

Trophic dynamics of several fish species in lakes of a climatically sensitive region, the Hudson Bay Lowlands

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Abstract Freshwater lakes in the Hudson Bay Lowlands (HBL) area of Ontario are expected to undergo considerable physical, chemical and biological changes related to climatic change; however, the nature of those changes is still very uncertain. As a first step to improve our understanding of fish communities within these subarctic lakes, we aimed to: (a) characterize trophic dynamics of several large-bodied species within three HBL lakes and (b) determine whether trophic dynamics of selected species in the HBL lakes differed from the same species in Southern Ontario lakes. We found that species-specific trophic position and littoral resource reliance varied significantly within and among the HBL lakes of differing biological communities, chemistry and morphometry. Although several significant differences were evident among lakes in the northern and southern regions, we did not find striking consistent differences in trophic dynamics. Based on observations of high variation in trophic position and/or littoral reliance, we can hypothesize that changes in

food resources resulting from climatic change would have little impact on most of the large-bodied species.

Keywords Subarctic lakes · Hudson Bay Lowlands · Trophic dynamics · Stable isotopes · Climate change

Introduction

Climatic change is emerging as a driving force behind many ecological changes within freshwater ecosystems (Mooij et al. 2005; Moss 2010). Some climatic factors that can influence biological communities in aquatic environments include changes in temperature, precipitation, water residence time, water level and ice cover (Jensen et al. 2007; Whitehead et al. 2009; Carter and Schindler 2012). Alteration of these factors can directly impact individual species or lead to shifts in community composition, biodiversity and altered trophic interactions among species (Brown et al. 2007; Keller 2007; Chessman 2009; Kratina et al. 2012).

The climate of Northern Ontario is expected to change dramatically by the latter part of this century. The northernmost areas are predicted to experience a substantial increase in annual (5–7 °C) and winter temperatures (9–10 °C) (Colombo et al. 2007). Consequently, freshwater lakes in the Hudson Bay Lowlands (HBL) area of Ontario are expected to undergo considerable physical, chemical and biological changes related to climatic change (McKenney et al. 2010; Rühländ et al. 2013); however, the nature of those changes is still very uncertain, especially for biota in lakes at higher trophic levels such as fish.

The HBL comprise one of the largest wetland complexes in the world and contain globally significant carbon stores (Macrae et al. 2004). The area is high in biodiversity

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and very sensitive to climate change (Far North Science Advisory Panel 2010). There are thousands of lakes and ponds across the landscape. Lakes of the HBL are largely unaffected by anthropogenic stressors such as acid rain and nutrient enrichment; however, given its ecological importance study of this area is key to developing an understanding of the potential impacts of climate change. Even though the HBL lakes are in a climatically sensitive region, they have received little research attention (Abraham et al. 2011); thus, there is generally a lack of information regarding how a warmer climate is likely to alter the biological communities within them.

In light of recent evidence of significant changes in lower trophic levels (plankton) from paleolimnological records within HBL lakes (Brazeau et al. 2013; Rühland et al. 2013), it is important that we assess whether and how fish communities will respond to climatic change. Climate change has the potential to directly and indirectly impact fish communities because they are ectotherms, and their activities and trophic interactions are highly dependent on temperature. Furthermore, as integrators in lake food webs (Vander Zanden and Vadeboncoeur 2002), it is of vital importance that we understand whether and how fish communities will change because loss or significant alterations in fish abundance or size composition can create changes that cascade throughout aquatic ecosystems.

One of the major challenges in freshwater ecology is predicting the consequences of environmental change on ecosystem structure and function. As a first step to improve our understanding of whether and how climate change can potentially alter food web structure and function of HBL lakes, we compare fish populations from the HBL lakes to those in warmer areas of Ontario including the Muskoka-Haliburton and Kawartha-Renfrew regions. Specifically, our objective is to determine whether trophic dynamics differ substantially among populations of several large-bodied fish species (that is, dominant piscivores and benthivores) in Northern versus Southern Ontario regions. This study is the first to apply stable isotope analyses to the examination of food web structure in subarctic HBL lakes. Stable isotope analysis is a very useful molecular technique for tracing energy flows and examining trophic relationships among predators and their prey and has been widely applied in aquatic food web studies (Peterson and Fry 1987; Fry 2006). We used carbon and nitrogen stable isotope data for two purposes here: (a) to characterize trophic interactions, energy transfer routes and niche overlap among large-bodied fish within three HBL lakes that are located in the Sutton Ridges area, a unique geological area within the HBL that offered the widest range of lake types, and (b) to determine whether the dietary carbon source and trophic position for large-bodied fish species differ between the HBL lakes in the north and southern Muskoka-

Haliburton and Kawartha-Renfrew lakes. We hypothesize that the wide ranging chemical, biological and morphometric differences among HBL lakes in the study area will result in significant variability of trophic interaction and energy transfer routes of selected large-bodied species within and among lakes. Further, if climate plays an overriding influence on trophic dynamics and energy transfer even in such variable systems, we would then expect that there will be significant and consistent differences between the northern HBL populations and those found in the southern lakes.

Methodology

Study lakes

Our data set consists of a total of nine lakes, three from each region (Table 1; Fig. 1). We used available data to select lakes in the Muskoka-Haliburton and Kawartha-Renfrew areas that contained at least one of the species found in the HBL lakes to facilitate comparison between regions. Within a given region, we selected lakes that ranged widely in morphometry and chemical characteristics. Lake areas and maximum depths ranged from 1,230 to 2,720 ha and 1.7–35.2 m in the HBL, 59–1,240 ha and 10–64 m in the Kawartha-Renfrew region, and 43.9–93.2 ha and 12–38 m in the Muskoka-Haliburton region.

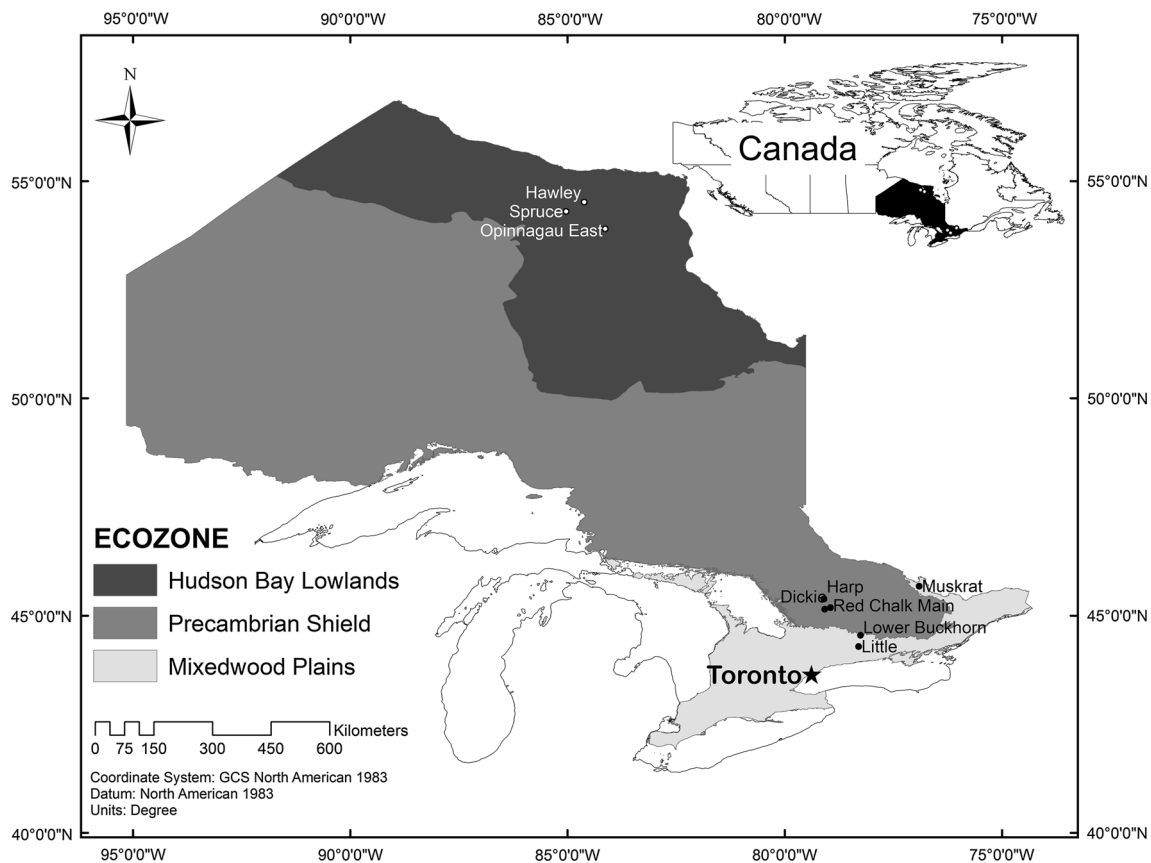
The geology of the surrounding lake catchments differs among regions. Catchments of the Kawartha-Renfrew lakes consist predominantly of calcareous bedrock, whereas the bedrock of the Muskoka-Haliburton lakes is primarily the granitic gneiss characteristic of the Precambrian Shield. The HBL lake catchments are more complex with a combination of Precambrian bedrock influencing the higher elevation lakes of the Sutton Ridge and more recent Paleozoic or calcareous bedrock surrounding the lower elevation lakes.

