Canadian Journal of Fisheries and Aquatic Sciences

Plenty of room at the bottom: Niche variation and segregation in large-bodied benthivores of boreal lakes

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2018-0180.R1
Manuscript Type:	Article
Date Submitted by the Author:	07-Sep-2018
Complete List of Authors:	Johnston, Thomas; Ontario Ministry of Natural Resources and Forestry, Aquatic Research and Monitoring Section Stasko, Ashley; Fisheries and Oceans Canada Central and Arctic Region Hamilton, Graeme; Laurentian University Department of Biology Nugent, Brett; Laurentian University Department of Biology Cott, Peter; Department of National Defence Gunn, John; Laurentian University
Keyword:	LAKES < Environment/Habitat, FRESHWATER FISHES < General, ISOTOPES < General, FEEDING < General, HABITAT < General
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

Plenty of room at the bottom: Niche variation and segregation in large-bodied benthivores of boreal lakes

Johnston, T.A. ^{1*}, Stasko, A.D. ², Hamilton, G.L. ², Nugent, B.K. ², Cott, P.A. ², and Gunn, J.M. ²

¹ Ontario Ministry of Natural Resources and Forestry, Cooperative Freshwater Ecology Unit, Vale Living With Lakes Centre, Laurentian University, Sudbury, ON P3E 2C6, Canada

² Department of Biology, Laurentian University, Cooperative Freshwater Ecology Unit, Vale Living With Lakes Centre, Sudbury, ON P3E 2C6, Canada

* Corresponding Author: Tom Johnston, Tel: 705-671-3828, E-mail: tjohnston@laurentian.ca

Abstract

Realized trophic niches of aquatic consumers are expected to reflect the particular abiotic and biotic conditions of the ecosystems they occupy. We examined patterns in the position, size, and shape of trophic niches of two common benthivorous fishes, white sucker (*Catostomus commersoni*) and lake whitefish (*Coregonus clupeaformis*), across boreal lakes using a stable isotope approach. In sympatry, white sucker niche positions reflected greater benthic reliance (higher $\delta^{13}\text{C}$) and lower trophic elevation (lower $\delta^{15}\text{N}$) compared to lake whitefish, and white sucker niche sizes (dispersion in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space) were also larger. Niche sizes of both species increased with maximum depth of lakes. Separation of trophic niche positions of the two species increased with increasing water clarity, but their niche sizes did not increase with increasing separation in their niche positions. White sucker occupied a niche position with slightly greater pelagic reliance, and trophic elevation, and had smaller trophic niches in the absence than in the presence of lake whitefish. Trophic niches of these benthivores appear to be shaped by both environmental factors and interspecific interactions.

Keywords: trophic ecology; food webs; freshwater; stable isotopes; fish; habitat

Introduction

The function and distribution of a species within an ecosystem is conceptualized as its niche - a space or ‘hyper-volume’ in ecological dimensions that a species occupies (Hutchinson 1957; Vandermeer 1972; Leibold 1995). The fundamental niche is the theoretical volume that could be occupied based solely on the phenotypic diversity of the species, and the realized niche is the smaller volume contained within that is actually utilized under constraints imposed by competitors, predators, available resources, and barriers to dispersal. Thus, the realized niche can be viewed as a flexible volume that can expand, contract, and move about within the more rigid fundamental niche according to prevailing conditions (Hutchinson 1957; Soberón and Arroyo-Peña 2017). Determining how external forces may influence the position, size and shape of the realized niche is important to our understanding of species interactions, ecosystem function, and eco-evolutionary dynamics.

The multidimensional nature of the niche concept makes empirical tests challenging, and the niche is often broken down into more tractable components. For example, a commonly studied component is the trophic niche, which is that portion of the niche defined by the food resources a species could (fundamental) or does (realized) utilize (e.g., Bearhop et al. 2004). A further challenge is that the choice of variables used to define the niche may influence interpretation of test results. Niche size (also termed width or breadth) has been quantified as dispersion in one or more traits, and is sometimes partitioned into within-phenotype and between-phenotype components (Van Valen 1965; Roughgarden 1972), or more recently, within-individual and between-individual components (Bolnick et al. 2003). Early studies tended to measure niche size using morphological traits as a proxy for resource use (Van Valen 1965; Roughgarden 1972). More recent studies have shifted towards direct functional measures of resource use, such as diet (Bolnick et al. 2002; Bolnick et al. 2003). Because diet is more responsive to changing conditions, this latter approach increases the perceived spatio-temporal

flexibility of the realized niche, and it has highlighted the importance of inter-individual variation to trophic niche size for a variety of taxa (Bolnick et al. 2007; Costa et al. 2008; Newsome et al. 2009; Vander Zanden et al. 2010). The use of diet as an indicator of niche size is also revealing the prevalence and magnitude of individual specialization, and the tendency for individuals to utilize restricted and divergent portions of the population's realized niche (Araujo et al. 2011). Such individual specialization has important consequences for understanding population and community dynamics (Bolnick et al. 2011).

Individual specialization, and consequently realized trophic niches, may be affected by various factors including the diversity and accessibility of habitats and food sources, and constraints imposed by predators and competitors (Lappalainen and Soininen 2006). Boreal lake fish communities provide excellent systems for testing the effects of these abiotic and biotic factors. Lakes are analogous to islands with fish communities isolated from each other to varying degrees, and experiencing different physical, chemical and biological conditions. Fishes of boreal lakes can be coarsely divided into three trophic guilds – forage fishes, benthivores, and piscivores. Large-bodied benthivores are a poorly-studied component of these systems. They are similar to forage fishes in that they primarily consume invertebrates, but also similar to piscivores in that they have longer lifespans and attain adult body sizes that render them less vulnerable to predation. Thus, in boreal lake food webs, large-bodied benthivores occupy a terminal node at the end of a relatively short trophic pathway. In this position, it would be expected that their adult trophic niches are shaped less by predation risk than by environmental conditions and competitive interactions.

Our objective in the current study was to compare and contrast the realized trophic niches of two widespread and common benthivorous fishes – white sucker (*Catostomus commersoni*) and lake whitefish (*Coregonus clupeaformis*) – and examine how the positions and dimensions of their trophic niches are related to abiotic and biotic conditions in boreal lakes. Both species can

attain large adult body sizes (> 1 kg) and long lifespans (> 10 years) (Scott and Crossman 1973). White sucker is classified as a coolwater species and occupies a wide variety of aquatic ecosystems, whereas lake whitefish is classified as a coldwater species and is primarily found in deeper lakes that stratify in the summer (Scott and Crossman 1973; Coker et al. 2001). However, lake whitefish will also occupy shallow lakes (< 10 m deep) and rivers in the northern part of their range where summer thermal conditions remain suitable. Differences in thermal preferences between these two species would be expected to contribute to some degree of segregation in both habitat and resource use, particularly in summer. Both species have been reported to consume a wide array of benthic invertebrates and there appears to be considerable scope for overlap in their prey resources (Scott and Crossman 1973; Coker et al. 2001), but there have been no studies, to our knowledge, comparing their trophic ecologies in shared environments.

Our central hypothesis is that the position and size of realized trophic niches of aquatic consumers vary according to the particular abiotic and biotic conditions in which they are found. This draws on facets of both niche theory (Van Valen 1965; MacArthur and Levins 1967; Roughgarden 1972; Vandermeer 1972) and foraging theory (Schoener 1971; Stephens and Krebs 1987). Specifically, we expect that trophic niche positions and sizes will reflect ecological necessity and/or ecological opportunity and that these will vary with the physical characteristics of the habitat. Using boreal lake populations of these two common benthivorous fishes we tested the following predictions: i) because lake whitefish prefer colder habitat, they will feed more in the offshore zone, and their trophic niche position will be based more on pelagic primary production compared to white sucker; also, because lake whitefish are thought to feed more frequently on higher trophic level organisms, such as fish, their trophic niche position will be more trophically elevated compared to white sucker; ii) because lake whitefish feed more in the colder, offshore zone which is structurally less complex than the warmer, nearshore zone they will have less opportunity for trophic diversification and therefore, will occupy a trophic niche

that is smaller compared to white sucker; iii) trophic niche sizes of both species will increase with decreasing lake productivity as there will be more pressure for trophic diversification (concurrently, increasing water clarity that accompanies decreasing productivity will create habitats that are perceived as more complex and providing more opportunity for trophic diversification); iv) because of its effect on lake thermal structure, lake depth is the primary physical characteristic influencing habitat segregation between these species, and separation of their trophic niches will increase with increasing lake depth; v) the trophic niche of each species will expand with increasing separation in their trophic niche positions, and be larger in the absence of the other species in response to reduced interspecific competition.

Materials and Methods

We tested our predictions by inferring trophic niche position, size, and shape from stable isotope compositions of individual lake whitefish and white sucker. Carbon and nitrogen stable isotope ratios, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were used as indices of energy source and trophic elevation, respectively (Peterson and Fry 1987; Fry 2006; Boecklen et al. 2011). Analyzing variance in $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ in isotopic bi-plot space (δ - δ space; Newsome et al. 2007) provides an effective means of quantifying trophic divergence among individuals or species (Fink et al. 2012; Layman et al. 2012), and has been proposed as an index of trophic niche size (Bearhop et al. 2004; Newsome et al. 2007).

