Prey consumption and trace element concentrations in double-crested cormorants (*Phalacrocorax auritus*) from Lake Winnipeg, Canada

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ABSTRACT

Double-crested cormorants (*Phalacrocorax auritus*) have generally increased throughout their range in North America over the last 40 years, leading to increased conflict with commercial and recreational fisheries that often view cormorants as competitors. Lake Winnipeg, Manitoba, Canada and adjacent large lakes support a significant portion of the continent's breeding population, and have high economic value for recreational and commercial fisheries; no recent assessment of cormorant diet has been conducted in this region. We measured stable isotopes (δ^{13}C, δ^{15}N, and δ^{34}S) in cormorant muscle and used a Bayesian mixing model approach to estimate cormorant diet composition throughout the Lake Winnipeg system, including the contribution of commercially and recreationally harvested walleye (*Sander vitreus*) and sauger (*Sander canadensis*). We estimated that cormorants occupied a trophic position around 4.0, which corresponds to a generalist diet, and consumed a small proportion of walleye (range of mean estimates: 6–12%) and sauger (range of mean estimates: 7–12%). We also examined the concentrations of 15 trace elements in cormorant muscle to evaluate the potential role that these birds played in contaminant flow and how these elements behaved trophically. Cd, Fe, Mn, Hg, and Se showed evidence of biomagnification in Lake Winnipeg's north basin, but only Hg biomagnified in the south basin; nutrient source (benthic vs. pelagic) had little effect on elemental concentrations. Our results add to the growing evidence that the two main basins of Lake Winnipeg are biologically distinct from each other, and that cormorants likely have little effect on the populations of harvested fishes.

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Introduction

Double-crested cormorant (*Phalacrocorax auritus*; hereafter "cormorants") populations throughout North America declined substantially over the past century due to organochlorine pesticide contamination and human persecution (Ludwig et al., 1996; Ontario Ministry of Natural Resources, 2006; Somers et al., 1993). However, over the past 40 years their numbers have generally increased (Ontario Ministry of Natural Resources, 2006; Weseloh et al., 2002; but see Wires et al., 2001) on lakes (Doucette et al., 2011; Weseloh et al., 2002), reservoirs (Caldwell et al., 1999), coastal regions (Wires et al., 2001), and aquaculture facilities (Dorr et al., 2004), likely due to a decline in organic pesticide use and increasing densities of prey items such as schooling fishes or farmed catfish (*Ictalurus* spp.). These upward population trends have generated considerable interest from

wildlife managers and the public (Belyea et al., 1997; Trapp et al., 1997; Wires et al., 2001) and have prompted research, especially on the Laurentian Great Lakes (Belyea et al., 1997; MacKinnon and Kennedy, 2014; Seefelt and Gillingham, 2008) and lakes in Saskatchewan (Doucette et al., 2011; Hall et al., 2014). The majority of studies have focused on cormorant consumption of commercially and recreationally-valuable fishes (Fielder, 2008; Hobson, 2009), their trophic niche (Doucette et al., 2011; Jones et al., 2010), and the effectiveness of population management programs (Dorr et al., 2010; Fielder, 2010). Cormorants nesting in Manitoba, however, have received little attention since diet studies conducted in the late 1980s (Hobson et al., 1989), despite the fact that Manitoba lakes (Lake Winnipegosis, Lake Winnipeg) support one of the continent's largest known cormorant breeding populations (Hatch, 1995; Nelson, 2005; Wires et al., 2001).

The relative sensitivity of cormorants to mercury (Hg), polychlorinated biphenyls (PCBs), and other persistent organic pollutants in the environment like dichlorodiphenyltrichloroethane (DDT) has made them an ideal indicator species for monitoring contaminant concentrations and their effects in aquatic systems (Golden and Rattner, 2003; Greichus et al., 1973; Ludwig et al., 1996; Somers et al., 1993). Cormorants are largely piscivorous, top predators within aquatic systems (Hobson, 2009), and therefore serve as integrators of the

energy and contaminants available from lower-trophic position (TP) organisms. Cormorant eggs, blood, and feathers, which can be sampled non-lethally, may be useful in intensive, long-term monitoring programs without negatively affecting populations or ecosystem function (Burger and Gochfeld, 2001; Caldwell et al., 1999; Ofukany et al., 2012).

A major challenge when using birds as "indicators" of contaminant concentrations in the environment is establishing a connection between concentrations in tissues and the source of consumer diets. Pellets, regurgitated prey items, and stomach contents are often used in diet reconstructions (Barrett et al., 2007; Seefelt and Gillingham, 2006), but these represent the bird's most recent meal, not the long-term nutrient and contaminant assimilation (Hobson, 2009). Stable isotopes of nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and potentially sulfur ($\delta^{34}S$) can help to quantitatively link the protein pool of consumers to their prey, and ultimately to the source of ingested contaminants (Hall et al., 2009; Rocque and Winker, 2004). The $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ values in cormorant tissues should reflect those in their prey tissues, as adjusted with known diet-to-tissue isotopic discrimination ($\Delta^{15}N$, $\Delta^{13}C$ and $\Delta^{34}S$) (Caut et al., 2009; Fry, 1988). Nitrogen stable isotope values ($\delta^{15}N$) are most often used to infer trophic position (TP), and to quantify contaminant biomagnification (Campbell et al., 2005; Gewurtz et al., 2006; Lavoie et al., 2013). Carbon and sulfur stable isotopes ($\delta^{13}C$, $\delta^{34}S$) can be used to link contaminant concentrations in tissues to prey or habitat types (Burgess and Hobson, 2006; Ofukany et al., 2012; Ofukany et al., 2014). Using stable isotopes to interpret trace element concentrations can link those concentrations with TP, nutrient source (e.g., along the benthic–pelagic continuum), and foraging ecology at the individual level (Jardine et al., 2006; Ricca et al., 2008), which is crucial for interpreting trace element and contaminant dynamics in an ecological context.

