

Trophic ecologies of double-crested cormorants and native piscivorous fishes in Lake
Nipissing, Ontario

by

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Abstract

Fisheries assessments have indicated a decline in Lake Nipissing's walleye (*Sander vitreus*) population in recent decades. This has coincided with an increase in double-crested cormorants (DCCO; *Nannopterum auritum*) on Lake Nipissing to conspicuous numbers (3,000 nests in 2012), fueling concerns that cormorant predation may be adversely affecting walleye recovery. I used carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) to examine the food web structure of Lake Nipissing, and in particular, the role of DCCO predation and competition in relation to four other native piscivores; walleye, northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*) and burbot (*Lota lota*). Trophic position (TP), estimated from $\delta^{15}\text{N}$, and trophic niche size (SEAc), inferred from the dispersion of individuals in $\delta^{13}\text{C} - \delta^{15}\text{N}$ isotopic space, were used to characterize piscivore niches. MixSIAR stable isotope mixing models (SIMM) were used to estimate the diet compositions of DCCO and piscivorous fishes. Among the piscivores, DCCO had the highest reliance on pelagic resources, the lowest trophic position, and the largest trophic niche size. Piscivorous fishes had higher levels of trophic niche overlap with each other than with DCCO. SIMMs predicted that DCCO diet was primarily composed of emerald shiner (*Notropis atherinoides*) and logperch (*Percina caprodes*) with low proportions of all other prey fishes. Emerald shiner and logperch also dominated the diets of piscivorous fishes indicating dietary overlap with DCCO to some extent. Juvenile walleye were a relatively small proportion of the diets of both DCCO and piscivorous fishes based on SIMM predictions. Currently, there is no indication of limitations in Nipissing's forage fish prey

base so potential for interspecific competition is considered low. The low likelihood of trophic niche overlap between DCCO and piscivorous fishes and the low contribution of juvenile walleye to DCCO diet suggests a low impact of DCCO predation on Nipissing's recovering walleye population. Stable isotope-based diet inference can complement bio-energetic models and other ecosystem assessment methods to improve our understanding of how DCCO interact with fish populations.

Keywords: freshwater, food web, invasive species, feeding ecology, predation, competition, stable isotopes

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Table of Contents

Abstract	iii
Acknowledgments.....	v
Table of Contents	vi
List of Tables	viii
List of Figures	x
List of Appendices	xiv
1.0 Introduction.....	1
2.0 Methods.....	9
2.1 Invertebrate and small-bodied fish sampling	9
2.2 Large-bodied fish sampling.....	12
2.3 Double-crested cormorant sampling	13
2.4 Sample preparation and stable isotope analysis	14
2.5 Data handling and statistical analyses.....	14
2.5.1 Trophic position analysis	15
2.5.2 SIBER isotopic niche analysis	17
2.5.3 Diet compositions of piscivores.....	18
3.0 Results.....	21
3.1 The Lake Nipissing food web in isotopic space.....	21
3.2 Trophic position analysis	21
3.3 SIBER isotopic niche analysis	25
3.4 Diets of DCCO and piscivorous fishes estimated by MixSIAR	32
4.0 Discussion.....	40

4.1 Using stable isotope analysis to interpret aquatic food webs.....	41
4.2 Lake Nipissing food web structure and trophic niche positions of DCCO and native piscivorous fishes	43
4.3 Trophic niche sizes of DCCO and piscivorous fishes.....	48
4.4 Trophic niche overlap between DCCO chicks and piscivorous fishes	50
4.5 Diet composition of DCCO and piscivorous fishes	51
4.6 Conclusions and fisheries management implications	61
Literature cited	64
Appendix.....	77

List of Tables

Table 1. Pairwise comparison matrix showing the probability of overlap between estimated mean trophic positions of double-crested cormorant chicks sampled from three nesting colonies on Lake Nipissing, Ontario, in June 2015. Trophic positions of double-crested cormorant chicks were estimated using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values standardized to a body mass of 1000 g.	24
Table 2. Pairwise comparison matrix showing the probability of overlap of mean trophic positions of double-crested cormorants and piscivorous fishes sampled from Lake Nipissing, Ontario, 2012 - 2016. Trophic positions of all taxa were estimated using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values standardized to a body mass of 1000 g.	27
Table 3. Pairwise comparison matrix for standardized ellipse areas (SEAc) of piscivores sampled from Lake Nipissing, Ontario, 2012 – 2016. Ellipse areas were calculated in SIBER using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to a body size of 1000 g. Values indicate the probability that a consumer in the row has a SEAc larger than the SEAc of the consumer in the column.	29
Table 4. Pairwise comparison matrix showing percentage overlap of standardized ellipse areas (SEAc) among piscivores sampled from Lake Nipissing, Ontario, 2012-2016. Ellipse areas, and their overlap, were calculated in SIBER using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to a body size of 1000 g.	31

Table 5. Summary of previous studies that have estimated DCCO diet composition in various locations on and near the Laurentian Great Lakes. 54

List of Figures

Figure 1. Map of Lake Nipissing showing sampling sites of double-crested cormorant chicks (Black stars; 1 = Hardwood Islands, 2 = Goose Islands, 3 = Gull Islands) and small-bodied forage fishes (Red circles; 4 = Goulais Point, 5 = Frank’s Point, 6 = Manitou Islands). 10

Figure 2. The food web positions of piscivores (red triangles) and potential prey fishes (blue squares) relative to two baseline invertebrates (black circles) within the $\delta^{13}\text{C} - \delta^{15}\text{N}$ isoscape of Lake Nipissing, Ontario, 2011-2016. Symbols are body size-adjusted means (± 1 SD); piscivore data were adjusted to 1000 g (BUR = burbot, DCCO = double-crested cormorant chicks, NP = northern pike, SMB = smallmouth bass, ADULT_WALL = large walleye), prey fish data were adjusted to 10 g (RSMELT = rainbow smelt, EMSHINER = emerald shiner, LPERCH = logperch, SPSHINER = spottail shiner, TPERCH = trout-perch, YPERCH = yellow perch, JUV_WALL = small walleye) and baseline invertebrate data were not adjusted for body size (CLAM = unionid clams, SNAIL = snails). 22

Figure 3. Trophic positions of double-crested cormorant chicks from three nesting colonies on Lake Nipissing, Ontario, in June 2015. Symbols are means with 95% credibility intervals. Cormorant chick trophic positions were calculated from muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values standardized to a body mass of 1000 g..... 23

Figure 4. Estimated trophic positions of various piscivores and forage fishes sampled from Lake Nipissing, Ontario, 2011 – 2016. Symbols are size-adjusted means with 95% credibility intervals. Trophic positions were calculated using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values adjusted to 1000 g body mass for piscivores (BUR = burbot, DCCO = double-crested cormorant chicks, NP = northern pike, SMB = smallmouth bass, ADULT_WALL = large walleye), and to 10 g for forage fishes (RSMELT = rainbow smelt, EMSHINER = emerald shiner, LPERCH = logperch, SPSHINER = spottail shiner, TPERCH = trout-perch, YPERCH = yellow perch, JUV_WALL = small walleye). 26

Figure 5. Comparison of isotopic niche sizes for five piscivores sampled from Lake Nipissing, Ontario, 2012 - 2016. Standardized ellipse areas (SEAc) were calculated from muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to a body size of 1000 g. Black dots represent means and shaded boxes indicate the 50, 75 and 95 % credible intervals. 28

Figure 6. Predicted proportional contributions of seven forage fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = juvenile walleye, YPERCH = yellow perch) to the diets of four piscivorous fishes (WALL-A = large walleye, NP = northern pike, SMB = smallmouth bass, BURB = burbot) sampled from Lake Nipissing, Ontario, 2012-2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g and 1000 g for prey and predator, respectively, and trophic enrichment factors from Vander Zanden and Rasmussen (2001). 33

Figure 7. Predicted proportional contributions of seven forage fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diet of double-crested cormorant (DCCO) chicks sampled from Lake Nipissing, Ontario, in June 2015. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g and 1000 g for prey and cormorant chicks, respectively, and trophic enrichment factors from four earlier studies (Source of TEF parameters). Estimates based on TEFs derived from DCCO are on the left (Craig et al. 2015a), all other estimates are based on TEFs derived from other fish-eating birds..... 34

Figure 8. Predicted proportional contributions of seven prey fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diets of double-crested cormorant chicks (DCCO, top) and walleye (WALL-A, bottom) sampled from Lake Nipissing, Ontario, 2012 -2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 1000 g for DCCO chicks and walleye, and adjusted to 5, 10, or 20 g for prey fishes. Trophic enrichment factors used for modeling were taken from Craig et al. (2015a) for DCCO chicks and from Vander Zanden and Rasmussen (2001) for walleye. Emerald shiner and logperch don't attain body masses of 20 g in Lake Nipissing and were not included as prey categories when modeling 20 g prey. 36

Figure 9. Predicted proportional contributions of seven prey fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diets of burbot (BURB, top) and adult walleye (WALL-A, bottom) sampled from Lake Nipissing, Ontario, 2012 -2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g for all prey species, and adjusted to 500, 1000, or 2000 g for burbot and walleye. Trophic enrichment factors used for modeling were taken from Vander Zanden and Rasmussen (2001). 38

Figure 10. Predicted proportional contributions of seven prey fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diet of walleye sampled from Lake Nipissing, Ontario, 2012 - 2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g and 1000 g for prey and predator, respectively, and trophic enrichment factors (Source of TEF parameters) derived from three earlier studies..... 39

List of Appendices

Table A1.1. Analysis of relationships between tissue $\delta^{13}\text{C}$ and body size (\log_{10} mass) for various biota sampled from Lake Nipissing from 2010 to 2017. Models included both \log_{10} mass and sampling year (class variable, fixed effect) without interaction terms, and significance of each are indicated (* partial-F test, $P < 0.05$). Model results for taxa with < 10 individuals analyzed are not included. $b_1 = \delta^{13}\text{C}$ vs \log_{10} mass slope. Size range gives the minimum – maximum body masses of each species used in analysis..... 77

Table A1.2. Analysis of relationships between tissue $\delta^{15}\text{N}$ and body size (\log_{10} mass) for various biota sampled from Lake Nipissing from 2010 to 2017. Models included both \log_{10} mass and sampling year (class variable, fixed effect) without interaction terms, and significance of each are indicated (* partial-F test, $P < 0.05$). Model results for taxa with < 10 individuals analyzed are not included. $b_1 = \delta^{15}\text{N}$ vs \log_{10} mass slope. Size range gives the minimum – maximum body masses of each species used in analysis..... 79

1.0 Introduction

Freshwater ecosystems only cover 0.8% of the Earth's surface but contain up to one third of all vertebrate species, including 40% of global fish diversity (Dudgeon et al. 2006). Freshwater ecosystems provide invaluable services such as drinking water, food, and recreation, and have immense aesthetic, cultural and spiritual significance. The recreational fishing industry is of noteworthy economic importance, for instance in 1995 Lake Ontario's recreational fishery generated \$53 million for the province of Ontario (Mills et al. 2003). The strong trophic linkages that characterize aquatic ecosystems may be particularly susceptible to disruptions from invasive species (Gallardo et al. 2016). Biological invasions within freshwater habitats have been studied extensively and a multitude of deleterious outcomes have been reported such as displacing native species by directly preying upon or outcompeting them for habitat or resources, habitat alteration, disease and parasite transfer, food web disruption, and increased contaminant bioaccumulation in higher trophic levels (Spencer et al. 1991; Swanson et al. 2003; Levine 2008; Liu et al. 2011). A more comprehensive understanding of how invasive species interact with native food webs is imperative in devising methods of mitigating their potential impacts.

The double-crested cormorant (hereafter DCCO; *Nannopterum auritum*, formerly *Phalacrocorax auritus*) is a migratory, colonial, fish-eating bird that is native and widely distributed in North America with a breeding range spanning all major flyways (Weseloh and Ewins 1994; Wires et al. 2001). Within the last thirty years,

DCCO populations have grown markedly in many regions throughout North America, with reports of expansion beyond their historical range (Wires et al. 2001; Wires and Cuthbert 2006; Doucette 2012; Bugajski et al. 2013). The DCCO is a highly opportunistic piscivore, capable of consuming a wide diversity of fishes; over 250 different fish species have been reported in their diet over their North American range (Wires et al. 2001). Due to a reputation for being efficient predators of fish and their high visibility as colonial nesters, DCCO have been implicated in the decline of economically-valuable fish populations within North America (Rudstam et al. 2004; Diana et al. 2006; Fielder 2010). Cormorant population control remains one of the most contentious issues in current wildlife management (Doucette et al. 2011; Ovegård 2017). In spite of this mass concern and controversy, relatively little is known of how DCCO may impact freshwater food webs (Doucette et al. 2011). A handful of studies have examined the potential impacts of cormorants on fisheries of interest, some vilifying DCCO (Birt et al. 1987; Coleman et al. 2016; Ovegård 2017), and others reporting that DCCO fish consumption has negligible effects (Wires et al. 2001; Coleman et al. 2005; Doucette et al. 2011). Ultimately, conclusions remain ambiguous, leaving a fragmented understanding of whether DCCO fish consumption is detrimental to fisheries.

Cormorants are typically regarded as pursuit-divers that are reliant on vision to detect and capture prey (Strod et al. 2004). However, it has recently been demonstrated that cormorants may possess poor visual acuity while in water and the ability to resolve

spatial detail begins to wane at distances of >1 m (White et al. 2007; Martin et al. 2008). Furthermore, it appears that many species of cormorant rarely perform high-speed diving pursuits of prey (Ropert-Coudert et al. 2006; Gómez-Laich et al. 2015). Instead of pursuit-foraging, diving cormorants may employ a close-quarter foraging strategy termed “single-strike lunging” analogous to that used by herons and egrets (Ardeidae); in which prey is seized at short range by rapid extension of the neck (Grémillet et al. 2006; White et al. 2007; Martin et al. 2008; Gómez-Laich et al. 2015). Cormorants may have increased dependence on other senses while foraging to compensate for limited visual capabilities. For example, cormorants are well adapted to hear in aquatic environments and may utilize underwater auditory cues to detect and capture prey as well as communicate with other conspecifics (Hansen et al. 2016, 2017; Johansen et al. 2016; Larsen et al. 2020). Although cormorants will forage alone, European shags *Phalacrocorax aristotelis* will frequently participate in social foraging behavior during non – breeding periods, aggregating on the water surface into “foraging rafts” (Evans et al. 2019) that perform cooperative dives to herd, flush or interrupt the cohesion of schooling fish (Cook et al. 2017). This group foraging strategy in cormorants may also improve foraging success by relaying social information to direct other conspecifics to locations of high prey densities (Van Eerden and Voslamber 1995; Cook et al. 2017).