Sample collection and processing

Lake whitefish and white sucker were sampled from 113 lakes in northern Ontario, Canada, primarily within the Boreal Shield Ecozone (Table S1). Lakes were distributed over 10°

latitude, and varied widely in surface area (range 64 – 91000 ha), maximum depth (range 1.8 – 39 m), and water clarity (Secchi depth range 0.3 – 9.4 m) (Table S1). Eighty-one of the sampled lakes contained both white sucker and lake whitefish populations, and 32 contained white sucker but not lake whitefish populations. Sampling was carried out during the open water season from 2008 to 2014, and each lake was usually sampled in a single year. Data were pooled across years for lakes sampled over multiple years. On a subset of our study lakes ($n = 24$) we also sampled macroinvertebrate primary consumers. Freshwater clams (Unionidae) and snails (Gastropoda) were collected to provide pelagic and benthic, respectively, isotopic baselines (Post 2002) that were used in some analyses of niche position and shape. Fish sampling for this program was reviewed and approved by the Ministry of Natural Resources and Forestry's Fisheries Animal Care Committee (ARMS-ACC-97, ARMS-ACC-97B) according to Canadian Council on Animal Care (CCAC) guidelines.

All fish were captured in benthic, multi-mesh, monofilament gill nets. These were usually of the North American Standard (NA1) configuration - 24.8 m long (8 panels of 3.1 m each) and 1.8 m high, with stretched mesh sizes of 38, 51, 64, 76, 89, 102, 114, and 127 mm (Sandstrom et al. 2013). Nets were set overnight, at all depths in each lake. Individuals spanning a wide range of body sizes were selected from the captured fish for stable isotope analysis. Fork length (FL, ± 1 mm), total length (TL, ± 1 mm), and round weight (RWT, ± 10 g) were measured and recorded for each fish, and a skinless dorsal muscle sample from the mid-body region was frozen for stable isotope analysis. Clams were collected by hand, dip net or clam rake from nearshore depositional zones (1-3 m deep), and snails were collected by hand from nearshore rocks, weeds or sunken logs (< 1 m deep). Clams and snails were weighed (± 0.1 g) and foot muscle (clams) or whole body without shell (snails) was retained and frozen for stable isotope analysis.

Tissue samples were dried in a Freezone 12 L freeze-drier (Labconco, Kansas City, MO, USA), and ground into a homogenous powder using a MM 400 ball mill (Retsch GmbH, Haan,

Germany). Carbon and nitrogen isotopic compositions of all tissues were analysed on a continuous-flow isotope ratio mass spectrometer (Thermo-Finnigan Delta Plus or Delta XP; ThermoFisher Scientific, Waltham, MA, USA) coupled to an elemental analyser (Carlo Erba NC2500; CEI, Wigan, UK, or Costech 4010; Costech Analytical Technologies, Valencia, CA, USA) at the Stable Isotopes in Nature Laboratory (University of New Brunswick, Fredericton, NB, Canada). Ratios of heavy to light isotopes were expressed in standard delta (δ) notation as parts per thousand (‰) relative to International Reference Standards of Vienna PeeDee Belemnite carbonate (V-PDB) and atmospheric nitrogen (AIR) for C and N, respectively. Lipid content of muscle in both fish species was considered low based on C:N ratios (mean 3.5 and 3.4 for lake whitefish and white sucker, respectively), and did not warrant lipid-extraction prior to isotope analysis (Post et al. 2007). Mean coefficients of variation for duplicate analyses of sample material were 0.10% for $\delta^{13}\text{C}$ and 0.32% for $\delta^{15}\text{N}$.

We examined trophic niches of these species in relation to environmental variables representing 1) climate, 2) ecosystem size, and 3) productivity, which in turn may influence resource availability and use. 1) Climate was represented by mean growing degree-days greater than 5 °C at the latitude and longitude of each lake for the period 1970-2000 calculated using a web-based tool (http://gmaps.nrcan.gc.ca/cl_p/climatepoints.php) developed by McKenney et al. (2006). 2) Ecosystem size was characterized both horizontally using lake surface area (km²) and vertically using lake maximum depth (m). Lake surface areas were determined from digitization of topographic maps, and maximum depths were determined from bathymetric surveys using sonar. 3) Ecosystem productivity was inferred from Secchi depth (m), an indicator of nutrient concentrations and algal biomass (Carlson 1977; Nürnberg 1996). Secchi depths were determined near the deepest part of the lake during the summer stratification period. We recognized that Secchi depth is also a well-established and direct measure of water clarity (Preisendorfer 1986) that can influence how habitat is perceived by visual consumers. We considered both of these

properties of Secchi depth data in our interpretation of results. Limnological data for sampled lakes were obtained from the Aquatic Habitat Inventory (AHI) database, maintained by the Ontario Ministry of Natural Resources and Forestry (Peterborough, ON, Canada). These data primarily originated from lake surveys conducted from the mid-1960s to the mid-1980s.

Statistical analyses

Statistical analyses used a combination of standard frequentist and information-theoretic approaches. Niche metrics were calculated in R version 3.1.2 (R Core Team 2014) using the packages “siar” (Parnell and Jackson. 2013) and “nicheROVER” (Lysy et al. 2014), and statistical analyses were performed using SAS/STAT® software procedures (SAS Institute Inc 2013). Fish data were culled in several steps prior to analysis. Robust regressions with MM estimation (Rousseeuw et al. 2012) of fish weight vs TL, and of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vs weight were used as a conservative approach to identify individual fish outliers. These outliers were only removed from analyses if deemed likely to have been a result of errors in sample handling or labelling, or data recording. Subsequently, dual-species lakes with a sample size of < 5 individuals of either species, and white sucker-only lakes with a sample size of < 5 individuals were eliminated. Fish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were adjusted to a weight of 1 kg using the slopes of regressions with $\log_{10}$ weight to account for observed covariation between isotope values and body size (Romanuk et al. 2011). The standard size of 1 kg was within the sample size range for most populations. However, restricted body size ranges in samples from a few populations resulted in covariance-adjusted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that were deemed outliers, and these were also eliminated from the data set. Finally, lake whitefish in northern lakes can sometimes diverge into distinct benthivorous and planktivorous morphotypes (Bodaly 1979; Doyon et al. 1998), particularly in lakes where the congeneric planktivore cisco, *Coregonus artedii*, is absent (Carl

and McGuinness 2006). For the purposes of this study, we wished to focus on the more prevalent, benthivorous form of lake whitefish, and we eliminated lake whitefish data from lakes that appeared to contain multiple morphotypes.

Niche metrics were calculated for each sample population following several recently published methods for analysing and interpreting variation among individuals or populations in isotopic dimensions. Our index of trophic niche position for a population was the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the sample. Our primary estimate of niche size for a given population was the area of a standard bivariate ellipse of the sample in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space, adjusted for small sample size (SEA_c) (Jackson et al. 2011). We scaled this ellipse up from the default 1 standard deviation (SD) to 2 SD to reduce boundary effects on estimates of niche overlap (Stasko et al. 2015). The centroid of this ellipse was the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the sample. The absolute range of $\delta^{13}\text{C}$ values covered by the 2 SD bivariate ellipse was considered an indicator of the breadth of carbon sources utilized (carbon range, CR) and the absolute range of $\delta^{15}\text{N}$ values covered by this ellipse was considered an indicator of the diversity of trophic elevations occupied (nitrogen range, NR). This is a more conservative approach than using the full range of isotopic values observed in the population, as originally proposed by Layman et al. (2007). Isotopic niches were also characterized by two other metrics – centroid distance (CD) and the standard deviation of nearest neighbour distance (SDNND)(Layman et al. 2007). The former is a measure of dispersion of individuals in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space, and hence, an alternate index of trophic niche size, whereas the latter is a measure of the evenness of the separation of individuals in niche space.

Trophic interactions between white sucker and lake whitefish were quantified for each of the lakes where species were found in sympatry, using three metrics based on the isotopic niche. First, the Euclidean distance between the species niche centroids in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space (DBC) was used as a measurement of their separation in mean trophic niche position (Turner et al. 2010).

Second, the standard ellipse area overlap (SEA_OV) was calculated as the percentage of the combined niche area (SEAc) of the two populations that was composed of shared space (Stasko et al. 2015). Third, the probability of isotopic niche overlap (PINO) was calculated as the median probability of finding a lake whitefish with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that fell within the isotopic niche of sympatric white sucker, computed over 10,000 iterations with $\alpha = 0.95$ using a Bayesian approach (Lysy et al. 2014; Swanson et al. 2015).

All of the variables used in statistical analyses are described in Table 1, and the analysis proceeded as follows. First, paired-comparisons tests, with lakes treated as replicates, were used to test the hypothesis that the mean trophic niche position, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, of white sucker differed from that of lake whitefish in lakes where they occurred in sympatry (prediction i). The same paired-comparisons approach was used to test whether isotopic niche dimensions (SEA_C, NR, and CR) differed between species (prediction ii). Only populations with minimum $n = 10$ samples / species were used in comparisons of isotopic niche dimensions to avoid biases from small sample sizes (Jackson et al. 2011).