The difference in geology among and within regions is reflected in the chemistry of the lakes; consequently, alkalinity, dissolved organic carbon (DOC) and total phosphorus (TP) concentrations are comparatively higher in the Kawartha-Renfrew and HBL lakes than in the Muskoka-Haliburton lakes (Table 1). Based on the Organization of Economic Cooperation and Development (OECD) classification (OECD 1982), the Muskoka-Haliburton lakes were all oligotrophic (TP range = 3.1–5.8 $\mu\text{g L}^{-1}$), whereas the HBL lakes ranged from oligotrophic to mesotrophic (6.6–19.7 $\mu\text{g L}^{-1}$), and the Kawartha-Renfrew lakes from mesotrophic to eutrophic (15.1–43.6 $\mu\text{g L}^{-1}$). Ranges in alkalinity in the HBL, Kawartha-Renfrew and Muskoka-Haliburton lakes were 63.1–106.0 $\text{mg L}^{-1} \text{CaCO}_3$, 75.0–123.0 $\text{mg L}^{-1} \text{CaCO}_3$

Table 1 Locations, morphometric characteristics and chemical properties of the study lakes

Region (Sampling year) Lake	Latitude	Longitude	Area (ha)	Z _{max} (m)	Secchi depth (m)	DOC (mgL ⁻¹)	Alkalinity (mgL ⁻¹ CaCO ₃)	TP (μgL ⁻¹)	pH
HBL (2010)									
Hawley	54.517	-84.617	1,240	35.2	5.1	5.8	106.0	6.6	8.1
Opinnagau East	53.900	-84.133	2,720	1.70	1.5	9.8	63.1	19.7	7.6
Spruce	54.300	-85.003	1,230	14.0	2.5	7.6	71.2	10.6	7.8
Kawartha-Renfrew (2009)									
Little	44.290	-78.300	59.0	10.0	3.4	8.0	97.9	16.0	8.0
Lower Buckhorn	44.550	-78.260	1,240	14.0	3.3	5.5	75.0	15.1	8.0
Muskrat	45.680	-76.910	1,220	64.0	1.9	10.0	123.0	43.6	8.1
Muskoka-Haliburton (2009)									
Dickie	45.150	-79.083	93.2	12.0	2.9	6.6	5.3	5.8	5.8
Harp	45.383	-79.100	71.4	37.5	4.2	4.8	3.9	3.8	6.0
Red Chalk Main (RCM)	45.183	-78.950	43.9	38.0	4.4	4.0	4.7	3.1	6.1

DOC is dissolved organic carbon; TP is total phosphorus; and Z_{max} is maximum depth at the time of sampling

**Fig. 1** Map of Ontario showing locations of the study lakes

and 3.9–4.7 mg L⁻¹ CaCO₃, respectively; whereas ranges in DOC concentrations were 5.8–9.8, 5.5–10.0 and 4.0–6.6 mg L⁻¹, respectively. The pH ranged from 7.6–8.1, 8.0–8.1 and 5.8–6.1 in the HBL, Kawartha-Renfrew and Muskoka-Haliburton lakes, respectively.

Climatically, the HBL is considerably cooler and drier than the Kawartha-Renfrew and Muskoka-Haliburton regions. The mean annual temperature for the HBL region between 2000 and 2010 was -5.7 ± 1.5 °C (mean and standard deviation for Churchill, Manitoba station) compared to 7.2 ± 1.1 and

5.4 ± 0.8 °C for the Kawartha-Renfrew (Peterborough and Kingston, Ontario stations) and Muskoka-Haliburton (Haliburton, Ontario station) regions, respectively (Environment Canada, <http://www.cccma.ec.gc.ca/hccd/>). The total precipitation was lower in the HBL with 558 ± 109 mm compared to 995 ± 118 and 1,184 ± 122 mm for the Kawartha-Renfrew and Muskoka-Haliburton regions, respectively (Environment Canada, <http://www.cccma.ec.gc.ca/hccd/>).

Biologically, the three HBL lakes differed widely in their phytoplankton, zooplankton, benthic invertebrate and fish communities (Keller et al. 2011, 2013). Phytoplankton biovolume and genera richness were highest in Opinnagau East Lake (1,249 mm³ m⁻³ and 69, respectively) and lowest in Hawley Lake (271.7 mm³ m⁻³ and 44, respectively). Zooplankton density was highest in Spruce Lake (5.40 × 10⁴ m⁻³) and lowest in Hawley Lake (1.91 × 10⁴ m⁻³), but zooplankton species richness was highest in Opinnagau East Lake (12) and lowest in Hawley Lake (8). The profundal benthic macro-invertebrate community of Hawley Lake (10 species) was richer compared to Opinnagau East Lake (6 species) and Spruce Lake (3 species). The fish species richness and diversity of Hawley Lake (15 species and Shannon $H' = 2.01$) were higher than that of Spruce Lake (10 species and Shannon $H' = 1.81$). A complete fish survey was not available for Opinnagau East Lake.

Sample collection

Fish and invertebrates

All fish and invertebrate samples used for stable isotope analyses were collected between 2009 and 2010 during the summer months when surface water temperatures were above 18 °C (18–20 °C for HBL, 21–23 °C for Kawartha-Renfrew and 20–21 °C for Muskoka-Haliburton regions). Fish were caught from throughout the lakes using standard gill netting methods developed by the Ministry of Natural Resources for the Broadscale Monitoring Program (Sandstrom et al. 2008) or the NORDIC Index Netting Program (Morgan and Snucins 2005). Multi-mesh gillnets (benthic) consisting of 12 different mesh sizes (stretched mesh sizes of 13–127 mm for Broadscale Monitoring and 10–110 mm for NORDIC Index nets) were randomly distributed across lakes, with the number of net sets dependent on lake area and depth. The number of benthic multi-mesh gillnets set ranged from four to ten in the HBL, 13–33 in the Kawartha-Renfrew region and 24–32 in the Muskoka-Haliburton region. We used either all of the fish caught or a random selection covering the full size range of the total catch obtained from each lake (see Table 2) for stable isotope analyses. For each fish, we recorded length and removed a

Table 2 Fish species, total catch, number of fish sampled for SIA (n) and fish size of SIA sampled fish in mm (mean ± SE) for the study lakes

Region	Lake	Fish species	Total catch	SIA Fish size mean ± SE (n)
HBL	Hawley	Lake trout	40	572.7 ± 28.4 (10)
		Lake whitefish	25	494.4 ± 24.8 (10)
		Northern pike	20	594.1 ± 15.0 (10)
		White sucker	27	443.5 ± 16.2 (10)
	Opinnagau East	Lake whitefish	50	440.3 ± 24.8 (10)
		Northern Pike	18	584.7 ± 65.3 (11)
		White sucker	63	522.6 ± 16.2 (10)
	Spruce	Lake whitefish	11	456.4 ± 19.6 (11)
		Northern pike	24	614.0 ± 42.6 (13)
		Walleye	37	485.3 ± 32.8 (12)
White sucker		33	482.3 ± 16.2 (10)	
Kawartha-Renfrew	Little	Walleye	11	338.2 ± 54.3 (9)
	Lower Buckhorn	Walleye	16	310.6 ± 37.2 (11)
	Muskrat	Northern pike	69	527.0 ± 53.5 (11)
		Walleye	69	465.0 ± 20.1 (12)
Muskoka-Haliburton	Dickie	White sucker	45	443.5 ± 54.3 (5)
		Northern pike	2	569.5 (2)
	Harp	White sucker	2	415 (2)
	Red Chalk Main	Lake trout	13	551.0 ± 18.7 (9)
White sucker		117	307.0 ± 64.5 (5)	

Fish species are as follows: Lake trout (*Salvelinus namaycush*); Lake whitefish (*Coregonus clupeaformis*); Northern pike (*Esox lucius*); Walleye (*Sander vitreus*) and White sucker (*Catostomus commersonii*)

skinless, dorsal muscle sample from the mid-region above the lateral line for isotope analyses.

