation (Chao and Jost 2012) and iNEXT software (Hsieh et al., iNEXT Online 1.2). For the emergent zone, we used abundance data to estimate species richness, whereas for the open water zone we used incidence data to account for variable survey area sizes. We calculated both Sorensen (1948) and Morisita (1959) indices to examine similarity of bird communities using diked and undiked wetlands, because the Sorensen index is calculated using species presence-absence data, whereas the Morisita index also incorporates species abundance. We calculated similarity indices between diked and undiked wetlands for all study areas and sites combined. To calculate the Morisita index, we used the number of detections per point in the emergent zone and bird abundance (detections per ha) in open water zone to account for differences in sizes of survey areas.

We used nonmetric multidimensional scaling (NMDS) to explore possible patterns in breeding bird abundance and composition of the emergent and open water zones among diked and undiked wetlands. We conducted separate analyses for emergent (point counts) and open water zones (timed-area surveys). To minimize the influence of rare or non-breeding transient species, we only included wetland-dependent and wetland-associated species observed at $\geq 25\%$ of the sites, which resulted in 24 species for the emergent and 16 species for the open water zone. We averaged bird abundance indices (detections per point or detections per ha of open water) by site and year before

analysis. We performed NMDS using the Bray-Curtis distance measure, 40 runs on the original data matrix, and a maximum of 400 iterations. A final solution was achieved when an instability value of 0.00001 was obtained or after 400 iterations. We conducted the Monte-Carlo permutation procedure (McCune and Grace 2002) with 50 randomized runs to evaluate if axes produced by NMDS explained more variation than by chance alone. We used multi-response permutation procedures (MRPP) to test for differences in bird communities between diked and undiked sites by wetland zone. We used Bray-Curtis distance measures and natural weighting ($n_j/\sum n_j$; Mielke 1984) in MRPP analyses. We conducted NMDS and MRPP analyses using PC-ORD v.4 (MjM Software, Gleneden Beach, OR).

Detectability.—To ensure patterns of detection were similar between the 2 wetland types for each species examined, we used the occupancy model described by MacKenzie et al. (2002) to estimate detection probability (p) for species observed during point counts. We estimated occupancy (ψ), or the estimated proportion of sites occupied after accounting for imperfect detection, and calculated naïve occupancy (observed proportion of sites occupied assuming perfect detection) for diked and undiked sites. Because some species were rare at these locations, we analyzed only those detected at ≥ 5 points in each wetland type (18 species). We conducted occupancy analyses using PRESENCE 5.5 (J. Hines, U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD). We modeled the occupancy parameter first using a default model with no covariates and single-variable models containing the following covariates: wetland type (diked or undiked), water depth, percent cover open water, percent cover floating vegetation, percent cover common reed, percent cover bulrush, and percent cover cattail. We selected occupancy covariates that were likely to influence bird use and differed between diked and undiked wetlands according to parametric and principal components analyses (see below). We assumed detection probability to be constant among sites and survey periods when modeling the occupancy parameter. We then used the best-supported (based on Akaike's Information Criterion [AIC] adjusted for small sample size [AIC_c]) occupancy configuration when modeling detection probability. We first compared 2 models, 1 with detectability assumed constant and the other with detection varying by survey period. We included the configuration best supported by our data in subsequent models. We next compared single-variable models with the following detection covariates: wetland type, wind speed, vegetation height, percent cover emergents, percent cover open water, and observer. For each species, we estimated mean occupancy and detection probabilities for diked and undiked wetlands using point estimates produced in the final best-approximating model.

Avian abundance.—We categorized bird species as wetland-dependent, wetland-associated, and non-wetland species according to Crowley et al. (1996) and Brown and Smith (1998) to indicate level of dependency on wetlands. We used the number of detections recorded within 50 m of each point as an index of density, because the number of

detections per ha dropped steeply for most species in the 50–100 m category and the 50-m distance threshold provided consistency with similar studies (e.g., Galloway et al. 2006). However, we used a 100-m boundary for pied-billed grebe (*Podilymbus podiceps*) and American bittern, because their calls were easily detected at ≥ 100 m. We calculated index values by dividing the number detected by the area surveyed. For timed-area surveys, we estimated bird abundance by dividing the number of birds detected by area of open water surveyed. Because most avian abundance indices were not normally distributed, we log transformed ($\log_e[x + 1]$; Bartlett 1947) abundance variables prior to analysis. We used mixed models (PROC MIXED; SAS Institute, Cary, NC) to compare avian abundance between diked and undiked coastal wetlands. Because several species were extremely rare, we compared only species detected at ≥ 10 points (emergent zone) or ≥ 10 survey areas (open water zone). The mixed model used to compare abundance in emergent zones (point counts) consisted of wetland type (i.e., diked and undiked), study area (i.e., St. Clair Flats and Saginaw Bay), and survey period (i.e., early, mid, and late season) as fixed effects, and year, site, and point count station as random effects. We used a repeated measures component to account for multiple surveys at the same point. We evaluated 3 commonly used covariance structures for each variable: autoregressive order 1, compound symmetric, and unstructured (Littell et al. 1996, Kincaid 2005). We compared models containing the repeated measures component with a standard mixed model with no repeated measures and selected the best-approximating model using AIC. For abundance in the open water zone, we used a mixed model consisting of wetland type, study area, and survey period as fixed effects, and year and site as random effects. We back-transformed parameter estimates from our models and expressed them as geometric means.

Wetland characteristics.—We compared wetland characteristics measured during quadrat sampling between diked and undiked wetlands. Because vegetation and physical variables were often not normally distributed, we transformed variables prior to analysis. We arcsine-square root transformed ($\arcsin\sqrt{p}$) percent variables and log transformed ($\log_e[x + 1]$) all other variables. We conducted analyses using a mixed model with wetland type, study area, and survey period as fixed effects, and year and site as random effects. We back-transformed parameter estimates and expressed them as geometric means in our results.

We performed a principal components analysis (PCA) on vegetation and physical variables using PROC PRINCOMP (SAS Institute). We averaged data for the 3 survey periods within a given year by point prior to analysis. We excluded variables that were highly correlated ($r \geq 0.70$) with similar variables or that had low frequencies of occurrence (i.e., $< 10\%$ of total quadrats), resulting in 14 variables in the PCA. We arcsine-square root transformed percent variables prior to analysis. We used correlation coefficients to form the cross-products matrix and did not rotate ordination axes. When evaluating the importance of the principal component loadings, we only considered loadings > 0.20 or < -0.20 ,

which is an approach similar to interpreting correlation coefficient significance at a 0.01 alpha level (Hair et al. 1987, McGarigal et al. 2000).

Avian abundance models.—We conducted multiple regression analysis (PROC REG; SAS Institute) to explore potential relationships between indices of avian abundance (detections/ha) in emergent zones and vegetation and physical variables collected during 2006 and 2007 point counts. We conducted the regression analysis for the same bird species analyzed via mixed models using vegetation and physical variables from quadrat sampling as our independent variables. We excluded variables highly correlated ($r \geq 0.60$) with other variables, resulting in 15 variables used in analyses. We employed forward stepwise and backward removal model selection procedures. The maximum P -value for model entry using forward stepwise selection was 0.20, whereas we retained variables with P -value ≤ 0.05 under the backward removal procedure. Final models from both selection procedures were similar, so we only report the forward stepwise models.