Double-crested cormorants are opportunistic predators and their prey selection appears to be linked to fish community characteristics within foraging areas (Gagliardi

et al. 2015; Koenigs et al. 2021). Their diets will shift according to prey availability as highlighted by the well documented shift in DCCO dietary preferences from alewife (*Alosa pseudoharengus*) to round goby (*Neogobius melanostomus*), following the introduction of round goby into the Great Lakes basin (Johnson et al. 2010b , 2015; Coleman et al. 2012; Madura and Jones 2016). Furthermore, DCCO have also demonstrated prey switching in response to seasonal changes in forage fish abundances (Belyea et al. 1997; Bur et al. 1997; Johnson et al. 2002; Diana et al. 2006; Koenigs et al. 2021). Size and type of prey consumed may also vary with the life stage of DCCO. The chicks of DCCO are altricial (nidicolous) consuming regurgitated boli of prey provided by the adults (Wires et al. 2001). Food boli for the chicks are mostly composed of intact prey (Johnson et al. 2008b) and they would presumably be fed smaller prey items than what adults could consume due to gape limitations (Somers et al. 2003). Although no direct comparisons between chick and adult diets have been made, a few studies found boli provided to chicks consisted mostly of relatively small prey items (Neuman et al. 1997; Doucette et al. 2011).

Traditional diet analysis methods, such as examining stomach contents and regurgitates, have been used to characterize diets of cormorants (Opačak et al. 2004; Yorio et al. 2010; Boström 2013; Ovegård 2017), and of DCCO in particular (Bur et al. 1997; Dalton et al. 2009; Göktepe et al. 2012; DeBruyne et al. 2013). Stable isotope analysis has also been used to explore cormorant feeding ecology (Bearhop et al. 1999; Hobson 2009; Bugajski et al. 2013; Craig et al. 2016). Studies have employed stable

isotope mixing models (SIMMs) to estimate the relative importance of different prey types to the DCCO diet (Jones et al. 2010; Doucette et al. 2011; Ofukany et al. 2015; King et al. 2017). Former diet studies using cast pellets, regurgitates and stomach contents have demonstrated that game fish species, particularly yellow perch (*Perca flavescens*) and walleye, make up relatively large proportions of DCCO diets in some waterbodies (Belyea et al. 1997; Johnson et al. 2002, 2015; Rudstam et al. 2004; Fielder 2008; Göktepe et al. 2012; Schultz et al. 2013; DeBruyne et al. 2017). However, other studies have reported that although walleye and yellow perch appeared in DCCO diet, they were of low relative importance (Bur et al. 1997; Doucette et al. 2011; King et al. 2017; Koenigs et al. 2021). Diet studies of DCCO have been undertaken in Ontario, but generally on populations nesting on the Laurentian Great Lakes (Bur et al. 1997; Johnson et al. 2008a, 2010a, 2010b, 2015) and because cormorant diets can vary substantially from region to region, Great Lakes results may not be applicable to other waterbodies.

Lake Nipissing (46° 17' N, 80° 00' W) has a surface area of 87,325 ha making it the third largest lake within Ontario's borders (OMNR 2012; Morgan 2013). Although large in surface area, Lake Nipissing is relatively shallow with a mean depth of 4.5 m (OMNR 2012; Morgan 2013). Due to its shallow depth and large fetch the majority of the lake is well mixed and remains unstratified year round, except for a small area of deep water (52 m maximum depth) near the French River outflow (Neary and Clark 1992). Lake Nipissing's drainage basin is situated on Precambrian metamorphic and igneous

bedrock mantled with vestigial sand and clay soils deposited from glacial Lake Algonquin (Neary and Clark 1992). Overall, Lake Nipissing is considered mesotrophic; due to its unique catchment geology, it has a slightly elevated pH and nutrient status, and slightly lower water clarity relative to other nearby shield lakes (Neary and Clark 1992). Lake Nipissing provides a medley of important ecosystem functions; although as one of northeastern Ontario's premier recreational fishing destinations it is particularly recognized for its fishing opportunities. The lake has also historically been a vital resource to local First Nation Communities by supporting subsistence and commercial fisheries.

Within Nipissing's fish community, walleye are arguably the most important species, socially and economically. Over the past two decades, fisheries assessments have indicated a decline in Lake Nipissing's walleye population, raising concern surrounding the precarious future of the invaluable fish stocks (Dunlop 1997; Morgan 2013). Surplus-production modeling indicated that Lake Nipissing walleye stocks had been overharvested from 1976 onwards and concluded that reducing annual harvest was the best course of action in returning stocks to sustainable numbers (Zhao and Lester 2013). There is also concern that recent alterations to Lake Nipissing's food web may be exacerbating the effects of overharvesting. One such alteration is the increase in abundance of spiny water flea (*Bythotrephes cederstroemi*), formerly identified as (*B. longimanus*), a predatory zooplankter, that may influence the composition of the native zooplankton community (Filion 2011; Korovchinsky and Arnott 2019). Another is

the notable increase in the abundance of nesting DCCO which has fueled concerns of stakeholders who suspect the bird may be adversely affecting walleye recovery.

Lake Nipissing contains the largest inland nesting population of DCCO in northeastern Ontario (OMNRF 2006). As of 2012, approximately 3,000 nests are built annually among the five main island colonies on Lake Nipissing (Smith 2017). In conjunction with the colonization of DCCO, Lake Nipissing has also experienced a dramatic increase in the biomass of yellow perch (Morgan 2013). A Broad-scale Monitoring survey conducted in 2015 indicated that yellow perch are the dominant species in Lake Nipissing's small-bodied fish assemblage, comprising 70% of the biomass in small-mesh (ON2) gillnet catches (MNRF, Biodiversity and Monitoring Section, unpubl data). A recent study has examined the diet composition of adult DCCO on Lake Nipissing using a molecular-based method to identify fish species in regurgitated cough pellets. The study concluded that yellow perch and trout-perch (*Percopsis omiscomaycus*) were the dominant prey items, comprising 43% and 27% respectively, while walleye was of minor importance accounting for only 7% of the overall DCCO diet (Lecours 2017). No study to date has used a carbon and nitrogen stable isotope approach to characterize and compare the diets of DCCO with other sympatric piscivores within the food web of Lake Nipissing.

My primary objective was to examine the role of DCCO within the Lake Nipissing food web, and in doing so, assess the potential for DCCO to predate directly upon or compete for similar resources with piscivorous fishes, particularly walleye. I

met this objective with the following approach. First, I characterized Lake Nipissing's food web through stable isotope analysis of various biota and examined relative positions of DCCO and other aquatic community members in the isoscape using various isotopic metrics. Second, I used stable isotope data with SIMMs to estimate the diets of DCCO and other native piscivores within Lake Nipissing's fish community. I had four key predictions associated with my objective:

- 1) The food web position of DCCO in isotopic space will be similar to that of native piscivorous fishes.

- 2) DCCO will exhibit low inter-individual diet variation compared to piscivorous fishes. Previous research suggests that the diets of DCCO tend to be comprised of the most prevalent species within forage fish communities. Because DCCO forage in cohesive flocks, members of the flock should encounter and target similar prey species. Because walleye forage in schools, another form of group foraging, they will have the smallest trophic niches among the piscivorous fishes, and a trophic niche size closest to that of DCCO.

- 3) DCCO and native piscivorous fishes will exhibit dietary overlap. Previous research has shown that DCCO and other piscivores may forage on similar prey, and Lake Nipissing's forage fish community is comprised of relatively few species, so DCCO and piscivores probably prey on a similar resource pool and their trophic niches should overlap.

- 4) The diets of DCCO and other native piscivores will be comprised primarily of yellow perch. Yellow perch currently dominate Lake Nipissing's forage fish assemblage and the high availability of this species should result in high predator-prey encounters, and high consumption of yellow perch by all piscivores.

2.0 Methods

2.1 Invertebrate and small-bodied fish sampling

Invertebrates and small-bodied fishes were sampled at three sites within Lake Nipissing's main basin: Goulais Point, Manitou Islands and Frank's Point (Fig 1). Goulais Point is on the northwest side of the basin, at the outlet of Cache Bay, and near the inflows of the Sturgeon and Veuve Rivers. This area is shallow (generally < 5 m deep), receives somewhat nutrient-enriched waters, and has slightly more turbid water than the other sites. The Manitou Islands site is located centrally, approximately 10 km offshore from the city of North Bay. This area is deeper (down to 20 m) and considered more mesotrophic. Frank's Point is located on the south-western portion of the lake, at the entrance to outlet bay, leading into the French River. Frank's Point is also the deepest location on the lake.

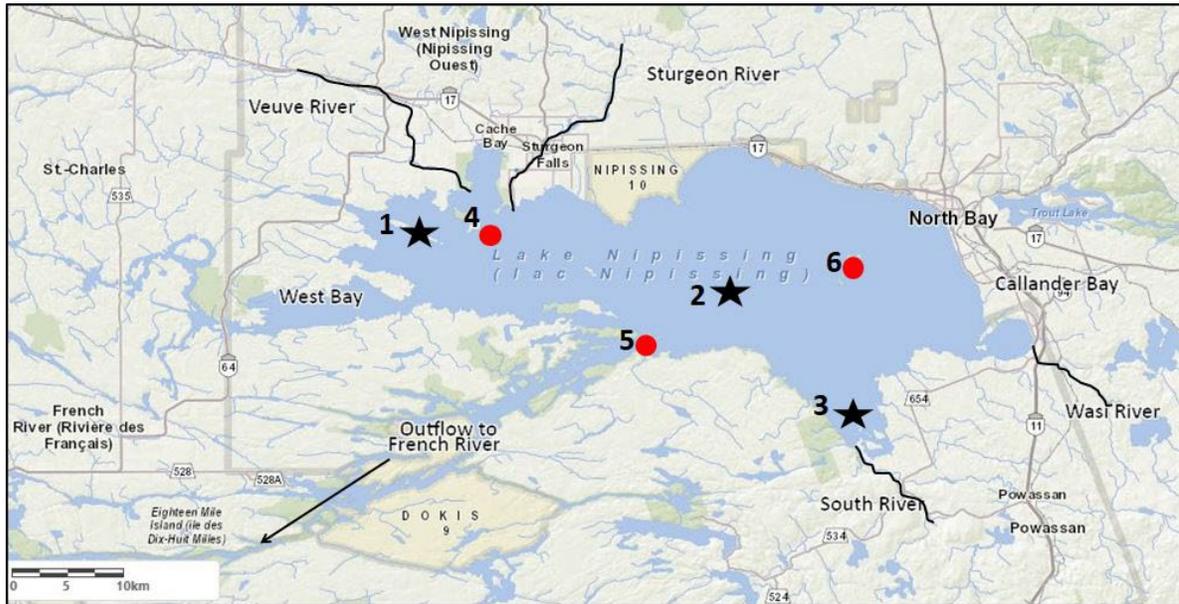


Figure 1. Map of Lake Nipissing showing sampling sites of double-crested cormorant chicks (Black stars; 1 = Hardwood Islands, 2 = Goose Islands, 3 = Gull Islands) and small-bodied forage fishes (Red circles; 4 = Goulais Point, 5 = Frank's Point, 6 = Manitou Islands).

Invertebrates were sampled at roughly monthly intervals over the open-water seasons of 2014 and 2015 at each of the three sites. Filter-feeding Unionid clams (*Bivalvia*, Unionidae) and surface-grazing snails (Gastropoda) were collected to represent the baselines of pelagic and benthic food webs, respectively. Unionid clams and snails are relatively long-lived, large-bodied primary consumers with isotopic values that tend to have low temporal variance making them suitable proxies for isotopic baseline values (Vander Zanden et al. 1997; Post 2002). Unionid clams were collected from nearshore depositional zones (1 – 2 m deep) either by wading and collecting by hand or dip net where visibility was good, or by dragging a clam rake over the substrate where visibility was poor. Snails were removed with fine forceps from the surfaces of rocks within the near shore zone (< 1 m deep). Unionid clams were stored in plastic freezer bags, snails were stored in 50 mL plastic centrifuge tubes, and both were placed on wet ice in the field and transferred to a -20 °C freezer upon returning to the laboratory. Invertebrates were later thawed, measured for whole body mass (g wet), and soft tissues removed for isotopic analysis; foot muscle was taken from unionid clams and whole viscera (body minus shell) was taken from snails and stored in glass vials at -20 °C.

Small-bodied fishes deemed to be available as prey to the dominant piscivores were primarily collected from the three sampling sites (Fig. 1) at approximately monthly intervals over the 2014 and 2015 open-water seasons. The exception was rainbow smelt (*Osmerus mordax*) which was sampled in 2011 and 2012. Small-bodied fishes were sampled with overnight sets of benthic, multi-mesh gill nets, primarily of the ON2

configuration with stretched mesh sizes of 13 to 38 mm (Sandstrom et al. 2013). Captured fish were put in Ziploc bags, transported on wet ice back to the laboratory and frozen whole at -20 °C. Fish were later thawed, measured for total length (mm) and whole body mass (g wet), and dissected for muscle tissue. Skinless, dorsal muscle tissue was removed from above the lateral line and stored in glass vials at -20 °C.

2.2 Large-bodied fish sampling

Samples of large-bodied fishes were acquired from concurrent fish community surveys and some supplemental sampling, primarily from 2012 to 2015. Community surveys were conducted using randomized sets of benthic, multi-mesh, monofilament gill nets over the whole lake at multiple depth strata; fish were selected haphazardly from catches in nets of the FWIN (Morgan 2002) and NA1 (Sandstrom et al. 2013) mesh configurations. Additional samples of adult walleye were obtained from trap nets set during spawning stock assessments. Burbot were rarely captured during gill net surveys but were sampled from walleye spawning stock assessment trap nets and by baited long-lines set near Frank's Point. For each species, individuals were selected to cover a wide body size range. Large-bodied fishes were usually processed in the field, but occasionally transported on ice back to the lab for processing. For each selected fish, total length (mm) and whole-body mass (g wet) were measured and recorded, and a sample of skinless, dorsal muscle tissue was removed from the mid-body above the lateral line and placed in

a glass scintillation vial. Muscle tissue of sampled large-bodied fishes has relatively low lipid content.