Benthic invertebrates were collected by the kick-and-sweep method (David et al. 1998) or an Ekman dredge (Luek et al. 2013). For the Kawartha-Renfrew and HBL lakes, kick-and-sweep sampling was done with a 500- μm mesh net at 5–10 locations within each lake. For the Muskoka-Haliburton lakes, a 15 cm \times 15 cm Ekman dredge was used to collect nine samples from three locations within each lake (Luek et al. 2013). All collected samples were sorted to obtain samples of Amphipoda, Chironomidae, Ephemeroptera and Corixidae.

Pelagic zooplankton samples were collected with a series of conical mesh nets. Zooplankton for the Kawartha-Renfrew and HBL lakes were collected with 75- and 200- μm mesh nets, whereas 84- and 128- μm mesh nets were used in the Muskoka-Haliburton lakes to collect zooplankton and *Chaoborus*, respectively (Luek et al. 2013).

Water chemistry

Water samples for chemical analyses were obtained from 0.5 m below the surface at the deepest station in each lake at the time of fish and invertebrate sampling. Chemical analyses were performed following the standard analytical protocols of the Ontario Ministry of the Environment (Ontario Ministry of the Environment 1983; www.desc.ca).

Stable isotope analyses

Carbon and nitrogen stable isotope analyses of dried and ground fish, zooplankton and benthic invertebrates were conducted in either the Water Quality Center at Trent University, the Environmental Quality Analysis Laboratory at the University of Regina or the Stable Isotope in Nature Laboratory at the University of New Brunswick. These are all accredited laboratories that routinely use a number of certified international standards for calibration when performing isotopic analyses.

For this multi-lake study, we calculated trophic position (TPos) of individual fish using a one source model as follows:

$$\text{TPos} = \frac{(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{base}})}{3.4\text{‰}} + 2$$

where $\delta^{15}\text{N}_{\text{fish}}$ is the nitrogen isotope value for fish, $\delta^{15}\text{N}_{\text{base}}$ is the isotope value for baseline organisms, 3.4 ‰ is the trophic fractionation value of $\delta^{15}\text{N}$ and 2 is the trophic position of the primary consumers used as baseline organisms (Post 2002; Anderson and Cabana 2007). Here, we calculated mean $\delta^{15}\text{N}_{\text{baseline}}$ values for each study lake using the $\delta^{15}\text{N}$ of a number of benthic invertebrates (Amphipoda, Chironomidae, Ephemeroptera and Corixidae) and zooplankton obtained from each lake.

Using the carbon isotopic data, we also estimated the reliance on littoral resources as follows:

$$\text{Littoral reliance} = \frac{(\delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{pelagic base}})}{(\delta^{13}\text{C}_{\text{littoral base}} - \delta^{13}\text{C}_{\text{pelagic base}})}$$

where $\delta^{13}\text{C}_{\text{fish}}$, $\delta^{13}\text{C}_{\text{pelagic base}}$ and $\delta^{13}\text{C}_{\text{littoral base}}$ are the fish and baseline carbon isotope values, respectively (adapted from Vander Zanden and Vadeboncoeur 2002). Here, we used zooplankton as the pelagic baseline and a number of benthic invertebrates (Amphipoda, Chironomidae, Ephemeroptera and Corixidae) as the littoral baseline organisms.

Isotopic niche space analysis

We used SIBER (Jackson et al. 2011) in the SIAR package (Parnell and Jackson 2013; R Core Team 2013) to calculate trophic niche space in isotopic dimensions of a given fish species in each lake. This method was first described by Layman et al. (2007) and written into a Bayesian model accessible in the R environment by Jackson et al. (2011). Species-specific trophic niche space was calculated for fish species within each of the study lakes. Then, trophic niche space was compared between fish species within each lake as well as between lakes for each fish species by calculating the likelihood that a given probability of a niche space size of one fish species in a specific lake is (a) larger than the niche of the same fish species in any other lake or (b) larger than the niche of any other fish species in the same lake. Any likelihood $90\% > p < 95\%$ was defined as marginally significant, while likelihoods $>95\%$ were considered significant.

The SIAR program also allows calculation of the trophic niche overlap between two given species (Jackson et al. 2011). This procedure is however not based on a Bayesian approach but rather uses a standard ellipse area calculation corrected for small sample size (Jackson et al. 2011). The procedure returns an area for each of the two input species trophic ellipses in the isotope space (radius of the standard ellipse represents 1 SD of variance in bivariate space) as well as the area of overlap. For this purpose, calculations were made using the percent of overlap between species focussing on the overlap of the trophic niche space of the top predators in the HBL lakes, namely northern pike (*Esox lucius*) and lake trout (*Salvelinus namaycush*) in Hawley Lake, and northern pike and walleye (*Sander vitreus*) in Spruce Lake.

Statistical analyses

Species-specific comparisons of trophic position and littoral reliance among lakes were carried out with parametric

and nonparametric statistics in the JMP 10 statistical program. One-way ANOVAs followed by post hoc Tukey HSD tests were primarily used to test for differences among lakes for a given species. In a few cases where Levene's test indicated that the assumption of homogeneity of variances was violated, we used nonparametric Wilcoxon tests followed by Dunn's paired comparisons to determine significant differences among lakes. Bonferroni-corrected critical p values were used to determine significance of ANOVAs and Wilcoxon results when necessary.

Results

Fish in HBL lakes

Isotopic values, trophic dynamics and energy pathways

The carbon and nitrogen isotopic values differed among large-bodied fish species within each of the three HBL lakes (Fig. 2, $\delta^{13}\text{C}$: ANOVA and Wilcoxon: $p \leq 0.008$; $\delta^{15}\text{N}$: ANOVA and Wilcoxon: $p \leq 0.0001$). Isotopic variability among species within lakes was highest in Hawley Lake, lowest in Opinnagau East Lake and intermediate in Spruce Lake (Fig. 2).

The calculated trophic position varied among species within the HBL lakes. In general, lake trout, northern pike and walleye occupied the highest trophic positions, whereas lake whitefish (*Coregonus clupeaformis*) and white sucker (*Catostomus commersonii*) occupied the intermediate and lowest trophic positions, respectively (Fig. 3). In Hawley Lake, lake trout trophic position (mean trophic position \pm SD = 4.75 ± 0.11) was significantly higher (Dunn: $p \leq 0.005$) than lake whitefish (3.45 ± 0.35) and white

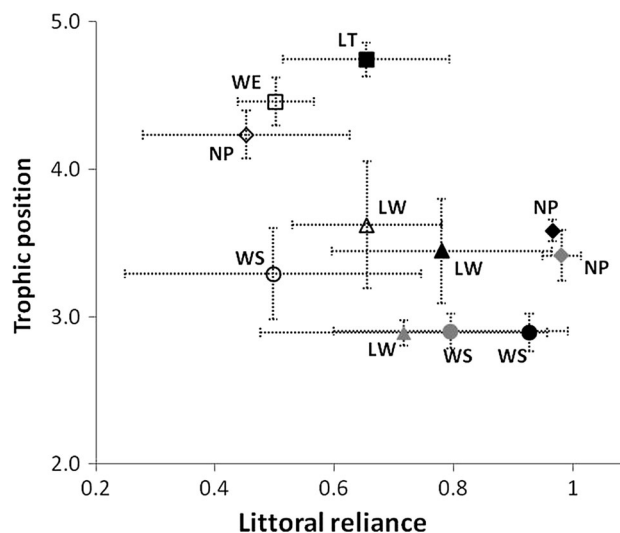


Fig. 3 Biplot of littoral reliance versus trophic position for large-bodied fish species (lake trout—LT, lake whitefish—LW, northern pike—NP, white sucker—WS and walleye—WE) in the HBL lakes: Hawley Lake (black symbols), Opinnagau East Lake (gray symbols) and Spruce Lake (open symbols). Symbols represent unadjusted means \pm SD

sucker (2.89 ± 0.13), but not northern pike (3.58 ± 0.07). In Spruce Lake, walleye trophic position (4.45 ± 0.16) was significantly higher (Dunn: $p \leq 0.009$) than lake whitefish (3.62 ± 0.43) and white sucker (3.29 ± 0.31), but not northern pike (4.23 ± 0.16). In Opinnagau East Lake, northern pike occupied a higher trophic position (3.41 ± 0.17) (Tukey HSD: $p < 0.001$) than lake whitefish (2.89 ± 0.43) and white sucker (2.90 ± 0.12). Lake whitefish trophic position was not significantly different from white sucker in any of the lakes ($p \geq 0.124$).

