Set for Success: Ecological Factors Facilitating Restoration of Self-Sustaining Lake Trout (*Salvelinus namaycush*) Populations in Acid-Damaged Lakes

by

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science (MSc) in Biology

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Abstract

Sudbury, Ontario, Canada is a site of extreme biodiversity loss due to widespread acidification from over a century of metal mining and smelting. Lake trout (*Salvelinus namaycush*) were the most widely and severely impacted of the resident sportfish but with massive emission reduction in recent years, their populations have since shown significant signs of recovery. The objective of my study was to identify conditions associated with lake trout recolonization and recruitment by conducting fish and water quality surveys on 31 once-damaged lakes across Sudbury's historic acid deposition zone. Lake trout biomass and odds of lake trout recruitment success increased in lakes with more depth of usable lake trout habitat, higher zooplankton biomass and a lower concentration of dissolved organic carbon. A history of hatchery stocking of lake trout was a top predictor of total lake trout biomass in standardized gillnet surveys but did not emerge in top models for predicting natural recruitment or the total biomass of natural lake trout in the lake.

These results demonstrate the importance of lake-specific ecological factors in the reestablishment of lake trout populations, regardless of whether the source of the population was hatchery stocking, migration from neighbouring lakes or residual populations that survived acidification. Overall, my study shows evidence that Sudbury's historically damaged lakes have been extensively recolonized and are no longer limited by acidic conditions. In many cases, they have shifted to simplified fish communities in which zooplankton may be a primary prey source for lake trout. Water chemistry factors, in particular the increase in concentration of dissolved organic carbon and the associated decrease in water clarity also emerged as potential factors shaping lake trout recovery in my study lakes.

Keywords

Lake trout (*Salvelinus namaycush*), acidification, Sudbury, stocking, zooplankton, dissolved organic carbon (DOC)

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List of Acronyms

AICc	Akaike's Information Criterion corrected for small sample sizes
Al	Aluminum
BsM	Broad-scale Monitoring
Ca	Calcium
Cu	Copper
DOC	Dissolved organic carbon
DO	Dissolved oxygen
MDL	Method detection limit
MECP	Ontario Ministry of the Environment, Conservation and Parks
MNDMNRF	Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry
Ni	Nickel
PC	Principal component
PCA	Principal component analysis
SO_4	Sulfate
TKN	Total Kjeldahl nitrogen
TP	Total phosphorus

1. Introduction

The recovery of lost or imperiled biodiversity is a critical area of active research in many fields of ecology and conservation science (Rahel and Olden 2008; Cazelles et al. 2019). However, the amount of conservation research per taxon is disproportionate to the actual distribution of organisms (Bonnet et al. 2002; Seddon et al. 2005). While a large research focus is put on mammals and birds, less attention is given to ectotherms such as amphibians, reptiles, and fish (Bonnet et al. 2002). A study done by Seddon et al. (2005) found that only 4% of vertebrate reintroduction research pertained to fish, despite fish representing 50% of vertebrate species. Freshwater fish are particularly underrepresented in this research, despite having had the highest extinction rates among all North American vertebrates throughout the 20th century (Burkhead 2012). As freshwater fish populations continue to decline, understanding the rehabilitation needs of individual species is critical.

The rehabilitation needs of lake trout (*Salvelinus namaycush*) in both the Great Lakes and the more than 5000 smaller lakes they occupy in North-America has been the focus of much research in recent years (Muir et al. 2021). Lake trout is a popular species for both recreational and commercial fishing, as well as indigenous subsistence harvesting (Riley et al. 2021). Historically, this apex predator was recognized as the second most important freshwater food fish in Canada (Martin and Olver 1980). Lake trout inhabit oligotrophic lakes of North America, thriving in cold (<10°C) and highly oxygenated (>6 mg/l) hypolimnetic habitat (Molot et al. 2003), but can also survive in what is considered marginal or “usable” habitat by Evans et al. (1991), with dissolved oxygen (DO) > 4 mg/L and temperature <15°C. A study by Guzzo & Blanchfield (2017) found that as air temperatures rise, the volume of optimal oxythermal lake trout habitat declines, a constraint that may limit lake trout abundance in the future as the climate continues to warm (Dillon et al. 2003; Evans 2007; Lester et al. 2021). Warmer temperatures also facilitate the northward invasion of warm-water species such as smallmouth bass (*Micropterus dolomieu*), that can out-compete lake trout for littoral prey, particularly in small lakes (Vander Zanden et al. 1999, 2004; Kaufman et al. 2009).

Lake trout have been the focal species for acidification research in Canada because the sensitive oligotrophic lakes they inhabit have particularly low buffering capacity to acidification (Gunn and Mills 1998). Extensive losses of lake trout populations in Canada were clearly linked to a single large Canadian source of acid deposition, from the metal smelters in Sudbury, Ontario (Matuszek et al. 1992). The damaging emissions of sulphur dioxide (SO_2) and metals from the Sudbury smelters began in 1888 and reached their peak in 1960 when Sudbury represented one of the largest point sources of SO_2 pollution in the world, with annual emissions of 2.5 M tonnes (Potvin and Negusanti 1995). Losses of lake trout were first documented in the 1940s and 50s, appearing to peak in the 60s with an estimated 94 lake trout lakes in the Sudbury area impacted by critically acidic conditions (Matuszek et al. 1992). Early netting assessments found that when lakes are acidified to a pH of less than 5.4-5.6, there is a loss of lake trout recruitment (i.e., death in the early developing stages of eggs, embryos and young juveniles) (Beggs and Gunn 1986; Gunn 1989; Matuszek et al. 1992). With a pH below 5.2, the entire population is usually extirpated (Beamish 1976; Beggs and Gunn 1986).

In recent decades, atmospheric SO_2 emissions from the Sudbury smelters and other sources have been greatly reduced in response to government regulations and improved technology, facilitating chemical recovery in many lakes beginning in the late 1970s and early 1980s (Keller et al. 1986, 2019; Gunn et al. 1988). Biological recovery was slower to occur, but progressed as various invertebrates and fish recolonized lakes, and some remnant stocks of lake trout and hatchery introduced trout began to reproduce (Gunn and Keller 1990; Gunn et al. 1995). From 2000 to 2005, Selinger et al. (2006) launched a large-scale regional assessment program to assess the status of recolonizing lake trout as water quality improved and during which nearly 250 000 lake trout were stocked in Northeastern Ontario. Of the 100 severely acid damaged lake trout lakes included in the assessment program (with the vast majority in the Sudbury area), 25 lakes had a native population that survived acidification, 10 had been successfully recolonized by self-sustaining lake trout through hatchery stocking, 34 lakes were considered chemically recovered and suitable for lake trout although self-sustaining populations were not yet present, and 31 lakes still required chemical recovery before lake trout could return. Analysis of these earlier data suggested that factors such as increased species richness, presence of competitors (e.g., smallmouth bass, rock bass and Coregonids) and angling pressure impeded lake trout recovery (Selinger et al. 2006; Kaufman et al. 2009), but like the much earlier work by Conlon et al. (1992), they lacked either the precision in their sampling methods, or access to associated limnological or food web data to better predict the population status in terms of standing crop biomass.

In more recent decades, there has been further evidence that suitable pH levels are returning to more Sudbury lakes as emissions continue to drop to less than 5% of historic highs (Keller et al. 2019). Such pH increases are also often accompanied by an increase in dissolved organic carbon (DOC) and decreases in calcium (Ca) concentrations (Williamson et al. 2015; Weyhenmeyer et al. 2019; Keller et al. 2019). In a recent study of 46 of Sudbury's acid sensitive lakes, Meyer-Jacob et al. (2020) found that since 1981, pH had increased by an average of 1.24, [DOC] had doubled, increasing by an average of 1.63 mg/L, and [Ca] had dropped by an average of 1.40 mg/L. Increased [DOC] in these Sudbury lakes is considered beneficial for lake trout because it can bind potential toxic metals (Schindler and Gunn 2003) and facilitates a quicker and shallower stratification, thus creating more cold water habitat (Snucins and Gunn 2000). At low [DOC], the thermocline is generally deeper and the hypolimnion is warmer due to increased light penetration; therefore an increase in [DOC] at least to pre-industrial levels should aid lake trout recovery, especially as climate continues to warm (Schindler and Gunn 2003). Approximately 70% of lake trout lakes in eastern North America have [DOC] between 3 and 5 mg/L which is also typical of the Sudbury area (Schindler and Gunn 2003). Essential for a wide variety of physiological functions in fish and aquatic invertebrates (such as cladoceran zooplankton), [Ca] declines may also negatively impact lake trout, particularly by impacting Ca rich food sources such as crustaceans which these fish rely upon (Jeziorski et al. 2014; Weyhenmeyer et al. 2019; Muir et al. 2021).

In addition to the chemical and physical changes, Sudbury's lake trout lakes have also seen major changes in species composition by shifting to simplified communities due to loss of cyprinids and other sensitive species when pH dropped below 6.0 (Matuszek et al. 1990). As a result, the littoral zones of many of these acid-damaged lakes are primarily occupied by only acid tolerant fish like the yellow perch *(Perca flavescens)*, with few if any other prey fish species (Matuszek et al. 1990). However, we know from studies in some other small Canadian boreal lakes, that lake trout can shift their diet from larger littoral prey to smaller pelagic prey to access food within areas that meet their thermal preferences (Guzzo and Blanchfield 2017; Vinson et al. 2021). For example, a pelagic planktivorous diet is common for the lean morph of lake trout in lakes smaller than 1000 ha when prey fish communities are less diverse (Vander Zanden et al. 2000; Vinson et al. 2021). Lake trout have also been detected shifting to a primarily invertebrate diet in the presence of smallmouth bass, but then returning to a piscivorous diet once the invasive predator was removed (Lepak et al. 2006). When forced to be planktivorous, lake trout appear to prefer cladocerans over copepods, even when the zooplankton population is primarily composed of copepods (Martin and Olver 1980). Konkle & Sprules (1986) provided evidence that lake trout were displaying size-selectivity for larger Cladocera to maximize energy intake. In the 95 guts they examined, 99% of the zooplankton eaten were *Daphnia* longer that 0.9mm (Konkle and Sprules 1986).

The recovery status of lake trout in Sudbury, in terms of population abundance and recruitment success, is currently unknown because there have been no extensive assessments since the regional survey program conducted by Selinger et al. (2006). However, very large investments have been made in further smelter emission reduction and fisheries managers have continued with extensive hatchery stocking of over 500 000 lake trout since the early 2000's.

The objectives of my research were to quantify the current status of lake trout populations in historically acidified lakes in the Sudbury area, and to identify important correlates of successful reproduction and high biomass. I hypothesized that lake trout biomass and recruitment would no longer be limited by lake acidity, but would be more strongly related to biological community composition as well as physical and chemical habitat characteristics, other than acidity. Based on long-term water quality monitoring information for the Sudbury region provided by the Ontario Ministry of the Environment, Conservation and Parks (MECP), I predicted that all surveyed lake trout lakes will have recovered to a pH above 5.4, no longer limiting reproduction. Due to the influence of DOC on hypolimnion volume, I predicted that higher [DOC] would be associated with a more abundant lake trout population. Regarding physical variables, I also predicted that lake trout biomass and recruitment success would be positively related to the availability of usable lake trout habitat in summer (<15°C and

DO>4mg/l) (Dillon et al. 2003; Evans 2007; Lester et al. 2021). Because fish communities were expected to be more simplified, I also predicted that lake trout population biomass and ability to reproduce would be positively related to alternate food sources such as zooplankton, especially in lakes where smallmouth bass had depleted littoral zone prey (Vander Zanden et al. 1999, 2004). More specifically, I predicted that the presence of large bodied taxa (Cladocera) would result in more lake trout biomass because lake trout appear to selectively consume larger zooplankton prey (Konkle and Sprules 1986). I also predicted that higher lake trout population biomass and more recruiting lake trout populations would be found in lakes with fewer fish species and lower predator biomass based on literature that lake trout do best in lakes with less competition for prey (Evans and Olver 1995; Selinger et al. 2006; Wilson and Mandrak 2021).

2. Methods

2.1 Study Area and Site Selection

Thirty-one lakes were sampled between June 17th, 2019 and September 10th, 2020 across an area outlined by Neary et al. (1990) as the Sudbury deposition zone (Figure 1). This 17 000 km^2 acid-impacted area was classified in the 1990s as the zone of highest total sulphur deposition in Ontario (Neary et al. 1990; Matuszek et al. 1992). A summary of the names, locations and general characteristics of my sample lakes can be found in Table 1. These lakes were primarily selected based on their previously documented acidity (historical pH < 6.0), their location within the Sudbury deposition zone and historical evidence that they once supported lake trout populations. Additional factors considered in lake selection were to include a wide range of historical pH (4.33-5.78) and to have both stocked and non-stocked lakes. A summary of historical lake trout stocking is provided in Table SI-1. Surface area and maximum depth data were obtained from GIS application 'Fish ON-Line' and historical pH (between 1975 and 1990) was obtained from Polkinghorne and Gunn (1981) and unpublished MECP data to represent the earliest recorded pH value after peak emissions in 1960.

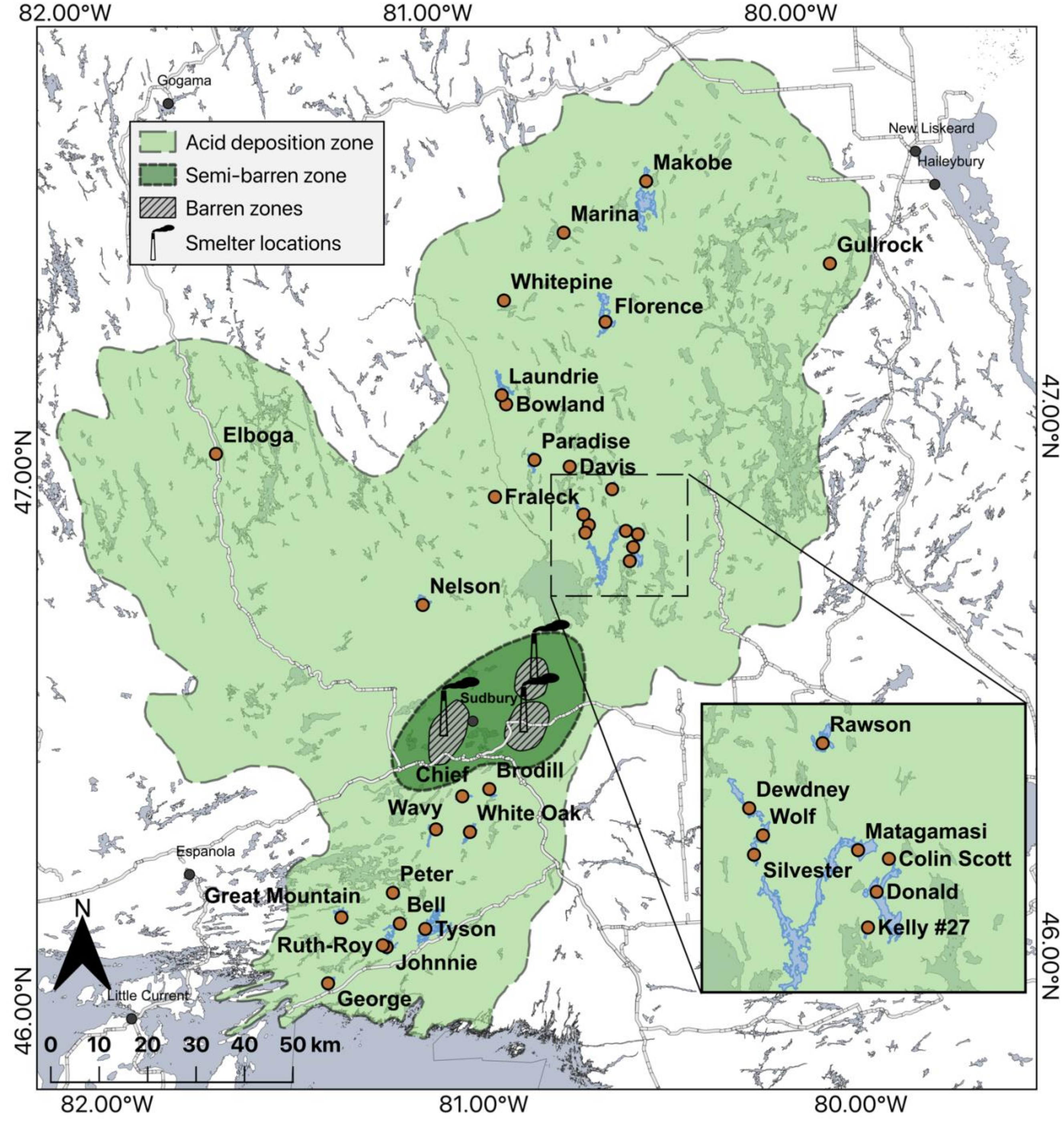

Figure 1 Location of the 31 lake trout lakes sampled in 2019 and 2020 across the Sudbury Deposition Zone (light green area), as defined by (Neary et al. 1990). This map was created by Calvin Kluke. Lake coordinates and other characteristics are presented in Table 1.

Table 1 Survey lake ID, locations and general characteristics. Lake location, surface area and maximum depth data was taken from the MNDMNRF GIS application 'Fish ON-Line'. Historical pH (1975-1990) was taken from Polkinghorne and Gunn (1981) unless otherwise indicated. Stocking presence (1) and absence (0) data was taken from unpublished MNDMNRF stocking data.

Survey ID	Lake	Township	Latitude	Longitude	Surface Area (ha)	Max depth (m)	Historical pH ('75-'90)	Stocking p/a
1	Brodill	Dill	46.37349	-80.94291	112.1	36	5.42[b]	0
2	Wavy	Eden	46.30407	-81.09151	306.3	34	4.33	1
3	Great Mountain	Hansen	46.14943	-81.35616	191.5	37.5	4.66	1
4	Chief	Tilton	46.3629	-81.01645	115.2	34	4.80[b]	1
5	White Oak	Tilton	46.2959	-81.00092	273.1	43	4.68	1
6	Elboga	Muldrew	47.02035	-81.63648	27.9	16.2	5.49	1
7	Davis	McConnell	46.96335	-80.67818	34.1	14	4.78	1
8	George	Killarney	46.02845	-81.40022	147.9	36.6	4.97	1
9	Johnnie	Carlyle	46.09046	-81.23923	342.3	33.6	4.82	1
10	Wolf	MacKelcan	46.85283	-80.63538	87.4	51.2[a]	4.45	0
11	Laundrie	Howey	47.10298	-80.85185	369.7	20.4	5.06	1
12	White Pine	McLeod	47.27834	-80.83164	66.9	19	5.40	1
13	Peter	Goschen	46.19041	-81.21546	132.4	30.5	5.78	1
14	Bowland	Howey	47.08558	-80.84123	108.4	28	4.90	1
15	Tyson	Sale	46.12037	-81.13381	1142.2	39.6	5.14	1
16	Gullrock	Brigstocke	47.31009	-79.93634	217.9	12.8	5.17[c]	1
17	Kelly #27	Kelly	46.78178	-80.53036	16.5	17	5.15	1
18	Nelson	Bowell	46.72163	-81.09598	315.8	50.3	5.70[e]	0
19	Bell	Goschen	46.13267	-81.20100	335.5	26.8	5.02	1
20	Matagamasi	MacKelcan	46.83813	-80.53597	1315.5	61	4.70	1
21	Marina	Corley	47.39802	-80.65811	37	16.8	5.30[d]	1
22	Florence	Florence	47.22803	-80.55814	1006.9	38.1	4.76[c]	1
23	Makobe	Trethewey	47.4845	-80.42426	2021.5	22.6	5.30[d]	0
24	Fraleck	Fraleck	46.91510	-80.88575	166	23.2	5.70	1
25	Paradise	Stobie	46.97737	-80.76971	487.4	35	5.52	0
26	Dewdney	Mackelcan	46.87357	-80.64921	176.1	34	4.43	0
27	Colin Scott	McCarthy	46.83075	-80.50410	43.9	43	4.80	1
28	Donald	Kelly	46.80184	-80.51650	502.2	60	4.67	1
29	Rawson	Sheppard	46.91885	-80.56735	158.6	26	5.20	0
30	Silvester	Mackelcan	46.84207	-80.64574	53.2	22[a]	4.48	0
31	Ruth-Roy	Carlyle	46.09572	-81.24740	54.5	18	4.44	0

[a] calculated from stratum depth data collected in 2019 or 2020 BsM survey
[b](Corston et al. 2014a, 2014b), [c](Keller et al. 2006), [d]unpublished MECP data, [e](Gunn et al. 1988)

2.2 Fish Community Assessment

The fish communities of the 31 lakes were sampled using a combination of multi-mesh gillnets. This included Broad-scale Monitoring program (BsM) large mesh gillnets (NA1), BsM small mesh gillnets (ON2) and NORDIC gillnets. The combined BsM small and large mesh nets have mesh sizes ranging from 13 mm to 127 mm (stretched) and the NORDIC nets have mesh sizes ranging from 10 mm to 110 mm (Morgan and Snucins 2005; Sandstrom et al. 2013). My surveys were based primarily on BsM gear and protocol, but NORDIC gear was included in an attempt to catch any unique species not caught by the BsM nets and perhaps more vulnerable to the smaller and finer mesh of the NORDIC nets (Morgan and Snucins 2005), based on thesis findings of Brekke (2017) that NORDIC nets are more successful at catching smaller bodied fish. However, these NORDIC gill nets were not deployed in eight of the survey lakes (Great Mountain, Nelson, Marina, Florence, Makobe, Colin Scott, Donald and Silvester) due to gear unavailability. The total number of BsM nets set per lake survey ranged from 16 to 45 depending on maximum depth and surface area of each lake (Sandstrom et al. 2013). Netting effort was distributed across depth strata proportional to stratum area, and randomized horizontally within each depth stratum (Sandstrom et al. 2013). Nets were set perpendicular to shore, and the depth of the anterior, middle and posterior point were recorded. Net set times, set locations (latitude and longitude) and lift times were also noted.

