

**MODELLING TROPHIC RECOVERY, INTERACTIONS, AND FOOD
WEB DYNAMICS ACROSS SMELTER-DAMAGED LAKES**

by

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Abstract

Unstable and simplified freshwater food webs threaten the long-term potential of Canadian fisheries due to lack of resiliency in response to stressors including pollutants, climate change, and invasive species. This study utilizes lakes in Sudbury, Ontario to highlight potential drivers and limiting factors of trophic recovery from acidification and heavy-metal pollution from historical nickel smelting emissions. Three lakes across the smelter-impact gradient were selected: one severely damaged lake with a barren watershed (Baby Lake), one severely damaged lake that received sub-watershed liming treatment but retained partial forest cover (Daisy Lake), and one minimally impacted lake with intact forest but had previously been limed to enhance a fish population (Nelson Lake). Two reference lakes far from Sudbury impacts were selected for comparison. Twenty Sudbury region lakes were examined to contextualize fish community assemblages and size data across the smelter deposition zone. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were quantified in yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieu*), and baseline organisms to develop quantitative population metrics and describe dietary niche partitioning in each study lake. The barren watershed lake had lowest trophic positioning, smallest body size and niche area, and greatest niche overlap among fish species. The semi-barren and forested watershed lakes were more similar to reference lakes than barren lake in isotopic metrics, signifying significant trophic recovery; however elevated niche overlap revealed additional recovery in these lakes is ongoing. Including stable isotopes in recovering lake studies provides ecosystem insights overlooked by traditional biomonitoring approaches that are critical in understanding freshwater food web responses.

Keywords: lake restoration, trophic ecology, acidification, stable isotope analyses, niche compression

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1 INTRODUCTION

Freshwater ecosystems are essential components of daily life in Canada, with uses ranging from clean drinking water and subsistence fishing to recreational use. The Canadian economy also relies upon our freshwater resources for hydroelectricity, commercial fishing and aquaculture, agriculture, and manufacturing and processing. Some of the very economies that utilize freshwater are directly responsible for the degradation of freshwater systems by discharging harmful effluents into the water or the surrounding air and soil. One of the symptoms of a stressed aquatic system is food web instability and simplification (McCann et al. 2005; McMeans et al. 2016; Burdon et al. 2017; Bartley et al. 2019). Food web instability and simplification pose threats to the long-term health of recreational and commercial fisheries and freshwater ecosystems in Canada. In a multi-stressor world with the additional stresses of pollutants, climate change, and over-fishing, understanding the responses of freshwater food webs to disturbance are paramount (Burdon et al. 2017; Bartley et al. 2019; Hayden et al. 2019). With an ever-growing population, the demand for resources and pressures on freshwater systems are high, thereby concentrating these pressures on the limited number of healthy lakes and rivers. Comprehending how these food webs respond to multiple stressors may provide insight into potential restoration techniques and is important in light of global change (Bartley et al. 2019; Bruder et al. 2019).

It is equally critical that priority is given to the protection and conservation of those healthy freshwater systems with diverse and stable food webs to prevent any future recovery needs. Diversity across all trophic levels maximizes the biological and resource potential of lakes by

filling the variety of niches available (Holt and Polis 1997; Hooper et al. 2005; Loreau and de Mazancourt 2013; Gonzalez et al. 2020; Ward et al. 2023). Healthy, diverse freshwater lakes foster a stable food web comprised of many weak consumer-resource interactions (McCann et al. 2000; Duffy et al. 2007; Loreau and de Mazancourt 2013; McMeans et al. 2016). Stable food webs are in turn more resilient in their response to disturbances due to their trophic topology that allows for density-dependent prey switching and omnivory (McCann et al. 2005; Duffy et al. 2007; Gellner and McCann 2012; McMeans et al. 2016). Behavioural changes in predation tactics provides relief to the prey species' population by reducing the pressure on that population and allowing for their recovery rather than decimation (Duffy et al. 2007). For example, in lakes, omnivorous predators may also couple aquatic food webs by foraging in the littoral zone productivity during periods when this habitat is productive and in the pelagic zone during high pelagic productivity (McMeans et al. 2016). This shift also benefits the predator population by reducing the energy spent hunting low-density prey, reducing energetic constraints on the predator that may cause reduced growth, condition, and fecundity (McCann et al. 2005; McMeans et al. 2016). Food web coupling may be linked to seasonal variation in benthic and pelagic resources, seasonal variation in habitat usage, relief from competition among predators, or a combination of these drivers (Duffy et al. 2007; Alp & Cucherousset 2022). This permits greater energetic efficiencies among consumers, producing larger body-sized individuals with greater reproductive potential, both of which are beneficial to commercial and recreation fisheries (McMeans et al. 2016). Food web coupling topologically builds resiliency into aquatic systems through the utilization of many resources and energetic pathways by facilitating switches between prey sources in response to stressors and environmental change (McCann et al. 2005; Duffy et al. 2007; Gellner and McCann 2012; Bartley et al. 2019).

Compounding effects of multi-stressors are intensified in areas such as Sudbury, Ontario, where over a century of nickel smelting activity has caused heavy metal pollution and acidification of many lakes (Keller 2009; Keller et al. 2019). Emissions of acidic sulphur dioxide (SO₂) and heavy metals originating from the ore roast yards and metal smelters in Sudbury commenced in the late 1800s and peaked in the 1960s (Dixit et al. 1996). At the height of SO₂ emissions, Sudbury represented the largest underground nickel mining complex and one of the largest point source emitters of SO₂ in the world (Winterhalder 1995). Over a century of SO₂ and heavy metal emissions resulted in over 7,000 lakes in the surrounding area becoming acid-damaged and many lakes within approximately 30 km of smelters becoming polluted with heavy metals beyond provincial water quality guidelines (Gunn et al. 2001; Keller 2009; Wesolek et al. 2010). Widespread declines of aquatic biodiversity and abundance across all trophic levels quickly followed, including the extinction of many fish communities (Keller 2009). Likewise, terrestrial ecosystems were badly damaged with extensive areas of barrens surrounding the smelters (Winterhalder 1995; Gunn et al. 2001; Keller 2009). Even the topsoil was stripped down to the bedrock as erosion intensified on the barren hillsides (Winterhalder 1995). The destruction of terrestrial ecosystems severed critical land-water linkages between lakes and their watersheds that transport essential nutrients to promote and sustain aquatic life (Wesolek et al. 2010; Tanentzap et al. 2014).

Following the closure of some smelters and the push for cleaner technology in the 1970s, Sudbury smelting operations dramatically reduced SO₂ and metal particulate emissions (Gunn et al. 2001). Today, SO₂ emissions have been reduced by over 95% compared to historic levels (Keller et al. 2019). While many lakes have recovered enough to sustain fish populations, some recovery lakes close to the historic smelters have lagged in both chemical and biological

recovery (Keller 2009; Gunn et al. 2016). In some cases, intensive restoration, known as the ‘Sudbury Method’ has been undertaken in catchments of particularly damaged watersheds (Gunn et al. 2001). The ‘Sudbury Method’ involves the application of dolomitic limestone (CaCO_3) to increase pH, followed by fertilizer, grass-seeding, and tree-planting (Gunn et al. 2001). Watershed restoration can restore terrestrial- aquatic linkages that are critical for transporting carbon and nutrients from the terrestrial catchment area into the lake (Szkokan-Emilson et al. 2011). In an effort to recover the diversity and ecosystem connectivity of these heavily damaged food webs, various restoration techniques have been applied to watersheds in the region (Gunn et al. 2001). Previous research demonstrates that watershed treatment can restore terrestrial-aquatic linkages that are critical for transporting carbon and nutrients from the terrestrial catchment area into the lake (Szkokan-Emilson et al. 2011; Tanentzap et al. 2014). Understanding how these restoration efforts have altered the food webs of these recovery lakes has not been well documented, but is absolutely critical to advance our understanding of both restoration ecology and freshwater biology and the intersection of these fields.

While chemical and biological recovery has been relatively well-documented and incorporated into long-term biomonitoring programs, this has not been the case for the trophic recovery of Sudbury’s smelter-damaged recovery lakes. Stable isotope studies of other smelter-damaged boreal freshwater systems show that these food webs often become simplified and unstable due to the lack of productivity, abundance, and diversity in the ecosystem (Hogsden et al. 2009; Luek et al. 2010; Layer et al. 2011). Additionally, the lack of prey resources spanning various trophic levels often results in trophic niche compression or alteration of the remaining consumers (McCann et al. 2005; Alp & Cucherousset 2022). Depending on which species remain in the system, there is also evidence that pollution tolerant or early colonizing species

may exhibit biological resistance (founder effect), wherein the species modifies its environment in such a way that promotes its resilience while hindering the success of other potentially competing species (Duffy et al. 2007; Layer et al. 2011; Henriksson et al. 2014). Yellow perch (*Perca flavescens*) is one such early colonist and rather tolerant species common in the Sudbury area that may create biological resistance in some cases (Lippert et al. 2007; Henriksson et al. 2014).

One of the few previous trophic ecology studies conducted in Sudbury recovery lakes found that application of the land reclamation techniques led to increases in fish growth through the input of higher abundance of terrestrially-derived carbon into the aquatic food web; however it is unknown how prominent the effects of the re-established land-water linkages will be as recovery continues to progress beyond these sub-watershed areas (Tanentzap et al. 2014). Though the biological recovery of fish, zooplankton, and benthic invertebrates has been more regularly measured in these recovery lake systems, aside from the Tanentzap (2014) study, there is limited research into the relative contribution and integration of these recovering community assemblages into the aquatic food web. There is potential for the recovery of lower trophic level communities to substantially influence the recovery of higher trophic level organisms through increased resources for consumers as well as omnivory (McCann et al. 2005; Vadeboncoeur 2005; Duffy et al. 2007). Quantifying trophic recovery and dynamics of fish communities through the use of stable isotope metrics of mean trophic positioning, niche area and proportion of overlap among niches, and proportion of littoral energy usage and how these metrics vary across fish communities and lakes provides insight into underlying factors limiting whole-lake recovery. These underlying factors may include lack of diverse (lake zone and trophic position) prey sources, high levels of competition for resources among species and communities, and

severed or impaired watershed connectivity. It is important to quantify the relative contributions of recovering communities into the whole-lake food web as they may act as stabilizing factors (Vadeboncoeur 2005).

Researching how chemical and biological recovery in smelter-damaged lakes are affected by restoration treatment is critical for understanding how these changes ultimately translate into food web recovery and stability. Stable isotope analyses, when applied in conjunction with traditional community ecology metrics, may provide a powerful method for evaluating the current state of aquatic food webs experiencing multi-stressors (Duffy et al. 2007; Bruder et al. 2019; Hayden et al. 2019; Alp & Cucherousset 2022). This study utilizes stable isotope metrics of trophic recovery as a novel tool for quantifying the current state of food web recovery in lakes recovering from smelter-damage. By quantifying and assessing the relative importance of different energy sources in recovering food webs using stable isotopes, the efficacy of freshwater restoration techniques may be evaluated (Pace et al. 2004; Bruder et al. 2019; Alp & Cucherousset 2022). As we enter the Decade of Ecosystem Restoration, it is essential to develop appropriate restoration techniques to globally recover the biological and resource potential of lakes and mitigate the effects of climate change, resource extraction, and intensive harvesting (United Nations 2019).

1.1 Objectives

The aim of this study is to determine the food web structure and trophic dynamics of three recovering Sudbury area lakes that varied widely in the original impact of the smelter emissions (barren, semi-barren, forested watersheds) in comparison to two distant reference lakes. Stable isotope analyses were conducted on the recovery lakes and reference lakes to understand variation in niche areas and positioning of consumers and relative usage of energetic pathways

(littoral vs. pelagic). More detailed isotopic analysis was undertaken for common fish species (yellow perch and smallmouth bass) within these two groups of lakes including, standard ellipse area calculations and degree of overlap, mean trophic positioning, and fish condition. Fish community structure was assessed for the recovery lakes and twenty regional lakes using catch-per-unit-effort (CPUE) metrics for each species present as well as for groups of species based on acid-tolerance and thermal guild. Size comparisons for yellow perch and smallmouth bass were conducted to contextualize CPUE findings in terms of local recovery across the smelter deposition zone. Collectively these methods were used to explore the use of stable isotope analyses and mixing models to evaluate the current food web structure of the three recovery lakes and assess their recovery status relative to other regional lakes and the two reference lakes. Stable isotope analyses provide ecosystem insights overlooked by traditional biomonitoring approaches, such as predator-prey interactions, competition, and resource use. Including stable isotope analyses with biomonitoring data is critical to increase our understanding of freshwater food web dynamics and responses to global change.

2 METHODS

2.1 Selection of study lakes

Three recovery lakes in the Sudbury region of the Ontario shield ecozone were selected across the smelter-impact gradient from the Coniston nickel smelters (Figure 1). Baby Lake and Daisy Lake are 11.9 ha and 36.1 ha lakes, respectively, that historically suffered intensive damage due to the close proximity (<4 km) to the Coniston smelters that operated from 1913 to 1972 (Corston et al. 2014a; Corston et al. 2014b). Baby Lake, being closer to the Coniston smelters, had a barren watershed without vegetation and topsoil, while Daisy Lake had some topographic relief that created a semi-barren watershed with pockets of intact forest cover (Figure S3; Figure S4; Dixit et al. 1996; Gunn et al. 2016). Water quality in these lakes has improved considerably since the smelter closure as demonstrated by significant increases in pH and exponential decreases in conductivity, nickel, and copper concentrations (Table S1; Corston et al. 2014a; Corston et al. 2014b). Benthic macroinvertebrate diversity and abundance has likewise improved, including the return of previously extirpated sensitive bioindicator species such as mayflies, stoneflies, and caddisflies (Wesolek et al. 2010). Fish species richness and abundance has also increased in both lakes since smelter emission reductions, although shifts in community structure have been noted (Corston et al. 2014a; Corston et al. 2014b). In semi-barren Daisy Lake, chemical and biological recovery is more pronounced due to partial retention of forest cover throughout the watershed and intensive restoration treatment to one catchment area in the early 1990s (Figure S4; Wesolek et al. 2010; Gunn et al. 2016). Unlike the semi-barren Daisy Lake, barren Baby Lake also lacks recovery assistance from delta ‘hotspots’ where stream inputs of terrestrially-derived nutrients (i.e. dissolved organic carbon, nitrogen, allochthonous materials) improve microsite conditions that influence recolonization of species (Figure S3;

Wesolek et al. 2010; Tanentzap et al. 2014). Nelson Lake is a 308.8 ha lake farther away from the Coniston smelters that only moderately acidified (pH 5.7) with elevated metal concentration (e.g. Cu 17-29 µg/L) but to a much lesser extent than that of the fully acidified and metal-contaminated Baby and Daisy Lakes (Dixit et al. 1991; Casselman and Gunn 1992; Dixit et al. 1996). The watershed surrounding Nelson Lake completely retained its original intact forest, unlike the barren and semi-barren Baby and Daisy Lakes (Figure S5; Gunn et al. 1988). Nelson Lake acidified to the degree that sportfish such as smallmouth bass and lake trout remained though were heavily impacted and the fish community shifted towards dominance by the acid-tolerant yellow perch (Figure 1; Table S1; Gunn et al. 1988). Nelson Lake received an extensive whole-lake neutralizing treatment in 1975 and 1976 that increased the pH to above 6.4 and reduced metal concentrations below the Provincial Water Quality Guidelines; however, liming alone was not responsible for the rapidly increasing lake trout population and their predation on perch (Casselman and Gunn 1988). The strong year classes of trout occurred prior to liming and appear to be linked to regional-scale recovery due to atmospheric emission reductions (Gunn et al. 1988; Casselman and Gunn 1992). These three recovery lakes each broadly represent the different degrees of watershed damage associated with smelter emissions (barren, semi-barren, intact forest).

Two reference lakes in the Ontario shield ecozone were selected: Tadenac Lake from Muskoka region and Richardson Lake from Kenora region both well outside of the influence of Sudbury's smelter deposition zone (Figure 1). Tadenac Lake is a relatively undisturbed 308 ha Precambrian shield lake in central Ontario with conductivity, alkalinity, pH, and metal concentrations typical of its geology (Figure 1; Table S1; Johnston et al. 2020). Tadenac Lake is also characterized as

oligotrophic as reflected by relatively low nutrient concentrations (Johnston et al. 2020).

Richardson Lake is a 194.8 ha Precambrian shield lake in northwestern Ontario with relatively elevated conductivity, alkalinity, pH, and calcium and phosphorous concentrations linked to its physical characteristics rather than anthropogenic impacts (Figure 1; Table S1). Both lakes contain similar fish species typical of Ontario boreal lakes, namely lake trout (*Salvelinus namaycush*), whitefishes (*Coregonus clupeaformis* and *Coregonus artedi*), northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), and perch (*Perca flavescens* and *Sander vitreus*) and also contain the invasive rainbow smelt (*Osmerus mordax*). Tadenac Lake and Richardson Lake were chosen as reference lakes due to their distance from any impacts associated with Sudbury metal smelting, smaller lake size (<310 ha), similar fish community assemblages, and availability of stable isotope ratio data for the only two common species across all three recovery lakes with large enough sample sizes (yellow perch and smallmouth bass). Though the fish assemblages and lake sizes of the reference lakes more closely resemble the forested recovery lake (Nelson Lake), the fish assemblages also resemble what would likely exist in the barren and semi-barren recovery lakes (Baby and Daisy Lakes) had their fish communities not been lost or severely impacted (Corston et al. 2014a; Corston et al. 2014b).