RESULTS

Emergent Zone

Using the MacKenzie et al. (2002) occupancy model, estimates of detection probability were similar between diked and undiked wetlands for 16 of 18 species analyzed (Table 1). Both pied-billed grebe and American coot (*Fulica americana*) had greater detection probabilities in undiked compared to diked wetlands. Although detection probability was similar between wetland types, the probability of detection varied by survey period for 11 of the 18 species analyzed (Table 2). Percent cover open water was also an influential covariate in several of the best-approximating models. Probability of detecting American bittern, Forster's tern (*Sterna forsteri*), marsh wren (*Cistothorus palustris*), and barn swallow (*Hirundo rustica*) increased with percent cover open water, whereas common yellowthroat (*Geothlypis trichas*) detectability was negatively related to percent cover open water (Table 2). Wind speed was another common covariate; black tern (*Chlidonias niger*), red-winged blackbird (*Agelaius phoeniceus*), yellow warbler (*Setophaga petechia*), and common grackle (*Quiscalus quiscula*) detection probabilities were negatively associated with wind speed.

All indicators of bird community composition showed a high degree of similarity between diked and undiked wetlands. Observed bird species richness was similar between wetland types, with 57 species seen or heard in diked and 53 species in undiked marshes. Forty-four species (67%) were common to both wetland types. Estimated species richness was also similar at 61 (95% CI 54.2–67.8) for diked wetlands and 58 (95% CI 52.1–64.8) for undiked wetlands. The Sorensen index of similarity was 0.80, indicating high similarity in species composition between diked and undiked sites. The Morisita index was 0.98, indicating an extremely high degree of similarity in bird assemblages between wetland types. Initial NMDS analysis suggested the data were best represented by 2 dimensions and a solution with

Table 1. Naïve occupancy (observed proportion of sites occupied) and model-estimated occupancy (ψ) and detection probability (p) for species detected during point counts conducted in emergent zones of diked and undiked Michigan coastal wetlands (2005–2007).

	Naïve occupancy		Estimated occupancy				Estimated detection probability ^a			
	Diked	Undiked	Diked		Undiked		Diked		Undiked	
			ψ	SE	ψ	SE	p	SE	p	SE
Wetland-dependent species										
Mallard	0.055	0.154	0.233	0.095	0.455	0.118	0.136	0.052	0.129	0.051
Pied-billed grebe	0.143	0.143	0.429	0.105	0.181	0.061	0.148	0.048	0.411	0.104
American bittern	0.418	0.187	0.694	0.120	0.370	0.094	0.359	0.078	0.292	0.075
Virginia rail	0.385	0.297	0.677	0.129	0.551	0.119	0.263	0.049	0.263	0.049
Sora	0.110	0.099	0.178	0.061	0.178	0.061	0.554	0.189	0.554	0.189
Common gallinule	0.066	0.077	0.116	0.047	0.075	0.028	0.576	0.170	0.588	0.168
American coot	0.176	0.176	0.311	0.066	0.218	0.049	0.364	0.107	0.719	0.114
Black tern	0.165	0.220	0.226	0.046	0.273	0.067	0.601	0.125	0.578	0.122
Forster's tern	0.110	0.308	0.165	0.053	0.605	0.125	0.337	0.063	0.263	0.060
Tree swallow	0.440	0.462	0.681	0.079	0.626	0.094	0.350	0.052	0.352	0.053
Marsh wren	0.868	0.912	0.948	0.022	0.893	0.040	0.918	0.022	0.842	0.038
Swamp sparrow	0.857	0.736	0.793	0.042	0.843	0.029	0.769	0.029	0.768	0.029
Red-winged blackbird	0.989	0.956	0.984	0.010	0.984	0.010	0.947	0.020	0.956	0.016
Wetland-associated species										
Barn swallow	0.242	0.330	0.512	0.114	0.738	0.104	0.216	0.040	0.181	0.041
Yellow warbler	0.220	0.143	0.273	0.048	0.167	0.039	0.576	0.109	0.670	0.095
Common yellowthroat	0.593	0.615	0.629	0.060	0.723	0.056	0.588	0.062	0.674	0.056
Common grackle	0.374	0.187	0.646	0.122	0.326	0.083	0.325	0.081	0.339	0.079
Non-wetland species										
Song sparrow	0.121	0.319	0.227	0.058	0.439	0.087	0.449	0.106	0.472	0.104

^a For species with survey period as a covariate, we only report the maximum detection probability observed from the 3 survey periods.

equal or less stress was not likely to occur by chance alone ($P=0.020$). After rerunning NMDS with only 2 dimensions, 78.3% of the variation in the original distance matrix was explained (final stress of 17.63). Results of NMDS were

consistent with the similarity indices and we found no clear visual distinction between wetland types (Fig. 2). Permutation tests indicated bird composition was similar between wetland types ($T=-0.49$, $P=0.270$).

Table 2. Best-approximating occupancy models and associated corrected Akaike's Information Criterion weights (w_i) and number of parameters (K) for species observed during point counts conducted at St. Clair Flats and Saginaw Bay, Michigan, USA, coastal wetlands, 2005–2007.

Species	Model ^a	w_i	K
Wetland-dependent species			
Mallard	$\psi(\text{SC}), p(\text{EM})$	0.320	4
Pied-billed grebe	$\psi(\text{W}), p(\text{WT})$	0.632	4
American bittern	$\psi(\text{WT}), p(\text{S}, \text{OW})$	0.607	6
Virginia rail	$\psi(\text{OW}), p(\cdot)$	0.232	3
Sora	$\psi(\cdot), p(\text{S})$	0.245	4
Common gallinule	$\psi(\text{W}), p(\text{S}, \text{OB})$	0.180	6
American coot	$\psi(\text{OW}), p(\text{S}, \text{WT})$	0.541	6
Black tern	$\psi(\text{SC}), p(\text{S}, \text{WI})$	0.409	6
Forster's tern	$\psi(\text{WT}), p(\text{OW})$	0.513	4
Tree swallow	$\psi(\text{PH}), p(\text{H})$	0.252	4
Marsh wren	$\psi(\text{W}), p(\text{S}, \text{OW})$	1.000	6
Swamp sparrow	$\psi(\text{OW}), p(\text{OB})$	0.715	4
Red-winged blackbird	$\psi(\cdot), p(\text{S}, \text{WI})$	0.373	5
Wetland-associated species			
Barn swallow	$\psi(\text{SC}), p(\text{OW})$	0.381	4
Yellow warbler	$\psi(\text{SC}), p(\text{S}, \text{WI})$	0.557	6
Common yellowthroat	$\psi(\text{OW}), p(\text{S}, \text{OW})$	0.656	6
Common grackle	$\psi(\text{WT}), p(\text{S}, \text{WI})$	0.375	6
Non-wetland species			
Song sparrow	$\psi(\text{W}), p(\text{S}, \text{OB})$	0.475	6

^a Variable notation: ψ , probability of occupancy; p , probability of detection; WT, wetland type; W, water depth; OW, percent open water; (\cdot), null; FL, percent floating vegetation; TY, percent *Typha*; PH, percent *Phragmites*; SC, percent *Schoenoplectus*; S, survey period; WI, wind speed; H, vegetation height; EM, percent cover total emergent; and OB, observer.