Lake surveys were conducted following the BsM protocol for gear deployment, set times, data recording and fish processing (Sandstrom et al. 2013). The only modification to the surveys was the addition of one NORDIC net set in each depth stratum. The NORDIC nets were set and lifted at the same times as the BsM nets, and NORDIC catches were processed as BsM catches, but all their data were recorded as NORDIC efforts. All captured fish were identified to species and measured for fork length (FL). Large-bodied fish (FL > 200mm) were further processed for total length (TL), round weight (RWT), sex, gonad maturity, and stomach contents, and species-specific ageing structures were collected (i.e., otoliths, cleithrum, pectoral ray etc.), as indicated in the BsM protocol (Sandstrom et al. 2013). Lake trout produced by the Ministry of Northern Development, Mines, Natural Resources and Forestry (MNDMNRF) fish culture stations are typically marked by unique fin-clipping prior to stocking. Juvenile are consistently marked when stocked but there are some inconsistencies with marking adult lake trout. In the context of this research, all captured lake trout without a fin clip were deemed to be of natural origin (i.e., due to successful reproduction) in order to remain consistent.

Lake trout catch data were used to calculate three indicators of population success (response variables) for my analyses. The first continuous response was total lake trout catch per unit effort (CPUE) and was calculated using equation (1):

$$\frac{\Sigma biomass\ of\ lake\ trout\ caught\ (g)}{number\ of\ BsM\ net\ sets} \qquad \text{(eq. 1)}$$

Only fish caught in BsM nets were used in this part of the analysis to remain consistent across all 31 lakes, since NORDIC nets were not used consistently across all surveys. Most juveniles were only measured for FL, so a RWT vs FL relationship for lake trout was fitted and used to estimate the missing RWT values (Figure SI-1a). Some of the fish caught fell outside the fitted curb, therefore some minor extrapolation was required. The second continuous response was natural lake trout CPUE and was calculated identically except only unclipped (i.e., natural) lake trout were included resulting in equation (2):

$$\frac{\Sigma biomass\ of\ natural\ lake\ trout\ caught\ (g)}{number\ of\ BsM\ net\ sets} \qquad \text{(eq. 2)}$$

As a categorical response, the presence or absence of lake trout recruitment was determined in each lake. If unclipped (i.e., naturally occurring) juvenile (≤ 300 mm) lake trout were caught in the BsM survey, the lake trout population was considered one where natural reproduction (i.e., recruitment) had recently taken place. This response was calculated using only BsM net catches to remain consistent and because recruitment status of lake trout did not change if NORDIC catches were also included. In other words, there were no instances where naturally occurring juvenile lake trout were caught in a NORDIC effort but not in a BsM effort.

Candidate biological predictors calculated using fish catch data are summarized in Table 2 and were all calculated using BsM catch only since NORDIC nets were not used consistently across all surveys. Smallmouth bass CPUE was calculated using equation (3):

$$\frac{\Sigma biomass\ of\ smallmouth\ bass\ caught\ (g)}{number\ of\ BsM\ net\ sets} \qquad \text{(eq. 3)}$$

Large piscivore CPUE was calculated similarly using equation (4):

$$\frac{\Sigma biomass\ of\ large\ piscivores\ caught\ (g)}{number\ of\ BsM\ net\ sets} \qquad \text{(eq. 4)}$$

All northern pike (*Esox lucius*), burbot (*Lota lota*), smallmouth bass, largemouth bass (*Micropterus salmoides*) and walleye (*Sander vitreus*) larger than 100g were classified as large piscivores. As with lake trout, RWT vs FL relationships were fitted for each species and used to estimate RWT where these data were lacking (Figure SI-1bcd). Some of the fish caught fell outside the fitted curb, therefore some minor extrapolation was required. Additional candidate predictors considered were fish species richness, presence of smallmouth bass, presence of yellow perch, presence of Coregoninae (includes whitefishes and ciscoes) and historical presence of lake trout stocking.

2.3 Water Quality Assessment

For each lake, water quality assessment occurred at the same time of the fish survey at a single location near the deepest point in the lake. A temperature (°C) and DO (mg/L) profile was taken using a ProODO YSI dissolved oxygen – temperature meter; measurements were taken just below the surface (0.5 m), at 1.0 m intervals from 1.0 to 16 m and at 2.0 m intervals thereafter, as indicated in the BsM protocol (Sandstrom et al. 2013). Dissolved oxygen – temperature profiles were not completed at Rawson Lake or Great Mountain Lake due to equipment malfunction. Depth of optimal (<10 °C and O_2 >6mg/L) and usable (<15 °C and O_2 >4 mg/L) lake trout habitat were calculated using DO – temperature profiles. To measure transparency, Secchi depth was measured on the shady side of the boat between 11:30 and 14:00 (Sandstrom et al. 2013). Water samples were collected using the surface grab method consistent with the MECP extensive water quality monitoring (Keller et al. 2006).

As for laboratory analyses of the water samples, pH was measured by MECP at the Vale Living with Lakes Centre using a MeterLab® PHM 220 pH meter (Radiometer Analytical, Copenhagen). The remainder of the water chemistry analyses were mostly completed by MECP at the Dorset Environmental Sciences Centre (DESC; Dorset, ON) and Laboratory Services Branch (Etobicoke, ON) in 2019 following standard protocols (Ontario Ministry of the Environment 1983). Chief and White Pine Lakes were not sampled for water chemistry in 2019, and 2018 MECP water chemistry data, also generated at DESC, were used. No water chemistry is included for Marina Lake because it was not sampled for water chemistry in 2019 due to unavailability of sampling gear and no 2018 data were available. The MECP laboratories were not accepting water samples in 2020 due to public health lockdown measures, therefore water samples collected during the 2020 lake surveys were analyzed at Testmark laboratory in Sudbury, Ontario, Canada. A comparison of analysis methods and results for samples analyzed by both MECP laboratories and Testmark found them to be mostly comparable other than some minor differences outlined in the next paragraph (Edwards and Patterson 2021). However, when

2019 water chemistry data were available from MECP laboratories for a lake surveyed in 2020, I used the 2019 MECP data. As a result, water chemistry data used in my analyses was from MECP for most lakes, and from Testmark for only four lakes (Paradise, Dewdney, Colin Scott, Rawson). Water chemistry parameters selected for use in the final dataset were alkalinity (total fixed endpoint), and concentrations of chloride, sulphate, DOC, reactive silicate, total phosphorous (TP), Ca, aluminum (Al), copper (Cu) and nickel (Ni). Parameters selected are standard water chemistry measures included in all BsM surveys.

There were some differences in the data provided by the laboratories. The DESC and Etobicoke laboratories each provided two TP estimates per lake because TP can be artificially raised in concentration if a piece of biota or other material enters the sample when collected. The mean of the two TP estimates was used for these lakes, unless they differed by more than 30%, in which case the lowest TP estimate was used. Estimates differed by > 30% for Bell, Elboga, Great Mountain, Peter and Tyson Lakes. Testmark laboratory only provided one TP estimate for each lake. For each datapoint, I compared the measured result to the method detection limit (MDL) and if the result was less than the MDL, half of the MDL was used as the final result. Testmark also provided duplicate determinations for some measurements including Ca, chloride, reactive silicate, sulphate, Cu, Al and Ni. If duplicates were provided, the mean of the two data points was used. All candidate chemical and physical predictors mentioned in this section are listed and defined in Table 2.

Table 2 List of candidate historical, physical, chemical, and biological predictors considered for predicting lake trout recruitment, total and natural lake trout CPUE.

Variable	Description	Units
Historical		
Stocking p/a	Presence of lake stocking, 0 = not stocked, 1 = stocked	n/a
Physical		
Lake Size	Surface area of the lake	Ha
Max Depth	Maximum depth of the lake	m
Optimal Depth	Depth of optimal lake trout habitat (<10 °C and O_2 >6mg/L)	m
Usable Depth	Depth of usable lake trout habitat (<15 °C and O_2 >4 mg/L)	m
Chemical		
Historical pH	Earliest recorded pH value between the years 1975 and 1990	n/a
Contemporary pH	Most recent pH value between the years 2018 and 2020	n/a
Secchi	Secchi	m
Chloride	Chloride	mg/l
Sulphate	Sulphate	mg/l
Alkalinity	Total fixed endpoint alkalinity	mg/l
DOC	Dissolved organic carbon	mg/l
Reactive Silicate	Reactive silicate	mg/l
TP	Total phosphorus	mg/l
Ca	Calcium	mg/l
Al	Aluminum	mg/l
Cu	Copper	mg/l
Ni	Nickel	mg/l
Biological		
Fish Species Richness	Number of fish species detected in BsM survey	n/a
Smallmouth p/a	Presence/absence of smallmouth bass	n/a
Smallmouth CPUE	Catch per unit effort of smallmouth bass	g/net
Yellow Perch p/a	Presence/absence of yellow perch	n/a
Zoo Density	Density of zooplankton	$\#m^3$
Zoo Biomass	Biomass of zooplankton	mg/m^3
Zoo Richness	Zooplankton species richness	n/a
Large Clad p/a	Presence of cladocera with a mean length >0.9mm, 0 = large cladocera absent, 1 = large cladocera present	n/a
Coregoninae p/a	Presence of coregonids, 0 = coregonids absent, 1 = coregonids present	n/a
Piscivore CPUE	Large piscivore catch per unit effort	g/net

2.4 Zooplankton Community Assessment

Zooplankton communities were sampled at the deepest point of each lake using a 30cm diameter Wisconsin net lowered to one meter above the bottom of the lake. After 30 seconds, the net was hauled vertically at a constant rate of approximately 1m/second. Bulk zooplankton samples were preserved with 14% formalin until identification. No zooplankton were collected on Marina or Makobe Lakes due to gear unavailability. Zooplankton were identified to species by zooplankton taxonomist Lynne M. Witty of Identazoop consulting (Capreol, ON) and density, biomass and total species richness were calculated for each lake (Table 2). Density was calculated by dividing the number of individuals of a species by the sample volume (haul depth × net diameter) × 1000 to convert to #individuals × m^3. Density of each species was then summed to estimate total zooplankton density of each lake. Biomass was calculated by multiplying the density of individual species by the calculated mean mass of that species within that sample and then divided by 1000 to end up with mg/m^3. Mean mass is calculated by measuring lengths from a subsample (minimum of 240 individuals) in each taxon, estimating their masses using taxon specific mass length regressions, and calculating the mean of these masses. Total zooplankton biomass density was the sum of individual species biomass densities for each lake. Nauplii, rotifers and other small zooplankton taxa that could not be identified to genus were binned and not included in these counts. The final predictor calculated for zooplankton was the presence or absence of Cladocera with a mean length larger than 0.9mm, based on the mean length of each species provided by the taxonomist for each individual lake.

2.5 Statistical analysis

All data handling, visualization, and statistical analyses were performed using R (v. 4.1.2) and alpha was set to 0.05 for all statistical tests. Regression models were used to investigate multiple chemical, physical and biological variables as potential predictors and determine which would be most suitable for predicting lake trout biomass and recruitment. Correlations between candidate predictors were assessed and a PCA of water chemistry variables was completed to reduce the number of predictors under consideration.

2.5.1 Preliminary Data Assessment

Scatterplots and boxplots of predictor and response variables (i.e., presence of lake trout recruitment, total lake trout CPUE and natural lake trout CPU) were used to identify outliers and determine the nature of relationships. If a strong relationship was identified between a response variable and a predictor, that predictor was retained for use in later analyses. Histograms and Shapiro-Wilk normality tests were used to determine distributions of each variable. Transformations of $\log_e(x + 1)$ were used when necessary to reduce the influence of extreme values, improve linear associations and better approximate univariate and multivariate normality (Quinn and Keough 2002).

A Pearson correlation matrix of all the continuous candidate predictor variables was completed before any multivariate analyses using the cor function in the 'stats' package (v 4.1.2). The argument 'use = "complete.obs"' was used to delete all missing values (NA's) on a casewise basis. A correlation threshold of $r < 0.7$ was used when selecting continuous predictors for future models. Including strongly correlated predictor variables within the same model can distort parameter estimation due to inflation of relationships from resulting multicollinearity

(Dormann et al. 2013). Notably strong correlations among predictor variables included: (1) optimal habitat depth and $\log_e$ usable habitat depth (r = 0.823), (2) $\log_e$ zooplankton density and $\log_e$ zooplankton biomass (r = 0.861) and (3) $\log_e$ piscivore CPUE and log smallmouth bass CPUE (r = 0.869) (Table SI-2a). In each of these three pairings, the latter variable was chosen for further modeling based on initial data exploration or sampling considerations. More specifically, $\log_e$ usable habitat depth was ultimately selected because it is not as stringent in its oxygen criteria and therefore less affected by seasonal oxygen depletion. As for zooplankton, $\log_e$ zooplankton biomass was selected because it demonstrated a strong univariate relationship with lake trout CPUE during data exploration. Finally, between smallmouth bass and piscivore CPUE, $\log_e$ smallmouth bass CPUE was selected because the negative effects of smallmouth bass on lake trout are prominent in the literature.

To reduce the number of chemical predictors under consideration and allow for the contemplation of other factors in the final models, a PCA was completed with all 13 chemical predictors listed in Table 2. Water chemistry data were not available for Marina Lake and it was excluded from this part of the analysis. Data were centered and scaled and PCA was performed through the ‘prcomp’ function (‘stats’ package v 4.1.2). The top three principal components (PC) were extracted for use in subsequent modelling. All three PCs were determined to represent a meaningful amount of chemical variation, based on broken stick analysis (Jackson 1993) using the ‘bstick’ function (‘vegan’ package 2.5-7) and all were above the point of inflection where PC variation starts to plateau (Figure SI-2) (Field et al. 2012). Univariate plots were used to interpret the contribution of individual water chemistry parameters in each PC and determine which variables were the primary drivers of relationships between response variables and PCs.

2.5.2 Assessing factors related to the presence of lake trout recruitment

Lake trout recruitment was modelled using a logistic regression where 0 represented lakes where unclipped juvenile lake trout were not detected and 1 represented lakes where unclipped juvenile lake trout were detected. All continuous predictors were converted to Z-scores in order to standardize variables. A combination of continuous and binary predictors (Quinn and Keough 2002) were included in the global model using the glm function (stats package v 4.1.2), such as $\log_e$ lake size, $\log_e$ usable habitat depth, $\log_e$ zooplankton biomass, $\log_e$ zooplankton species richness, $\log_e$ smallmouth bass CPUE, presence of Cladocera > 0.9mm, presence of coregoninae, presence of yellow perch, presence of lake trout stocking, $\log_e$ fish species richness, as well as water chemistry PC1, PC2 and PC3. Predictors selected were not strongly correlated with one another ($r < 0.7$; see section 2.5.1 above) and were relevant based on previous research and preliminary findings from exploratory plots. All combinations of the global model were run, allowing each model to have up to one predictor variable per 10 observations resulting in a criterion of a maximum of three predictors per model. Models were assessed and ranked using the glmulti package (v 1.0.8) to calculate Akaike's Information Criterion corrected for small sample sizes (AICc). Models with a ΔAICc of < 2 from the top model were retained for interpretation (Burnham and Anderson 2004). Relative strengths of models were determined bason on Akaike weights and relative strengths of predictors were based on standardized model coefficients. Univariate logistic regressions were used to visualize the relationship between the presence of lake trout recruitment and each individual predictor that emerged in the top models.

2.5.3 Assessing factors related to lake trout biomass

Individual models for each continuous response of total and natural lake trout CPUE as a function of various predictors were fitted and ranked in a similar fashion. All continuous predictors were standardized using Z-score conversion. The global model for both responses was run using lm function (stats package v 4.1.2) and with the same predictors listed for the logistic regression global model (see section 2.5.2). Similar to the logistic regression, all predictor combinations of the global model were run using the glmulti package (v 1.0.8) with a maximum of three predictors per model. Top models for both responses were ranked and assessed for strength based on the same criteria as the logistic regression (see section 2.5.2). I verified homoskedasticity and normality of residuals in top models to satisfy the assumptions of regression. Univariate linear regressions were used to visualize the relationship of each response variable with the individual predictions that were selected for in the top models.

3. Results

3.1 General description of fish communities and lake characteristics

Lake specific results of all candidate chemical, physical and biological predictors, including those mentioned in this section, can be found in Table SI-3a and b. Contemporary pH of the 31 lakes surveyed ranged from 5.76 to 7.11, all suitable to sustain a reproducing lake trout population (Figure 2). The study showed ~20% increase in pH from a historical (1975-1990) average of 5.00 to a contemporary (2018-2020) average of 6.39. As for physical parameters, surveyed lakes varied from 16.5 ha (Kelly#27 Lake) to 2021.5 ha (Makobe Lake) in surface area, and 12.8 m (Gullrock Lake) to 61 m (Matagamasi Lake) in maximum depth. Depth of usable lake trout habitat varied from less than 1m in Gullrock Lake to a maximum of 41 m in Nelson Lake. Zooplankton biomass also varied widely across all lakes, with a minimum of 5.26 mg/m^3 in Ruth-Roy Lake to a maximum of 67.45 mg/m^3 in White Pine Lake.

The composition of fish communities across the sample lakes was highly variable. Fish species richness ranged from no fish species caught in Ruth-Roy Lake to 13 fish species in Johnnie Lake. Thirty different fish species were caught across all BsM and NORDIC efforts and only one fish species, slimy sculpin (*Cottus cognatus*), was caught solely in NORDIC nets (Table SI-4a and SI-4b). Species richness of Bell, Elboga and George Lake increased when NORDIC catch data were included. Pumpkinseed (*Lepomis gibbosus*), brook stickleback (*Culaea inconstans*), slimy sculpin, lake whitefish (*Coregonus clupeaformis*) and brown bullhead (*Ameiurus nebulosus*) were caught in NORDIC nets but not BsM nets in Bell, Elboga and George Lakes (Table SI-4a and b). Smallmouth bass were present in 18 of the 31 lake trout lakes with CPUE ranging from 118.08 g/net in Brodill Lake to 1603.88 g/net in Paradise Lake.

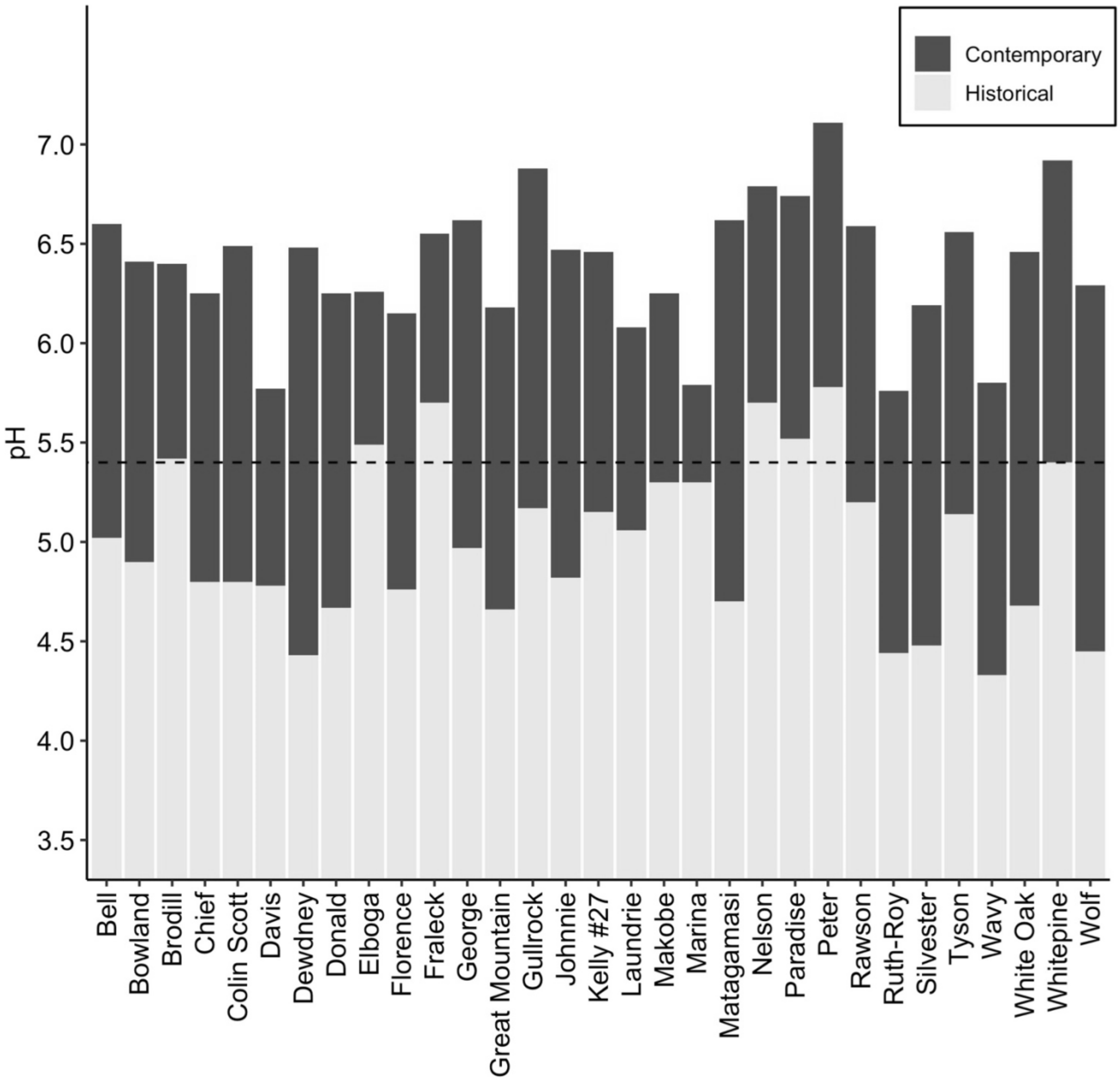

Figure 2 Stacked bar plot of historical (1975-1990; light grey) and contemporary (2018-2020; dark grey) pH across surveyed lakes. The dashed line represents the lake pH threshold of 5.4 above which lake trout reproduction is no longer limited.