Data from 20 Sudbury regional broadscale monitoring (BsM) lakes were utilized to compare the current status and recovery state of the recovery lakes in relation to lakes in the broader local region (Table S6). These lakes were included to specifically compare fish community assemblages and size distributions throughout the smelter deposition zone. Similarly, these lakes span a smelter-impact gradient given the proximity to the nickel smelters, ranging from 14 km to 103 km (Table S6). A gradient of lake sizes were used as well with lakes ranging from 16.5 ha to

1,315.5 ha and a median lake size of 140.2 ha (Table S6). Sudbury regional lakes were grouped into Northeastern lakes (NE BsM Lakes) and Southwestern (SW BsM Lakes) based on primary wind direction in relation to the smelters, which are typically southwesterly (Table S6). These 20 regional lakes contextualize the use of the three recovery lakes as being representative of the broader deposition zone in terms of fish community assemblages and the prevalence and size distributions of certain species (i.e. yellow perch) across communities.

2.2 Field sampling

Fish community sampling – Fish community were sampled in accordance with Ontario Ministry of Natural Resources and Forestry (OMNRF) Broad-scale Monitoring (BsM) protocols. BsM protocols implement large-mesh and small-mesh gill-net gangs that are each set and distributed evenly and proportionally to the area and bathymetry of the lake (Sandstrom et al. 2013). A minimum of two nets per depth stratum were set in the afternoon and remained in place overnight for 16-22 hours with retrieval the following morning. In addition to the BsM protocol, one multi-mesh NORDIC net was set per stratum to fish at the same time as a BsM net for the given stratum for the Sudbury recovery and regional lakes to target smaller sizes and potentially other species not typically caught in BsM nets (Brekke 2016). Each NORDIC net was set following the Swedish standardized protocol such that nets were set randomly within the depth strata and perpendicular to the shoreline to fish for 16-22 hours (Appelburg 2000). NORDIC nets were also used in the survey of Tadenac Lake to measure species richness and were primarily set at depths greater than 10 m (Johnston et al. 2020). NORDIC nets were not used during the survey of Richardson Lake. As the reference lakes utilized different applications of NORDIC nets than the recovery and regional lakes there is potential bias in species richness values against

the reference lakes (Brekke 2016). Netting surveys occurred in July 2009 for Richardson Lake, June 2012 for Tadenac Lake, and Sudbury regional and recovery lakes were surveyed between June and September 2019.

All captured fish were enumerated by individual net and identified to species. Additional measurements were conducted on selected small- and large-bodied species. Small-bodied fishes had total length (TLEN) measured while large-bodied fishes were measured for fork length (FLEN), TLEN, and total weight and sex, and maturity level. Axial muscle tissue samples dorsal to the lateral line were collected for quantification of stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) from up to 20 fish per species. Small-bodied fish for tissue sample were kept whole and frozen for later processing in the lab, while large-bodied fish tissue samples were collected in the field. All tissue samples were kept on ice in the field until transfer to a laboratory where samples were stored at -20°C for processing. For the three primary recovery lakes where greater than 10 individuals per species were captured, a subset of 10 tissue samples per species were selected proportionally to the size distributions of the given species and were analyzed for stable isotopes.

Baseline organisms collection – Ephemeroptera (mayfly), zooplankton, and clams were collected from the lakes as baseline organisms for stable isotope analyses with the Sudbury recovery lakes undergoing more extensive sampling techniques. All three Sudbury recovery lakes were sampled for baseline organisms in summer 2019 while those in the two reference lakes (Tadenac Lake and Richardson Lake) were collected at the time of the fish community surveys in 2012 and 2009, respectively (Johnston et al. 2020). For these recovery lakes, Ephemeroptera were

collected with forceps from the undersides of submerged rocks along the shoreline in multiple locations across the shoreline from each cardinal direction. In the two reference lakes, Ephemeroptera were also collected with forceps but sites were selected randomly along the shoreline (Johnston et al. 2020). Ephemeroptera samples from all lakes were then pooled and homogenized to create a whole-lake composite sample reflective of the entire lake system (Guzzo et al. 2011; Johnston et al. 2020). In the two reference lakes, Ephemeroptera were also collected with forceps but sites were selected randomly along the shoreline (Johnston et al. 2020). Zooplankton were sampled using multiple vertical hauls being taken with Wisconsin nets (80µm mesh) from 1 m above the bottom at deep points from each cardinal direction for the Sudbury recovery lakes. Hauls were completed from several locations within each of the lake basins until a 1-L homogenized jar sample was filled. Zooplankton communities from the two reference lakes were sampled using vertical hauls with coarser mesh (500µm) Wisconsin nets at the deepest point of the lake (Sandstrom et al. 2013; Johnston et al. 2020). Across all lakes, clams (Unionidae) were collected by searching and dip-netting in the nearshore areas and snorkelling in the deep areas (Johnston et al. 2020). No clams were available as baseline organisms for the recovery lakes. All available baseline organisms from the Sudbury recovery lakes were collected in late-summer 2019, kept on ice, and stored at -20°C until further processing.

2.3 Stable isotope analysis

Prior to the stable isotope analyses, all isotope samples were further processed. Small-bodied fish samples were thawed, measured (TLLEN, weight), and had skinless axial muscle tissue samples removed. Clams were measured for weight and a foot muscle samples was removed (Johnston et

al. 2020). Ephemeroptera and zooplankton whole individuals were retained as stable isotope samples from all lakes and rinsed using carbon-neutral deionized water (Johnston et al. 2020). All isotope samples were then placed in glass scintillation vials and then dried at 0.10 mBar and -45C in a Labconco FreeZone 12 freeze-drier for 7 days (Johnston et al. 2020). Samples were then ground into a fine powder using a Retsch MM 400 ball mill and then analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope composition at the Stable Isotopes in Nature Laboratory (SINLAB) in Fredericton, New Brunswick (Johnston et al. 2020). Samples were analyzed using a Thermo Finnigan Delta Plus Conflo isotope ratio mass spectrometer connected to a Costech 4010-XP elemental analyzer (Jardine et al. 2003; Logan et al. 2008). Stable isotope ratios were reported as isotope delta (δ) in parts per thousand (‰) relative to international standards (atmospheric air for N and Vienna PeeDee Belemnite for C) using the formula:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

where R represents the ratios of heavy to light isotopes ($^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$) in sample and standard materials.

2.4 Data analysis

All data processing, statistical analyses, and figures were completed using R statistical computing software (“R” Version 4.0.0, R Core Team 2020). Initial data manipulation was completed using the ‘dplyr’ package and data visualizations were completed using the ‘ggplot2’ package (Wickham et al. 2016; Wickham et al. 2022).

Stable isotope analyses – All stable isotope data remained unadjusted for body size. Although this may have increased variability in our results, the relationships between stable isotope signatures and body size are known to also vary with fish species and population (Persaud et al. 2012). As well, there was a limited size range for yellow perch across all lakes and for smallmouth bass in the barren lake that would skew isotopic results if scaled to a common FLEN. Lakes with multiple determinants for baseline organism stable isotopes were averaged to give a single C and N value. Baseline organism $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ biplots were visually assessed to determine which organisms or combinations of organisms were best-suited as littoral and pelagic baselines across lakes (Figure S7; Figure S8). Mixed zooplankton and clams were used as a pelagic baseline and Ephemeroptera were used as the littoral baseline organism based on our visual assessments and in accordance with literature (Figure S7; Figure S8; Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 2001; Post 2002; Vuorio et al. 2007). Scatterplots of trophic positioning of common fish species with each individual and mixed baseline organisms were also visually assessed to determine if consumers are utilizing pelagic, littoral, or both food webs (Figure S8; Figure S9). From our visual assessment, it was determined that a two end member mixing model would best estimate the trophic positioning of yellow perch and smallmouth bass across lakes (Figure S7; Figure S8). As such, we utilized Post's (2002) equation for calculating trophic position using two food webs:

$$\text{Trophic position} = \lambda + (\delta^{15}\text{N} - [\delta^{15}\text{N}_{\text{base1}} \times \alpha + \delta^{15}\text{N}_{\text{base2}} \times (1 - \alpha)]) / \Delta_n$$

where α is the proportion of nitrogen derived from the base of food web one.

Mean trophic position with standard deviation was calculated for both yellow perch and smallmouth bass for the three recovery lakes and two reference lakes using base R functions (R Core Team 2020). A two-way ANOVA ‘aov’ with Tukey’s pairwise comparisons were used to determine significant differences in trophic positioning for each species across lakes (R Core Team 2020).

Proportion littoral energy usage was calculated for yellow perch and smallmouth bass following Vander Zanden and Vadeboncoeur’s (2002) mixing model equation:

$$\textit{Proportion littoral contribution} = (\delta^{13}\text{C}_c - \delta^{13}\text{C}_p) / (\delta^{13}\text{C}_l - \delta^{13}\text{C}_p)$$

where $\delta^{13}\text{C}_c$, $\delta^{13}\text{C}_l$, and $\delta^{13}\text{C}_p$ are the mean $\delta^{13}\text{C}$ of the consumer, littoral prey, and pelagic prey, respectively, and no trophic enrichment in $\delta^{13}\text{C}$ is assumed (trophic fractionation = 0‰).

For instances where the consumer $\delta^{13}\text{C}$ values fell outside of 0-1 (0-100%), values were set to either 0 or 1 (Vander Zanden and Vadeboncoeur 2002; Figure S13). This adjustment was needed for 44% of our data from the five lakes. Mean proportion littoral energy usage with standard deviation was calculated using base R functions with an additional two-way ANOVA and Tukey’s pairwise comparisons to determine significant differences in littoral energy use for each species across the five lakes (R Core Team 2020).

Fish condition was calculated for yellow perch and smallmouth bass as the ratio of C:N from the isotope sample. C:N ratio is used as a proxy for lipid content given that lipids are relatively enriched in C compared to proteins which are composed primarily of N (Sweeting et al. 2006;

Dempson et al. 2010). Fish with greater C:N values, and thereby greater lipid content, are said to be in higher condition (Dempson et al. 2010). Mean C:N values with standard deviation were calculated for both common fish species across all five lakes.

Quantitative population metrics of stable isotope data were used to determine dietary niche partitioning via the ‘stable isotope Bayesian ellipses in R’ (SIBER) package (Layman et al. 2007; Jackson et al. 2011). The position, area, range ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), and overlap of dietary niches were calculated using the ‘SIBER’ package for smallmouth bass and yellow perch across the five lakes (Jackson et al. 2011). We utilized Bayesian probabilistic methods with noninformative and Wishart priors to estimate the probabilistic ($\alpha = 95\%$) elliptical niche regions for each species (Jackson et al. 2011). Markov Chain Monte Carlo methods were used to draw 10,000 posteriors that are then used to calculate the aforementioned niche metrics (Rossi, Allenby & McCulloch 2005; Jackson et al. 2011). Maximum likelihood estimated means and covariances of each species were then used to calculate the standard ellipse area corrected for small sample size (SEA_c) and area of niche overlap between the species within each lake (Jackson et al. 2011). Sample size was accounted for in SEA by applying a correction of $(n - 2)$ to estimates of two-dimensional variance and covariance instead of Bessel’s correction $(n - 1)$ (Jackson et al. 2011). Range for each isotope was calculated by subtracting the minimum and maximum $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from each other for each species within each lake. The range in $\delta^{13}\text{C}$ details the extent (littoral – pelagic) of basal resources consumed, whereas the $\delta^{15}\text{N}$ range details the extent of trophic levels occupied by each fish community.

Community structure – CPUE was calculated for all fish species present within each of the three recovery lakes and Sudbury regional lakes. CPUE was calculated by dividing the total number of caught individuals of a given species (catch) by the total number of gill-nets that were set during the survey period (effort). CPUE calculations were also conducted for groupings of fish species based on acid-sensitivity and thermal guild. Fish species were classified in terms of acid-sensitivity into three groups based on the minimum pH threshold required for successful reproduction from the literature: acid-tolerant (pH<4.5), acid-sensitive (pH 4.5-5.5), and highly acid-sensitive (pH>5.5) (Magnuson et al. 1984; Matuszek et al. 1990; Conlon et al. 1992). Classification of fish species based on thermal guild was determined based on Coker et al.'s (2001) classification and final temperature preferendum (FTP) data from the MNRF and Fisheries and Oceans Canada (Hasnain et al. 2010; Minns 2010). Fish species were then assigned one of three groups based on the literature review and data: warm water fish (>25°C), cool water fish (19°C - 25°C), and cold water fish (<19°C). Collectively, the different CPUE measures (catch by species, pH tolerance, temperature preferendum) were used to determine and compare the fish community assemblages with additional context of recovery signals (acid-sensitivity) and theoretical niche overlap (thermal guild) across the region.

Mean FLEN measured in millimetres for yellow perch and smallmouth bass were calculated with standard deviation in the three Sudbury recovery lakes and 20 regional lakes with the given species present. Plots of mean FLEN values were compared by visual assessment to observe any noticeable trends or differences in body size from the three recovery lakes and the regional lakes.

Another metric of fish condition, Fulton's Index (or Fulton's condition factor), was calculated for both common fish species. Fulton's Index employs an allometrically-scaled length-weight relationship of an individual and relates that to overall condition such that values closer to one are better condition and those closer to zero are poorer condition (Fulton 1904; Froese 2006).

The formula for Fulton's index is:

$$K = W/L^3$$

where K is Fulton's index of condition, W is weight of individual in grams, and L is length of individual in centimetres.

Mean Fulton's index with standard deviation were calculated for both common fish species across the three recovery lakes and also compared to the 20 regional lake samples. The Fulton's Index values were visually compared to the C:N condition proxy to examine congruency and relative accuracy of each condition measure.

3 RESULTS

3.1 Smallmouth bass and yellow perch size

Smallmouth bass were found to be smaller in the barren watershed lake (Baby Lake) than any other lake ($n = 16$) with a mean FLEN of 132.50 mm and standard deviation of 19.82 mm (Figure S9). Smallmouth bass in the intact forest lake (Nelson Lake) were discovered to have smaller mean FLEN (177.16 mm \pm 105.86 mm) than both the regional lakes to the northeast (NE BsM lakes) (mean FLEN = 227.22 mm \pm 73.07 mm) and the regional lakes to the southwest (SW BsM lakes) (mean FLEN = 225.91 mm \pm 95.36 mm) lakes (Figure S9). Semi-barren Daisy Lake contained smallmouth bass with the largest mean FLEN (259.07 mm \pm 93.05 mm) of any lake (Figure S9). Conversely, netting surveys revealed that the barren watershed lake had the largest yellow perch of the recovery lakes (mean FLEN = 91.94 mm \pm 17.32 mm; Figure S10). Yellow perch from the intact forest lake had a greater size (mean FLEN = 89.63 mm \pm 29.97 mm) than those from the semi-barren lake (mean FLEN = 74.82 mm \pm 16.91 mm) (Figure S10). Across all recovery lakes ($n = 3$), yellow perch were smaller than in the NE BsM lakes (mean FLEN = 100.57 mm \pm 33.54 mm) and SW BsM lakes (mean FLEN = 104.48 mm \pm 29.70 mm; Figure S10).

3.2 Fish community dynamics

Overall species richness as determined by BsM netting surveys was found to be equal across all three recovery lakes with a total of 7 different species present. Sudbury regional lakes had similar species richness values with the NE BsM averaging 6.22 \pm 2.22 species and SW BsM averaging 8.18 \pm 3.94 fish species. The reference lakes had higher species richness as Richardson Lake contained 11 different species and Tadenac Lake had 15 fish species.

CPUE for smallmouth bass was lowest in the barren lake (CPUE = 0.40) followed by the forested lake (CPUE = 1.79) (Figure S11). The semi-barren lake was determined to have a greater smallmouth bass CPUE (3.16) than SW BsM lakes (mean CPUE = 2.15 ± 1.36) but not NE BsM lakes (mean CPUE = 4.33 ± 3.26 ; Figure S11). On the other hand for yellow perch, the semi-barren lake had the lowest CPUE (11.79), which was still greater than the SW BsM lakes (mean CPUE = 8.89 ± 13.05) but not the forested lake (CPUE = 14.82; Figure S11). The barren lake had the highest yellow perch CPUE (27.55), which was greater than the NE BsM lakes (mean CPUE = 15.62 ± 20.00) and all lakes included in the study (Figure S11).

When fish species were grouped by acid sensitivity, the barren lake was dominated by acid-tolerant ($\text{pH} < 4.5$) species with a CPUE of 27.60, which far exceeds the forested lake (mean CPUE = 14.85), semi-barren lake (mean CPUE = 14.00), and SW BsM lakes (mean CPUE = 12.27 ± 11.16 ; Figure 2). Both the forested and semi-barren lakes had lower abundance of acid-tolerant species than NE BsM lakes (mean CPUE = 16.35 ± 19.96), though were higher than the mean SW BsM CPUE (Figure 2). Prevalence of acid-sensitive fish linearly increased with watershed damage for the three recovery lakes (Figure 2). The barren lake had the lowest CPUE of acid-sensitive fish (2.95), followed by the semi-barren lake (CPUE = 3.47), and the forested lake (CPUE = 6.05; Figure 2). SW BsM lakes had a depressed abundance of acid-sensitive fish (mean CPUE = 2.94 ± 1.68) while NE BsM lakes had an average CPUE (mean CPUE = 5.09 ± 2.91 ; Figure 2). The barren lake was devoid of any highly acid-sensitive fish species (CPUE = 0.00; Figure 2). The forested lake had a relatively reduced abundance of highly acid-sensitive fish (CPUE = 0.10), which was below the mean CPUE for NE and SW BsM lakes (mean CPUE

= 0.59 ± 0.34 and 0.76 ± 0.65 , respectively; Figure 2). The semi-barred watershed lake was determined to have a relatively elevated abundance of highly acid-sensitive fish (CPUE = 0.89; Figure 2).