Patterns in species occupancy and abundance estimates were similar between diked and undiked sites. Probability of occupancy appeared to differ between diked and undiked wetlands for 4 of 18 species examined (Table 1), and of the 21 species abundant enough to compare indices of abundance between wetland types, only 3 differed significantly (Table 3). Red-winged black bird, marsh wren, and swamp sparrow (*Melospiza georgiana*) collectively comprised >65% of all individuals observed and their occupancies and relative abundances were similar between wetland types. Tree swallow (*Tachycineta bicolor*) and Virginia rail each comprised approximately 2% of all birds detected, whereas all other species accounted for <2% of the total number of birds observed during point counts. Pied-billed grebe occupancy was greater in diked than undiked sites, but abundance did not differ significantly. American bittern had greater occupancy and was 3 times more abundant ($F_{1,409} = 10.62$, $P = 0.001$) in diked wetlands relative to undiked sites. Least bittern was 4 times more abundant ($F_{1,409} = 9.34$, $P = 0.002$) in diked sites, but was too rare to reliably estimate occupancy probabilities. Forster's tern had greater probability of occupancy and was the only species more abundant in undiked wetlands, with mean abundance over 5 times greater ($F_{1,409} = 7.74$, $P = 0.006$). Common grackle occupancy was greater in diked than undiked sites and the difference between indices of abundance was nearly significant ($F_{1,409} = 3.52$, $P = 0.061$). Consistent with abundance comparisons, wetland type was included in best-supported occupancy models for American bittern, Forster's tern, and common grackle (Table 2).

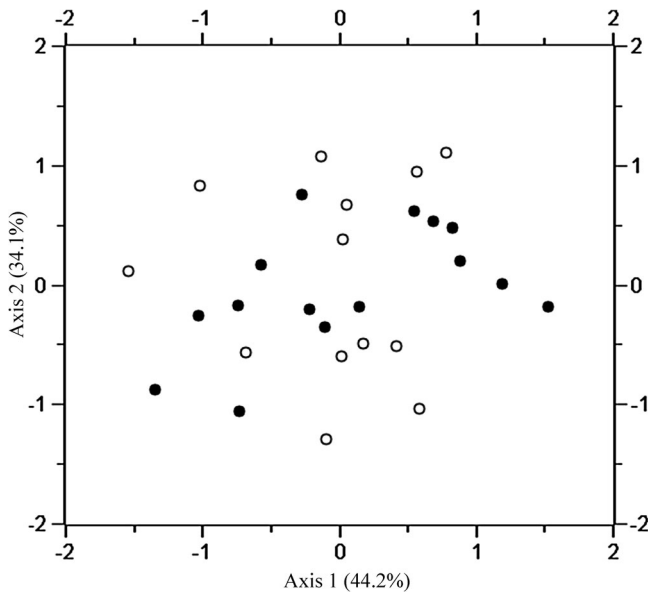


Figure 2. Nonmetric multidimensional scaling plot for birds sampled in the emergent zones of diked (●) and undiked (○) coastal marshes at St. Clair Flats and Saginaw Bay, Michigan, USA, 2005–2007.

Water depth, percent cover open water, and percent cover bulrush were the occupancy covariates most often occurring in best-approximating models (Table 2). Pied-billed grebe, common gallinule (*Gallinula galeata*), and marsh wren occupancy was positively related to water depth, whereas song sparrow occupancy was negatively associated with water depth. Percent cover open water was included in the best-

supported models of 4 species, with Virginia rail and American coot occupancy being positively related and swamp sparrow and common yellowthroat occupancy negatively associated. Probability of occupancy by mallard (*Anas platyrhynchos*), black tern, and barn swallow was positively associated with percent cover bulrush, whereas occupancy of yellow warbler was negatively related.

Open Water Zone

We observed more differences between wetland types in the bird communities of open water than in the emergent zone. Mean size of survey areas differed by wetland type ($F_{1,269} = 4.25, P = 0.040$), with diked survey areas averaging 3.67 ha (SE = 1.87, $n = 144$) and undiked sites 9.38 ha (SE = 2.09, $n = 143$). Observed species richness was 32 for both diked and undiked wetlands, with 25 species (64%) common to both wetland types. Estimated species richness was 38 (95% CI 30.1–46.2) at undiked sites compared to 33 (95% CI 29.2–36.7) at diked wetlands, but the confidence intervals overlapped considerably. The Sorensen index of similarity was 0.73, indicating high similarity in bird species composition between wetland types. The Morisita similarity index was 0.62 between diked and undiked wetlands, suggesting a moderate level of similarity. Initial NMDS on timed-area data indicated the solution was unlikely to result from chance alone ($P = 0.020$) and the data set was best represented by 3 dimensions. We recalculated NMDS with 3 dimensions and observed a final stress of 11.58. The 3 dimensions explained 78.9% of the total variance in the original distance matrix. Diked and undiked wetlands did

Table 3. Least squares geometric means and lower and upper 95% confidence limits (lower [LCL] and upper [UCL]) by wetland type for breeding bird abundances (bird detections/ha) measured during point counts conducted in emergent zones of St. Clair Flats and Saginaw Bay, Michigan, USA, coastal wetlands, 2005–2007 (n indicates the number of point counts conducted). P -Values with an asterisk indicate a significant difference between wetland types ($P < 0.05$).

Bird abundance	No. points with detections		Diked ($n = 294$)			Undiked ($n = 311$)			P
	Diked	Undiked	Mean	LCL	UCL	Mean	LCL	UCL	
Wetland-dependent species									
Canada goose	6	4	0.03	0.01	0.04	0.01	0.00	0.03	0.390
Mallard	5	14	0.02	-0.02	0.06	0.05	0.01	0.09	0.129
Pied-billed grebe	13	13	0.02	0.00	0.04	0.02	0.00	0.05	0.793
American bittern	38	17	0.06	0.04	0.08	0.02	0.01	0.04	0.001*
Least bittern	14	1	0.04	0.02	0.06	0.01	-0.01	0.02	0.002*
Virginia rail	35	27	0.20	0.14	0.26	0.15	0.09	0.21	0.282
Sora	10	9	0.04	0.01	0.07	0.03	0.01	0.06	0.613
Common gallinule	6	7	0.04	0.02	0.07	0.02	0.00	0.04	0.086
American coot	16	16	0.09	0.02	0.16	0.10	0.03	0.17	0.855
Black tern	15	20	0.08	0.01	0.15	0.13	0.06	0.21	0.211
Forster's tern	10	28	0.04	-0.04	0.12	0.21	0.12	0.30	0.006*
Willow flycatcher	8	4	0.04	0.02	0.07	0.02	0.00	0.05	0.261
Tree swallow	40	42	0.21	0.04	0.41	0.33	0.15	0.54	0.352
Marsh wren	79	83	1.89	1.22	2.76	1.31	0.79	1.96	0.202
Swamp sparrow	78	67	1.02	0.49	1.72	0.94	0.45	1.60	0.785
Red-winged blackbird	90	87	2.69	2.00	3.53	2.44	1.81	3.21	0.438
Wetland-associated species									
Barn swallow	22	30	0.08	0.00	0.16	0.17	0.09	0.25	0.099
Yellow warbler	20	13	0.18	0.07	0.31	0.13	0.03	0.25	0.518
Common yellowthroat	54	56	0.43	0.23	0.67	0.53	0.31	0.77	0.387
Common grackle	34	17	0.20	0.10	0.31	0.10	0.01	0.20	0.061
Non-wetland species									
Song sparrow	11	29	0.10	-0.01	0.21	0.20	0.09	0.32	0.175