The estimated littoral resource reliance differed significantly among species (Fig. 3) within all of the HBL lakes

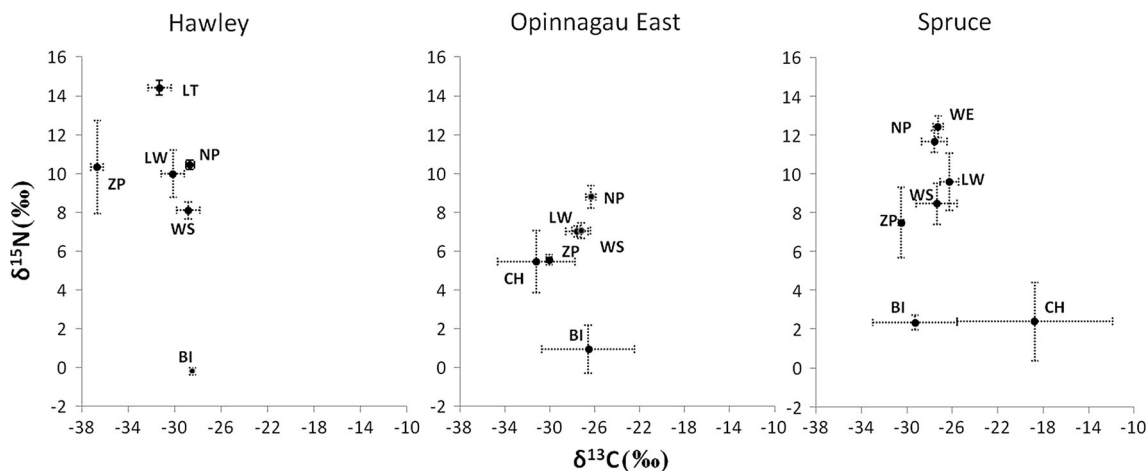


Fig. 2 Biplots of uncorrected $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for the large-bodied fish species (lake trout—LT, lake whitefish—LW, northern pike—NP, white sucker—WS and walleye—WE) and baseline sources

(zooplankton—ZP, chironomids—CH and other benthic invertebrates—BI) in the HBL lakes: Hawley Lake, Opinnagau East Lake and Spruce Lake. Symbols represent unadjusted mean \pm SD

(Wilcoxon: $p \leq 0.008$). In Opinnagau East Lake, northern pike were more reliant on littoral sources (mean littoral reliance proportion \pm SD = 0.98 ± 0.03) compared to lake whitefish (0.72 ± 0.24) and white sucker (0.80 ± 0.20) (Dunn: $p \leq 0.013$). In Spruce Lake, northern pike (0.45 ± 0.17) were less reliant on littoral sources compared to lake whitefish (0.65 ± 0.13) (Dunn: $p = 0.01$). In Hawley Lake, lake trout (0.65 ± 0.14) were less reliant on littoral sources compared to northern pike (0.97 ± 0.03) and white sucker (0.93 ± 0.07).

Niche space

The SIBER model indicated that there were differences in trophic niche space among fish species within lakes, as well as for some fish species among lakes (Table 3). In deep Hawley Lake, northern pike and lake trout occupied the smallest niche spaces of the four sampled fish species. White sucker and lake whitefish were lower in the food web, but occupied significantly larger niches. In Opinnagau East Lake, lake whitefish had a significantly larger niche space than white suckers, but there were no other trophic niche differences among species in the fish community in this shallow lake. In Spruce Lake, the smallest of the three HBL lakes, northern pike and walleye occupied similar sizes of trophic niches, while white suckers had the smallest trophic niche space of the community.

For the three fish species that were present in all of the HBL lakes: northern pike, white sucker and lake whitefish, species-specific analysis of differences in trophic niche spaces among lakes revealed differences in trophic niche sizes only for northern pike and white sucker. Northern pike had the largest trophic niche in Spruce Lake, while niche space in Opinnagau East Lake and Hawley Lake were not different from each other. White sucker exhibited the largest trophic niche space in Hawley Lake, with Opinnagau East Lake and Spruce Lake being significantly smaller, but not different from each other.

The calculated isotopic niche spaces indicated that overlap of northern pike with other predators varied in Spruce Lake and Hawley Lake. Northern pike and walleye had overlapping trophic niche spaces in Spruce Lake (27.7 % of walleye niche space was shared with northern pike, where as 10.4 % of northern pike niche space was shared with walleye), but northern pike and lake trout did not overlap in their trophic niches in Hawley Lake (0 % for the two species).

Regional comparison among fish species and lakes

Trophic dynamics

Significant differences in the trophic position occupied by northern pike, walleye and white sucker were found

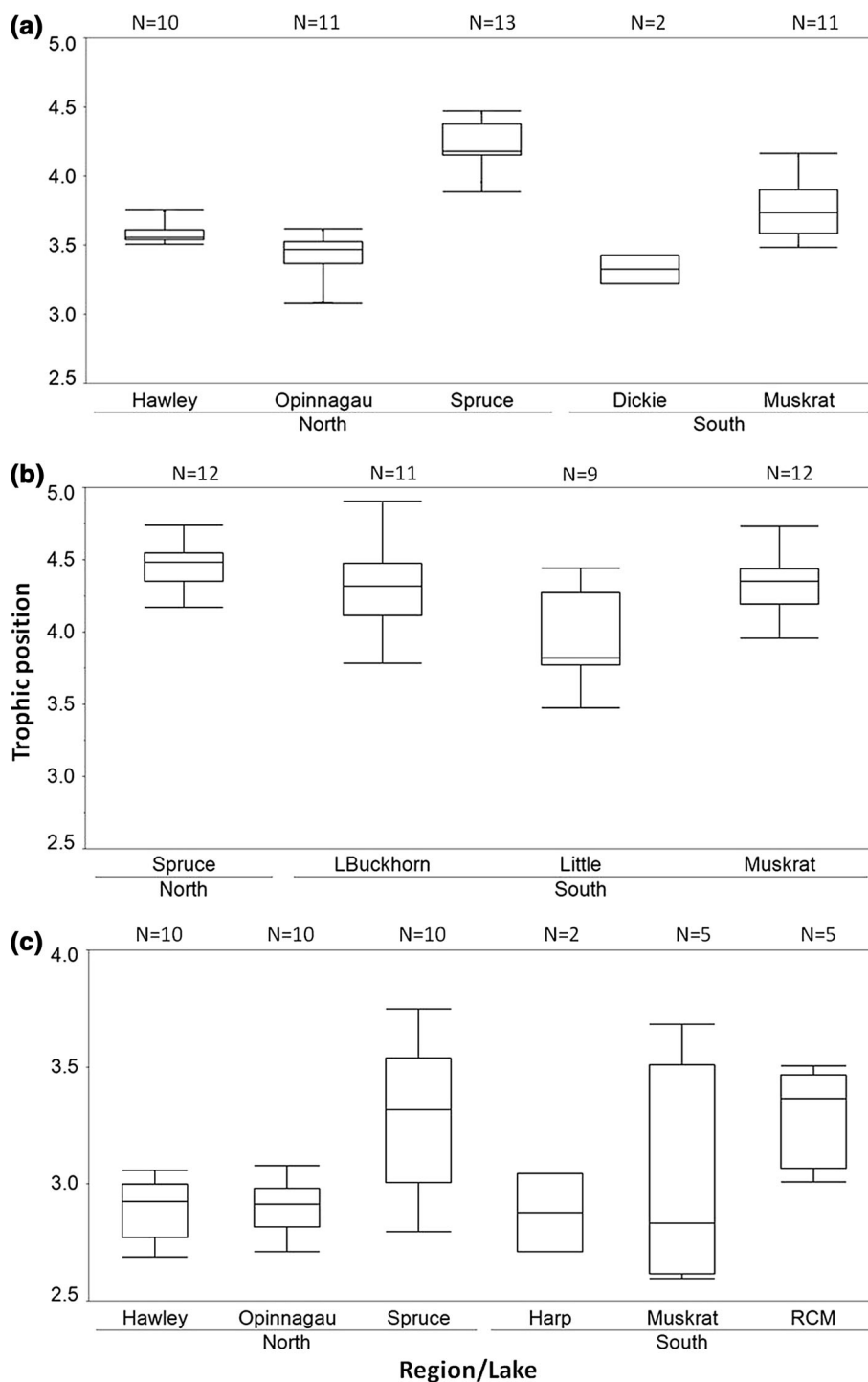
between northern and southern lakes (Fig. 4; Table 4). The trophic position of northern pike varied among four lakes (Fig. 4a; Wilcoxon $p < 0.0001$), with the highest trophic positions recorded in the northern Spruce Lake population. The northern pike population from southern Muskrat Lake was significantly different from northern Hawley Lake but not Spruce Lake or Opinnagau East Lake. Walleye trophic position varied among the four lakes in which they were found (Fig. 4b; Wilcoxon $p < 0.0001$), with the northern population from Spruce Lake having the highest trophic position compared to the southern populations. The southern Little Lake walleye population had a significantly lower trophic position compared to northern Spruce Lake and southern Muskrat Lake and Lower Buckhorn Lake. The trophic position of white sucker differed among five lakes (Fig. 4c; Wilcoxon $p = 0.006$), with the highest positions recorded within the Spruce Lake population. The trophic position of northern Hawley Lake white suckers was significantly lower than those collected from Red Chalk Main in the south and Spruce Lake in the north.