Based on final temperature preferendum, all lakes were dominated by cool water fish species with varying abundance of warm and cool water fishes (Figure S12). The barren lake was dominated by cool water fishes and devoid of any cold water fish species (CPUE_{warm} = 0.50; CPUE_{cool} = 30.05; CPUE_{cold} = 0.00; Figure S12). The semi-barren lake was similarly dominated by cool water fishes and lacking any cold water fish species, but had a greater abundance of warm water fishes than the barren lake (CPUE_{warm} = 2.00; CPUE_{cool} = 16.37; CPUE_{cold} = 0.00; Figure S12). The forested lake was dominated by cool water fishes but was found to have a greater abundance of cold water fishes (lake trout) than warm water fishes (CPUE_{warm} = 0.026; CPUE_{cool} = 19.77; CPUE_{cold} = 1.20; Figure S12). NE BsM lakes had nearly equal prevalence of warm and cold water fishes (mean CPUE_{warm} = 1.23 ± 1.15 ; mean CPUE_{cool} = 19.79 ± 18.94 ; mean CPUE_{cold} = 1.296 ± 1.00) while SW BsM lakes had greater prevalence of cold than warm water fishes (mean CPUE_{warm} = 0.89 ± 0.57 ; mean CPUE_{cool} = 12.18 ± 11.68 ; mean CPUE_{cold} = 3.22 ± 2.26 ; Figure S12).

3.3 Trophic positioning

Whole-lake mean trophic position (TP) was found to significantly differ across lakes ($F_{4, 356} = 37.95$, $p < 2e^{-16}$) from a two-way ANOVA with Tukey's pairwise comparisons. The barren lake's whole-lake mean TP was significantly lower (mean TP = 2.94 ± 0.51) than all other lakes. The mean TP for Tadenac Lake (reference lake) was the next lowest (mean TP = 3.60 ± 0.42), which

was significantly less than the other reference lake, Richardson Lake, (mean TP = 3.82 ± 0.37) but was not significantly different from the semi-barren (3.64 ± 0.44) or forested lakes (3.64 ± 0.34). The barren lake was found to have significantly reduced TP while the semi-barren and forest lake TPs were similar to the two reference lakes.

Across lakes, the mean TP of smallmouth bass differed significantly ($F_{4,59} = 18.26$, $p = 8.27e^{-10}$; Figure 3). Two-way ANOVA with Tukey's pairwise comparisons revealed that smallmouth bass in the barren were of significantly lower TP (mean TP = 3.16 ± 0.094 , $p < 0.001$) than all other recovery lakes ($n = 3$) and reference lakes ($n = 2$; Figure 3). No significant difference ($p < 0.05$) in smallmouth bass TP was found among any of the other lakes (Figure 3). Generally, smallmouth bass TP was found to increase with decreasing watershed damage across the recovery lakes (Figure 3). The semi-barren lake had the next lowest smallmouth bass TP (mean TP = 3.69 ± 0.15) followed by the reference lakes (Tadenac Lake mean TP = 3.77 ± 0.19 ; Richardson Lake mean TP = 3.81 ± 0.18 ; Figure 3). The forest recovery lake had the highest smallmouth bass TP of all lakes (mean TP = 3.85 ± 0.20 ; Figure 3).

Conversely, a two-way ANOVA found that the mean TP of yellow perch did not differ significantly across lakes ($F_{4,57} = 0.752$, $p = 0.561$; Figure 3). However, the same general trend of increasing TP with decreasing watershed damage among the recovery lakes was observed for yellow perch as well (Figure 3). Yellow perch in the barren lake also had the lowest TP (mean TP = 3.12 ± 0.28), followed by a reference lake (Richardson Lake mean TP = 3.22 ± 0.16 ; Figure 3). The semi-barren lake (3.28 ± 0.49) and other reference lake (Tadenac Lake = 3.28 ± 0.19) were found to have equal yellow perch TP, though TP was more variable in the semi-barren lake

population (Figure 3). Again, the forested recovery lake had the highest TP for yellow perch (mean TP = 3.30 ± 0.30) of all lakes (Figure 3).

3.4 Trophic niche dynamics

Standard Ellipse Area (niche area) corrected for small sample size (SEA_c) was smallest in the barren lake for both smallmouth bass and yellow perch ($SEA_c = 0.70$, $SEA_c = 1.80$, respectively; Table 1). The reference lakes had the next smallest niche area for smallmouth bass (Tadenac Lake $SEA_c = 0.83$; Richardson Lake $SEA_c = 0.84$; Table 1; Figure 4). The semi-barren lake had the second largest niche area for smallmouth bass ($SEA_c = 1.32$), while the forested lake was found to have the largest niche area ($SEA_c = 4.56$; Table 1; Figure 4). For yellow perch, the forested recovery lake had the second smallest niche area ($SEA_c = 1.84$) next to the barren lake (Table 1; Figure 4). The reference lakes had the next largest niche areas for yellow perch (Richardson Lake $SEA_c = 2.29$; Tadenac Lake $SEA_c = 4.04$), though the magnitude of SEA_c difference between reference lakes was considerable (Table 1; Figure 4). Yellow perch in the semi-barren lake were found to have the largest niche area ($SEA_c = 8.35$; Table 1; Figure 4).

The range and mean in $\delta^{13}C$ values were determined for each population of smallmouth bass and yellow perch (Table 1). For smallmouth bass, a reference lake (Tadenac Lake) had the smallest range in $\delta^{13}C$ (range $\delta^{13}C = 1.3$), followed by the barren lake (range $\delta^{13}C = 2.0$), semi-barren lake (range $\delta^{13}C = 2.6$), other reference lake (Richardson Lake; range $\delta^{13}C = 3.7$), then the forested watershed lake (range $\delta^{13}C = 6.8$; Table 1). Smallmouth bass mean $\delta^{13}C$ values with standard deviation were also found to vary among populations with the barren lake being the most depleted in $\delta^{13}C$ ($\delta^{13}C = -28.6 \pm 0.8$), followed by semi-barren lake ($\delta^{13}C = -27.8 \pm 0.8$), a

reference lake (Tadenac Lake; $\delta^{13}\text{C} = -25.7 \pm 0.4$), the forested lake ($\delta^{13}\text{C} = -25.7 \pm 2.1$), and finally the other reference lake (Richardson Lake; $\delta^{13}\text{C} = -25.2 \pm 1.2$) being the least depleted in $\delta^{13}\text{C}$ (Table 1). For yellow perch $\delta^{13}\text{C}$ range, the forested lake was found to be the smallest (range $\delta^{13}\text{C} = 2.5$), followed by a reference lake (Richardson Lake; range $\delta^{13}\text{C} = 5.6$), the barren lake (range $\delta^{13}\text{C} = 5.8$), the other reference lake (Tadenac Lake; range $\delta^{13}\text{C} = 7.9$), and finally the semi-barren lake with the largest range (range $\delta^{13}\text{C} = 8.4$; Table 1). Yellow perch mean $\delta^{13}\text{C}$ values with standard deviation were also calculated for each population. The semi-barren lake yellow perch were found to be the most depleted in $\delta^{13}\text{C}$ (mean $\delta^{13}\text{C} = -30.2 \pm 2.4$), followed by the barren lake (mean $\delta^{13}\text{C} = -29.4 \pm 1.5$), forested lake (mean $\delta^{13}\text{C} = -27.8 \pm 0.9$), and reference lakes (Tadenac Lake mean $\delta^{13}\text{C} = -27.2 \pm 1.9$; Richardson Lake mean $\delta^{13}\text{C} = -24.9 \pm 1.7$; Table 1).

Similarly, the range and mean in $\delta^{15}\text{N}$ values were also calculated for each population of both fish species. For smallmouth bass, the barren lake had the smallest range in $\delta^{15}\text{N}$ (range $\delta^{15}\text{N} = 1.0$), followed by one of the reference lake (Richardson Lake; range $\delta^{15}\text{N} = 1.4$), the semi-barren lake (range $\delta^{15}\text{N} = 2.1$), reference lake (Tadenac Lake; range $\delta^{15}\text{N} = 2.2$), then the forested lake with the largest range (range $\delta^{15}\text{N} = 2.6$; Table 1). Smallmouth bass (SMB) and yellow perch (YP) mean $\delta^{15}\text{N}$ values with standard deviation were also calculated across lakes and similar trends were observed in both species (Table 1). The population with the most depleted mean $\delta^{15}\text{N}$ for both fish species was found to be the forested lake (mean $\delta^{15}\text{N}_{\text{SMB}} = 6.7 \pm 0.8$; mean $\delta^{15}\text{N}_{\text{YP}} = 5.6 \pm 0.8$), followed by the barren lake (mean $\delta^{15}\text{N}_{\text{SMB}} = 7.2 \pm 0.4$; mean $\delta^{15}\text{N}_{\text{YP}} = 6.5 \pm 0.4$), semi-barren lake (mean $\delta^{15}\text{N}_{\text{SMB}} = 7.8 \pm 0.6$; mean $\delta^{15}\text{N}_{\text{YP}} = 6.9 \pm 1.3$), and references

lakes with the least depleted mean $\delta^{15}\text{N}$ for smallmouth bass (Richardson Lake mean $\delta^{15}\text{N}_{\text{SMB}} = 9.4 \pm 0.4$ and mean $\delta^{15}\text{N}_{\text{YP}} = 7.4 \pm 0.4$; Tadenac Lake mean $\delta^{15}\text{N}_{\text{SMB}} = 9.6 \pm 0.6$ and mean $\delta^{15}\text{N}_{\text{YP}} = 7.9 \pm 0.6$; Table 1). For yellow perch $\delta^{15}\text{N}$ range, the barren lake also had the smallest range (range $\delta^{15}\text{N} = 1.2$), followed by a reference lake (Richardson Lake; range $\delta^{15}\text{N} = 1.7$), the forested lake (range $\delta^{15}\text{N} = 2.2$), the other reference lake (Tadenac Lake; range $\delta^{15}\text{N} = 2.2$), and finally the semi-barren lake with the largest range (range $\delta^{15}\text{N} = 4.2$; Table 1).

Proportion of niche overlap between smallmouth bass and yellow perch within each lake was determined using the SIBER package (Jackson et al. 2011; Table 1). The highest proportion of dietary niche area overlap was found in the barren lake populations (proportion overlap = 0.2102), followed by the forested lake with the next highest proportion of overlap (0.1608), semi-barren lake (proportion overlap = 0.1586), and reference lakes which had the least niche overlap between fish populations (Tadenac Lake proportion overlap = 0.0722; Richardson Lake 1.5134 e^{-17} ; Table 1).

3.5 Littoral energy usage

Mean proportion of littoral energy usage was calculated using the methods and adjustment described by Vander Zanden and Vadeboncoeur (2002) and contrasted between populations using two-way ANOVAs with Tukey's pairwise comparison. Smallmouth bass in Tadenac Lake (a reference lake) were found to forage extensively on littoral sources (mean proportion littoral energy usage (adj.) = 1.000 ± 0.00), as all individuals were found to have proportions of littoral energy use greater than 100% prior to adjustment (Figure S13; Figure 5). Forested lake smallmouth bass were the next most reliant on littoral energy sources (mean proportion littoral

energy usage (adj.) = 0.977 ± 0.0531), followed by the other reference lake (Richardson Lake; mean proportion littoral energy usage (adj.) = 0.937 ± 0.0596). Smallmouth bass in the barren (mean proportion littoral energy usage (adj.) = 0.749 ± 0.228) and semi-barren lakes (mean proportion littoral energy usage (adj.) = 0.726 ± 0.110) were determined to be significantly less reliant on littoral energy sources than those in the forested lake ($p_{\text{Baby}} = 0.0001$, $p_{\text{Daisy}} < 0.00001$), and reference lakes (Tadenac Lake $p_{\text{Baby}} = 0.00002$, $p_{\text{Daisy}} < 0.00001$; Richardson Lake $p_{\text{Baby}} = 0.004$, $p_{\text{Daisy}} < 0.00001$; Figure 5). Yellow perch in Richardson Lake were found to forage the most on littoral energy sources (mean proportion littoral energy usage (adj.) = 0.928 ± 0.121) though was not significantly greater ($p > 0.05$) than the yellow perch populations in the forested lake (mean proportion littoral energy usage (adj.) = 0.875 ± 0.110) or Tadenac Lake (mean proportion littoral energy usage (adj.) = 0.679 ± 0.454 ; Figure 5). The barren lake yellow perch had significantly less use of littoral energy sources (mean proportion littoral energy usage (adj.) = 0.582 ± 0.269 ; $p = 0.045$) than one of the reference lakes (Richardson Lake), but not the forested lake or other reference lake (Tadenac Lake; Figure 5). Yellow perch from the semi-barren lake were found to have the lowest mean proportion of littoral energy usage (0.398 ± 0.314) though was not significantly different ($p > 0.05$) from the Tadenac Lake (reference lake) or barren lake populations (Figure 5).

3.6 Fish condition

Fish condition, as assessed by mean C:N ratio, was calculated for each population of smallmouth bass and yellow perch. Smallmouth bass in the barren and semi-barren lakes were found to have significantly higher C:N ratio (C:N = 3.403 ± 0.0472 , $p = 0.0012$; C:N = 3.366 ± 0.114 , $p = 0.00018$, respectively) than a reference lake (Tadenac Lake) population (C:N = 3.213 ± 0.0848),

but not the forested lake (C:N = 3.310 ± 0.0492) or other reference lake (Richardson Lake) populations (C:N = 3.272 ± 0.124 ; Figure S14 (A)). No significant difference ($p > 0.05$) was found between the reference lakes or forested lake populations (Figure S14 (A)). Similar results were found when examining the yellow perch populations of each lake (Figure S14 (A)). Yellow perch in the barren and semi-barren lakes were found to have significantly greater C:N ratio (C:N = 3.322 ± 0.0605 , $p = 0.042$; C:N = 3.342 ± 0.0739 , $p = 0.0064$) than a reference lake (Tadenac Lake) population (C:N = 3.237 ± 0.0661 ; Figure S14 (A)). No significant differences ($p > 0.05$) were found among the barren, semi-barren, or forested lakes (C:N = 3.255 ± 0.122), and the other reference lake (Richardson Lake; C:N = 3.263 ± 0.0668) populations, nor between the reference lakes and forested lake yellow perch populations (Figure S14 (A)).

Mean Fulton's Index (FI) was a metric also used to quantify and compare fish condition.

Richardson Lake (reference lake) was determined to contain the smallmouth bass population with the highest FI (mean FI = 1.850 ± 0.112) that was found to be significantly greater than the semi-barren (mean FI = 1.651 ± 0.124 , $p = 0.011$), barren (mean FI = 1.627 ± 0.121 , $p = 0.040$), forested (mean FI = 1.522 ± 0.182 , $p < 0.0001$), and reference lake (Tadenac Lake; mean FI = 1.490 ± 0.148 , $p < 0.0001$) populations (Figure S14 (B)). Smallmouth bass in the semi-barren lake had a significantly greater ($p = 0.021$) mean FI than those from a reference lake (Tadenac Lake), while no significant differences ($p > 0.05$) were found between barren, forested, or reference lake (Tadenac Lake) populations (Figure S14 (B)). In terms of yellow perch population comparisons, the population from the barren lake had a significantly greater mean FI (mean FI = 1.318 ± 0.115) than the reference lake (mean FI = 1.128 ± 0.148 , $p = 0.0054$) and forested Lake (mean FI = 1.026 ± 0.167 , $p = 0.00026$) populations, but not the semi-barren lake (mean FI =

1.180 ± 0.119, $p = 0.102$) population (Figure S14 (B)). No significant difference ($p > 0.05$) in mean FI was found between the semi-barren, forested, and reference lake (Tadenac Lake), yellow perch populations. Mean FI was not calculated for one of the reference lake's (Richardson Lake) yellow perch population as size data was not captured during sampling.