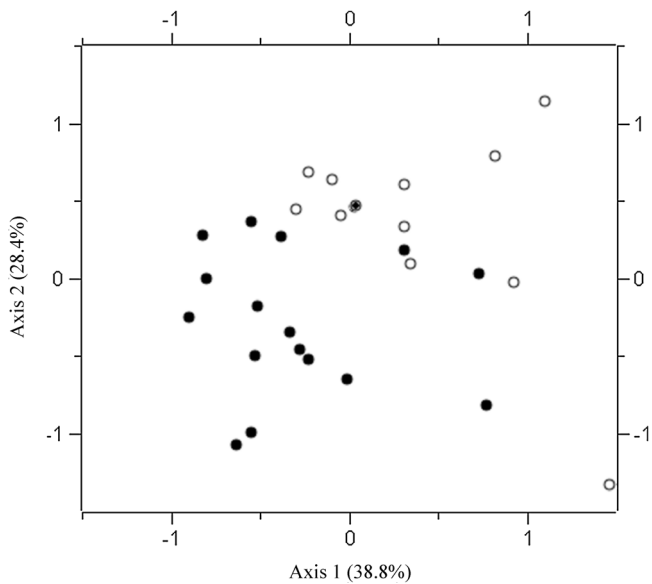


Figure 3. Nonmetric multidimensional scaling plot for birds sampled in the open water zones of diked (●) and undiked (○) coastal marshes at St. Clair Flats and Saginaw Bay, Michigan, USA, 2005–2007.

not separate along axes 1 or 3, but a gradient by wetland type was apparent along axis 2 (Fig. 3), indicating some differences in the bird communities of the open water zone. Permutation tests indicated bird composition of the open water zone differed by wetland type ($T = -9.25$, $P < 0.001$).

Seven of the 16 species abundant enough to compare differed significantly by wetland type (Table 4). Wood duck (*Aix sponsa*) was the most common species observed in the open water zone of diked wetlands and made up about 20% of the birds observed. Mallard was most abundant at undiked sites, accounting for 29% of observations. The next most common species at diked wetlands were black tern, Canada

goose (*Branta canadensis*), mallard, and pied-billed grebe, each of which made up 6–11% of the total birds detected. Forster's tern, black tern, pied-billed grebe, and American coot were the next most common species at undiked sites, accounting for 5–9% of all birds observed. All other species in both wetland types made up <5% of the total birds detected. We estimated over 10 times greater ($F_{1,269} = 28.06$, $P < 0.001$) mean Canada goose abundance and nearly 13 times greater ($F_{1,269} = 14.29$, $P < 0.001$) wood duck abundance in diked compared to undiked sites (Table 4). Common gallinule abundance was >3 times greater in diked wetlands ($F_{1,269} = 5.79$, $P = 0.017$), whereas American coot abundance was nearly 3 times greater in undiked sites ($F_{1,269} = 4.36$, $P = 0.038$). We found mean indices of abundance of ring-billed gull (*Larus delawarensis*) were 4 times greater ($F_{1,269} = 9.30$, $P = 0.003$), herring gull (*L. argentatus*) over 4 times greater ($F_{1,269} = 4.03$, $P = 0.046$), and Forster's tern 5 times greater ($F_{1,269} = 12.74$, $P < 0.001$) in undiked wetlands relative to diked wetlands.

Wetland Characteristics

Several vegetation and physical variables differed between diked and undiked wetlands. Open water–aquatic bed was the most common cover type category in both wetland types, but mean coverage was greater ($F_{1,1507} = 13.08$, $P < 0.001$) in diked sites. Diked wetlands also had greater mean cover of floating vegetation ($F_{1,1507} = 9.63$, $P = 0.002$), persistent deep-water vegetation ($F_{1,1507} = 4.98$, $P = 0.026$), and cattail ($F_{1,1507} = 14.86$, $P < 0.001$) than undiked wetlands (Table 5). We found more shallow-water vegetation in undiked compared to diked wetlands, with greater mean percent cover of both persistent ($F_{1,1507} = 8.68$, $P = 0.003$) and non-persistent ($F_{1,1507} = 12.33$, $P = 0.001$) shallow-water plants. Undiked wetlands also had greater coverage of bulrush ($F_{1,1507} = 31.53$, $P < 0.001$), common reed

Table 4. Least squares geometric means and lower and upper 95% confidence limits (lower [LCL] and upper [UCL]) by wetland type for bird abundances (bird detections/ha) measured during timed-area surveys conducted in open water zones of St. Clair Flats and Saginaw Bay, Michigan, USA, coastal wetlands, 2005–2007 (n indicates the number of surveys conducted). P -Values with an asterisk indicate a significant difference between wetland types ($P < 0.05$).

Bird abundance	Diked ($n = 144$)			Undiked ($n = 143$)			P
	Mean	LCL	UCL	Mean	LCL	UCL	
Wetland-dependent species							
Canada goose	0.31	0.23	0.40	0.03	-0.03	0.10	$\leq 0.001^*$
Mute swan	0.15	0.03	0.29	0.09	-0.04	0.23	0.486
Wood duck	0.63	0.39	0.91	0.05	-0.12	0.24	$\leq 0.001^*$
Mallard	0.20	0.03	0.49	0.63	0.28	1.07	0.063
Pied-billed grebe	0.18	0.03	0.34	0.17	0.02	0.35	0.982
Great blue heron	0.11	0.03	0.18	0.04	-0.03	0.12	0.121
Great egret	0.03	0.04	0.09	0.07	0.00	0.15	0.359
Black-crowned night-heron	0.04	-0.04	0.13	<0.01	-0.09	0.09	0.474
Common gallinule	0.07	0.03	0.11	0.02	-0.02	0.06	0.017*
American coot	0.04	-0.01	0.10	0.11	0.05	0.17	0.038*
Ring-billed gull	0.01	-0.01	0.02	0.04	0.03	0.06	0.003*
Herring gull	<0.01	-0.02	0.03	0.04	0.01	0.07	0.046*
Black tern	0.36	0.09	0.69	0.18	-0.08	0.50	0.376
Forster's tern	0.04	-0.04	0.13	0.20	0.10	0.31	$\leq 0.001^*$
Wetland-associated species							
Killdeer	0.04	-0.02	0.10	0.01	-0.05	0.07	0.284
Caspian tern	0.10	0.06	0.14	0.09	0.05	0.13	0.578

Table 5. Least squares geometric means and lower and upper 95% confidence limits (lower [LCL] and upper [UCL]) for vegetation and physical variables measured during quadrat sampling conducted at St. Clair Flats and Saginaw Bay, Michigan, USA, coastal wetlands, 2006–2007 (*n* indicates the number of quadrats sampled). *P*-Values with an asterisk indicate a significant difference between wetland types ($P < 0.05$).