Lake trout were caught in all but two lakes (Brodill, Ruth-Roy), and only stocked lake trout (i.e., all fin-clipped) were caught in three lakes (Fraleck, Peter, Wavy). When looking at evidence of recruitment within the 26 lakes where unclipped lake trout were caught, 17 lakes had evidence of recent recruitment (unclipped juveniles captured) and 9 lakes did not. Total and natural lake trout CPUE both ranged from a minimum of 0 g/net (Brodill, Ruth-Roy) to a maximum of 3228.1 g/net in Makobe Lake where only naturally-produced lake trout were caught. The high biomass in Makobe Lake can be attributed to the fact that all but six of the lake trout caught throughout the survey were above 1 kg. Despite Makobe Lake's abundance of lake trout, no juvenile lake trout smaller than 200 mm were caught. Colin Scott Lake was unique in the fact that it was the single lake where lake trout was the only fish species captured in the survey, and still had a relatively high natural lake trout CPUE of 723.38 g/net and natural juveniles present. Dewdney Lake was also distinctive in that stocked lake trout were found throughout the survey despite having no records of being stocked by the provincial government; it is likely that this population was recolonized from lake trout migrating from a neighbouring lake (MNDMNRF 2020). Evidence of lake trout migration was also found in the same chain of Dewdney, Wolf and Silvester Lake, where lake trout were still extirpated of when surveyed in the early 2000s (Selinger et al. 2006) and were never stocked with lake trout, yet now have reproducing lake trout populations, other than Silvester Lake where only adult lake trout were caught.

3.2 Conditions associated with sustainable lake trout populations

3.2.1 Patterns in water chemistry across lake trout lakes

The PCA of water chemistry identified three PCs for use in subsequent modelling (Table SI-5). Based on PC variable loadings of above 0.3, historic and contemporary pH, $\log_e$ alkalinity and [Ca] dominated and loaded negatively on PC1. PC2 was dominated by $\log_e$ Secchi depth (-), $\log_e$ chloride (+), [SO_4] (-), DOC (+) and $\log_e$ [Al] (+). PC3 was dominated and loaded positively by $\log_e$ [Cu] and $\log_e$ [Ni]. PC1 explained 27% of variance, PC2 explained 25% of variance and PC3 explained 16% of variance. In general, lower values of pH and alkalinity were associated with lower values of calcium on PC1, seeming to represent various ionic measures (Figure 3). Higher [DOC], chloride and [Al] were associated with lower secchi and [SO_4] on PC2, seeming to represent parameters associated to DOC and water clarity (Figure 3).

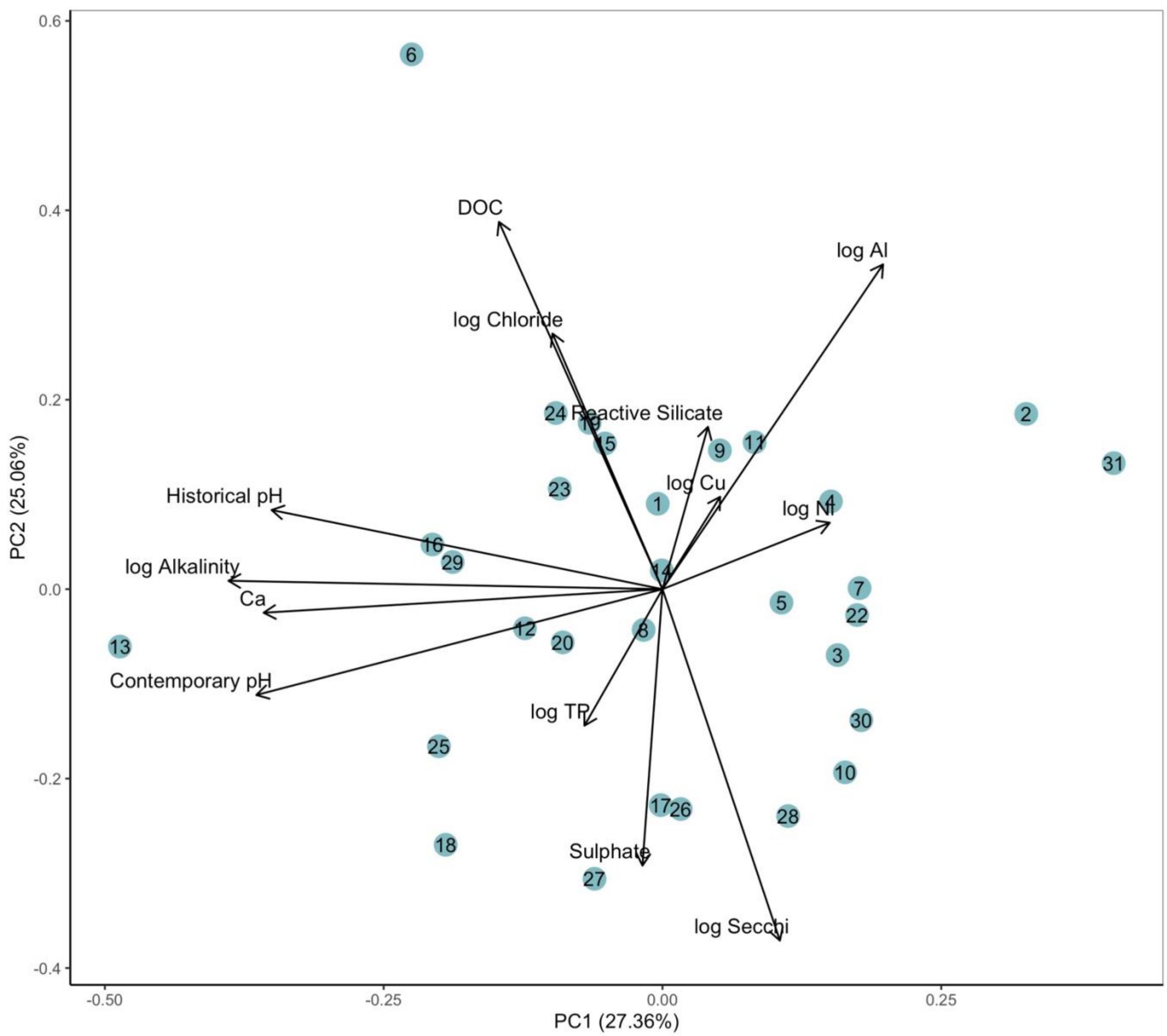

Figure 3 Biplot of the first two principal components resulting from a Principal Components Analysis of 13 water chemistry variables across 30 surveyed lakes (blue points). Lake labels correspond to survey ID provided in Table 1. PC1 and PC2 explained 27.36% and 25.06% of variance, respectively.

3.2.2 Predicting lake trout recruitment

A single top model emerged for predicting lake trout recruitment, because the potential second top model did not meet the inclusion criteria of a ΔAICc < 2 (Table 3). Biological, physical and chemical predictor were all important in this top-ranked logistic regression model, which had an Akaike weight of 0.58, indicating relatively strong predictive power. Variables that were retained as predictors of lake trout recruitment were $\log_e$ usable lake trout habitat depth, $\log_e$ zooplankton biomass and PC2 (Secchi/chloride/[SO_4]/[DOC]/[Al]) (Table 3). Lake trout recruitment had a positive significant relationship with zooplankton biomass ($p = 0.04$) and a negative significant relationship with [DOC] and decreased Secchi depth ($p = 0.02$). The association between lake trout and depth of usable lake trout habitat was positive but not statistically significant.

The univariate relationships of lake trout recruitment with each individual emergent model predictor displayed similar results. Lake trout recruitment and $\log_e$ usable depth displayed a positive association but no significance (Figure 4). The univariate relationship between presence of recruitment and $\log_e$ zooplankton biomass was positive but unlike the multi predictor model (Table 3), this relationship was also not significant (Figure 5). The regression between lake trout recruitment and water chemistry PC2 was the only one considered statistically significant ($p=0.009$; Figure 6). When broken down into the five dominant variables of PC2, the strongest relationships were with $\log_e$ secchi (coef: 3.77 ± 1.53; $p=0.01$), [DOC] (coef: -0.99 ± 0.40; $p=0.01$) and $\log_e$ [Al] (coef: 36.31 ± 15.68; $p=0.02$), although all relationships were at least marginally significant. Overall, the strongest predictor of lake trout recruitment was water chemistry PC2.

Table 3 Results of a top ranked logistic regression model to determine factors facilitating lake trout recruitment in acid-damaged lakes. All combinations of predictors were modelled, with a maximum criterion of three predictor variables per model. Models with a ΔAICc (Akaike's information criterion corrected for small sample size) < 2 were selected, the second model exceeded a ΔAICc < 2, and only the first model was kept.

Model metrics				Standardized coefficients (Mean ± SE)		
Rank	AICc	ΔAICc	Weight	Usable Depth[a]	Zoo Biomass[a]	PC2
1	32.47	0	0.58	0.93±0.65	1.80±0.87*	-2.76±1.16*

[a] transformation of $\log_e(x+1)$ applied
significance levels: *** p<0.001; ** p<0.01; * p<0.05, ^ p<0.1; no asterisk = non-significant

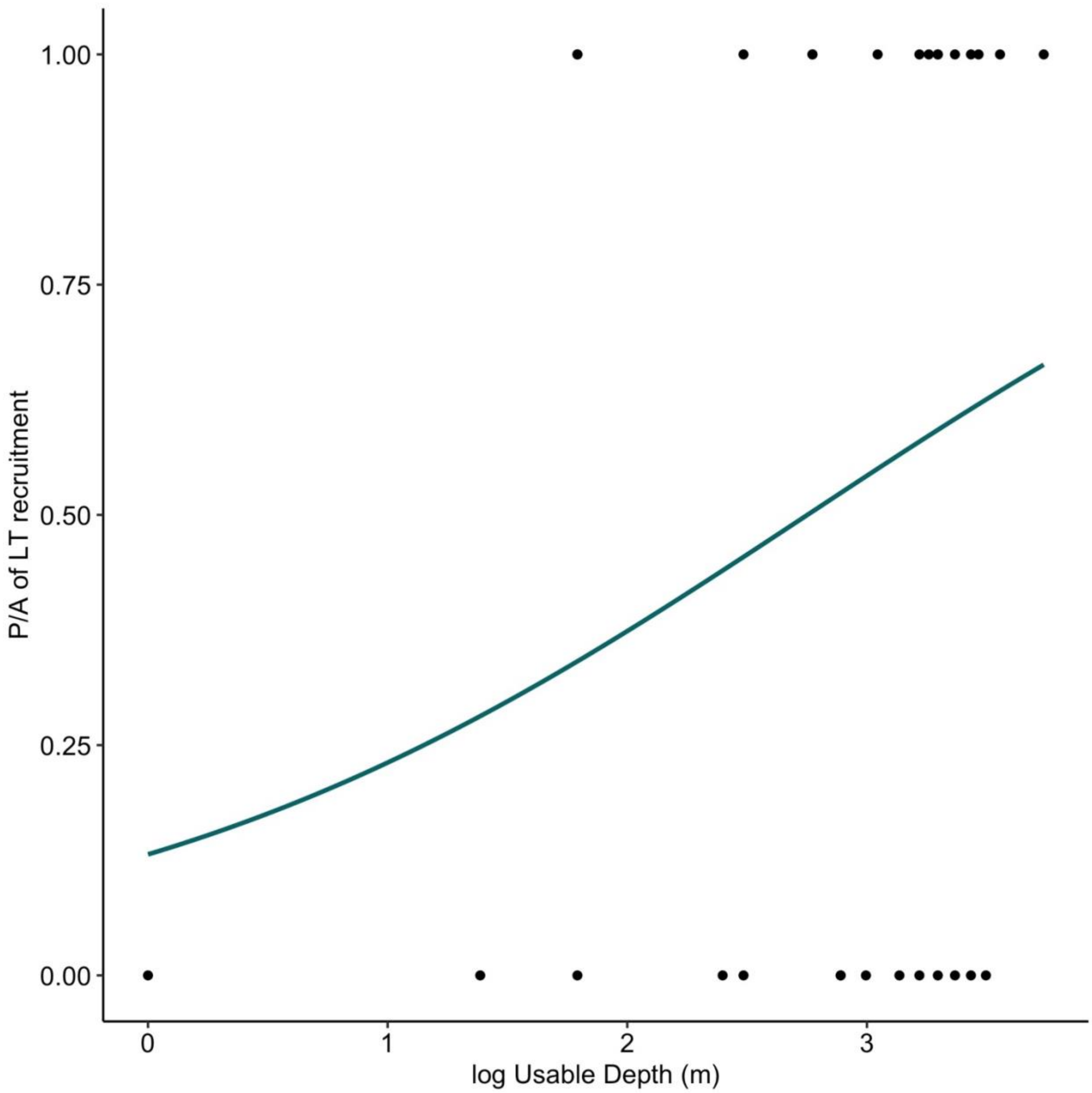

Figure 4 Logistic regression of lake trout recruitment and $\log_e$ usable depth of lake trout habitat. Regression coefficient is 0.69 ± 0.55 (p=0.21). Fit line represents maximum likelihood estimation of model parameters.

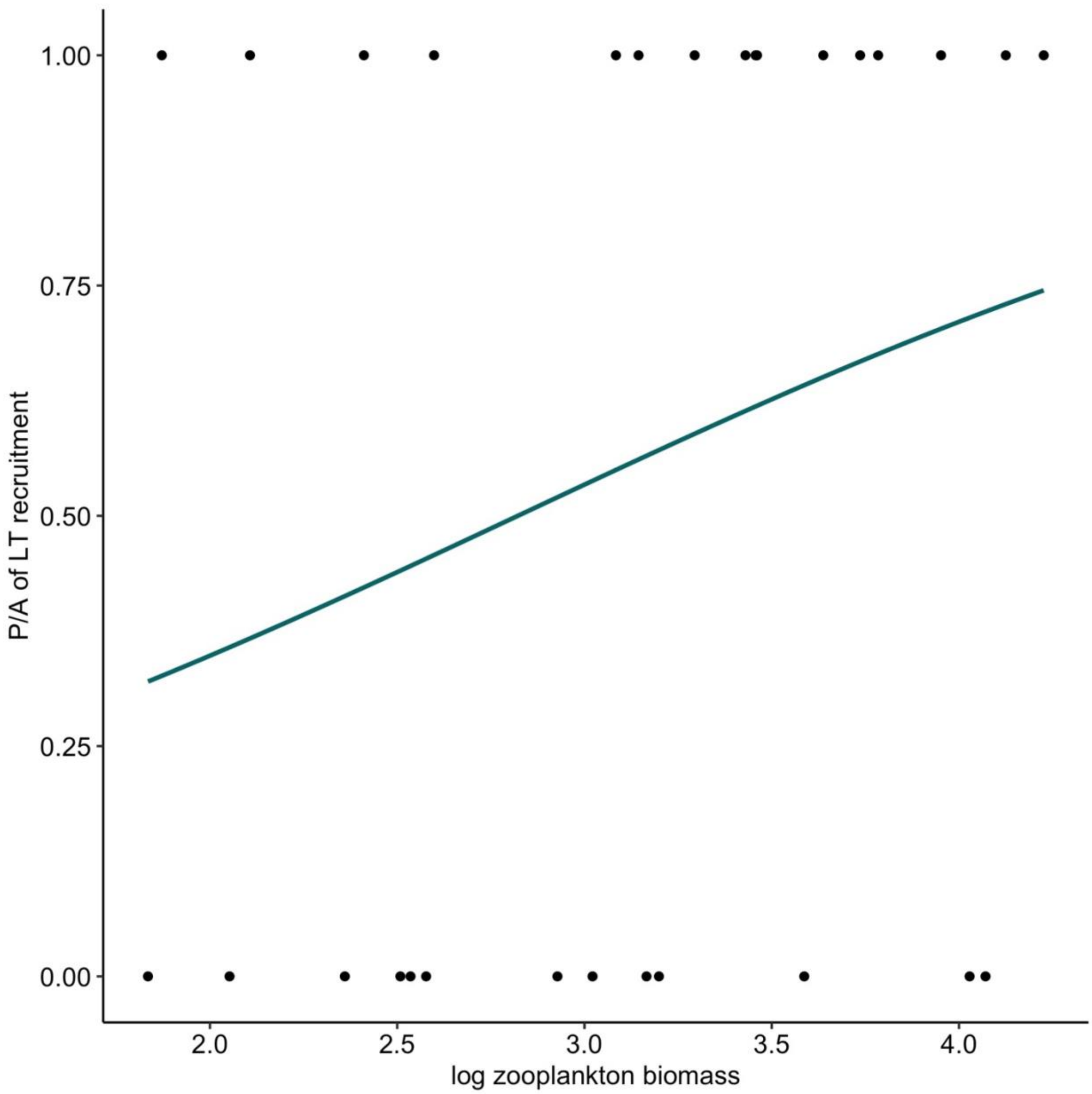

Figure 5 Logistic regression of lake trout recruitment and $\log_e$ zooplankton biomass. Regression coefficient is 0.76 ± 0.57 ($p=0.18$). Fit line represents maximum likelihood estimation of model parameters.

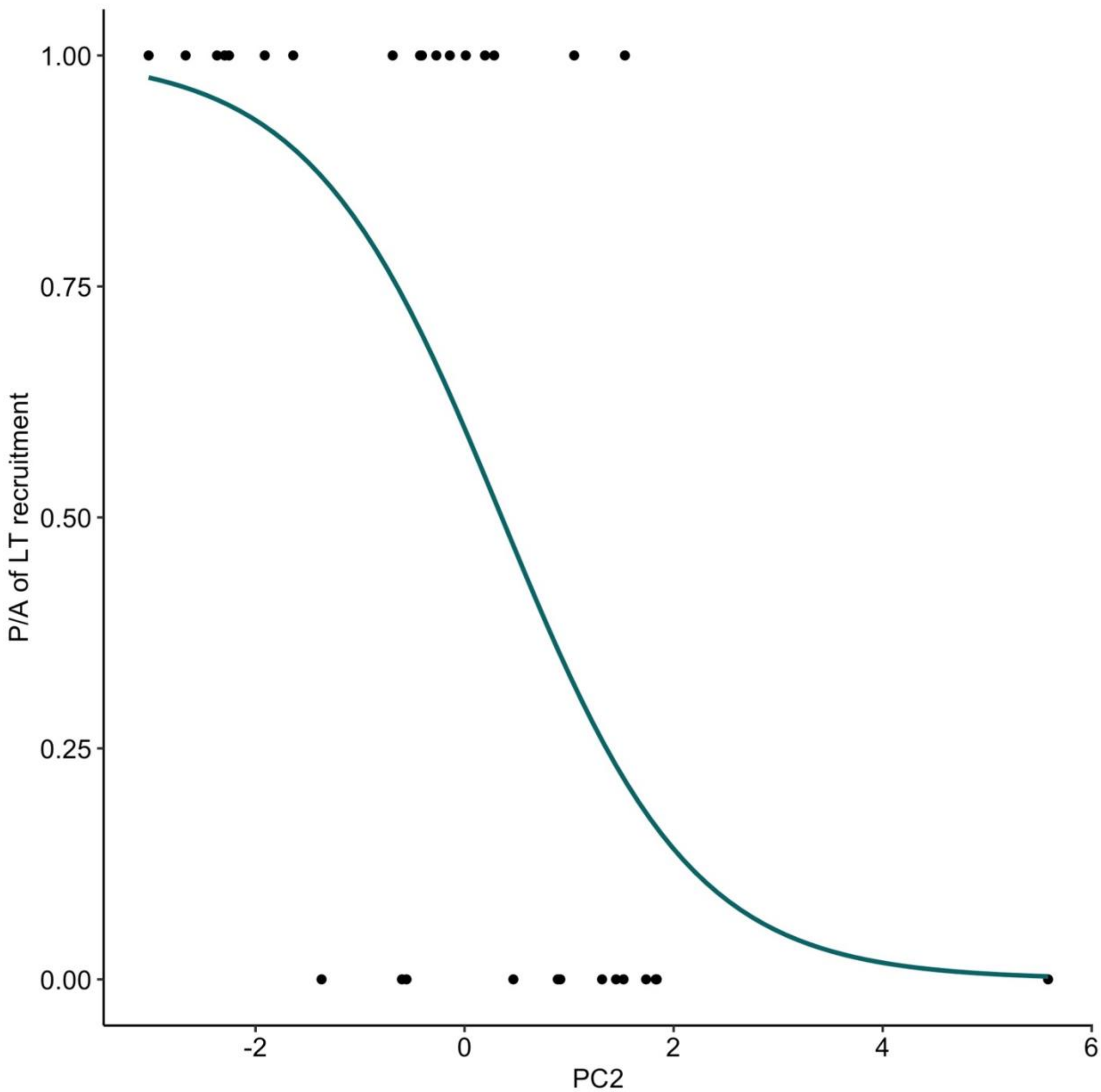

Figure 6 Logistic regression of lake trout recruitment and water chemistry PC2 (Secchi/chloride/[SO4]/[DOC]/[Al]). Regression coefficient is -1.10 ± 0.42 (p=0.009). Fit line represents maximum likelihood estimation of model parameters. Models of individual water chemistry parameter from PC2 can be found in Figure 7.