To determine whether fish size could have affected the above trophic position comparisons, we tested whether size of a given species varied among lakes using total length as an indicator of fish size. There was no difference in body size among lakes for northern pike (ANOVA: $F_{2,35} = 1.28$, $p = 0.29$, respectively). For white sucker, even though a significant difference in size was evident among lakes (ANOVA: $F_{3,33} = 4.66$, $p = 0.009$), the regression between total length and trophic position was not significant (Regression: $r^2 = -0.01$, $p = 0.59$). For walleye, significant differences in size were evident among lakes (Wilcoxon: $\chi^2 = 12.10$, $p = 0.007$) and a significant relationship was found between total length and trophic position (Regression: $r^2 = 0.34$, $p < 0.0001$).

Energy pathways

Several species-specific differences in the reliance on littoral resources were evident among lakes (Fig. 5; Table 4). For northern pike, the population from northern Spruce Lake had a significantly lower reliance on littoral sources compared to southern Muskrat Lake and northern Hawley Lake and Opinnagau Lake (Fig. 5a, Dunn: $p \leq 0.0001$). Walleye from southern Muskrat Lake had a significantly greater littoral reliance compared to northern Spruce Lake and southern Lower Buckhorn (Fig. 5b, Dunn: $p \leq 0.009$). Walleye from southern Little Lake also had a greater reliance on littoral sources compared to northern Spruce Lake (Dunn: $p = 0.0002$). The white sucker population from northern Spruce Lake was less reliant on littoral carbon sources compared to southern Muskrat Lake and northern Hawley Lake (Fig. 5c, Dunn: $p \leq 0.003$).

Fig. 4 Trophic position of the large-bodied fish species: (a) northern pike, (b) walleye and (c) white sucker in lakes from the northern (HBL) and southern (Kawartha-Renfrew and Muskoka-Haliburton). Boxes represent 25 and 75 % quantiles with median line and capped lines represent ranges. *N* indicates the number of individual fish data points for each lake



Discussion

Trophic dynamics and energy pathways in the HBL lakes

Overall, the energy pathways and trophic positions of dominant large-bodied fish species were very different

among the three HBL lakes which varied in chemistry, morphometry and biological communities. In general, Opinnagau East Lake and Hawley Lake fish were more reliant on littoral food, whereas Spruce Lake fish appeared to be more dependent on pelagic resources. These differences were supported by variability in the phytoplankton and zooplankton communities (Keller et al. 2011, 2013). In

Table 3 Summary of trophic niche space comparisons of species within the three Hudson Bay Lowland lakes

Lake	Species 1	Species 2	Statistical comparison	Likelihood
Hawley	Lake trout	Lake whitefish	Lake trout < Lake whitefish	0.98
	Lake trout	White sucker	Lake trout < White sucker	0.83
	Lake whitefish	White sucker	Lake whitefish < White sucker	0.32
	Northern pike	Lake trout	Northern pike < Lake trout	0.95
	Northern pike	Lake whitefish	Northern pike < Lake whitefish	0.99
	Northern pike	White sucker	Northern pike < White sucker	0.99
	White sucker	Lake trout	White sucker < Lake trout	0.16
	White sucker	Lake whitefish	White sucker < Lake whitefish	0.67
Opinnagau East	Northern pike	Lake whitefish	Northern pike < Lake whitefish	0.93
	Northern pike	White sucker	Northern pike < White sucker	0.41
	White sucker	Lake whitefish	White sucker < Lake whitefish	0.96
Spruce	Northern pike	Lake whitefish	Northern pike < Lake whitefish	0.51
	Walleye	Lake whitefish	Walleye < Lake whitefish	0.73
	Walleye	Northern pike	Walleye < Northern pike	0.86
	White sucker	Lake whitefish	White sucker < Lake whitefish	0.97
	White sucker	Northern pike	White sucker < Northern pike	0.99
	White sucker	Walleye	White sucker < Walleye	0.94

Spruce Lake, there were more pelagic basal food resources as both phytoplankton biovolume and zooplankton density were high; however, the similarity between zooplankton and benthic invertebrate carbon isotopic values suggests that there may have been some exchange of carbon resources between the littoral and pelagic pathways. In contrast to Spruce Lake, in deeper oligotrophic Hawley Lake, the pelagic pathway was weaker as both phytoplankton biovolume and zooplankton density were the lowest among the three HBL lakes. This is further supported by lake chemistry which shows that Hawley Lake has a lower TP concentration, hence lower pelagic productivity, compared to Spruce Lake (6.6 and 10.6 $\mu\text{g L}^{-1}$, respectively). In mesotrophic Opinnagau East Lake, fish appeared to be primarily littoral despite a high open water phytoplankton biovolume and moderate zooplankton density because of the shallow nature of the lake.

In Hawley Lake, the differences in trophic position and lack of overlap in isotopic niche area for piscivorous northern pike and lake trout indicate that they were likely exploiting different food sources and habitats. A separation in diet is possible for these piscivores since Hawley Lake is relatively deep; thereby accommodating physical habitat separation with lake trout primarily occupying deeper coldwater and northern pike remaining in fairly shallow but cool water (Scott and Crossman 1973; Casselman and Lewis 1996). Diet separation was also facilitated by the ample abundance of prey species within the lake since 12 species of the resident 15 species (Keller et al. 2011) can readily serve as potential food sources. Lake whitefish was one of two large-bodied planktivores that could have served as an important route of pelagic energy for lake