2.3 Double-crested cormorant sampling

DCCO chicks were sampled rather than adults because it was presumed that a higher proportion of the nestling body would be derived from locally-captured prey, and thus, more closely reflect Lake Nipissing's food web. Double-crested cormorants have established several nesting colonies on Lake Nipissing, and the three containing the largest cormorant populations – Hardwood Islands, Goose Islands, and Gull Islands – were sampled (Fig. 1). From mid-June to late July 2014, chick mortalities were retrieved opportunistically from nests during colony surveys. Difficulties were encountered acquiring sufficient sample sizes with this approach and a lethal sampling program was adopted in 2015 taking 10 nestlings from each of the three colonies in late June. At this stage of development, the nestlings were large (roughly 1 kg) and had left their nests but were not yet fledged. Nestlings were selected at random, captured by net, and euthanized by cervical dislocation. Collected carcasses were then bagged, transported to the lab on wet ice, and frozen at -20 °C. Chicks were later thawed, measured for whole body mass (g), and muscle samples were collected and placed in glass vials. Muscle samples were removed from the thigh in 2014 and the breast in 2015.

2.4 Sample preparation and stable isotope analysis

All tissue samples were freeze-dried for 7 days (< 0.20 mBar, < - 45 °C) using a Labconco Freezone 12 L freeze drier. The freeze-dried tissue was then ground into a homogenous fine powder using a mortar and pestle or a ball mill (Retsch MM 400). Analyses of carbon and nitrogen isotope compositions were carried out on subsamples of the powdered tissues using a Finnigan Mat Delta Plus continuous-flow isotope ratio mass spectrometer coupled with a Thermoquest NC2500 element analyzer (EA-CFIRMS) at the Stable Isotopes in Nature Laboratory (SINLAB) of the University of New Brunswick (Fredericton, NB, Canada). Stable isotope ratios were expressed as parts per thousand (‰ or per mil) delta values ($\delta^{15}\text{N}$ or $\delta^{13}\text{C}$), calculated using the formula: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$, in which R represents the ratio of heavy to light isotopes ($^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$). Random duplicate analyses were performed every 20 samples and no less than 20% of each run was composed of standard reference material. Samples were adjusted to meet International Reference Standards (IRS) of atmospheric nitrogen and Vienna Pee-Dee Belemnite for carbon.

2.5 Data handling and statistical analyses

All statistical analyses were performed, and graphics produced using R software version 3.1.2. (R Core Team 2013). Prior to statistical analysis, raw data were scrutinized for outliers by visually examining diagnostic residuals plots from isotope ratio vs body size relationships, and $\delta^{15}\text{N}$ vs $\delta^{13}\text{C}$ biplots. To account for body size/ontogenetic

variation, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were standardized to a common body mass (Persaud et al. 2012; Johnston et al. 2021). Adjustments were made with population-level estimates of the slopes (b_1) of isotope ratio vs \log_{10} body mass relationships. This was performed using a least-squares regression approach using the equation:

$$\text{adjusted } \delta X_i = \text{observed } \delta X_i - b_1 \times (\log_{10}M_i - \log_{10}M_s)$$

where δX_i is the stable isotope ratio ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) of individual i , M_i is the measured body mass of individual i , M_s is the selected standard body mass, and b_1 is the regression slope for the population. Standard body masses used for adjustments were 10 g for small-bodied fishes, and 1000 g for large-bodied fishes and DCCO chicks, unless specified otherwise. Observed relationships of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with body mass for various Lake Nipissing biota are summarized in Appendix 1.

2.5.1 Trophic position analysis

Trophic positions (TP) were estimated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the population level using the Bayesian framework outlined in the R package, *tRophicPosition* (Quezada-Romegialli et al. 2018). This approach builds upon conventional methodologies of estimating trophic positions from isotopic data (Cabana and Rasmussen 1994; Vander Zanden et al. 1997; Post 2002) and offers some novel advantages such as considering two different baselines (benthic vs. pelagic). The technique uses trophic fractionation, the stepwise enrichment of ^{15}N relative to ^{14}N at each trophic transfer, to calculate a

continuous measure of distance, estimating the amount of times biomass or energy has been transferred within a food chain between primary production and a consumer of interest. Trophic positions were calculated using mean trophic fractionations of $0.4 \text{ ‰} \pm 1.3 \text{ ‰}$ for $\delta^{13}\text{C}$, and $3.4 \text{ ‰} \pm 0.98 \text{ ‰}$ for $\delta^{15}\text{N}$, which describes the average increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from one trophic level to the next within aquatic food webs (Post 2002). Post *et al.* (2002) derived these factors from 56 and 107 estimates of trophic fractionation from nitrogen and carbon, respectively, and deemed them robust after testing their applicability in calculating trophic positions of piscivorous fish from food webs of 25 lakes. The trophic fractionation factors used in trophic position calculations are an estimate of the average increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at each trophic transfer across a food web, from basal organisms to target consumers and differ from trophic enrichment factors (TEFs) used in SIMM diet modeling that instead describe an increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between a specific consumer and its immediate prey. Clam and snail tissue isotopic ratios represented the pelagic and benthic baseline endpoints, respectively, and models were run using sufficient iterations to allow convergence. Two separate modeling exercises were implemented. First, mean trophic positions of DCCO were estimated for each of the three nesting colonies sampled during the open water season of 2015. Second, the model was used to generate and compare mean trophic positions of the various small-bodied forage fishes, piscivorous fishes and DCCO chicks using isotopic data pooled across sampling years. To examine trophic position differences between species, pairwise comparisons were made to evaluate the probability of trophic positions overlapping using Bhattacharyya coefficients (Quezada-Romegialli *et al.* 2018).

2.5.2 SIBER isotopic niche analysis

The R statistical software package SIBER was used to calculate and compare isotopic niche positions, sizes, and shapes for populations and to examine the potential for isotopic niche overlap between DCCO and native piscivorous fishes (Jackson et al. 2011). A population's isotopic niche is thought to closely align with its trophic niche and therefore considered an appropriate proxy of trophic niche. The isotopic niche size of each species was inferred from the dispersion of individuals in $\delta^{13}\text{C} - \delta^{15}\text{N}$ space, estimated as Standardized Ellipse Area adjusted for small sample size (SEAc, units of $\%o^2$). The SEAc represents 1 SD in bivariate space and captures about 40% of the data points (Jackson et al. 2011). As an index of trophic niche size, SEAc is less prone to sample size bias than measures based on polygon or convex hull methods. I calculated SEAc for each of the three cormorant colonies and each native piscivorous fish population using data pooled across sampling years. Additional metrics were calculated using SIBER to examine shape and structure of isotopic niches of piscivores at the population level. Carbon range (CR) and nitrogen range (NR) provided measurements of the breadth of dietary carbon sources and range of trophic elevations, respectively, used by a population (Layman et al. 2007). The mean nearest neighbour distance (NND) provided an estimate of trophic redundancy or trophic evenness, and mean centroid distance (CD) provided a measure of trophic diversity in the population (Layman et al. 2007). Isotopic niche overlap was calculated using the equation:

$$\% \text{ Isotopic Overlap} = \left(\frac{\left((\text{area of overlap between } SEA_{sp1} \text{ and } SEA_{sp2}) \times 2 \right)}{SEA_{sp1} + SEA_{sp2}} \right) \times 100$$

where SEA_{SP1} and SEA_{SP2} represent ellipse areas of the two populations being evaluated for isotopic overlap. The % isotopic overlap is expressed as the proportion of overlap between the two ellipses in relation to the total area available for isotopic niche interaction. It is important to note that overlap occurs on both niches and therefore must be accounted for in the equation by multiplying the overlap area by 2. Differences in SEAc between populations were assessed in pairwise comparisons. Probabilities were calculated from Bayesian posterior estimates generated from the SEAc of each group. Distributions of simulated isotopic ellipses were generated for each piscivore from the observed data. I then calculated the proportion of draws within a piscivore's distribution of isotopic ellipses that was larger than that of another species, which is also representative of the probability that one piscivore's isotopic ellipse is larger than another. The Bayesian model was run using sufficient iterations (number of SEAc simulations performed) to allow model convergence.

2.5.3 Diet compositions of piscivores

The Bayesian stable isotope mixing model software package MixSIAR (version 3.1.10) was used to estimate the relative contributions of different forage fish species to the diets of DCCO, walleye, northern pike, smallmouth bass and burbot in Lake

Nipissing (Stock et al. 2018). The MixSIAR package offers a few advantages over other mixing model software such as the ability to account for error associated with consumer and source isotopic compositions and trophic enrichment factors (TEFs)(Stock et al. 2018). Model inputs included individual-based $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the piscivores, means and SDs of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for small-bodied forage fishes purported to be likely prey sources, and trophic enrichment factors (TEFs) obtained from earlier published research. For primary modeling, the isotopic data of prey and piscivores were adjusted to standard body masses of 10 g and 1000 g, respectively. I selected trophic enrichment factors specific to piscivorous freshwater fish (0.8 ‰ for $\delta^{13}\text{C}$, 3.4 ‰ for $\delta^{15}\text{N}$) from Vander Zanden and Rasmussen (2001) for primary simulation modeling of piscivorous fishes consuming small-bodied forage fishes. Trophic enrichment factors for primary modeling of DCCO consuming small-bodied forage fishes were acquired from a controlled feeding study by Craig et al. (2015a) (-1.1 +/- 1.2 ‰ for $\delta^{13}\text{C}$, 3.9 +/- 0.7 ‰ for $\delta^{15}\text{N}$).

Examining the relationship between a model's inputs and its outputs can be very useful for understanding model uncertainty and testing robustness of results. A sensitivity analysis was performed by manipulating model inputs and noting the effect on MixSIAR predicted dietary proportions. To test the effect of adjusting isotope data to different predator and prey body sizes, MixSIAR modeling was performed using piscivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values adjusted to 500, 1000 and 2000 g body mass, and forage fish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values adjusted to 5, 10 and 20 g body mass. Emerald shiner (*Notropis atherinoides*)

and logperch (*Percina caprodes*) do not attain body masses of 20 g in Lake Nipissing and consequently were omitted as prey categories from any simulations performed using prey body masses adjusted to 20 g.

To gauge the sensitivity of model predictions to TEF selection, the outputs of primary model simulations using TEFs from Vander Zanden and Rasmussen (2001) (for piscivorous fish) and Craig et al. (2015) (for DCCO) were compared to outputs from simulations using various other TEFs. Alternate TEFs for piscivorous fishes included estimates from a laboratory diet shift experiment with juvenile walleye (0.94 +/- 0.12 ‰ for $\delta^{13}\text{C}$, 1.8 +/- 0.21‰ for $\delta^{15}\text{N}$) (Schumann et al. 2018), and also unpublished TEFs derived for walleye of northern Ontario lakes (0.21 ‰ for $\delta^{13}\text{C}$, 2.61‰ for $\delta^{15}\text{N}$). These latter TEFs were estimated following the procedures described by Vander Zanden and Rasmussen (2001), in which median differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were calculated between 10 g yellow perch and 500 g walleye sampled from 39 northern Ontario lakes (T.A. Johnston, unpubl. data from Boreal Food Webs database, Cooperative Freshwater Ecology Unit). Alternative TEFs for DCCO were acquired from laboratory feeding studies of ring-billed gulls (*Larus delawarensis*) (0.3 +/- 0.4 ‰ for $\delta^{13}\text{C}$, 1.4 +/- 0.1‰ for $\delta^{15}\text{N}$) (Hobson and Clark 1992) and great cormorant (*Phalacrocorax carbo*) (2.1 ‰ for $\delta^{13}\text{C}$, 2.4‰ for $\delta^{15}\text{N}$) (Mizutani et al. 1991), and a meta-analysis of other piscivorous birds (0.92 +/- 0.27 ‰ for $\delta^{13}\text{C}$, 1.7 +/- 0.43‰ for $\delta^{15}\text{N}$) (Caut et al. 2009).

3.0 Results

3.1 The Lake Nipissing food web in isotopic space

Lake Nipissing's food web in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space is illustrated in Figure 2. As expected, at the base of the food web, unionid clams had low $\delta^{13}\text{C}$, reflecting pelagic primary production, and snails had high $\delta^{13}\text{C}$, reflecting benthic primary production. In general, food web positions of forage fishes and piscivores appeared to be aggregated more closely to each other than anticipated within $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space (Fig. 2). In the $\delta^{13}\text{C}$ dimension, most forage fishes and piscivores appeared to be collectively positioned closer to unionid clams than snails (Fig. 2), suggesting a relatively stronger dependence on pelagic production. The exception was logperch, which stood apart from the other fishes with an elevated $\delta^{13}\text{C}$ (Fig. 2). Also unexpected was that the food web position of DCCO chicks was more closely aligned with forage fishes than with piscivorous fishes; DCCO had both lower $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ relative to the piscivorous fishes (Fig. 2).

3.2 Trophic position analysis

Mean TPs of DCCO chicks ranged from 3.40 at the Gull Islands to 4.10 at the Goose Islands (Fig. 3). Mean TPs of DCCO chicks at Goose Islands and Hardwood Islands displayed a high degree of similarity (90%), while the mean TP of DCCO chicks at Gull Islands exhibited a low probability of overlapping with those of the other two colonies (Table 1).