A better understanding of cormorant diet and trace element concentrations in Lake Winnipeg is important for the conservation and management of this ecosystem (Wires et al., 2001), and will add to our understanding of trophic interactions and contaminant dynamics in an aquatic system cumulatively impacted by eutrophication, exotic species introduction, and commercial fishing pressures (Environment Canada, Manitoba Water Stewardship, 2011; Manitoba Water Stewardship, 2010; Stewart and Watkinson, 2004). Harvests of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and lake whitefish (*Coregeonus clupeaformis*) on Lake Winnipeg are valued at approximately $20 - million/year (Environment Canada, Manitoba Water Stewardship, 2011). Given the extent and the long history of cormorant–fisheries conflicts in North America (Dorr et al., 2004; Hobson et al., 1989; Trapp et al., 1997), our goal was to identify which fish species are most frequently consumed by cormorants nesting on Lake Winnipeg. The potential prey base is diverse, with an abundant array of forage fishes (Hobson et al., 2012; Lumb et al., 2012). We predicted that commercially important (and high TP) fish would represent a relatively small proportion of cormorant diet because of the abundance of alternative prey such as lower TP forage fish (Doucette et al., 2011; Hobson et al., 1989). Our objectives were to use a comprehensive multi-isotopic ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$) approach to estimate cormorant diet composition and inform future regulatory and management decisions. We also investigated whether cormorant diet data could be linked to concentrations of Al, As, Cd, Fe, Mn, Hg, and Se in muscle tissue because the trophodynamics of Hg and other potentially toxic elements are poorly known for Lake Winnipeg and concentrations accumulating in high-TP consumers are not well characterized (Fox et al., 2002; Ofukany et al., 2012, 2014).

Materials and methods

Sample collection

Forty adult cormorants were collected from breeding colonies in Lake Winnipeg, Manitoba, Canada (53° 17′N, 97° 58′W; Fig. 1) from May–August 2009 (n = 23) and June–August 2010 (n = 17). Hatch-year cormorants (n = 12) were collected from the Black and Devil's Island colonies in the lake's south basin between July and August 2010. Only the Eagle, George, and Cox Island colonies were accessed in the north basin during 2010; no birds were collected from Cox Island in 2010 because of breeding failure. All collections were conducted by trained personnel, and complied with the appropriate Manitoba Conservation permits (WB09813 and WB11121) and firearms regulations. Whole cormorant carcasses were immediately frozen ($-20\ ^{\circ}C$) until they were transported to the National Hydrology Research Centre laboratory in Saskatoon, Saskatchewan, Canada.

Stable isotope values ($\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$) for potential prey and competing fishes were obtained simultaneously (Ofukany et al., 2014). In 2009 and 2010, fishes were obtained from beam trawls which were towed alongside the *MV Namao* (Lumb et al., 2012), and from commercial gillnets (2010 only). Fish samples were immediately frozen ($-20\ ^{\circ}C$). Fish collections and analyses are described in greater detail by Ofukany et al. (2014).

Each cormorant was thawed, and mass (g) and tarsus length (mm) were measured. The left pectoral muscle was sub-divided into three sample aliquots: one for stable isotope analysis, one for trace element determination and a third for Hg analysis. Specimens were sexed based on visual examination of the reproductive organs (Seefelt and Gillingham, 2006).

Stable isotope analyses

The samples were oven-dried (60 °C) and homogenized using a ball mill grinder prior to isotopic assays (Logan et al., 2008). Because lipid content varies and lipids are depleted in ^{13}C relative to other compounds, they were extracted from small aliquots of dried muscle samples prior to $\delta^{13}C$ analysis (Bodaly et al., 2007; Sotiropoulos et al., 2004). These aliquots were rinsed multiple times with a 2:1 (v/v) chloroform:methanol mixture, then allowed to dry in a fume hood overnight (Doucette et al., 2010). Because $\delta^{15}N$ values are altered by chemical lipid extraction (Doucette et al., 2010; Sotiropoulos et al., 2004), and the effects of chloroform:methanol treatments on $\delta^{34}S$ values are unknown, $\delta^{15}N$ and $\delta^{34}S$ analyses were completed using untreated muscle samples.

The sample weights of 1.00 ± 0.01 mg and 10.00 ± 0.10 mg of dried, unextracted muscle, and 1.00 ± 0.01 mg of lipid-extracted muscle were weighed into tin capsules for $\delta^{15}N$, $\delta^{34}S$, and $\delta^{13}C$ analyses, respectively (Wayland and Hobson, 2001). Values of $\delta^{15}N$, $\delta^{34}S$, and $\delta^{13}C$ in the muscle were quantified via continuous-flow isotope-ratio mass spectrometry and calibrated using secondary organic isotopic reference materials BWB ($\delta^{15}N = 14.4$‰, $\delta^{13}C = -18.5$‰, $\delta^{34}S = 17.5$‰), PUGEL ($\delta^{15}N = 5.6$‰, $\delta^{13}C = -12.6$‰) and CFS ($\delta^{34}S = -3.8$‰). Control reproducibility was better than ± 0.2‰ for $\delta^{15}N$ and $\delta^{13}C$ and ± 0.3‰ for $\delta^{34}S$.

All $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ values for the cormorant muscle are expressed in per mil (‰) relative to the isotopic reference materials' atmospheric nitrogen (N_2), Vienna Pee Dee Belemnite (VPDB), and Vienna Cañon Diablo Troilite (VCDT), respectively, where $\delta X = (R_A/R_S - 1)$, and X was ^{15}N, ^{13}C and ^{34}S, R_A was the ratio of the heavy to light isotope (example: $^{13}C/^{12}C$) in the sample, and R_S was the ratio in the standard.

