Migrating ducks and submersed aquatic vegetation respond positively after invasive common carp (*Cyprinus carpio*) exclusion from a freshwater coastal marsh

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Abstract

Invasive carp can negatively affect waterbirds through habitat degradation, including removal of submersed aquatic vegetation (SAV). At a freshwater coastal marsh of great ecological and cultural significance, we excluded invasive common carp (*Cyprinus carpio*) with the goal of restoring the marsh to historical conditions to support fall-migrating waterfowl. We used a multi-pronged approach to assess the response of ducks and SAV to carp exclusion by leveraging historical duck and SAV surveys and collecting new data for six years post-exclusion on density and distribution of ducks within the marsh, SAV response, and refueling performance (as indexed by plasma-lipid metabolites) by two species of diving ducks. We found that fall-migrating duck numbers and total SAV extent rebounded to historical levels (1970s). There was a 339% increase in diving duck density and a nearly 400% increase in dabbling duck density between the pre- (i.e., 2000s) and post-exclusion periods. Diving ducks were more likely to be observed associated with SAV within the marsh, whereas dabbling ducks responded to emergent vegetation extent and water levels. Refueling performance was stable post-exclusion, despite increased numbers of ducks using the marsh, indicating that marsh habitat quality was sufficient. Some aspects of the marsh recovery remain in question, including possible shifts in SAV community composition. Overall, the carp exclusion has successfully improved the quality of habitat for migrating ducks.

Keywords: coastal wetland; *Cyprinus carpio*; invasive species; plasma lipid metabolites; submersed aquatic vegetation; waterfowl

Introduction

Invasive species affect native organisms through a variety of mechanisms resulting in significant alterations to the structure and functioning of food webs and ecosystems and biodiversity loss. These mechanisms include habitat alteration (including structure and biochemical composition), competition, hybridization, and consumption (Ricciardi and MacIsaac 2011; Emery-Butcher et al. 2020). The direct effects of aquatic invasive species, such as mussels and certain fish species, are well documented (MacIsaac et al. 2011). Cascading effects of aquatic invasions on terrestrial vertebrates that depend on aquatic systems are less well studied, but the presence of invasive fish has been observed to have negative effects on herbivorous and invertivorous waterbirds, typically reducing the number of birds using affected habitat (Ivey et al. 1998; Bajer et al. 2009; Laguna et al. 2016; Maceda-Veiga et al. 2017).

Common carp (*Cyprinus carpio*; hereafter, carp) act as invasive ecosystem engineers, with cascading effects that can result in shifts between stable states (Emery-Butcher et al. 2020). High carp biomass negatively impacts water clarity and submersed aquatic vegetation (SAV) communities indirectly by increasing suspended solids and turbidity and lowering light penetration (Parkos et al. 2003; Badiou and Goldsborough 2010), and directly through uprooting and stem breakage of SAV during carp feeding and spawning activities (Tryon 1954; Crivelli 1983). Healthy SAV assemblages are desirable as they serve as spawning, refuge, and feeding habitat for many species of fish (Randall et al. 1995; Weaver et al. 1997). SAV also supports great densities of aquatic macroinvertebrates, which are food sources for both fish and ducks (Bartonek and Hickey 1969; Keast 1984; Anteau and Afton 2008a), and the vegetative parts are consumed by some duck species (Anderson and Low 1976; DuBowy 1985). A number of studies have demonstrated that carp have detrimental effects on duck forage in marshes (e.g., Batzer et al. 2000; Anteau et al. 2011). However, reducing carp numbers can restore lost ecosystem functions to varying degrees, depending on the local conditions and control measures used (e.g., Ivey et al. 1998; Schrage and Downing 2004; Bonneau and Scarnecchia 2014, 2015).

Carp-degraded habitats may not provide sufficient food for migrating waterbirds, which need to acquire nutrient and fat reserves to help fuel migration (Hanson et al. 1990). Triglyceride and β-hydroxybuterate are plasma-lipid metabolites which can be used to estimate real-time energy income or catabolism rates in birds (Williams et al. 1999; Smith et al. 2021), and have been used to assess refueling rates of individual birds (Guglielmo et al. 2005), monitor refueling performance at stopover sites (Schaub and Jenni 2001), and assess habitat condition (e.g., Guglielmo et al. 2002; Seaman et al. 2006; Lyons et al. 2008; Anteau and Afton 2011; Janke et al. 2019). Presumably, birds in a healthy environment with abundant food will be accumulating fat while birds at sites with limited food resources will be catabolizing fat, with those differences reflected in plasma-metabolite concentrations.

Delta Marsh, Manitoba, Canada is a large freshwater coastal wetland on the south end of Lake Manitoba. It has local, regional, and international importance (Batt 2000), with sections protected under provincial designations (Wildlife Management Area, Game Bird Refuge), and international recognition as a Ramsar site (1982) and Important Bird and Biodiversity Area (1999). In addition to its ecological importance, Delta Marsh has great cultural significance —

first, to the Indigenous Peoples of the area and later as a famed waterfowl hunting destination (Suggett et al. 2015). However, the presence of carp, as well as hybrid cattail (*Typha* x *glauca*), nutrient loading from the surrounding agricultural land, and the stabilization of water levels in Lake Manitoba have led to the degradation of the marsh (Batt 2000). Most fish, including carp, overwinter in Lake Manitoba and migrate into the marsh each spring (Lapointe 1986). An earlier attempt at carp exclusion in the 1960s and 1970s, as well as recent experimental pond manipulations (Hnatiuk 2006; Hertam 2010), showed that reducing carp numbers at Delta Marsh resulted in improved habitat conditions (i.e., increased water clarity and SAV). Because of its relatively large size and connectivity, carp control options are limited — the only approach deemed viable was the installation of exclusion screens on channels connecting the marsh to the lake. In 2013, we initiated carp exclusion and an associated research and monitoring program.

In this study, we used a multi-pronged approach to assess the response of diving and dabbling ducks and their habitat to carp exclusion at Delta Marsh. The primary objective of carp exclusion was to restore capacity of the marsh to sustain historic levels of migrating ducks. We evaluated the success of the restoration by three metrics: a return to historical (1970s) levels of 1) the number of ducks using the marsh during fall migration and 2) extent of SAV; and, 3) marsh habitat of sufficiently high quality to meet energetic needs of those migrating birds. We leveraged historical duck and SAV surveys and collected new data on duck density and distribution within the marsh, SAV response, and nutrient acquisition by two species of diving ducks. Because diving ducks are wetland-obligate foragers (i.e., not feeding on waste grains in nearby fields as some dabbling ducks might), our expectation was that diving ducks would have a more pronounced response to marsh degradation by carp and any improvement in marsh conditions post-exclusion. We predicted that the exclusion of large carp from Delta Marsh would promote the return of a robust SAV community. In turn, we predicted that diving duck density would increase and that they would be observed associated with areas of the marsh with greater SAV. We expected that diving duck condition, as indexed by plasma-lipid metabolites, would improve through time as conditions in the marsh improved. In contrast, we anticipated that dabbling duck density and spatial patterns within the marsh would be influenced by habitat characteristics, such as emergent vegetation extent (e.g., Webb et al. 2010), that are independent of carp abundance and the restoration.

Methods

Study area

Delta Marsh stretches approximately 32 km along the south end of Lake Manitoba, occupying ~ 18,500 ha (Fig. 1). There is a forested beach ridge between the lake and the marsh, with four channels connecting the marsh to the lake. The marsh consists of a series of large and small open bays, isolated ponds, former river channels, flooded emergent vegetation, wet meadows, and low prairie, and is divided into three units (west, center and east) by anthropogenic structures (Fig.1). Water levels of the marsh track those of Lake Manitoba, with an average water depth in the open-water areas of approximately 1.0–1.3 m. Dominant emergent vegetation consists of *Phragmites australis* (common reed), *Typha* x *glauca*, *Scolochloa festucacea* (common rivergrass), and *Schoenoplectus acutus* var. *acutus* (hardstem bulrush). Dominant submersed aquatic vegetation includes *Myriophyllum sibiricum* (northern water milfoil), *Stuckenia pectinata* (sago pondweed), and *Ceratophyllum demersum* (hornwort/coontail). Carp are believed to have first entered Lake Manitoba and Delta Marsh around 1947 (Atton 1959). Between 1964 and 1982 there were various efforts to exclude carp from the marsh (e.g., dams and chain-link fence across marsh-lake channels, screened culverts). However, the infrastructure sometimes fell into disrepair and there were often challenges managing vegetation build-up on structures, and these efforts provided only partial exclusion of carp from the marsh, so the infrastructure was removed in 1982.

The construction or retrofitting of new carp exclusion structures, together with associated dykes, was done in the winter of 2012–2013. Based on fish migration monitoring during 2009–2012, recommendations were made that carp exclusion screens be positioned seasonally each spring. Delayed positioning of the screens maintains unimpeded access into the marsh for large native fish for as long as possible prior to the peak of carp migration. A screen opening size of 70 mm between vertical steel bars was selected to allow access to the marsh by most native fish while excluding the majority of large carp (> 70 mm maximum body width anterior to the pectoral fin, ~470 mm fork length). Large carp are broad and deep-bodied, with somewhat laterally compressible bodies (e.g., French et al 1999; Hillyard et al. 2010). Carp exclusion occurred for the west and center units of the marsh, and for most areas (~93% of the total area of the main water bodies) of the east marsh (hereafter, east marsh or east unit). The screens are lifted each year in mid- to late-July.

Duck density

We used historical aerial survey data to characterize duck density during fall migration at Delta Marsh pre-carp exclusion, with surveys conducted in 26 years between 1965 and 2012 (Table A1). In the post-exclusion period (2013–2018), we conducted 2–5 aerial surveys annually (Table A1). In all years except 2018, surveys were conducted from a fixed-wing aircraft. In 2018, we were unable to access a suitable fixed-wing aircraft and conducted surveys from a rotary-wing aircraft. Aircraft speed during surveys was 130–150 km hr^{-1} at 30–65 m above ground level (AGL) for fixed-wing surveys and 90–110 km hr^{-1} at 50–60 m AGL for rotary-wing surveys. Flights were not initiated under inclement weather conditions including fog, precipitation, or when wind gusts exceeded 40 km h^{-1}. Surveys were flown between 800 and 1400 hours, though were generally started later (after 1000 hours) in the post-exclusion period to minimize overlap with duck hunting activity on the marsh. Between 1965 and 2012, surveys were flown along seven strip transects running east-west (Fig. 1, top panel). From 2013 onward, to reduce observer fatigue, we flew surveys along 17 strip transects, spaced 1.61 km apart and oriented north-south (Fig. 1, bottom panel). North-south transects were divided into two or three segments to capture changes in habitat (large bays, small bays, and isolated ponds).