Vegetation/physical variable	Diked (<i>n</i> = 771)			Undiked (<i>n</i> = 750)			<i>P</i>
	Mean	LCL	UCL	Mean	LCL	UCL	
Percent cover—plant categories							
Open water—aquatic bed	73.8	61.6	84.5	40.0	26.9	53.9	≤0.001*
Emergent vegetation	23.9	15.2	34.0	25.7	16.3	36.4	0.758
Surface litter	13.0	6.5	21.2	31.0	20.9	42.2	0.004*
Persistent deep-water	16.9	9.9	25.3	6.3	2.1	12.7	0.026*
Persistent shallow-water	1.0	0.0	3.8	8.0	3.4	14.3	0.003*
Floating vegetation	1.9	0.7	3.7	<0.1	0.2	0.5	0.002*
Submersed vegetation	1.1	0.2	2.6	0.2	0.0	1.1	0.139
Non-persistent shallow-water	0.1	<0.1	0.4	0.8	0.4	1.3	0.001*
Non-persistent deep-water	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.060
Exposed sediments	<0.1	<0.1	0.1	0.3	0.1	0.6	0.017*
Percent cover—dominant taxa							
Cattail	16.3	9.7	24.3	1.8	0.1	5.7	≤0.001*
Common reed	0.2	0.1	1.7	3.4	1.0	7.2	0.023*
Bulrush	<0.1	<0.1	0.2	1.8	1.0	2.8	≤0.001*
Sedge	0.2	<0.1	0.6	0.1	<0.1	0.5	0.554
Rush	<0.1	<0.1	0.1	0.2	<0.1	0.8	0.078
Grass	<0.1	<0.1	0.1	0.2	<0.1	0.6	0.025*
Stem density							
Cattail ^a	11.78	6.76	20.06	1.58	0.52	3.38	≤0.001*
Bulrush ^a	0.10	-0.19	0.49	2.88	1.80	4.37	≤0.001*
Common reed ^a	0.46	-0.14	1.48	2.80	1.16	5.67	0.013*
Trees and shrubs ^b	0.24	0.08	0.42	0.04	0.10	0.20	0.084
Vegetation height (m)	1.55	1.22	1.92	1.44	1.11	1.82	0.663
Visual obstruction (m)	1.17	0.85	1.56	0.81	0.52	1.16	0.127
Water depth (m)	0.30	0.22	0.39	0.09	0.02	0.17	≤0.001*
Organic sediment depth (m)	0.40	0.30	0.50	0.24	0.15	0.34	0.007*

^a No. stems per 0.25 m² quadrat.

^b No. stems >2 m tall per 20 m² (i.e., within 2.5-m radius of quadrat center).

($F_{1,1507} = 5.20$, $P = 0.023$), and grass ($F_{1,1507} = 5.02$, $P = 0.025$) compared to diked marshes. We observed greater mean percent cover of surface litter ($F_{1,1506} = 8.41$, $P = 0.004$) and exposed sediments ($F_{1,1507} = 5.70$, $P = 0.017$) in undiked than diked sites. Mean cattail stem density was greater ($F_{1,1505} = 20.11$, $P < 0.001$) in diked wetlands, whereas densities of bulrush ($F_{1,1507} = 31.53$, $P < 0.001$) and common reed ($F_{1,1498} = 6.13$, $P = 0.013$) were greater in undiked marshes. Mean water depth ($F_{1,1494} = 13.89$, $P < 0.001$) and organic sediment depth ($F_{1,1323} = 7.33$, $P = 0.007$) was greater in diked wetlands.

Our PCA confirmed differences observed in parametric comparisons of wetland characteristics. Although diked and undiked point count stations overlapped in principal component (PC) scores, undiked wetlands tended to have greater PC 1 scores and lower PC 2 scores (Fig. 4). Undiked sites usually had shallower water, denser and taller vegetation, and more common reed compared to diked wetlands, whereas diked sites tended to have greater water and organic sediment depths, greater percent cover open water, submersed vegetation, and floating plants, and more cattail.

Avian Abundance Models

Stepwise multiple regression analysis using avian point count and wetland characteristic data from 2006 to 2007 resulted in

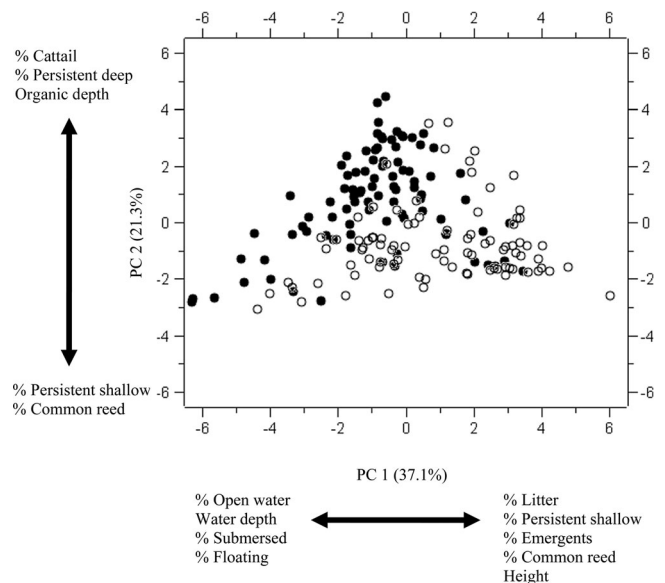


Figure 4. Biplot of principal components (PC) analysis conducted using 14 vegetation and physical variables gathered during quadrat sampling at avian point count stations within coastal marshes at St. Clair Flats and Saginaw Bay, Michigan, USA, 2006–2007. Point count stations are coded by wetland type (● = diked and ○ = undiked marsh).

significant ($P < 0.05$) models for all species analyzed. Four variables were most often associated with bird abundance: percent cover emergent vegetation (12 species), percent cover bulrush (11 species), water depth (10 species), and percent cover floating vegetation (9 species). Abundance indices of most wetland-dependent species were negatively associated with total emergent and floating vegetation and positively related to water depth and bulrush cover (Table 6). Four wetland-dependent species were also positively associated with sedge cover.

DISCUSSION

We expected diked wetlands to support more species and greater abundances of wetland birds than undiked sites, but our results suggested a more ambiguous reality. In the emergent zone, we observed differences in occupancy probabilities of only 4 species (3 greater in diked, 1 in undiked) and abundance of 3 species (2 greater in diked, 1 in undiked). Measures of species richness, similarity indices, and multivariate analyses all indicated similar bird communities in diked and undiked wetlands. We observed more differences in the open water zone, with abundance of 7 species differing (3 greater in diked, 4 greater in undiked). Multivariate analysis indicated statistically significant separation of bird communities in the open water zone; however, similarity indices and species richness estimates suggested the differences were small. The larger open water areas in undiked wetlands, plus their connection to the Great Lakes, may have resulted in increased use by gulls, Forester's tern, and American coot. Conversely, the smaller more interspersed open-water areas in diked wetlands may have been more suitable to Canada goose, wood duck, and common gallinule. However, apparent regular use of mowed dike tops for feeding and loafing suggests Canada geese may have been less abundant had diked wetlands lacked this upland component.

Most diked sites had not been completely drawn down for many years (e.g., 8 yr), resulting in simplified marshes dominated by floating cattail mats and aquatic bed zones of floating and submersed plants. Early managers of impounded wetlands observed declines in waterfowl use with increasing time since initial flooding, leading them to use drawdowns (i.e., dewatering) to rejuvenate waterfowl habitats (Griffith 1948, Hartman 1949, Kadlec 1962, Harris and Marshall 1963, Whitman 1976). Notably, mallards, a typical focal species for wetland management, made up a greater proportion of the birds observed and tended to have greater abundance at undiked sites. Weller and Fredrickson (1973) found Virginia rail densities peaked in an experimentally manipulated marsh during the first year of reflooding following a drawdown, when the site consisted of sparse and well-dispersed annual and immature perennial vegetation. Densities subsequently decreased in the 3 following years as dense stands of perennial emergent plants established and then increased in the next 2 years as vegetation/open water ratios approached 50:50 (Weller and Fredrickson 1973). We found abundance of several wetland-dependent bird species was positively associated

with percent cover bulrush and negatively related to floating vegetation; least bittern and marsh wren were the only wetland-dependent species positively related to cattail cover. Johnson and Dinsmore (1986) suggested managers encourage diverse stands of robust, moderately robust, and fine emergents, and seed producing plants to attract Virginia rails and soras. Abundance of both bird species was positively related to percent cover of sedge in our study. Relatively stable water levels in our diked study sites over many years likely reduced diversity of microhabitats for bird nesting and foraging.