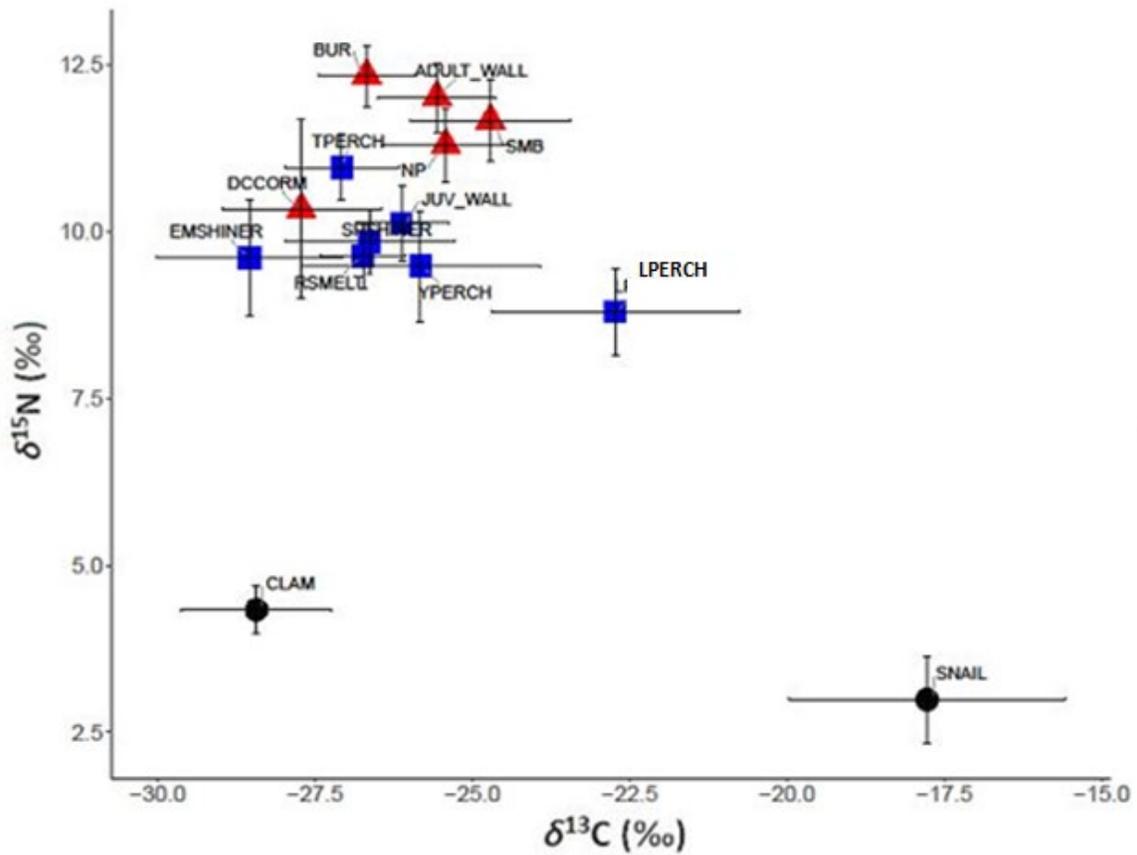


Figure 2. The food web positions of piscivores (red triangles) and potential prey fishes (blue squares) relative to two baseline invertebrates (black circles) within the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ isoscape of Lake Nipissing, Ontario, 2011-2016. Symbols are body size-adjusted means (± 1 SD); piscivore data were adjusted to 1000 g (BUR = burbot, DCCO = double-crested cormorant chicks, NP = northern pike, SMB = smallmouth bass, ADULT_WALL = large walleye), prey fish data were adjusted to 10 g (RSMELT = rainbow smelt, EMSHINER = emerald shiner, LPERCH = logperch, SPSHINER = spottail shiner, TPERCH = trout-perch, YPERCH = yellow perch, JUV_WALL = small walleye) and baseline invertebrate data were not adjusted for body size (CLAM = unionid clams, SNAIL = snails).

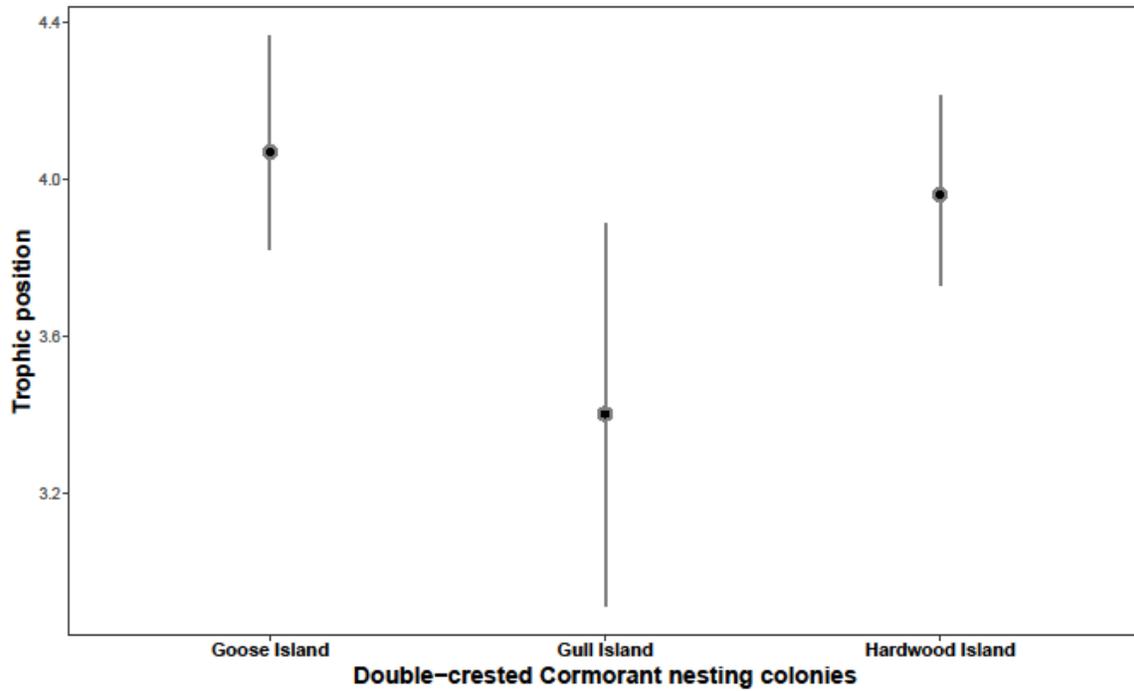


Figure 3. Trophic positions of double-crested cormorant chicks from three nesting colonies on Lake Nipissing, Ontario, in June 2015. Symbols are means with 95% credibility intervals. Cormorant chick trophic positions were calculated from muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values standardized to a body mass of 1000 g.

Table 1. Pairwise comparison matrix showing the probability of overlap between estimated mean trophic positions of double-crested cormorant chicks sampled from three nesting colonies on Lake Nipissing, Ontario, in June 2015. Trophic positions of double-crested cormorant chicks were estimated using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values standardized to a body mass of 1000 g.

	Goose Island	Gull Island	Hardwood Island
Goose Island	1.00	0.21	0.90
Gull Island		1.00	0.26
Hardwood Island			1.00

Interspecific comparisons revealed that burbot occupied the highest TP among consumers analyzed (4.40) followed by walleye (4.36) and smallmouth bass (4.30) (Fig. 4). The mean TP of forage fishes varied from 3.52 (logperch) to 4.00 (trout-perch) (Fig. 4). All piscivores exhibited mean TPs higher than those of forage fishes with the notable exception of DCCO that had an estimated mean TP (across colonies) of 3.80. Piscivorous fishes demonstrated relatively high probabilities of overlap in TP with each other (Table 2). Probabilities were lowest between northern pike and walleye (0.55) and between northern pike and burbot (0.42) but were generally high (> 0.78) in all other pairwise comparisons (Table 2). In contrast, probabilities of TP overlap with DCCO chicks were consistently low (< 0.16) for all piscivorous fishes analyzed (Table 2).

3.3 SIBER isotopic niche analysis

Double-crested cormorant chicks had the largest isotopic niche size, inferred from SEAc, indicating the highest inter-individual dietary variation among the piscivores analyzed (Fig. 5). Among the piscivorous fishes, smallmouth bass had the largest SEAc and burbot had the smallest SEAc (Fig. 5). Based on SEAc posterior distributions, DCCO chicks had a high probability ($> 90\%$) of having a larger SEAc than all the piscivorous fishes (Table 3). Among piscivorous fish, smallmouth bass had a high probability ($> 80\%$) of having a larger SEAc than all other species, and burbot had a high probability ($> 85\%$) of having a smaller SEAc than all other species (Table 3).

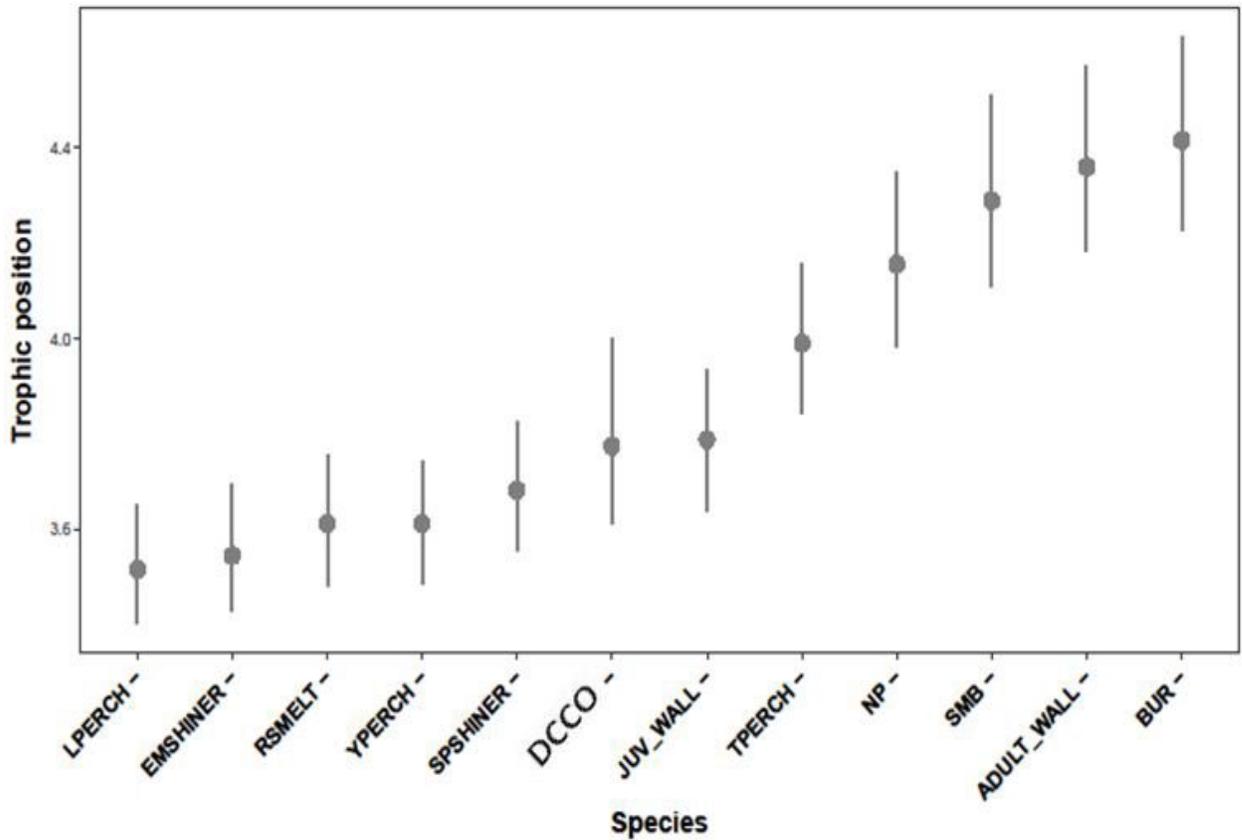


Figure 4. Estimated trophic positions of various piscivores and forage fishes sampled from Lake Nipissing, Ontario, 2011 – 2016. Symbols are size-adjusted means with 95% credibility intervals. Trophic positions were calculated using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values adjusted to 1000 g body mass for piscivores (BUR = burbot, DCCO = double-crested cormorant chicks, NP = northern pike, SMB = smallmouth bass, ADULT_WALL = large walleye), and to 10 g for forage fishes (RSMELT = rainbow smelt, EMSHINER = emerald shiner, LPERCH = logperch, SPSHINER = spottail shiner, TPERCH = trout-perch, YPERCH = yellow perch, JUV_WALL = small walleye).

Table 2. Pairwise comparison matrix showing the probability of overlap of mean trophic positions of double-crested cormorants and piscivorous fishes sampled from Lake Nipissing, Ontario, 2012 - 2016. Trophic positions of all taxa were estimated using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values standardized to a body mass of 1000 g.

	Adult Walleye	Northern pike	Smallmouth bass	Burbot
Double-crested cormorant	0.02	0.16	0.05	0.01
Adult Walleye	1.00	0.55	0.93	0.96
Northern pike		1.00	0.79	0.42
Smallmouth bass			1.00	0.82
Burbot				1.00

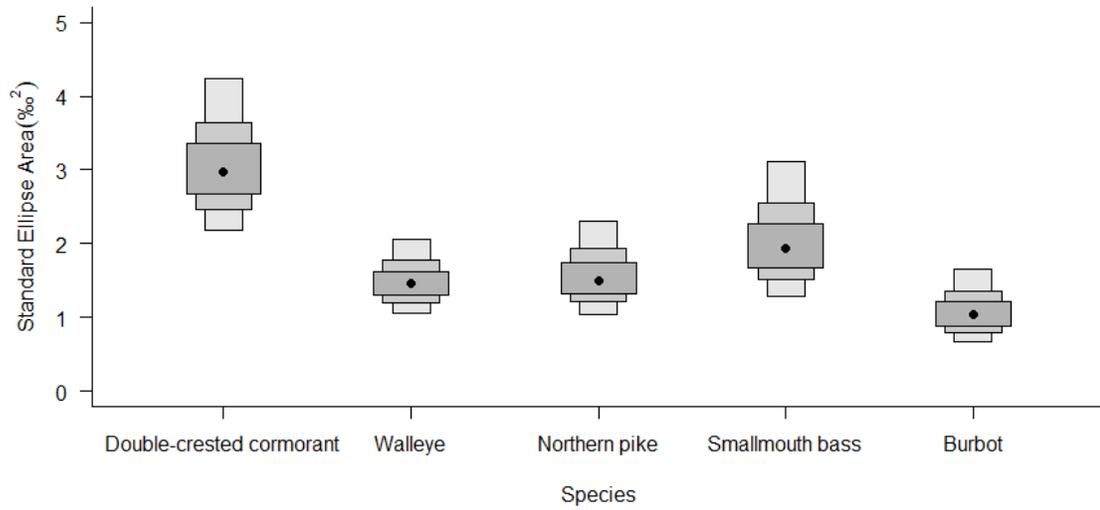


Figure 5. Comparison of isotopic niche sizes for five piscivores sampled from Lake Nipissing, Ontario, 2012 - 2016. Standardized ellipse areas (SEAc) were calculated from muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to a body size of 1000 g. Black dots represent means and shaded boxes indicate the 50, 75 and 95 % credible intervals.

Table 3. Pairwise comparison matrix for standardized ellipse areas (SEAc) of piscivores sampled from Lake Nipissing, Ontario, 2012 – 2016. Ellipse areas were calculated in SIBER using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to a body size of 1000 g. Values indicate the probability that a consumer in the row has a SEAc larger than the SEAc of the consumer in the column.

	Double-crested cormorant	Walleye	Northern pike	Smallmouth bass	Burbot
Double-crested cormorant	0	0.99	0.99	0.92	0.99
Walleye		0	0.41	0.11	0.86
Northern pike			0	0.18	0.89
Smallmouth bass				0	0.98
Burbot					0

Interspecific comparisons were also made with respect to other isotopic niche metrics. Smallmouth bass, walleye and DCCO chicks had very similar CRs (range 4.76 – 4.80). Trends in NR were similar to those for SEAc, with the highest NR in DCCO chicks (5.61) and lowest NR in burbot (1.53), and intermediate NR in the other piscivores (range 2.04 – 2.42). Similarly, interspecific trends in CD, an alternate measure of isotopic dispersion, corresponded with those of SEAc, with DCCO having the largest CD and burbot having the lowest CD. Walleye had the lowest mean NND, indicating that isotopic similarity among individuals was higher in walleye than in Nipissing's other piscivores. Burbot and DCCO chicks had the lowest and also very similar mean NND values indicating both had the lowest levels of trophic similarity relative to the other piscivore populations.