Voice recorders were used to record duck species and counts. All scaup (lesser [*Aythya affinis*] and greater [*Aythya marila*], hereafter, scaup) were classified together as the species are difficult to distinguish on aerial surveys. Otherwise, if species could not be identified, foraging guild (diving or dabbling duck) was recorded. One or two observers counted all ducks within a 200 m strip on one (one observer) or both (two observers) sides of the aircraft. The portion of birds observed in flocks which extended past the strip transect were not counted. In 2013 and 2014, a dependent double-observer method (Nichols et al. 2000) was used to estimate detection probability. During these years, on approximately every other transect, two observers recorded ducks on the same side of the aircraft. For data analysis, duck counts were normalized to account for different total area surveyed (based on number of transects and observers) and different sampling effort across years and decades.

Marsh characterization

SAV beds at Delta Marsh were mapped in the summers of 1974, 1997, 2009, 2010, 2014, and 2016–2018. Mapped areas and techniques varied each year depending on project objectives, available resources, and mapping technology. SAV was surveyed by boat and, in earlier years, was combined with aerial photo interpretation. Until 2014, vegetation beds were drawn on maps and later digitized. SAV species was recorded. Only in 2017 and 2018 was percent cover of each SAV species within vegetation beds estimated. Detailed methods can be found in the Supplementary Information. To facilitate comparison of SAV among years, we only included areas of the marsh that were mapped both pre- and post-exclusion and that intersect contemporary duck survey transects in the west and east marsh units.

We calculated multiple transect segment- or marsh-scale variables that might influence duck distribution within the marsh. To characterize inter-annual fluctuations in the extent of duck habitat, we developed a Landsat-based landcover classification that allowed us to separate upland, emergent vegetation, and open-water areas (detailed methods in the Supplementary Information). Combined with the mapped SAV, we calculated annual, transect segment-specific estimates of percent cover for emergent vegetation, open water, SAV, and sago pondweed. We estimated the percent cover of sago pondweed because it is an important food item for canvasback (*Aythya valisineria*; e.g., Bartonek and Hickey 1969). Percent cover was based on total duck habitat within a segment, rather than total segment area, with guild-specific definitions of duck habitat. For diving ducks, we considered available duck habitat to include open water and SAV, whereas dabbling ducks included those habitats plus emergent (deep marsh) vegetation. We used on-site windspeed to calculate 18-hour lagged windspeed as previous analysis showed it was influential on turbidity in the marsh (see Supplementary Information). We calculated average weighted fetch distance (Rohweder et al. 2012; using ArcGIS 10.7 [ESRI Inc., Redlands, CA]) of each segment based on wind direction(s) in the hour preceding surveys as a proxy for the relative exposure of different segments that might influence duck settling patterns (i.e., sheltered segments had shorter fetch distance). As an additional measure of possible dabbling duck habitat, we calculated annual estimates of the percent shallowly flooded area (< 41 cm deep; Pöysä 1983) within a segment based on marsh bathymetric data (Geard 2015), bare earth LiDAR data (from the Manitoba Land Initiative), and average daily water levels as measured by the Water Survey of Canada Westbourne gauge on Lake Manitoba (~13 km west of Delta Marsh). Water levels in Delta Marsh generally track the water levels measured at that gauge on Lake Manitoba (Ducks Unlimited Canada, unpublished data). We used distance between a segment centroid and the nearest hunting access point as a proxy for level of duck hunting disturbance (hereafter, hunting disturbance).

Between 2013 and 2018, to assess the effectiveness of the carp exclusion measures, we quantified the abundance of large carp present in Delta Marsh. We used a standard gang gillnet and a separate 241 mm gillnet set throughout the east marsh in June. See the Supplementary Information for detailed methods.

Plasma and ingesta sample collection and analysis

We selected two diving duck species (canvasback and lesser scaup) for measurement of plasma-lipid metabolites. The marsh has historically been an important stopover site for both species during fall migration, and those species feed on the SAV, or the associated invertebrate community, that the carp exclusion effort targeted. We collected male canvasbacks and lesser scaup in 2013–2014 and 2016–2018 in the center and east units of the marsh by shooting them over decoys, although we pass shot some birds if the opportunity presented itself. To minimize the body condition bias associated with collecting birds over decoys (Bain 1980; Pace and Afton 1999), we only collected birds from flocks of two or more birds. We also spread collections out within each flock and across the marsh by collecting no more than two birds per flock and limiting collections to a maximum of four birds of each species per day from a given location. Furthermore, any bias should be consistent through time and thus should not affect conclusions. We started collections half an hour before sunrise (i.e., legal shooting light) and, when possible, we collected birds through the diving duck fall migration period — typically, mid-September to freeze-up (early November).

Immediately after shooting (postmortem), we collected ~ 1 ml of blood via cardiac puncture using a 20-gauge needle, transferred the blood to a 1.5 ml heparinized vial, and gently mixed the sample to prevent clotting. Blood was stored in a cool environment and centrifuged within six hours (10 minutes at 6000 rpm, to separate blood plasma from the whole blood). Blood plasma was then transferred into a non-heparinized vial and stored in a cooler until being transferred to a -45°C chest freezer (within two hours of centrifuging). Birds were weighed using a 2500 g Pesola scale (to the nearest 10 g) and we recorded their age (either hatch year [HY; young-of-the-year] or after hatch year [AHY; adult]). We removed the ingesta from the esophagus-proventriculus for diet analyses, preserving the samples in 99% isopropyl alcohol. In the laboratory, we sorted food items into groups (e.g., amphipods, chironomid larvae, sago pondweed tubers). For each group, we measured food volumes by water displacement to the nearest 0.1 ml.

Plasma samples were analyzed for concentrations of the plasma-lipid metabolites triglyceride (TRIG) and β-hydroxybutyrate (BOHB) at the Northern Prairie Wildlife Research Center, Jamestown, ND (2013 and 2014) and at the Advanced Facility for Avian Research, University of Western Ontario (2016 to 2018). We measured hemoglobin concentration in 2016–2018 to determine whether hemolysis in samples was enough to affect metabolite concentration estimates (Janke 2016). We did not find extensive hemolysis (i.e., hemoglobin concentrations >

1 g/dL) and, therefore, did not exclude any samples from analysis for this reason. We calculated a Refueling Index (RFI; Anteau and Afton 2008b; Janke et al. 2019) which composites TRIG and BOHB to provide a relative account of lipid accumulation or catabolism. Higher RFI scores indicate better refueling performance.

Statistical analysis

For all analyses, we used a modelling approach wherein we ran sets of models driven by *a priori* hypotheses, then ranked the models using Akaike Information Criterion (AIC) or Akaike Information Criterion corrected for small sample size (AIC_c), as appropriate. We followed criteria outlined in Burnham and Anderson (2002), wherein the model with the lowest AIC is deemed best-approximating, and models with ΔAIC values ≤ 2 and < 4 (ΔAIC being the difference between the best-approximating and lower ranked models) are considered well-supported and plausible, respectively. We interpreted covariate effects from the best-approximating model. Often, the best-approximating model contained imprecisely estimated covariate effects (i.e., the ratio of the estimated effect to standard error was < ~2 or, in additive models, smooth terms that were not statistically significant [$p > 0.05$]). We did not simplify these models; instead, we only plot and interpret meaningful effects.

Analyses of duck density: Long-term trends

We used negative binomial generalized linear models (SAS PROC GENMOD; SAS Institute, Inc., Cary, NC) to estimate densities of diving and dabbling ducks and canvasback and scaup recorded during Delta Marsh duck surveys. Models included effects of year or decadal grouping (1960s through 1990s, 2000–2012 [hereafter, 2000s], and 2013–2017), survey timing (with "mid"-season surveys between September 16 and October 15 and "late"-season after October 15), and their interaction. We used Tukey-Kramer adjusted pairwise comparisons to compare duck densities among decadal groupings. Early surveys (i.e., those before September 16) were excluded from analyses as they were not conducted consistently through all years. We did not use counts from 2018 to estimate long-term trends in duck density due to the different aircraft type used that year. To calculate detection probability, models were fit as dependent double-observer data using the multinomPois function in the R package 'unmarked' (Fiske and Chandler 2011). We considered survey number and foraging guild as predictors of waterfowl abundance and direction of aircraft travel and foraging guild as predictors of detection probability. See Supplementary Information for a detailed description of the analysis of detection probability.

Analyses of duck density: Spatial patterns

We used generalized additive mixed models (gamm in the mgcv package in R; Wood 2011) for modeling spatial patterns of duck density within the marsh during fall migration 2014 and 2016–2018. The total number of diving or dabbling ducks per segment and survey occasion was modeled using a negative binomial distribution (log-link function) and scaled for habitat availability by including the natural log of guild-specific available habitat area (km^2) as an offset variable. Each model included an effect of year to account for fluctuation in yearly populations and smoothed random effects of segment and survey occasion to account for repeated surveying of the fixed transects. Segments varied in their accessibility by boat and 100 out of 180 segment-years (i.e., segment access varied by year) were not surveyed in their entirety during SAV surveys. Exploratory modelling revealed that results were robust when segments with less than 50% survey coverage were excluded (resulting in n = 124 segment-years for analysis). For the analysis of diving ducks, we excluded segment-survey data with no SAV observed (percent SAV = 0) or dominant SAV species = *Potamogeton pusillus* (n = 2), resulting in n = 109 segment-years for analysis. For models of diving ducks, we had four variables of primary interest including percent SAV and dominant SAV species, open water, and sago pondweed. We also considered five covariates that might influence diving duck distribution or modify the effects of primary interest including: day of the year, time of day, mean fetch distance, and proxies for turbidity and hunting disturbance. For models of dabbling ducks, the variables of primary interest were percent emergent vegetation, shallowly flooded area, and SAV. We also considered the effects of time of day, fetch distance, water level, and a proxy for hunting disturbance. Several sets of candidate models were run (Tables A5, A6), each characterized by one or two primary effects of interest. To allow exploration of nonlinear effects of covariates, each quantitative covariate was fit as a smoothed function, allowing a basis dimension up to k = 5 and interactions were specified using tensor products. A maximum likelihood method was used to allow for comparison of fit among models differing in their fixed effects. Stability of selected smoothing parameters was assessed by examining changes in the effective degrees of freedom with increasing basis dimension (up to k = 20). For each candidate model, we also considered alternative simplified models, including: (i) smooth effects of quantitative covariates but excluding interactions; (ii) linear effects of covariates but excluding interactions; and (iii) primary variable linear effects only. For the analysis of diving ducks, we also re-fit the top models with primary effects of open water, sago pondweed, and open water + sago pondweed on the SAV subset (n = 109 segment-years) in order to contrast AIC values across all models considered. We modelled detection estimates for this analysis of spatial patterns of duck density differently than for the analysis of long-term trends in duck density, using only 2014 data and considering different predictors of abundance and detection probability. We held the abundance process fixed and included effects of the amount of duck habitat available, foraging guild, and percent SAV within a transect segment. Detection process covariates included: foraging guild, direction of aircraft travel, percent SAV, and an interaction between foraging guild and direction. See Supplementary Information for more details of the analysis.