Second, relationships between various niche metrics and environmental conditions in the lakes (predictions iii and iv) were examined using both correlation analyses, and a model selection approach (Johnson and Omland 2004; Anderson 2008). Environmental variables were normalized (converted to Z-scores; STANDARD procedure) prior to model fitting to reduce scaling effects. Niche size and niche interaction metrics were regressed against all combinations of environmental variables (maximum three per model; GLMSELECT procedure) and fitted models were ranked by Akaike's Information Criterion adjusted for small sample size (AICc). Following ranking, the relative explanatory power of each independent variable was assessed by summing Akaike weights (w_i) across all models containing it. Some variables were log_e-transformed prior to analyses to linearize relationships and/or normalize residuals.

Finally, potential competitive effects of lake whitefish on white sucker were assessed by comparing the trophic niche position (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), size (SEAc), and shape (CR) of white sucker populations between lakes with and without lake whitefish (prediction v). We started with a one-way analysis of variance (ANOVA; GLM procedure) with community type (lake whitefish present or absent) as the fixed-effect class variable. Results were then compared with analysis of covariance models (ANCOVA; GLM procedure) including environmental covariates. We predicted that the influence of lake whitefish presence on the white sucker niche would diminish with increasing lake depth, as greater depth would allow greater habitat segregation between the species. Though lake depth was the primary covariate of interest, we also repeated this analysis with other environmental covariates identified as potentially influential in the preceding model selection analyses. In addition, for the subset of lakes with invertebrate isotope data, we used combinations of clam and snail $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as covariates to account for the potential influence of variation in baseline stable isotope ratios among lakes.

Results

Trophic niche positions, sizes and shapes in sympatry

Across study lakes containing both species, niche positions of white sucker and lake whitefish were positively correlated with each other both in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ dimensions ($r > 0.65$, $n = 75$, $P < 0.001$) (Fig. 1). On average, white sucker was 1.45 ‰ more enriched in ^{13}C (paired-comparisons $t = 6.42$, $n = 75$, $P < 0.001$), and 1.57 ‰ less enriched in ^{15}N (Signed rank $S = -1424$, $n = 75$, $P < 0.001$) compared to lake whitefish (Fig. 1). Unlike niche positions, trophic niche sizes, as represented by SEAc and CD, were not strongly correlated between the two species ($r < 0.05$, $n = 57$, $P > 0.70$). White sucker tended to have larger trophic niches than lake whitefish; both SEAc and CD were significantly greater in white sucker than lake whitefish

(Table 2). There was no significant difference in SDNND between species (Table 2), indicating that the evenness of the distribution of individuals in isotopic niche space was similar for both. The mean ratio of white sucker to lake whitefish SEAc was 2.1 (range 0.28 to 8.0). The larger niche size of white sucker was primarily due to the use of a broader range of carbon sources compared to sympatric lake whitefish, as indicated by a significantly larger CR. There was no significant difference in trophic diversity, represented by NR, between the species (Table 2).

Environmental effects on niches in sympatry

Trophic niche sizes of both species, represented by SEAc, were related to environmental characteristics of the lakes (Table 3). For both species, models relating niche size to ecosystem size received the strongest support. For white sucker, the strongest univariate model was a positive relationship between SEAc and lake maximum depth, but models that included both a positive depth and negative area effect ranked highest (Table 3). Across white sucker models, lake depth and area were similar in explanatory power ($\Sigma w_i = 1.02$ and 0.90 , respectively) whereas GDD and Secchi depth were relatively weaker predictors ($\Sigma w_i = 0.28$ and 0.25 , respectively). Likewise, for SEAc of lake whitefish, lake depth was the strongest univariate predictor, and a positive component of all top-ranked models ($\Sigma w_i = 1.00$, Table 3), however, GDD was the next strongest predictor and had a negative effect ($\Sigma w_i = 0.71$, Table 3). There was a weak, positive relationship between SEAc and Secchi depth for white sucker but not for lake whitefish (Table 3). Also, the difference in SEAc between species was most strongly related to lake area ($r = -0.33$, $n = 57$, $P = 0.0097$), and only weakly related to Secchi depth ($r = 0.14$, $n = 57$, $P = 0.29$).

Trophic niche interactions were also weakly, but significantly related to environmental conditions. The distance between niche positions (DBC) of white sucker and lake whitefish was

positively correlated with $\log_e$ maximum depth ($r = 0.38$, $n = 75$, $P < 0.001$) (Fig. 2) but was even more strongly positively correlated with Secchi depth ($r = 0.51$, $n = 75$, $P < 0.001$) (Fig. 2). Secchi depth was the strongest predictor overall ($\Sigma w_i = 0.99$; Table 4), whereas lake area or depth tended to fall into lower ranking models ($\Sigma w_i = 0.24$ and 0.25 , respectively; Table 4). Most of the shift in niche position between species along these environmental gradients was due to changes in white sucker position. For example, whereas both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of lake whitefish were essentially invariable with respect to increasing Secchi depth, white sucker $\delta^{13}\text{C}$ increased and $\delta^{15}\text{N}$ decreased (Fig. 3). As would be expected, niche overlap tended to decline with increasing DBC; there were significant negative correlations between SEA_OV and DBC ($r = -0.70$, $n = 57$, $P < 0.001$), and between PINO and DBC ($r = -0.54$, $n = 64$, $P < 0.001$). As with DBC, niche overlap was most strongly related to Secchi depth, either alone or in combination with lake area or GDD, both for SEA_OV (Table 4) and PINO (results not shown). Finally, SEAc did not increase significantly for either species as DBC increased ($r < 0.13$, $n = 57$, $P > 0.36$), suggesting that their niche sizes were not constrained by the proximity of their niche positions in $\delta^{13}\text{C} - \delta^{15}\text{N}$ space.

White sucker trophic niches in lakes with and without lake whitefish

Sampled lakes containing both white sucker and lake whitefish differed in several respects from those containing only white sucker. Lakes with both species were from significantly warmer climatic areas (higher GDD), and were both significantly deeper and larger in area (one-way ANOVA, $P < 0.05$). They also tended to have higher Secchi depth, though this difference was not significant ($P > 0.05$). For the smaller subset of lakes with baseline invertebrate data, lakes with both white sucker and lake whitefish tended to have clams and snails with both higher (less negative) mean $\delta^{13}\text{C}$ and lower mean $\delta^{15}\text{N}$, though this trend was only significant for snail $\delta^{13}\text{C}$.

Given these lake differences, and the observed relationships between niche metrics and environmental variables in the preceding analyses, we chose to compare white sucker niches between these two groups of lakes using multiple ANCOVA models with a variety of environmental variables as covariates.

In terms of trophic niche position, the overall trend was that white sucker had lower (more negative) $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ in the absence than in the presence of lake whitefish, and these differences were statistically significant based on one-way ANOVA (Table 5, COV = none). However, results were more varied for models including covariates. White sucker $\delta^{13}\text{C}$ was significantly positively related to maximum depth, area, and Secchi depth across lakes, and the addition of any as covariate eliminated the significance of the $\delta^{13}\text{C}$ difference between lakes with and without lake whitefish (Table 5). Relationships between white sucker $\delta^{15}\text{N}$ and environmental covariates were more complex, and effects for some (GDD, Secchi depth) were stronger in lakes without lake whitefish (Table 5). But, significantly higher white sucker $\delta^{15}\text{N}$ in the absence of lake whitefish was still evident after covariate adjustment (Table 5). Among these models, white sucker mean predicted $\delta^{13}\text{C}$ was 0.7 – 1.6 ‰ lower and mean predicted $\delta^{15}\text{N}$ was 0.5 – 0.7 ‰ higher in the absence of lake whitefish (Table 5). In the smaller subset of lakes with invertebrate isotope data, both white sucker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were positively related to the corresponding ratios in clams and snails, but there was no significant difference in either white sucker $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between lakes with and without lake whitefish (Table 5). However, it should also be noted that neither white sucker $\delta^{13}\text{C}$ nor $\delta^{15}\text{N}$ differed between lakes with and without lake whitefish in this smaller subset of lakes when analyzed without baseline isotope covariates (one-way ANOVA, $P > 0.05$).

The relationship between white sucker trophic niche dimensions and lake whitefish presence or absence was more straightforward. White sucker had significantly larger SEAc and CR in the presence of lake whitefish than in their absence based on one-way ANOVA (Table 6,

COV = none). White sucker SEAc and CR were positively related to maximum depth, Secchi depth and GDD, and negatively related to lake area across lakes (Fig. 4, Table 6), and the addition of any as covariate only altered the test outcome for the lake whitefish effect in two cases (Table 6). Among these models, white sucker mean predicted SEAc was 17-31% smaller and mean predicted CR was 5-21% smaller in the absence of lake whitefish (Table 6). In the smaller subset of lakes with invertebrate isotope data, neither white sucker SEAc nor CR were significantly related to the $\delta^{13}\text{C}$ endpoint separation at the base of the food web (clam $\delta^{13}\text{C}$ minus snail $\delta^{13}\text{C}$), and neither varied significantly in relation to presence or absence of lake whitefish (Table 6). In this smaller set of lakes, the lake whitefish effect was also not significant when SEAc and CR were analyzed without baseline isotope covariates (one-way ANOVA, $P > 0.05$).