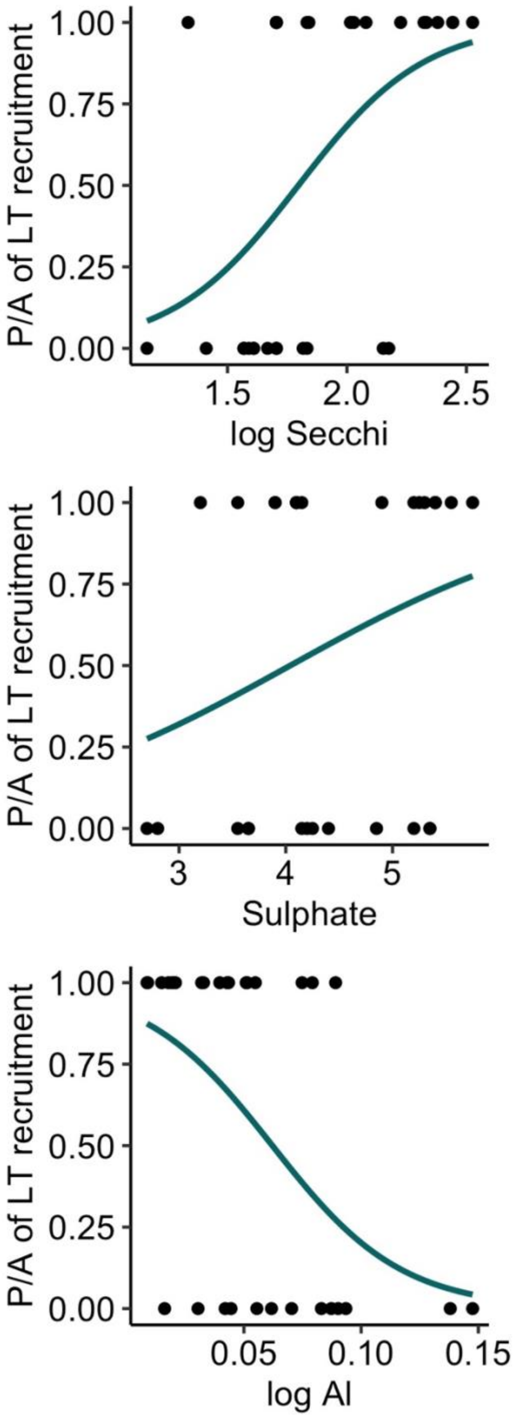

Figure 7 Logistic regressions of the univariate relationships between lake trout recruitment and $\log_e$ secchi (coef: 3.77 ± 1.53; p=0.01), $\log_e$ chloride (coef: -10.97 ± 5.80; p=0.06), sulphate (coef: 0.72 ± 0.47; p=0.1), DOC (coef: -0.99 ± 0.40; p=0.01) and $\log_e$ Aluminum (coef: -36.31 ± 15.68; p=0.02). Each water chemistry parameter was a primary contributor to PC2. Fit lines represent maximum likelihood estimation of model parameters.

3.2.3 Predicting total lake trout biomass

One top model emerged for predicting total lake trout CPUE based on ΔAICc values. The single model performed well with a weight of 0.51 and an R^2 of 0.47, whereas the second model dropped to a weight of 0.12 and was not kept for interpretation (Table 4). The predictors present in this top model included $\log_e$ usable lake trout habitat depth, $\log_e$ zooplankton biomass and the presence of lake trout stocking. All parameter estimates were statistically significant ($p<0.05$) other than $\log_e$ usable lake trout habitat depth, which was still marginally significant ($p<0.1$; Table 4). Total lake trout CPUE had positive relationships with depth of usable lake trout habitat, zooplankton biomass, and the presence of lake trout stocking (Table 4).

The univariate regression plots of $\log_e$ total lake trout CPUE with each individual top model predictor followed a similar trend but the univariate relationships were not as strong. No significant relationship was present between $\log_e$ total lake trout CPUE and $\log_e$ usable depth (Figure 8), a strong positive relationship was present with $\log_e$ zooplankton biomass ($p=0.005$; Figure 9) and no relationship was present with lake trout stocking (Figure 10). Overall, the strongest predictor of total lake trout biomass was zooplankton biomass.

Table 4 Results of a top ranked multiple regression model to determine factors contributing to total lake trout catch per unit effort in acid-damaged lakes. All combinations of predictors were modelled, with a maximum criterion of three predictor variables per model. Models with a ΔAICc (Akaike's information criterion corrected for small sample size) < 2 were selected, the second model exceeded a ΔAICc < 2, and only the first model was kept. R squared is adjusted.

Model metrics					Standardized coefficients (Mean ± SE)		
Rank	AICc	ΔAICc	Weight	R^2	Usable Depth[a]	Zoo Biomass[a]	Stocking p/a
1	102.80	0	0.51	0.47	0.51±0.27^	1.17±0.29***	1.67±0.61*

[a] transformation of $\log_e(x+1)$ applied
significance levels: *** p<0.001; ** p<0.01; * p<0.05, ^ p<0.1; no asterisk = non-significant

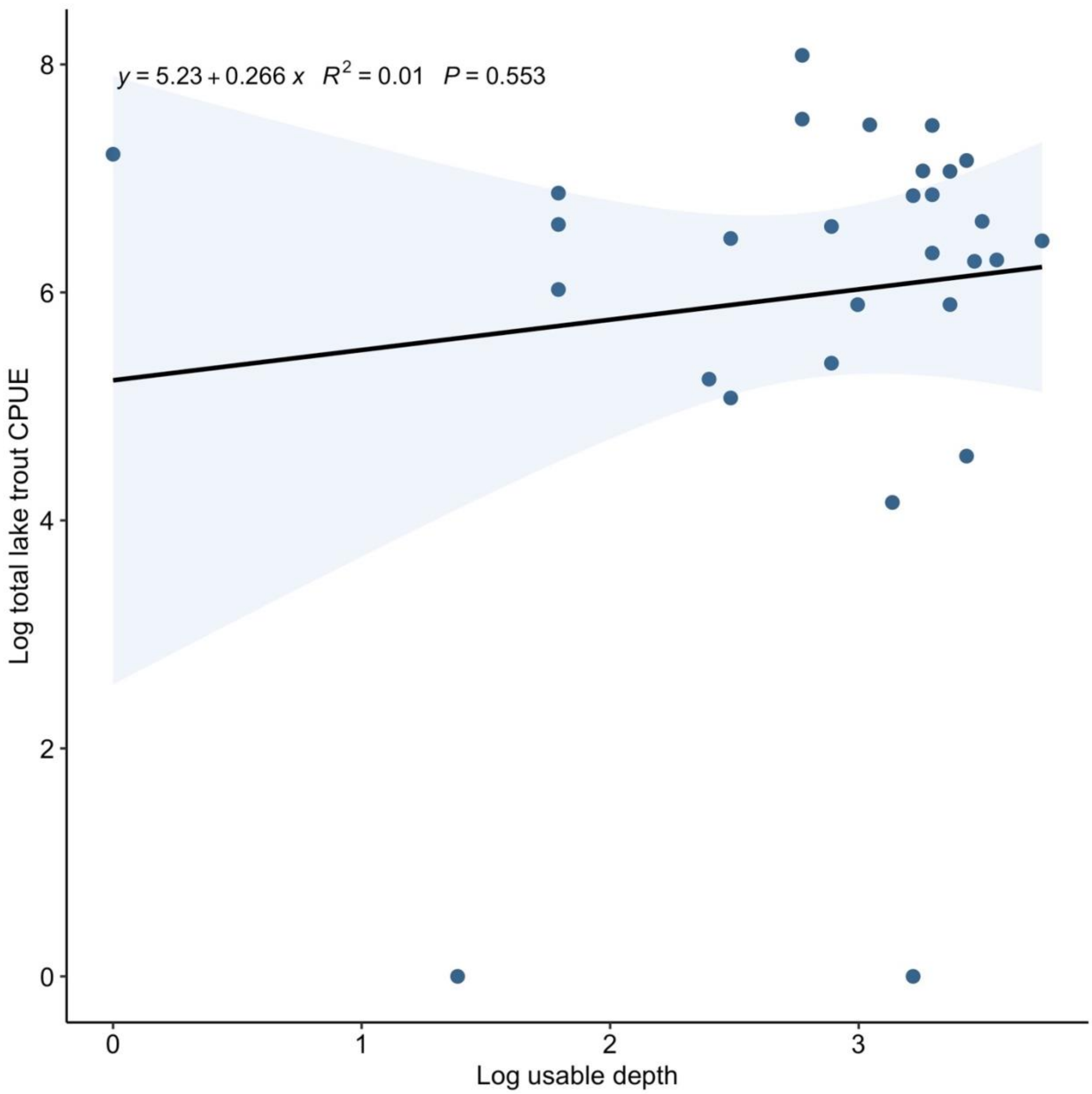

Figure 8 Linear regression of $\log_e$ total lake trout catch per unit effort and $\log_e$ usable depth of lake trout habitat. Line represents ordinary least squares regression fit, and blue shading represents a 95% confidence interval.

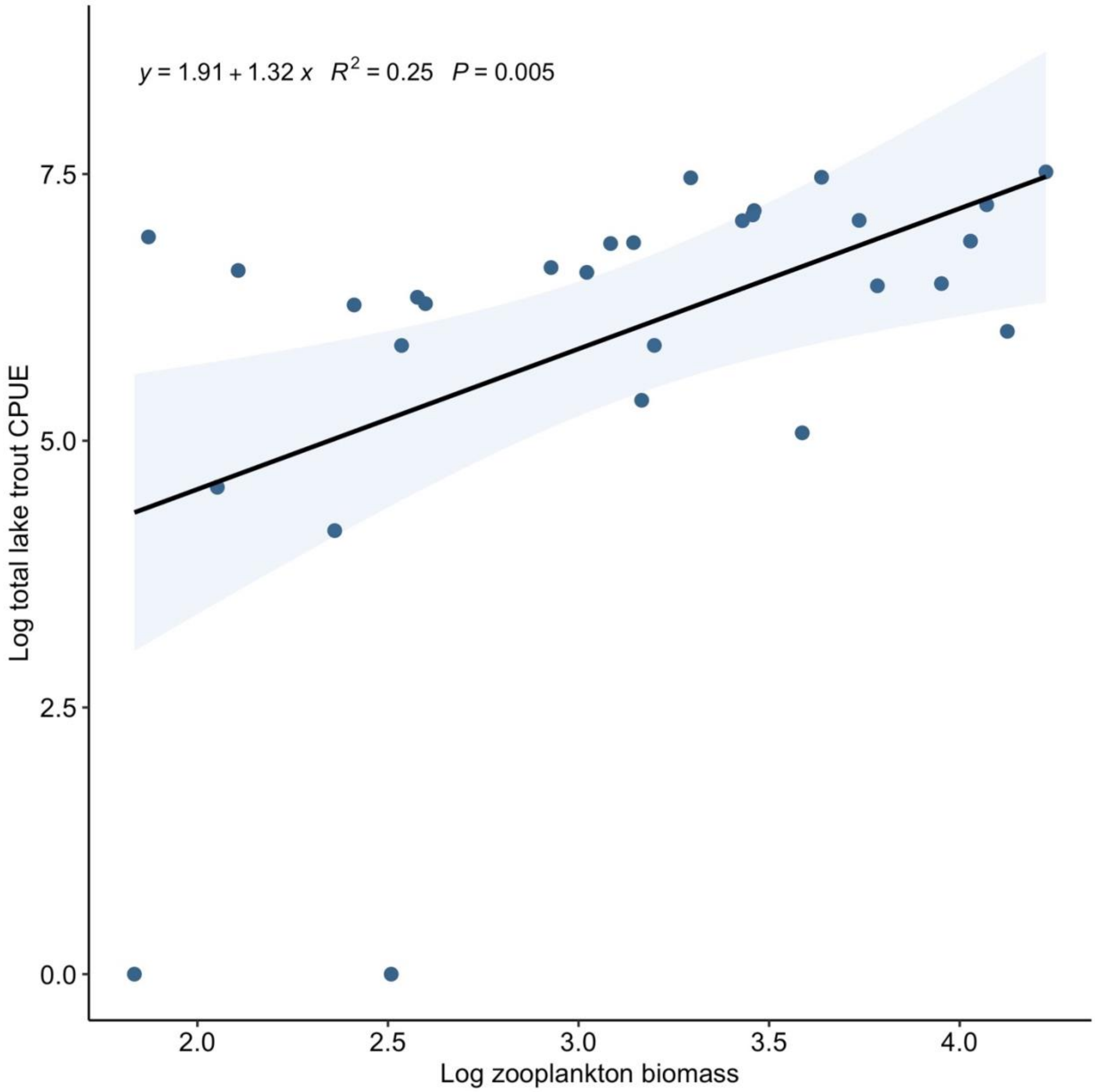

Figure 9 Linear regression of $\log_e$ total lake trout catch per unit effort and $\log_e$ zooplankton biomass. Line represents ordinary least squares regression fit, and blue shading represents a 95% confidence interval.

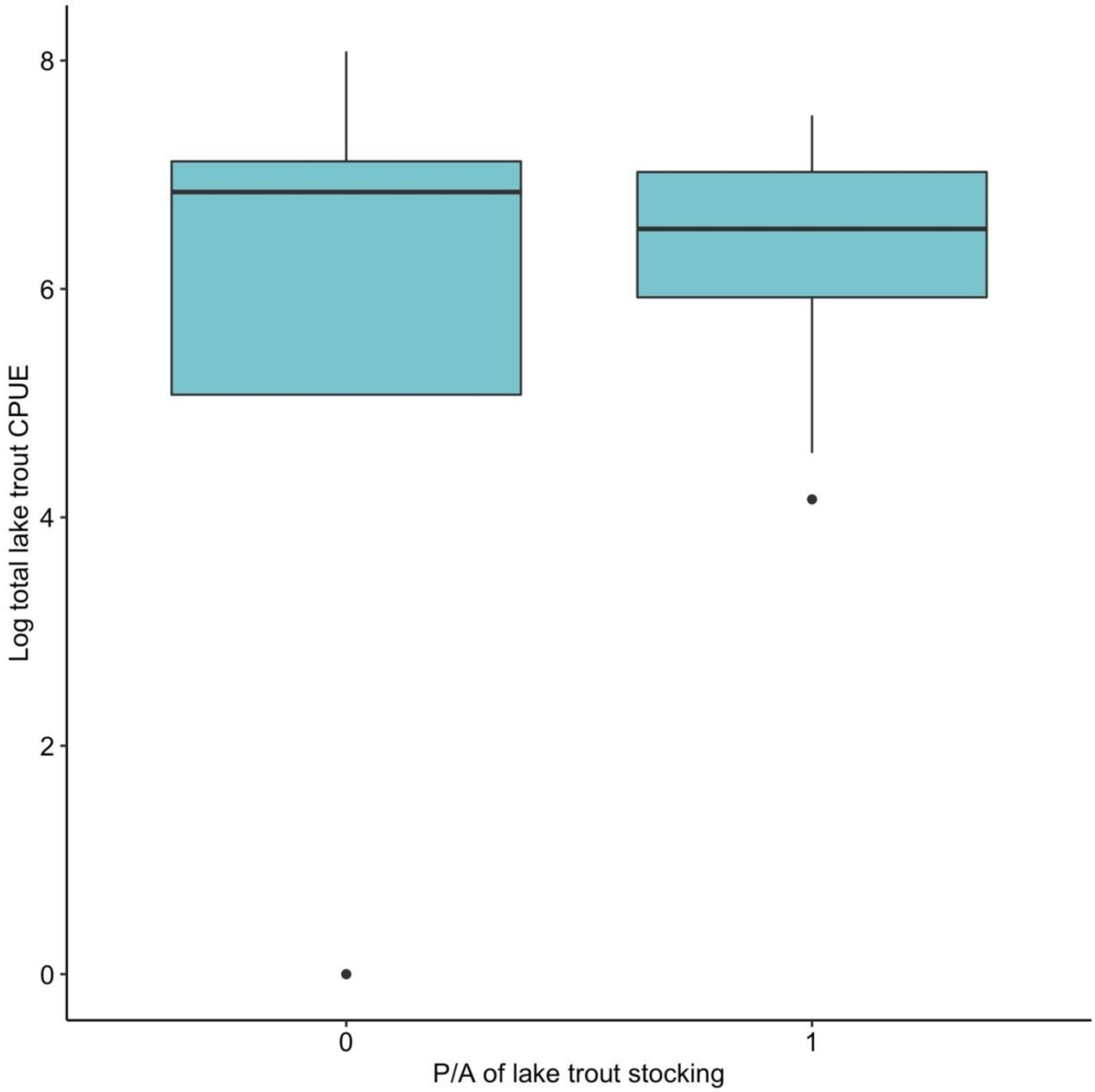

Figure 10 Box plot of $\log_e$ total lake trout catch per unit effort in relation to the presence (1) or absence (0) of lake trout stocking. A Welch two sample t-test resulted in a p value of 0.3.

3.2.4 Predicting natural lake trout biomass

Physical, biological and chemical predictors all accounted for variance of natural lake trout CPUE. Only one top model emerged for predicting natural lake trout CPUE, because the potential second top model did not meet the criterion of $\Delta AICc < 2$ (Table 5). The model selected performed well and represented a Akaike weight of 0.61, whereas the following potential model dropped to a weight 0.16. As indicated in Table 5, variables that were retained as predictors of natural lake trout CPUE were $\log_e$ usable lake trout habitat depth, $\log_e$ zooplankton biomass and PC2 (Secchi/chloride/[SO_4]/[DOC]/[Al]). Natural lake trout CPUE had a positive relationship with zooplankton biomass ($p = 0.002$) and a negative relationship with [DOC] and decreased Secchi depth ($p = 0.03$). The association with depth of usable lake trout habitat was positive although the coefficient was small and non-significant (Table 5).

The univariate relationships of $\log_e$ natural lake trout CPUE with each emergent predictor were very similar to those found in the top model. A non-significant relationship was present with $\log_e$ usable depth (Figure 11), a strong positive relationship was present with $\log_e$ zooplankton biomass ($p=0.01$; Figure 12) and a marginally significant negative relationship was present with water chemistry PC2 ($p=0.07$; Figure 13). When broken down to univariate relationships with PC2's primary contributor variables, the only statistically significant relationship present was between $\log_e$ natural lake trout CPUE and $\log_e$ aluminum ($p=0.02$; Figure 14). The strongest predictor of natural lake trout biomass was zooplankton biomass.

Across all three response variables of lake trout recruitment, total and natural lake trout CPUE, $\log_e$ usable depth of lake trout habitat and $\log_e$ zooplankton biomass were selected as predictors in top models. The relationship with $\log_e$ zooplankton biomass was always statistically significant and was the strongest relationship in predicting total and natural CPUE. Water chemistry PC2 was the strongest predictor of lake trout recruitment. The single top model of usable depth, zooplankton biomass and PC2 selected for predicting lake trout recruitment was identical to the model selected for predicting natural lake trout CPUE. Both linear multiple regression models met model assumptions for normality and homoscedasticity based on visual assessment of residuals.

Table 5 Results of a top ranked multiple regression model to determine factors contributing to natural lake trout catch per unit effort in acid-damaged lakes. All combinations of predictors were modelled, with a maximum criterion of three predictor variables per model. Models with a ΔAICc (Akaike's information criterion corrected for small sample size) < 2 were selected, the second model exceeded a ΔAICc < 2, and only the first model was kept. R squared is adjusted.