Elemental analysis

The muscle samples were dried at 60 °C, homogenized, and digested using high purity nitric acid (HNO_3; 70% v/v) and 30% v/v analytical grade hydrogen peroxide (H_2O_2) (Ashoka et al., 2009). One method blank, one DORM-2 reference material (National Research Council Canada; Ottawa), and one duplicate sample was included for every 10 muscle samples. Concentrations of Al, As, Cd, Cu, Fe, Mn, and Se in muscle were quantified using inductively-coupled plasma mass
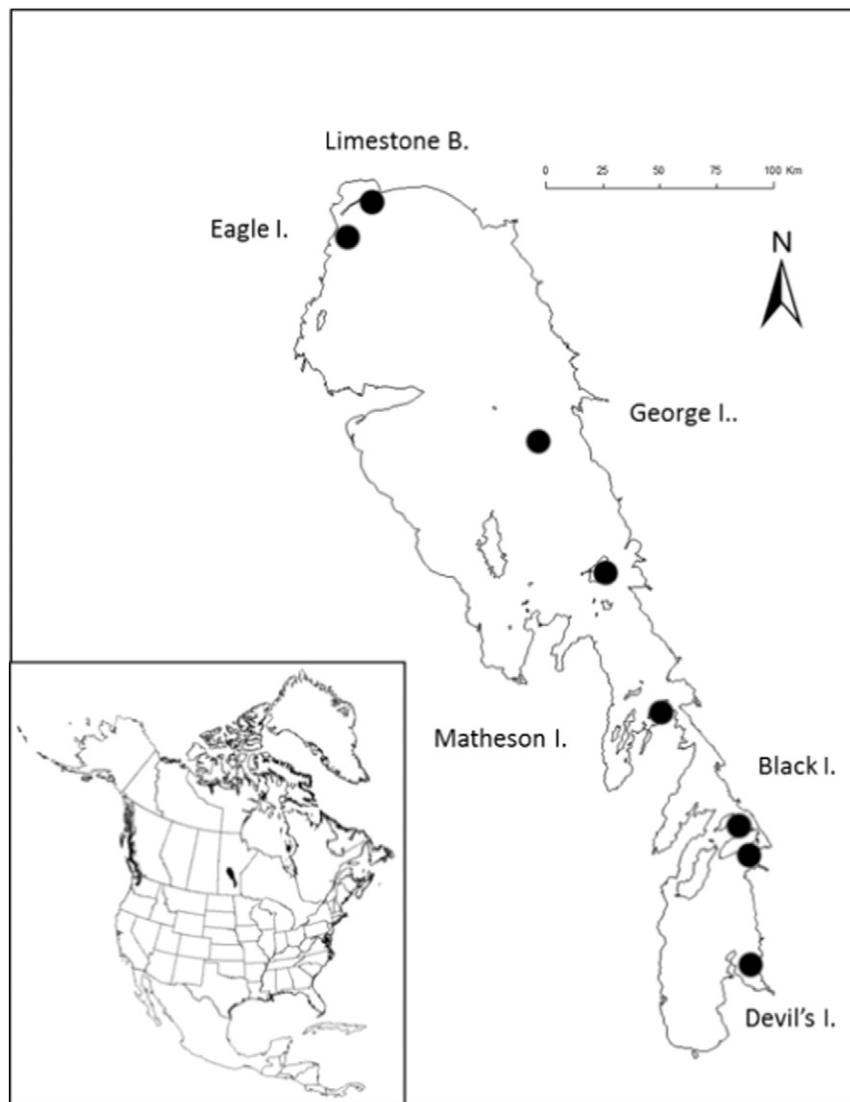
Fig. 1. Cormorant sample collection sites on Lake Winnipeg, Canada. Circles represent collection sites for May–August 2009 and June–August 2010. Some colonies were on small, unnamed islands, so regional landmarks (e.g., George Island) were used as location identifiers. The north and south basins are separated by the narrows approximately one-third of the way from the south end of the lake.

spectrometry (ICP-MS) at the Toxicology Centre, University of Saskatchewan, Saskatoon, Canada. Recoveries from DORM-2 reference material and coefficients of variation (CVs) on the duplicate samples were accepted when within ±20% and ±15%, respectively. Limits of detection (LoD) for Al, As, Cd, Cu, Fe, Mn, and Se were 0.9 µg/g, 5.2×10^{-4} µg/g, 1.7×10^{-4} µg/g, 1.8×10^{-3} µg/g, 0.1 µg/g, 1.1×10^{-3} µg/g and 7.2×10^{-4} µg/g dry mass (dw), respectively.

Mercury analysis

The samples of fresh cormorant muscle were microwave digested (U.S. EPA, 1996) and analyzed for total Hg (hereafter "Hg") via cold vapor atomic fluorescence spectroscopy at the Saskatchewan Research Council Environmental Analytical Laboratory in Saskatoon, Canada. Blanks, reference material (DORM-2), and duplicates were included with every 10 samples. Recoveries of Hg from DORM-2 were 85–100%, and the CVs of the duplicate samples were within 15%. The limit of detection (LoD) was 0.01 µg/g fresh mass (fw). We used percent moisture values for each muscle sample (75.1 ± 2.4%) to convert the fw Hg values to units of µg/g dw.

Statistical analyses

The stable isotope values of zooplankton ($\delta^{15}N_{Zoop}$), dissolved inorganic carbon ($\delta^{13}C_{DIC}$) and dissolved sulfate ($\delta^{34}S_{DS}$) in Lake Winnipeg are spatially heterogeneous (Hobson et al., 2012). Distinctive variation in the baseline $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values of the north and south basins of Lake Winnipeg confound the interpretation of isotopic data for consumers (Hobson et al., 2012; Post, 2002). To remove the effects of basin baseline variability, isotopic data for cormorant muscle were adjusted according to:

$$\delta X_{Adjusted} = \delta X_{Consumer} - \delta X_{Baseline}$$

where X was one of ^{15}N, ^{13}C and ^{34}S, and $\delta X_{Baseline}$ was the mean $\delta^{15}N_{Zoop}$ (north = +3.4 ± 1.9‰, n = 31; south = +9.6 ± 2.8‰, n = 27), $\delta^{13}C_{DIC}$ (north = −3.4 ± 2.0‰, n = 31; south = −8.4 ± 1.0‰, n = 30) or $\delta^{34}S_{DS}$ (north = −4.7 ± 3.1‰, n = 30; south = −8.2 ± 2.5‰, n = 29) value for the basin where a given cormorant was captured. A basin-specific correction was chosen as we assumed that cormorants did not travel outside of these large areas to forage (Wires et al., 2001; see also Table 1), and that their prey were

Table 1
Mean ± SD δ^{15}N, trophic position (TP), δ^{34}S and δ^{13}C for cormorants nesting on Lake Winnipeg. Stable isotope data for muscle is baseline corrected (Equation 5.2). Isotopic units are per mil (‰).

Group	Location	n	δ^{15}N (‰)	TP	δ^{13}C (‰)	δ^{34}S (‰)
North basin, adult	All	32	+9.4 ± 0.8	5.6 ± 0.5	−21.9 ± 0.7	−0.3 ± 1.6
	Cox Island	7	+10.1 ± 0.4	5.9 ± 0.2	−22.7 ± 0.4	−1.5 ± 1.8
	Eagle Island 2009	3	+9.3 ± 0.2	5.5 ± 0.1	−21.5 ± 0.1	+2.3 ± 1.0
	Eagle Island 2010	10	+8.7 ± 0.3	5.1 ± 0.2	−21.4 ± 0.3	−0.6 ± 0.5
	George Island	10	+9.7 ± 0.7	5.7 ± 0.4	−21.7 ± 0.4	−0.6 ± 1.4
	Limestone Bay	1	+10.9	6.4	−23.8	+1.5
	Matheson Island	1	+11.0	6.5	−21.7	+1.3
South basin, adult	All	8	+5.2 ± 0.9	4.0 ± 0.5	−17.7 ± 1.0	+4.0 ± 1.6
South basin, hatch-year	All	12	+5.5 ± 0.9	4.1 ± 0.5	−18.3 ± 0.4	+0.4 ± 1.2

also representative of the two major basins (Hobson et al., 2012; Ofukany et al., 2014).