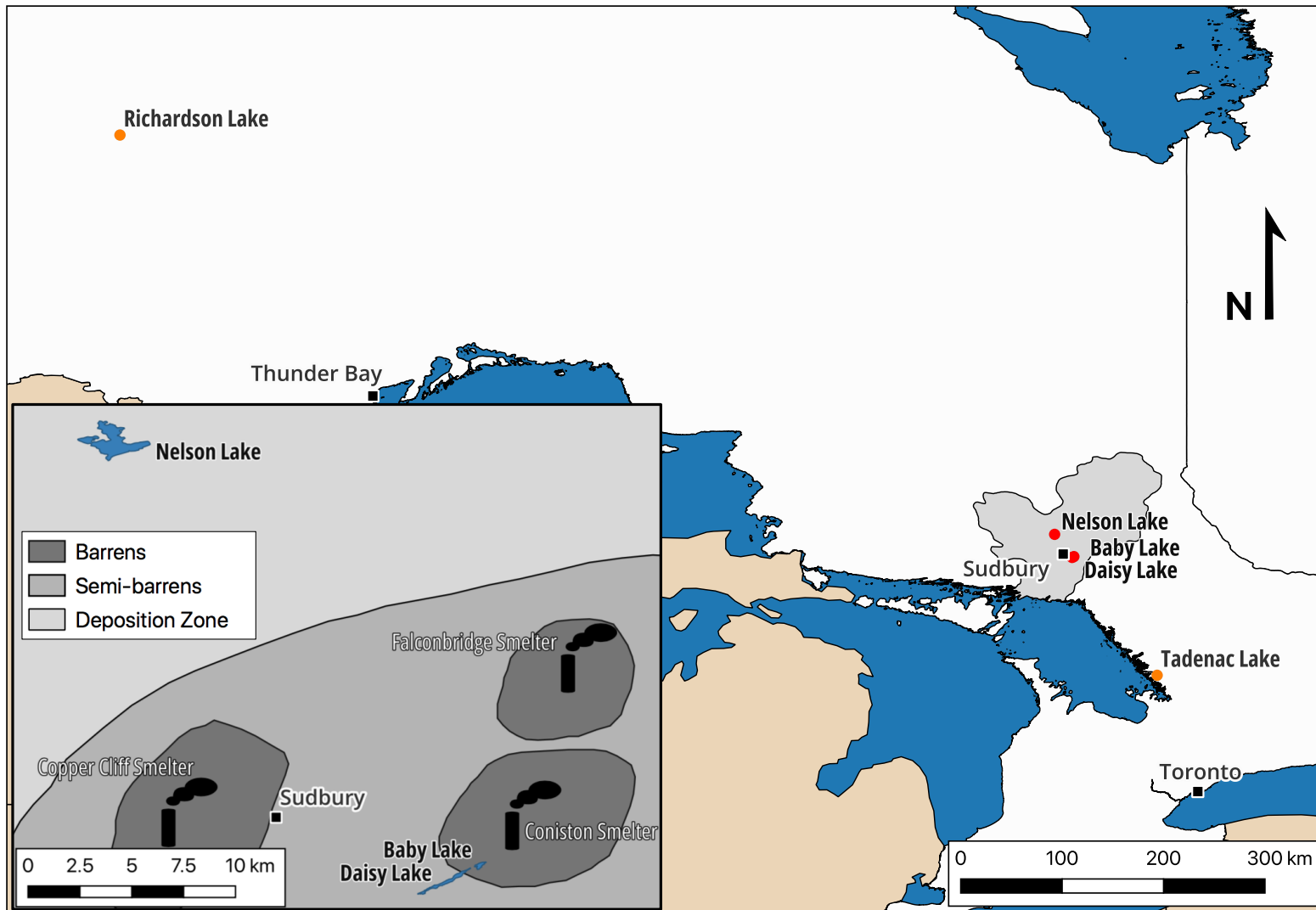


Figure 1 Spatial distribution of recovery lakes and reference lakes across Ontario. Recovery lakes are denoted by red circles and reference lakes are denoted by orange symbols. Map generated using QGIS 3.28.2 with data sourced from Land Information Ontario database and QGIS.

Table 1 Niche area (SEA_c) and proportion of niche overlap (95% CI) for two common fish species, smallmouth bass and yellow perch, across lakes. SEA_c and niche overlap were calculated using SIBER package maximum likelihood methods (Jackson et al. 2011).

Lake group	Lake	Species	n	SEA_c	Mean $\delta^{13}C \pm sd$	Range $\delta^{13}C$	Mean $\delta^{15}N \pm sd$	Range $\delta^{15}N$	Proportion overlap (95%)
Recovery	Baby Lake (barren watershed)	Smallmouth bass	6	0.70	-28.6 ± 0.8	2.0	7.2 ± 0.4	1.0	0.2102
		Yellow perch	11	1.80	-29.4 ± 1.5	5.8	6.5 ± 0.4	1.2	
	Daisy Lake (semi-barren watershed)	Smallmouth bass	21	1.32	-27.8 ± 0.8	2.6	7.8 ± 0.6	2.1	0.1586
		Yellow perch	11	8.35	-30.2 ± 2.4	8.4	6.9 ± 1.3	4.2	
	Nelson Lake (intact forested watershed)	Smallmouth bass	13	4.56	-25.7 ± 2.1	6.8	6.7 ± 0.8	2.6	0.1608
		Yellow perch	8	1.84	-27.8 ± 0.9	2.5	5.6 ± 0.8	2.2	
Reference	Richardson Lake	Smallmouth bass	10	0.84	-25.2 ± 1.2	3.7	9.4 ± 0.4	1.4	$1.5134e^{-17}$
		Yellow perch	15	2.29	-24.9 ± 1.7	5.6	7.4 ± 0.4	1.7	
	Tadenac Lake	Smallmouth bass	14	0.83	-25.7 ± 0.4	1.3	9.6 ± 0.6	2.2	0.0722
		Yellow perch	17	4.04	-27.2 ± 1.9	7.9	7.9 ± 0.6	2.2	

* SEA_c = standard ellipse area corrected for small sample size with $p = 0.95$ ellipses.

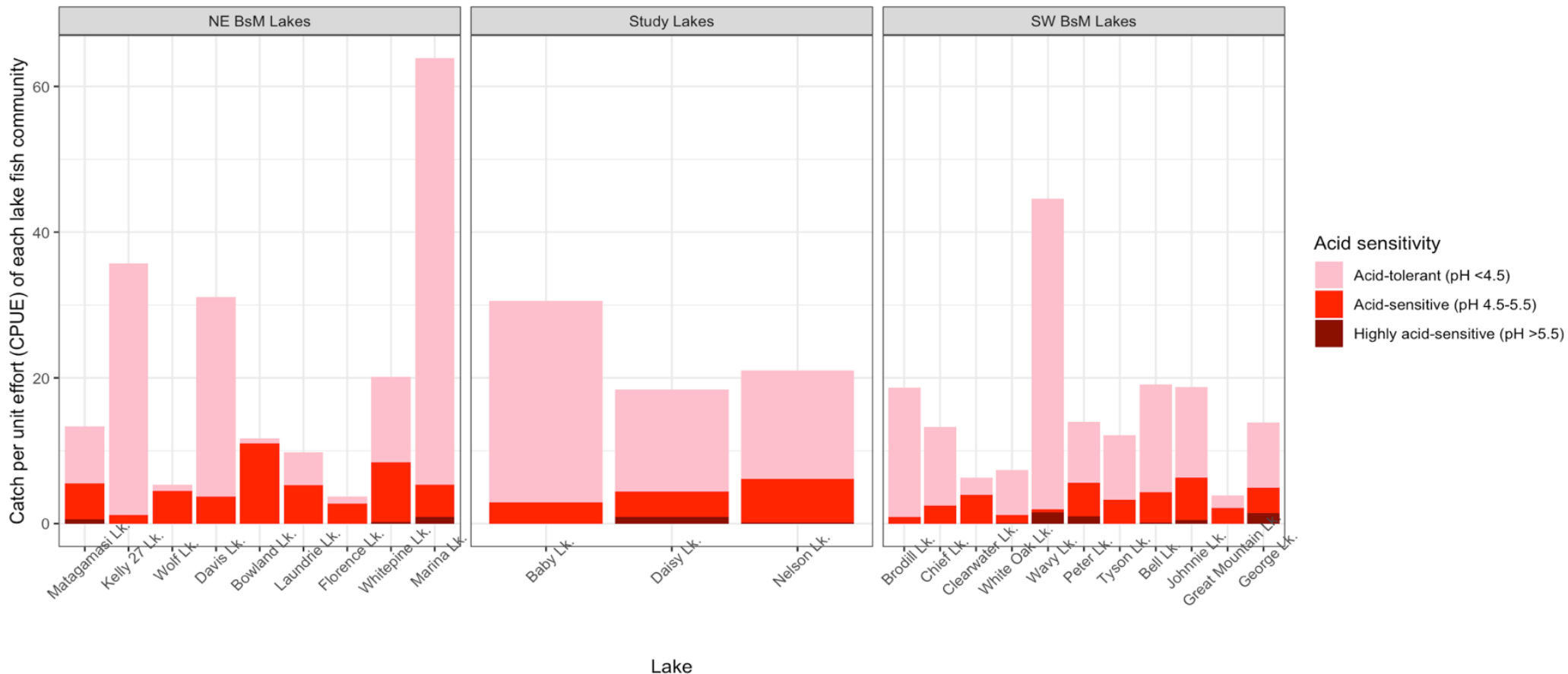


Figure 2 Catch per unit effort (CPUE) of Sudbury region lakes by fish species sensitivity to lake acidity. Acid sensitivity was determined based on minimum pH threshold for successful reproduction (Magnuson et al. 1984; Matuszek et al. 1990; Conlon et al. 1992). Acid sensitivity is denoted by shading of colour; Acid-tolerant (pH<4.5) fish species (light red), acid-sensitive (pH 4.5-5.5) fish species (red), and highly acid-sensitive (pH>5.5) fish species (dark red). Lakes within each lake category are ordered by increasing distance from Coniston nickel smelters.

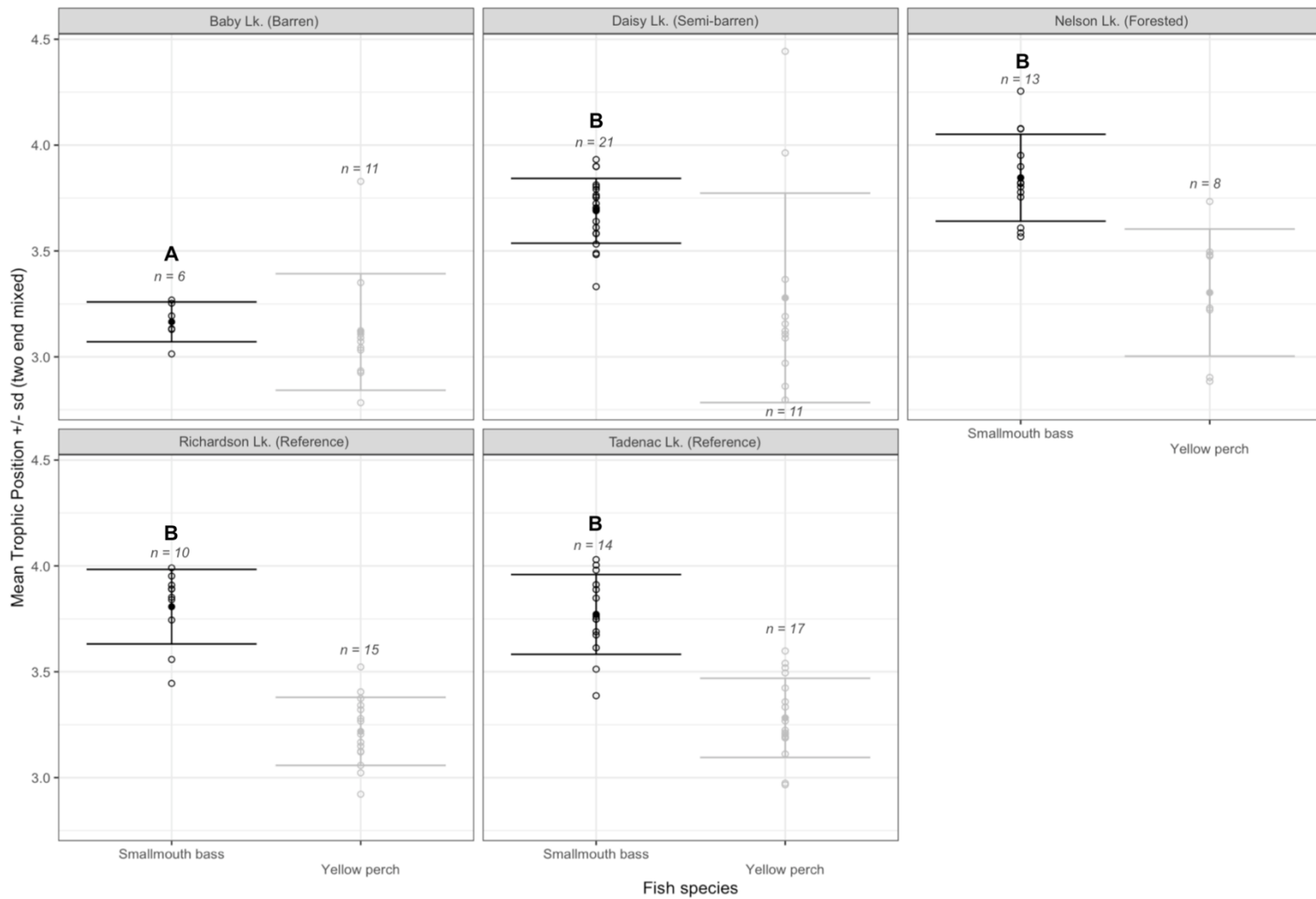


Figure 3 Mean trophic position (\pm standard deviation) for smallmouth bass and yellow perch across lakes calculated using a two end member mixing model. Fish species are distinguished by shading of colour. Significant differences ($p < 0.05$) across smallmouth bass populations are denoted by different letters.

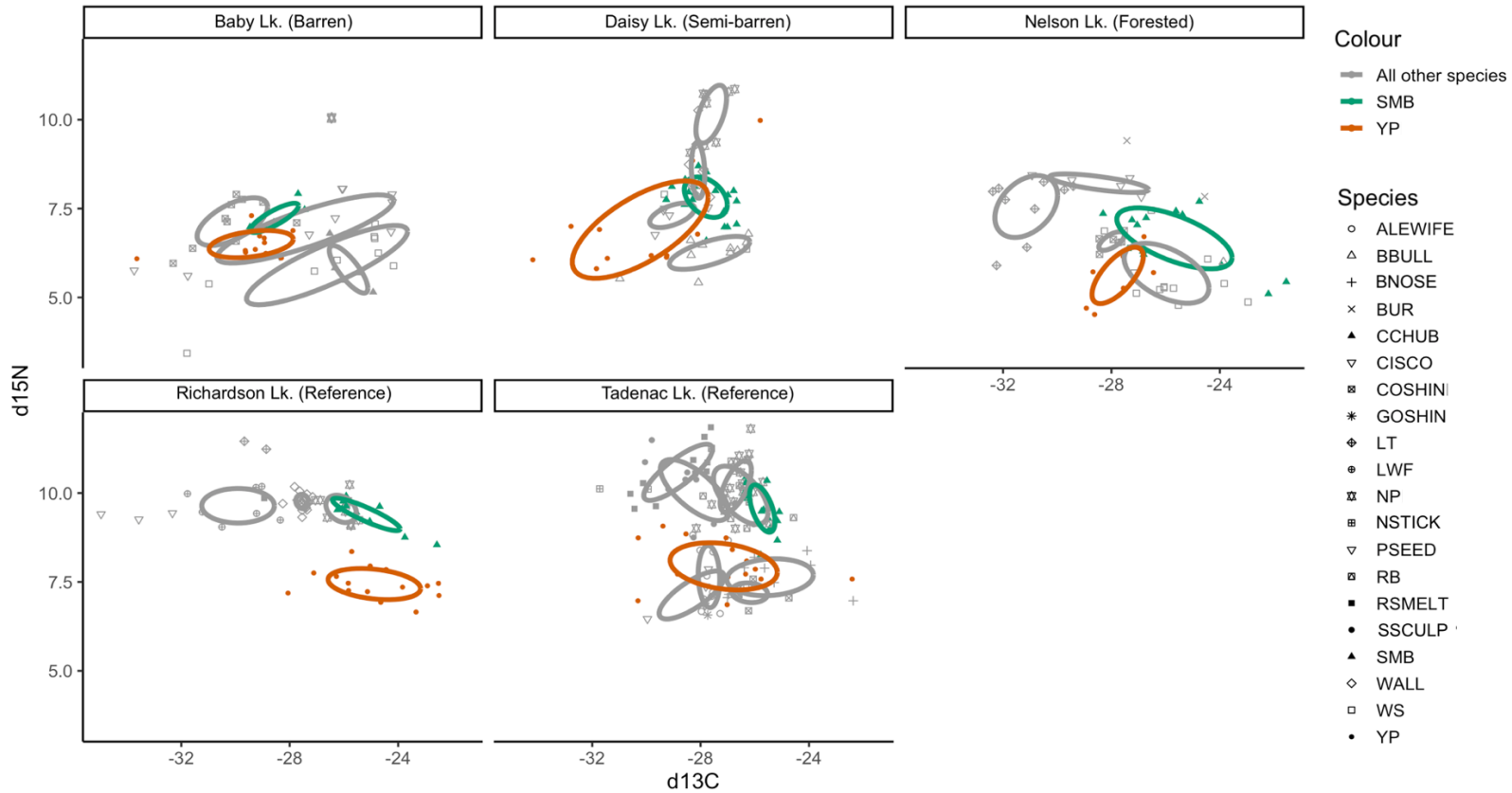


Figure 4 Standard Ellipse Areas and raw values for each fish species within each lake. Ellipses for focal species (smallmouth bass [SMB] and yellow perch [YP]) are highlighted by colour. Ellipses were not plotted for species with only one isotope sample. Fish species are distinguished by symbol. Sample sizes for consumer isotope values within each lake are reported in each panel.