Other analyses

Based on normally distributed and homoscedastic model residuals, we used a general linear model (in the R programming environment; R Core Team 2019) to examine the influence of year, sampling date (day of the year), sampling time (hours after sunrise), species, age, body mass, ingesta (present or absent), and sampler (blood drawer) on RFI. RFI was standardized within species before analysis.

To interpret findings relative to patterns in carp exclusion, we estimated large carp presence in the marsh. We first used the R package 'omnr.gillnet' (Walker et al. 2013) to estimate relative selectivity coefficients by 20 mm fork length classes (e.g., 70 = 61 to 80 mm) for carp caught in the standard gang gillnet. We then calculated catch per unit effort (CPUE; the number of carp > 70 mm maximum body width caught per net set [standard gang gillnet plus 241 mm gillnet]) using GLMMs (SAS PROC GLIMMIX; using a log link function and negative binomial distribution).

Results

Duck density: Long-term trends

Detection probabilities in 2013 and 2014 were high and consistent between years, ranging from 0.94 to 0.98 (SE = 0.001–0.008) for diving ducks and 0.88 to 0.91 (SE = 0.003–0.012) for dabbling ducks (Table A3). Because detection was high, and to maximize comparability of recent surveys to historical data, we did not adjust duck counts for detection. In the best-approximating model of diving duck abundance, only the effect of decadal grouping was well estimated. Statistical contrasts revealed the highest diving duck densities in the 1960s–1980s and 2013–2017, with the lowest densities in the 2000s (Fig. 2). There was a 339% increase in diving duck density between the 2000s and the post-exclusion period. Scaling duck densities to a marsh area of 170 km^2, total daily diving duck abundance at Delta Marsh was at its lowest in the 2000s (1,836 ± 238 SE) but rebounded to 8,058 ± 1,751 after carp exclusion. For dabbling ducks, the best-approximating model included well-estimated effects of decadal grouping, survey timing, and their interaction. Mid-season, dabbling duck densities were highest in the 1960s–1970s and 1990s, and lowest in the 2000s (Fig. 2). The highest late-season dabbling duck densities occurred in the 1960s–1980s and 2013–2017, and the lowest in the 1990s–2000s. Late-season dabbling duck densities increased nearly 400% between the 2000s and the post-exclusion period. Total daily dabbling duck abundance post-exclusion was 12,070 ± 2,720 (mid-season) and 10,999 ± 2,482 (late-season) compared with 6,766 ± 918 and 2,210 ± 306 (mid- and late-season, respectively) in the 2000s. For canvasback, the best-approximating model had well-estimated effects of decadal grouping and survey timing. Statistical contrasts revealed the lowest canvasback densities in the 1990s–2000s (Fig. 3), with a > 1000% increase in canvasback densities between the 2000s and post-exclusion period. Total daily canvasback abundance at Delta Marsh ranged from 204 ± 34 in the 2000s to 3,315 ± 1,003 post-exclusion. Decadal grouping and survey timing were well estimated in the best-approximating model of scaup abundance, with the lowest scaup densities occurring in the 2000s (Fig. 3) and a ~ 250% increase in scaup density between the 2000s and post-exclusion period. Total daily scaup abundance at Delta Marsh was 1,088 ± 221 in the 2000s and 3,876 ± 1,258 in the post-exclusion period. Within the post-exclusion period, there was no consistent increase in the number of diving ducks observed at the marsh in the fall, but duck densities were relatively low in 2014 (Table 1).

Duck density: Spatial patterns

Detection probability varied with the direction of aircraft travel, foraging guild, and percent SAV cover within a segment (Table A4). Averaging over the effect of direction of travel, detection probability of diving ducks increased with percent SAV, ranging from 0.87 (SE = 0.017) to 0.94 (SE = 0.009) as SAV increased from 0 to 20% (the 90th percentile of SAV range). Dabbling duck detection also increased with percent SAV, but from 0.90 (SE = 0.010) to 0.94 (SE = 0.007) as SAV increased from 0 to 10% (the 90th percentile of SAV range for that guild).

The best-approximating model of spatial patterns of diving duck density included well-estimated effects of percent SAV, dominant SAV species, and distance to the nearest hunting access point (Table 2). Most segments had relatively low percent SAV (mean = 23%, SD = 0.27 and range = 0–100%; Table A7). Diving ducks were positively associated with SAV cover and were found in greater numbers on segments farther from hunting access points (Fig. 4). Density of diving ducks was intermediate on segments where the dominant SAV species was sago pondweed (estimated marginal mean [emmean] = 295.9, 95% confidence limits [CLs] = 210.6, 415.7) or northern water milfoil-dominated segments (emmean = 415.7, 95% CLs = 210.6, 820.6). Densities were lowest on segments dominated by hornwort (emmean = 141.2, 95% CLs = 78.3, 252.1). Although the effect of mean fetch distance was not well estimated in the best-approximating model, it was well estimated in well-supported and plausible models (Table 2). Diving ducks were more abundant on segments with lower fetch distance (i.e., more sheltered segments). Consistent with the direction of the effect of SAV on density, diving duck density was lower with increasing percent of open water within a segment. From the best-approximating model, our estimated effect of percent SAV on diving duck abundance was $\beta = 2.323$. If percent SAV increases from 0 to 20%, then we estimate a 59% increase in diving ducks (i.e., $\exp(0.20*2.323) - 1$). From our detection probability analyses, we estimated that we were detecting 87% of diving ducks when percent SAV = 0 and 94% of diving ducks when percent SAV = 20. Adjusting for differences in detection probability, we estimate that the increase in diving ducks may have been more modest, with a 46% increase (i.e., $\exp(0.20*2.323)*(0.87/0.94)) - 1$) in density over the 0–20% SAV range.

The best-approximating model of dabbling duck use of the marsh included a well-estimated interaction between emergent vegetation extent and water level (Table 3, Fig. 5). Dabbling duck abundance increased with emergent vegetation cover. However, this effect levelled off around 60% cover, and was more pronounced when water levels were low. Other covariates in the best-approximating model were not statistically significant.

SAV

Total SAV extent rebounded to historical levels post-exclusion. Within the east marsh, total SAV extent declined from 1974 through to a low in 2009, then increased following carp exclusion in 2013 (Fig. 6). In the west marsh, the change in SAV was more complicated — SAV extent increased after 2013 but with a decline in 2018 (Fig. 6). In late July and early August 2018, extensive beds of sago pondweed were observed in the west marsh. However, many of these beds had disappeared by the time SAV was surveyed 15–17 August of that year. We speculate that SAV decreased due to early senescence caused by low water levels and grazing by ducks. The area of sago pondweed increased post-exclusion, with substantial inter-annual variation, but did not rebound to historical levels.

Plasma-lipid metabolites and ingesta

We collected 272 blood samples at Delta Marsh; 261 had complete data suitable for inclusion in statistical models. Birds collected included 148 canvasback (94 HY, 54 AHY) and 124 lesser scaup (19 HY, 105 AHY). Thirty-two collected canvasbacks had food in their esophagus-proventriculus compared to nine lesser scaup. Of the canvasbacks, five crops contained only sago pondweed (primarily tubers), four contained a mix of plant and animal material, and the remainder (n = 23) contained chironomid larvae. By volume, chironomid larvae were the most abundant food item, followed by sago pondweed, with negligible contributions from other animal and plant food items (Fig. 7). Only animal material was found in the crops of scaup, consisting of mostly amphipods, but also some snails and chironomid larvae.

TRIG concentrations (mmol L^{-1}) ranged from 0.336 to 5.789 and BOHB (mmol L^{-1}) from 0.0480 to 3.078. The best-approximating model of RFI included well-estimated effects of year, sampling date and time, mass, as well as age, species, and their interaction. Effects of the presence/absence of ingesta and sampler were not well estimated. RFI increased seasonally ($\beta = 0.014 \pm 0.0060$, $P = 0.017$) and throughout the morning ($\beta = 0.10 \pm 0.044$, $P = 0.020$). The age-species interaction indicated an age effect in canvasback (HY emmean = -0.034, 95% CL = -0.34, -0.27; AHY emmean = -0.69, 95% CL = -1.14, -0.24) but not in lesser scaup (HY emmean = 0.44, 95% CL = -0.16, 1.03; AHY emmean = 0.33, 95% CL = -0.045, 0.71). Although there was no discernable improvement in RFI through years, there was some detectable inter-annual variation with species (especially canvasback) showing poorer refueling performance in 2014 and peak RFI coinciding with peak duck densities (Table 1).

Discussion

Overall, the exclusion of common carp from Delta Marsh was successful with respect to the response of both ducks and SAV. Although our hypotheses were not always supported, we observed a remarkable rebounding of duck numbers and total SAV area to historical levels (1970s). Diving ducks were more likely to be observed associated with SAV within Delta Marsh, whereas dabbling ducks responded to other habitat characteristics. Refueling performance did not increase throughout the post-exclusion period, but stable RFI, despite increased duck use of the marsh, indicates that Delta Marsh is providing adequate quality habitat for migrating diving ducks.

Duck response to carp exclusion

After carp exclusion, fall-migrating duck density reached levels comparable to historical abundance. Although modifications to the survey design following carp exclusion may have influenced duck numbers (i.e., increased observed ducks), we are confident that they cannot explain the magnitude of the increase in duck density. For example, our results show an almost 350% increase in diving duck abundance between the 2000s and the period after carp exclusion began, whereas changes related to methodology were relatively small (addition of detection probability adjustment would change diving duck densities by ~ 5%). Furthermore, although duck density at Delta Marsh might be influenced by factors outside the marsh, the magnitude and timing of changes in duck density observed does not reflect, for example, continental population trends (Figs. A2, A3). Instead, we suggest that diving duck numbers at Delta Marsh have been driven by habitat conditions, noting that low diving duck densities in the 1990s and 2000s occurred after earlier carp exclusion measures ceased in 1982 (duck surveys in the 1980s period precede this management change). Our findings are consistent with observed increases in diving ducks after complete fish-removal in a gravel pit lake (Phillips 1992) and a shallow prairie lake (Hanson and Butler 1994). Finally, our analysis of spatial patterns of diving duck density supports this interpretation of a habitat-driven response — within the marsh, diving ducks were found in higher densities in areas with more SAV.