We estimated the cormorant TP on a basin-specific scale in order to compare δ^{15}N data across systems (Hobson, 2009; Hobson et al., 2012) using the equation:

$$TP_{Cormorant} = TP_{Fish} + \left(\delta^{15}N_{Cormorant} - \delta^{15}N_{Fish}\right)/1.70‰$$

based on δ^{15}N values in the cormorant muscle ($\delta^{15}N_{Cormorant}$), the lowest mean $\delta^{15}N_{Fish}$ and TP_{Fish} of potential prey fishes and a diet-tissue discrimination factor of +1.70‰ (Caut et al., 2009; Hobson, 2009). Estimates of the cormorant TP were based on white sucker (*Catostomus commersonii*; δ^{15}N = 6.8 ± 1.2‰, TP = 4.0 ± 0.04, n = 55) in the north basin and emerald shiner (*Notropis atherinoides*, δ^{15}N = 3.7 ± 1.5, TP = 3.1 ± 0.4, n = 60) in the south, as these were the potential prey species with the lowest δ^{15}N values (Hobson, 2009; Ofukany et al., 2014).

All the statistical tests were conducted in R Version 3.0.2 (R Development Core Team, 2014). Shapiro–Wilk's goodness-of-fit test and Levene's test were used to determine whether the cormorant data were normally-distributed and had homogenous variances, respectively (Blanco et al., 2009; Levene, 1960; Shapiro and Wilk, 1965). The mean (±SD) δ^{15}N, δ^{13}C and δ^{34}S values of fishes and cormorants from each basin were used to plot food web structure in terms of three-dimensional isotopic space (Fig. 2).

We used the stable isotope analysis in the R (SIAR) package to estimate the proportional contribution of various fish species to cormorant diet (Parnell et al., 2010). We used stable isotope values of fish muscle collected during the ice-free seasons of 2009 and 2010, to match when cormorants were collected (Ofukany et al., 2014). We further reduced potential prey sources by removing fishes with fork lengths of >400 mm, which cormorants cannot ingest (Doucette et al., 2011), and species with <5 individuals with total lengths of ≤400 mm. Because the number of potential sources (prey species) in the north (n = 12) and south basin (n = 11) far exceed the number of isotopic tracers (n = 3), sources with statistically similar isotope values were pooled (Phillips and Gregg, 2003) using a Wilcoxon rank sum test with a Bonferroni correction for multiple comparisons to compare the isotopic profiles of all the prey species within each basin (Dalgaard, 2008; Hobson et al., 2012). Bonferroni corrections are conservative, and may therefore group prey species more frequently than other statistical methods. Sources were pooled only when there were no significant differences in δ^{15}N, δ^{13}C, and δ^{34}S between two species at the p ≤ 0.05 level (Phillips and Gregg, 2003).

We used diet-tissue isotope discrimination factors of Δ^{15}N = +1.70 ± 0.43‰, Δ^{13}C = 0.92 ± 0.27‰ and Δ^{34}S = 1.9 ± 1.0‰ (Caut et al., 2009; Moreno et al., 2010). Because no value the for avian muscle is currently known, a SD of 1.0 was applied to Δ^{34}S. The mixing models were run using non-informative priors, 1 000 000 iterations, a burn-in of 40 000, thinned by 15 for a final total of 64 000 posterior draws (Bond and Diamond, 2011; Hobson et al., 2011). The initial burn-in

and thinning interval were SIAR default values. Results were presented in terms of mean contributions (%) and 95% credible intervals.

Akaike's Information Criterion (Akaike, 1974) corrected for small sample sizes (AIC$_c$) was used to evaluate which dietary (δ^{15}N, δ^{13}C and δ^{34}S), morphological (sex, mass, tarsus length) and locational (nesting colony) parameters best explained the trace element concentrations in the cormorant muscle (Anderson, 2008; Burnham and Anderson, 2002). The model set included general linear models and a null model (Anderson, 2008; Irvine et al., 2009). Over-parameterization and very large candidate model sets can lead to unreliable results, so the number of parameters per model was maintained at roughly n/10, and the number of models considered at any one time never exceeded the sample size (n) (Anderson, 2008). Models were ranked using the R package *AICcmodavg* (Mazerolle, 2013) in terms of its ΔAIC$_c$ value and Akaike mass (w_i) (Burnham and Anderson, 2002). Any model with ΔAIC$_c$ ≥ 10.00 was deemed to be a poor fit, and any competing model with ΔAIC$_c$ ≤ 2.00 was considered to be a relatively good fit (Mazerolle, 2006; Symonds and Moussalli, 2011). If the top-ranking model did not have w_i ≥ 0.90, model-averaging was used to identify which parameters had the strongest influence on the element of interest (Burnham and Anderson, 2002). The overall effect of a given parameter was averaged over a 95% confidence set of models (Σw_i ≥ 0.95), and if the 95% unconditional confidence interval around the model-averaged estimate excluded zero, the parameter was identified as having a strong effect on the dependent variable (Pluess et al., 2012).

Results

Cormorant diet

The isotopic profiles of cormorants collected from Lake Winnipeg's north and south basins exhibited a bimodal pattern similar to that previously identified for baseline nutrients ($\delta^{13}C_{DIC}$, $\delta^{34}S_{DS}$), primary consumers ($\delta^{15}N_{Zoop}$) and fishes (Hobson et al., 2012; Ofukany et al., 2014; Table 1).