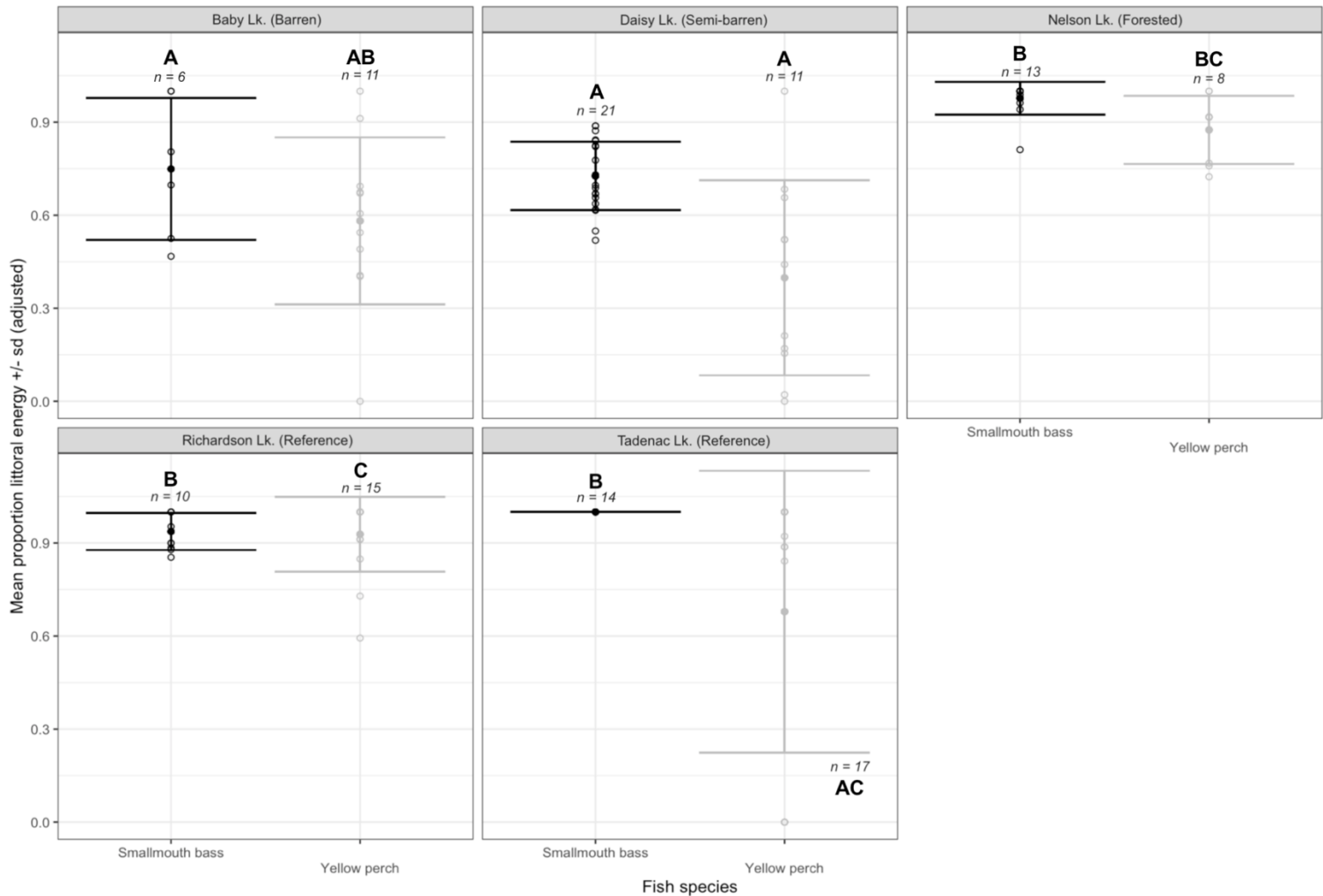


Figure 5 Mean proportion of littoral energy usage (\pm standard deviation) for smallmouth bass and yellow perch across lakes. Fish species are distinguished by shading of colour. Proportion of littoral energy usage was calculated and adjusted using the methods of Vander Zanden and Vadeboncoeur (2002). Significant differences ($p < 0.05$) across populations of each species are denoted by different letters as determined by Tukey's pairwise comparisons.

4 DISCUSSION

4.1 Stable isotope analyses as recovery indicators

Trophic positioning – Compared to all other recovery lakes, the barren watershed lake (Baby Lake) exhibited a significantly reduced whole-lake and smallmouth bass mean TP and though not significantly different, yellow perch TP was lowest in the barren lake as well (Figure 3). Collectively, this demonstrates the barren lake having an energetically compressed and truncated food web (McCann et al. 2005). This is not the case for the semi-barren watershed (Daisy Lake) or intact forested watershed (Nelson Lake) lakes, where the smallmouth bass, yellow perch, and whole-lake mean TP is comparable to the distant reference lakes. Common fish species and whole-lake mean TP was observed to linearly increase with decreasing watershed smelter-damage across these recovery lakes (Figure 3). Inherent variability is introduced in stable isotope analyses of these recovery lakes as a result of considerable habitat variability at the within-lake scale with certain sites lagging in recovery of suitable benthic invertebrate habitat, a key food resource to smallmouth bass and yellow perch (Guzzo et al. 2011). While within-lake variability in baseline stable isotope signatures was accounted for by pooling baseline samples from multiple sites, there is potential for this variability to be present among mobile predators like yellow perch. This may provide explanation as to why significant differences in TP were present in smallmouth bass and not yellow perch across recovery lakes. The comparability of the semi-barren and forested lakes to the reference lakes signals trophic recovery has occurred in these lakes while recovery in the barren lake remains ongoing. Quantifiable and comparable differences in TP at the whole-lake and species scales suggests that TP could be used as a metric to assess lake health across the landscape.

Niche area and overlap – The barren lake was determined to have the smallest niche areas (SEA_c) for both common species and the greatest proportion of niche overlap of any lake, providing further evidence of food web truncation in this smelter-damaged lake (Table 1; Figure 4). SEA_c is directly linked to the ranges of $\delta^{13}C$ and $\delta^{15}N$ of each species as determined through maximum likelihood analyses (Jackson et al. 2011). The reduced SEA_c of smallmouth bass and yellow perch in the barren lake represents the simplicity of the food web thereby restricting $\delta^{15}N$ range via energy transfer and the lack of diverse (pelagic and benthic) prey sources linked to $\delta^{13}C$ range (McCann et al. 2005; Sherwood et al. 2002). Additionally, Baby Lake fish populations face the issue of high degrees of niche overlap, a measure of interspecific competition (Table 3). This supports the notion that the fish community in the barren lake is experiencing energetic compression and signifies the lake being at an earlier stage in recovery compared to the semi-barren and forested watershed lakes. It should be noted, however, that all three recovery lakes have considerably more niche overlap than the two reference lakes (Table 1; Figure 4). This suggests that though recovery processes are well-underway with the semi-barren and forested lakes, the end-point of recovery has not yet been met. As well, SEA_c and proportion of niche overlap could potentially be used as yet another quantitative metric of recovery status for industrially-damaged lake systems and highlight those systems which may benefit from restoration treatment. Both metrics appear to be more sensitive to interspecific community-level dynamics and underscore the diversity of energy sources, or lack thereof, within recovering lakes than considering TP alone.

Stable isotope analyses – SI metrics, namely TP, SEA_c , and proportion of niche overlap, when combined with summary statistics of isotopes by species, create a powerful toolset for

quantitatively evaluating lake health (Gray et al. 2014). These metrics provide insight into functional community interactions beyond those determined solely via community ecology metrics, such as species richness and diversity indices, as SI metrics consider energy sources and pathways, which affect community structure, ecosystem processes, and lake productivity (Gray et al. 2014).

4.2 Community structure and size classes

The fish community in the barren lake was found to be heavily-dominated by the acid-tolerant yellow perch compared to the other recovery and regional lakes (Figure S11). Yellow perch in the barren lake had an even stronger hold on the fish community until recently when smallmouth bass recolonized the lake (Corston et al. 2014a). Similar to other lakes in the Sudbury region, such as the semi-barren Daisy Lake, the re-establishment of predator fish populations has resulted in a dramatic decline in the proportion of yellow perch present in the barren lake (Lippert et al. 2007; Corston et al. 2014b; Figure S11). Given that the tolerant and hardy yellow perch is often the first to colonize these smelter-damaged lake systems before tapering off as recovery progresses, there is potential to use the proportion of yellow perch catch as a recovery metric (Keller 2009). Consideration should be taken to address potential underlying factors that may contribute to prolonged simple or perch-dominated assemblages, such as dispersal limitation of predatory fish species and degree of hydrologic connectedness. CPUE results should generally be used with caution as high variability and limited sample sizes restrict the ability to analyze statistically significant differences in relative abundance (Maunder et al. 2006; Carruthers et al. 2012; Maunder and Piner 2015). Here general trends in proportion of yellow perch in each population are observed from CPUE catch data to aid in the interpretation of trophic niche

metrics, like SEA_c and proportion of overlap. The trophic niche approach is a stronger means of assessing fish community structure in recovering lakes than CPUE which lacks statistical and interpretive power without supplementary costly data of individual weight and growth rates (Maunder et al. 2006; Maunder and Piner 2015).

Smallmouth bass in the barren Baby Lake had much smaller mean FLEN than all other lakes in Sudbury (Figure S9). Smallmouth bass size may be truncated in the barren lake due to their recent colonization of the system, meaning the captured bass were quite immature in their growth. Analyses of the aging structures sampled from captured individuals would provide insight but were not undertaken for this study. If not due to age, smallmouth bass may experience body truncation because growth is suppressed due to limited food availability and acidity and heavy metal stress, shifting the size structure to be smaller in the barren lake (Figure S8; Figure S9).

Baby Lake yellow perch population did not exhibit body truncation to the same degree as with smallmouth bass (Figure S11). Yellow perch in the barren lake had the largest mean FLEN of all recovery and reference lakes ($n=5$), though was reduced compared to the NE and SW BsM lake means (Figure S11). Differential size class truncation between smallmouth bass and yellow perch populations are likely due to age differences but may include physiological differences that allow yellow perch to be more acid-tolerant and therefore reach greater sizes in stressed systems (Magnuson et al. 1984; Schindler et al. 1985; Matuszek et al. 1990; Conlon et al. 1992). Given the increased predation pressure from the newly invaded smallmouth bass and northern pike, yellow perch may be experiencing selection towards morphometric forms with deeper bodies as

a response (Lippert et al. 2007). Body morphometrics were not examined in this study but should be considered in future fish inventories as a proxy of predation pressure and trophic interaction strength. Additional netting surveys would be able to parse the effects of cohort cycling in yellow perch on mean body size, as observed in Scandinavian lakes (Ohlberger et al. 2013).

Regional trends of larger perch (mean FLEN) in lakes either dominated by perch or with less diverse fish community assemblages were also observed (Figure S10; Figure S11). This trend, while congruent among recovery lakes (n=3), does not hold true for the barren lake when considered on the regional scale (Figure S11). Barren lake yellow perch may have smaller mean FLEN compared to the regional means due to energetic bottlenecks from low productivity within the lake (Figure S11; Figure S15; Sherwood et al. 2002). Energetic costs of foraging on smaller prey sources such as zooplankton and small benthic invertebrates (i.e. chironomids) are high and this lack of diverse prey sources in the barren lake may be causing a growth bottleneck within the perch population (Sherwood et al. 2002). Availability of different sized prey is critical as perch grow to facilitate natural switches between prey sources with size as more energy is spent on foraging to sustain basal metabolic requirements (Sherwood et al. 2002). Repressed TP and lower reliance on littoral food sources by the barren lake yellow perch population indicate that a significant component of their diet is comprised by zooplankton and other low-level pelagic organisms (Figure 3; Figure 5).

4.3 Evidence of trophic niche compression

Consistently reduced TP at the species and whole-lake scales in the barren lake (Baby Lake) compared to all other lakes points to trophic niche compression (Figure 4). To some degree

reduced TP in Baby Lake may be due to smaller lake size (11.9 ha); however, Daisy Lake (semi-barren lake) is not considerably larger (36.1 ha) and lake size was accounted for in the study design by only including relatively smaller lakes < 310 ha (Post et al. 2002). It is possible that the realized size, that is the suitable habitat to occupy, within the barren lake is further reduced from its entire 11.9 ha due to lack of refuges, its relatively small watershed with minimal delta 'hotspots', and basin homogeneity. All of these components greatly restrict the buffering capacity of behaviourally-mitigated (i.e. usage of refugia) TP reductions in fish (McCann et al. 2005).

Resource scarcity, a symptom of reduced lake productivity, results in energetic constraints in food webs and inefficient transfers of the available energy (Sherwood et al. 2002; McCann et al. 2005). While the barren lake has a relatively high density of small (FLEN and RWT) yellow perch, relative densities of smallmouth bass (also small) and northern pike are low (Figure S11). Coupled with reduced benthic invertebrate and cyprinid abundance and diversity, it becomes evident that the barren lake suffers from low productivity (Figure S11; Figure S15; Corston et al. 2004a; Wesolek et al. 2010). This has manifested in a myriad of whole-lake reduced TP, constricted niche areas (SEA_c), and high proportion of niche overlap among fish species (Table 1; Figure 3). Interestingly, with the exception of yellow perch SEA_c in the semi-barren lake, each of these metrics appear to increase with decreasing degree of smelter damage (Table 1; Figure 3). The degree of separation in TP between yellow perch and smallmouth bass within each lake also increases with increasing distance from smelter (Figure 3). Increased proportion of niche overlap as a result of smelter-damage, resource scarcity, and habitat homogeneity, leads to food web compression as demonstrated in the case of the barren lake (McCann et al. 2005; Burdon et al.

2019). Future studies should expand to include additional lakes along the smelter depositional gradient to determine if trends in TP, niche overlap, and SEA_c hold true.

4.4 Prevalence of omnivory and food web implications

In spatially compressed food webs, such as the barren Baby Lake, relative reductions in TP may also reflect omnivorous feeding strategies among species (McCann et al. 2005). Omnivory is likely occurring in the barren lake as supported by highly variable proportions of littoral energy usage in both yellow perch and smallmouth bass (Figure 5). Stomach content analyses were not undertaken on either species in the barren lake as the minimum threshold for size was not met by any individual under the sampling protocol (Sandstrom et al. 2013). It is unlikely that smallmouth bass or yellow perch would be able to sustain their population size and basal metabolic requirements in the absence of omnivorous feeding strategies due to the low productivity of the barren lake, as supported by previous fishery inventories and benthic invertebrate studies (Figure S15; Wesolek et al. 2010; Corston et al. 2014a).

Omnivory can impose a stabilizing effect on food webs by coupling benthic and pelagic zones and reducing dependence and pressure on specific species or trophic levels (McCann et al. 2005; Gellner and McCann 2012). Although the degree of omnivory required to elicit any meaningful stabilizing effect increases with increasing niche overlap among species (McCann et al. 2005; Gellner and McCann 2012). For a food web such as that of the barren lake, a greater degree of omnivory is required among consumers given the larger niche overlap between yellow perch and smallmouth bass compared to other lakes (Table 1; McCann et al. 2005). Achieving a meaningful level of omnivory among consumers in the barren lake may prove difficult given the

lack of diverse prey base in both the littoral and pelagic lake zones. This may spell bad news for the barren Baby Lake food web when considering the introduction and future establishment of a new top predator, northern pike, as high-level consumers tend to drive stronger top-down control and trophic cascades in compressed food webs (McCann et al. 2005). Without significant prey refugia, the establishment of northern pike minus appropriate stability afforded by omnivory may have strong de-stabilizing effects on this stressed food web (McCann et al. 2005; Gellner and McCann 2012). Food web stability and adaptiveness to change is ever important in light of global trends of increasing warming and introduction of invasive species.

Generalism in yellow perch from the semi-barren Daisy Lake is reflected by a considerably larger SEAc, TP variability, and variability in littoral energy usage (Table 1; Figure 4; Figure 5). The benefits of a large and diverse littoral zone with significant refugia from predator species and an abundant diverse prey base of forage fish and benthic invertebrates contribute to the high-degree of omnivory exhibited by these fish (Wesolek et al. 2010; Corston et al. 2014b). Meaningful degrees of omnivory among yellow perch creates many weak interactions that builds resiliency into the semi-barren lake food web.

4.5 Biological resistance and other factors

Historical severe smelter damage is known to continue influencing community structure even after chemical recovery through a process deemed biological resistance (Keller and Yan 1998; Keller 2009). This has been observed in recovering lakes as unusually simple aquatic food webs dominated by acid-tolerant yellow perch, which is most prominent in the barren lake (Figure S12; Keller 2009). The persistence of yellow perch may now be inhibiting the colonization and

establishment of other communities across trophic levels directly or indirectly by consumption and competition for resources or habitat (Elton 1958; Keller 2009). Biological resistance contributes to the ‘lag’ seen between chemical and biological recovery and may even transcend lake systems by limiting dispersal (Keller & Yan 1998; Layer et al. 2011). It is possible that biological resistance by yellow perch is responsible for greatly restricting the successful establishment of northern pike (first detected in 2006) and smallmouth bass (first observed in 2018) in barren Baby Lake. Yellow perch may likewise be inhibiting the recovery of benthic invertebrate and zooplankton communities via consumption or perhaps there are resistant species within their respective communities out-competing species of their guild. The effects of biological resistance in smelter-damaged lake systems remain poorly understood and difficult to quantify; however, further incorporating trophic interactions into biological studies in the Sudbury region may advance our understanding of the impacts.

4.6 Conclusion

Rebuilding a healthy lake system from a barren landscape is a significant and decades-long undertaking. From achieving chemical recovery to permit initial recolonization and the succession of community assemblages that follow or cannot overcome biological resistance, recovery is an ongoing process, often without a clear endpoint. In the Sudbury region, some lakes have undergone significant recovery to the point where sensitive top predators and bioindicators like lake trout and amphipods have re-established, while other lakes have achieved new community assemblages or have lingering residual effects of smelter-damage (Figure S15; Keller et al. 2019; Louste-Fillion 2022). The suite of quantitative biological metrics available to measure and understand these recovering systems is ever-growing.

In this study, the usage of SIA to analyze interactions between species and communities and relative usage of energetic pathways was explored. Trophic positioning of both fish species, smallmouth bass and yellow perch, were found to increase with decreasing watershed damage among the recovery lakes. The barren watershed lake (Baby Lake) demonstrated considerable niche compression with the lowest trophic positioning, smallest body size and niche area, and greatest niche overlap among fish species. The semi-barren (Daisy Lake) and forested watershed (Nelson Lake) lakes exhibited trophic dynamics more similar to reference lakes than the barren watershed lake, signifying significant trophic recovery. Elevated niche overlap in the semi-barren and forested watershed lakes relative to the reference lakes revealed greater resource competition among consumers and that additional recovery in these lakes is ongoing. Including stable isotopes in recovering lake studies provides ecosystem insights overlooked by traditional biomonitoring approaches that are critical in understanding freshwater food web responses.