Model metrics					Standardized coefficients (Mean ± SE)		
Rank	AICc	ΔAICc	Weight	R^2	Usable Depth[a]	Zoo Biomass[a]	PC2
1	123.66	0	0.61	0.36	0.15±0.41	1.44±0.42**	-0.93±0.40*

[a] transformation of $\log_e(x+1)$ applied
significance levels: *** p<0.001; ** p<0.01; * p<0.05, ^ p<0.1; no asterisk = non-significant

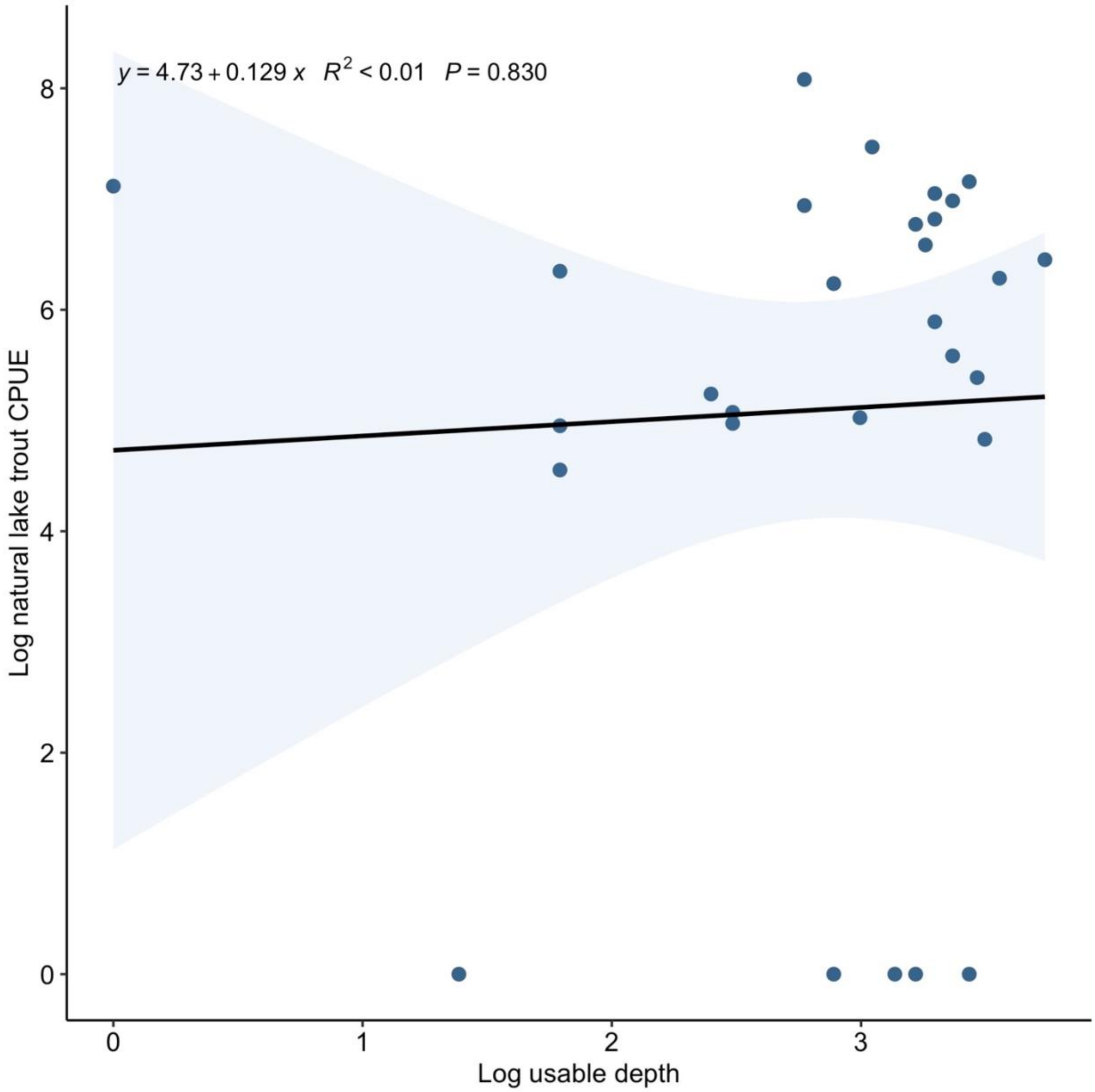

Figure 11 Linear regression of $\log_e$ natural lake trout catch per unit effort and $\log_e$ usable depth of lake trout habitat. Line represents ordinary least squares regression fit, and blue shading represents a 95% confidence interval.

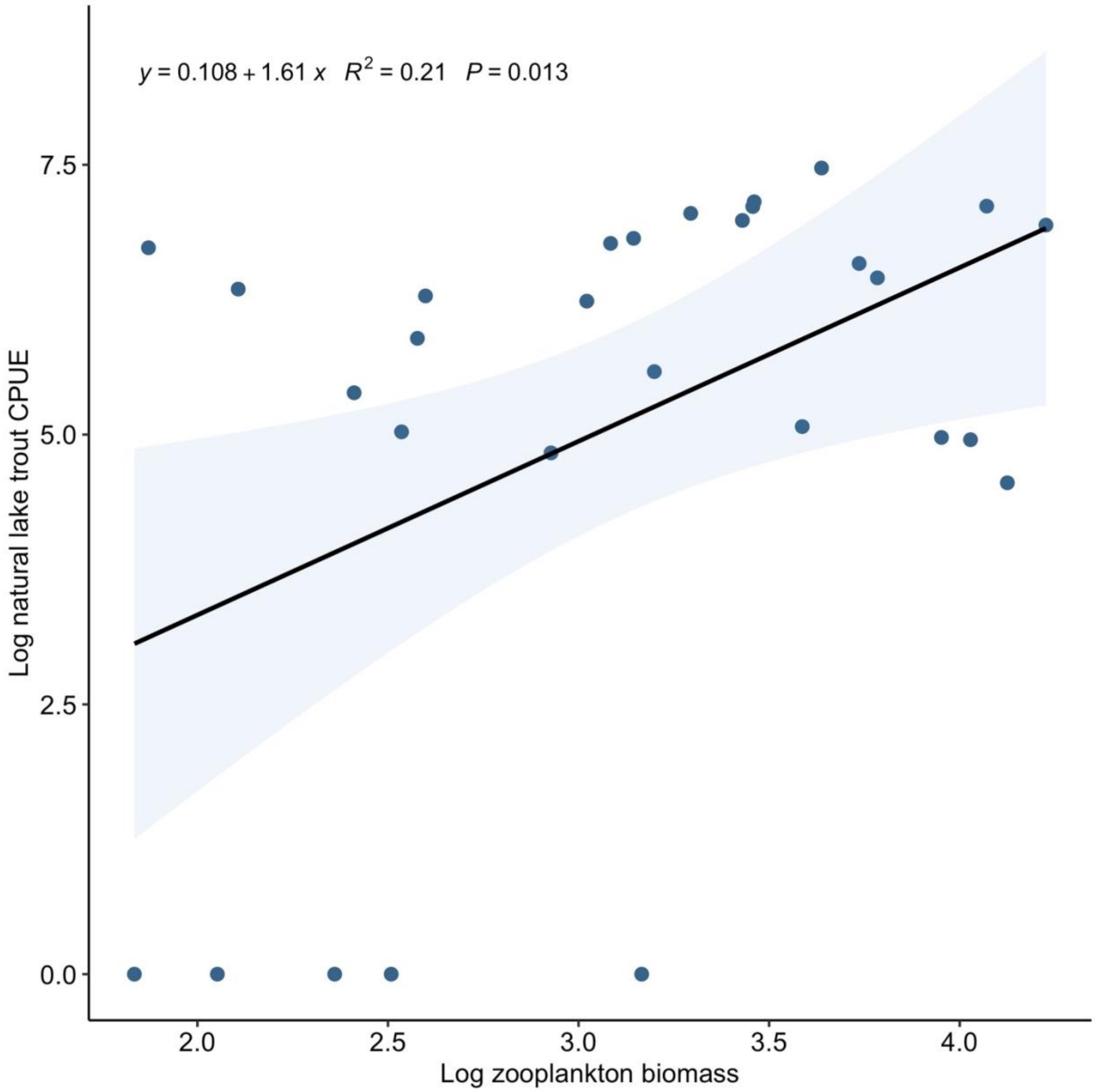

Figure 12 Linear regression of loge natural lake trout catch per unit effort and loge zooplankton biomass. Line represents ordinary least squares regression fit, and blue shading represents a 95% confidence interval.

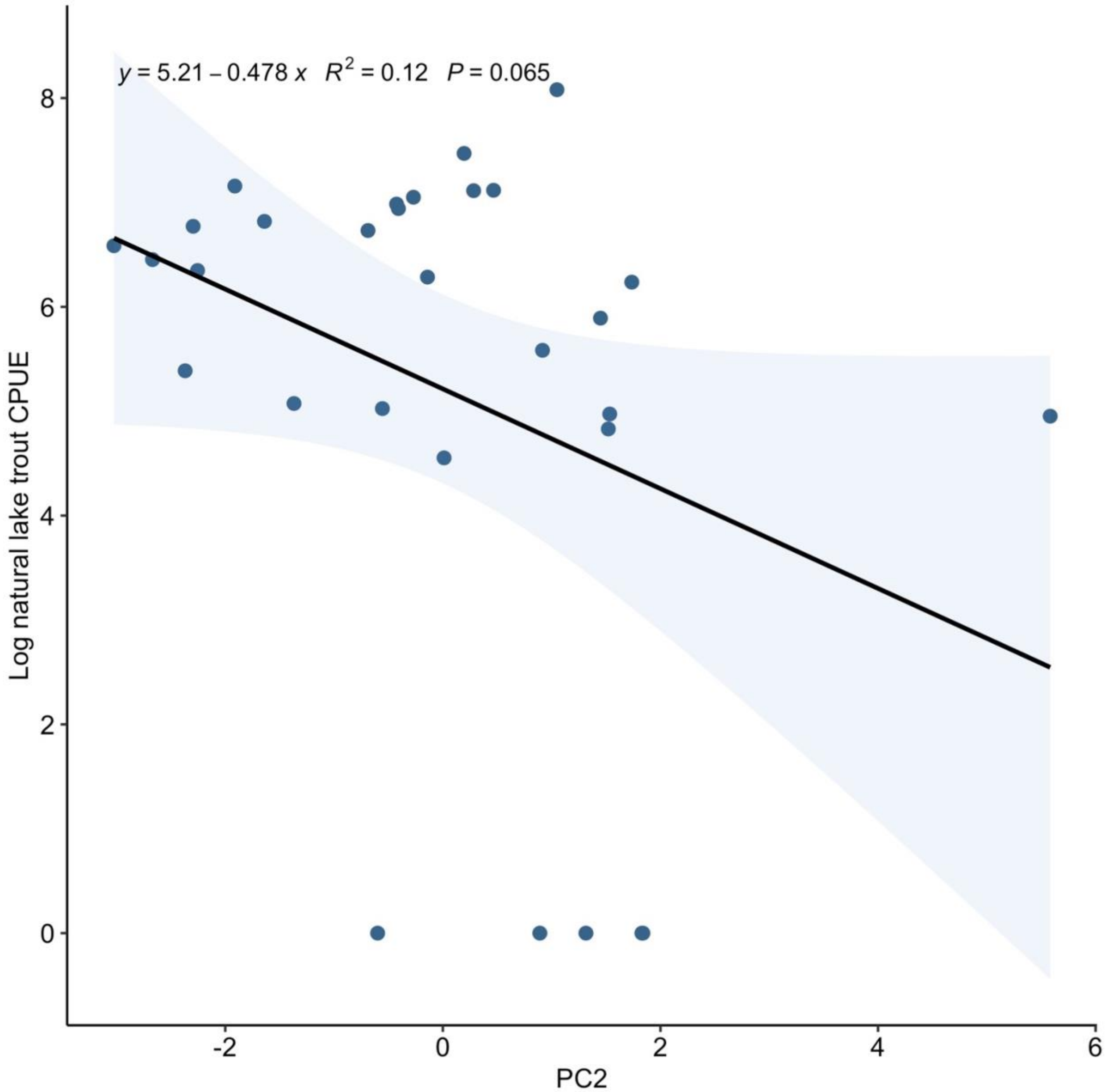

Figure 13 Linear regression of $\log_e$ natural lake trout catch per unit effort and water chemistry PC2 (Secchi/chloride/[SO4]/[DOC]/[Al]). Models of each individual water chemistry parameter from PC2 can be found in Figure 14. Line represents ordinary least squares regression fit, and blue shading represents a 95% confidence interval.

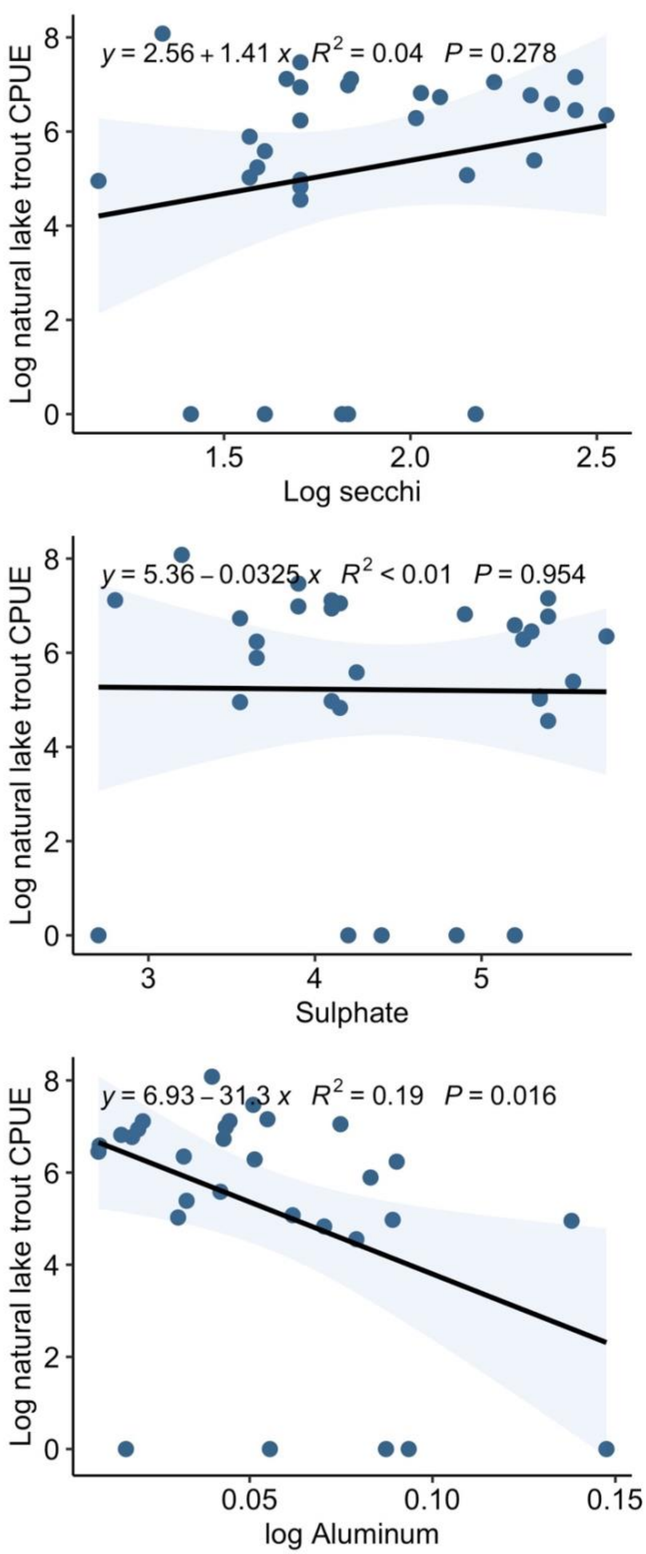

Figure 14 Linear regressions of the univariate relationships between lake trout recruitment and loge secchi, $\log_e$ chloride, sulphate, dissolved organic carbon and $\log_e$ Aluminum. Each water chemistry parameter was a primary contributor to water chemistry PC2. Lines represent ordinary least squares regression fits, and shading represents 95% confidence intervals.

4. Discussion

The findings of this study indicate that damaged lake trout lakes across Sudbury's acid deposition zone are on a clear path to recovery from acidification. Contemporary pH across study lakes has risen and is now at an average of 6.39. Lake trout have been introduced or naturally colonized in all but two of the study lakes and are successfully reproducing in more than half of them. The majority of these restored trout populations have returned by means of ministry stocking or migration from neighbouring lakes, though a few populations appear to have survived through the acidification period and can now successfully reproduce. Despite returning to less acidic conditions, lake trout now face changes in community composition and water chemistry. Fewer cyprinids and other prey fish species are now present, smallmouth bass have invaded and zooplankton are now likely a primary food source for lake trout, making a lake like Colin Scott possible, where lake trout are the only fish species present. Chemically, the increase in pH was accompanied by an increase in [DOC] and water colour causing a shift in the structure of the water column to a shallower thermocline. The results of my study provide an updated chemical, physical and biological characterization of Sudbury's unique lake trout lakes, and identify which conditions have aided in lake trout population biomass recovery and successful reproduction.

4.1 Influence of historical management

Not surprisingly, the history of hatchery stocking emerged as a significant predictor in the top model for predicting total lake trout CPUE, but did not contribute to any top models for lake trout successful recruitment or natural lake trout CPUE. This was to be expected since total lake trout CPUE was calculated using both natural and stocked lake trout caught. It was imperative that this work go beyond an assessment of recovery based on the persistence of the fish stocked in them (twenty-two of the 31 surveyed lakes were stocked) to determine whether aspects of the recovered environment allowed for lake trout populations to thrive. This was confirmed when stocking was not selected as a predictor in any top models for lake trout recruitment or for natural lake trout CPUE. This finding suggests that the fish stocking history itself is not enough to predict that an abundant and reproducing lake trout population will occur. The environment in which these fish are stocked is also key to their success in terms of creating a self-sustaining population. For this reason, I conclude that total lake trout CPUE is not a useful condition of lake trout population health because stocked fish are making up the majority of the catch and focus the remainder of my discussion on hypotheses and predictions related to the success of natural lake trout CPUE and recruitment success.

4.2 Influence of water chemistry parameters

Chemical predictors were frequently retained in top CPUE and recruitment models. As previously predicted, all surveyed lakes have recovered to a pH of above 5.4. Acid-recovery indicators such as pH and alkalinity were represented by PC1, which never emerged in any of the top models, further confirming that lake trout no longer seem to be limited by lake acidity. In contrast, PC2 (positively associated with DOC, negatively associated with Secchi) was retained as a predictor for both lake trout recruitment and natural lake trout CPUE. The relationship of each response with PC2 was negative, suggesting that lake trout recruitment and natural lake trout CPUE were negatively associated with [DOC] and positively associated with water clarity. This was not as I predicted based on the role of [DOC] in expanding cold water habitat (Snucins and Gunn 2000; Schindler and Gunn 2003), but consistent with literature on lake browning when high [DOC] can reduce productivity through shading (Karlsson et al. 2009) or may be related to lakes with more anoxia (Dillon et al. 2003). The significant univariate relationships of lake trout recruitment with $\log_e$ Secchi and [DOC] indicates that these variables are largely contributing to this negative relationship with PC2 (Figure 7). The average [DOC] of lakes without recruitment was 4.43 mg/L, approaching the maximum [DOC] of 5mg/L historically found in 90% of eastern North America's lake trout lakes (Schindler and Gunn 2003). Although increasing [DOC] is beneficial in creating more cold-water habitat, there appears to be a maximum to the beneficial range of [DOC]. Dissolved organic carbon concentrations across surveyed lakes ranged from 1.7 mg/L to 7.2 mg/L and all lakes with [DOC] above 4.6 mg/L (n=8) were without recruitment except White Pine Lake ([DOC] = 5.4mg/L). These results along with the negative (although non-significant) univariate relationship of $\log_e$ natural lake trout CPUE and [DOC] seem to demonstrate an inflection point of around 5mg/L at which [DOC] is no longer beneficial (Figure 14). A recent study by Jarvis et al. (2020) found a negative relationship between lake trout production and [DOC] and uses the decline in whole-lake primary production caused by decreased light attenuation (or Secchi) found by Karlsson et al. (2009) as a potential explanation. A decline in primary production results in a decline in biomass of higher trophic levels like zooplankton and fish (Karlsson et al. 2009). However, in both studies, DOC range extended to 16.8 mg/L, whereas lakes of my study only reached a maximum [DOC] of 7.2 mg/L. A negative relationship is therefore possible but further research should take place in order to determine a more precise point at which [DOC] may be harmful to lake trout.

Chloride was another water chemistry parameter that contributed to PC2 (loaded positively; Table SI-5). When plotted univariately, no relationship was found between natural lake trout biomass and chloride but a marginally significant relationship (p=0.06; Figure 7) was present between lake trout recruitment and $\log_e$ chloride. The primary driver of this relationship is likely Elboga lake, a lake with no recruitment and with the highest chloride concentration of 15.7 mg/L compared to an average of 0.74 mg/L across survey lakes, likely due to road salt runoff from Ontario Highway 144. A recent study on a lake of similar size to Elboga, found that elevated chloride concentrations can inhibit spring mixing due to road salt induced density differences across the water column (Wiltse et al. 2020). Without lake turnover, anoxic conditions are more prevalent and lake trout habitat is less abundant. The bottom 4m of Elboga Lake were anoxic (<2mg/L of DO), however Elboga's temperature and oxygen profile was taken in late August when seasonal oxygen depletion is most prevalent (Dillon et al. 2003).