Like diving ducks, use of Delta Marsh by fall-migrating dabbling ducks tended to be lower in the 1990s and 2000s, although the decadal patterns differed by survey period (i.e., middle or late) and did not fully match the patterns in carp exclusion. Although dabbling ducks may be less influenced by SAV abundance than diving ducks, and thus less affected by carp use of the marsh, carp affect more than just SAV. For example, carp can depress abundance of food items that may influence marsh habitat quality for dabbling ducks (e.g., benthic invertebrates; Zambrano et al. 2001; Bonneau and Scarnecchia 2014, 2015). We suggest that although dabbling ducks responded positively to carp exclusion, their numbers were also influenced by marsh water levels and corresponding changes in the extent of emergent vegetation and suitable foraging habitat. Consistent with this interpretation, and the literature demonstrating the importance of hemi-marsh conditions for dabbling ducks in the non-breeding period (e.g., Webb et al. 2010; Stafford et al. 2007; Osborn et al. 2017), our analysis revealed that dabbling ducks were found at higher densities in areas with greater emergent vegetation cover, up to ~ 60% cover. However, this effect was water level dependent — it is unclear whether this pattern reflects accessibility of food items or whether it could be driven by greater visibility of ducks (i.e., more ducks visible outside the emergent vegetation when water levels are low). The shallowly flooded area variable was meant to test the food accessibility hypothesis more directly. However, maximum shallowly flooded areas occurred in 2014, with these flooded areas extending into upland areas with dense vegetation that may not have been attractive to dabbling ducks. Although the discontinuance of planting lure crops (to keep waterfowl off unharvested agricultural fields) in the area (Table A1) could have contributed to the decline of at least some species of dabbling ducks in the 1990s and 2000s, it cannot explain the subsequent increase in abundance in the post-exclusion period nor low abundance in the 1980s.

Rapid recovery of multiple communities post-carp exclusion

Numerous marsh characteristics showed rapid recovery after the installation of carp exclusion structures, with changes evident in the first open-water season post-exclusion. Although not all carp were prevented from accessing the marsh, post-exclusion carp CPUE was less than half of pre-exclusion levels (Table A2) and negative effects of carp on vegetation and waterfowl may only occur at high carp density (Bajer et al. 2009). Other studies of carp eradication or exclusion efforts have documented rapid (< 1 year) response of macrophytes (Schrage and Downing 2004; Laguna et al. 2016) and aquatic macroinvertebrates (Schrage and Downing 2004; Bonneau and Scarnecchia 2015). The speed of recovery at Delta Marsh may have been further augmented by unusual conditions during the two years pre-restoration — in 2011, there was a major flood resulting in unusually low numbers of large carp using the marsh in 2012. Ducks appeared to be readily able to perceive and respond to either habitat changes or reduced number of large carp (Weier and Starr 1950; Ivey et al. 1998), thereby facilitating a rapid multi-trophic-level recovery.

Although total SAV area rebounded, sago pondweed area remained below historical levels (Fig. 6). From 2009 onward, there were fewer pure sago pondweed beds in the east marsh but more mixed-species beds (Fig. A1), which may affect the attractiveness of the beds for foraging. Hansel-Welch et al. (2003) observed that SAV community composition changed through time after fish removal from a shallow lake; it is possible that five years of post-exclusion monitoring was not long enough to observe full sago pondweed reestablishment. However, other carp-removal studies have observed a rapid rebounding of SAV, including sago pondweed (Schrage and Downing 2004; Laguna et al. 2016). Alternatively, abiotic conditions in the marsh may no longer be as suitable for sago pondweed. Anderson (1978) previously identified that water depth and wave action affect the distribution of sago pondweed in Delta Marsh. Over time, islands and shorelines have eroded at Delta Marsh, thereby increasing wind and wave exposure. Furthermore, sago pondweed thrives in more brackish conditions than northern water milfoil and hornwort (Stewart and Kantrud 1972), but specific conductance in Lake Manitoba and the marsh has declined through time (Lake Manitoba/Lake St. Martin Regulation Review Committee 2013). With the return of high numbers of migrating ducks, duck herbivory could also be restricting sago pondweed reestablishment (Anderson and Low 1976; Van Onsem and Triest 2018).

Within the post-exclusion period, canvasback and scaup numbers fluctuated little, although 2014 stood out as having lower abundance of both species (Table 1). Low duck counts were not associated with greater carp CPUE (i.e., more large carp present in the marsh), although low carp numbers in 2014 may be misleading as a severe storm damaged exclusion screens and breached dykes in early July (i.e., after gillnet sampling was completed). Alternatively, 2014 also stood out with respect to high water levels — although diving ducks are often associated with deeper water (e.g., Austin et al. 2017), they may avoid foraging in water that is too deep (Anderson and Low 1976; Carbone and Houston 1994) and foraging efficiency declines with increasing depth (e.g., Lovvorn 1994; Lovvorn and Gillingham 1996). Notably, patterns in duck density at Delta Marsh tracked patterns in RFI, with high duck counts in years with higher RFI. Migrating ducks may be able to detect favorable habitat conditions (Haas et al. 2007), resulting in both greater use of the marsh and birds with better refueling status. Our diet analyses confirmed that migrating canvasbacks are consuming sago pondweed at Delta Marsh, though it was not the most abundant food item observed (Fig. 7). Available historical data indicate that, in the fall, canvasbacks in southern Manitoba consumed mainly plant materials, especially sago pondweed tubers (Bartonek and Hickey 1969). However, sample sizes in both our study and Bartonek and Hickey (1969) were small and collection of ducks over decoys introduces biases to the description of duck diets (Callicutt et al. 2011). Thus, further work would be needed to elucidate what food items these migrating canvasbacks and scaup are relying on. Importantly, Delta Marsh appears to provide sufficient food resources such that greater numbers of ducks using the marsh does not result in worse RFI.

Conclusions

Multiple lines of evidence indicate that restoration of Delta Marsh via exclusion of large carp successfully improved the habitat quality for migrating ducks, as evidenced by more birds returning, yet maintaining a consistent refueling status. The rebounding of fall-migrating ducks using the marsh to historical levels corresponded with a rapid recovery of total SAV extent. Sago pondweed, which was historically an important food item for migrating canvasbacks, has not completely rebounded. It is unclear if sago pondweed needs more time to recover or whether underlying shifts in marsh conditions may inhibit its recovery. Finally, this study highlights the benefits of maintaining large carp exclusion at Delta Marsh — even imperfect exclusion of an invasive species can dramatically improve conditions for migrating ducks, thereby helping to safeguard the ecological and cultural benefits of this important system.

References

Anderson MG (1978) Distribution and production of sago pondweed (*Potamogeton Pectinatus* L.) on a northern prairie marsh. Ecology 59:154–160. https://doi.org/10.2307/1936642

Anderson MG, Low JB (1976) Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. Journal of Wildlife Management 40:233–242

Anteau MJ, Afton AD (2008a) Amphipod densities and indices of wetland quality across the upper-Midwest, USA. Wetlands 28:184–196. https://doi.org/10.1672/07-53.1

Anteau MJ, Afton AD (2008b) Using plasma-lipid metabolites to index changes in lipid reserves of free-living lesser scaup (*Aythya affinis*). Auk 125:354–357. https://doi.org/10.1525/auk.2008.06255

Anteau MJ, Afton AD (2011) Lipid catabolism of invertebrate predator indicates widespread wetland ecosystem degradation. PLoS ONE 6:e16029. http://dx.doi.org/10.1371/journal.pone.0016029

Anteau MJ, Afton AD, Anteau ACE, and Moser EB (2011) Fish and land use influence *Gammarus lacustris* and *Hyalella azteca* (Amphipoda) densities in large wetlands across the upper Midwest. Hydrobiologia 664:69–80. https://doi.org/10.1007/s10750-010-0583-2

Atton FM (1959) The invasion of Manitoba and Saskatchewan by carp. Transactions of the American Fisheries Society 88:203–205

Austin JE, O'Neil ST, Warren JM (2017) Habitat selection by postbreeding female diving ducks: influence of habitat attributes and conspecifics. Journal of Avian Biology 48:295–308. https://doi.org/10.1111/jav.01063

Badiou PHJ, Goldsborough LG (2010) Ecological impacts of an exotic benthivorous fish in large experimental wetlands, Delta Marsh, Canada. Wetlands 30:657–667. https://doi.org/10.1007/s13157-010-0071-5

Bain GAC (1980) The relationship between preferred habitat, physical condition and hunting mortality of canvasbacks (*Aythya valisineria*) and redheads (*Aythya americana*) at Long Point, Ontario. Thesis, University of Western Ontario

Bajer PG, Sullivan G, Sorensen PW (2009) Effects of a rapidly increasing population of common carp on vegetative cover and waterfowl in a recently restored Midwestern shallow lake. Hydrobiologia. 632:235–245. https://doi.org/10.1007/s10750-009-9844-3

Bartonek JC, Hickey JJ (1969) Food habits of canvasbacks, redheads, and lesser scaup in Manitoba. Condor 71:280–290

Batt BDJ (2000) The Delta Marsh. In: Murkin HR, van der Valk AG, and Clark WR (ed). Prairie wetland ecology: the contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, pp 17–33

Batzer DP, Pusateri CR, Vetter R (2000) Impacts of fish predation on marsh invertebrates: Direct and indirect effects. Wetlands 20:307–312.

Bonneau JL, Scarnecchia DL (2014) The zooplankton community of a turbid great plains (USA) reservoir in response to a biomanipulation with common carp (*Cyprinus carpio*). Transactions of the Kansas Academy of Science 117:181–192

Bonneau JL, Scarnecchia DL (2015) Response of benthic macroinvertebrates to carp (*Cyprinus carpio*) biomanipulation in three tributaries of a eutrophic, Great Plains reservoir, USA. Transactions of the Kansas Academy of Science 118:13–26.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York

Callicutt JT, Hagy HM, Schummer ML (2011) The food preference paradigm: A review of autumn–winter food use by North American dabbling ducks (1900–2009). Journal of Fish and Wildlife Management 2:29–40.

Carbone C, Houston AI (1994) Patterns in the diving behavior of the pochard, *Aythya ferina*: A test of an optimality model. Animal Behaviour 48:457–465. https://doi.org/10.1006/anbe.2003.2090

Crivelli AJ (1983) The destruction of aquatic vegetation by carp. Hydrobiologia 106:37–41.