Future studies should encompass a greater number of regional lakes across various sizes for SIA to determine how results scale across the landscape and in larger lake settings. Though there is considerable regional spread across the smelter-deposition zone among the recovery lakes, these findings are limited to one lake representing each category of watershed damage (barren, semi-barren, intact forest) and additional lakes with similar food web structure from each category should be included to corroborate results.

In conjunction with traditional community ecology metrics, SIA metrics can be utilized to 1) highlight lakes that may benefit from restoration treatment, 2) facilitate the development of

targeted restoration efforts to accelerate recovery using methods that will translate into lake health, 3) evaluate the success of conservation actions and restoration treatments, and 4) act as an early indicator of ecosystem health (i.e. food web stability) in long-term monitoring studies for preventative conservation management. Restoring industrially-impacted lakes, such as those in the Sudbury region, will help relieve the mounting pressure on current lake productivity and fisheries. Recovering lake systems provides increasing resiliency to our threatened freshwater resources against pressures like climate change, invasive species, and shoreline development, while helping to achieve federal and global biodiversity targets.

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APPENDICES

Appendix 1: *Historic and current water chemistry parameters, watershed condition, and current fish assemblages across study lakes.*

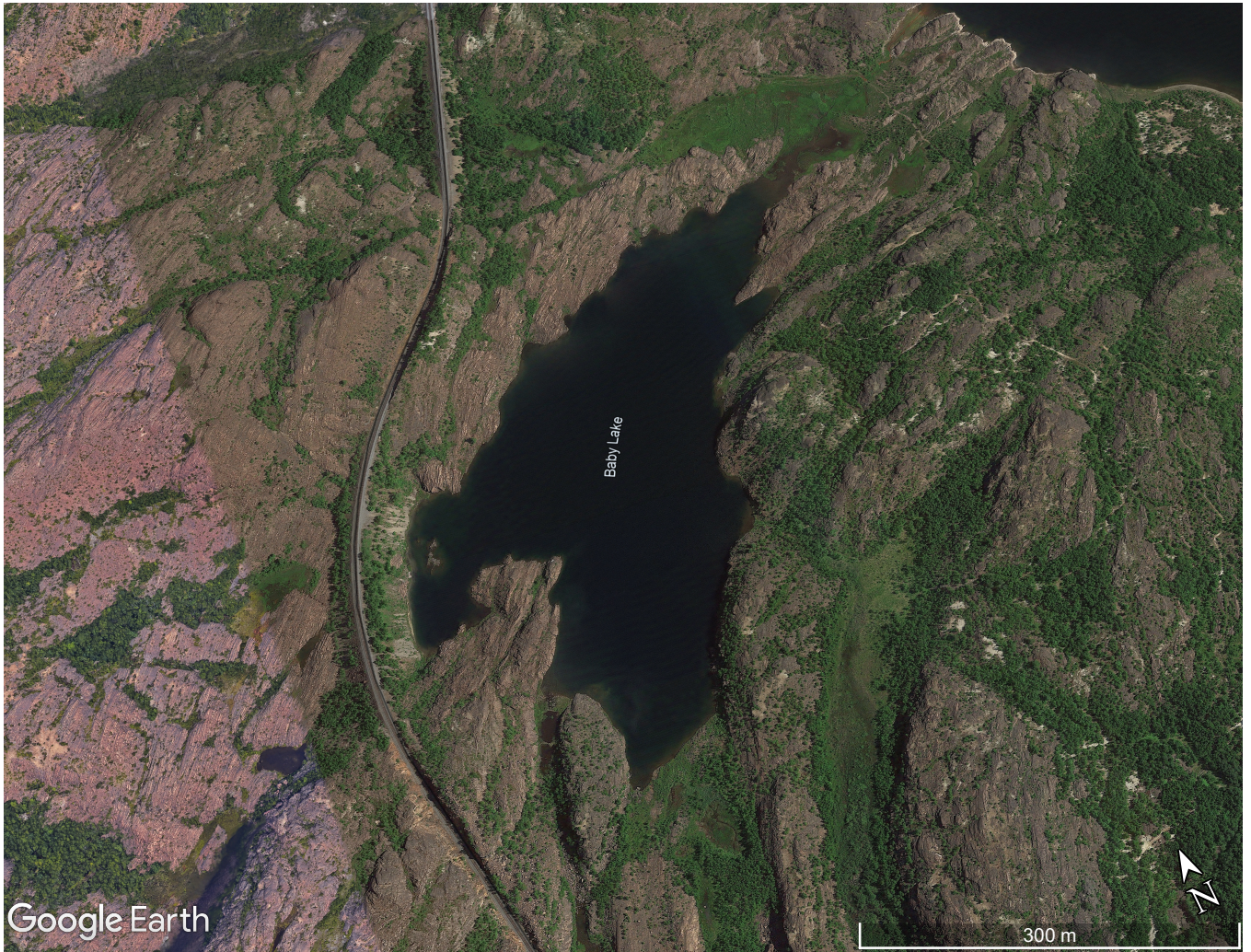
S1. Sudbury recovery lakes and distant reference lakes smelter-impact level, restoration treatment details, and historic (prior to improving trends) and current water chemistry parameters. Historic water chemistry values retrieved from: MOE 1982, Dixit et al. 1996, Keller et al. 2004, Corston et al. 2014a, and Corston et al. 2014b.

Lake	Smelter impact to watershed	Restoration treatment		pH	Conductivity (µS/cm)	Copper (µg/L)	Nickel (µg/L)	Current fish species present	Stable isotope sampling date
Baby Lake	Barren	No treatment	<i>Historic</i>	4.05	140	780	3200	YP, COSHIN, WS,	July 2019
			<i>Current</i>	6.7	39.77	9.1	56	PSEED, SMB, CCHUB, NP	
Daisy Lake	Semi-barren	Intensive catchment reclamation (1991)	<i>Historic</i>	4.5	55*	87*	370*	YP, SMB, BBULL,	July 2019
			<i>Current</i>	6.54	35.7	8.2	36.4	WALL, NP, PSEED, WS	
Nelson Lake	Intact forest	Lake liming (1975/76). Treatment was determined to have negligible effects (Gunn et al. 1988)	<i>Historic</i>	5.7	46	22	17	YP, WS, SMB, LT,	August 2019
			<i>Current</i>	6.56	22.7	2.3	3.6	COSHIN, BUR, BBULL	
Tadenac Lake	No smelter impact	No treatment	<i>Current</i>	6.7	21.2	0.5	0.3	SMB, YP, LGAR, ALE, LT, RSMELT, NP, GOSHIN, COSHIN, BNOSE, NSTICK, RB, PSEED, SMB, LMB, SSCULP	June 2012
Richardson Lake	No smelter impact	No treatment	<i>Current</i>	7.45	72.4	N/A	N/A	SMB, YP, WALL, NP, LT, RSMELT, LWF, CIS	July 2009

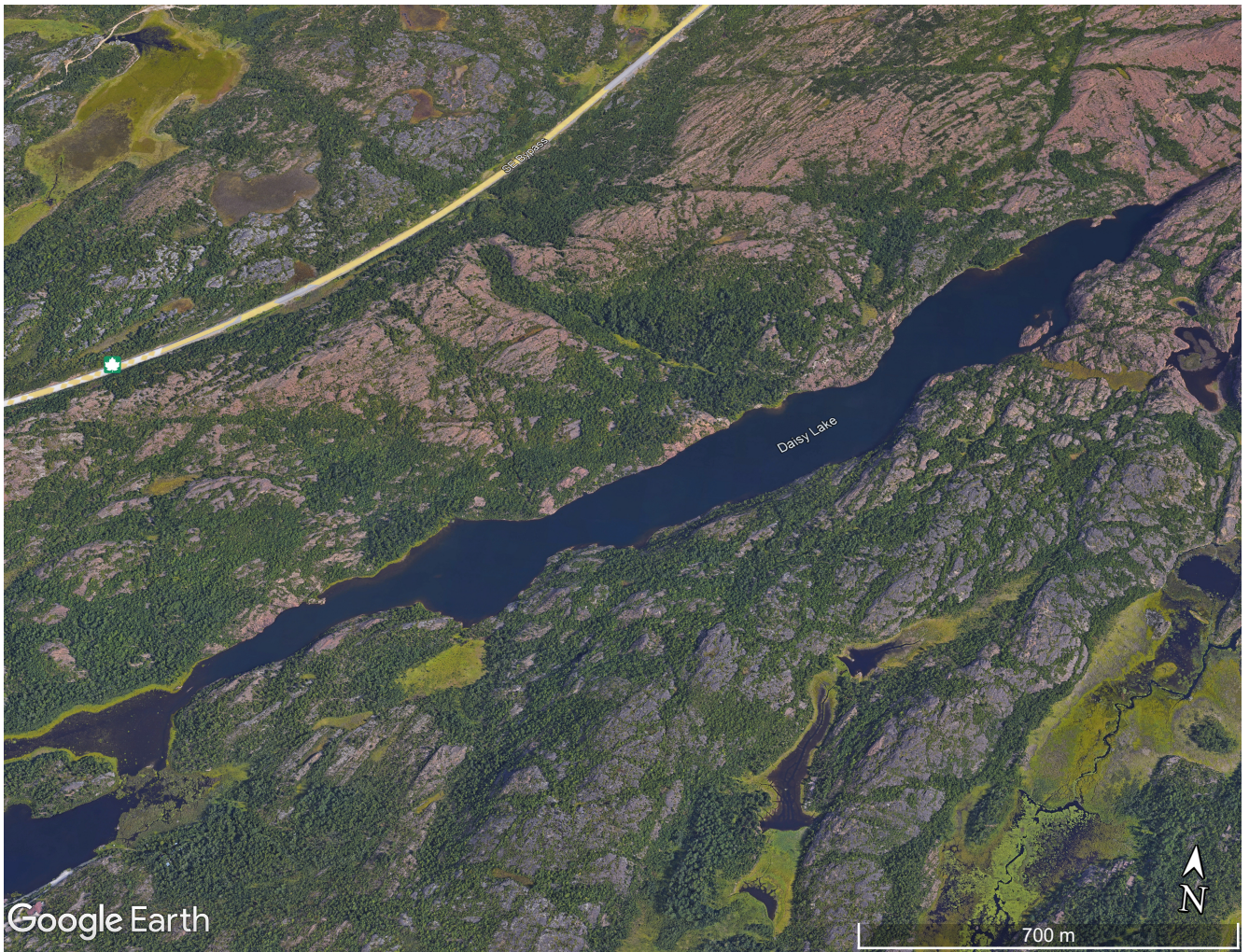
**Historic water chemistry parameters measured significantly later for Daisy Lake (1990) than Baby and Nelson (1972 and 1975). Inferred Ni concentrations from sediment cores shows historic concentrations peaked at nearly 500 µg/L (Dixit et al. 1996).*

S2. List of fish species abbreviations with scientific and common names.

Abbreviation	Scientific name	Species common name
ALE	<i>Alosa pseudoharengus</i>	Alewife
AT	<i>Salvelinus fontinalis timigamiensis</i>	Aurora trout
BBULL	<i>Ameiurus nebulosus</i>	Brown bullhead
BNOSE	<i>Pimephales notatus</i>	Bluntnose minnow
BT	<i>Salvelinus fontinalis</i>	Brook trout
BUR	<i>Lota lota</i>	Burbot
CCHUB	<i>Semotilus atromaculatus</i>	Creek chub
CIS	<i>Coregonus artedi</i>	Cisco
COSHIN	<i>Luxilus cornutus</i>	Common shiner
EBD	<i>Rhinichthys atratulus</i>	Eastern blacknose dace
GOSHIN	<i>Notemigonus crysoleucas</i>	Golden shiner
IODA	<i>Etheostoma exile</i>	Iowa darter
LGAR	<i>Lepisosteus osseus</i>	Longnose gar
LMB	<i>Micropterus salmoides</i>	Largemouth bass
LPERCH	<i>Percina caprodes</i>	Logperch
LT	<i>Salvelinus namaycush</i>	Lake trout
LWF	<i>Coregonus clupeaformis</i>	Lake whitefish
NP	<i>Esox lucius</i>	Northern pike
NRD	<i>Chrosomus eos</i>	Northern redbelly dace
NSTICK	<i>Pungitius pungitius</i>	Ninespine stickleback
PDACE	<i>Margariscus nachtriebi</i>	Pearl dace
PSEED	<i>Lepomis gibbosus</i>	Pumpkinseed
RB	<i>Ambloplites rupestris</i>	Rock bass
RSMELT	<i>Osmerus mordax</i>	Rainbow smelt
SMB	<i>Micropterus dolomieu</i>	Smallmouth bass
SPLAKE	<i>Salvelinus fontinalis x Salvelinus namaycush</i>	Splake
SSCULP	<i>Cottus cognatus</i>	Slimy sculpin
WALL	<i>Sander vitreus</i>	Walleye
WS	<i>Catostomus commersonii</i>	White sucker
YP	<i>Perca flavescens</i>	Yellow perch



S3. Google Earth satellite image of the barren Baby Lake watershed in July 2019. Significant portions of the watershed catchments remain unforested.



S4. Google Earth satellite image of the semi-barren Daisy Lake watershed in July 2019. The northeast catchment remains sparsely vegetated.

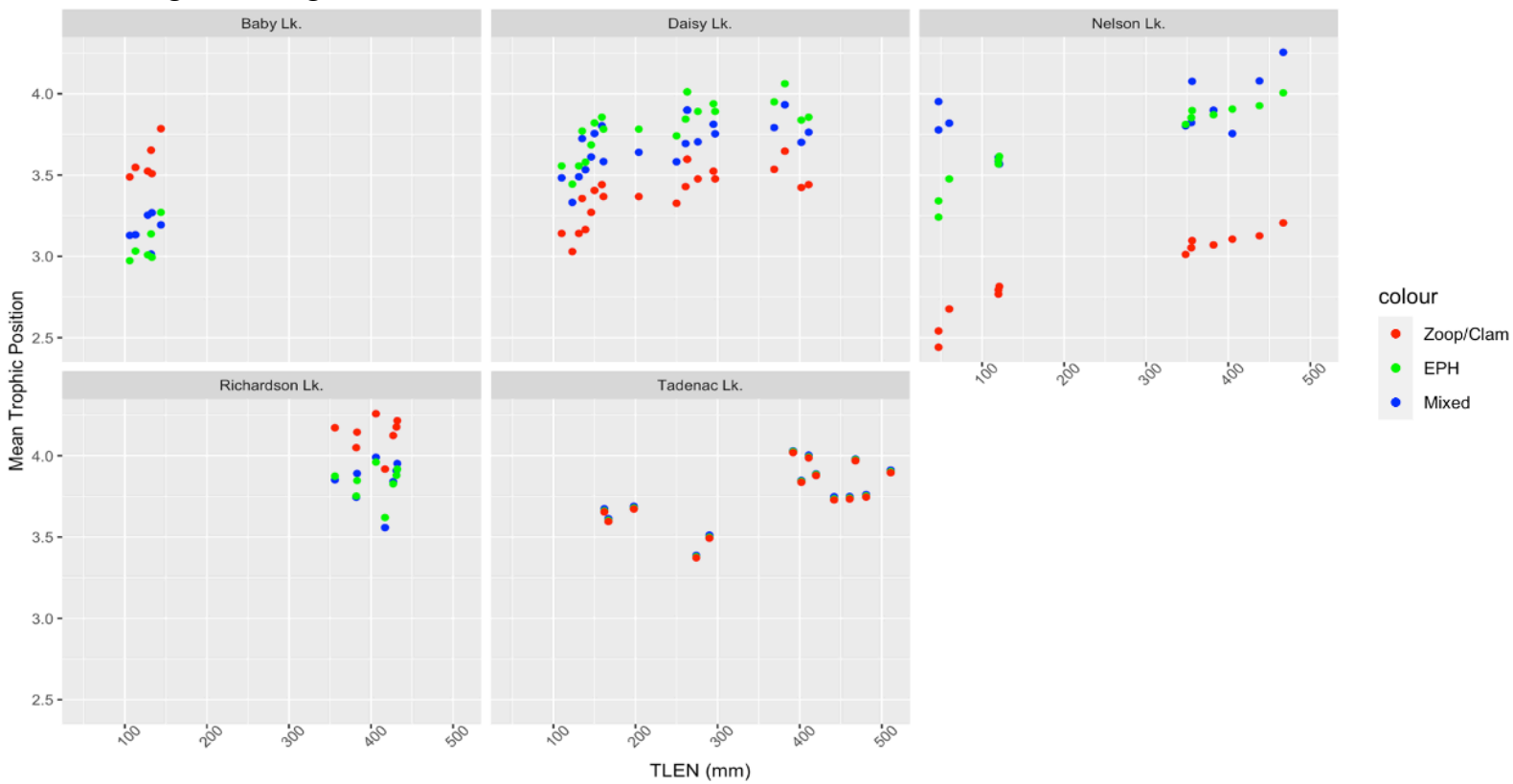


S5. Google Earth satellite image of the intact forested watershed of Nelson Lake. Imagery of the northern part of the lake was captured in April 2020, the remaining imagery was captured in July 2019.