Galloway et al. (2006) observed greater indices of abundance for marsh-nesting obligate birds, marsh-nesting generalists, and area-sensitive marsh-nesting obligates in diked Great Lakes coastal wetlands. In addition, they found greater cumulative species richness in diked compared to undiked sites for several marsh bird groups and only aerial forager species richness was greater in undiked wetlands. Differences between our study and Galloway et al. (2006) could be due to analytical methods (e.g., bird group vs. species comparisons), study duration, hydrologic regimes, human disturbance, invasive species impacts, and landscape context. Management may have also differed, as Galloway et al. (2006) noted some of their publicly owned study wetlands in Ontario were actively managed to maintain high plant and structural diversity. Although our point count methods were similar, we also conducted open water surveys not done by Galloway et al. (2006). We observed more differences in the bird communities of the open water compared to emergent zone and believe timed-area surveys provided a better index of use for species focusing activity in open water or along marsh edges (e.g., waterfowl, herons, common gallinule, American coot, gulls, terns). Unlike our multi-year study, Galloway et al. (2006) sampled during only 1 breeding season, which did not account for inter-annual variation in wetland condition or bird use. Because our study occurred during a period of low water levels and water level fluctuations and depths can affect plant communities and bird use of Great Lakes coastal wetlands (Steen et al. 2006, Timmermans et al. 2008), further study during periods of higher water levels would expand our understanding of bird use of diked and undiked wetlands.

Despite mixed results in bird community comparisons, we found clear differences in the vegetation and physical characteristics of diked and undiked coastal wetlands. Diked sites had deeper water, more organic sediments, and greater percent cover of open water, floating plants, and cattail compared to undiked wetlands, whereas undiked sites had greater percent cover and density of common reed and bulrush. Other studies have noted similar vegetation patterns (Albert and Brown 2008), including greater cattail cover in diked Great Lakes coastal wetlands and greater common reed cover in undiked sites (Herrick and Wolf 2005). Galloway et al. (2006) observed greater native plant species richness and coverage in diked than undiked sites in both emergent and open water zones. Several authors suggested wetland plant species are distributed along gradients of disturbance, fertility, and organic matter content based on

Table 6. Vegetation and physical variables^a included in significant ($P < 0.05$) multiple regressions of avian abundances (bird detections/ha) estimated at 182 point count stations in Michigan coastal wetlands, 2006–2007. A positive (+) or negative (–) sign denotes a significant explanatory variable in the final model, whereas 0 indicates the variable was not significant and excluded. We provide P -values for differences in avian abundances by wetland type (i.e., diked or undiked) from our mixed model analysis as reference. P -Values with an asterisk indicate a significant difference between wetland types ($P < 0.05$). The number of species positively or negatively associated with each variable is provided by species group and for all species combined.

Species	No. points with species observed	Water depth	Organic depth	Emergent	Floating	Submersed	Bare	Cattail	Bulrush	Common reed	Grass	Sedge	Rush	Non. deep	Non. shallow	Woody	R^2	Type	P -value
Wetland-dependent																			
Canada goose	10	0	+	–	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.390	
Mallard	19	0	0	–	0	0	0	0	+	0	0	0	0	0	0	0	0.07	0.129	
Pied-billed grebe	26	+	–	–	–	–	0	0	0	0	0	0	0	0	0	0	0.11	0.793	
American bittern	55	+	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0.06	0.001*	
Least bittern	15	+	0	0	–	0	0	+	0	+	0	0	0	0	0	+	0.18	0.002*	
Virginia rail	62	0	0	–	0	0	0	0	0	0	0	+	0	0	0	0	0.07	0.282	
Sora	19	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0.08	0.613	
Common gallinule	13	+	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0.04	0.086	
American coot	32	+	0	–	–	0	0	0	+	0	0	0	0	0	0	0	0.15	0.855	
Black tern	35	0	0	–	0	0	0	0	+	0	0	+	0	0	0	0	0.08	0.211	
Forster's tern	38	0	0	–	–	0	0	0	+	0	0	0	0	–	0	0	0.14	0.006*	
Willow flycatcher	12	0	0	0	0	0	0	0	–	0	0	0	–	+	+	+	0.52	0.261	
Tree swallow	82	+	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0.16	0.352	
Marsh wren	162	+	0	–	–	0	0	+	+	0	0	0	0	+	0	0	0.31	0.202	
Swamp sparrow	145	–	0	+	+	0	0	0	0	–	0	+	0	0	0	+	0.33	0.785	
Red-winged blackbird	177	0	0	–	+	–	0	0	0	0	–	0	0	0	0	0	0.12	0.438	
No. species (+)	7	1	1	1	2	0	0	2	6	1	0	4	0	2	2	3			
No. species (–)	1	1	1	9	6	3	0	0	1	1	1	0	1	1	0	0			
Wetland-associated																			
Barn swallow	52	–	–	–	0	0	0	+	+	0	0	0	0	0	0	0	0.16	0.099	
Yellow warbler	33	0	0	0	+	0	0	0	–	0	0	0	0	0	+	+	0.32	0.518	
Common yellowthroat	110	–	0	+	0	+	0	0	–	+	0	0	0	0	+	0	0.31	0.387	
Common grackle	51	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0.03	0.061	
No. species (+)	2	0	0	1	1	1	0	2	1	1	0	0	0	0	2	1			
No. species (–)	2	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0			
Non-wetland																			
Song sparrow	40	0	–	0	0	0	0	0	–	0	+	0	0	+	+	+	0.24	0.175	
No. species (+)	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1			
No. species (–)	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0			
Total no. species (+)	7	1	2	3	1	1	0	4	7	2	1	4	0	3	5	5			
Total no. species (–)	3	3	10	6	3	3	0	0	4	1	1	0	1	1	0	0			

^a Water depth; depth of organic sediments (organic depth); and percent cover of emergent, floating, and submersed vegetation, exposed sediments (bare), cattail (*Typha* spp.), bulrush (*Scheuchzeria* spp.), common reed (*Phragmites australis*), grass, sedge (*Carex* spp.), rush (*Juncus* spp.), non-persistent deep-water emergents (non. deep), non-persistent shallow-water emergents (non. shallow), and shrubs/trees (woody).

competitive abilities (e.g., Wilson and Keddy 1986; Day et al. 1988; Gaudet and Keddy 1988, 1995; Moore et al. 1989). Broad-leaved species such as cattails outcompete other species under high fertility and low disturbance (Wisheu and Keddy 1992), which was likely reflected at our diked sites because of stabilized water levels and trapped organic matter and nutrients (Herrick et al. 2007). Invasive common reed expanded rapidly over an extended period of low Great Lakes water levels (1997–2012), reducing plant diversity at many of our undiked study sites and other parts of the Great Lakes (Tulbure et al. 2007, Tulbure and Johnston 2010).

A few bird species benefitted from the deep-water marshes provided by the diked wetlands we examined. We found greater abundance of American and least bitterns and common gallinules in diked wetlands and all 3 species were positively associated with water depth, thus may have been attracted to higher water levels of the diked sites. American bitterns in Maine preferred impounded and beaver-created wetlands over wetlands of glacial origin (Gibbs et al. 1992). Bogner and Baldassarre (2002) suggested vegetation type and emergent/open water ratios influenced abundance of least bitterns and Weller (1961) found most least bittern nests in cattail and bulrush marshes near open water. Our diked wetlands appeared to have greater interspersed of emergent vegetation and open water compared to undiked sites. Likewise, common gallinules typically breed in permanently flooded deep-water marshes interspersed with open areas (Bannor and Kiviat 2002).