All Nipissing's piscivores demonstrated some sharing of isotopic niche space, as inferred from SEAc overlap. I found that DCCO chicks had the least isotopic overlap with other piscivores, ranging from 30.6 % with smallmouth bass to 44.3% with walleye (Table 4). Piscivorous fishes generally had greater SEAc overlap among each other (range 41.9 – 66.5 %) than with DCCO chicks (Table 4). Among the piscivorous fishes, walleye was found to overlap the most and burbot was found to overlap the least with the others (Table 4).

Table 4. Pairwise comparison matrix showing percentage overlap of standardized ellipse areas (SEAc) among piscivores sampled from Lake Nipissing, Ontario, 2012-2016. Ellipse areas, and their overlap, were calculated in SIBER using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to a body size of 1000 g.

	Walleye	Northern pike	Smallmouth bass	Burbot
Double-crested cormorant	44.3	34.8	30.6	42.1
Walleye	100	63.8	66.5	57.6
Northern pike		100	65.2	41.9
Smallmouth bass			100	47.1
Burbot				100

3.4 Diets of DCCO and piscivorous fishes estimated by MixSIAR

Initial model simulations with MixSIAR were performed using stable isotope data adjusted to body sizes of 10 g for prey species and 1000 g for consumers. Under these conditions, the diets of piscivorous fishes were predicted to be relatively similar in composition with emerald shiner predicted to make the largest dietary contribution (range 40 – 59 %) and logperch predicted to make the second largest contribution (range 23 – 53 %) for most species (Fig. 6). Each of the other prey species were predicted to contribute relatively little to the piscivorous fish diets (< 10 % each). Juvenile walleye and yellow perch were each predicted to contribute < 5 % to piscivore diets. Using the same base model configuration of 1000 g consumer and 10 g prey for DCCO chicks, but with TEF estimates specifically for DCCO (Craig et al. 2015), emerald shiner and logperch were also estimated to be the dominant DCCO prey items with contributions of 27% and 18%, respectively (Fig. 7). However, the DCCO chick diet was predicted to be more diverse than that of the piscivorous fishes, with yellow perch, spottail shiner and rainbow smelt also making notable contributions (> 10 % each) (Fig. 7).

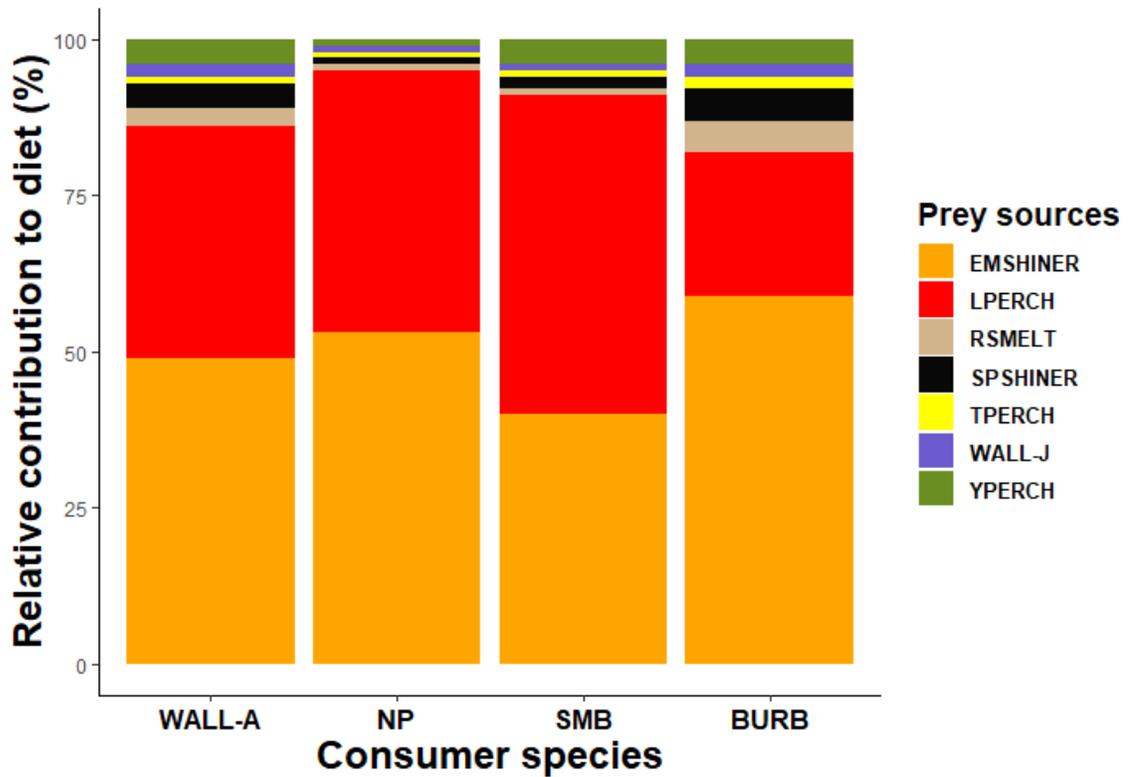


Figure 6. Predicted proportional contributions of seven forage fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SP SHINER = spottail shiner, TPERCH = trout-perch, WALL-J = juvenile walleye, YPERCH = yellow perch) to the diets of four piscivorous fishes (WALL-A = large walleye, NP = northern pike, SMB = smallmouth bass, BURB = burbot) sampled from Lake Nipissing, Ontario, 2012-2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g and 1000 g for prey and predator, respectively, and trophic enrichment factors from Vander Zanden and Rasmussen (2001).

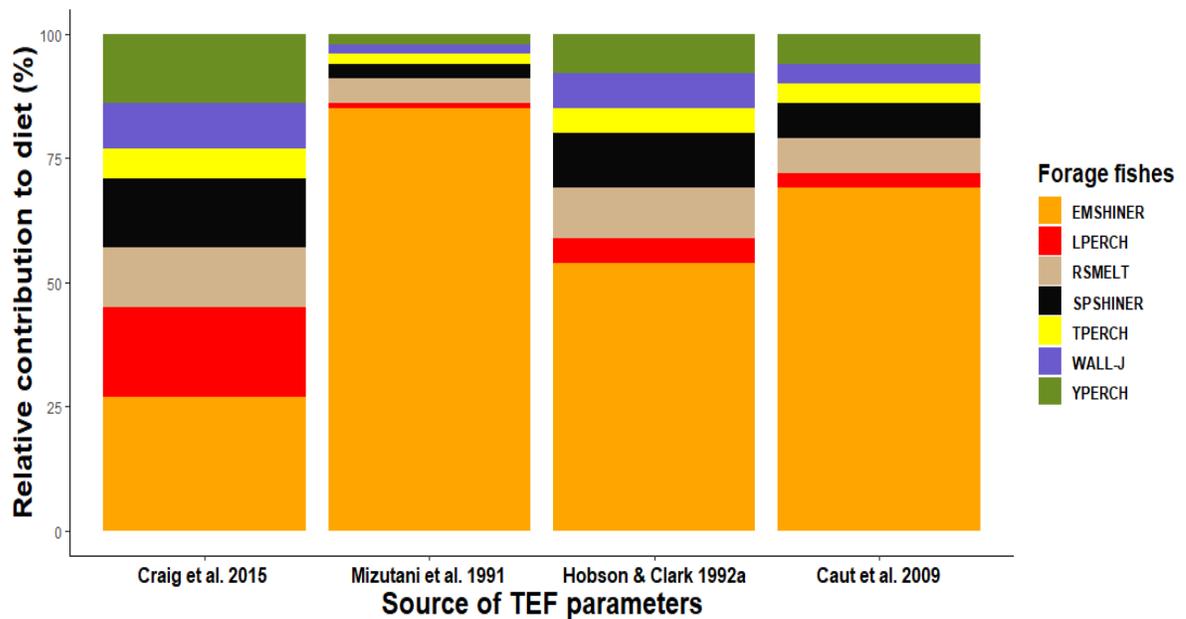


Figure 7. Predicted proportional contributions of seven forage fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diet of double-crested cormorant (DCCO) chicks sampled from Lake Nipissing, Ontario, in June 2015. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g and 1000 g for prey and cormorant chicks, respectively, and trophic enrichment factors from four earlier studies (Source of TEF parameters). Estimates based on TEFs derived from DCCO are on the left (Craig et al. 2015a), all other estimates are based on TEFs derived from other fish-eating birds.

The effects of predator:prey body size ratios on MixSIAR diet predictions were examined by adjusting the input stable isotope data to various standard body sizes for both prey (5 g, 10 g and 20 g) and predator (500 g, 1000 g and 2000 g). Increasing standard prey sizes from 5 g to 10 g produced only minor shifts in estimated mean dietary proportions of 1000 g DCCO chicks and walleye (Fig.8). Similarly, there were only minor changes in the predicted diets of burbot, northern pike and smallmouth bass when standard prey size was moved from 5 g to 10 g (results not shown). However, adjusting prey size to 20 g had a much larger effect on model outputs of all piscivores. Emerald shiner and logperch do not attain this body size in Lake Nipissing and were eliminated as prey categories in the analysis. With only five prey categories available at 20 g, yellow perch was predicted to be the dominant prey item for most piscivores, comprising 66 % of the walleye diet and 31 % of the DCCO chick diet (Fig. 8). As with other standard prey sizes, DCCO chick diet was predicted to be more diverse than walleye diet at 20 g prey size (Fig. 8). Increasing standard prey size to 20 g also increased the relative contributions of other prey categories to piscivore diets, including increasing the contribution of juvenile walleye to the DCCO chick diet to 17% (Fig. 8).

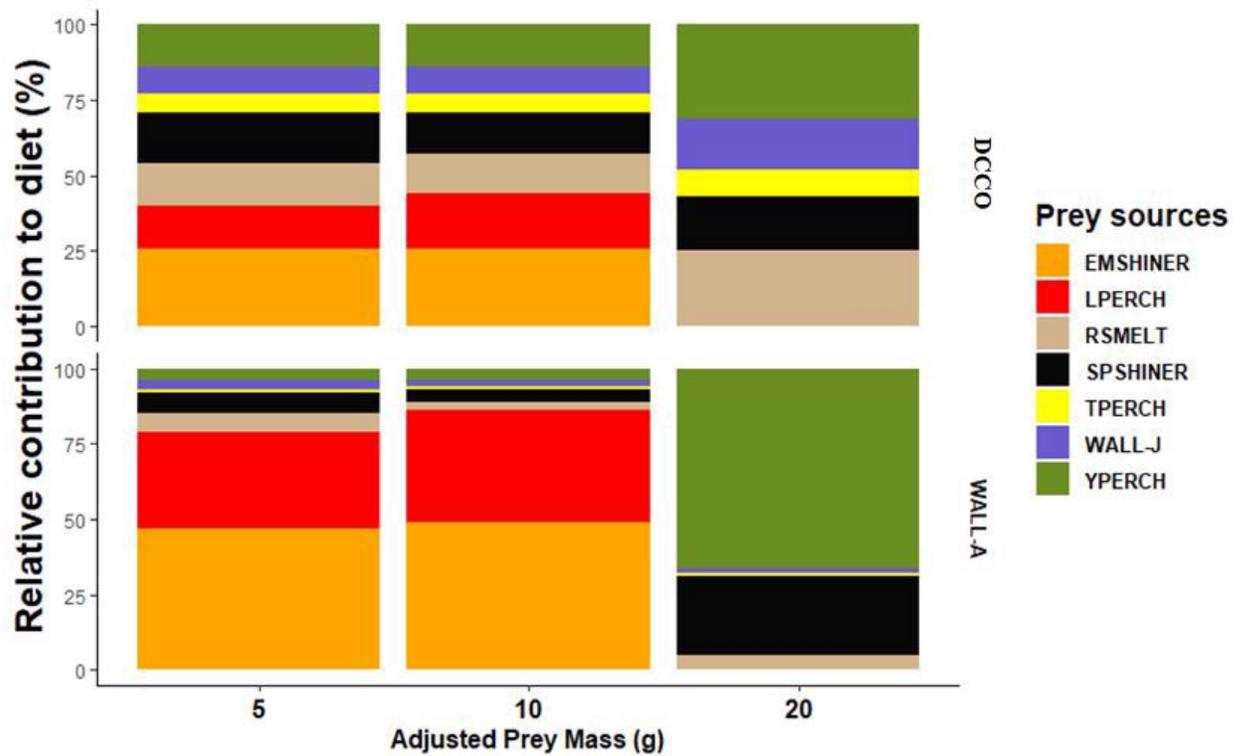


Figure 8. Predicted proportional contributions of seven prey fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diets of double-crested cormorant chicks (DCCO, top) and walleye (WALL-A, bottom) sampled from Lake Nipissing, Ontario, 2012 -2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 1000 g for DCCO chicks and walleye, and adjusted to 5, 10, or 20 g for prey fishes. Trophic enrichment factors used for modeling were taken from Craig et al. (2015a) for DCCO chicks and from Vander Zanden and Rasmussen (2001) for walleye. Emerald shiner and logperch don't attain body masses of 20 g in Lake Nipissing and were not included as prey categories when modeling 20 g prey.

Shifting consumer body mass from 500 g to 2000g while maintaining prey standard mass at 10 g was found to diversify the predicted diets of most piscivorous fishes. In both burbot and walleye, the dietary importance of emerald shiner decreased, while the combined contributions of spottail shiner, rainbow smelt, trout-perch, juvenile walleye and yellow perch increased with increasing consumer body size (Fig.9). I did not model DCCO chick diet at different standard body sizes because cormorant chicks were relatively uniform in size and were represented poorly over the 500 g to 2000 g size range.

I also found that MixSIAR estimates of piscivore diet composition were sensitive to the choice of TEFs used as model inputs. For 1000 g DCCO chicks feeding on 10 g prey, predicted diet compositions were more diverse when using TEFs developed specifically for DCCO than when using TEFs derived from other fish-eating birds (Fig. 7). Models using these latter TEFs predicted a much higher proportion of emerald shiner in the diet (Fig. 7). For 1000 g walleye feeding on 10 g prey, predicted diet compositions based on TEFs from Vander Zanden and Rasmussen (2001) were dominated by emerald shiner and logperch, whereas predicted diet compositions from models using TEFs derived specifically for walleye were more diverse (Fig. 10). Models using lab-based TEFs for small walleye (Schumann et al 2018) predicted trout-perch to be the dominant prey whereas models using field-based TEFs for larger walleye (T.A. Johnston, unpubl. data) predicted logperch to be the dominant prey (Fig. 10).