Discussion

This study illustrates the nature and scale of variation in the position, size and shape of realized trophic niches of aquatic consumers. It is somewhat unique in boreal lake food web research in that we used both a multi-species and multi-ecosystem approach, and our focal fish species were benthivores rather than piscivores. Our approach was to use an isotopic characterization of trophic niches across a large number of populations in lakes representing a wide diversity of ecosystem size and shape, and limnological and climatic conditions. We have shown how realized trophic niches differ between two co-habiting, large-bodied benthivorous fishes, and also demonstrated how their niches vary with respect to environmental conditions in the boreal lakes they inhabit. Observed differences between sympatric white sucker and lake whitefish populations generally followed our predictions based on previously reported habitat preferences and feeding ecologies of these species. However, the influence of environmental

conditions on their realized trophic niches, and their niche interactions, was not always as predicted, and some surprising patterns emerged.

There have been numerous investigations on the ecology of our target benthivores, but most have been limited to one or a few populations, have not involved direct comparisons of co-habiting populations, and have used a gut content rather than stable isotope approach for trophic analyses. Previous research has suggested considerable potential for niche overlap, both in habitat use and food resources, between these two species. Though lake whitefish generally prefer offshore, deepwater habitat in summer, they will utilize habitats at varying depths in the cooler seasons (Quadri 1961; Baldwin and Polacek 2011). Similarly, although white sucker is generally associated with nearshore, shallower habitats (Coker et al. 2001) they have been shown to forage in all three lake layers (down to 20 m depth) during stratification in boreal lakes (Logan et al. 1991). Dietary studies of both species have documented a diversity of prey items that can vary ontogenetically (Pothoven and Nalepa 2006), and seasonally (Barton 1980; Herbst et al. 2013), as well as among waterbodies. Prey items consumed by lake whitefish include aquatic insects, molluscs, amphipods, mysids, zooplankton, small fishes, and fish eggs (Quadri 1961; Watson 1963; Dumont and Fortin 1978; Pothoven et al. 2001; Lumb et al. 2007; Herbst et al. 2013). White sucker reportedly consume a variety of aquatic insects, amphipods, and zooplankton (Barton 1980; Logan et al. 1991; Saint-Jacques et al. 2000), and will even add detritus to their diet when invertebrate prey are scarce (Ahlgren 1990; Ahlgren 1996). Overall, dietary analyses have suggested that lake whitefish may include relatively more molluscs and fish tissue in their diets than white sucker (Coker et al. 2001).

Despite their dietary similarities, white sucker and lake whitefish populations are frequently found co-habiting in lakes across their common ranges, suggesting that their niches are sufficiently distinct to allow co-existence. In terms of relative trophic niche positions, our results

clearly demonstrated that white sucker derive relatively more energy from benthic primary production, and feed at a lower trophic level compared to lake whitefish. In terms of trophic niche size, our results also showed that white sucker tend to have larger trophic niches than sympatric lake whitefish, as predicted, and this was primarily due to white sucker's use of a broader range of carbon sources. This latter result may be due, in part, to white sucker occupying more nearshore habitats than lake whitefish in boreal lakes; nearshore habitats are closer to terrestrial ecosystems and probably support greater allochthonous-based production, which has $\delta^{13}\text{C}$ signatures similar to autochthonous pelagic sources (Solomon et al. 2011), and fish in the nearshore may thus have access to a wider $\delta^{13}\text{C}$ diversity in food resources. Our indices of trophic niche size, SEAc and CD, reflect inter-individual variation in isotopic composition, and thus, the degree of dietary variation in a population. White sucker occupy a wider diversity of aquatic habitats than lake whitefish across their shared native ranges (Scott and Crossman 1973; Coker et al. 2001) and this may be facilitated, in part, by white sucker's greater capacity for trophic divergence, through either individual specialization (Matthews and Mazumder 2004) or diverging selectivity within a generalist population (Vander Zanden et al. 2010). In some lakes, lake whitefish have diverged into distinct benthivorous and planktivorous morphotypes (Bodaly 1979; Doyon et al. 1998), a pattern not reported for white sucker populations. In the current study, we restricted our analyses to lakes believed to contain only the more common benthivorous form, but it is possible that lake whitefish populations containing both benthivorous and planktivorous morphotypes occupy larger trophic niches.

Environmental influences on the trophic niches of these benthivores were evident at multiple levels. Not surprisingly, niche positions in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space of co-habiting white sucker and lake whitefish populations were positively correlated across lakes. This reflects the common influence of the baseline (background) ecosystem biogeochemistry on the isotopic compositions of resident biota (Cabana and Rasmussen 1996). Similarly, we found strong positive correlations

between isotopic composition of white sucker and isotopic compositions of clams and snails in a smaller subset of our study lakes (Table 5). It has also been suggested that inter-individual variability in isotopic compositions of consumers should increase with the diversity of isotopic compositions in their available prey sources (Matthews and Mazumder 2004). However, we did not find evidence of this in our analyses. Trophic niche sizes of co-habiting lake whitefish and white sucker populations, represented by either SEAc or CD, were not strongly correlated across lakes, suggesting that they are not influenced in the same way by the shared isotopic diversity of available prey. Similarly, we found no significant relationships between indices of niche size or carbon range in white sucker and the separation of clam and snail isotopic compositions lower in the food web (Table 6). Indeed, baseline separation of clam and snail $\delta^{13}\text{C}$ was the only covariate that did not exert any significant influence over white sucker trophic niche dimensions in our analysis. Collectively, our results suggest that baseline isotopic conditions in lakes have a much stronger influence on isotopic-based indices of niche position, than niche size or shape, at least for our target species.

We predicted that waterbody productivity and/or water clarity could influence the realized trophic niches of our target species, and included Secchi depth as the representative environmental variable in our analyses. Specifically, we predicted that trophic niche sizes of both species would increase with increasing Secchi depth because both declining productivity and increasing perceived habitat complexity would cause greater divergence in feeding ecologies among individuals. Our results did not support this prediction; the observed relationship between SEAc and Secchi depth was weak in white sucker and absent in lake whitefish. For both species, models relating niche size to ecosystem size received much stronger support (discussed further, below). Though niche size was not strongly related to Secchi depth in either of our target benthivores, the separation of their trophic niche positions did increase with increasing Secchi depth, primarily due to the white sucker niche position moving to higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$.

Previously reported relationships between niche size, position, or separation and Secchi depth appear to vary among species, presumably reflecting differences in how the physical environment influences their foraging strategies. In a study of two piscivores in small (100-200 ha) boreal lakes, the trophic niche size (SEAc) of the light-adapted species (smallmouth bass, *Micropterus dolomieu*) decreased with increasing Secchi depth, but neither the niche size of the dark-adapted species (walleye, *Sander vitreus*), nor niche separation (DBC) between them were strongly related to water clarity (Stasko et al. 2015). In a series of larger boreal lakes, walleye reliance on nearshore relative to offshore production was found to decline with increasing water clarity (Tunney et al. 2018). In contrast, in small Swedish lakes, Eurasian perch (*Perca fluviatilis*), which primarily consumed zooplankton and benthos, were more diverse morphologically, and relied more on nearshore production at higher water clarity (Bartels et al. 2012; Bartels et al. 2016).

The size and morphometry of boreal lakes can influence the availability and diversity of habitats and resources for resident fishes. Lake depth, in particular, has been associated with variation in abundance of both white sucker (Trippel and Harvey 1987) and lake whitefish (Marshall and Ryan 1987). We found that trophic niche size, represented by SEAc, was positively related to maximum depth for both white sucker and lake whitefish across our study lakes. Because of its effect on lake thermal structure, we predicted that lake depth would be the primary physical characteristic controlling habitat and trophic segregation between our target benthivores. Niche overlap among co-habiting nearshore and offshore fishes in northern Finnish lakes was found to be highest in shallow lakes and decline with increasing lake depth (Hayden et al. 2014). Similarly, we found that trophic niche separation of benthivores increased with lake maximum depth, as predicted, but was more strongly related to Secchi depth (discussed further, above). When comparing our models containing ecosystem size variables, maximum depth and area, we found that maximum depth tended to be the stronger predictor. However, niche size of

fishes has been positively associated with lake area in other species (Bartels et al. 2016). An interesting finding in our study was that white sucker trophic niche size was both positively related to depth and negatively related to area. This may reflect the role of basin shape. In Ontario lakes, the relative use of nearshore and offshore food sources by lake trout (*Salvelinus namaycush*) was found to depend on lake shape; lake trout used nearshore resources more in lakes that were uniform in shape than in lakes that were reticulate (Dolson et al. 2009).