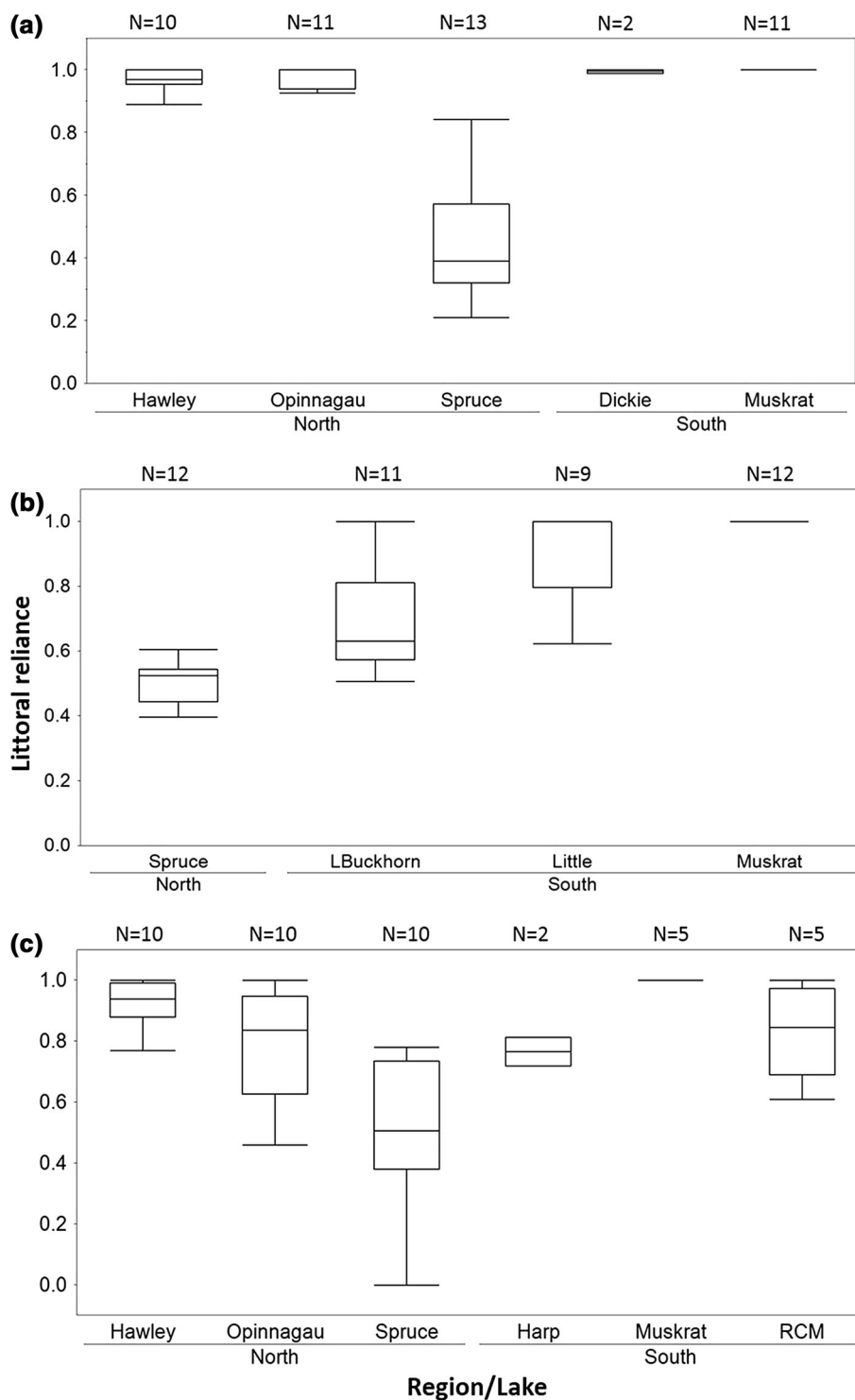
trout; whereas white sucker was one of two large-bodied benthivorous fish species that served as an important energy route of littoral carbon to piscivorous northern pike.

In Hawley Lake, the differences in trophic position between lake whitefish and white sucker suggest that they were utilizing very different habitats and/or food sources. Typically, white suckers are opportunistic benthic feeders capable of foraging on a wide array of benthic resources (Scott and Crossman 1973). In contrast, lake whitefish can be pelagic planktivores even though they can exploit benthic resources when competitors are present (Carl and McGuinness 2006).

In Spruce Lake, the comparable littoral reliance, trophic position and isotopic niche overlap of piscivorous northern pike and walleye indicate that they probably share many food sources in common and/or they were consuming food sources with similar isotopic values. Coexistence between pike and walleye was likely facilitated by spatial and temporal differences in prey selection and feeding habits even though there was some niche overlap between species. While large individuals of walleye and northern pike can venture and forage within both the littoral and pelagic area (Scott and Crossman 1973; Andersen et al. 2008; Bozek et al. 2011), body size differences between species lead to differences in prey selection. Spruce Lake contains a moderately rich prey fish community with eight species of the ten resident fish species (Keller et al. 2011) serving as potential prey. Further, northern pike is primarily a diurnal feeder which contrasts with the crepuscular feeding of walleye (Scott and Crossman 1973; Ryder 1977).

The shallow nature of Opinnagau East Lake appears to influence trophic interaction among the fish species

Fig. 5 Littoral reliance of the large-bodied fish species: (a) northern pike, (b) walleye and (c) white sucker in lakes from the northern (HBL) and southern (Kawartha-Renfrew and Muskoka-Haliburton). Boxes represent 25 and 75 % quantiles with median line and capped lines represent ranges. *N* indicates the number of individual fish data points for each lake



present, resulting in northern pike primarily feeding in the littoral zone and lake whitefish and white sucker having similar trophic dynamics and energy pathways. A strong littoral energy pathway to pike is expected in a shallow waterbody such as Opinnagau East Lake. The nearly identical trophic position and similar littoral reliance of lake whitefish and white sucker in this very shallow lake

($Z_{max} = 1.7$ m) indicate that they were feeding on a comparable composition of food items. The diet similarity between these two species may be a result of the very shallow nature of Opinnagau East Lake with little opportunity for the typical separation of open water and littoral food sources. The trophic dynamics or isotopic overlap described above for the three species in Opinnagau East

Table 4 Summary of statistical comparisons for trophic position and littoral reliance of large-bodied fish species in Northern (HBL) and Southern (Kawartha-Renfrew and Muskoka-Haliburton) lakes

Species	Region	Lakes	Trophic position		Littoral reliance	
			Among lakes	Post-hoc comparison	Among lakes	Post-hoc comparison
Northern pike	Northern	Hawley	Wilcoxon	<u>SPR MUS HAW OPP</u>	Wilcoxon	<u>SPR MUS OPP HAW</u>
		Oppinagan	$\chi^2 = 34.28$		$\chi^2 = 34.48$	
		Spruce	$p < 0.0001$		$p < 0.0001$	
	Southern	Muskrat				
Walleye	Northern	Spruce	ANOVA	<u>SPR LBU MUS LIT</u>	Wilcoxon	<u>SPR LBU LIT MUS</u>
	Southern	Lower Buckhorn	$F_{3,43} = 6.52$		$\chi^2 = 34.48$	
		Little	$p = 0.0011$		$p < 0.0001$	
		Muskrat				
White sucker	Northern	Hawley	Wilcoxon	<u>RCM SPR OPP MUS HAW</u>	Wilcoxon	<u>MUS HAW RCM OPP SPR</u>
		Oppinagan	$\chi^2 = 14.59$		$\chi^2 = 21.88$	
		Spruce	$p = 0.006$		$p = 0.0002$	
	Southern	Muskrat				
		RCM				

Post hoc comparisons are based on Tukey HSD and Dunn pairwise tests. Underlines group lakes with means that are not significantly different

Lake is unusual for deeper thermally stratified lakes, but is likely a common scenario across the HBL landscape since the majority of lakes are very shallow.

Potential climate change impacts on fish in the HBL lakes?

We extended our study to a regional comparison in order to speculate about the potential impacts of climate change on the trophic ecology of these large-bodied fish species. Recent evidence indicated that climatic change has the potential to impact plankton and fish within HBL lakes and rivers (Gunn and Snucins 2010; Rühland et al. 2013). Examination of paleolimnological data shows that long-term changes in the algal community have resulted from climatic warming within four HBL lakes (Rühland et al. 2013). Warm temperatures in 2001 led to significant mortalities of brook charr (*Salvelinus fontinalis*) and white sucker downstream from Hawley Lake in the Sutton River (Gunn and Snucins 2010). However, the potential for more widespread effects on fish in the HBL is not known.

From our findings, it is unlikely that climatic warming would have a dramatic impact on the trophic ecology of northern pike. The regional comparison between HBL and southern lakes indicated that despite climatic, morphometric and chemical differences among regions and lakes, the trophic position and littoral reliance of pike populations from two of the three HBL lakes were similar to Muskrat Lake in

the south. Pike can tolerate temperatures up to 29 °C even though they are mesothermal; nevertheless, excessively warm temperatures have been found to affect growth and recruitment to some extent (Casselman 1996, 2002; Casselman and Lewis 1996). Instead, for northern pike, climate change effects will likely be more indirect via alteration of prey availability (Winfield et al. 2008). However, our survey of the three HBL lakes suggests that pike are quite versatile in food use and will likely adapt to changing food sources as their variable trophic position and energy pathways among lakes indicate considerable diet plasticity. Furthermore, the ability of pike to feed on benthic invertebrates and conspecifics (Bry et al. 1992; Venturelli and Tonn 2005) will likely aid in their trophic adaptability as the climate changes.