Other chemical variables contributing to PC2 included [SO_4] (loaded negatively) and [Al] (loaded positively; Table SI-5). A marginally significant positive relationship was found when lake trout recruitment was plotted univariately with [SO_4] (Figure 7). This was not as I expected because a decrease in [SO_4] is a sign of chemical recovery from acidification (Keller et al. 2019). This marginal relationship is likely an indirect effect of decreased [SO_4] on [DOC] increase and Secchi decrease (Keller et al. 2019). Aluminum was likely another contributor to the negative relationship between lake trout and PC2. Univariate relationships of both lake trout recruitment and $\log_e$ natural lake trout CPUE with $\log_e$ Al were negative and statistically significant (Figure 7; Figure 14). Elboga and Ruth Roy Lake both had the most elevated [Al] of all surveyed lakes with 0.15 and 0.16 mg/L respectively and little to no natural lake trout present (140.5 g/net in Elboga and 0 g/net in Ruth-Roy). A similar study by Conlon et al. (1992) also found a negative relationship between lake trout presence and [Al] and determined a maximum [Al] of 0.16 mg/L in lakes with lake trout present. At concentrations of 0.2mg/L, Al toxicity can adversely affect growth and ability to feed in alevin lake trout (Gunn and Noakes 1987).

4.3 Influence of physical habitat characteristics

The physical predictor of usable depth of lake trout habitat came up in top models for both lake trout responses, although this positive relationship was never statistically significant (Table 3; Table 5). I had predicted this positive relationship based on the extensive literature surrounding the availability of oxythermal habitat for lake trout as a limiting factor in lake trout colonization and abundance (Dillon et al. 2003; Evans 2007; Jarvis et al. 2020; Lester et al. 2021). Although depth of lake trout habitat did contribute to my top models, the relationship may not have been strong because of the potential lack of precision of depth in estimating how much lake trout habitat is available in each lake. Volume of lake trout habitat may have been a stronger predictor because lake size and bathymetry were so variable across waterbodies and volume is frequently used in research in which lake trout habitat is measured (Dillon et al. 2003; Guzzo et al. 2017; Jarvis et al. 2020). Jarvis et al. (2020) found that lake volume below the thermocline was the strongest predictor of lake trout production ($kg \cdot ha^{-1} \cdot year^{-1}$) in a boosted regression tree analysis of 239 Ontario lakes, however these study lakes had a much broader range of surface area (21–34 518 ha) and maximum depth (12–125.95 m) relative to my study lakes. Additionally, a strong relationship with depth of usable lake trout habitat was not detected because availability of oxythermal habitat may not yet be a concern in my study lakes. Sudbury's systems are unique in that [DOC] is just now returning to pre-industrial levels (Meyer-Jacob et al. 2020) and has not yet reached the point at which oxygen depletion may take place. Research has shown an association between elevated [DOC] and a decline in lake DO, but study lakes had [DOC] > 10mg/L and small surface areas (<25 ha) (Craig et al. 2015; Couture et al. 2015).

4.4 Influence of biological community composition

As predicted, zooplankton biomass was a significant predictor for both lake trout recruitment and natural lake trout CPUE. Zooplankton are likely one of the primary prey for lake trout in my study lakes based on limited prey fish availability in the Sudbury region. Of the 31 lakes sampled for this project, no cyprinids were detected in 13 lakes and in the other 18, the majority contained only 3 or fewer cyprinid species (White Pine lake had four and Gullrock lake had six species of cyprinids; Table SI4a and 4b). In addition to having so few cyprinids, 18 of the survey lakes were invaded by the warm water smallmouth bass, likely further depleting the prey fish available (Vander Zanden et al. 1999, 2004; Kaufman et al. 2009). A positive relationship between lake trout and zooplankton was therefore to be expected and further speaks to the adaptability of lake trout (Gunn and Louste-Fillion *in-review*). Smallmouth bass CPUE did not emerge in any top models, despite my prediction. Smallmouth bass out-competing lake trout for littoral prey and reducing lake trout abundance is prominent in the literature (Vander Zanden et al. 1999, 2004; Kaufman et al. 2009) but may not have been detected in my lakes because prey fish were already depleted from acidification and lake trout have likely adapted to feed on pelagic zooplankton. Smallmouth bass were also only detected in 18 of my surveyed lakes, therefore a larger sample size may have been necessary to detect a relationship with smallmouth bass CPUE.

The presence of large Cladocera and fish species richness were both factors that were predicted to emerge as drivers of lake trout reproduction and abundance but did not. The presence of large-bodied zooplankton taxa was predicted to result in a more productive lake trout population based on the theory by Konkle and Sprules (1986) that lake trout size select zooplankton prey. I have not found extensive literature on this theory, but lake trout are visual predators with good eyesight that permits them to hunt in the dark hypolimnion (Marsden et al. 2021). My sample size was limited with only 10 replicates without the presence of large Cladocera, therefore more research should take place before this theory can be refuted. Fish species richness was predicted to negatively impact lake trout production based on literature that lake trout do best in more simple food webs, with less competition for prey (Evans and Olver 1995; Wilson and Mandrak 2003; Selinger et al. 2006). In general, my study lakes were low in fish species richness (range of 0-13, median of 7; Table SI-3b) and low in large piscivore CPUE (nine lakes were without large piscivores: Table SI-3b), so complexity of fish communities was likely not at a level to exert a negative influence. This combined with lake trout likely depending on invertebrates as a primary prey source, could explain why fish species richness was not identified as an important predictor in my models.

4.5 Management implications

My study shows that simply stocking a lake is not enough to generate an abundant and reproducing lake trout population. The physical, chemical and biological environment in which reintroduction occurs are critical. Stocking lake trout may actually be harmful to already established reproducing lake trout population because of increased competition for prey and the potential of cannibalism. For example, Makobe Lake, although never stocked, had the highest lake trout biomass but no detection of juvenile lake trout of < 200mm in total length. This could be because juvenile lake trout are difficult to detect in a BsM survey (Brekke 2017) or perhaps because lake trout themselves are a stress on recruitment. Loss of native lake trout from stocked lake trout and loss of juvenile lake trout from cannibalistic adults have both been documented elsewhere (Evans and Willox 1991; Evans 2007). Rawson Lake showed clear evidence of lake trout cannibalism with the largest lake trout caught (>5kg, nearly 5x bigger than the second largest lake trout at 1.2kg) having stomach contents full of juvenile lake trout. The presence of natural recruitment should therefore be determined first and the potential for negative effects on natural population production need to be considered before stocking decisions are made.

Chemically and physically, the most important predictors to emerge were [DOC] and usable depth of lake trout habitat. In my study, the majority of lakes with [DOC] above 5 mg/L had lower lake trout biomass and less evidence of recruitment. In cases of higher [DOC], volume of lake trout habitat and zooplankton biomass should both be considered before lake trout are stocked. A biological factor that was previously considered when selecting which lakes to stock with lake trout is whether an abundance of prey fish is available for them to feed on. My study findings that a lake trout population can survive without any other fish species present, demonstrates that lake trout can be stocked in a lake without prey fish, as long as an abundant zooplankton population is available. My study did not find smallmouth bass to be as detrimental to lake trout as predicted, perhaps due to the ability of Sudbury's lake trout to survive with so few prey fish in their ecosystems. Another management relevant finding in my thesis was the ability of lake trout to travel between interconnected lakes like Dewdney, Wolf and Silvester, a trait that has been found in lake trout before based on interconnectivity of lakes and scarcity of local prey (Binder et al. 2021). This finding will inform the ministry to prioritize stocking the most upstream lakes and to hesitate stocking lakes that will likely be colonized from neighbouring lakes, since it is best not to mix strains of lake trout.

Conclusion

By evaluating determinants of lake trout vulnerability and resilience, this study contributes to understanding ecological recovery trajectories and ongoing challenges for the restoration of aquatic biodiversity in the region. Sudbury, Ontario faced widespread acidification and biodiversity loss and the return of reproducing and abundant lake trout speaks to the importance of effective pollution control, regulations and technologies. The unique systems these lake trout inhabit have simplified fish communities with few prey fish and lake trout populations still manage to achieve substantial biomass and successfully reproduce. My results show that an abundant zooplankton population and a limited concentration of DOC and aluminum are associated with thriving lake trout populations. Future studies including stable isotope analyses to confirm lake trout diet could strengthen my findings that lake trout CPUE is dependent on zooplankton biomass and that lake trout can survive in systems without prey fish to feed on. The relationship between lake trout and [DOC] should also be investigated further to determine a clear threshold of [DOC] or associated variable at which lake trout biomass begins to decline. Finally, other measures of lake trout population recovery status should also be explored such as number of age classes within the population and yearly growth of juvenile fish. Overall, my research findings provide an update on the status of lake trout populations in historically acidified lakes in the Sudbury area, identify important determinants of a recruiting and abundant lake trout population and should help ensure the best management practices in the future.

Literature Cited

Beamish, R.J. 1976. Acidification of lakes in Canada by acid precipitation and the resulting effects on fishes. Water. Air. Soil Pollut. **6**(2–4): 501–514. Springer. doi:10.1007/BF00182888.

Beggs, G.L., and Gunn, J.M. 1986. Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. *In* Acidic Precipitation. *Edited by* H.C. Martin. Springer Netherlands, Dordrecht. pp. 711–717. doi:10.1007/978-94-009-3385-9_73.

Binder, T.R., Marsden, J.E., Kornis, M.S., Goetz, F.W., Hellström, G., Bronte, C.R., Gunn, J.M., and Krueger, C.C. 2021. Movement ecology and behavior. *In* The lake charr *salvelinus namaycush*: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 203–252. doi:10.1007/978-3-030-62259-6_1.

Bonnet, X., Shine, R., and Lourdais, O. 2002. Taxonomic chauvinism. Trends Ecol. Evol. **17**(1): 1–3. Elsevier Current Trends. doi:10.1016/S0169-5347(01)02381-3.

Brekke, L.J. 2017. Comparison of two indexed gill-netting protocols for fish community surveys in northern lakes. Laurentian University.

Burkhead, N.M. 2012. Extinction rates in north American freshwater fishes, 1900-2010. Bioscience **62**(9): 798–808. Oxford Academic. doi:10.1525/bio.2012.62.9.5.

Burnham, K.P., and Anderson, D.R. 2004. Model selection and multimodel Inference. *In* Model selection and multimodel inference, Second edi. Springer New York. doi:10.1007/b97636.

Cazelles, K., Bartley, T., Guzzo, M.M., Brice, M.H., MacDougall, A.S., Bennett, J.R., Esch, E.H., Kadoya, T., Kelly, J., Matsuzaki, S. ichiro, Nilsson, K.A., and McCann, K.S. 2019.

Homogenization of freshwater lakes: Recent compositional shifts in fish communities are explained by gamefish movement and not climate change. Glob. Chang. Biol. **25**(12): 4222–4233. Blackwell Publishing Ltd. doi:10.1111/gcb.14829.

Conlon, M., Gunn, J.M., and Morris, J.R. 1992. Prediction of lake trout (*Salvelinus namaycush*) presence in low- alkalinity lakes near Sudbury, Ontario. *In* Canadian Journal of Fisheries and Aquatic Sciences. doi:10.1139/f92-304.

Corston, A., Gillespie, M., and Gunn, J. 2014a. Chief Lake urban lakes fisheries study. Sudbury, Ontario.

Corston, A., Gillespie, M., and Gunn, J. 2014b. Brodill Lake urban lakes fisheries study. Sudbury, Ontario.

Couture, R.M., De Wit, H.A., Tominaga, K., Kiuru, P., and Markelov, I. 2015. Oxygen dynamics in a boreal lake responds to long-term changes in climate, ice phenology, and DOC inputs. J. Geophys. Res. G Biogeosciences **120**(11): 2441–2456. Blackwell Publishing Ltd. doi:10.1002/2015JG003065.

Craig, N., Jones, S.E., Weidel, B.C., and Solomon, C.T. 2015. Habitat, not resource availability, limits consumer production in lake ecosystems. Limnol. Oceanogr. **60**(6): 2079–2089. doi:10.1002/lno.10153.

Dillon, P.J., Clark, B.J., Molot, L.A., and Evans, H.E. 2003. Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes. Can. J. Fish. Aquat. Sci. **60**(8): 959–970. doi:10.1139/f03-082.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., and Lautenbach, S. 2013.

Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.). **36**(1): 27–46. doi:10.1111/j.1600-0587.2012.07348.x.

Edwards, B.A., and Patterson, A. 2021. Personal communication on comparibility of MECP's laboratories and Testmark laboratory. Ontario Ministry of the Environment Conservation and Parks.

Environment, O.M. of the. 1983. Handbook of analytical methods for environmental sampling. Ontario Ministry of the Environment, Toronto, ON. Available from https://archive.org/details/handbookofanalyt00ontauoft.

Evans, D.O. 2007. Effects of hypoxia on scope-for-activity and power capacity of lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **64**(2): 345–361. NRC Research Press Ottawa, Canada . doi:10.1139/F07-007.

Evans, D.O., Casselman, J.M., and Willox, C.C. 1991. Effects Of exploitation loss Of nursery habitat and stocking on lake trout populations in Ontario. *In* Lake trout synthesis, response to stress working group. Ontario Ministry of Natural Ressources, Toronto, ON. p. 193. Available from https://www.worldcat.org/title/effects-of-exploitation-loss-of-nursery-habitat-and-stocking-on-the-dynamics-and-productivity-of-lake-trout-populations-in-ontario-lakes-lake-trout-synthesis-response-to-stress-working-group/oclc/36369793.

Evans, D.O., and Olver, C.H. 1995. Introduction of lake trout (*Salvelinus namaycush*) to inland lakes of Ontario, Canada: Factors contributing to successful colonization. J. Great Lakes Res. **21**: 30–53. Elsevier. doi:10.1016/S0380-1330(95)71082-6.

Evans, D.O., and Willox, C.C. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. Can. J. Fish. Aquat. Sci. **48**(Suppl.1): 134–147. doi:10.1139/f91-312.

Field, A., Miles, J., and Field, Z. 2012. Discovering statistics using R. *In* Choice Reviews Online. SAGE Publications Ltd, London. doi:10.5860/choice.50-2114.

Gunn, J., Keller, W., Negusanti, J., Potvin, R., Beckett, P., and Winterhalder, K. 1995. Ecosystem recovery after emission reductions: Sudbury, Canada. Water, Air, Soil Pollut. **85**(3): 1783–1788. doi:10.1007/BF00477238.

Gunn, J.M. 1989. Survival of lake charr (*Salvelinus namaycush*) embryos under pulse exposure to acidic runoff water. Aquat. Toxicol. water Qual. Manag. **22**: 23–45.

Gunn, J.M., and Keller, W. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature **345**(6274): 431–433. doi:10.1038/345431a0.

Gunn, J.M., and Louste-Fillion, J. 2022. Adaptability of lake charr (*Salvelinus namaycush*) in a changing world: Newly recolonized landscapes reveal the significance of traits shaped during the Pleistocene. Environ. Biol. Fishes: 21.

Gunn, J.M., McMurtry, M.J., Casselman, J.M., Keller, W., and Powell, M.J. 1988. Changes in the fish community of a limed lake near sudbury, Ontario: Effects of chemical neutralization or reduced atmospheric deposition of acids? Water. Air. Soil Pollut. **41**(1–4): 113–136. doi:10.1007/BF00160348.

Gunn, J.M., and Mills, K.H. 1998. The potential for restoration of acid-damaged lake trout lakes. Restor. Ecol. **6**(4): 390–397. John Wiley & Sons, Ltd. doi:10.1046/j.1526-100X.1998.06409.x.

Gunn, J.M., and Noakes, D.L.G. 1987. Latent effects of pulse exposure to aluminum and low pH on size, ionic composition, and feeding efficiency of lake trout (*Salvelinus namaycush*) Alevins . Can. J. Fish. Aquat. Sci. **44**(8): 1418–1424. doi:10.1139/f87-170.

Guzzo, M.M., and Blanchfield, P.J. 2017. Climate change alters the quantity and phenology of habitat for lake trout (*Salvelinus namaycush*) in small boreal shield lakes. Can. J. Fish. Aquat. Sci. **74**(6): 871–884. Canadian Science Publishing. doi:10.1139/cjfas-2016-0190.

Guzzo, M.M., Blanchfield, P.J., and Rennie, M.D. 2017. Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. Proc. Natl. Acad. Sci. U. S. A. **114**(37). doi:10.1073/pnas.1702584114.

Jackson, D.A. 1993. Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. Ecology **74**(8): 2204–2214. doi:10.2307/1939574.

Jarvis, L.A., McMeans, B.C., Giacomini, H.C., and Chu, C. 2020. Species-specific preferences drive the differential effects of lake factors on fish production. Can. J. Fish. Aquat. Sci. **77**(10): 1625–1637. Canadian Science Publishing. doi:10.1139/cjfas-2020-0105.

Jeziorski, A., Tanentzap, A.J., Yan, N.D., Paterson, A.M., Palmer, M.E., Korosi, J.B., Rusak, J.A., Arts, M.T., Keller, W.B., Ingram, R., Cairns, A., and Smol, J.P. 2014. The jellification of north temperate lakes. Proc. R. Soc. B Biol. Sci. **282**(1798). The Royal Society. doi:10.1098/rspb.2014.2449.

Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., and Jansson, M. 2009. Light limitation of nutrient-poor lake ecosystems. Nature **460**(7254): 506–509. Nature Publishing Group. doi:10.1038/nature08179.

Kaufman, S.D., Snucins, E., Gunn, J.M., and Selinger, W. 2009. Impacts of road access on lake trout (*Salvelinus namaycush*) populations: Regional scale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*). Can. J. Fish. Aquat. Sci. **66**(2): 212–223. doi:10.1139/F08-205.

Keller, W. (Bill), Heneberry, J., McLachlan, E., and MacPhee, S. 2006. Data report: 25 years of extensive montoring of acidified lakes in the Sudbury area, 1981 to 2005. Sudbury, Ontario.

Keller, W., Pitblado, J.R., and Conroy, N.I. 1986. Water quality improvements in the Sudbury, Ontario, Canada area related to reduced smelter emissions. *In* Water, Air, & Soil Pollution. doi:10.1007/BF00284223.

Keller, W.B., Heneberry, J., and Edwards, B.A. 2019. Recovery of acidified Sudbury, Ontario, Canada, lakes: A multi-decade synthesis and update. Environ. Rev. **27**(1): 1–16. doi:10.1139/er-2018-0018.

Konkle, B.R., and Sprules, W.G. 1986. Planktivory by stunted lake trout in an Ontario lake. Trans. Am. Fish. Soc. **115**(4): 515–521. doi:10.1577/1548-8659(1986)115<515:pbslti>2.0.co;2.

Lepak, J.M., Kraft, C.E., and Weidel, B.C. 2006. Rapid food web recovery in response to removal of an introduced apex predator. Can. J. Fish. Aquat. Sci. **63**(3): 569–575. doi:10.1139/f05-248.

Lester, N.P., Shuter, B.J., Jones, M.L., and Sandstrom, S. 2021. A general, life history-based model for sustainable exploitation of lake charr across their range. *In* The lake charr *Salvelinus namaycush*: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 429–485. doi:10.1007/978-3-030-62259-6_1.

Marsden, J.E., Binder, T.R., Riley, S.C., Farha, S.A., and Krueger, C.C. 2021. Habitat. *In* The lake charr *Salvelinus namaycush*: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 167–202. doi:10.1007/978-3-030-62259-6_1.

Martin, N.V., and Olver, C.H. 1980. The lake charr, *Salvelinus namaycush*. *In* Charrs: Salmonid fishes of the genus *Salvelinus*. *Edited By* E.K. Balon. Dr. W Junk Publishers, Springer, Netherlands.

Matuszek, J.E., Goodier, J., and Wales, D.L. 1990. The occurrence of cyprinidae and other small fish species in relation to pH in Ontario lakes. Trans. Am. Fish. Soc. **119**(5): 850–861. doi:10.1577/1548-8659(1990)119<0850:toocao>2.3.co;2.

Matuszek, J.E., Wales, D.L., and Gunn, J.M. 1992. Estimated impacts of SO2 emissions from Sudbury smelters on Ontario's sportfish populations. Can. J. Fish. Aquat. Sci. **49**(Suppl.1): 87–94. NRC Research Press Ottawa, Canada . doi:10.1139/f92-303.

Meyer-Jacob, C., Labaj, A.L., Paterson, A.M., Edwards, B.A., Keller, W. (Bill), Cumming, B.F., and Smol, J.P. 2020. Re-browning of Sudbury (Ontario, Canada) lakes now approaches pre-acid deposition lake-water dissolved organic carbon levels. Sci. Total Environ. **725**: 138347. Elsevier B.V. doi:10.1016/j.scitotenv.2020.138347.