Climate could have a variety of direct and indirect effects on the feeding ecology of lacustrine benthivores. Lakes in warmer climates would be expected to have warmer epilimnia, and potentially higher and more diverse secondary production. Using the Outlying Mean Index (OMI) approach (Dolédec et al. 2000), both niche position and size in Finnish fish communities were shown to vary over a 7 ° latitudinal gradient, but patterns differed among species (Lappalainen and Soininen 2006). Our index of climate, GDD, was the second strongest predictor of lake whitefish trophic niche size (SEAc), but was not a strong predictor of white sucker niche size. Lake whitefish niche size was negatively related to GDD. This finding is likely linked to the colder thermal preference of lake whitefish relative to white sucker. The difference between epilimnion and hypolimnion temperatures in summer is greater in warmer climates, and lake whitefish may be more restricted to the hypolimnion, and utilize a narrower diversity of resources in warmer climates. Other studies have also linked characteristics of trophic niches to climate for coldwater fish species. For example, lake trout have been found to occupy more offshore and trophically-elevated food web positions under warmer conditions across a climatic gradient of Ontario lakes (Tunney et al. 2014).

In addition to the effects of physical habitat on trophic niches of benthivores, biotic interactions probably also play a major role; in fact, some of the observed relationships between trophic niche characteristics and physical habitat may be mediated through effects on the biotic

community. There is some evidence of food limitation and intraspecific competition in both of our study species in boreal lakes. White sucker growth is negatively related to population density, and positively related to benthos abundance (Chen and Harvey 1995), and higher predation pressure (Bertolo and Magnan 2005). Populations of both white sucker and lake whitefish have exhibited increased growth following population reductions (Healey 1980; Brodeur et al. 2001). However, to our knowledge, this is the first study to investigate trophic interactions, and potentially competition, between these two species. We predicted that the trophic niche of each species would expand with increasing separation in their trophic niche positions, and be larger in the absence of the other species in response to reduced interspecific competition. Our results did not support either of these predictions. In sympatry, niche size (SEAc) did not increase significantly for either species as the distance between niche positions increased. Furthermore, comparison of white sucker niche position, size and shape between lakes with and without lake whitefish yielded some unexpected results.

White sucker tended to be more ^{13}C -depleted and ^{15}N -enriched in the absence than in the presence of lake whitefish. However, sampled lakes with both species differed from those with only white sucker in several respects, and after accounting for some of this environmental variation, the observed difference in $\delta^{13}\text{C}$ was less pronounced, but the observed shift in $\delta^{15}\text{N}$ persisted. Thus, overall, the niche position of white sucker may be slightly more pelagic and trophically elevated in lakes without lake whitefish. Regarding trophic niche size and shape, contrary to our prediction, white sucker had significantly larger trophic niche size and carbon breadth in the presence rather than the absence of lake whitefish for most analyses, regardless of the adjustment for environmental covariation. Thus, interspecific interactions with lake whitefish appear to contribute to trophic diversification in white sucker. This suggests that the area of trophic niche overlap between these species may contain preferred niche space for white sucker, and in the absence of lake whitefish, white sucker individuals may tend to converge towards this

space. This is consistent with the observed shift in white sucker food web position towards the expected position of lake whitefish when the latter are absent. An alternate explanation is that dual-species lakes tend to have particular conditions, that were not represented well by our environmental variables, that allow greater scope for trophic diversification. These conditions may be related to the biotic community composition, such as the diversity and abundance of prey. Prey community composition has been shown to be a strong predictor of niche interactions of piscivores in both north-temperate and sub-arctic lakes (Eloranta et al. 2015; Stasko et al. 2015), but similar studies on benthivores appear to be lacking.

Using stable isotope-based metrics we have been able to test predictions about the realized trophic niches of two common benthivorous fishes across a northern landscape. Because our estimate of trophic niche size reflects only inter-individual variability, or individual specialization, it may be conservative. Nevertheless, we were able to clearly demonstrate relationships between niche metrics, including niche size, and environmental conditions in boreal lakes both for individual species, and their interaction. Given the widespread use of stable isotope analysis in aquatic ecology, it is likely that this approach to exploring predictions from food web and niche theory will increase in future, and we offer the following suggestions. First, much of the research on freshwater food webs to date has placed emphasis on apex predators, particularly game fish species. For a more complete understanding of ecosystem function, we feel it is important to diversify the approach, and consider other components of the food web; it is possible, perhaps likely, that the influence of environmental factors on the niche varies with food web position. Second, a more thorough analysis of the relationships between consumer niche metrics and biotic variables, such as prey abundance and/or diversity, may provide insights into the mechanisms underlying the patterns we observed between niche metrics and lake physical characteristics. Finally, the use of individual-level dispersion in C-N isotopic space as a measure

of population trophic niche size could benefit from studies that quantify the dietary and non-dietary contributions to this dispersion, though this may require controlled laboratory trials.

Acknowledgements

We thank the many staff and students who have contributed to the Boreal Food Webs research program (Cooperative Freshwater Ecology Unit, Laurentian University) over the past decade. Funding and in-kind support were provided by the Ontario Ministry of Natural Resources and Forestry, the Natural Sciences and Engineering Research Council's (NSERC) Strategic Network Grants, Discovery Grants, and Canadian Graduate Scholarship Programs, and the Department of Fisheries and Oceans. Constructive criticisms on earlier drafts were provided by Tim Johnson and two anonymous reviewers.

Literature Cited

- Ahlgren, M.O. 1990. Diet selection and the contribution of detritus to the diet of the juvenile white sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci. **47**: 41-48. doi: 10.1139/f90-004
- Ahlgren, M.O. 1996. Selective ingestion of detritus by a north temperate omnivorous fish, the juvenile white sucker, *Catostomus commersoni*. Environ. Biol. Fishes, **46**: 375-381. doi: 10.1007/bf00005016
- Anderson, D.R. 2008. Model based inference in the life sciences: A primer on evidence. ed. Springer Science+Business Media LLC, New York
- Araujo, M.S., Bolnick, D.I., and Layman, C.A. 2011. The ecological causes of individual specialisation. Ecol. Lett. **14**: 948-958. doi: 10.1111/j.1461-0248.2011.01662.x
- Baldwin, C.M., and Polacek, M. 2011. Abundance and seasonal shifts in vertical and horizontal distribution of lake whitefish (*Coregonus clupeaformis*) in a western United States reservoir. Journal of Freshwater Ecology **26**: 171-183. doi: 10.1080/02705060.2011.554216
- Bartels, P., Hirsch, P.E., Svanbäck, R., and Eklov, P. 2012. Water transparency drives intra-population divergence in Eurasian perch (*Perca fluviatilis*). Plos One **7**: 1-10. doi: 10.1371/journal.pone.0043641
- Bartels, P., Hirsch, P.E., Svanbäck, R., and Eklöv, P. 2016. Dissolved organic carbon reduces habitat coupling by top predators in lake ecosystems. Ecosystems **19**: 955-967. doi: 10.1007/s10021-016-9978-x
- Barton, B.A. 1980. Spawning migrations, age and growth, and summer feeding of white suckers and longnose suckers in an irrigation reservoir. Canadian Field-Naturalist **94**: 300-304. doi:
- Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., and MacLeod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Anim. Ecol. **73**: 1007-1012. doi: 10.1111/j.0021-8790.2004.00861.x
- Bertolo, A., and Magnan, P. 2005. The relationship between piscivory and growth of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) in headwater lakes of the Canadian Shield. Can. J. Fish. Aquat. Sci. **62**: 2706-2715. doi: 10.1139/f05-174