Based on our limited data, it is unclear whether climatic change will affect walleye trophic dynamics. Even though we found some differences in trophic position and littoral reliance between populations in the northern and southern lakes, we cannot rule out that the differences may not have been attributable to body size differences among populations. It is possible that trophic position and littoral reliance differences between Spruce Lake and the southern lakes were due to size differences of the animals; the larger size of Spruce Lake walleye can explain their higher trophic position compared to Little Lake, and their lower littoral reliance compared to the southern lakes. Walleye are able to readily feed on whatever species are available to them, but as they grow and increase in size they are able to take

larger fish as prey because they are gape-limited predators (Scott and Crossman 1973; Graeb et al. 2005). Furthermore, larger fish are able to forage away from the littoral zone, especially when there is niche overlap and interspecific competition with other piscivores such as northern pike (see above discussion).

White suckers too will likely be able to adapt to diet changes under climate change. From past studies based on stomach analyses rather than isotopic inference, suckers are known to exhibit diet plasticity and also the ability to tolerate a relatively wide range of environmental conditions, despite their preference for coolwater habitats (Lyons et al. 2009). Here, we present several lines of evidence to support this inference. First, in agreement with previous studies, we found that suckers are obligatory benthic feeders (Scott and Crossman 1973); hence, they should adapt to changes in benthic food type and availability. Second, this species is ubiquitous across the various climatic zones of North America; a distribution pattern confirmed in this study since they were found in the HBL and southern lakes. Third, the regional comparisons indicate that there were no consistent differences in trophic position and littoral reliance between northern and southern populations. In fact, a couple of notable similarities in populations were evident in lakes that are quite different in morphology; the Hawley Lake white suckers were similar to the southern population in Muskrat Lake, and the Spruce Lake population was similar to the Red Chalk Main population. Although food changes are unlikely to affect suckers, extreme heating, such as the documented 2001 Sutton River event (Gunn and Snucins 2010), could lead to some mortality.

Lake whitefish populations in shallow lakes are probably among the most vulnerable of the northern populations of the HBL. Lake whitefish is known to be a coolwater species with a preference for thermal habitats between 15 and 20 °C during warm summer months, which they are able to access as they vertically migrate through the water column diurnally (Edsall 1999; Gorsky et al. 2012). In the small number of deep lakes, such as Hawley Lake, in HBL, lake whitefish should be able to avoid thermal stress by moving to cooler hypolimnetic waters. However, the real concern with future warming is that there may be a lack of suitable thermal habitat in shallow systems which are typical of the HBL region such as Opinnagau East Lake.

Most of the lakes in the HBL region are very shallow and often large and windswept, such as Opinnagau East Lake, which may facilitate rapid equilibration with air temperature. With climate warming, the coolwater species white sucker and lake whitefish in such lakes may potentially be exposed to an increased incidence of summer episodes of direct thermal stress. However, on the other hand, a shorter ice-covered period with future warming may reduce the incidence of winterkill in such shallow

lakes. Given the recent evidence of increasing productivity in HBL lakes (Brazeau et al. 2013; Rühland et al. 2013), fish growth and/or abundance may be expected to generally increase in these systems.

Lake trout are very rare in the HBL, restricted to only Hawley Lake of the HBL lakes in this study and three other comparatively deep lakes (Aquatuk Lake, North Raft Lake and Sutton Lake) within close proximity in the Sutton Ridges area, where an outcrop of the Precambrian Shield protrudes through the sedimentary rock of the Lowlands. In temperate areas, warming air temperatures have not been shown to significantly reduce the coldwater habitat available for lake trout in lakes of sufficient depth to thermally stratify (Keller et al. 2005). In fact, coldwater habitat has sometimes increased with climate warming, due in part to the effects of increased DOC on thermal stratification (Keller et al. 2005, 2007).

Hawley Lake has undergone a dramatic shift in thermal structure with the warmer air temperatures of recent decades in the HBL. In contrast to the very weakly stratified or unstratified thermal conditions observed during the 1970s and 1980s, Hawley Lake was strongly stratified during a particularly intense heating episode in 2001 (Gunn and Snucins 2010). Since then, all measured lake temperature profiles (2009–2012) have shown much stronger thermal stratification than in the 1970s and 1980s (W. Keller, Laurentian University, Sudbury, Ontario; *unpublished data*) although stratification was not as strong as in 2001.

We speculate that the impacts of climatic change on lake trout in the HBL lakes will likely be dampened considerably because of the morphometry of native lake trout lakes. For example, lake trout in deep Hawley Lake will not likely be directly threatened as the climate warms in the next few decades, but they will occupy a more strongly thermally stratified habitat similar to that of lake trout populations in southern areas. This scenario is also likely for Sutton Lake, a large, deep ($Z_{\max} > 25$ m) lake immediately upstream of Hawley Lake. However, in the other two, shallower, HBL lakes with lake trout populations, North Raft and Aquatuk lakes ($Z_{\max} < 15$ m), surface warming and increased hypolimnetic oxygen depletion with increased productivity could start to reduce the habitat favorable for lake trout (Dillon et al. 2003).

Important next steps for the HBL region

Prior to our study, very little was known about the lake food webs of the HBL region in Northern Ontario. Here, we have characterized fish communities in three HBL lakes and extended our investigation to a regional comparison in order to speculate about potential impacts of climate change on the trophic ecology of select species. We show that energy pathways and trophic position varied among

the three HBL lakes which differed in chemistry, morphometry and biological communities; and that most of the large-bodied species exhibit wide variability in their apparent diet and therefore will likely adapt to changing food resources resulting from climatic change. However, we must acknowledge that in focusing on vulnerability of diet changes, we are only addressing a narrow range of potential climate change effects and our inferences are limited by the size of our dataset. Nevertheless, we believe that these are valuable first steps which can be used to direct future research to quantitatively assess whether climate change will impact large-bodied species found within the HBL lakes.

In light of forecasted dramatic climate change in this sensitive region, it is imperative that we characterize the biological communities in more lakes and determine potential impacts on food web dynamics. There is a general lack of data for HBL lakes because access is limited and costly expeditions are required for work in this vast, very remote area. Despite this, we strongly recommend sampling of additional HBL systems for stable isotopes, especially shallow systems such as Opinnagau East Lake which are characteristic of the region. Stable isotopes are ideal for studying food web dynamics in these lakes because we are able to obtain invaluable time-integrated information even from snapshot sampling. Future research should also involve application of habitat availability models (e.g., Dillon et al. 2003; Lester et al. 2004), especially those that consider the potential impact of multiple factors such as hydrology, climate, nutrient inputs, water clarity and land-use changes (Jones et al. 2006). This will allow for more quantitative determination of species-specific changes in optimal habitat within the HBL lakes. Furthermore, combining assessments of food web dynamics and optimal habitat modeling will allow for a more comprehensive evaluation of potential climate change impacts on fish communities in HBL lakes.