American coot and Forster's tern abundances were greater in undiked compared to diked wetlands. Weller and Fredrickson (1973) suggested American coots pioneer new habitats quickly, whereas common gallinules tended to move into sites several years after reflooding. Given the negative association of American coot with floating vegetation and positive relationship with bulrush cover, vegetation differences between wetland types likely accounted for differing coot abundance. The dynamic nature of plant communities associated with undiked wetlands due to annual, seasonal, and seiche-driven water-level changes may also be better suited to American coot. Differences in Forster's tern abundance were likely influenced by food availability and proximity to nesting sites. Fish are a primary component of Forster's tern diets (McNicholl et al. 2001). Connections to the Great Lakes, shallower water depths, and lesser amounts of aquatic vegetation at undiked wetlands likely increased access to forage fish. Studies of Lake Erie coastal wetlands indicated differences between diked and undiked sites in fish species richness and abundance, age class frequencies, lengths, and body condition for some species (Johnson et al. 1997, Markham et al. 1997). Foraging may have been more difficult for Forster's terns in diked wetlands because of greater coverage of floating vegetation. Forster's terns were observed nesting only in undiked wetlands on mats of dead bulrush and abundance was positively associated with bulrush cover; bulrush was uncommon and sparse in diked wetlands.

MANAGEMENT IMPLICATIONS

Diked coastal wetlands in Michigan are generally managed to increase waterfowl use and provide recreational opportunities to hunters and wildlife watchers. We observed many similarities in the bird communities of diked and undiked wetlands and a small number of species were more abundant in 1 type or another. Given our observation of greater water depths and dominance of cattail and floating vegetation in diked wetlands, we recommend active water-level management to encourage growth of vegetation we found associated with abundance of desired game species (e.g., mallard) and species of conservation concern (e.g., rails, terns), while retaining habitat for bitterns and gallinules. Conducting periodic late-season complete drawdowns coupled with other disturbances (e.g., fire, mowing, disking) could improve habitats for these species by stimulating plant growth and increasing vegetation and structural diversity. Managing diked wetlands for shallower water depths during non-drawdown years could also increase preferred foraging habitat and availability of invertebrate and plant foods for mallards and other marsh birds. However, because drawdowns encourage growth of invasive plant species, we advise experimental dewatering using an adaptive management approach. Concurrent monitoring of bird and vegetation response to water-level manipulations would allow consideration of management risk versus reward, plus provide locally collected data to develop explicit management objectives.

ACKNOWLEDGMENTS

Financial support was provided by the Federal Aid in Restoration Act under Pittman-Robertson project W-147-R, United States Department of Interior, Fish and Wildlife Service via the Upper Mississippi River and Great Lakes Region Joint Venture, Rocky Mountain Goats Foundation, and Michigan State University (MSU) Graduate School. J. Schafer (Michigan Department of Natural Resources [DNR]) helped initiate the project and provided substantial logistical support. Valuable input was provided by T. Burton and K. Millenbah of MSU. Many DNR personnel provided advice, equipment, and logistical support, including B. Avers, D. Avers, M. Donovan, T. Gierman, A. Karr, and D. Luukkonen. We thank the following individuals for conducting field work: J. Bobick, A. Boetcher, K. Borland, J. Gehring, J. List, R. Loiselle, B. Noel, M. Perkins, C. Provence, M. Sanders, E. Ter Haar, and S. Warner.

LITERATURE CITED

- Albert, D. A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. General Technical Report NC-178, U.S., Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA.
- Albert, D. A., and P. W. Brown. 2008. Analysis of vegetation in adjacent diked-undiked coastal wetlands. Michigan Natural Features Inventory Report, 2008-14, Lansing, USA.
- Bannor, B. K., and E. Kiviat. 2002. Common moorhen (*Gallinula chloropus*). Account 685 in A. Poole, and F. Gill, editors. The birds of North America. The Birds of North America, Philadelphia, Pennsylvania, USA.
- Bartlett, M. S. 1947. The use of transformations. *Biometrics* 3:39–52.