DuBowy PJ (1985) Feeding ecology and behavior of postbreeding male blue-winged teal and northern shovelers. Canadian Journal of Zoology 63:1292–1297. https://doi.org/10.1139/z85-194

Emery-Butcher HE, Beatty SJ, Robson BJ (2020) The impacts of invasive ecosystem engineers in freshwaters: A review. Freshwater Biology 65:999–1015. https://doi.org/10.1111/fwb.13479

Fiske I, Chandler R (2011) Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23. http://dx.doi.org/10.18637/jss.v043.i10

French, JRP, Wilcox DA, Nichols SJ (1999) Passing of northern pike and common carp through experimental barriers designed for use in wetland restoration. Wetlands 19:883–888. https://doi.org/10.1007/BF03161790

Geard N (2015) Bathymetry, substratum and emergent vegetation distributions during an extreme flood event in Delta Marsh, Manitoba. Thesis, University of Manitoba. http://hdl.handle.net/1993/30845

Guglielmo CG, Cerasale DJ, Eldermire C (2005) A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological Biochemical Zoology 78:116–125. https://doi.org/10.1086/425198

Guglielmo CG, O'Hara PD, Williams TD (2002) Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living western sandpipers (*Calidris mauri*). Auk 119:437–445. http://dx.doi.org/10.1642/0004-8038(2002)119[0437:EAISOV]2.0.CO;2

Haas K, Kohler U, Diehl S, Kohler P, Dietrich S, Holler S, Jaensch A, Niedermaier M, Vilsmeier J (2007) Influence of fish on habitat choice of water birds: a whole system experiment. Ecology 88:2915–2925. https://doi.org/10.1890/06-1981.1

Hansel-Welch N, Butler MG, Carlson TJ, Hanson MA (2003) Changes in macrophyte community structure in Lake Christina (Minnesota), a large shallow lake, following biomanipulation. Aquatic Botany 75:323–337. http://dx.doi.org/10.1016/S0304-3770(03)00002-0

Hanson AR, Ankney CD, Dennis DG (1990) Body weight and lipid reserves of American black ducks and mallards during autumn. Canadian Journal of Zoology 68:2098–2104. https://doi.org/10.1139/z90-292

Hanson MA, Butler MG (1994) Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Canadian Journal of Fisheries and Aquatic Sciences 51:1180–1188. https://doi.org/10.1139/f94-117

Hertam SC (2010) The effects of common carp (*Cyprinus carpio* L.) on water quality, algae and submerged vegetation in Delta Marsh, Manitoba. Thesis, University of Manitoba. http://hdl.handle.net/1993/4207

Hillyard KA, Smith BB, Conallin AJ, Gillanders BM (2010) Optimising exclusion screens to control exotic carp in an Australian lowland river. Marine and Freshwater Research 61:418-429. https://doi.org/10.1071/MF09017

Hnatiuk SD (2006) Experimental manipulation of ponds to determine the impact of common carp (*Cyprinus carpio* L.) in Delta Marsh, Manitoba: Effects on water quality, algae, and submersed vegetation. Thesis, University of Manitoba. http://hdl.handle.net/1993/7963

Ivey GL, Cornely JE, Ehlers BD (1998) Carp impacts on waterfowl at Malheur National Wildlife Refuge, Oregon. Transactions of the 63rd North American Wildlife and Natural Resources Conference:66–74

Janke AK (2016) A physiological assessment of wetland habitats for spring-migrating ducks in the agricultural landscapes of the southern Prairie Pothole Region. Dissertation, South Dakota State University.

Janke AK, MJ Anteau, JD Stafford (2019) Prairie wetlands confer consistent migrant refueling conditions across agradient of agricultural land use intensities. Biological Conservation 229:99–112. https://doi.org/10.1016/j.biocon.2018.11.021

Keast A (1984) The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. Canadian Journal of Zoology 62:1289–1303. https://doi.org/10.1139/z84-186

Laguna C, Lopez-Perea JJ, Vinuela J, Florin M, Feliu J, Chicote A, Cirujano S, Mateo R (2016) Effects of invasive fish and quality of water and sediment on macrophytes biomass, and their consequences for the waterbird community of a Mediterranean floodplain. Science of the Total Environment 551:513–521. https://doi.org/10.1016/j.scitotenv.2016.02.059

Lake Manitoba and Lake St. Martin Regulation Review Committee Report (LM & LSMRRC) (2013) Finding the right balance: a report to the Minister of Infrastructure and Transportation. https://www.gov.mb.ca/asset_library/en/2011flood/regulation_review_report.pdf. Accessed 1 March 2020

Lapointe GD (1986) Fish movement and predation on macroinvertebrates in a lakeshore marsh. Thesis, University of Minnesota

Lovvorn JR (1994) Biomechanics and foraging profitability: An approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 279:223–233. https://doi.org/10.1007/BF00027856

Lovvorn JR, Gillingham MP (1996) Food dispersion and foraging energetics: A mechanistic synthesis for field studies of avian benthivores. Ecology 77:435–451. http://dx.doi.org/10.2307/2265620

Lyons JE, Collazo JA, Guglielmo CG (2008) Plasma metabolites and migration physiology of semipalmated sandpipers: Refueling performance at five latitudes. Oecologia 155:417–427. https://doi.org/10.1007/s00442-007-0921-x

Maceda-Veiga A, Raquel L, Green AJ (2017) Dramatic impact of alien carp *Cyprinus carpio* on globally threatened diving ducks and other waterbirds in Mediterranean shallow lakes. Biological Conservation 212:74–85. http://dx.doi.org/10.1016/j.biocon.2017.06.002

MacIsaac HJ, Tedla RA, Ricciardi A (2011) Patterns and rate of growth of studies in invasion ecology. In: Richardson DM (ed) Fifty years of invasion ecology: The legacy of Charles Elton. 1st edn. Blackwell Publishing Ltd., West Sussex, UK, pp 51–60.

Nichols JD, Hines JE, Sauer JR, Fallon FW, Fallon JE, Heglund PJ (2000) A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408. https://doi.org/10.1093/auk/117.2.393

Osborn JM, Hagy HM, McClanahan MD, Davis JB, Gray MJ (2017) Habitat selection and activities of dabbling ducks during non-breeding periods. Journal of Wildlife Management 81:1482–1493. https://doi.org/10.1002/jwmg.21324

Pace RM, Afton AD (1999) Direct recovery rates of lesser scaup banded in northwest minnesota: Sources of heterogeneity. Journal of Wildlife Management 63:389–395. https://doi.org/10.2307/3802524

Parkos III J, Santucci Jr. VJ, Wahl D (2003) Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. Canadian Journal of Fisheries and Aquatic Sciences 60:182–192. https://doi.org/10.1139/f03-011

Phillips VE (1992) Variation in winter wildfowl numbers on gravel pit lakes at Great Linford, Buckinghamshire, 1974–79 and 1984–91, with particular reference to the effects of fish removal. Bird Study 39:177–185. https://doi.org/10.1080/00063659209477116

Pöysä H (1983) Morphology-mediated niche organization in a guild of dabbling ducks. Scandinavian Journal of Ornithology 14:317–326. http://dx.doi.org/10.2307/3676325

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Randall RG, Minns CK, Cairns VW, Moore JE (1995) The relationship between an index of fish production and submersed aquatic macrophytes and other features at three littoral areas in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 53:35–44. https://doi.org/10.1139/f95-271

Ricciardi A, MacIsaac HJ (2011) Impacts of biological invasions on freshwater ecosystems. In: Richardson DM (ed) Fifty years of invasion ecology: The legacy of Charles Elton. 1st edn. Blackwell Publishing Ltd., West Sussex, UK, pp 211–224.

Rohweder J, Rogala JT, Johnson BL, Anderson D, Clark S, Chamberlin F, Potter D, and Runyon K (2012) Application of wind fetch and wave models for habitat rehabilitation and enhancement projects – 2012 update. Contract report prepared for U.S. Army Corps of Engineers' Upper Mississippi River Restoration – Environmental Management Program

Schaub M, Jenni L (2001) Stopover durations of three warbler species along their autumn migration route. Oecologia 128:217–227. http://dx.doi.org/10.1007/s004420100654

Schrage LJ, Downing JA (2004) Pathways of increased water clarity after fish removal from Ventura Marsh; a shallow, eutrophic wetland. Hydrobiologia 511:215–231. http://dx.doi.org/10.1023/B:HYDR.0000014065.82229.c2

Seaman DAA, Guglielmo CG, Elner RW, Williams TD (2006) Landscape-scale physiology: Site differences in refueling rates indicated by plasma metabolite analysis in free-living migratory sandpipers. Auk 123:563–574. https://doi.org/10.1093/auk/123.2.563

Smith EJ, Anteau MJ, Hagy HM, Jacques CN (2021) Plasma metabolite indices are robust to extrinsic variation and useful indicators of foraging habitat quality in Lesser Scaup. Ornithology 138:1–11.

Stafford JD, Horath MM, Yetter AP, Hine CS, Havera SP (2007) Wetland use by mallards during spring and fall in the Illinois and central Mississippi river valleys. Waterbirds, 30:394–402. https://doi.org/10.1675/1524-4695(2007)030[0394:WUBMDS]2.0.CO;2

Stewart RE, Kantrud HA (1972) Vegetation of prairie potholes, North Dakota, in relation to quality of water and other environmental factors. U.S. Bureau of Sport Fisheries and Wildlife and the U.S. Geological Survey, Washington, D.C., Professional Paper 585-D. https://doi.org/10.3133/pp585D

Suggett G, Goldsborough G, the Delta Marsh History Group (2015) Delta: A prairie marsh and its people. Delta Marsh History Group, Portage la Prairie, MB, Canada.

Tryon Jr. CA (1954) The effect of carp exclosures on growth of submerged aquatic vegetation in Pymatuning Lake, Pennsylvania. Journal of Wildlife Management 18:251–254. https://doi.org/10.2307/3797722

Van Onsem S, Triest L (2018) Turbidity, waterfowl herbivory, and propagule banks shape submerged aquatic vegetation in ponds. Frontiers in Plant Science 9:1–18. https://doi.org/10.3389/fpls.2018.01514

Walker S, Addison P, Sandstrom S, Lester N (2013) Contact retention selectivity of three types of gillnet gangs. Ontario Ministry of Natural Resources, Aquatic Research Series 2013-07.