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References

- Abraham KF, McKinnon LM, Jumeau Z, Tully SM, Walton LR, Stewart HM (2011) Hudson plains ecozone: status and trends assessment. in canadian biodiversity: ecosystem status and trends 2010, Technical Ecozone Report. Canadian Council of Resource Ministers, Ottawa, ON 445 pp
- Andersen M, Jacobsen L, Gronkjaer P, Skov C (2008) Turbidity increases behavioural diversity in northern pike, *Esox lucius* L., during early summer. *Fish Manag Ecol* 15:377–383
- Anderson C, Cabana G (2007) Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. *J North Am Benthol Soc* 26:273–285
- Bozek MA, Haxton TJ, Raabe JK (2011) Walleye and sauger habitat. In: Barton BA (ed) *Biology, management, and culture of walleye and sauger*. American Fisheries Society, Bethesda, pp 133–197
- Brazeau ML, Poulain AJ, Paterson AM, Keller W, Sanei H, Blais JM (2013) Recent changes in mercury deposition and primary productivity inferred from sediments of lakes from the Hudson Bay Lowlands, Ontario, Canada. *Environ Pollut* 173:52–60
- Brown LE, Hannah DM, Milner AM (2007) Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Glob Change Biol* 13:958–966
- Bry C, Basset E, Rognon X, Bonamy F (1992) Analysis of sibling cannibalism among pike, *Esox lucius*, juveniles reared under semi-natural conditions. *Environ Biol Fishes* 35:75–84
- Carl LM, McGuinness F (2006) Lake whitefish and lake herring population structure and niche in ten south-central Ontario lakes. *Environ Biol Fish* 75:315–323
- Carter JL, Schindler DE (2012) Responses of zooplankton populations to four decades of climate warming in lakes of southwestern Alaska. *Ecosystems* 15:1010–1026
- Casselman JM (1996) Age, growth and environmental requirements of pike. In: Craig JF (ed) *Pike: biology and exploitation*. Chapman & Hall, London, pp 69–101
- Casselman JM (2002) Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the great lakes basin. *Am Fish Soc Symp* 32:39–60
- Casselman JM, Lewis CA (1996) Habitat requirements of northern pike (*Esox lucius*). *Can J Fish Aquat Sci* 53(Suppl 1):161–174
- Chessman BC (2009) Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Glob Change Biol* 15:2791–2802
- Colombo SJ, McKenney DW, Lawrence KM, Gray PA (2007) Climate change projections for Ontario: practical information for policymakers and planners. *Climate Change Research Report CCRR—05*. Ontario Ministry of Natural Resources
- David SM, Sommers KM, Reid RA, Hall RJ, Girard RE (1998) Sampling protocols for the rapid bioassessment of streams and lakes using benthic macroinvertebrates. Ontario Ministry of Environment, ON 65 pp
- Dillon PJ, Clark BJ, Molot LA, Evans HE (2003) Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes. *Can J Fish Aquat Sci* 60:959–970
- Edsall TA (1999) The growth-temperature relation of juvenile lake whitefish. *Trans Am Fish Soc* 128:962–964
- Fry B (2006) *Stable isotope ecology*. Springer Science+Business Media, New York
- Gorsky D, Zydlewski J, Basley D (2012) Characterizing seasonal habitat use and diel vertical activity of lake whitefish in Clear Lake, Maine, as determined with acoustic telemetry. *Trans Am Fish Soc* 141:761–771
- Graeb BDS, Galarowicz T, Wahl DH, Dettmers JM, Simpson MJ (2005) Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. *Can J Fish Aquat Sci* 62:2010–2020
- Gunn J, Snucins E (2010) Brook charr mortalities during extreme temperature events in Sutton River, Hudson Bay Lowlands, Canada. *Hydrobiologia* 650:79–84

- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602
- Jensen OP, Benson BJ, Magnuson JJ, Card VM, Futter MN, Soranno PA, Stewart KM (2007) Spatial analysis of ice phenology trends across the Laurentian Great Lakes region during a recent warming period. *Limnol Oceanogr* 52:2013–2026
- Jones ML, Shuter BJ, Zhao Y, Stockwell JD (2006) Forecasting effects of climate change on Great Lakes Fisheries: models that link habitat supply to population dynamics can help. *Can J Fish Aquat Sci* 63:457–468
- Keller W (2007) Implications of climate warming for Boreal Shield lakes: a review and synthesis. *Environ Rev* 5:99–112
- Keller W, Heneberry J, Leduc J (2005) Linkages between weather, dissolved organic carbon and coldwater habitat in a Boreal Shield lake recovering from acidification. *Can J Fish Aquat Sci* 62:340–346
- Keller W, Paterson AM, Somers KM, Dillon PJ, Heneberry J, Ford A (2008) Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes. *Can J Fish Aquat Sci* 65:786–795
- Keller W, Paterson A, Jones C, Heneberry J, Winter J, Johnston T, Haslam L, Gunn J, Houle J, White M, MacPhee S, Smol J, Rühland K, Blais J, Poulain A, Brazeau M, Wolfe B, Wilson H, Mueller D, Persaud A, Dillon P, Finkelstein S (2011) Progress Report—Aquatic ecosystem studies in the Hawley Lake/Sutton River area of the Hudson Bay Lowlands, 2009–2010. Cooperative Freshwater Ecology Unit, Laurentian University, ON 50 pp
- Keller W, MacPhee S, Sarrazin-Delay C, Gunn J, Smol J, Rühland K, Hargan K, Jeziorski A, Hadley K, Blais J, Poulain A, Brazeau M, Wolfe B, White H, Mueller D, Koponen L, Persaud A, Dillon P, Finkelstein S, Bunbury J, Packalen M, Paterson A, Jones C, Heneberry J, Winter J, Johnston T, Haslam L, and Houle J (2013) Second Progress Report—Aquatic ecosystem studies in the Hawley Lake/Sutton River area of the Hudson Bay Lowlands, 2009–2012. Cooperative Freshwater Ecology Unit, Laurentian University, ON 52 pp
- Kratina P, Greig HS, Thompson PL, Carvalho-Pereira TSA, Shurin JB (2012) Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology* 93:1421–1430
- Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol Lett* 10:937–944
- Lester NP, Dextrase AJ, Kushneriuk RS, Rawson MR, Ryan PA (2004) Light and temperature: key factors affecting walleye abundance and production. *Trans Am Fish Soc* 133:588–605
- Luek A, Morgan GE, Wissel B, Gunn JM, Ramcharan CW (2013) Impaired littoral energy pathways cause a shift to pelagic resources by fish in recovering lake food webs. *Ecol Freshw Fish* 22:348–360
- Lyons J, Zorn T, Stewart J, Seelbach P, Wehrly K, Wang L (2009) Defining and characterizing coolwater streams and their fish assemblages in Michigan and Wisconsin, USA. *North Am J Fish Manag* 29:1130–1151
- Macrae ML, Bello RL, Molot LA (2004) Long-term carbon storage and hydrological control of CO₂ exchange in tundra ponds in the Hudson Bay Lowland. *Hydrol Process* 18:2051–2069
- McKenney DW, Pedlar JH, Lawrence K, Gray P, Colombo SJ, Crins WJ (2010) Current and projected future climatic conditions for ecoregions and selected natural heritage areas in Ontario. Climate Change Research Report CCCR-16. Ontario Ministry of Natural Resources
- Mooij WM, Hulsmann S, De Senerpont Domis LN, Nolet BA, Bodelier PLE, Boers PCM, Pires LMD, Gons HJ, Ibelings BW, Noordhuis R, Portielje R, Wolfstein K, Lammens EHRR (2005) The impact of climate change on lakes in the Netherlands: a review. *Aquat Ecol* 39:381–400
- Morgan GE, Snucins E (2005) Manual of instructions and provincial biodiversity Benchmark values NORDIC index netting. Ontario Ministry of Natural Resources
- Moss B (2010) Climate change, nutrient pollution and the bargain of Dr. Fautus. *Freshw Biol* 55:175–187
- Ontario Ministry of the Environment (1983) Handbook of analytical methods for environmental samples. Volume 1 & 2. Ontario Ministry of the Environment, ON 686 pp
- Organization for Economic Co-operation and Development (1982) Eutrophication of waters: monitoring, assessment and control. Organization for economic and co-operative development, Paris, France
- Parnell A, Jackson AL (2013) SIAR: Stable isotope analysis in R. R package version 4.2. <http://CRAN.R-project.org/package=siar>
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* 83:703–718
- R Core Team (2013) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing, Vienna, Austria
- Rühland KM, Paterson AM, Keller W, Michelutti N, Smol JP (2013) Global warming triggers the loss of a key Arctic refugium. *Proc R Soc B* 280:1887–1895
- Ryder RA (1977) Effects of ambient light variations on behavior of yearling, subadult, and adult wall-eyes (*Stizostedion vitreum vitreum*). *J Fish Res Board Can* 34:1481–1491
- Sandstrom S, Rawson M, Lester N (2008) Manual for broad-scale fish community monitoring; using large mesh and small mesh gillnets. Peterborough, Ontario Ministry of Natural Resources, ON 32 pp
- Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada, 966 pp
- Vander Zanden MJ, Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83:2152–2161
- Venturelli PA, Tonn WM (2005) Invertivory by northern pike (*Esox lucius*) structures communities of littoral macroinvertebrates in small boreal lakes. *J North Am Benthol Soc* 24:904–918
- Whitehead PG, Wilby RL, Battarbee RW, Kernan M, Wade AJ (2009) A review of the potential impacts of climate change on surface water quality. *Hydrol Sci J* 54:101–123
- Winfield IJ, Ben James J, Fletcher JM (2008) Northern pike (*Esox lucius*) in a warming lake: changes in population size and individual condition in relation to prey abundance. *Hydrobiologia* 601:29–40