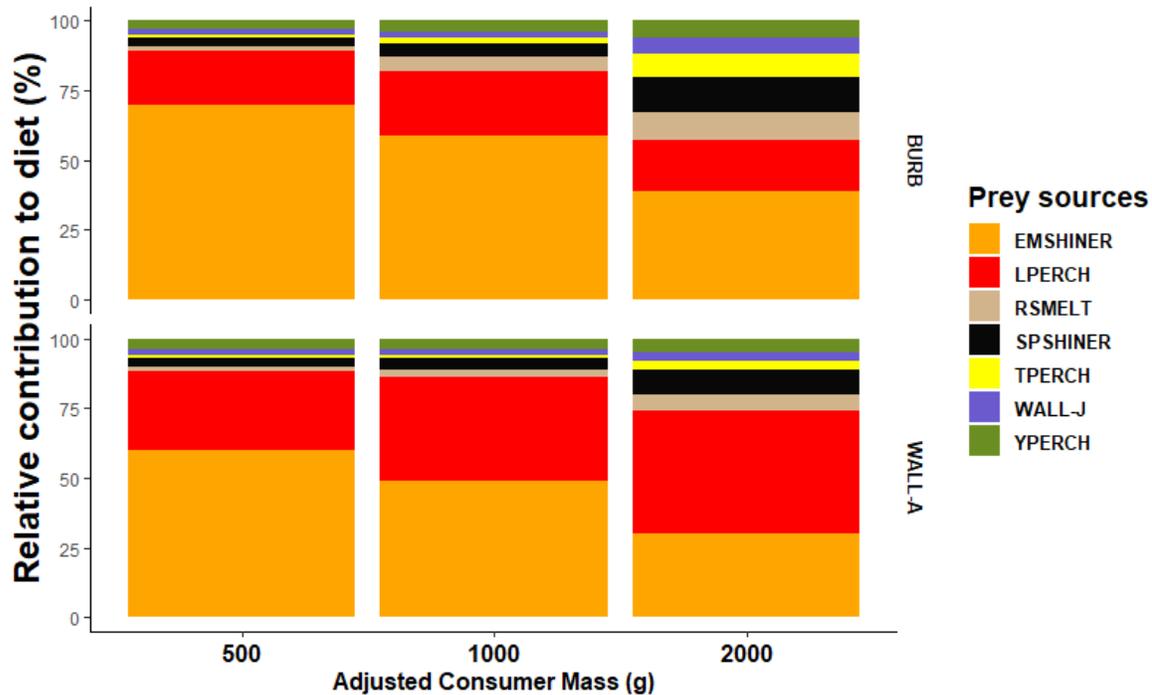


Figure 9. Predicted proportional contributions of seven prey fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diets of burbot (BURB, top) and adult walleye (WALL-A, bottom) sampled from Lake Nipissing, Ontario, 2012 -2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g for all prey species, and adjusted to 500, 1000, or 2000 g for burbot and walleye. Trophic enrichment factors used for modeling were taken from Vander Zanden and Rasmussen (2001).

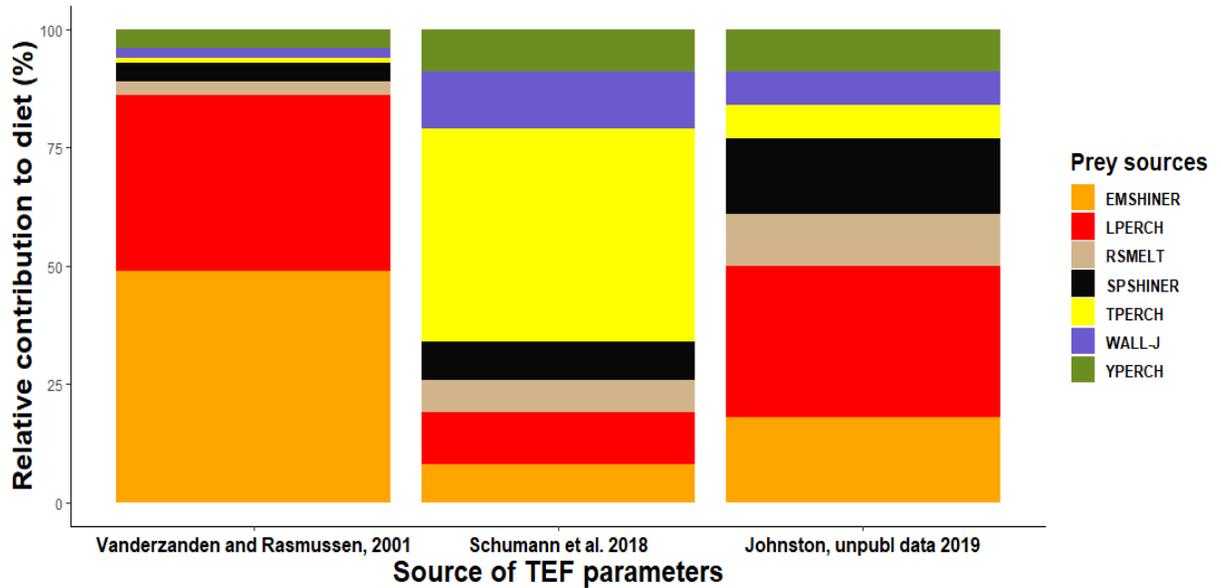


Figure 10. Predicted proportional contributions of seven prey fishes (EMSHINER = emerald shiner, LPERCH = logperch, RSMELT = rainbow smelt, SPSHINER = spottail shiner, TPERCH = trout-perch, WALL-J = small walleye, YPERCH = yellow perch) to the diet of walleye sampled from Lake Nipissing, Ontario, 2012 - 2016. Dietary proportions were estimated with MixSIAR using muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data adjusted to 10 g and 1000 g for prey and predator, respectively, and trophic enrichment factors (Source of TEF parameters) derived from three earlier studies.

4.0 Discussion

The aim of this study was to determine the ecological role of DCCO within Nipissing's food web and to better understand predatory and competitive interactions between DCCO and Nipissing's native piscivores. This was carried out using a comprehensive carbon and nitrogen stable isotope approach to characterize and compare the food web and trophic positions, dietary niche, and diet composition of DCCO nestlings relative to walleye and three other co-occurring predatory fishes. Analysis of isotopic niche characteristics revealed DCCO nestlings may have a higher reliance on pelagic basal carbon sources and feed at a lower trophic level than sympatric populations of walleye and three other co-occurring predatory fish within Nipissing's food web. Piscivorous fishes had higher trophic niche overlap with each other than with DCCO. On the other hand, DCCO nestlings appeared to occupy a larger niche space than predatory fish, which may suggest cormorants express greater dietary variation between individuals and draw nutritional support from a larger pool of resources. Emerald shiner and logperch were the most important prey fish within the diets of Nipissing's piscivores, although diet composition did vary between DCCO and predatory fish. The diet composition of predatory fish was much more focused and primarily composed of emerald shiner and logperch, while DCCO diet tended to have greater diversity with moderate contributions from other forage fishes.

4.1 Using stable isotope analysis to interpret aquatic food webs

There are a few commonly used methods to evaluate trophic structures within aquatic food webs and each approach varies in the type of information provided and its interpretation. Stomach content analysis yields granular dietary information revealing taxonomic details on the prey in a consumer's diet but is sensitive to a few inherent drawbacks and biases including: potential prey misidentification, a short-term dietary time-frame sometimes reflecting only a single feeding event, and biases resulting from differences in prey digestion rates in which easily digestible prey are difficult to detect and less digestible prey may be overemphasized. On the other hand, stable isotope ratios reflect dietary nutrients assimilated over time, providing a longer-term representation of diet. Stable isotope analysis provides a valuable tool for evaluating trophic ecologies and food web structure but like most analytical frameworks it is not infallible, and interpretation of stable isotope data is also subject to assumptions and limitations.

Examining relative food web positions of consumers in isotopic space provides a generalized overview of food web structure and offers a way to conceptualize the various trophic roles and interactions of consumers. However, this simplified representation of Nipissing's food web may not capture potential intraspecific isotopic variability that may be present within consumer food web positions due to various factors such as ontogeny. Therefore, it is important that inferences remain broad when assessing relationships between mean food web positions of consumers in isotopic space.

Inferring trophic niche size and shape from variance ellipses in $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ space and evaluating the overlap of these niche spaces between species is an informative method for highlighting potential for dietary overlap and competition. However, it is important to note that it is possible that two consumer species can have distinct diets while also having similar isotopic compositions (e.g., one consumer's isotopic composition could actually represent the average of two isotopically extreme prey). Without direct observational data or detailed gut contents it is difficult to determine whether isotopic overlap between species is a result of feeding on similar prey or feeding on different prey with similar isotopic values (Layman et al. 2012).

A key assumption for using stable isotope ratios to estimate trophic position is the use of fixed trophic enrichment factors to represent the average enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with each trophic transfer in the food web. Early studies reported that muscle tissue from consumers is typically enriched by 0 - 1 ‰ in $\delta^{13}\text{C}$ and 3 - 4 ‰ in $\delta^{15}\text{N}$ with each trophic step (DeNiro and Epstein 1981; Minagawa and Wada 1984) while later studies point out that trophic enrichment factors especially those for $\delta^{15}\text{N}$, can vary among taxa (Caut et al. 2009) and this variation may influence trophic position estimates. Individual specific trophic enrichments of $\delta^{15}\text{N}$ between consumer and prey are likely to range from 2 to 5‰. Earlier studies have stated that a fixed mean trophic fractionation of 3.4‰ may be a valid assumption when averaged over multiple trophic transfers in aquatic food webs (Post 2002). Others have found that trophic enrichment of $\delta^{15}\text{N}$ may decrease with increasing trophic elevation and have argued for the use of scaled trophic enrichment

factors to reflect this variation (Hussey et al. 2014). A study comparing trophic positions of freshwater piscivorous fish calculated using both fixed trophic enrichment factors and scaled trophic enrichment factors found the two methods produced relatively similar estimates (Nawrocki et al. 2020). Trophic discrimination factors may be the crux in many stable isotope analysis applications representing a potential source of uncertainty that could influence interpretation. This highlights the need for more controlled diet rearing experiments to obtain species-specific trophic discrimination factors.

4.2 Lake Nipissing food web structure and trophic niche positions of DCCO and native piscivorous fishes

As expected, unionid clams and snails displayed a clear separation with respect to each other along the $\delta^{13}\text{C}$ axis, illustrating the two distinct sources of available carbon and energy within Lake Nipissing's food web, the benthic (primarily nearshore) and pelagic (primarily offshore) habitats. The food web positions of forage fishes in isotopic space appeared to be tightly aggregated and located close to piscivores except for logperch that had a higher $\delta^{13}\text{C}$ relative to the rest of the forage fish community, indicative of a higher reliance on benthic primary production. Based on previous research demonstrating that DCCO and piscivorous fishes may consume similar prey and have similar muscle $\delta^{15}\text{N}$ values (Doucette et al. 2011) and considering that the bulk of Lake Nipissing's forage fish community is composed of few species (yellow perch, trout

perch, shiners (*Notropis spp.*)), I anticipated that the food web positions of DCCO and native piscivorous fishes would be very similar. However, this prediction did not align with my results. Within $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space standardized for body size, DCCO chicks pooled from all three colonies exhibited a higher reliance on pelagic basal resources (lower $\delta^{13}\text{C}$) than the co-habiting piscivorous fishes. This result closely aligns with similar research conducted on three lakes in Saskatchewan, Canada, that also found adult DCCO had a more pelagic (lower $\delta^{13}\text{C}$) signal than that of walleye and northern pike (Doucette et al. 2011), and although no comparison with co-habiting predators was made, young-of-the-year DCCO from Lake Winnipeg, Canada, also procured dietary carbon from pelagic basal resources (Ofukany et al. 2015).

Also contrary to my predictions, trophic position (calculated from $\delta^{15}\text{N}$) of DCCO chicks was lower relative to all four piscivorous fishes examined in Lake Nipissing. Adult DCCO consume large fish up to 400 mm in length and can assume top-predator roles within aquatic food webs (Wires et al. 2001; Doucette 2012). For example, adult DCCO nesting on lakes in Saskatchewan, Canada, held trophic positions just under walleye, but higher than burbot and northern pike in two lakes and held the highest trophic position among all piscivores in a third (Doucette et al. 2011; Doucette 2012). However, I examined DCCO nestlings in the current study and some research has suggested that diet may vary between nestlings and adults. DCCO chicks probably have a smaller gape size than adults, reducing the maximum prey size that they can consume (Neuman et al. 1997; Somers et al. 2003). Thus, DCCO adults may exhibit size-selective

foraging during nesting, collecting smaller size prey with lower $\delta^{15}\text{N}$ values to feed their young, but collecting larger prey items to feed themselves. As of this current study, adult DCCO and chick prey-size selection have not been explicitly compared, but there is some evidence to support differences between the two life stages. For example, bolus regurgitates intended for chick provisioning collected from DCCO in Lake Ontario and Lake Huron were mostly comprised of smaller prey species (Neuman et al. 1997); moreover, yellow perch < 10 cm in length (roughly < 12 g in mass) comprised over 85% of the biomass within juvenile DCCO regurgitates collected from two lakes in Saskatchewan, Canada (Willis et al. 1991; Doucette et al. 2011; Doucette 2012).

Northern pike, smallmouth bass and walleye were closely bound in C-N isotopic space in Lake Nipissing, suggesting that these three piscivores may rely on similar nutritional support. Northern pike and smallmouth bass utilize shallow, vegetated nearshore habitats, where both species employ similar ambush foraging tactics, so it may be expected the two predators encounter and consume similar prey (Brown et al. 2009; Harvey 2009). Also, previous studies have suggested that northern pike, smallmouth bass and walleye may utilize similar resources and overlap in diet to some degree (Vander Zanden et al. 1997; Fayram et al. 2005; Stasko 2012). It is also worth noting that the mean $\delta^{13}\text{C}$ values of walleye, northern pike and smallmouth bass closely aligned with that of the mean $\delta^{13}\text{C}$ of Nipissing's most abundant forage fish, yellow perch, which may be a potential food source of the three piscivores. Compared to the other piscivores, burbot had the most depleted mean $\delta^{13}\text{C}$ signature inferring that most of this species' energy is

assimilated from offshore basal sources. Adult burbot have been known to be predominantly piscivorous and tend to occupy cooler deeper waters during summer months (McPhail and Paragamian 2000; Cott et al. 2011). So, it may not be surprising that burbot occupy a food web position that strongly reflects offshore energy pathways.