MNDMNRF. 2020. Unpublished NMDMNRF stocking data. Sudbury, Ontario.

Molot, L., Dillon, P., and Clark, B. 2003. Lake trout (*Salvelinus namaycush*) habitat volumes and boundaries in Canadian Shield lakes. *In* Boreal Shield watersheds: Lake trout ecosystems in a changing environment. *Edited by* J.M. Gunn, R.J. Steedman, and R.A. Ryder. Lewis Publishers. pp. 111–117. doi:10.1201/9780203495087.ch6.

Morgan, G.E., and Snucins, E. 2005. Manual of instructions and provincial biodiversity benchmark values: NORDIC Index Netting. *In* Ministry of Natural Resources. Peterborough, Ontario.

Muir, A.M., Bennion, D., Hansen, M.J., Riley, S.C., and Gunn, J.M. 2021. Distribution. *In* The lake charr *Salvelinus namaycush*: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 13–40. doi:10.1007/978-3-030-62259-6_1.

Neary, B.P., Dillon, P.J., Munro, J.R., and Clark, B.J. 1990. The acidification of Ontario lakes : an assessment of their sensitivity and current status with respect to biological damage. doi:10.5962/bhl.title.29191.

Polkinghorne, D., and Gunn, J. 1981. Sudbury district lake trout lakes - A description of the lakes and the changes produced by man. Sudbury District.

Potvin, R.R., and Negusanti, J.J. 1995. Declining industrial emissions, improving air quality, and reduced damage to vegetation. *In* Restoration and recovery of an industrial region: progress in restoring the smelter-damaged landscape near Sudbury, Canada. *Edited by* J.M. Gunn. Springer, New York, NY. pp. 51–65. doi:10.1007/978-1-4612-2520-1_4.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. *In* Austral Ecology. Cambridge University Press, New York. doi:10.1046/j.1442-9993.2003.01318.x.

Rahel, F.J., and Olden, J.D. 2008, June 1. Assessing the effects of climate change on aquatic invasive species. John Wiley & Sons, Ltd. doi:10.1111/j.1523-1739.2008.00950.x.

Riley, S.C., Hansen, M.J., Krueger, C.C., Noakes, D.L.G., and Muir, A.M. 2021. Introduction. *In* The lake Charr: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 1–12. doi:10.1007/978-3-030-62259-6_1.

Sandstrom, S., Rawson, M., and Lester, N. 2013. Manual of instructions for broad-scale fish community monitoring using North American (NA1) and Ontario small mesh (ON2) gillnets. Peterborough, Ontario.

Schindler, D., and Gunn, J. 2003. Dissolved organic carbon as a controlling variable in lake trout and other Boreal Shield lakes. *In* Boreal Shield watersheds: Lake Trout ecosystems in a changing environment. pp. 133–146. doi:10.1201/9780203495087.ch8.

Seddon, P.J., Soorae, P.S., and Launay, F. 2005. Taxonomic bias in reintroduction projects. Anim. Conserv. **8**(1): 51–58. John Wiley & Sons, Ltd. doi:10.1017/S1367943004001799.

Selinger, W., Lowman, D., Kaufman, S., and Malette, M. 2006. The status of lake trout populations in northeastern Ontario (2000-2005). *In* Ontario Ministry of Natural Resources, Timmins, Ont. Ontario Ministry of Natural Resources. Available from http://www.mnr.gov.on.ca/264857.pdf.

Snucins, E., and Gunn, J. 2000. Interannual variation in the thermal structure of clear and colored lakes. Limnol. Oceanogr. **45**(7): 1639–1646. American Society of Limnology and Oceanography Inc. doi:10.4319/lo.2000.45.7.1639.

Vinson, M.R., Chavarie, L., Rosinski, C.L., and Swanson, H.K. 2021. Trophic ecology. *In* The lake charr *Salvelinus namaycush*: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 287–314. doi:10.1007/978-3-030-62259-6_1.

Weyhenmeyer, G.A., Hartmann, J., Hessen, D.O., Kopáček, J., Hejzlar, J., Jacquet, S., Hamilton, S.K., Verburg, P., Leach, T.H., Schmid, M., Flaim, G., Nõges, T., Nõges, P., Wentzky, V.C., Rogora, M., Rusak, J.A., Kosten, S., Paterson, A.M., Teubner, K., Higgins, S.N., Lawrence, G., Kangur, K., Kokorite, I., Cerasino, L., Funk, C., Harvey, R., Moatar, F., de Wit, H.A., and Zechmeister, T. 2019. Widespread diminishing anthropogenic effects on calcium in freshwaters. Sci. Rep. **9**(1): 1–10. doi:10.1038/s41598-019-46838-w.

Williamson, C.E., Overholt, E.P., Pilla, R.M., Leach, T.H., Brentrup, J.A., Knoll, L.B., Mette, E.M., and Moeller, R.E. 2015. Ecological consequences of long-term browning in lakes. Sci. Rep. **5**(July): 1–10. Nature Publishing Group. doi:10.1038/srep18666.

Wilson, C., and Mandrak, N. 2003. History and evolution of lake trout in Shield lakes. doi:10.1201/9780203495087.ch2.

Wilson, C., and Mandrak, N. 2021. Paleoecology. *In* The lake charr *Salvelinus namaycush*: Biology, ecology, distribution, and management, Fish & Fis. *Edited by* A.M. Muir, C.C. Krueger, M.J. Hansen, and S.C. Riley. Springer International Publishing. pp. 41–67. doi:10.1007/978-3-030-62259-6_1.

Wiltse, B., Yerger, E.C., and Laxson, C.L. 2020. A reduction in spring mixing due to road salt runoff entering Mirror Lake (Lake Placid, NY). Lake Reserv. Manag. **36**(2): 109–121. Taylor and Francis Ltd. doi:10.1080/10402381.2019.1675826.

Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature **401**(6752): 464–467. Nature Publishing Group. doi:10.1038/46762.

Vander Zanden, M.J., Olden, J.D., Thorne, J.H., and Mandrak, N.E. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecol. Appl. **14**(1): 132–148. doi:10.1890/02-5036.

Vander Zanden, M.J., Shuter, B.J., Lester, N.P., and Rasmussen, J.B. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **57**(4): 725–731. Canadian Science Publishing. doi:10.1139/cjfas-57-4-725.

Supplemental Information

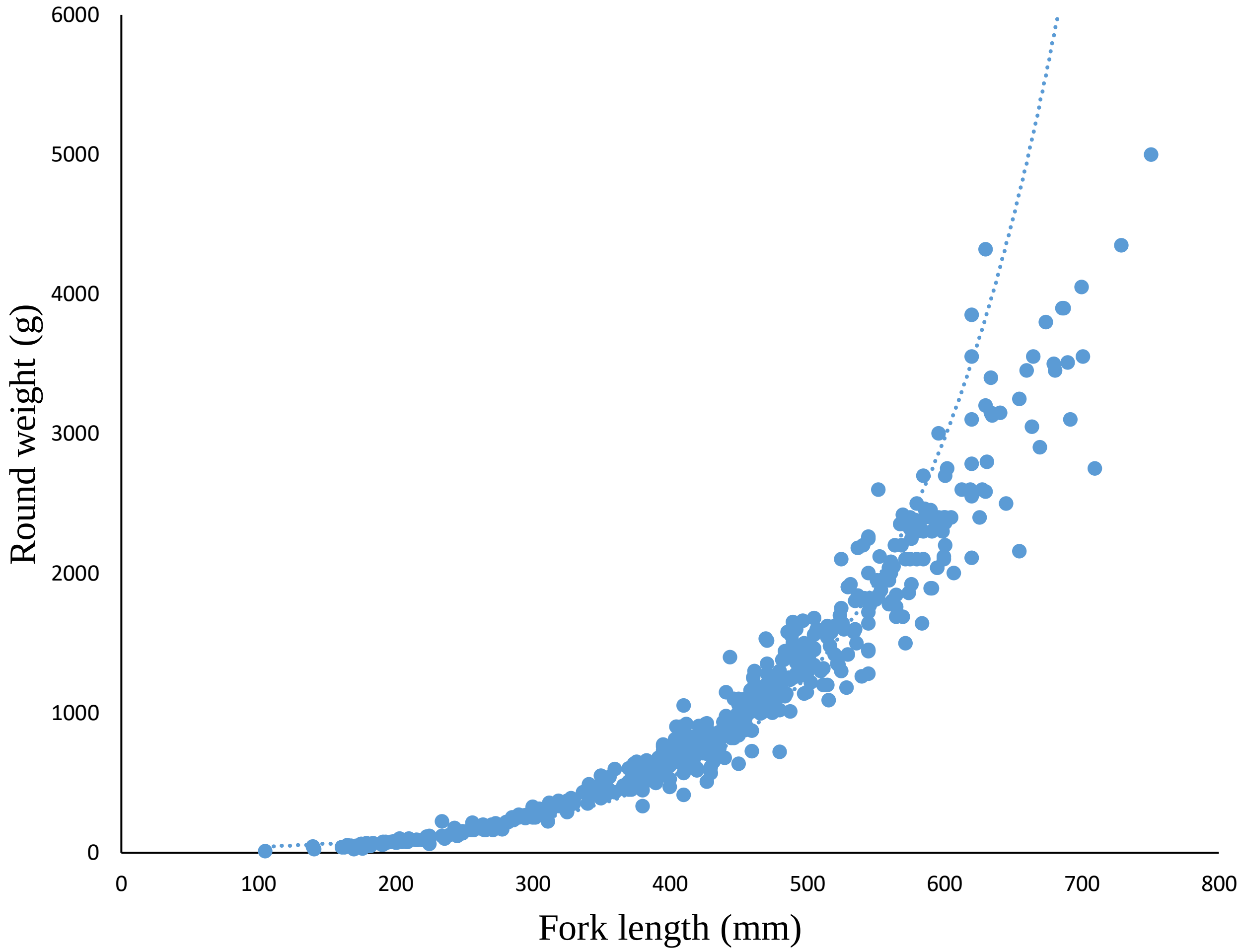

Figure SI-1a Relationship between round weight and fork of lake trout used to estimate missing weights of individuals not measured in field. $R^2 = 0.944$, n = 596 fish, trendline $y = 17.925e^{0.0085x}$.

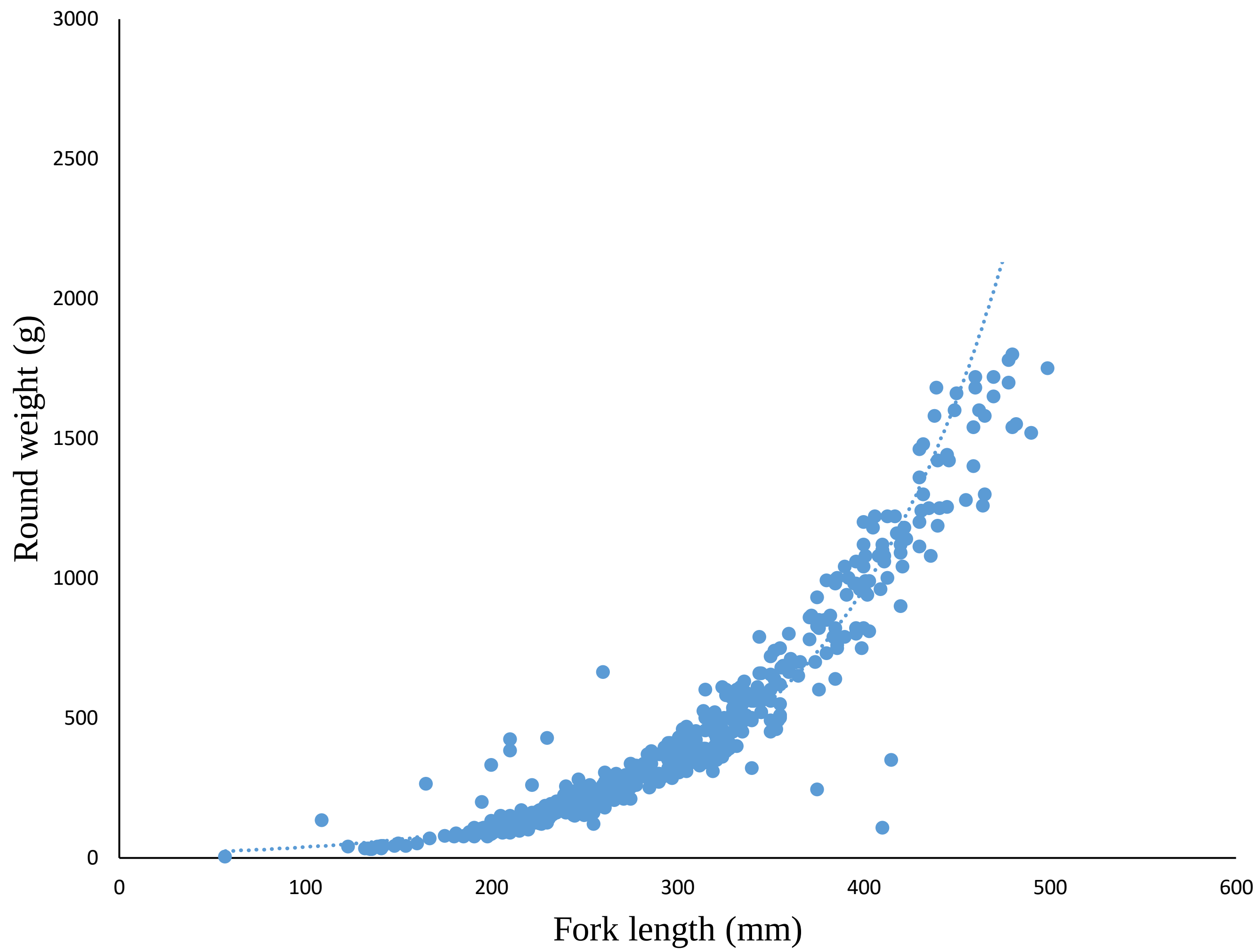

Figure SI-1b Relationship between round weight and fork of smallmouth bass used to estimate missing weights of individuals not measured in field. $R^2 = 0.914$, n = 577 fish, trendline $y = 13.381e^{0.0107x}$.

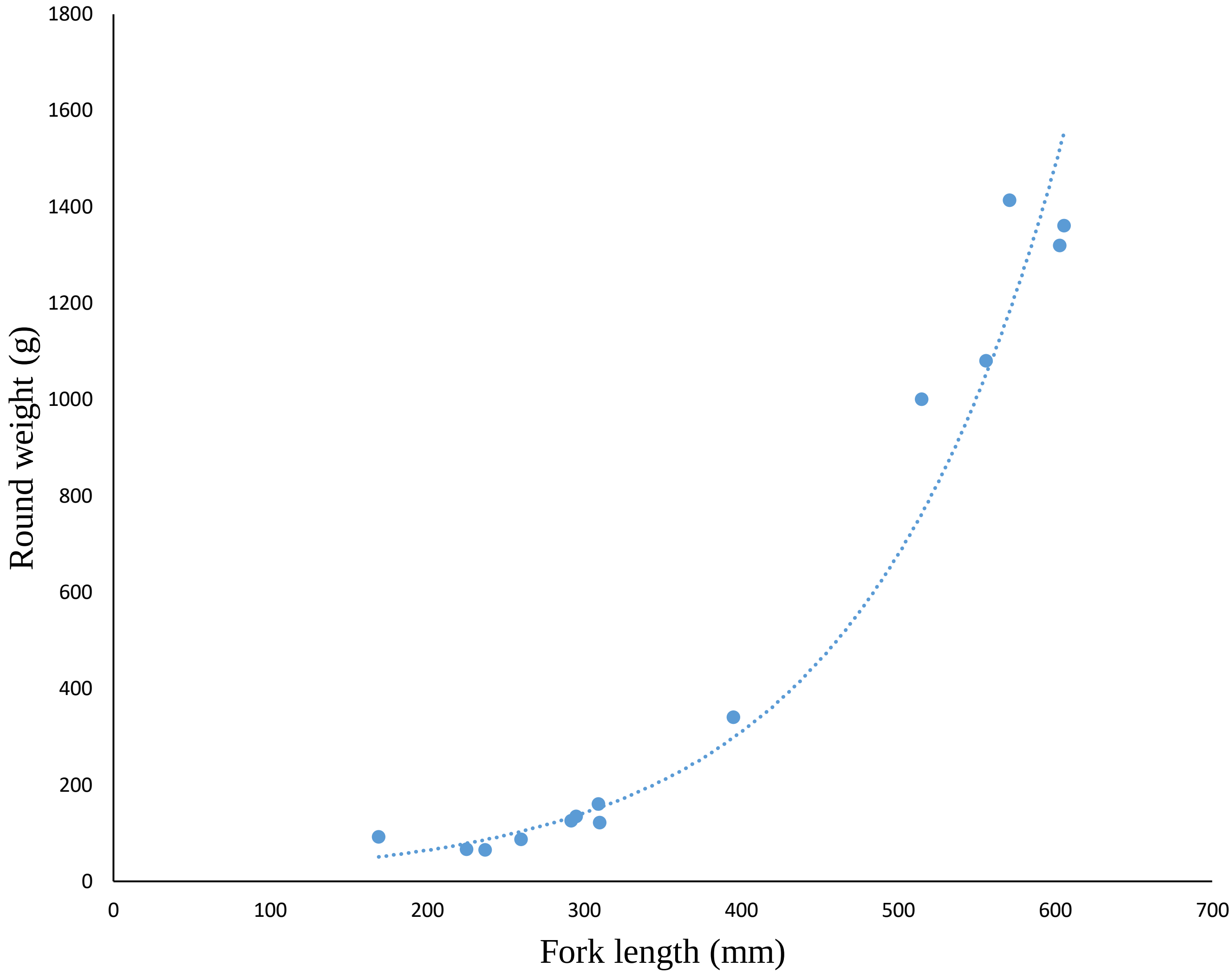

Figure SI-1c Relationship between round weight and fork of burbot used to estimate missing weights of individuals not measured in field. $R^2 = 0.955$, n = 14 fish, trendline $y = 13.529e^{0.0078x}$.

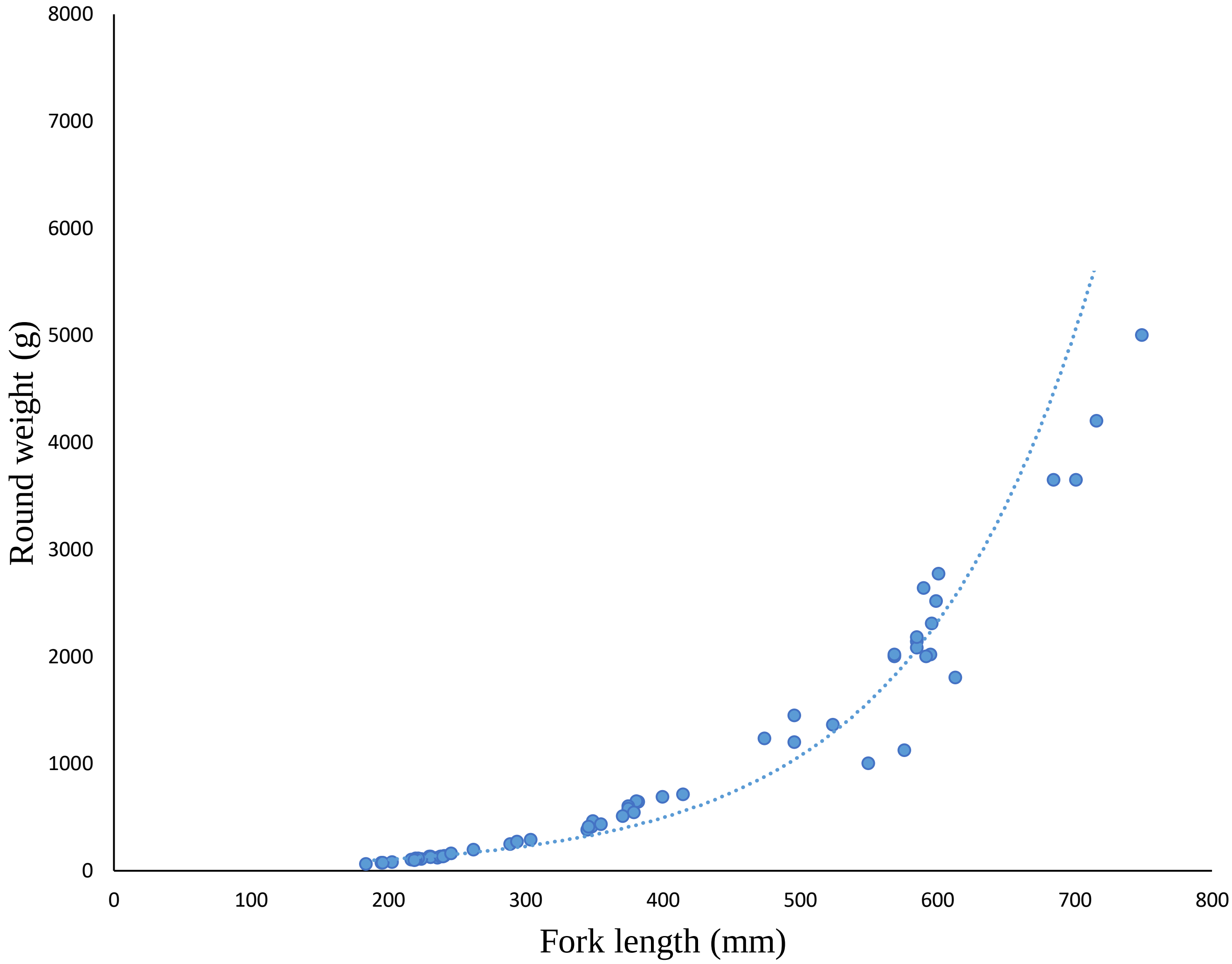

Figure SI-1d Relationship between round weight and fork of walleye used to estimate missing weights of individuals not measured in field. $R^2 = 0.935$, n = 60 fish, trendline $y = 22.607e^{0.0077x}$.