In the south basin, adult (TP = 4.0 ± 0.5, n = 8) and hatch-year (TP = 4.1 ± 0.5, n = 12) cormorants occupied similar TPs as sauger (TP = 3.9 ± 0.4, n = 111) and walleye (TP = 3.6 ± 0.5, n = 152) collected in 2009 and 2010 (Ofukany et al., 2014). Walleye and sauger from the north basin had TPs of 5.0 (sauger: SD = 0.06, n = 34; walleye: SD = 0.4, n = 124) (Ofukany et al., 2014), which was slightly lower than the cormorants from Eagle Island (2009: TP = 5.5 ± 0.1, n = 3; 2010: TP = 5.1 ± 0.2, n = 10; Table 1). However, the cormorants from Cox Island, Matheson Island and near Limestone Bay occupied TPs nearly 1–1.5 steps above walleye and sauger from the north basin (Table 1).

No colony-related, annual or seasonal differences in δ^{15}N, δ^{13}C and δ^{34}S were observed within adult (SB DCCO) or hatch-year cormorants (HY DCCO) collected from the south basin (ANOVAs, all p < 0.05). Therefore, one SIAR model was conducted for adults (n = 8) and for hatch-year birds (n = 12) from the south basin. The number of
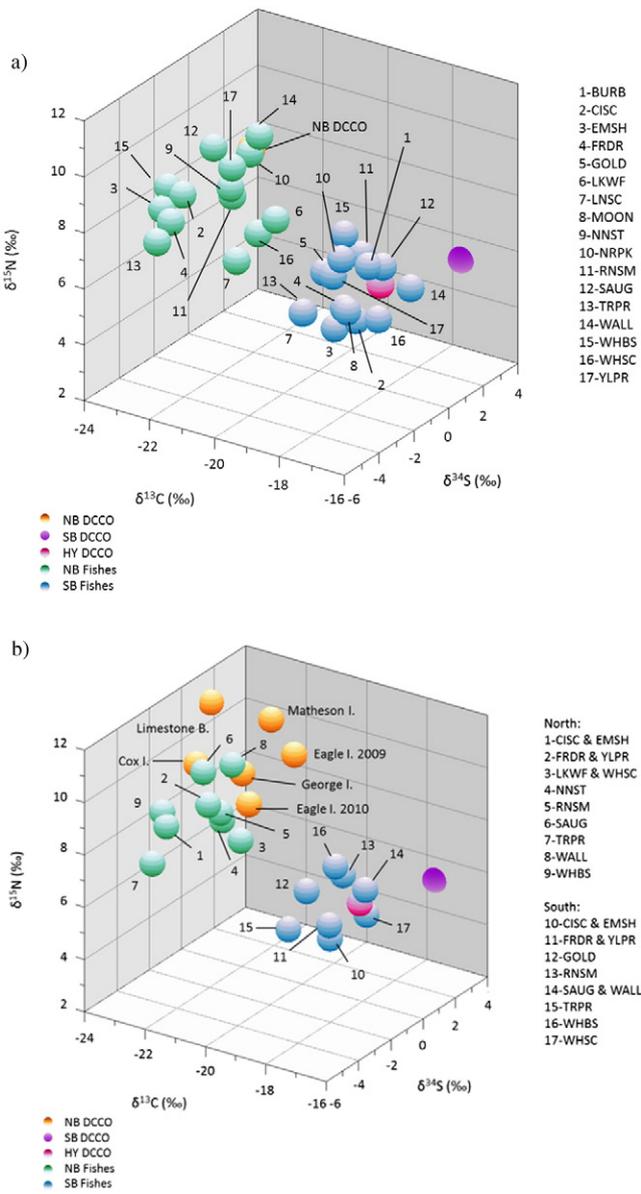
Fig. 2. a. Isotopic food web structure for cormorants and fishes collected from Lake Winnipeg during 2009 and 2010. Each point represents the mean $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ values in the north or south basin. Species codes: BURB = burbot (*Lota lota*); CISC = cisco (*Coregonus artedi*); EMSH = emerald shiner (*Notropis atherinoides*); FRDR = freshwater drum (*Aplodinotus grunniens*); GOLD = goldeye (*Hiodon alosoides*); LKWF = lake whitefish (*Coregonus clupeaformis*); LNSC = longnose sucker (*Catostomus catostomus*); MOON = mooneye (*Hiodon tergisus*); NNST = ninespine stickleback (*Pungitius pungitius*); NRPK = northern pike (*Esox lucius*); RNSM = rainbow smelt (*Osmerus mordax*); SAUG = sauger (*Sander canadensis*); TRPR = troutperch (*Percopsis omiscomaycus*); WALL = walleye (*Sander vitreus*); WHBS = white bass (*Morone chrysops*); WHSC = white sucker (*Catostomus commersonii*); YLPR = yellow perch (*Perca flavescens*). Cormorants (DCCO) are separated as to north and south basin adults and hatch year cormorants (HY DCCO). b. Isotopic food web structure for cormorants and their potential prey. Points represent the mean $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ values of cormorant groups, and potential prey sources (fishes with FL < 400 mm) used in stable isotope mixing models. Abbreviations as in Fig. 2a.

potential sources in the south basin was thereby reduced from n = 12 to n = 8, since $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values of ciscoes, freshwater drum (*Aplodinotus grunniens*) and sauger were indistinguishable from those of the emerald shiner, yellow perch (*Perca flavescens*) and walleye, respectively (Bonferroni, p ≤ 0.05).

In the north basin, $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ values for the cormorant muscle (NB DCCO) varied among colonies and between years. The cormorants collected from Eagle Island in 2009 and 2010 had the lowest

$\delta^{15}N$ values of all north basin cormorants (ANOVA, Tukey HSD; $F_{4, 25}$ = 13.09, p < 0.0001), individuals from Eagle Island in 2009 had greater $\delta^{34}S$ values than all the cormorants collected in 2010 (ANOVA, Tukey HSD; $F_{6, 23}$ = 8.35, p < 0.0001), and Cox Island (2009) birds had $\delta^{13}C$ values which were significantly lower than those from all other colonies, except Limestone Bay (ANOVA, Tukey HSD; $F_{4, 10}$ = 17.1, p = 0.0002). Based on these differences, separate mixing models were developed in SIAR for 1) Cox Island (2009), 2) Eagle Island (2009), 3) Eagle Island (2010) and 4) George Island (2009, 2010). Limestone Bay (n = 1) and Matheson Island (n = 1) cormorants fell outside the isotopic mixing space, and were therefore excluded from the SIAR analyses (Table 1; Electronic Supplementary Material, Table S1). The number of prey sources in the north basin was reduced by pooling ciscoes with emerald shiner, freshwater drum with yellow perch, and lake whitefish with white sucker, based on similar $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values (Bonferroni, p ≤ 0.05).