The higher trophic positions observed in piscivorous fish compared to DCCO chicks may be because the former typically consume larger prey than what is provisioned to DCCO chicks. Although adult cormorants have been known to consume large fish, they appear to prefer prey of 150 mm in length or less, and the average lengths of fish found in nestlings regurgitates may be less than 100 mm (Harrisamf and Wanless 1993; Neuman et al. 1997; Wires et al. 2001; Doucette et al. 2011; Andrews et al. 2012; Ovegård 2017). Interactions between piscivorous fishes and prey tend to be determined by size constraints. Gape size increases with body size in piscivorous fishes and a larger gape permits ingestion of larger prey (Mihalitsis and Bellwood 2017; Gaeta et al. 2018). Larger size prey fishes comprise a large proportion of the diets of adult walleye, northern pike and smallmouth bass (Gaeta et al. 2018; Grausgruber and Weber 2020). At 1000 g mass, walleye, smallmouth bass and northern pike would be predicted to have maximum ingestible prey sizes of 154mm, 155mm and 179 mm, respectively (Gaeta et al. 2018). These piscivore maximum prey-size constraints align more with the typical prey sizes consumed by adult DCCO and might suggest piscivorous fish have the capacity to ingest larger forage fish with higher $\delta^{15}\text{N}$ levels than what adult DCCO provision to their chicks.

Isotopic compositions of DCCO chicks were found to vary among nesting colonies. Juvenile DCCO from Goose Island and Hardwood Island occupied similar trophic positions (calculated from $\delta^{15}\text{N}$), while DCCO chicks from Gull Island seemed to occupy a lower trophic position. One potential explanation for the observed differences between nesting colonies is variability in the aquatic habitat structure surrounding each cormorant colony resulting in differences in forage fish assemblages (Neuman et al. 1997). Within large lakes, regional differences in morphometry (e.g., depth, substrate), vegetation, and habitat structure can result in spatial variation in the species composition of available forage fishes (Benson and Magnuson 1992). As well, DCCO from different breeding colonies may differ in their preferred foraging locations within the lake (Coleman et al. 2005; Ridgway et al. 2006). Thus, adult DCCO nesting in different colonies may draw resources from markedly different fish assemblages. Another tenable explanation to consider could be that some adults might collect prey for their young outside of Lake Nipissing. DCCO can fly long distances to foraging locations. For example, within the Laurentian Great Lakes, breeding DCCO make average foraging flights of 3 - 13 km from their breeding colony and maximum foraging flight distances of 40 km have been reported (Custer and Bunck 1992; Neuman et al. 1997). Long flights to distant foraging areas may be motivated by a decrease in prey availability within the immediate vicinity of the nesting site. For example, breeding DCCO in central Saskatchewan foraged for their young within the nesting colony lake during periods when prey densities were abundant, but when prey densities decreased, cormorants focused foraging in other lakes (~20 km from colony) containing higher abundances of the same

prey species (Bugajski et al. 2013). There are four large lakes ($\geq 12 \text{ km}^2$) located within 20 km of Lake Nipissing that DCCO could potentially forage within; Trout Lake, Lake Nosbonsing, Restoule Lake and Tomiko Lake. It is unknown if these other lakes contain higher prey abundances than Lake Nipissing to warrant the extra energy expenditure associated with long distance flights, especially during stages of chick rearing when energy demands are high.

4.3 Trophic niche sizes of DCCO and piscivorous fishes

Previous research suggests DCCO diet largely consists of the most readily abundant and available species within forage fish communities (Belyea et al. 1997; Bur et al. 1997; Johnson et al. 2002; Diana et al. 2006; Koenigs et al. 2021). Lake Nipissing's forage fish community at the time of this study was dominated by just a handful of species, with yellow perch estimated to comprise 70% of the small-bodied fish assemblage, according to lake-wide gill net surveys. The select few species that numerically dominate Lake Nipissing's forage fish community would be expected to account for the largest proportion of DCCO diet resulting in low inter-individual dietary variation represented by a small isotopic niche. Moreover, because DCCO can forage collectively, aggregated in flocks (Dorr et al. 2021) and tend to forage on highly abundant and available species (Koenigs et al. 2021), I hypothesized that this foraging behavior should increase the likelihood of flock members encountering and targeting similar prey, resulting in further reduction of inter-individual dietary variation. Based

on these postulates, I predicted that DCCO would have a small trophic niche relative to the other piscivorous fish analyzed. This prediction ran contrary to my results, in that DCCO exhibited the largest isotopic niche overall which suggests that there is greater dietary variation among individuals and that DCCO draw prey from a more expansive pool of potential resources than piscivorous fishes. Aligning with my results, adult DCCO at breeding colonies on six lakes within Saskatchewan, Ontario, Canada, were also found to exhibit large isotopic niches at the population level, and stomach content analysis indicated strong individual specialization in prey consumed (Doucette 2012). I did not attempt to determine if Nipissing's DCCO population is comprised of generalists, specialists or a combination of the two at the individual level; this would require monitoring individual consumers over time. Consumer isotope values that vary temporally indicate a generalist behavior, and conversely, isotope values that remain relatively uniform over time indicate a specialist behavior (Fink et al. 2012). The isotopic niche size of DCCO populations may vary from region to region and the amount of inter-individual dietary variation within a population of DCCO may depend on the suite of resources present within the foraging habitats available to that population. For example, an assessment of colonial water bird habitats within New York Harbour, N.Y., U.S.A., revealed that a DCCO population within a nesting region with access to a diverse range of resources and habitats exhibited the largest isotopic niche of the six water birds examined, while two other DCCO colonies located in areas with lower prey diversity exhibited isotopic niches five and twenty times smaller (Craig et al. 2015b).

4.4 Trophic niche overlap between DCCO chicks and piscivorous fishes

Trophic niche overlap may serve as an index of the potential for interspecific competition through partial or complete sharing of resources or habitats by two or more populations. I looked at trophic niche overlap to examine potential competition between DCCO and piscivorous fishes of Lake Nipissing. Because Nipissing's small-bodied fish assemblage is dominated by a few species, I predicted that DCCO and piscivorous fishes would likely exploit similar resources and thus overlap in trophic niche to some degree. This prediction was correct in that DCCO shared some overlap in isotopic niches with all piscivorous fishes including walleye, though in most cases piscivorous fishes overlapped more with each other than with DCCO.

Prior research has reported trophic niche overlap between walleye and DCCO in other aquatic ecosystems. For example, DCCO and walleye had varying overlap of isotopic niches across three lakes in Saskatchewan, Canada; however, the two piscivores shared only a limited portion of available niche space, and the potential for competition was considered to be relatively low (Doucette et al. 2011). DCCO and walleye within western Lake Erie feed on similar prey items from July to October with the greatest diet similarity occurring in August (Bur et al. 1997; Stapanian et al. 2002). However, bioenergetics modeling predicted that total annual DCCO predation within western Lake Erie only accounted for 1.7% of the forage fish biomass supporting walleye, suggesting DCCO predation represents a low potential for competitive interaction (Madenjian and Gabrey 1995). Walleye and DCCO are both considered adaptive generalists capable of

exploiting a wide range of prey species and demonstrate a reliance on the most abundant prey within foraging areas (Doucette et al. 2011; Herbst et al. 2016; Koenigs et al. 2021). They may also potentially share a preference for similar foraging habitats within water depths of 3 to 12 m, so overlap in dietary resources may be possible (Coleman et al. 2005; Bozek et al. 2011; Peat et al. 2015; Herbst et al. 2016).

4.5 Diet composition of DCCO and piscivorous fishes

Many studies have highlighted the flexible foraging behavior of DCCO, pointing out that while they are capable of consuming a wide range of prey fish they will often focus on accessible and abundant species (Bur et al. 1997; Johnson et al. 2008a; DeBruyne et al. 2013; Coleman et al. 2016; DeBruyne et al. 2017; Dorr and Fielder 2017; King et al. 2017; Koenigs et al. 2021). Recent lake-wide fish community surveys have indicated that yellow perch are the most numerically abundant fish species in Nipissing's small-bodied fish community. Based on this, I anticipated that yellow perch would be the dominant prey source within the diets of DCCO and piscivorous fishes. However, most SIMM simulations did not support this prediction. For DCCO, SIMMs indicated that emerald shiner was the primary prey item and yellow perch was third in relative importance; SIMMs also indicated that the DCCO diet was quite diverse with four of seven prey types having mean contributions between 13 and 18 %. Similarly, for piscivorous fishes, SIMM outputs indicated emerald shiner and logperch constituted over

80 % of the diet, while yellow perch was of relatively low importance. Although not as abundant as yellow perch, emerald shiner and logperch are also of high relative abundance within Nipissing's forage fish assemblage based on gill net surveys. With no current indication of resource limitation, it may not be possible to know whether DCCO interact competitively with Nipissing's other piscivores.

DCCO have shown dietary preference for less-abundant non-percid species while nesting in lakes containing percid-dominant fish communities (DeBruyne et al. 2017). Emerald and spottail shiners, have contributed a major part of DCCO dietary fraction in locations where DCCO and shiners coincide (DeBruyne et al. 2012; Hundt et al. 2013). For example, emerald shiners comprised large portions of DCCO diet from colonies in Lakes Erie, Ontario and Huron (Madenjian and Gabrey 1995; Bur et al. 1997; Neuman et al. 1997; Stapanian et al. 2002; Somers et al. 2003; King et al. 2017), were consumed heavily by DCCO within the Upper Niagara River (Coleman et al. 2012), and constituted a fairly large portion of young-of-the-year DCCO diet within Lake Winnipeg (Ofukany et al. 2015). On the other hand, logperch were found to comprise a relatively small percentage of DCCO diet within Lake Winnebago, Wisconsin (Koenigs et al. 2021), the Upper Niagara River (Coleman et al. 2012), Lake Champlain, USA – Canada (DeBruyne et al. 2012), Leech lake, Minnesota (Göktepe et al. 2012; Hundt et al. 2013), and Lake Huron, USA (Neuman et al. 1997; DeBruyne et al. 2017). Although consumed in lower frequency during most years in Lake Oneida, logperch made large contributions to DCCO diet in 1995 and 1998 (Rudstam et al. 2004; DeBruyne et al. 2013).

Based on SIMM outputs, DCCO chicks appeared to have a more generalized diet, consuming smaller proportions of many prey types rather than consuming larger proportions of just a few prey types like piscivorous fishes. Contrary to my results, a suite of earlier studies have reported DCCO diet to consist of primarily one or two species composing 50 % or more of the total diet (Bur et al. 1997; Seefelt and Gillingham 2004, 2006; Johnson et al. 2010b, 2015; Andrews et al. 2012; DeBruyne et al. 2012; Van Guilder and Seefelt 2013; Hundt et al. 2013; King et al. 2017; Koenigs et al. 2021) (See Table 5). Many of these studies were based on waterbodies containing small-bodied fish assemblages dominated in abundance by just a few species. Conversely, adult and young-of-the-year DCCO on Lake Winnipeg fed on nine prey types in fairly equal measures, with each prey type contributing between 10 and 13% to DCCO diet (Ofukany et al. 2015). The bulk of prey fish community biomass within Lake Winnipeg is largely shared by six common species (Sheppard et al. 2015; ECCC 2020); which may be more akin to Lake Nipissing's current fish assemblage, in which Nipissing's ten most common forage fish species are believed to be of high densities ($> 25 \text{ g} / 100 \text{ m of net} / \text{night}$).

Table 5. Summary of previous studies that have estimated DCCO diet composition in various locations on and near the Laurentian Great Lakes.

Lake (location) and years	Life history stage(s)	Analysis type	Primary prey species (estimated % of diet)	Reference
Erie (west basin), 1997	Adult, juvenile	Stomach contents	Gizzard shad (70%), Emerald shiner (27%)	Bur et al. 1997
Erie, 2009-2010	Adult, chick	Regurgitates	Round goby (70%), Cyprinidae (14 %)	King et al. 2017
Erie, 2009-2010	Adult, chick	Stable Isotope Mixing Model	Round goby (35 %), Alewife (38 %)	King et al. 2017
Leech, MN, 2004 - 2006	Adult, chick	Regurgitates	Yellow perch (34 - 79%), <i>Notropis spp</i> (19 - 52 %)	Hundt et al. 2013
Michigan (north end), 2000 - 2001	Adult, juvenile	Regurgitates, stomach contents	Alewife (> 70 %)	Seefelt and Gillingham 2004
Michigan (north end), 2010	Chick	Regurgitates	Round goby (67 %), Alewife (29 %)	Van Guilder and Seefelt 2013
Ontario (east end), 2003 - 2007	Adult	Regurgitates	Round goby (86 - 97 %)	Johnson et al. 2010a
Ontario (west end), 2006 - 2007	Chick	Regurgitates	Alewife (87 - 93 %)	Andrews et al. 2012
Ontario (west end), 2009 - 2010	Adult, chick	Regurgitates	Round goby (25 - 42 %), Alewife (51 - 56 %), Cyprinidae (4 - 13 %)	King et al. 2017

Table 5. Continued.

Lake (location) and years	Life history stage(s)	Analysis type	Primary prey species (estimated % of diet)	Reference
Ontario (west end), 2009 - 2010	Adult, chick	Stable Isotope Mixing Model	Round goby (17 - 26 %), Alewife (30 - 33 %), Emerald shiner (41 - 54 %)	King et al. 2017
Winnebago, WI, 2015 - 2017	Adult	Stomach contents	Freshwater drum (15 - 93 %), Gizzard shad (18 - 78 %)	Koenigs et al. 2021

A 2014 – 2015 study of adult DCCO diet on Lake Nipissing based on molecular analysis of regurgitated cough pellets estimated a composition with 43% yellow perch, 27% trout-perch, and only 7% walleye (Lecours 2017). Notably absent from the adult DCCO diet estimates were any *Notropis* species (shiners), which was unexpected given that they are relatively abundant in the Lake Nipissing fish community. Using regurgitates to infer diet can have some drawbacks such as under-representation or omission of rapidly digested prey and may present a bias for over-estimation of digestion-resistant prey (Duffy and Laurenson 1983; Johnstone et al. 1990; Brugger 1993; Seefelt and Gillingham 2006; Johnson et al. 2010b). Regurgitate diet assessments have sometimes underestimated shiners within DCCO diets when compared alongside other methods of diet investigation (i.e. stomach contents, isotope analysis) (Seefelt and Gillingham 2006; King et al. 2017).