- 598 Bodaly, R.A. 1979. Morphological and ecological divergence within the lake whitefish
599 (*Coregonus clupeaformis*) species complex in Yukon Territory. J. Fish. Res. Board Can.
600 **36**: 1214-1222. doi: 10.1139/f79-175
- 601 Boecklen, W.J., Yarnes, C.T., Cook, B.A., and James, A.C. 2011. On the use of stable isotopes in
602 trophic ecology. Ann. Rev. Ecol. Evol. Syst. **42**: 411-440. doi: 10.1146/annurev-ecolsys-
603 102209-144726
- 604 Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M., and Svanbäck, R. 2002. Measuring
605 individual-level resource specialization. Ecology **83**: 2936-2941. doi: 10.2307/3072028
- 606 Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., and Forister,
607 M.L. 2003. The ecology of individuals: Incidence and implications of individual
608 specialization. Am. Nat. **161**: 1-28. doi: 10.1086/343878
- 609 Bolnick, D.I., Svanbäck, R., Araujo, M.S., and Persson, L. 2007. Comparative support for the
610 niche variation hypothesis that more generalized populations also are more
611 heterogeneous. Proc. Nat. Acad. Sci. USA **104**: 10075-10079. doi:
612 10.1073/pnas.0703743104
- 613 Bolnick, D.I., Amarasekare, P., Araujo, M.S., Buerger, R., Levine, J.M., Novak, M., Rudolf,
614 V.H.W., Schreiber, S.J., Urban, M.C., and Vasseur, D.A. 2011. Why intraspecific trait
615 variation matters in community ecology. Trends Ecol. Evol. **26**: 183-192. doi:
616 10.1016/j.tree.2011.01.009
- 617 Brodeur, P., Magnan, P., and Legault, M. 2001. Response of fish communities to different levels
618 of white sucker (*Catostomus commersoni*) biomanipulation in five temperate lakes. Can.
619 J. Fish. Aquat. Sci. **58**: 1998-2010. doi: 10.1139/cjfas-58-10-1998
- 620 Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen
621 isotopes. Proc. Nat. Acad. Sci. USA **93**: 10844-10847. doi: 10.1073/pnas.93.20.10844
- 622 Carl, L.M., and McGuinness, F. 2006. Lake whitefish and lake herring population structure and
623 niche in ten south-central Ontario lakes. Environ. Biol. Fishes, **75**: 315-323. doi:
624 10.1007/s10641-006-0030-4
- 625 Carlson, R.E. 1977. A trophic state index for lakes. Limnol. Oceanogr. **22**: 361-369. doi:
626 10.4319/lo.1977.22.2.0361
- 627 Chen, Y., and Harvey, H.H. 1995. Growth, abundance, and food supply of white sucker. Trans.
628 Am. Fish. Soc. **124**: 262-271. doi: 10.1577/1548-8659(1995)124<0262:gaafso>2.3.co;2
- 629 Coker, G., Portt, C.B., and Minns, C.K. 2001. Morphological and ecological characteristics of
630 Canadian freshwater fishes. Can. Manuscr. Rep. Fish. Aquat. Sci. **2554**: iv + 89 p.

- Costa, G.C., Mesquita, D.O., Colli, G.R., and Vitt, L.J. 2008. Niche expansion and the niche variation hypothesis: Does the degree of individual variation increase in depauperate assemblages? *Am. Nat.* **172**: 868-877. doi: 10.1086/592998
- Dolédec, S., Chessel, D., and Gimaret-Carpentier, C. 2000. Niche separation in community analysis: a new method. *Ecology* **81**: 2914-2927. doi: 10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2
- Dolson, R., McCann, K., Rooney, N., and Ridgway, M. 2009. Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos* **118**: 1230-1238. doi: 10.1111/j.1600-0706.2009.17351.x
- Doyon, J.-F., Schetagne, R., and Verdon, R. 1998. Different mercury bioaccumulation rates between sympatric populations of dwarf and normal lake whitefish (*Coregonus clupeaformis*) in the La Grande complex watershed, James Bay, Quebec. *Biogeochemistry* **40**: 203-216. doi: 10.1023/A:1005951009950
- Dumont, P., and Fortin, R. 1978. Quelques aspects de la biologie du grand corégone *Coregonus clupeaformis* des lacs Hélène et Nathalie, territoire de la Baie James. *Can. J. Zool.* **56**: 1402-1411. doi: 10.1139/z78-193
- Eloranta, A.P., Kahilainen, K.K., Amundsen, P.-A., Knudsen, R., Harrod, C., and Jones, R.I. 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecol. Evol.* **5**: 1664-1675. doi: 10.1002/ece3.1464
- Fink, P., Reichwaldt, E.S., Harrod, C., and Rossberg, A.G. 2012. Determining trophic niche width: an experimental test of the stable isotope approach. *Oikos* **121**: 1985-1994. doi: 10.1111/j.1600-0706.2012.20185.x
- Fry, B. 2006. *Stable Isotope Ecology*. Springer Science Business Media, LLC, New York
- Hayden, B., Harrod, C., and Kahilainen, K.K. 2014. Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water-adapted fish. *Ecology* **95**: 538-552. doi: 10.1890/13-0264.1
- Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Can. J. Fish. Aquat. Sci.* **37**: 255-267. doi: 10.1139/f80-033
- Herbst, S.J., Marsden, J.E., and Lantry, B.F. 2013. Lake whitefish diet, condition, and energy density in Lake Champlain and the lower four Great Lakes following dreissenid invasions. *Trans. Am. Fish. Soc.* **142**: 388-398. doi: 10.1080/00028487.2012.747991
- Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**: 415-427. doi: 10.1101/sqb.1957.022.01.039

- 665 Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche widths
666 among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim.*
667 *Ecol.* **80**: 595-602. doi: 10.1111/j.1365-2656.2011.01806.x
- 668 Johnson, J.B., and Omland, K.S. 2004. Model selection in ecology and evolution. *Trends Ecol.*
669 *Evol.* **19**: 101-108. doi: 10.1016/j.tree.2003.10.013
- 670 Lappalainen, J., and Soininen, J. 2006. Latitudinal gradients in niche breadth and position—
671 regional patterns in freshwater fish. *Naturwissenschaften* **93**: 246-250. doi:
672 10.1007/s00114-006-0093-2
- 673 Layman, C.A., Arrington, D.A., Montana, C.G., and Post, D.M. 2007. Can stable isotope ratios
674 provide for community-wide measures of trophic structure? *Ecology* **88**: 42-48. doi:
675 10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2
- 676 Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R.,
677 Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., and Bearhop, S. 2012.
678 Applying stable isotopes to examine food-web structure: an overview of analytical tools.
679 *Biol. Rev.* **87**: 545-62. doi: 10.1111/j.1469-185X.2011.00208.x
- 680 Leibold, M.A. 1995. The niche concept revisited: mechanistic models and community context.
681 *Ecology* **76**: 1371-1382. doi: 10.2307/1938141
- 682 Logan, C., Trippel, E.A., and Beamish, F.W.H. 1991. Thermal stratification and benthic foraging
683 patterns of white sucker. *Hydrobiologia*, **213**: 125-132. doi: 10.1007/BF00014998
- 684 Lumb, C.E., Johnson, T.B., Cook, H.A., and Hoyle, J.A. 2007. Comparison of lake whitefish
685 (*Coregonus clupeaformis*) growth, condition, and energy density between Lakes Erie and
686 Ontario. *J. Great Lakes Res.* **33**: 314-325. doi: 10.3394/0380-
687 1330(2007)33[314:COLWCC]2.0.CO;2
- 688 Lysy, M., Stasko, A.D., and Swanson, H.K. 2014. nicheROVER: (Niche) (R)egion and Niche
689 (Over)lap metrics for multidimensional ecological niches. R package ver 1.0. . Available
690 at: <http://CRAN.R-project.org/package=nicheROVER>
- 691 MacArthur, R., and Levins, R. 1967. The limiting similarity, convergence, and divergence of
692 coexisting species. *Am. Nat.* **101**: 377-385. doi: 10.2307/2459090
- 693 Marshall, T.R., and Ryan, P.A. 1987. Abundance patterns and community attributes of fishes
694 relative to environmental gradients. *Can. J. Fish. Aquat. Sci.* **44**: s198-s215. doi:
695 10.1139/f87-323
- 696 Matthews, B., and Mazumder, A. 2004. A critical evaluation of intrapopulation variation of $\delta^{13}\text{C}$
697 and isotopic evidence of individual specialization. *Oecologia* **140**: 361-371. doi:
698 10.1007/s00442-004-1579-2

- McKenney, D.W., Pedlar, J.H., Papadopol, P., and Hutchinson, M.F. 2006. The development of 1901-2000 historical monthly climate models for Canada and the United States. *Agricult. For. Meteorol.* **138**: 69-81. doi: 10.1016/j.agrformet.2006.03.012
- Newsome, S.D., del Rio, C.M., Bearhop, S., and Phillips, D.L. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.* **5**: 429-436. doi: 10.1890/060150.1
- Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.T., Ralls, K., Staedler, M.M., Fogel, M.L., and Estes, J.A. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* **90**: 961-974. doi: 10.1890/07-1812.1
- Nürnberg, G.K. 1996. Trophic state of clear and colored, soft- and hardwater lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake Reser. Manage.* **12**: 432-447. doi: 10.1080/07438149609354283
- Parnell, A., and Jackson, A. 2013. SIAR: Stable Isotope Analysis in R. R package version 4.2. ed. Available from <http://CRAN.R-project.org/package=siar>,
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Ann. Rev. Ecol. Syst.* **18**: 293-320. doi: 10.1146/annurev.ecolsys.18.1.293
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**: 703-718. doi: 10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montana, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**: 179-189. doi: 10.1007/s00442-006-0630-x
- Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., and Brandt, S.B. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. *N. Am. J. Fish. Manage.* **21**: 876-883. doi: 10.1577/1548-8675(2001)021<0876:cidabc>2.0.co;2
- Pothoven, S.A., and Nalepa, T.F. 2006. Feeding ecology of lake whitefish in Lake Huron. *J. Great Lakes Res.* **32**: 489-501. doi: 10.3394/0380-1330(2006)32[489:feolwi]2.0.co;2
- Preisendorfer, R.W. 1986. Secchi disk science: visual optics of natural waters. *Limnol. Oceanogr.* **31**: 909-926. doi: 10.4319/lo.1986.31.5.0909
- Quadri, S.U. 1961. Food and distribution of lake whitefish in Lac la Ronge, Saskatchewan. *Trans. Am. Fish. Soc.* **90**: 303-307. doi: 10.1577/1548-8659(1961)90[303:fadolw]2.0.co;2