The contribution of potential prey fishes to cormorant diet varied with location, year, and age-class (Table 2a–f). In the north basin, troutperch (*Percopsis omiscomaycus*), ciscoes/emerald shiner and ninespine stickleback (*Pungitius pungitius*) were most frequently consumed by cormorants. At Cox Island, most potential sources had mean contribution values between 10 and 13% and 95% credible intervals ranging from 0 to 24% (Table 2), suggesting that the cormorants nesting on this island were likely feeding on a range of prey items, predominantly troutperch and ciscoes/emerald shiners.

The cormorants from George Island in 2009 and 2010 exhibited a similar dependence on ciscoes/emerald shiner (mean = 14%; 95% credible interval = 1–26%) and troutperch (mean = 16%; 95% credible interval = 2–28%; Table 2). Troutperch were also the predominant prey item for the cormorants from Eagle Island in 2010 (mean = 21%, 95% credible interval = 10–32%; Table 2). In 2009, Eagle Island birds were less reliant on troutperch (Table 2) and consumed more ninespine stickleback (mean = 14%, 95% credible interval = 0–26%).

The diet of south basin cormorants differed from their north basin counterparts. White sucker (mean = 19%, 95% credible interval = 0–37%) were the predominant prey item consumed by the cormorants nesting on the Black and Devil's Island colonies (Table 3). The mixing models for adults and hatch-year cormorants nesting in the south basin predicted a similar dependence on ciscoes/emerald shiner (Tables 2 and 3). Hatch-year cormorants, however, consumed troutperch in greater amounts than other sources (mean = 31%, 95% credible interval = 9–56%).

Contribution of commercially harvested fish

The proportion of walleye and sauger consumed by cormorants varied depending on colony location and cormorant age class. Based

Table 2
The mean (95% credible interval) % contributions of several prey groups to the diet of adult double-crested cormorants from the north basin of Lake Winnipeg, estimated using stable isotope mixing models. Prey items were grouped based on similar $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values.

Prey item	Cox Island (n = 7)	George Island (n = 10)	Eagle Island 2009 (n = 3)	Eagle Island 2010 (n = 10)
Cisco & emerald shiner (%)	13 (0–24)	14 (1–26)	12 (0–22)	13 (1–24)
Freshwater drum & yellow perch (%)	10 (0–21)	8 (0–18)	10 (0–20)	10 (0–20)
Lake whitefish & white sucker (%)	10 (0–21)	10 (0–20)	12 (0–24)	11 (0–22)
Ninespine stickleback (%)	11 (0–21)	13 (1–23)	14 (0–26)	11 (0–21)
Rainbow smelt (%)	11 (0–22)	12 (0–23)	12 (0–24)	11 (0–22)
Sauger (%)	11 (0–21)	7 (0–17)	9 (0–19)	7 (0–17)
Troutperch (%)	13 (0–24)	16 (2–28)	10 (0–21)	21 (10–32)
Walleye (%)	10 (0–20)	7 (0–16)	10 (0–20)	6 (0–15)
White bass (%)	12 (0–23)	13 (1–24)	11 (0–22)	11 (0–20)

Table 3
The mean (95% credible interval) % contributions to the diet of adult and hatch-year double-crested cormorants from the south basin of Lake Winnipeg, estimated using stable isotope mixing models. Prey items were grouped based on similar $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values.

Prey item	Adults (n = 8)	Hatch-year (n = 12)
Cisco & emerald shiner (%)	16 (0–32)	16 (0–30)
Freshwater drum and yellow perch (%)	13 (0–26)	15 (0–29)
Goldeye (%)	9 (0–22)	11 (0–24)
Rainbow smelt (%)	11 (0–25)	7 (0–19)
Sauger and walleye (%)	12 (0–26)	6 (0–15)
Troutperch (%)	10 (0–22)	31 (9–56)
White bass (%)	10 (0–22)	7 (0–18)
White sucker (%)	19 (0–37)	8 (0–19)

on the 95% credible interval, <15% of hatch-year cormorant diet consisted of walleye and sauger (range of mean estimates: 6–12%). Similarly, walleye and sauger made the smallest contributions of all the prey species to the diets of the cormorants nesting on George Island (Table 2), Eagle Island in 2009 (Table 2), and Eagle Island in 2010 (Table 2). Adult cormorants from the south basin consumed the highest relative proportion of walleye and sauger, yet these species represented, on average, only about 12% of the cormorant diet (95% credible interval = 0–26%).

Trace element concentrations

Concentrations of Al in the cormorant muscle were consistently below the detection limit. Recoveries of Cu from DORM-2 (78%) and CVs on the duplicate samples (CV ≤ 17%) fell outside the acceptable range for the cormorants collected and analyzed in 2010; therefore these values were not included in the statistical analyses. Copper concentrations for the cormorants collected in 2009 were within acceptable limits, and have been included (Table 4).

The concentrations of Al, As, Cd, Cu, Fe, Mn, Hg and Se in the pectoral muscle of the cormorants were log-transformed prior to statistical testing (Campbell et al., 2005). The mean rankings of log-transformed Cd, Hg, and Se concentrations were not significantly different among adult cormorants from either basin or hatch-year birds (Table 4; Kruskal–Wallis test; Cd: $H = 4.51$, df = 2, p = 0.10; Hg: $H = 4.44$, df = 2, p = 0.11; Se: $H = 5.37$, df = 2, p = 0.07). Similarly, log-transformed concentrations of Cu in the muscle of north and south basin adults (2009 only) were similar (Mann–Whitney U-test; $U = 84$, p = 0.13). The mean ranked log(As) values were highest in adult cormorants from the north basin, and did not differ between age classes in the south basin (Kruskal–Wallis test: $H = 16.78$, df = 2, p = 0.0002). This was the only element that differed in its concentration between the north and south basin adults. Log(Fe) and log(Mn) were significantly different among adults and hatch-year birds, with hatch-year individuals having lower mean ranked values than adults (Kruskal–Wallis test; Fe: $H = 11.47$, df = 2, p = 0.003; Mn: $H = 13.96$, df = 2, p = 0.0009).