Weaver MJ, Magnuson JJ, Murray CK (1997) Distribution of littoral fishes in structurally complex macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 54:2277–2289. http://dx.doi.org/10.1139/f97-130

Webb EB, Smith LM, Vrtiska MP, Lagrange TG (2010) Effects of local and landscape variables on wetland bird habitat use during migration through the rainwater basin. Journal of Wildlife Management 74:109–119. http://dx.doi.org/10.2193/2008-577

Weier LJ, Starr DF (1950) The use of rotenone to remove rough fish for the purpose of improving migratory waterfowl refuge areas. Journal of Wildlife Management 14:203–205. https://doi.org/10.2307/3796333

Williams TD, Guglielmo CG, Egeler O, Martyniuk CJ (1999) Plasma lipid metabolites provide information on mass change over several days in captive western sandpipers. Auk 116:994–1000. https://doi.org/10.2307/4089679

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Statistical Methodology Series B 73:3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Zambrano L, Scheffer M, Martínez-Ramos M (2001) Catastrophic response of lakes to benthivorous fish introduction. Oikos 94:344–350. https://doi.org/10.1034/j.1600-0706.2001.940215.x

Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Field data were collected by Robert Emery, Paige Kowal, Dale Wrubleski, Frank Baldwin, Cameron Meuckon, and Howard Singer. Statistical analysis was done by Llwellyn Armstrong, with contributions from Lauren Bortolotti, Michael Anteau, Vanessa Harriman, and other coauthors. The first draft of the manuscript was written by Lauren Bortolotti and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets used in this study are available from the corresponding author on reasonable request.

Table 1. Estimated (model-based) density and refueling index (RFI) of fall-migrating canvasbacks and lesser scaup, modelled catch per unit effort (CPUE; number of carp > 70 mm maximum body width per gillnet set), and 95% confidence limits at Delta Marsh, Canada, 2013–2018. Diving duck densities are derived from a negative binomial model including the effect of year (for 2013–2017) or an intercept-only model (for 2018). RFI values for canvasback and scaup represent estimated marginal means from the best-approximating model, with other quantitative covariates set to mean values. Mean water levels (standard deviation; meters above sea level, masl) are from the Water Survey of Canada Westbourne gauge on Lake Manitoba and represent the period over which diving ducks were collected (Sept. 13–Nov. 8). NA = not applicable as data were not collected.

Year	Canvasback density (per km^2)	Scaup density (per km^2)	Canvasback RFI	Scaup RFI	Carp CPUE	Water level (masl)
2013	19.2 (9.9, 37.6)	15.8 (11.5 21.6)	-0.34 (-0.81, 0.14)	0.41 (-0.15, 0.97)	9.78 (4.88, 19.57)	247.59 (0.08)
2014	9.0 (4.2, 19.4)	6.3 (3.6, 10.9)	-0.81 (-1.21, -0.41)	-0.060 (-0.57, 0.45)	2.34 (0.99, 5.55)	248.15 (0.10)
2015	20.0 (9.9, 40.4)	34.2 (24.8, 47.0)	*NA*	*NA*	6.07 (2.98, 12.35)	247.49 (0.08)
2016	39.7 (20.3, 77.7)	33.3 (24.2, 45.9)	0.022 (-0.37, 0.42)	0.77 (0.26, 1.28)	1.67 (0.64, 4.38)	247.51 (0.06)
2017	12.6 (6.0, 26.2)	25.2 (17.9, 35.6)	-0.39 (-0.79, 0.014)	0.36 (-0.11, 0.83)	5.18 (2.47, 10.84)	247.66 (0.11)
2018	38.6 (4.8, 311.0)	73.9 (30.5, 179.2)	-0.30 (-0.75, 0.14)	0.44 (-0.02, 0.91)	8.96 (4.52, 17.78)	247.32 (0.06)

Table 2. The best-approximating models of fall-migrating diving duck density at Delta Marsh, Canada, 2014 and 2016–2018, for each subset of models evaluating variables of primary interest including percent submersed aquatic vegetation (SAV), open water (OW), and sago pondweed (SAGO) within a transect segment. Other covariates were: dominant SAV species, distance to the nearest duck hunting access point (dist_hunt), average weighted fetch distance, time of day, and day of the year (date). An "s" before a covariate in the model structure denotes a smoothed variable and "ti" a tensor product (i.e., interaction). Akaike Information Criterion (AIC) is an estimator of the expected Kullback-Leibler information (i.e., the discrepancy between the candidate model and the true model generating the data). ΔAIC is the difference between the AIC of the candidate model and the overall best-approximating model (AIC = 3553.68). Covariates in bold text were well estimated (i.e., the ratio of the estimated effect to standard error was > ~2 or smooth terms were statistically significant).

Model[1]	Total effective degrees of freedom[2]	AIC[3]	ΔAIC
SAV + **SAV species** + **dist_hunt** + fetch	29.7	3553.68	0
OW + **dist_hunt** + **fetch**	28.4	3553.82	0.14
OW + SAGO + **dist_hunt** + **fetch**	29.0	3556.59	2.91
s(SAGO) + **s(dist_hunt)** + **s(fetch)** + **s(time)** + s(date) + **ti(SAGO, time)** + ti(SAGO, date)	31.0	3560.43	6.75

[1]All models include effects of year and smoothed random effects of transect segment and survey occasion and were refit on the SAV subset for AIC comparability.

[2]Total effective degrees of freedom is non-integer even when all covariate effects are linear due to inclusion of smoothed random effects.

[3]AIC = -2*Maximum log-likelihood + 2*Total effective degrees of freedom.

Table 3. The best-approximating models of fall-migrating dabbling duck density at Delta Marsh, Canada, 2014 and 2016–2018, for each subset of models evaluating variables of primary interest including percent emergent vegetation (EV), submersed aquatic vegetation (SAV), and shallowly flooded area (< 41 cm deep) within a transect segment. Other covariates considered were: distance to the nearest duck hunting access point (dist_hunt), average weighted fetch distance, time of day, and water level. An "s" before a covariate in the model structure denotes a smoothed variable and "ti" a tensor product (i.e., interaction). Covariates in bold text were well estimated (i.e., the ratio of the estimated effect to standard error was > ~2 or smooth terms were statistically significant).

Model[1]	**Total effective degrees of freedom**[2]	**AIC**[3]	**ΔAIC**
s(EV) + s(dist_hunt) + s(fetch) + s(time) + **s(water level)** + **ti(EV, water level)**	21.8	4128.68	0
SAV + Shallow Flooded	39.0	4134.14	5.46
EV + Shallow Flooded	30.0	4137.21	8.53

[1]All models include effects of year and smoothed random effects of transect segment and survey occasion.

[2]Total effective degrees of freedom is non-integer even when all covariate effects are linear due to inclusion of smoothed random effects.

[3]AIC = -2*Maximum log-likelihood + 2*Total effective degrees of freedom.

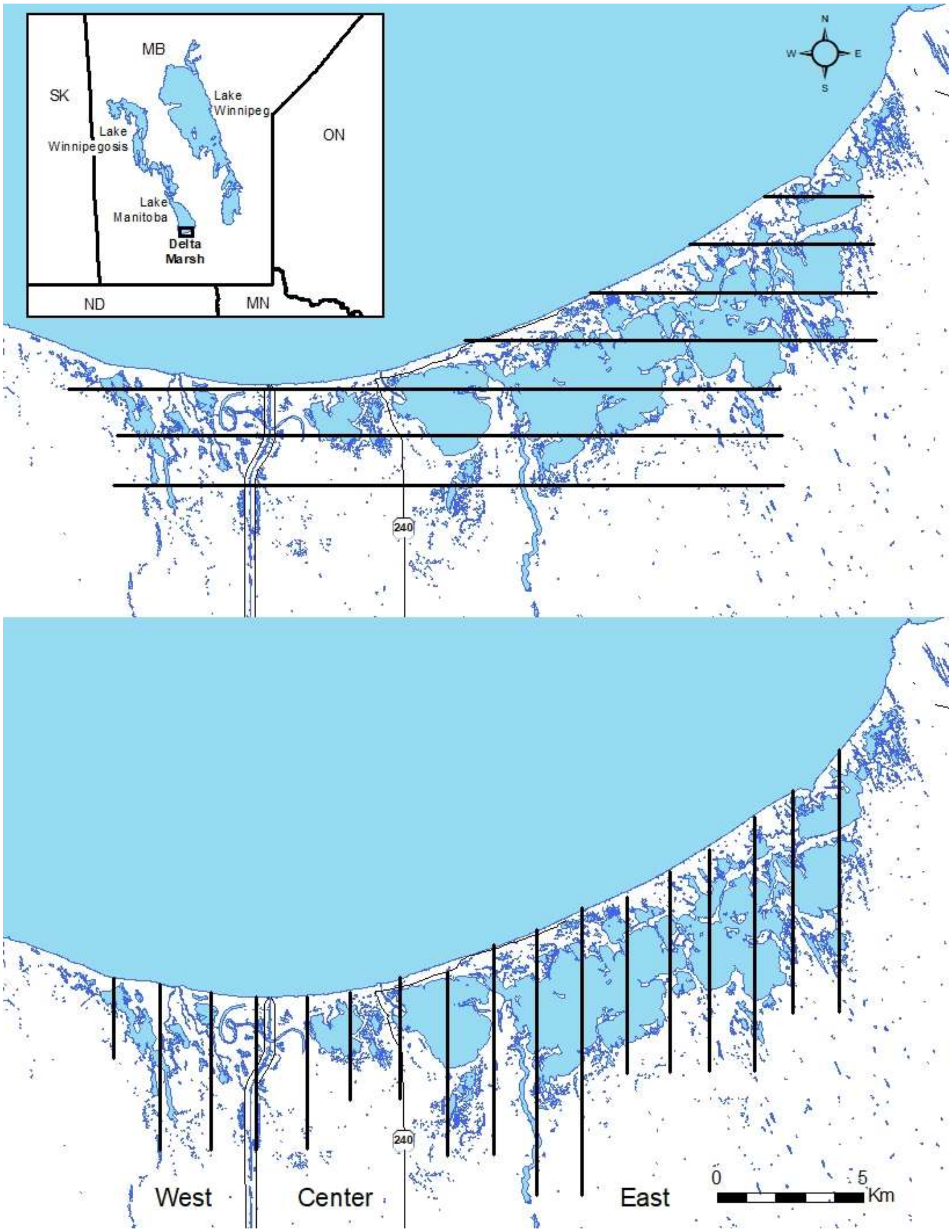

Fig. 1. Location of Delta Marsh, Manitoba, Canada (inset) and the location of aerial duck survey transects in 1965–2012 (top panel) and 2013–2018 (the post-exclusion period; bottom panel) at Delta Marsh. The west, center, and east marsh units span 4, 2, and 11 transects, respectively.