- 733 R Core Team. 2014. R: a language and environment for statistical computing, version 3.1.2. ed. R
734 Foundation for Statistical Computing, Vienna, Austria, Available at [https://www.r-](https://www.r-project.org)
735 [project.org](https://www.r-project.org).
- 736 Romanuk, T.N., Hayward, A., and Hutchings, J.A. 2011. Trophic level scales positively with
737 body size in fishes. *Global Ecology and Biogeography* **20**: 231-240. doi: 10.1111/j.1466-
738 8238.2010.00579.x
- 739 Roughgarden, J. 1972. Evolution of niche width. *Am. Nat.* **106**: 683-718. doi: 10.1086/282807
- 740 Rousseeuw, P., Croux, C., Todorov, V., Ruckstuhl, A., Saliban-Barrera, M., Verbeke, T., Koller,
741 M., and Maechler, M. 2012. robustbase: Basic robust statistics. R package ver. 0.9-2.
742 Available at: <http://CRAN.R-project.org/package=robustbase>
- 743 Saint-Jacques, N., Harvey, H.H., and Jackson, D.A. 2000. Selective foraging in the white sucker
744 (*Catostomus commersoni*). *Can. J. Zool.* **78**: 1320-1331. doi: 10.1139/cjz-78-8-1320
- 745 Sandstrom, S., Rawson, M., and Lester, N. 2013. Manual of Instructions for Broad-scale Fish
746 Community Monitoring; using North American Gillnets (NA1) and Ontario Small Mesh
747 Gillnets (ON2). Version 2013.2. 35 p.
- 748 SAS Institute Inc. 2013. SAS OnlineDoc® Version 9.4. SAS Institute Inc, Cary, NC
- 749 Schoener, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* **2**: 369-404. doi:
750 10.2307/2096934
- 751 Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. *Bull. Fish. Res. Board Can.*
752 **184**: 966 p.
- 753 Soberón, J., and Arroyo-Peña, B. 2017. Are fundamental niches larger than the realized? Testing
754 a 50-year-old prediction by Hutchinson. *PloS one* **12**: e0175138. doi:
755 10.1371/journal.pone.0175138
- 756 Solomon, C.T., Carpenter, S.R., Clayton, M.K., Cole, J.J., Coloso, J.J., Pace, M.L., Vander
757 Zanden, M.J., and Weidel, B.C. 2011. Terrestrial, benthic, and pelagic resource use in
758 lakes: results from a three-isotope Bayesian mixing model. *Ecology* **92**: 1115-1125. doi:
759 10.1890/10-1185.1
- 760 Stasko, A.D., Johnston, T.A., and Gunn, J.M. 2015. Effects of water clarity and other
761 environmental factors on trophic niches of two sympatric piscivores. *Freshw. Biol.* **60**:
762 1459-1474. doi: 10.1111/fw.b.12581
- 763 Stephens, D.W., and Krebs, J.R. 1987. Foraging theory. Princeton University Press, Princeton,
764 NJ, USA

- Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D., and Reist, J.D. 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* **96**: 318-324. doi: 10.1890/14-0235.1
- Trippel, E.A., and Harvey, H.H. 1987. Abundance, growth, and food supply of white suckers (*Catostomus commersoni*) in relation to lake morphometry and pH. *Can. J. Zool.* **65**: 558-564. doi: 10.1139/z87-086
- Tunney, T.D., McCann, K.S., Lester, N.P., and Shuter, B.J. 2014. Effects of differential habitat warming on complex communities. *Proc. Nat. Acad. Sci. USA* **111**: 8077-8082. doi: 10.1073/pnas.1319618111
- Tunney, T.D., McCann, K.S., Jarvis, L., Lester, N.P., and Shuter, B.J. 2018. Blinded by the light? Nearshore energy pathway coupling and relative predator biomass increase with reduced water transparency across lakes. *Oecologia* doi: 10.1007/s00442-017-4049-3
- Turner, T.F., Collyer, M.L., and Krabbenhoft, T.J. 2010. A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology* **91**: 2227-2233. doi: 10.1890/09-1454.1
- Van Valen, L. 1965. Morphological variation and width of ecological niche. *Am. Nat.* **99**: 377-390. doi: 10.1086/282379
- Vander Zanden, H.B., Bjorndal, K.A., Reich, K.J., and Bolten, A.B. 2010. Individual specialists in a generalist population: results from a long-term stable isotope series. *Biol. Lett.* **6**: 711-714. doi: 10.1098/rsbl.2010.0124
- Vandermeer, J.H. 1972. Niche theory. *Ann. Rev. Ecol. Syst.* **3**: 107-132. doi: 10.2307/2096844
- Watson, N.H.F. 1963. Summer food of lake whitefish, *Coregonus clupeaformis* Mitchill, from Heming Lake, Manitoba. *J. Fish. Res. Board Can.* **20**: 279-286. doi: 10.1139/f63-025

Table 1. Definitions and calculations for dependent and independent variables used in analyses.

Variable	Definition
<i>Niche metrics of individual populations</i>	
SEAc	Standard ellipse area, an index of niche size. Calculated as area of a 2 SD variance ellipse in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bivariate space corrected for small sample size (‰^2).
CR	Carbon range, an index of the breadth of carbon sources utilized. Calculated as shadow of a 2 SD variance ellipse in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space that is cast along $\delta^{13}\text{C}$ axis (‰).
NR	Nitrogen range, an index of the range of trophic elevations occupied. Calculated as shadow of a 2 SD variance ellipse in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space that is cast along $\delta^{15}\text{N}$ axis (‰).
CD	Centroid distance, an index of niche size. Calculated as mean distance from population food web position (mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$) to each individual in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space (‰).
SDNND	Standard deviation of nearest neighbour distance, an index of dispersion of individuals in niche space. Calculated in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space, as described (‰).
<i>Niche interaction metrics</i>	
DBC	Distance between centroids, an index of niche separation. Calculated as distance between mean positions of two populations in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space (‰).
SEA_OV	Standard ellipse area overlap, an index of niche overlap. Percentage of combined niche area (SEAc) of two populations that is composed of shared space.
PINO	Probability of isotopic niche overlap (%). Median probability of finding an individual of species 1 with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that fall within the isotopic niche of species 2
<i>Environmental characteristics</i>	
ZMAX	Lake maximum depth (m), an index of ecosystem size in vertical dimension.
AREA	Lake surface area (km^2), an index of ecosystem size in horizontal dimension.
SECCHI	Secchi depth (m), an index of water clarity and ecosystem productivity.
GDD	Mean annual cumulative growing degree-days above 5 °C for the period 1971-2000, an index of climate.

Table 2. Tests of differences between white sucker (WS) and lake whitefish (LWF) in trophic niche size and shape based on various isotopic niche metrics (defined in Table 1). Paired-comparisons t-tests and Signed Rank tests were used in cases where differences between species were normally distributed and not normally distributed, respectively (n = number of lakes where ≥ 10 individuals of each species were sampled).

Niche metric	n	Trend	Test	Statistic	P
SEAc	57	WS > LWF	Paired-comparison t	3.19	0.0023
CD	57	WS > LWF	Paired-comparison t	3.50	< 0.001
SDNND	57	WS > LWF	Signed Rank S	178	0.15
CR	57	WS > LWF	Paired-comparison t	3.63	< 0.001
NR	57	WS > LWF	Paired-comparison t	1.06	0.29

Table 3. Comparison of linear models relating niche size ($\log_e$ SEAc) to environmental variables (defined in Table 1) for white sucker and lake whitefish populations in sympatry in 68 boreal lakes. For each species, models were constructed for all one, two and three variable combinations, and subsets of the 15 fitted models are shown. AIC_c = Akaike's Information Criterion corrected for small sample size, Δ_i = difference between AIC_c value of a given model and the top-ranked model, w_i = Akaike weight.

Variables in model (effect)	Rank	AIC_c	Δ_i	w_i	Adj - R^2
White sucker					
ZMAX (+), $\log_e$ AREA (-)	1	6.22	0.00	0.47	0.15
ZMAX (+), $\log_e$ AREA (-), GDD (+)	2	8.04	1.82	0.19	0.15
ZMAX (+), $\log_e$ AREA (-), SECCHI (+)	3	8.51	2.29	0.15	0.14
GDD (+), $\log_e$ AREA (-)	4	11.69	5.47	0.03	0.08
ZMAX (+)	6	11.84	5.62	0.03	0.07
SECCHI (+)	8	12.66	6.44	0.02	0.05
GDD (+)	11	13.54	7.32	0.01	0.04
$\log_e$ AREA (-)	12	13.85	7.63	0.01	0.04
Intercept only	15	15.23	9.01	0.01	0.00
Lake whitefish					
$\log_e$ ZMAX (+), GDD (-)	1	6.70	0.00	0.36	0.23
$\log_e$ ZMAX (+), GDD (-), SECCHI (-)	2	7.58	0.88	0.23	0.23
$\log_e$ ZMAX (+), GDD (-), $\log_e$ AREA (+)	3	8.82	2.12	0.12	0.22
$\log_e$ ZMAX (+), SECCHI (-)	4	9.09	2.39	0.11	0.20
$\log_e$ ZMAX (+)	5	9.24	2.54	0.10	0.19
Intercept only	8	21.98	15.28	0.00	0.00
$\log_e$ AREA (+)	9	22.15	15.45	0.00	0.01
SECCHI (+)	11	22.52	15.82	0.00	0.01
GDD (-)	12	24.16	17.46	0.00	< 0.01

Table 4. Comparison of linear models relating distance between trophic niche centroids (DBC) and niche overlap (SEA_OV) of white sucker and lake whitefish to environmental variables (defined in Table 1) in boreal lakes with sympatric populations. Models were constructed for all one, two and three variable combinations, and a subset of the 15 fitted models is shown. AIC_c = Akaike's Information Criterion corrected for small sample size, Δ_i = difference between AIC_c value of a given model and the top-ranked model, w_i = Akaike weight.