Factors affecting elemental concentrations

The $\delta^{15}N$ composition of muscle had a strong positive effect on most elements (Cd, Fe, Mn, Hg, and Se) measured in adult cormorants from the north basin, suggesting that the cormorants feeding at higher TPs accumulated greater amounts of these trace elements in the muscle (ESM Table S2). The strongest effect of $\delta^{15}N$ or TP on elemental concentrations was observed for Hg ($\beta = 0.96$, SE = 0.13, 95% CI = 0.71–1.21); for every 1‰ increase in $\delta^{15}N$, log(Hg) increased by a factor of 0.96, and Hg concentrations would more than double (2.61 times larger). Every 1‰ increase in $\delta^{15}N$ was also varied with an approximate 1.5-fold (1.46 and 1.47, respectively) increase in Cd and Se concentrations (Cd: $\beta = 0.38$, SE = 0.10, 95% CI = 0.18–0.57; Se: $\beta = 0.39$, SE = 0.07, 95% CI = 0.26–0.53). The rate of biomagnification was also similar for Fe and Mn in north basin birds (Fe: $\beta = 0.28$, SE = 0.06, 95% CI = 0.16–0.40; Mn: model-averaged estimate = 0.26, unconditional SE = 0.06, 95% unconditional CI = 0.13–0.38).

In the south basin, $\delta^{15}N$ composition had a positive effect on Hg in adult birds only (model-averaged estimate = 0.50, unconditional SE = 0.23, 95% unconditional CI = 0.05–0.95), although the rate of increase in Hg with increasing $\delta^{15}N$ was only half that of the north basin birds.

The only negative correlation between $\delta^{15}N$ composition and trace element concentrations in the cormorant muscle was for log(Fe) in south basin adults ($\beta = -0.07$, SE = 0.03, 95% CI = −0.13 to −0.02).

Effects of size and sex

Body size and sex had little influence on Hg and other trace element concentrations in the cormorant muscle. There was no effect of the tarsus length on any elemental concentration. Body mass was included in the top-ranking models for Se in north basin adults and Hg in hatch-year birds (ESM Table S2); however, the influence of mass was weak in both instances (NB DCCO: $\beta = 0.00$, SE = 0.00, 95% CI = 0.00–0.00; HY DCCO: model-averaged estimate = 0.00, unconditional SE = 0.00, 95% unconditional CI = 0.00–0.00). Sex did have a strong effect on log(Hg) concentrations in HY DCCO however, with males accumulating less Hg in the pectoral muscle than females (model-averaged estimate$_{Males}$ = −0.28, unconditional SE = 0.14, 95% unconditional CI = −0.55 to −0.01).

Influence of nutrient source

Few models containing $\delta^{13}C$ or $\delta^{34}S$ were ranked within the top models ($\Delta AIC_c \leq 2.00$; ESM Table S2). Hatch-year cormorants, which obtain dietary carbon from pelagic sources (lower $\delta^{13}C$), rather than near the sediment (higher $\delta^{13}C$), had higher concentrations of As in the muscle (model-averaged estimate = −0.25, unconditional SE = 0.11, unconditional CI = −0.47 to −0.03). Adult cormorants from the north basin, which are increasingly reliant on water-column sources of sulfate (higher $\delta^{34}S$ values), accumulated more As in the muscle ($\beta = 0.19$, SE = 0.06, 95% CI = 0.07–0.31).

Table 4
Mean ± SD concentrations of Al, As, Cd, Cu, Fe, Mn, Hg, and Se measured in pectoral muscle of cormorants from Lake Winnipeg. Concentrations are expressed in units of μg/g dry mass. LoD: level of detection.

Group	Al	As	Cd	Cu	Fe	Mn	Hg	Se
North basin adults (n = 32)	<LoD	0.14 ± 0.10	0.10 ± 0.05	20.86 ± 1.72[a]	247.92 ± 103.35	2.00 ± 0.82	1.79 ± 1.23	1.60 ± 0.63
South basin adults (n = 8)	<LoD	0.09 ± 0.10	0.06 ± 0.03	16.72 ± 5.83	232.10 ± 94.18	1.71 ± 0.27	3.78 ± 2.91	1.32 ± 0.38
South basin hatch-year birds (n = 12)	<LoD	0.07 ± 0.01	0.06 ± 0.01	NA[b]	161.15 ± 43.33	1.28 ± 0.30	2.00 ± 0.61	1.08 ± 0.18

[a] 2009 (n = 15) data only; 2010 analytical batch did not pass QA/QC.
[b] Analytical batch did not pass QA/QC.

Discussion

Cormorant diet

The diet of adult cormorants nesting on Lake Winnipeg differed from those of hatch-year birds, and varied among the north and south basins and among colonies. Regardless of location, fishes of little direct commercial value comprised the largest proportions of cormorant diet (Tables 2 and 3). Trophic positions (TPs) of adult cormorants from the north basin were similar to those of the cormorants nesting on Prairie lakes (i.e., Canoe, Dore and Last Mountain lakes) in Saskatchewan (TP = 5.3 ± 0.4), where ciscoes and ninespine stickleback were among the most heavily-consumed fishes (Doucette et al., 2011).

The proportions of yellow perch in the cormorant diet at Last Mountain Lake (mean estimate = 44%), and in regurgitated samples from Lake Winnipegosis in 1987 (27.6% of biomass) (Hobson et al., 1989) were larger than we have estimated for the Lake Winnipeg cormorants. The highest mean yellow perch contribution identified from isotope mixing models was for hatch-year cormorants in the south basin (Table 3), and the mean estimate (15%) was similar to the percent biomass estimate of 13% from regurgitations in lakes Huron, Michigan and Superior in the late 1980s (Ludwig et al., 1989). Hatch-year cormorants consumed similar amounts of yellow perch and ciscoes/emerald shiner (mean = 16%, 95% credible interval = 0–30) and more troutperch (mean = 31%, 95% credible interval = 9–56; Table 3).

Walleye and sauger with fork lengths of ≤400 mm were marginally important as prey items for the cormorants at Cox Island (mean dietary contributions of 10% and 11%, respectively; Table 2). We acknowledge that the cormorants from Cox and Matheson islands may have had access to walleye and sauger discarded as waste from nearby commercial fish packing stations (Fox et al., 2002; Manitoba Water Stewardship, 2010). A single cormorant collected near Limestone Bay was likely feeding within the Bay (northwest of the north basin, Fig. 1), which could potentially confound the results of our baseline correction.