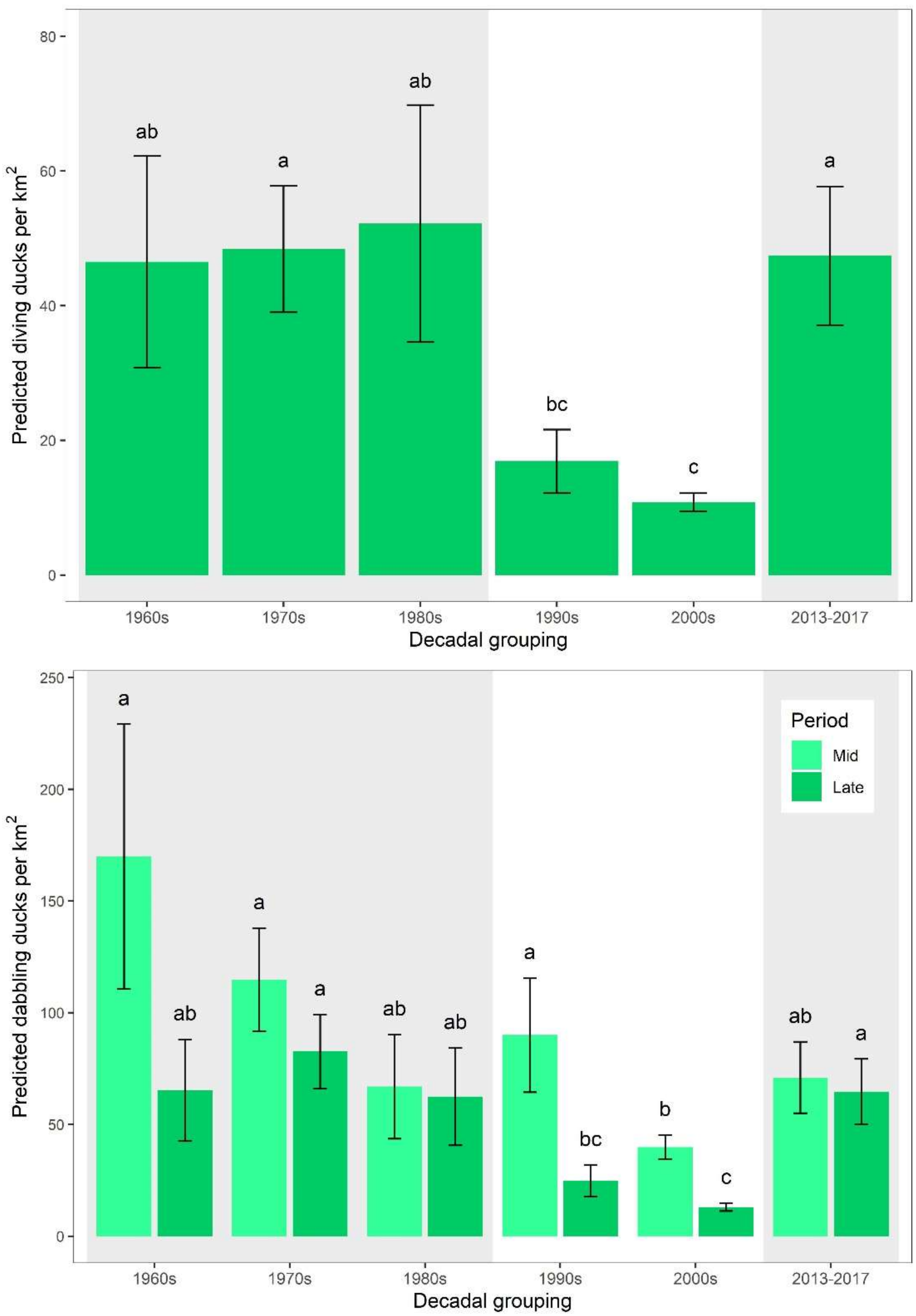

Fig. 2. Change in model-estimated diving (top panel) and dabbling (bottom panel) duck density (± 1 standard error) during fall aerial surveys at Delta Marsh through time. Gray shaded areas show time periods when there was at least partial exclusion of large common carp from Delta Marsh, Canada. "Mid" survey periods represent surveys conducted September 16–October 15 and "Late" periods those conducted after October 15. There is no statistical difference (as determined from Tukey-Kramer adjusted pairwise comparisons) among decadal groupings sharing the same letter within a survey period (i.e., Mid or Late).

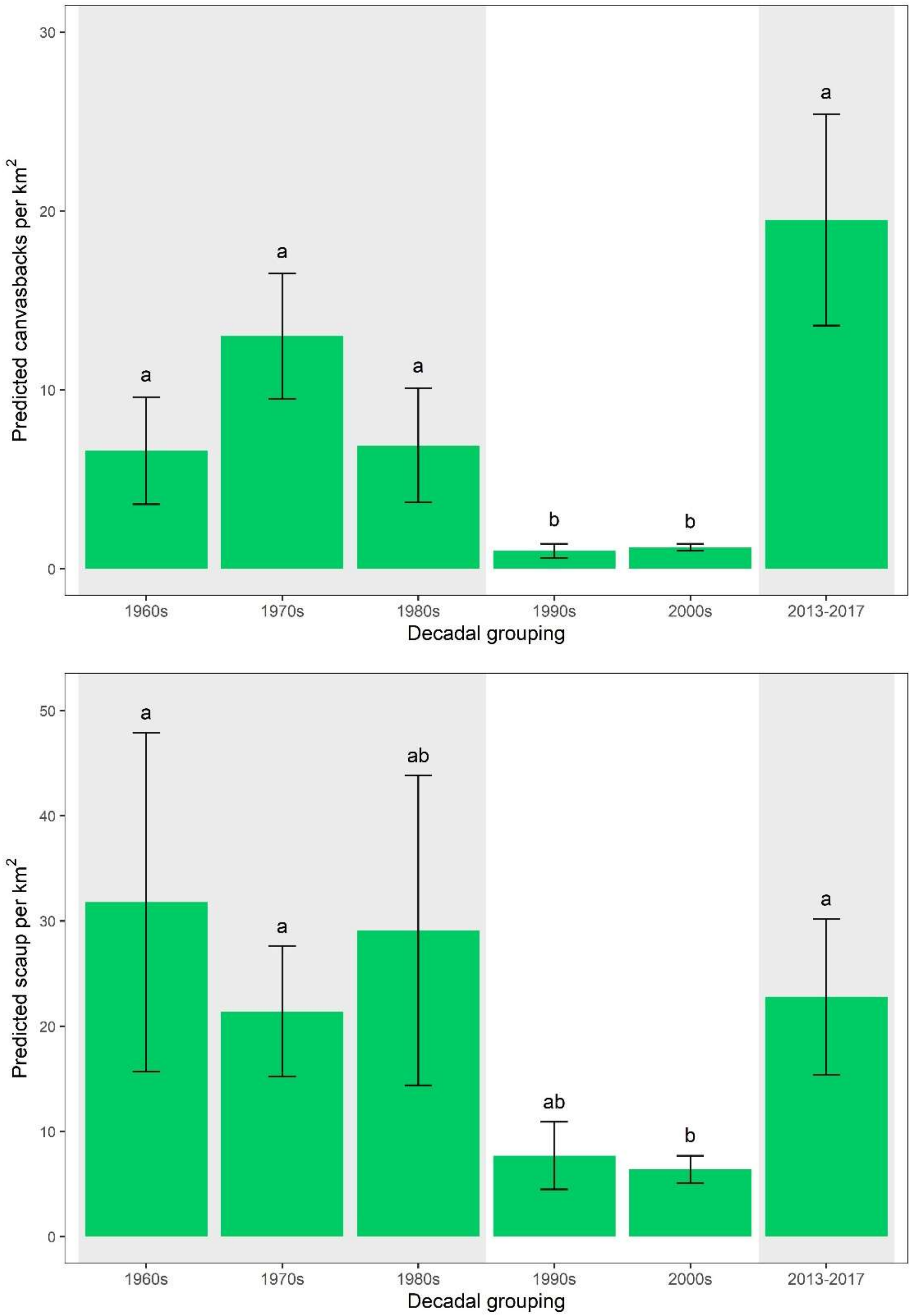

Fig. 3. Change in model-estimated canvasback (top panel) and scaup (bottom panel) density (± 1 standard error) during fall aerial surveys at Delta Marsh, Canada through time. Gray shaded areas show time periods when there was at least partial exclusion of large common carp from Delta Marsh. There is no statistical difference (as determined from Tukey-Kramer adjusted pairwise comparisons) among decadal groupings sharing the same letter.

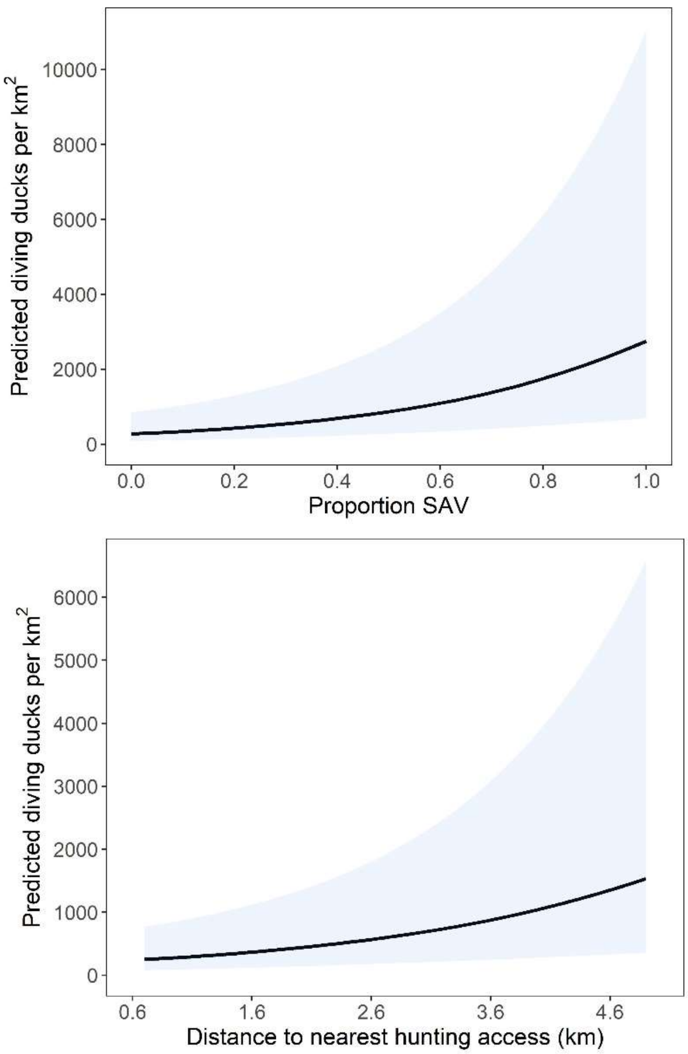

Fig. 4. Effect of the proportion of submersed aquatic vegetation (SAV) within a transect segment (top panel) and distance to the nearest duck hunting access point (bottom panel) on the density of diving ducks at Delta Marsh, Canada during fall aerial surveys, 2014 and 2016–2018. Shaded areas show 95% confidence intervals. Conditional duck density estimates come from the best-approximating model, with continuous covariates set to median values, year effects averaged, and random effects of day of the year and segment set to zero.