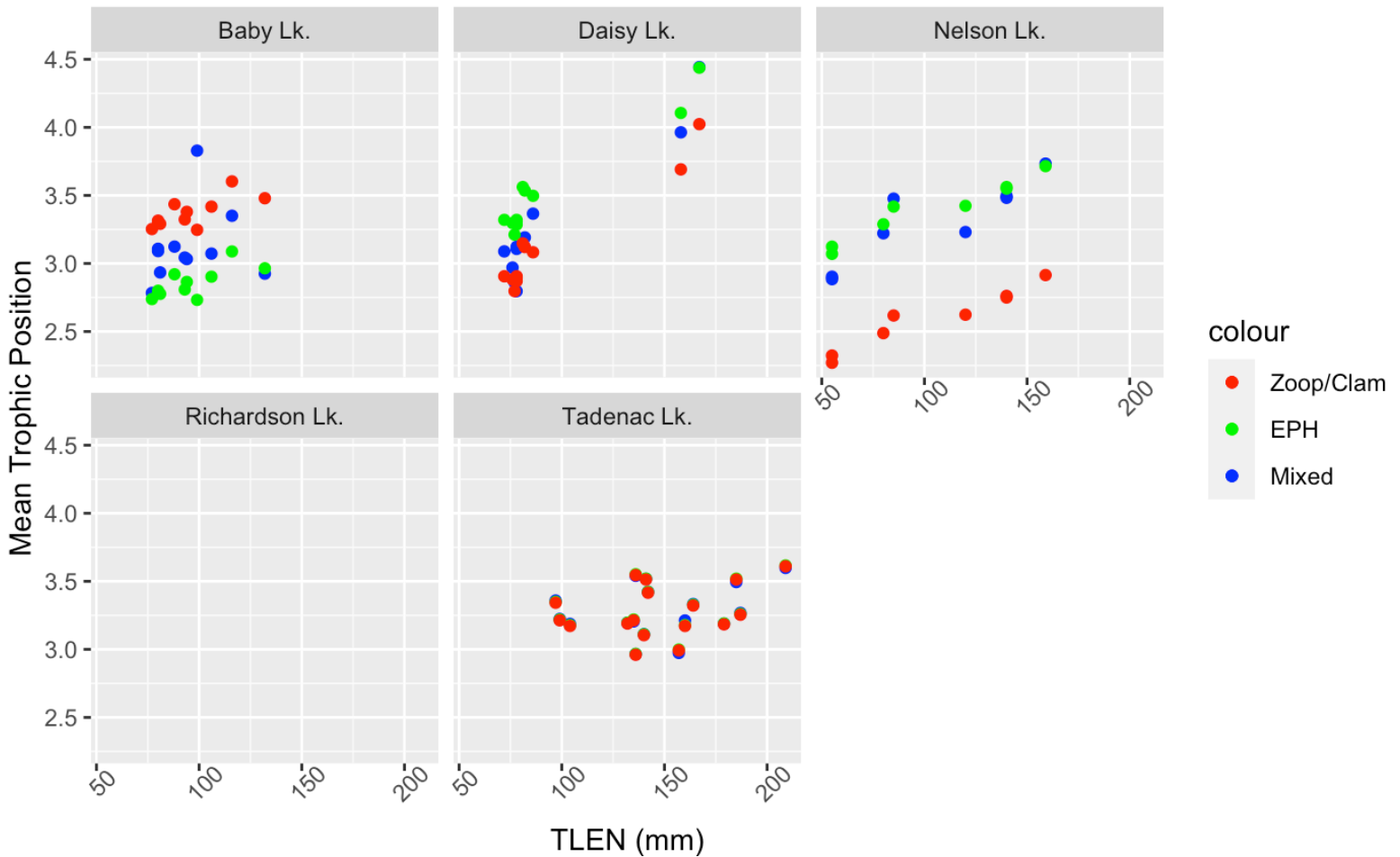
S6. Northeast and southwest Broadscale monitoring (BsM) lakes locations and general characteristics.

Region	Lake	Survey date	Lat/Long	Area (ha)	Depth (m)	Secchi (m)	Fish species abbreviation
North-east	Matagamasi	Sept. 2019	46.75472, -80.61115	1315.5	61	n/a	LT, NP, SMB, WS, BBULL, BUR, RB, YP, WALL
	Kelly 27	Aug. 2019	46.78178, -80.53036	16.5	17	11.50	LT, NRD, YP
	Wolf	July 2019	46.85283, -80.63538	87.4	51.2	10.50	LT, SMB, WS, YP
	Davis	July 2019	46.96335, -80.67818	34.1	14	4.50	LT, WS, GOSHIN, BBULL, YP
	Bowland	Aug. 2019	47.08558, -80.84123	108.4	28	4.50	LT, WS, SMB, YP
	Laundrie	July 2019	47.10298, -80.85185	386.7	26	4.50	LT, SMB, WS, CCHUB, YP
	Florence	June 2019	47.23387, -80.54145	1006.9	38.1	9.40	BT, LT, WS, GOSHIN, COSHIN, CCHUB, PSEED, YP
	Whitepine	July 2019	47.27834, -80.83164	66.9	19	4.50	LT, WS, GOSHIN, COSHIN, CCHUB, PDACE, BUR, YP
	Marina	Aug. 2019	47.39802, -80.65811	37	16.8	3.90	BT, LT, AT, WS, GOSHIN, EBD, PSEED, YP, WALL
South-west	Brodill	June 2019	46.37472, -80.94165	112.1	36	5.15	WS, PSEED, SMB, YP
	Chief	June 2019	46.36290, -81.01645	115.2	34	4.00	LT, WS, CCHUB, PDACE, PSEED, YP, IODA
	Clearwater	Aug. 2019	46.36898, -81.05081	75.6	21	7.80	BBULL, SMB, YP, PSEED, (CCHUB)
	White Oak	June 2019	46.29590, -81.00092	273.1	43	6.50	LT, CIS, NRD, GOSHIN, BNOSE, BBULL, PSEED, YP
	Wavy	June 2019	46.30407, -81.09151	306.3	34	4.00	WALL, YP, LT
	Peter	July 2019	46.19041, -81.21546	132.4	30.5	5.25	LT, SMB, NP, CIS, WS, GOSHIN, BNOSE, BBULL, RB, PSEED, YP, LPERCH
	Tyson	Aug. 2019	46.12037, -81.13381	1142.2	39.6	4.50	LT, CIS, NP, WS, GOSHIN, BBULL, RB, PSEED, SMB, LMB, YP
	Bell	Sept. 2019	46.13267, -81.20100	335.5	26.8	4.50	LT, SPLAKE, LWF, CIS, NP, WS, GOSHIN, CCHUB, RB, PSEED, SMB, YP, LPERCH
	Johnnie	July 2019	46.09046, -81.23923	342.3	33.6	3.80	LT, LWF, CIS, NP, WS, GOSHIN, BNOSE, BBULL, RB, PSEED, SMB, YP, LMB
	Great Mountain	June 2019	46.14943, -81.35616	191.5	37.5	7.00	LT, CIS, PSEED, SMB
	George	July 2019	46.02845, -81.40022	147.9	36.6	5.25	LT, LWF, CIS, WS, EBD, BNOSE, CCHUB, BBULL, RB, PSEED, YP, SMB

Appendix 2: Variation in trophic positioning of common fish species (smallmouth bass and yellow perch) calculated using different baseline organisms to support decisions in baseline organism usage.

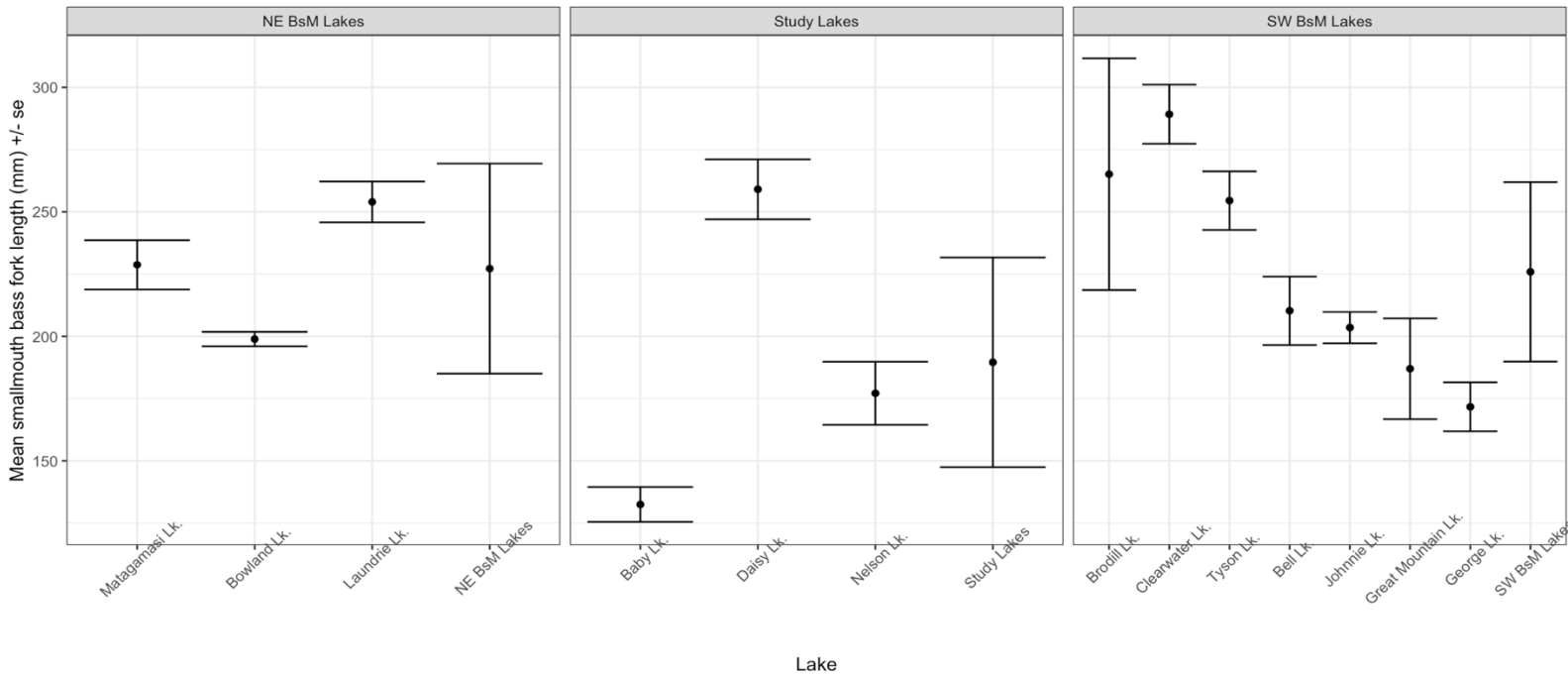


S7. Variation in trophic positioning of smallmouth bass with total length (mm) across lakes calculated using different baseline organisms. Colours denote baseline organisms; Zooplankton and clam (red), *Ephemeroptera* (green), and mixed zooplankton/clam and *Ephemeroptera* (blue).

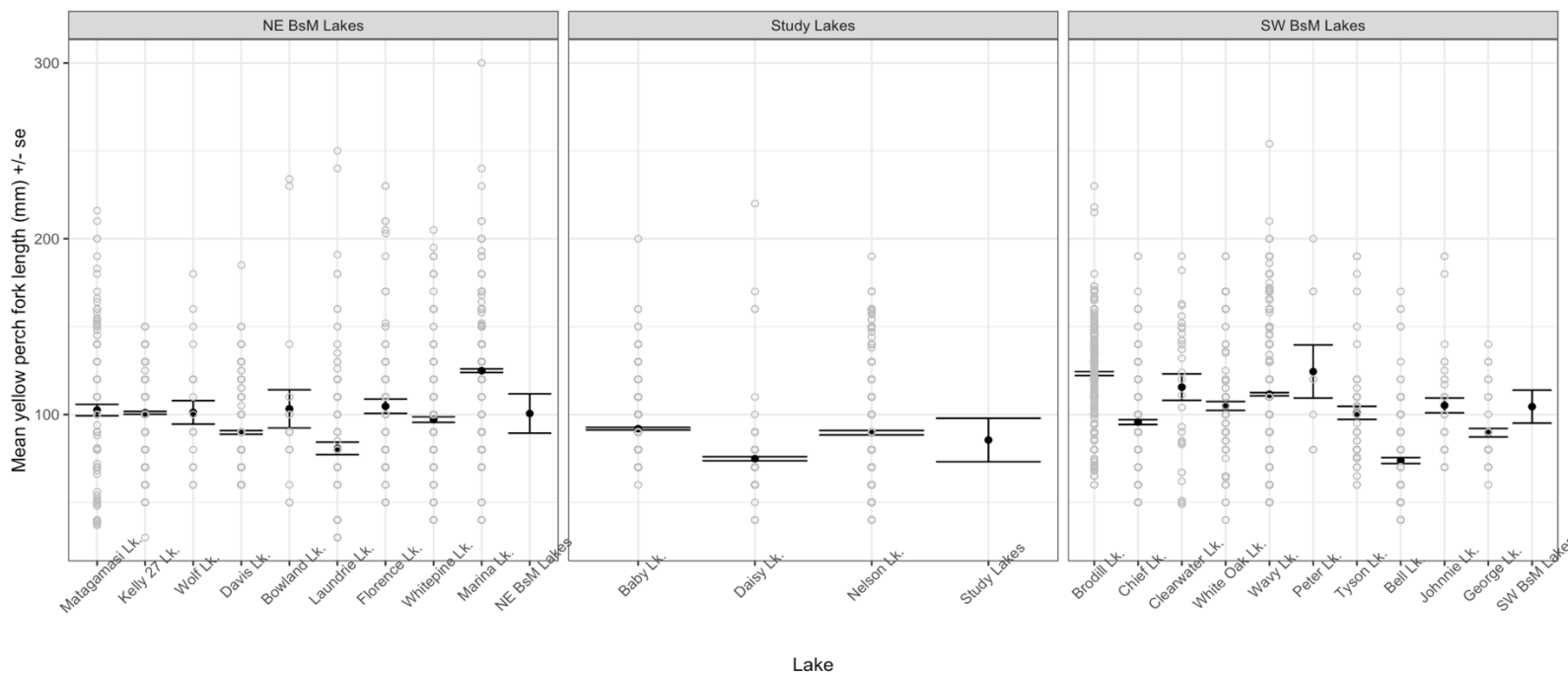


S8. Variation in trophic positioning of yellow perch with total length (mm) across lakes calculated using different baseline organisms. Size data was not collected for Richardson Lake yellow perch as is reflected by the blank panel. Colours denote baseline organisms; Zooplankton and clam (red), *Ephemeroptera* (green), and mixed zooplankton/clam and *Ephemeroptera* (blue).

Appendix 3: Variation in mean fork length among smallmouth bass and yellow perch communities across Sudbury region lakes.

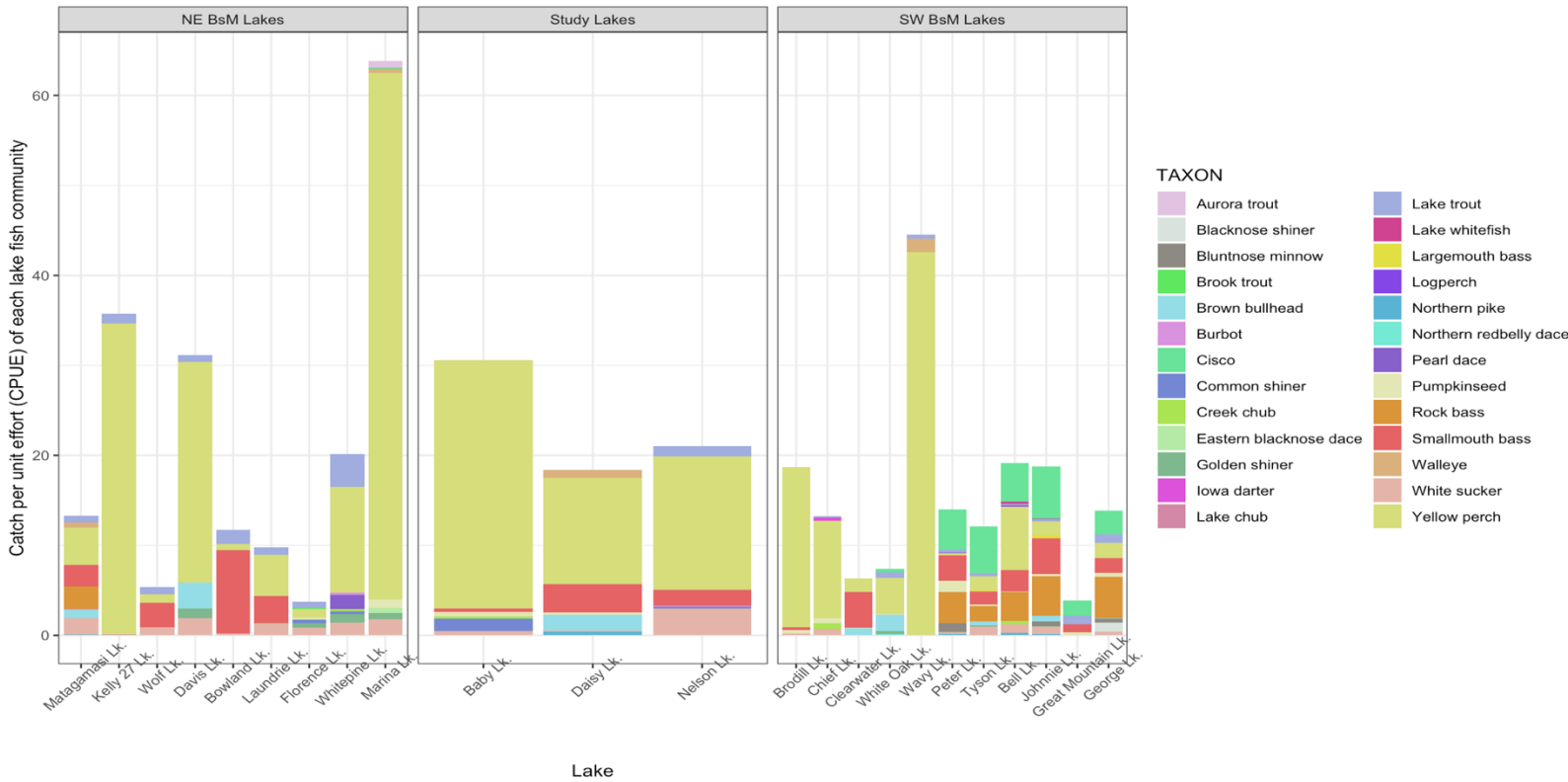


S9. Mean fork length (mm) of smallmouth bass (\pm standard error) between recovery lakes and lakes across the Sudbury region from BsM netting surveys. Lake categories were determined firstly based on whether the lake was one of the primary sample lakes of this study then by predominant direction of the lake relative to the Coniston nickel smelters. Lakes within each lake category are ordered by increasing distance from Coniston nickel smelters.