- Bogner, H. E., and G. A. Baldassarre. 2002. Home range, movement, and nesting of least bitterns in western New York. *Wilson Bulletin* 114: 297–308.
- Bookhout, T. A., K. E. Bednarik, and R. W. Kroll. 1989. The Great Lakes marshes. Pages 131–156 in L. M. Smith R. L. Pederson, and R. M. Kaminski, editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, USA.
- Brasher, M. G., J. D. Steckel, and R. J. Gates. 2007. Energetic carrying capacity of actively and passively managed wetlands for migrating ducks in Ohio. *Journal of Wildlife Management* 71:2532–2541.
- Brewer, R., G. A. McPeck, and R. J. Adams. 1991. *The atlas of breeding birds of Michigan*. Michigan State University Press, East Lansing, USA.
- Brown, M., and J. J. Dinsmore. 1986. Implications of marsh size and isolation for marsh bird management. *Journal of Wildlife Management* 50:392–397.
- Brown, S. C., and C. R. Smith. 1998. Breeding season bird use of recently restored versus natural wetlands in New York. *Journal of Wildlife Management* 62:1480–1491.
- Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533–2547.
- Conway, C. J. 2005. Standardized North American marsh bird monitoring protocols. U.S. Geological Survey Wildlife Research, Report 2005-04, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, Arizona, USA.
- Crowley, S., C. Welsh, P. Cavanaugh, and C. Griffin. 1996. Weighing—birds: habitat assessment procedures for wetland-dependent birds in New England. University of Massachusetts, Department of, Forestry and Wildlife Management, Amherst, USA.
- Day, R. T., P. A. Keddy, J. McNeill, and T. Carleton. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69:1044–1054.
- Galloway, M., L. Bouvier, S. Meyer, J. Ingram, S. Doka, G. Grabas, K. Holmes, and N. Mandrak. 2006. Evaluation of current wetland dyking effects on coastal wetlands and biota. Pages 187–229 in L. Mortsch J. Ingram A. Hebb, and S. Doka, editors. *Great Lakes coastal wetland communities: vulnerability to climate change and response to adaptation strategies*. Environment Canada and the Department of, Fisheries and Oceans, Toronto, Ontario, Canada.
- Gaudet, C. L., and P. A. Keddy. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* 334:242–243.
- Gaudet, C. L., and P. A. Keddy. 1995. Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology* 76:280–291.
- Gibbs, J. P., S. Melvin, and F. A. Reid. 1992. American bittern (*Botaurus lentiginosus*). Account 18 in A. Poole P. Stettenheim, and F. Gill, editors. *The birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Griffith, R. 1948. Improving waterfowl habitat. *Transactions of the North American Wildlife Conference* 13:609–617.
- Hair, J. F. Jr., R. E. Anderson, and R. L. Tatham. 1987. *Multivariate data analysis*. Second edition. MacMillan Publishing, New York, New York, USA.
- Harris, S. W., and W. H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. *Ecology* 44:331–343.
- Hartman, G. F. 1949. Management of central Wisconsin flowages. *Wisconsin Conservation Bulletin* 14:19–22.
- Herrick, B. M., M. D. Morgan, and A. T. Wolf. 2007. Seed banks in diked and undiked Great Lakes coastal wetlands. *American Midland Naturalist* 158:191–205.
- Herrick, B. M., and A. T. Wolf. 2005. Invasive plant species in diked vs. undiked Great Lakes wetlands. *Journal of Great Lakes Research* 31: 277–287.
- Johnson, D. L., W. E. Lynch, and T. W. Morrison. 1997. Fish communities in a diked Lake Erie wetland and an adjacent undiked area. *Wetlands* 17:43–54.
- Johnson, R. R., and J. J. Dinsmore. 1986. Habitat use by breeding Virginia rails and soras. *Journal of Wildlife Management* 50:387–392.
- Jude, D. J., and J. Pappas. 1992. Fish utilization of Great Lakes coastal wetlands. *Journal of Great Lakes Research* 18:651–672.
- Kadlec, J. A. 1962. Effects of a drawdown on a waterfowl impoundment. *Journal of Wildlife Management* 43:267–281.
- Kaminski, R. M., and H. H. Prince. 1981a. Dabbling duck activity and foraging responses to aquatic macroinvertebrates. *Auk* 98:115–126.
- Kaminski, R. M., and H. H. Prince. 1981b. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. *Journal of Wildlife Management* 45:1–15.
- Keddy, P. A., and A. A. Reznicek. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research* 12:25–36.
- Keough, J. R., T. A. Thompson, G. R. Guntenspergen, and D. A. Wilcox. 1999. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. *Wetlands* 19:821–834.
- Kincaid, C. 2005. Guidelines for selecting the covariance structure in mixed model analysis. Paper 198-30 in *Proceedings of the Thirtieth Annual SAS® Users Group International Conference*. SAS Institute, April 10–13, 2005, Philadelphia, Pennsylvania, USA.
- Krieger, K. A., D. M. Klarer, R. T. Heath, and C. E. Herdendorf. 1992. A call for research on Great Lakes coastal wetlands. *Journal of Great Lakes Research* 18:525–528.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS® system for mixed models. SAS Institute, Cary, North Carolina, USA.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier Publishing, Inc., Amsterdam, The Netherlands.
- MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* 42:1105–1114.
- Markham, C. A., W. E. Lynch, Jr., D. L. Johnson, and R. W. Petering. 1997. Comparison of white crappie populations in diked and undiked Lake Erie wetlands. *Ohio Journal of Science* 97:72–77.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. Springer, New York, New York, USA.
- McLaughlin, D. B., and H. J. Harris. 1990. Aquatic insect emergence in two Great Lakes marshes. *Wetlands Ecology and Management* 1:111–121.
- McNicholl, M. K., P. E. Lowther, and J. A. Hall. 2001. Forster's tern (*Sterna forsteri*). Account 595 in A. Poole, and F. Gill, editors. *The birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
- Mielke, P. W. Jr. 1984. Meteorological applications of permutation techniques based on distance functions. Pages 813–830 in P. R. Krishnaiah, and P. K. Sen, editors. *Handbook of statistics*. Volume 4. Elsevier Science Publishers, Amsterdam, The Netherlands.
- Mitchell, L. R., S. Gabrey, P. P. Marra, and R. M. Erwin. 2006. Impacts of marsh management on coastal-marsh bird habitats. *Studies in Avian Biology* 32:155–175.
- Moore, D. R. J., P. A. Keddy, C. L. Gaudet, and I. C. Wisheu. 1989. Conservation of wetlands: do infertile wetlands deserve a higher priority? *Biological Conservation* 47:203–217.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Series E (Biology)* 3:65–80.
- Murkin, H. R., R. M. Kaminski, and R. D. Titman. 1982. Responses by dabbling ducks and aquatic invertebrates to an experimentally manipulated cattail marsh. *Canadian Journal of Zoology* 60:2324–2332.
- Prince, H. H. 1985. Avian communities in controlled and uncontrolled Great Lakes wetlands. Pages 99–119 in H. H. Prince, and F. M. D'Itri, editors. *Coastal wetlands, Proceedings of the first Great Lakes Coastal Wetlands Colloquium*. Lewis Publishers, Chelsea, Michigan, USA.
- Provence, C. D. 2008. Effects of diking and plant zonation on invertebrate communities of Lake St. Clair coastal marshes. Thesis, Michigan State University, East Lansing, USA.
- Riffell, S. K., B. E. Keas, and T. M. Burton. 2001. Area and habitat relationships of birds in Great Lakes coastal wet meadows. *Wetlands* 21:492–507.

- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295–297.
- Sorensen, T. A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Kongelige Danske Videnskaberne Selskabs Biologiske Skrifter* 5:1–34.
- Steen, D. A., J. P. Gibbs, and S. T. A. Timmermans. 2006. Assessing the sensitivity of wetland bird communities to hydrologic change in the eastern Great Lakes region. *Wetlands* 26:605–611.
- Thiet, R. K. 2002. Diversity comparisons between diked and undiked coastal freshwater marshes on Lake Erie during a high-water year. *Journal of Great Lakes Research* 28:285–298.
- Timmermans, S. T. A., S. S. Badzinski, and J. W. Ingram. 2008. Associations between breeding marsh bird abundances and Great Lakes hydrology. *Journal of Great Lakes Research* 34:351–364.
- Tulbure, M. G., and C. A. Johnston. 2010. Environmental conditions promoting non-native *Phragmites australis* expansion in Great Lakes coastal wetlands. *Wetlands* 30:577–587.
- Tulbure, M. G., C. A. Johnston, and D. L. Auger. 2007. Rapid invasion of a Great Lakes coastal wetland by non-native *Phragmites australis* and *Typha*. *Journal of Great Lakes Research* 33(Special Issue 3):269–279.
- Weller, M. W. 1961. Breeding biology of the least bittern. *Wilson Bulletin* 73:11–35.
- Weller, M. W., and L. H. Fredrickson. 1973. Avian ecology of a managed glacial marsh. *Living Bird* 12:269–291.
- Weller, M. W., and C. S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Department of Zoology and Entomology, Special Report 43, Agricultural and Home Economics Experiment Station, Iowa State University, Ames, USA.
- Whitman, W. R. 1976. Impoundments for waterfowl. Canadian Wildlife Service Occasional Paper, 22, Ottawa, Ontario, Canada.
- Wilcox, D. A. 1993. Effects of water-level regulation on wetlands of the Great Lakes. *Great Lakes Wetlands* 4(1–2):11.
- Wilcox, D. A. 1995. The role of wetlands as nearshore habitat in Lake Huron. Pages 223–245 in M. Munawar T. Edsall, and J. Leach, editors. *The Lake Huron ecosystem: ecology, fisheries, and management*. SPB Academic Publishing, Amsterdam, The Netherlands.
- Wilcox, D. A., J. A. Meeker, and J. Elias. 1993. Impacts of water-level regulation on the wetlands of the Great Lakes. Phase 2 Report to Working Committee 2, International Joint Committee Water-levels Reference Study, Ottawa, Ontario, Canada, and Washington, D.C., USA.
- Wilcox, D. A., and T. H. Whillans. 1999. Techniques for restoration of disturbed coastal wetlands of the Great Lakes. *Wetlands* 19:835–857.
- Wilson, S. D., and P. A. Keddy. 1986. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology* 67:1236–1242.
- Wisheu, I. C., and P. A. Keddy. 1992. Competition and centrifugal organization of plant communities: theory and tests. *Journal of Vegetation Science* 3:147–156.

Associate Editor: David King.