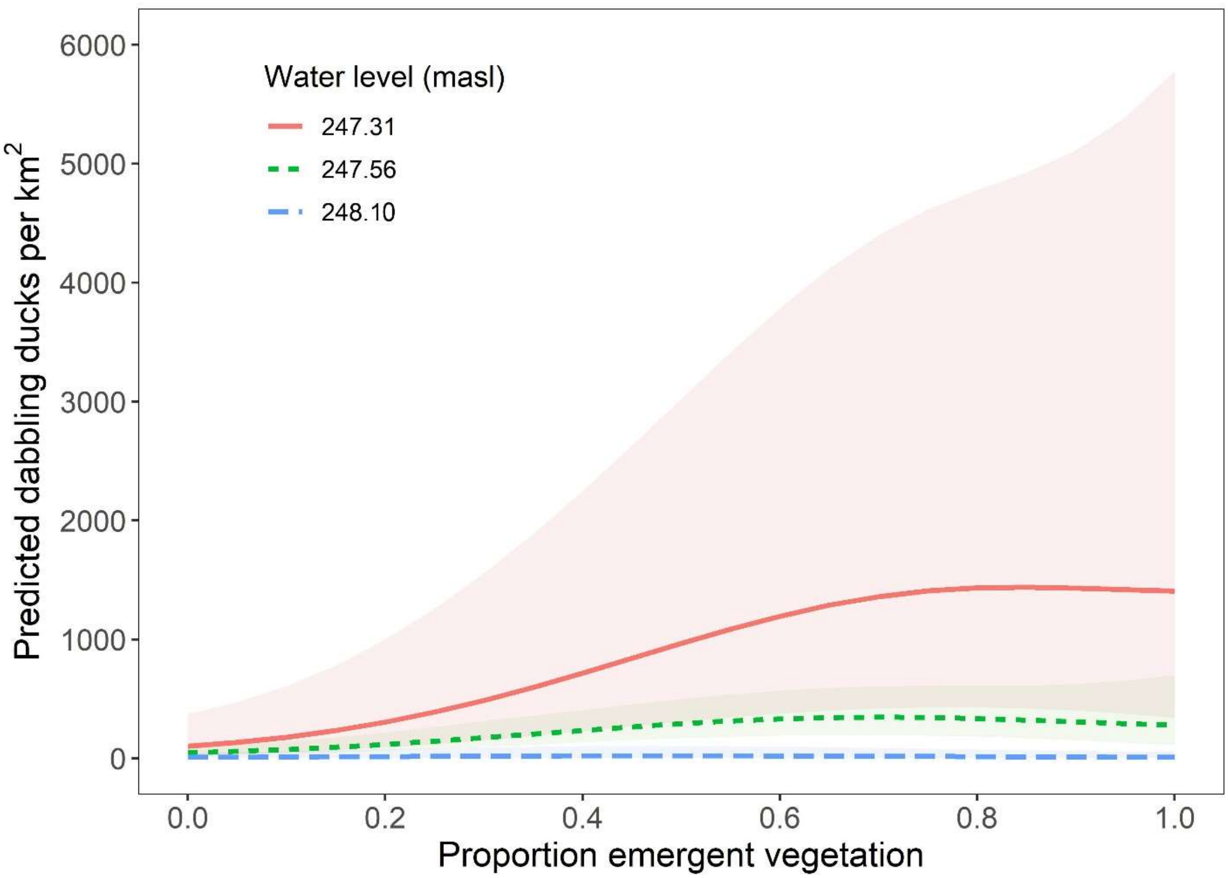

Fig. 5. Effect of the proportion of emergent vegetation within a transect segment for three Lake Manitoba water levels (meters above sea level, masl) on the density of dabbling ducks at Delta Marsh, Canada during fall aerial surveys, 2014 and 2016–2018. Shaded areas show 95% confidence intervals. Conditional duck density estimates come from the best-approximating model, with continuous covariates set to median values, year effects averaged, and random effects of day of the year and segment set to zero.

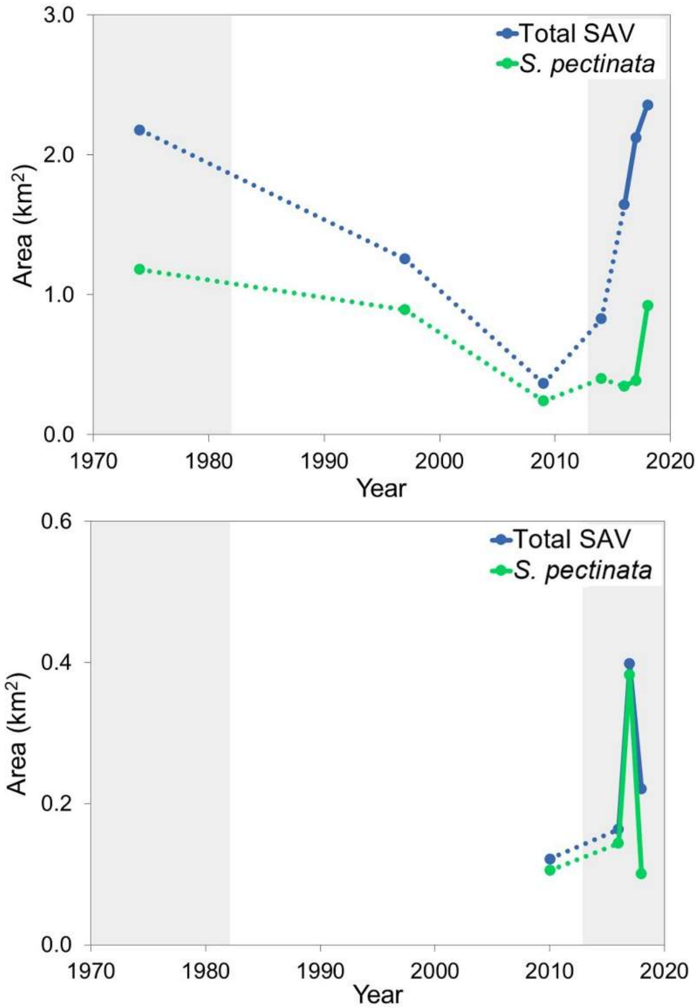

Fig. 6. Areal extent (km^2) of total submersed aquatic vegetation (SAV; in blue) and sago pondweed (*Stuckenia pectinata*; in green) in duck survey transects in the east (top panel) and west (bottom panel) marsh units, Delta Marsh, Canada. The east marsh was surveyed in 1974, 1997, 2009, 2014, and 2016–2018 and the west marsh in 2010 and 2016–2018. Dotted lines connect non-consecutive survey years; solid lines connect consecutive survey years. Gray shaded areas show time periods when there was at least partial exclusion of large common carp from Delta Marsh.

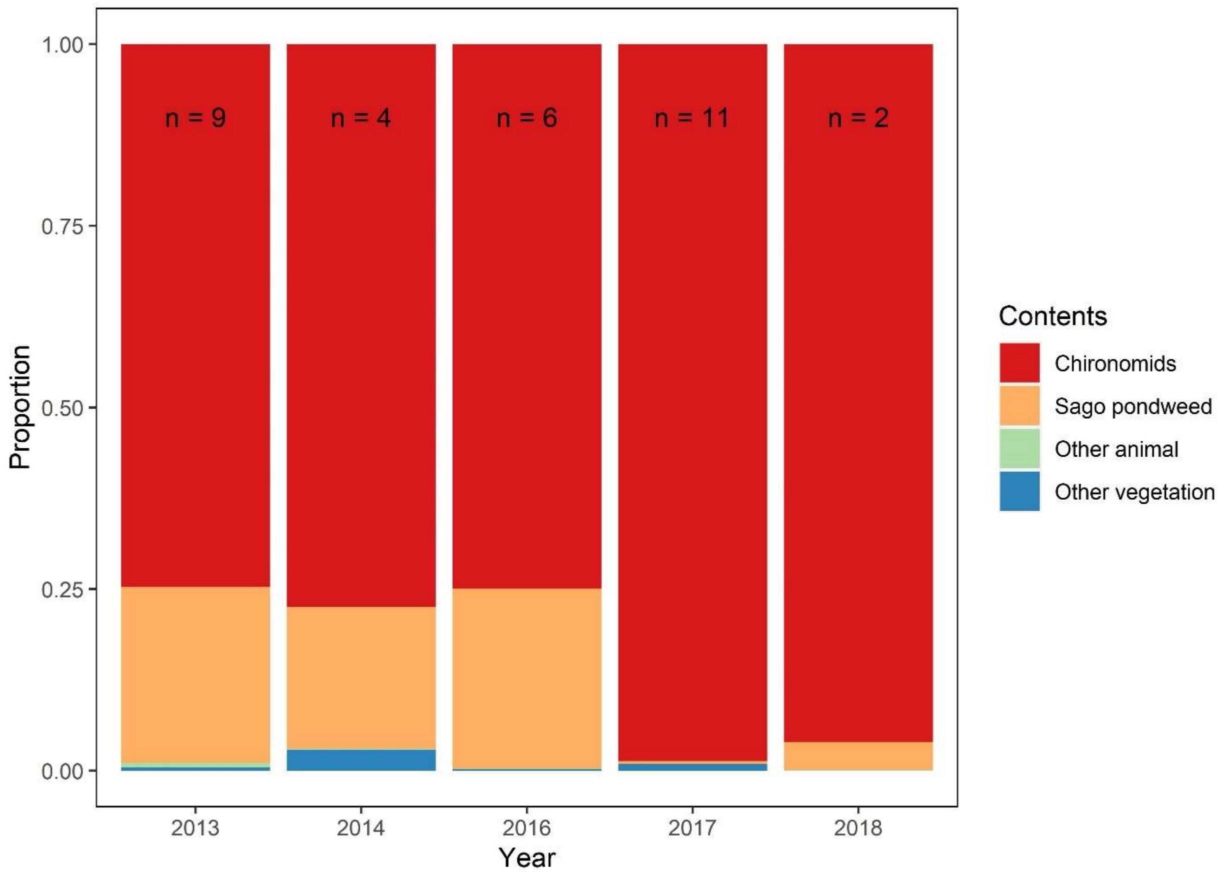

Fig. 7. Proportion of esophagus-proventriculus contents, by volume, for canvasbacks collected at Delta Marsh, Canada in 2013–2014 and 2016–2018. Contents include chironomid larvae, sago pondweed tubers and nutlets, other animal matter (snails, leeches, clams, amphipods), and other vegetation (plant achenes, nutlets and seeds). Sample sizes (n) are the number of birds collected with food items in each year.