Variables in model (effect)	Rank	AIC_c	Δ_i	w_i	Adj - R^2
DBC ($n = 75$ lakes)					
SECCHI (+), GDD (+)	1	117.82	0.00	0.29	0.26
SECCHI (+)	2	117.99	0.17	0.26	0.25
SECCHI (+), $\log_e$ ZMAX (+)	3	119.73	1.91	0.11	0.24
SECCHI (+), GDD (+), $\log_e$ AREA (-)	4	119.96	2.14	0.10	0.26
SECCHI (+), GDD (+), $\log_e$ ZMAX (+)	5	120.08	2.26	0.09	0.25
GDD (+)	10	128.68	10.86	0.00	0.14
$\log_e$ ZMAX (+)	11	128.94	11.12	0.00	0.13
Intercept only	14	138.45	20.63	0.00	0.00
$\log_e$ AREA (-)	15	140.29	22.47	0.00	< 0.01
SEA_OV ($n = 57$ lakes)					
SECCHI (-), $\log_e$ AREA (+)	1	392.63	0.00	0.26	0.18
SECCHI (-)	2	392.74	0.11	0.25	0.16
SECCHI (-), GDD (+)	3	394.31	1.68	0.11	0.15
SECCHI (-), $\log_e$ AREA (+), GDD (+)	5	394.41	1.78	0.11	0.17
SECCHI (-), $\log_e$ AREA (+), $\log_e$ ZMAX (+)	6	394.89	2.26	0.08	0.17
$\log_e$ AREA (+)	9	400.25	7.62	0.01	0.04
$\log_e$ ZMAX (-)	10	401.03	8.40	0.00	0.03
Intercept only	12	401.37	8.74	0.00	0.00
GDD (-)	14	402.84	10.21	0.00	< 0.01

Table 5. Tests for differences in white sucker trophic niche position in isotopic space between lakes with and without lake whitefish. For each dependent variable (muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) a one-way ANOVA and multiple ANCOVA models are compared. Covariates (COV) include environmental variables (defined in Table 1) and indices of isotopic baseline. Models using isotopic covariates are based on a smaller subset of lakes. b_i = common covariate slope, b_A and b_P = covariate slopes in absence and presence, respectively, of lake whitefish, Mean_A and Mean_P = least-square means in absence and presence, respectively, of lake whitefish

COV	Covariate effect				Lake whitefish effect (with covariate)				
	b_i	F	df_{error}	P	F	df_{error}	P	Mean_P	Mean_A
White sucker niche position - $\delta^{13}\text{C}$									
none	.	.	.	.	5.65	107	0.019	-27.2	-28.5
ZMAX	0.039	22.0	106	< 0.001	1.44	106	0.23	-27.4	-28.0
$\log_e$ AREA	0.46	6.35	106	0.013	1.26	106	0.26	-27.3	-28.0
SECCHI	0.60	25.2	106	< 0.001	3.14	106	0.079	-27.3	-28.2
GDD	0.002	2.8	106	0.10	7.24	106	0.0083	-27.1	-28.7
Clam $\delta^{13}\text{C}$	0.80	8.67	21	0.008	0.84	21	0.37	-27.1	-28.1
Snail $\delta^{13}\text{C}$	0.43	6.75	21	0.017	0.00	21	0.99	-27.4	-27.4
White sucker niche position - $\delta^{15}\text{N}$									
none	.	.	.	.	6.97	107	0.010	7.50	8.10
ZMAX	-0.008	5.45	106	0.022	3.77	106	0.055	7.54	7.99
$\log_e$ AREA	0.08	1.06	106	0.31	7.99	106	0.006	7.47	8.17
SECCHI	significant interaction, $b_A > b_P$				.	105	0.009	7.55	8.13
GDD	significant interaction, $b_A > b_P$				.	105	0.049	7.48	7.94
Clam $\delta^{15}\text{N}$	0.52	21.6	21	< 0.001	0.17	21	0.69	7.57	7.45
Snail $\delta^{15}\text{N}$	0.75	38.7	21	< 0.001	0.25	21	0.62	7.57	7.44

Table 6. Tests for differences in dimensions of white sucker trophic niches in isotopic space between lakes with and without lake whitefish. For each dependent variable (SEAc and CR, defined in Table 1) a one-way ANOVA and mutiple ANCOVA models are compared. Covariates (COV) include environmental variables (defined in Table 1) and an index of isotopic baseline (Base $\delta^{13}\text{C}$ = snail $\delta^{13}\text{C}$ - clam $\delta^{13}\text{C}$). Models using isotopic covariates are based on a smaller subset of lakes. b_i = common covariate slope, b_A and b_P = covariate slopes in absence and presence, respectively, of lake whitefish, Mean_A and Mean_P = least-square means in absence and presence, respectively, of lake whitefish

COV	Covariate effect				Lake whitefish effect (with covariate)				
	b_i	F	df_{error}	P	F	df_{error}	P	Mean_P	Mean_A
<i>White sucker niche area - log_e SEAc</i>									
none	.	.	.	.	10.0	93	0.002	2.24	1.71
log _e ZMAX	0.21	7.53	92	0.007	4.69	92	0.033	2.20	1.82
log _e AREA	-0.12	5.42	92	0.022	15.4	92	< 0.001	2.29	1.59
SECCHI	0.093	6.33	92	0.014	8.33	92	0.005	2.22	1.75
GDD	significant interaction, $b_A > b_P$				.	91	< 0.001	2.26	1.56
Base $\delta^{13}\text{C}$	-0.019	0.13	16	0.72	0.13	16	0.73	2.25	2.14
<i>White sucker niche breadth - log_e CR</i>									
none	.	.	.	.	5.62	93	0.020	1.72	1.45
log _e ZMAX	0.18	11.8	92	< 0.001	1.46	92	0.23	1.69	1.55
log _e AREA	-0.12	11.2	92	0.0012	13.52	92	< 0.001	1.77	1.68
SECCHI	0.094	14.9	92	< 0.001	3.99	92	0.049	1.71	1.49
GDD	0.001	17.9	92	< 0.001	11.06	91	0.001	1.75	1.39
Base $\delta^{13}\text{C}$	0.037	1.08	16	0.31	0.00	16	1.00	1.79	1.78

Figure captions

Figure 1. Muscle isotopic compositions ($\delta^{13}\text{C}$, top; $\delta^{15}\text{N}$, bottom) of white sucker vs lake whitefish in 75 boreal lakes with co-habiting populations. Symbols are population means ($n \geq 5$ per species) adjusted to a body size of 1 kg, solid lines are fitted OLS regressions, and dashed lines are 1:1 agreement reference lines. One lake with very elevated $\delta^{15}\text{N}$ in both species is out of range in the bottom panel.

Figure 2. Relationship between trophic niche separation in isotopic space (DBC, defined in Table 1) of white sucker and lake whitefish and lake maximum depth (top) and Secchi depth (bottom). Symbols represent population pairs ($n \geq 5$ per species) from 75 boreal lakes and solid lines are fitted OLS regressions.

Figure 3. Muscle isotopic compositions ($\delta^{13}\text{C}$, top; $\delta^{15}\text{N}$, bottom) vs Secchi depth of white sucker (open circles, dashed lines) and lake whitefish (closed triangles, solid lines) in 75 boreal lakes with co-habiting populations. Symbols are population means adjusted to a body size of 1 kg, and lines are fitted OLS regressions. One lake with very elevated $\delta^{15}\text{N}$ in both species is out of range in the bottom panel.

Figure 4. Relationship between white sucker trophic niche area in isotopic space (SEAc, defined in Table 1) and lake maximum depth (top) and Secchi depth (bottom) in 95 boreal lakes. Symbols represent white sucker populations ($n \geq 10$ per population) from boreal lakes with cohabiting lake whitefish ($n = 68$ lakes; open circles and dashed lines) and without lake whitefish ($n = 27$ lakes; closed circles and solid lines). Lines are fitted OLS regressions.

Figure 1

31

32

33 **Figure 2**

Figure 3

37

38 **Figure 4**