Different diet assessment techniques may predict over different time scales and consequently may also vary in their ability to detect differences in diet over time. Regurgitates and pellets indicate what individuals have eaten recently, while stable isotope ratios integrate diet information over a longer period of time; the duration of time depending on the type of tissue sampled. For example, recalcitrant tissue with slow turn-over rates such as bone provides dietary information assimilated over years while more metabolically-active tissues such as blood plasma and liver have a higher turn-over rate reflecting diet over days and weeks (Madigan et al. 2021). DCCO quickly adapt to shifts in forage fish community structure by switching to newly abundant prey (Johnson et al.

2010a; Coleman et al. 2012; Koenigs et al. 2021). Stable isotope analyses performed using tissue with slower turnover rates may be unable to detect sudden shifts in diet, whereas more direct methods such as analyses of stomach contents and regurgitates could identify a switch in prey.

Diet composition has been shown to differ between rearing and non-rearing stages in several other species of piscivorous birds (Shealer 1998; Davoren and Burger 1999; Morgenthaler et al. 2016). Optimal foraging theory predicts that for multiple-prey loaders, such as cormorants that transport multiple prey items within the crop to provision nestlings, adults should optimize each chick provisioning trip by selecting high energy prey (i.e., fatty species, gravid individuals), and while self-feeding with no transportation energy demands adults should feed on the prey that is most available (Barrett et al. 2007). The caloric densities of forage fish can vary between species; for example, within Lake Winnipeg the average energy densities of emerald shiner and yellow perch were 6820 +/- 1220 Joules/gram and 5040 +/- 640 Joules/gram, respectively (Sheppard et al. 2015). Variation between adult and nestling diet composition has been reported in DCCO (Neuman et al. 1997; Somers et al. 2003; Doucette 2012; Hundt et al. 2013) and other congeneric species (Harrisamf and Wanless 1993; Boström 2013; Buttu et al. 2019). Adult DCCO may also collect smaller prey to be fed to chicks than when self-feeding to accommodate the feeding constraints of the smaller gape size of chicks (Neuman et al. 1997; Somers et al. 2003; Doucette 2012).

Based on recent fish community surveys, juvenile walleye represent a relatively small percentage of the total biomass comprising Lake Nipissing's diverse small-bodied fish community. Thus, it is not surprising that SIMMs predicted that juvenile walleye were only marginally important within the diets of piscivorous fishes and DCCO nestlings. DCCO diet has been found to be highly variable and may be dependent on the current structure of small-bodied fish communities present within foraging areas. Overall, studies that found walleye present in DCCO diet, but of lower importance in comparison to other species, have been from lakes with relatively low walleye densities (Bur et al. 1997; Neuman et al. 1997; Doucette et al. 2011; Coleman et al. 2012; Hundt et al. 2013; Ofukany et al. 2015; DeBruyne et al. 2017; King et al. 2017; Koenigs et al. 2021). Conversely, studies that point to a prevalence of walleye within DCCO diet were conducted on lakes with walleye-dominant fish communities, such as Lake Oneida (Rudstam et al. 2004; DeBruyne et al. 2013). Furthermore, later research on Lake Oneida noted that DCCO diet shifted away from walleye to predominantly emerald shiner and gizzard shad coinciding with strong year-classes occurring between 2006 and 2009 (Coleman et al. 2016) and seasonal increases in density (DeBruyne et al. 2013). And shortly after round goby were introduced into eastern Lake Ontario and quickly became established in high abundances, DCCO diet promptly reflected the shift in fish communities by switching from a diet previously dominant in alewife to round goby (DeBruyne et al. 2012). These studies emphasize that DCCO prey selection can vary seasonally as well as annually and can be highly dependent on the prevailing species composition of small-bodied fish communities.

Correct discrimination factors or TEF's may be critical when using SIMMs to obtain accurate estimates of assimilated diets. TEF's are usually considered to be specific for a given consumer because of interspecific differences in metabolic rates and thought to remain constant throughout the consumer's lifespan. However, studies have demonstrated that TEF's may vary within a particular species due to an array of factors. Muscle tissue incorporation rates of ^{15}N vary with body size in various species of caiman (Villamarín et al. 2018) and arapaima (Jacobi et al. 2020). Differences in the nutritional content of diet, particularly nitrogen, have been associated with $\delta^{15}\text{N}$ TDF variation in guppy (*Poecilia reticulata*), zebrafish (*Danio rerio*), fathead minnow (*Pimephales promelas*), bluegill (*Lepomis macrochirus*) (Blanke et al. 2017), juvenile herring (*Clupea harengus*) (Aberle and Malzahn 2007) and Mozambique tilapia (*Oreochromis mossambicus*) (Kadye et al. 2020). TDF's have also been shown to vary among individuals of different ontogenetic stages associated with changes in metabolic rates in Eurasian perch (*Perca fluviatilis*) (Scharnweber et al. 2021) and walleye (Overman and Parrish 2001). When modeling DCCO, I used species-specific TEF's derived from a laboratory controlled-feeding experiment (Craig et al. 2015a) and when modeling piscivorous fish I used TEF's that are widely accepted to represent muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ fractionation rates of most freshwater fish (Vander Zanden and Rasmussen 2001). Modeling DCCO diet using alternative TEFs did not change the order of relative importance of prey items but did reduce predicted diet diversity.

My estimates of piscivorous fish diet composition from SIMMs remained relatively stable across models using alternative TEFs. However, modeling piscivorous fish using TEFs selected from Schumann et al. (2018) did alter the order of importance of prey items within the diet; this particular study derived a TEF for $\delta^{15}\text{N}$ that was considerably lower (1.9 ‰) than typical TEF values used to describe fractionation in freshwater fish (3.4 ‰). The TEFs estimated by Schumann et al. (2018) were for very young walleye and considering that TEFs can vary with body size, growth and ontogeny it may be inappropriate to utilize them when modeling diets of larger mature fish like those found in my study (Jacobi et al. 2020; Scharnweber et al. 2021).

Another critical aspect when applying SIMMs is ensuring inclusion of all potential prey types considered available to the consumer. Failing to include important prey types or inclusion of prey types seldom consumed could lead to spurious estimates. When evaluating the influence of shifting prey size on diet estimates, the largest prey size category (20 g) exceeded the maximum size of two species of prey fish and subsequently, those two prey species were omitted from modeling the 20 g category. Exclusion of the two prey types had a substantial impact on the estimated diet composition of all piscivores. It is difficult to be certain whether any important prey types were overlooked or excluded in diet estimation. Due to insufficient sample sizes, Centrarchidae such as rock bass (*Ambloplites rupestris*) were excluded as potential prey from diet modeling but are believed to be in high abundance within Nipissing's small-bodied fish assemblage. When seasonally abundant, non-fish prey such as spiny water flea (*Bythotrephes*

longimanus) and burrowing mayfly nymphs (Ephemeroidea) have been important within the diets of walleye and northern pike. Other non-fish prey such as crayfish have been found in relatively large numbers in regurgitates of DCCO from the lower Laurentian Great Lakes, as well as from inland lakes in Saskatchewan, Canada (Neuman et al. 1997; Doucette et al. 2011). However, two assessments of Lake Nipissing DCCO regurgitates, one performed during the years 1993 to 1995 (Jorgensen, MNRF, unpubl data) and one more recently (Lecours 2017) both failed to detect any non-fish prey. Future studies might consider a form of direct observation such as stomach contents or pellet analysis prior to modeling piscivore diet to assist in identifying important prey items.

4.6 Conclusions and fisheries management implications

The results of this research have several implications that may be considered when developing management planning to address Nipissing's DCCO population. During my study period, juvenile walleye did not appear to be a major component within the diets of cormorants or piscivorous fishes, suggesting it is unlikely that cormorant or piscivorous fish predation is a major factor contributing to walleye mortality or declines in recruitment. Piscivorous fish within Lake Nipissing were predicted to feed primarily on emerald shiner and logperch. Emerald shiner was also nutritionally important to cormorant, suggesting some similarity in diet to predatory fish, but DCCO diet composition was slightly more diverse and contained moderate

amounts of other species of forage fish. And, although diet composition was similar to some extent, isotopic niche analyses revealed predatory fish and DCCO occupied fairly different niche space and may suggest the potential for competitive interaction between DCCO and predatory fish is relatively low. In light of the similarity in diet observed between predatory fish and DCCO there may be a possibility of competition at some level. At the time of my study, according to lake wide community surveys, Lake Nipissing's prey fish populations appeared to be abundant with no indication that prey were limiting. If at some point, prey fish densities were to decline and favored prey species such as emerald shiner and logperch were to become limiting, interspecific competition may be expected to occur.

Stable isotope analysis provides an informative and powerful means to understand trophic relationships and potential competition between consumers that might otherwise be difficult to resolve solely using traditional diet analysis methods. Future research intending to model piscivore diet might consider combining direct methods such as stomach and pellet content data in conjunction with stable isotope analyses. Integrating the two approaches might provide a more complete picture of diet that could assist in disentangling diet similarities/differences between consumers as well as reveal details on species and size classes of prey that could be used to establish criteria for selection of prey categories in SIMM modeling.

At the time of this study, there appears to be limited research on whether the diet composition of DCCO varies between life-history stages. One interesting avenue of

future research might be to compare the diet compositions of adult and juvenile DCCO to uncover whether these two segments of the population interact with fish populations differently. Other studies have demonstrated that DCCO diet is variable and strongly associated with fish population dynamics and in turn may shift along with future food web alterations. This outlines the importance of continuing to perform studies such as the current one that examines diet composition, trophic relationships and overall food web patterns and can be used to track future cormorant dietary shifts, if they should occur.

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Appendix

Relationships between C and N isotopic composition and body size for biota sampled from Lake Nipissing, 2010 – 2017

Table A1.1. Analysis of relationships between tissue $\delta^{13}\text{C}$ and body size (\log_{10} mass) for various biota sampled from Lake Nipissing from 2010 to 2017. Models included both \log_{10} mass and sampling year (class variable, fixed effect) without interaction terms, and significance of each are indicated (* partial-F test, $P < 0.05$). Model results for taxa with < 10 individuals analyzed are not included. $b_1 = \delta^{13}\text{C}$ vs \log_{10} mass slope. Size range gives the minimum – maximum body masses of each species used in analysis.

Species	Body size (\log_{10} mass) effect				Year effect?	Full model R^2
	b_1	partial-F	df_{error}	P		
<i>Piscivores</i>						
Burbot	1.09	6.28	25	0.019 *	*	0.75
Double-crested cormorant	-0.56	0.37	39	0.54		0.15
Northern pike	0.44	0.25	23	0.62	*	0.40
Smallmouth bass	1.26	9.38	34	0.0043 *	*	0.52
Walleye	0.32	5.94	158	0.016 *	*	0.34
<i>Forage fishes</i>						
Cisco	0.27	0.13	28	0.72	*	0.37
Emerald shiner	-4.02	32.3	79	< 0.001 *	*	0.31
Logperch	2.61	12.1	84	< 0.001 *		0.16
Rainbow smelt	-0.56	1.76	31	0.19	*	0.48
Spottail shiner	-2.84	57.5	107	< 0.001 *	*	0.53
Trout-perch	0.82	8.92	121	0.0034 *	*	0.27
Yellow perch	0.86	25.0	290	< 0.001 *	*	0.13

Table A1.1. Continued.

Species	Body size (\log_{10} mass) effect				Year effect?	Full model R^2
	b_1	partial-F	df_{error}	P		
<i>Benthivores</i>						
Freshwater drum	0.58	0.65	17	0.43		0.15
Lake sturgeon	0.73	1.76	18	0.20		0.09
Lake whitefish	2.39	0.98	11	0.34		0.09
White sucker	3.24	7.62	27	0.010 *		0.37
<i>Invertebrates</i>						
Clams	1.09	11.1	166	0.0011 *	*	0.20
Crayfish	-3.82	3.49	11	0.089		0.34
Burrowing mayflies	-0.72	1.91	44	0.17	*	0.15
Flathead mayflies	-0.68	0.64	100	0.43		0.04
Snails	-0.58	2.10	80	0.15		0.08

Table A1.2. Analysis of relationships between tissue $\delta^{15}\text{N}$ and body size (\log_{10} mass) for various biota sampled from Lake Nipissing from 2010 to 2017. Models included both \log_{10} mass and sampling year (class variable, fixed effect) without interaction terms, and significance of each are indicated (* partial-F test, $P < 0.05$). Model results for taxa with < 10 individuals analyzed are not included. $b_1 = \delta^{15}\text{N}$ vs \log_{10} mass slope. Size range gives the minimum – maximum body masses of each species used in analysis.

Species	Body size (\log_{10} mass) effect				Year effect?	Full model R^2
	b_1	partial-F	df_{error}	P		
<i>Piscivores</i>						
Burbot	1.38	10.80	25	0.0031 *		0.55
Double-crested cormorant	-1.65	3.64	39	0.064		0.18
Northern pike	1.71	8.76	23	0.0070 *	*	0.36
Smallmouth bass	-0.02	0.01	34	0.94		0.10
Walleye	0.71	89.30	156	< 0.001 *	*	0.77
<i>Forage fishes</i>						
Cisco	0.92	11.80	28	0.0018 *	*	0.64
Emerald shiner	1.69	26.1	79	< 0.001 *	*	0.41
Logperch	1.03	25.8	84	< 0.001 *	*	0.29
Rainbow smelt	0.45	4.12	31	0.051		0.16
Spottail shiner	1.77	99.8	107	< 0.001 *	*	0.62
Trout-perch	0.99	20.40	121	< 0.001 *	*	0.21
Yellow perch	0.89	133.0	291	< 0.001 *	*	0.45

Table A1.2. Continued.

Species	Body size (log ₁₀ mass) effect				Year effect?	Full model R ²
	b ₁	partial-F	df _{error}	P		
<i>Benthivores</i>						
Freshwater drum	0.79	7.60	17	0.013 *		0.38
Lake sturgeon	-0.14	0.41	18	0.53		0.02
Lake whitefish	-0.46	1.52	11	0.24		0.41
White sucker	0.31	0.26	27	0.610		0.01
<i>Invertebrates</i>						
Clams	0.25	4.1	166	0.045 *		0.04
Crayfish	1.19	1.29	11	0.29		0.11
Burrowing mayflies	0.51	3.02	44	0.089		0.08
Flathead mayflies	-0.19	0.76	100	0.38		0.02
Snails	0.17	1.84	82	0.18	*	0.17