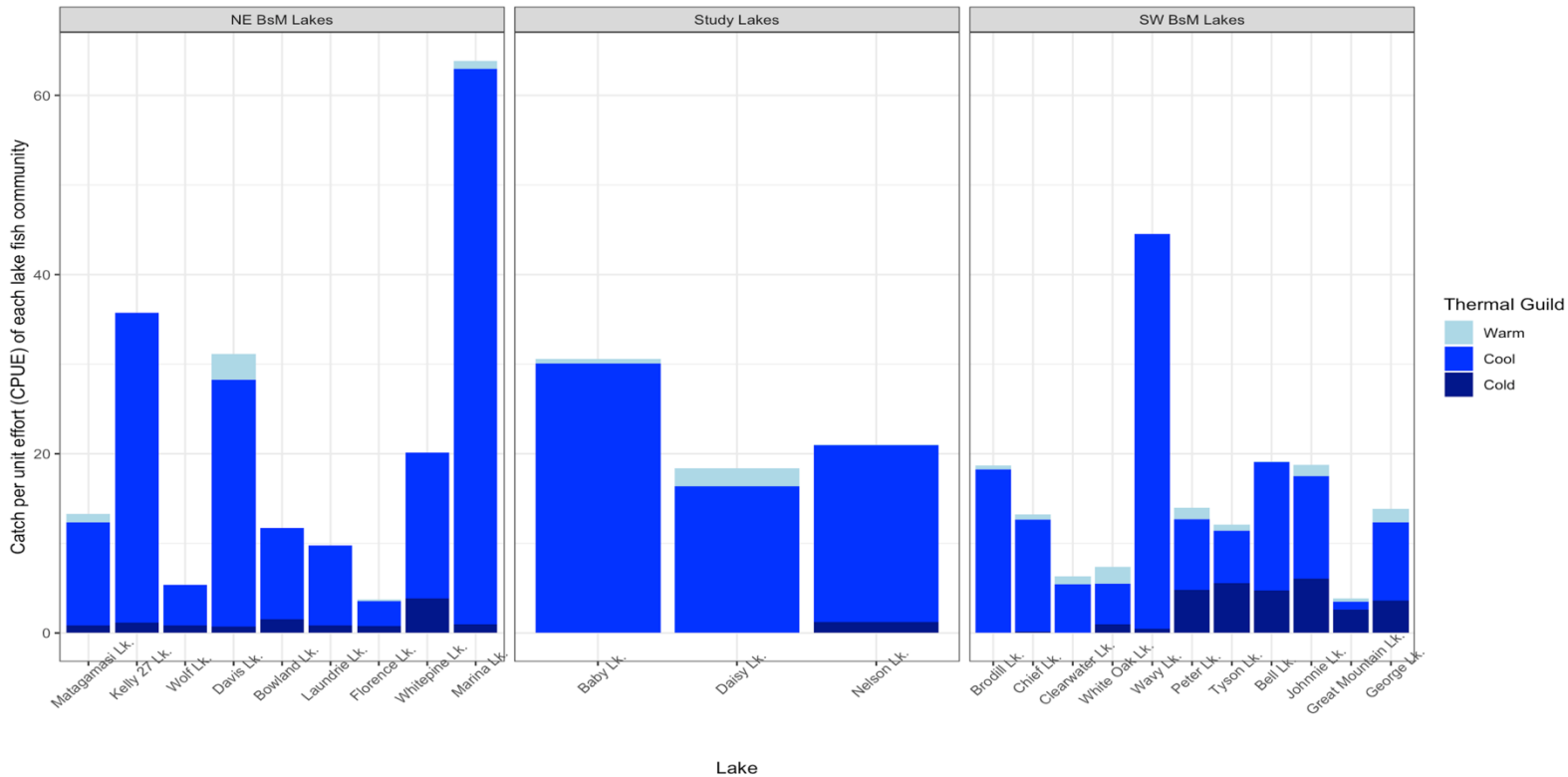


S10. Mean fork length (mm) of yellow perch (\pm standard error) between recovery lakes and lakes across the Sudbury region. Lake categories were determined firstly based on whether the lake was one of the primary sample lakes of this study then by predominant direction of the lake relative to the Coniston nickel smelters. Lakes within each lake category are ordered by increasing distance from Coniston nickel smelters.

Appendix 4: Catch per unit effort (CPUE) among different fish community groups across Sudbury region lakes.

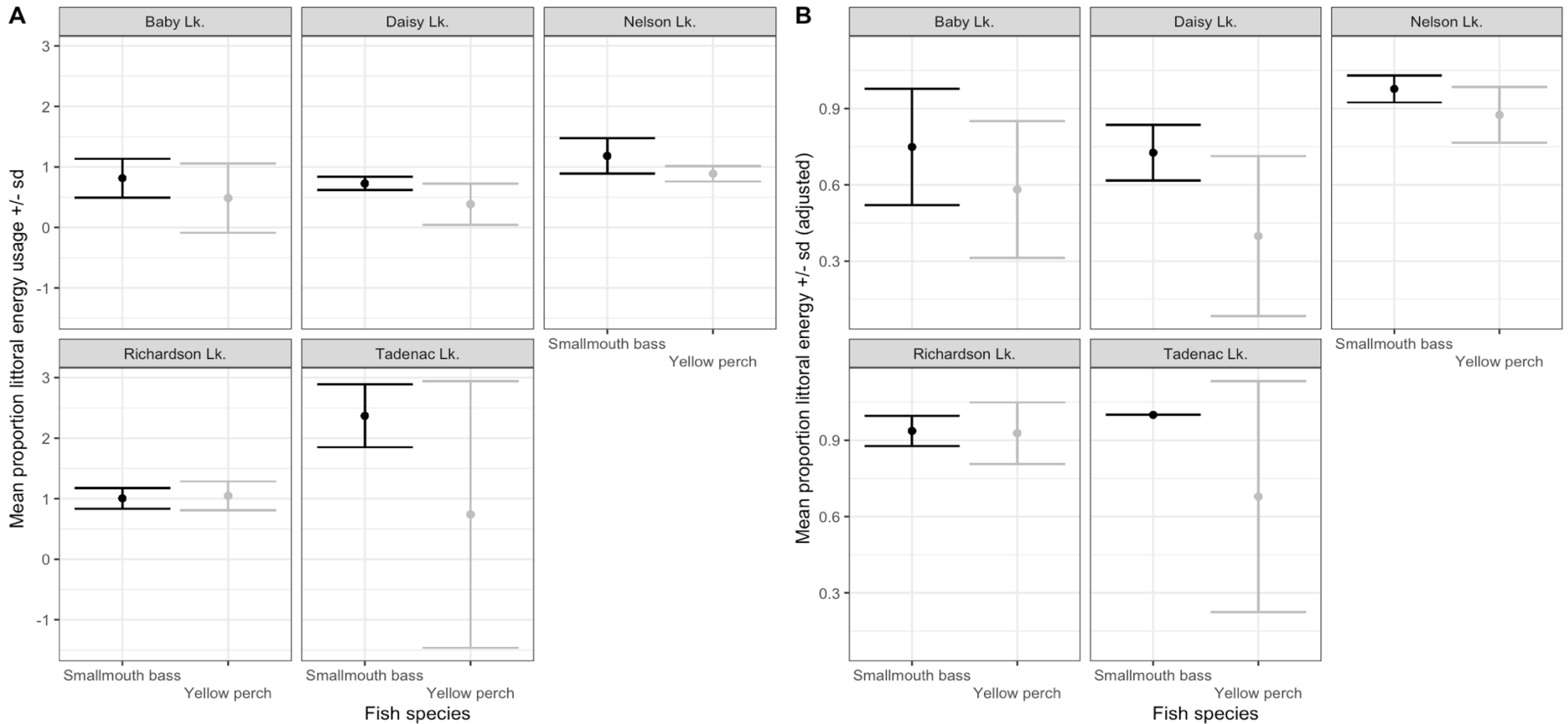


S11. Catch per unit effort (CPUE) for all fish species across lakes in the Sudbury region. Fish species are denoted by colour. Lake categories were determined firstly based on whether the lake was one of the primary sample lakes of this study then by predominant direction of the lake relative to the Coniston nickel smelters. Lakes within each lake category are ordered by increasing distance from Coniston nickel smelters.



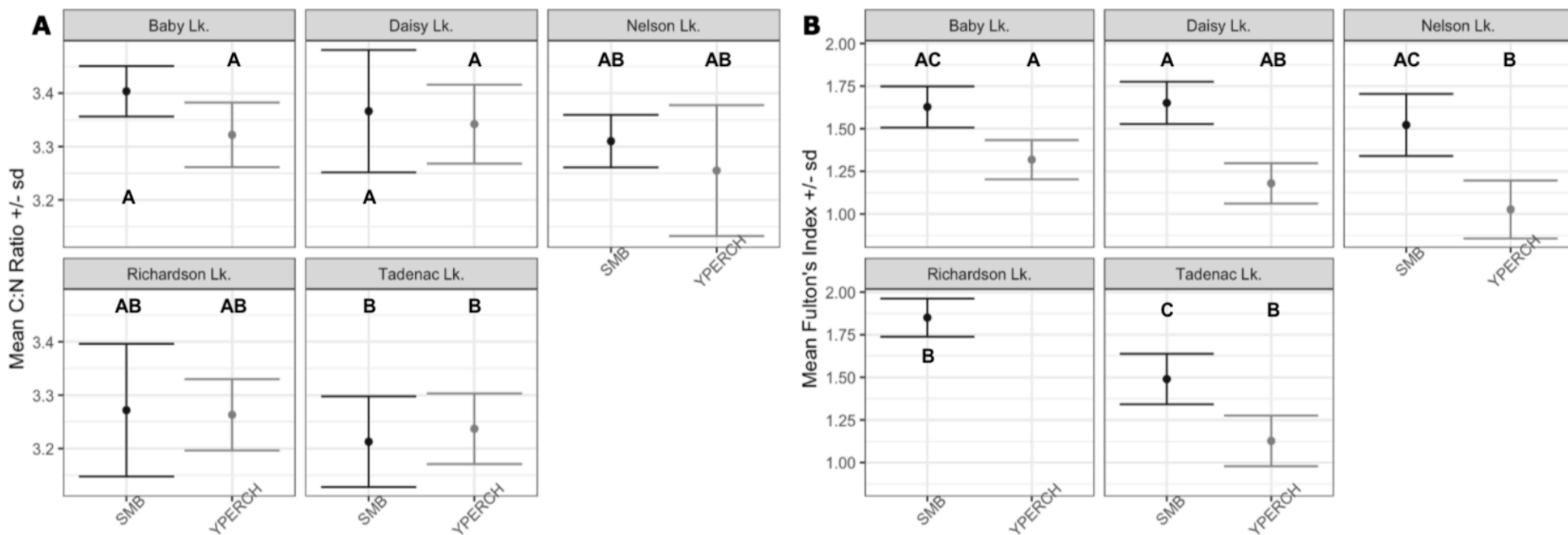
S12. Catch per unit effort (CPUE) of Sudbury region lakes by fish species preferred thermal guild. Thermal guilds were determined based on Coker et al.'s (2001) classification and using the final temperature preferendum (FTP) data for each species published by the Ontario Ministry of Natural Resources and Fisheries and Oceans Canada (Hasnain et al. 2010; Minns 2010). Thermal guilds are denoted by shading of colour; Warm water (>25°C) fish species (light blue), cool water (19°C - 25°C) fish species (blue), and cold water (<19°C) fish species (dark blue). Lakes within each lake category are ordered by increasing distance from Coniston nickel smelters.

Appendix 5: Comparison of adjusted and unadjusted mean proportion of littoral energy usage across study lakes (recovery and reference) as calculated using Vander Zanden (2002) equation.



S13. Mean proportion of littoral energy usage (\pm standard deviation) in smallmouth bass and yellow perch across recovery and reference lakes. **(A)** shows unadjusted mean proportion of littoral energy usage calculated using Vander Zanden (2002) equation: percentage contribution of littoral = $(\delta^{13}C_c - \delta^{13}C_p) / (\delta^{13}C_l - \delta^{13}C_p)$; **(B)** shows adjusted mean proportion of littoral energy usage, where if the $\delta^{13}C$ value of the individual was outside of either endpoint ($>100\%$ littoral reliance or $<0\%$ littoral reliance), values were set at either 100% or 0% (Vander Zanden 2002).

Appendix 6: Comparison of mean C:N ratio and mean Fulton's Index as condition factor metrics across fish species

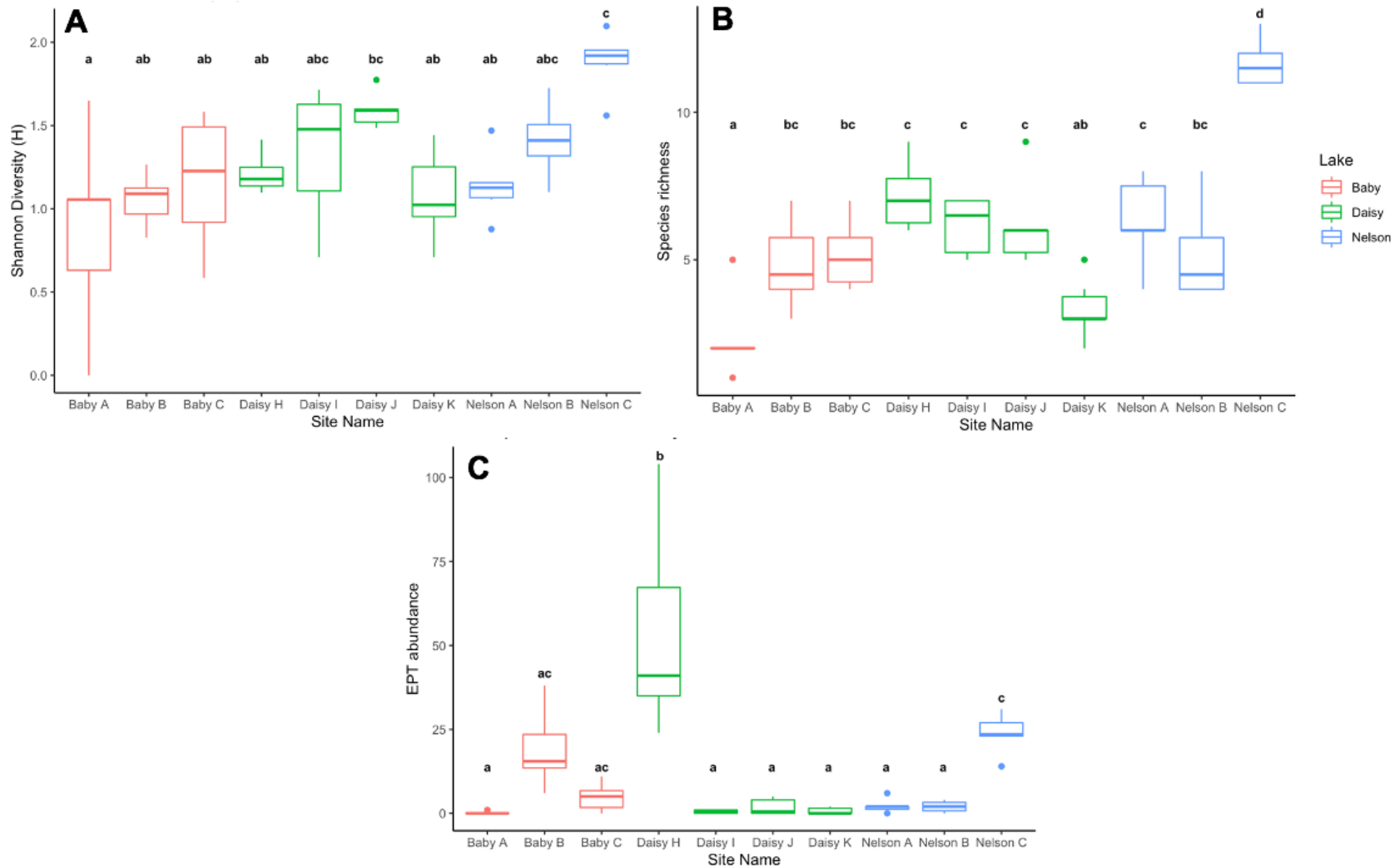


Smallmouth bass and Yellow perch communities by Lake

Smallmouth bass and Yellow perch communities by Lake

S14. Mean isotopic and morphometric condition factor proxies (\pm standard deviation) for smallmouth bass and yellow perch across lakes. Fish species are denoted by shading of colour. **(A)** shows $^{13}\text{C}:^{15}\text{N}$ ratio of condition (\pm standard deviation). **(B)** shows Fulton's index of condition (\pm standard deviation).

Appendix 7: Benthic invertebrate community data from recovery lakes (n=3) sampled in 2019.



S15. Two-way ANOVA with contrasts of current **(A)** Shannon-Weiner diversity, **(B)** species richness, **(C)** Ephemeroptera, Plecoptera, and Trichoptera (EPT) abundance measures for benthic invertebrates across delta zones ($n = 58$). Letters above each site type indicate statistically significant ($p = 0.05$) differences. Benthic invertebrate communities were sampled using artificial leaf pack substrates according to methods described in Wesolek et al. 2010.