Little historical dietary data are available for the cormorants or other aquatic birds nesting on Lake Winnipeg. Adult herring gulls (*Larus argentatus*) collected near Grand Rapids (north basin) from 1991–1993 occupied a mean TP of 3.7 (Fox et al., 2002), much lower than that of north basin cormorants. However, gull $\delta^{13}C$ value (−24.8 ± 0.7‰), when corrected based on $\delta^{13}C_{DIC}$ ($\delta^{13}C \approx -20.5‰$), was higher than the cormorant muscle $\delta^{13}C$ (Table 1), and may indicate that gulls were more benthically linked than the cormorants. Importantly, the gull data from 1991–1993 precede the recent eutrophication and food web perturbations, including record floods, and changes in the flow rates that govern current nutrient dynamics in the lake (Environment Canada, Manitoba Water Stewardship, 2011).

Mercury & other trace elements

Although the variables best explaining elemental concentrations in the cormorant muscle differed by colony location and bird age class, the concentrations of many elements such as Al (<LoD), Cd, Cu, Hg, and Se did not differ between basins or among age classes. We predicted that Hg would be lower in hatch-year birds because they had not been exposed to Hg in the previous winter (Ofukany et al., 2012). Hatch-year cormorants had TPs similar to those of burbot (*Lota lota*), northern pike (*Esox lucius*), sauger, and white bass (*Morone chrysops*); the $\delta^{13}C$ and $\delta^{34}S$ values for this group of birds were similar to those of sauger (Ofukany et al., 2014), but Hg concentrations in hatch-year cormorants (2.00 ± 0.61 μg/g dw) were approximately double that of the sauger (1.10 ± 0.60 μg/g dw) (Ofukany et al., 2014; Table 4). This was surprising, as the stable isotope values of these two species were similar, and much of the young cormorants Hg is sequestered in newly-formed feathers, rather than in the muscle (Caldwell et al., 1999). Although

this accounts for only 35–68%, some Hg must be sequestered in internal tissues (Monteiro and Furness, 2001).

Unlike Hg in hatch-year cormorant muscle, the concentrations in the muscle of adults were a function of $\delta^{15}N$, or TP. There was a 0.50-fold increase in log-transformed Hg with every 1‰ increase in $\delta^{15}N$ for adults collected in the south basin, similar to the 0.48-fold increase reported for a variety of seabirds from Kongsfjorden, Svalbard (Jaeger et al., 2009). The cormorants from Lake Winnipeg had much higher Hg concentrations than Svalbard seabirds (largest mean ± SE = 1.07 ± 0.20 μg/g dw for glaucous gulls (*Larus hyperboreus*); assuming 70% moisture; Table 4) (Jaeger et al., 2009). Hg concentrations of Lake Winnipeg cormorants were generally lower than those measured in the muscle of a common loon (*Gavia immer*; Hg = 5.0 μg/g dw, n = 1), American coot (*Fulica americana*; Hg = 1.13 μg/g dw, n = 1) and herring gulls (mean Hg = 5.67 μg/g dw, range = 2.2 to 13.33 μg/g dw, n = 5) from Tadenac Lake, Ontario (Wren et al., 1983).

The biomagnification of Cd and Mn in the north basin cormorants was unexpected. Trophic position has a negative effect on the Cd concentrations in birds, fishes and other organisms collected from the Northwater Polynya, Baffin Bay (Campbell et al., 2005), and the bioaccumulation of Cd found in seabirds collected from the Barents Sea is the result of age effects (Savinov et al., 2003). Although Cd appears to show biomagnification in the cormorants in Lake Winnipeg's north basin, the mean concentration (0.10 ± 0.05 μg/g dw, n = 32; Table 4) was an order of magnitude lower than that found in seabirds from the Northwater Polynya, assuming a moisture content of 70% (Campbell et al., 2005).

The concentrations of Mn were unrelated to $\delta^{15}N$ in the Northwater Polynya food web, or in the food web of Tadenac Lake (Campbell et al., 2005; Wren et al., 1983). Herring gulls collected from Tadenac Lake had muscle Mn concentrations similar to those in rainbow smelt (*Osmerus mordax*), northern pike and other fishes, ranging from 2.0 to 4.7 μg/g dw. The Mn concentrations measured in the muscle of adult cormorants from the north basin (2.00 ± 0.82 μg/g dw; Table 4), and in adult and hatch-year cormorants from Lake Winnipeg's south basin (mean = 1.71 ± 0.27 μg/g dw and 1.28 ± 0.30 μg/g dw, respectively) were similar to Mn in the fish muscle (range: 0.38–2.11 μg/g dw) (Ofukany et al., 2014).

Arsenic in cormorants (around 0.1 μg/g; Table 4) were similar to, or lower than the concentrations observed in Lake Winnipeg fish (range of means: 0.1–0.8 μg/g; Ofukany et al., 2014), adding further evidence that As rarely bioaccumulates across trophic levels in the freshwater systems (Blight, 2011). It is currently unclear why metal concentrations differ between basins and why the relationships between the cormorant and fish tissue $\delta^{15}N$ and metal concentrations do not show the same patterns in each basin. Each basin drains different watersheds and is subject to different nutrient loads (Schindler et al., 2012; Wassenaar and Rao, 2012). Possibly, productivity differences between basins or overall foodweb length may be a factor but clearly, future research is needed to resolve these questions.

Conclusions

Affirming several previous studies, we found that commercially valuable walleye and sauger represented a relatively small proportion of the diet of adult and hatch-year cormorants throughout Lake Winnipeg. Although it is possible that some of the cormorants were consuming wastes from commercial processing facilities, or preying on netted fish, these phenomena need further investigation and likely represent incidental occurrences only. Although cormorants are migratory, and are exposed to concentrations of contaminants throughout the year (Ofukany et al., 2012), the concentrations of most elements were correlated to $\delta^{15}N$ values in the muscle, representing cormorant dietary habits over about a six-week period prior to capture (Hobson, 2009). The concentrations of As in the cormorant muscle were lower than those in Lake Winnipeg fishes, and Cd, Mn, and Se were similar in fish

and avian samples. The concentrations of Hg were greater in the cormorants relative to fishes, despite the absence of carry-over effects in hatch-year birds (Ofukany et al., 2012). Characterizing the cormorant diet in an isotopically variable system, such as Lake Winnipeg, is challenging, and must account for the differences in isotopic baseline values throughout the lake. Linking trace element concentrations with individual foraging ecology using stable isotopes can vastly improve understanding of contaminant and nutrient flow within and among systems (Jardine et al., 2006).

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2015.03.008.

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