Table SI-1 Summary of historical lake trout stocking across surveyed lakes. Stocking years begin as early as 1980 and number (#) of lake trout stocked were calculated starting in 2001 because the number of fish stocked was not documented prior to that year. All data provided by MNDMNRF Sudbury and North Bay District Office. Stocked lake trout included a combination of yearlings, 2 year-olds and adults.

Lake	Stocking years	# of lake trout stocked[c]
Bell	84-89, 92, 01, 03, 20	1700
Bowland	early 80's[a]	0[d]
Brodill		0
Chief	08, 21	1400
Colin Scott	87, 88, 89, 01-19 (every 2 yrs)	5500
Davis	84, 85, 01-19 (every 2 yrs)	4800
Dewdney		0
Donald	87, 88, 01-04, 06-18 (every 2 yrs)	55000
Elboga	03, 04, 08, 10, 13, 16, 19, 21	4000
Florence	01, 02, 03, 09, 10, 14, 19	53400
Fraleck	84,85,86, 04, 06, 08, 10, 13, 15, 17, 19, 21	5700
George	84-92,02,04	600
Great Mountain	01,04,06	700
Gullrock	88, 98, 99, 00, 06, 08, 09, 10, 11	8600
Johnnie	01, 03, 07, 20	2200
Kelly #27	04, 06, 08, 10, 13, 15, 17, 19	4000
Laundrie	80-86, 05-19 (every 2 yrs)	28000
Makobe		0
Marina[b]	03, 05, 08, 10	2000
Matagamasi	98-04, 05-19 (every 2 yrs), 20, 21	134900
Nelson		0
Paradise		0
Peter	84, 85, 89-92, 04, 06, 07- 21 (every 2 yrs)	5900
Rawson		0
Ruth-Roy		0
Silvester		0
Tyson	81-94, 02, 03-05, 08, 10, 12, 14, 16, 17, 19, 21	39200
Wavy	09, 11, 13, 14, 16, 18, 19, 21	11400
White Oak	1996	0[d]
White Pine	80, 81	0[d]
Wolf		0

[a]Specic stocking year unknown
[b]Transferred to Kirkland Lake District after 2010 so no further stocking data were provided
[c]Number rounded to the nearest 100
[d]Lakes were only stocked prior to 2001 so the number of fish stocked since 2001 is 0

Table SI-2a Correlation matrix of continuous candidate predictors. Bolded values indicate correlated variables (r ≥ 0.7).

	Max Depth	log Lake Size	Optimal Depth	log Usable Depth	log Species Richness	log Zoo Density	log Zoo Biomass	log Zoo Richness	log Smallmouth CPUE	log Piscivore CPUE	PC1	PC2	PC3
Max Depth	1	0.466	0.519	0.669	0.027	-0.142	-0.223	0.382	0.428	0.446	0.098	-0.505	0.228
log Lake Size	0.466	1	0.462	0.433	0.435	-0.017	-0.194	0.438	0.45	0.648	-0.057	0.001	0.093
Optimal Depth	0.519	0.462	1	**0.823**	0.271	-0.064	-0.214	0.342	0.26	0.336	0.031	-0.231	0.452
log Usable Depth	0.669	0.433	**0.823**	1	0.24	-0.06	-0.215	0.397	0.427	0.52	0.022	-0.28	0.442
log Species Richness	0.027	0.435	0.271	0.24	1	0.495	0.206	0.461	0.343	0.345	-0.573	0.203	0.144
log Zoo Density	-0.142	-0.017	-0.064	-0.06	0.495	1	**0.861**	0.422	0.088	-0.029	-0.507	0.111	-0.218
log Zoo Biomass	-0.223	-0.194	-0.214	-0.215	0.206	**0.861**	1	0.402	-0.075	-0.214	-0.265	0.028	-0.331
log Zoo Richness	0.382	0.438	0.342	0.397	0.461	0.422	0.402	1	0.389	0.397	-0.421	-0.248	0.075
log Smallmouth CPUE	0.428	0.45	0.26	0.427	0.343	0.088	-0.075	0.389	1	**0.869**	-0.31	-0.17	-0.057
log Piscivore CPUE	0.446	0.648	0.336	0.52	0.345	-0.029	-0.214	0.397	**0.869**	1	-0.158	-0.056	0.013
PC1	0.098	-0.057	0.031	0.022	-0.573	-0.507	-0.265	-0.421	-0.31	-0.158	1	0.029	0.03
PC2	-0.505	0.001	-0.231	-0.28	0.203	0.111	0.028	-0.248	-0.17	-0.056	0.029	1	0
PC3	0.228	0.093	0.452	0.442	0.144	-0.218	-0.331	0.075	-0.057	0.013	0.03	0	1

Table SI-2b Correlation matrix of water chemistry parameters included in the Principal Components Analysis. Bolded values indicate correlated variables (r ≥ 0.7).

	Historical pH	**Contemporary pH**	**log Secchi**	**log Chloride**	**Sulphate**	**log Alkalinity**	**DOC**	**Reactive Silicate**	**log TP**	**Ca**	**log Al**	**log Cu**	**log Ni**
Historical pH	1	0.626	-0.27	0.242	-0.049	0.59	0.369	-0.047	0.037	0.651	-0.194	0.053	-0.183
Contemporary pH	0.626	1	-0.022	-0.064	0.063	**0.768**	0.068	-0.272	0.176	0.63	-0.648	-0.053	-0.273
log Secchi	-0.27	-0.022	1	-0.45	0.537	-0.18	**-0.803**	-0.292	0.229	-0.123	-0.451	-0.262	-0.138
log Chloride	0.242	-0.064	-0.45	1	-0.221	0.309	0.53	0.192	-0.101	0.23	0.436	-0.04	-0.06
Sulphate	-0.049	0.063	0.537	-0.221	1	0.001	-0.567	-0.047	0.185	0.353	-0.608	0.027	0.114
log Alkalinity	0.59	**0.768**	-0.18	0.309	0.001	1	0.302	-0.096	0.381	0.683	-0.407	-0.083	-0.236
DOC	0.369	0.068	**-0.803**	0.53	-0.567	0.302	1	0.308	-0.185	0.189	0.566	0.099	-0.019
Reactive Silicate	-0.047	-0.272	-0.292	0.192	-0.047	-0.096	0.308	1	0.393	-0.336	0.35	0.255	0.283
log TP	0.037	0.176	0.229	-0.101	0.185	0.381	-0.185	0.393	1	-0.105	-0.352	-0.137	-0.162
Ca	0.651	0.63	-0.123	0.23	0.353	0.683	0.189	-0.336	-0.105	1	-0.427	0.004	-0.129
log Al	-0.194	-0.648	-0.451	0.436	-0.608	-0.407	0.566	0.35	-0.352	-0.427	1	-0.037	0.042
log Cu	0.053	-0.053	-0.262	-0.04	0.027	-0.083	0.099	0.255	-0.137	0.004	-0.037	1	**0.936**
log Ni	-0.183	-0.273	-0.138	-0.06	0.114	-0.236	-0.019	0.283	-0.162	-0.129	0.042	**0.936**	1

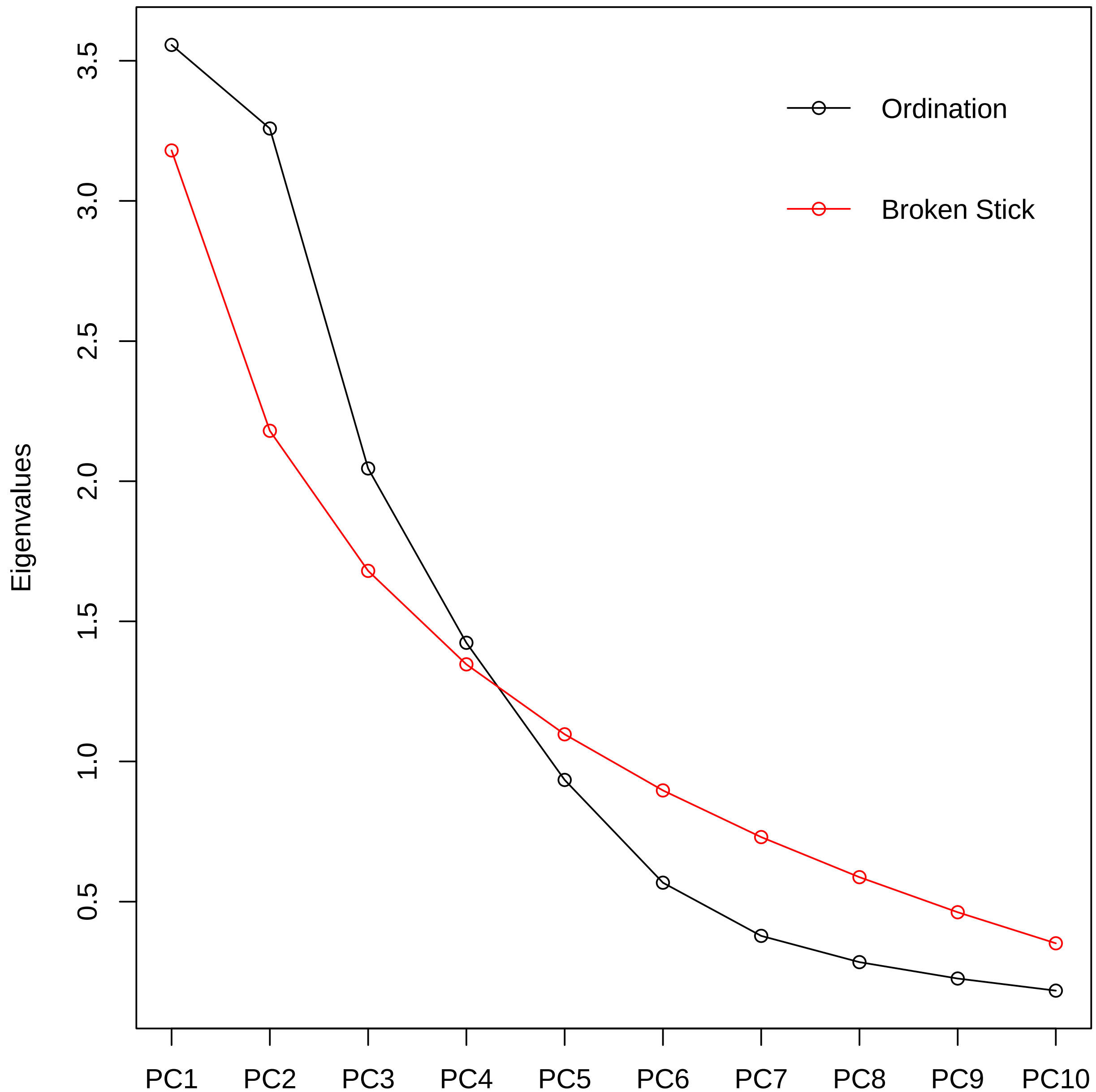

Figure SI-2 Screeplot representing eigenvalues of each principal component (black) and broken stick analysis threshold (red). Top three principal components were extracted and results of variable loadings of these principal components can be found in Table SI-5.

Table SI-3a Lake specific results of candidate predictors. Surface area, max depth and historical pH can all be found in table 1

Lake	Optimal Depth (m)	Usable Depth (m)	Contemporary pH	Secchi (m)	Chloride (mg/L)	Sulphate (mg/L)	Alkalinity (mg/L)	DOC (mg/L)	Reactive Silicate (mg/L)	TP (mg/L)	Ca (mg/L)	Al (mg/L)	Cu (mg/L)	Ni (mg/L)
Brodill	20	24	6.4	5.15	0.3	4.85	4.05	3.8	1.56	0.006	1.5	0.0571	0.007	0.0366
Wavy	27	30	5.8	4	0.2	4.4	2.42	4.4	1.68	0.0051	0.96	0.098	0.005	0.0283
Great Mountain	NA	NA	6.18	7	0.24	3.55	2.82	2.7	0.68	0.0062	0.94	0.0438	0.001	0.0033
Chief	26	28	6.25	4	0.38	4.25	2.82	3.2	1.4	0.0041	1.3	0.0429	0.0065	0.0386
White Oak	32	34	6.46	6.5	0.34	5.25	3.16	3.4	1.68	0.0048	1.3	0.0527	0.004	0.0262
Elboga	0	5	6.26	2.2	15.7	3.55	5.56	7.2	1.64	0.006	1.72	0.148	0.001	0.001
Davis	2	5	5.77	4.5	0.16	5.4	2.42	3.3	1.06	0.0048	1.38	0.0824	0.001	0.0063
George	26	28	6.62	5.25	0.36	3.9	3.64	2.6	1.04	0.0049	1.24	0.0444	0.001	0.0025
Johnnie	25	26	6.47	3.8	0.21	3.65	3.19	4.9	1.22	0.0043	1.16	0.0866	0.002	0.0055
Wolf	26	30	6.29	10.5	0.18	5.4	2.55	2	1.2	0.0036	1.34	0.0564	0.001	0.0049
Laundrie	5	11	6.08	4.5	0.14	4.1	2.72	5.4	1.56	0.0069	1.28	0.0932	0.001	0.0018
White Pine	13	15	6.92	4.5	0.13	4.1	3.53	3.3	1.08	0.0037	1.28	0.0197	0.0025	0.001
Peter	18	22	7.11	5.25	0.32	5.2	7.25	4.8	0.92	0.0026	2.54	0.0163	0.002	0.0036
Bowland	11	20	6.41	4.5	0.13	3.9	3.45	3.8	1.1	0.0056	1.36	0.0523	0.001	0.0013
Tyson	31	32	6.56	4.5	0.88	4.15	3.78	5.5	1.34	0.0052	1.26	0.0729	0.002	0.007
Gullrock	0	0	6.88	4.3	0.13	2.8	5.54	4.6	0.5	0.0067	1.5	0.0455	0.001	6.00E-04
Kelly #27	0	5	6.46	11.5	0.17	5.75	3.2	2.5	1.02	0.0031	1.48	0.0325	0.001	0.0054
Nelson	31	41	6.79	10.5	0.23	5.3	4.14	1.8	0.48	0.0025	1.78	0.0087	0.002	0.0038
Bell	15	17	6.6	4.5	0.2	3.65	4.09	6.2	1.18	0.0076	1.42	0.0944	0.002	0.0061
Matagamasi	1	19	6.62	3.8	0.44	5.35	4.21	3.3	1.04	0.0042	1.68	0.0309	0.002	0.0061
Marina	9	10	5.79	3.9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Florence	19	26	6.15	8.25	0.13	4.15	2.58	3.3	1.32	0.0059	1.04	0.0777	0.001	0.0013
Makobe	11	15	6.25	2.8	0.11	3.2	4.18	4	1.1	0.0046	1.52	0.0405	9.00E-04	5.00E-04
Fraleck	16	17	6.55	3.1	0.13	4.2	3.48	4.9	1.92	0.0046	1.4	0.0912	0.001	0.003
Paradise	24	26	6.74	6.6	0.1	4.9	5	3.1	1.88	0.078	1.4	0.015	0.002	0.002
Dewdney	20	24	6.48	9.2	0.2	5.4	5	2.3	2.09	0.054	1.08	0.018	5.00E-04	0.003
Colin Scott	16	25	6.49	9.8	0.1	5.2	5	1.9	0.56	0.031	1.38	0.009	5.00E-04	0.004
Donald	28	31	6.25	9.3	0.2	5.55	2.56	1.7	0.68	0.0023	1.44	0.0333	0.001	0.005
Rawson	NA	NA	6.59	5.3	0.1	4.1	5	4.4	1.97	0.001	1.9	0.021	0.002	0.002
Silvester	5	11	6.19	7.6	0.17	5.35	2.5	2	1.22	0.0037	1.3	0.0637	0.001	0.0057
Ruth-Roy	1	3	5.76	7.8	0.21	2.7	2.12	2.8	1.28	0.0039	0.62	0.159	0.001	0.006

Table SI-3b Lake specific results of candidate predictors. Stocking p/a can be found in table 1.

Lake	Species Richness	Yellow perch p/a	Smallmouth bass p/a	Coregoninae p/a	Smallmouth bass CPUE (g/net)	Piscivore CPUE (g/net)	Zoo Density	Zoo Biomass	Zoo Richness	Large Clad p/a	Tot Lake trout CPUE (g/net)	Nat Lake trout CPUE (g/net)	Lake trout Recruitment p/a
Brodill	4	1	1	0	118.08	112.08	7554.2	11.286	13	1	0	0	0
Wavy	3	1	0	0	0	574.38	6292.1	6.786	13	0	94.96	0	0
Great Mountain	4	0	1	1	167.75	124.54	4329.9	5.499	12	0	1001.67	837.08	1
Chief	7	1	0	0	0	0	22337.4	23.503	13	0	361.67	265	0
White Oak	8	1	0	1	0	0	10346	12.442	16	1	535.37	535.37	1
Elboga	6	0	0	0	0	0	42125.5	55.165	14	1	963.02	140.53	0
Davis	5	1	0	0	0	0	38576.7	60.864	14	0	412.86	93.93	1
George	10	1	1	1	161.59	79.19	40566.2	29.87	12	0	1165.89	1078.48	1
Johnnie	13	1	1	1	704.17	729.12	13290.6	12.16	17	0	568.71	361	0
Wolf	4	1	1	0	244.29	119.08	14882	30.84	15	1	1282.08	1282.08	1
Laundrie	5	1	1	0	974.19	916.15	29092.1	51.04	14	1	646.37	143.52	1
White Pine	8	1	0	0	0	0	51034.5	67.453	14	1	1843.57	1033.14	1
Peter	12	1	1	1	984.25	1040	28945.2	9.593	13	0	62.92	0	0
Bowland	4	1	1	0	1150.38	887.46	30475.7	36.997	15	1	1753.54	1753.54	1
Tyson	11	1	1	1	489.24	584.76	17159.6	17.686	13	0	751.21	124.24	0
Gullrock	7	0	0	0	0	0	39970.3	57.601	15	1	1355	1231.32	0
Kelly #27	4	1	0	0	0	0	3533.6	7.224	10	0	731.02	570.36	1
Nelson	7	1	1	0	377.39	361.11	46266.8	42.994	21	1	633.18	633.18	1
Bell	11	1	1	1	573.12	940.5	16390.3	19.524	16	0	718.33	510	0
Matagamasi	9	1	1	0	662.8	1639.3	14228.4	11.624	17	1	361.43	151.2	0
Marina	10	1	0	0	0	211.88	NA	NA	NA	NA	187.5	187.5	0
Florence	8	1	0	0	0	145.79	17530	25.956	15	1	1744.39	1151.76	1
Makobe	11	0	0	1	0	109.26	NA	NA	NA	NA	3228.14	3228.14	1
Fraleck	7	1	1	0	248.71	1035.24	15726.9	22.702	16	1	215.9	0	0
Paradise	11	1	1	1	1603.88	1852.08	13729.3	22.205	21	1	949.46	913.63	1
Dewdney	4	1	1	0	319.08	151.12	12437.6	20.847	16	1	941.69	871.69	1
Colin Scott	1	0	0	0	0	0	19137	40.935	17	1	1170.04	723.38	1
Donald	3	1	1	0	541.1	456.27	7070.8	10.147	14	1	528.96	217.63	1
Rawson	5	1	1	0	815.75	746.62	18875.8	30.723	16	1	1231.72	1226.63	1
Silvester	4	1	1	0	439.24	287.33	21533.7	35.119	14	1	158.81	158.81	0
Ruth-Roy	0	0	0	0	0	0	3333.4	5.263	8	1	0	0	0

Table SI-4a List of fish species organized by fish type caught in both NORDIC and BsM nets in each lake. Species richness values indicated by #. Three # values differ from fish species richness values used in analysis (see Table SI-2) because species richness used in my study was calculated using only BsM nets to remain consistent across all lakes.

		Piscivores									***Benthivores***				***Pelagic prey***		
Lake	**#**	**bt**	**lt**	**at**	**np**	**br**	**rb**	**smb**	**lmb**	**wal**	**lw**	**lns**	**ws**	**bb**	**cis**	**bs**	**ss**
Bell	12[a]		6		8		94	69			5		27		126		
Bowland	4		45					267					7				
Brodill	4							8					6				
Chief	7		4										19				
Colin Scott	1		41														
Davis	5		12										29	43			
Dewdney	4		29					100					9				
Donald	3		24					66									
Elboga	8[a]		35									91	192			6[b]	3[b]
Florence	8	14	69										87				
Fraleck	7		6				2	54		37			57				
George	12[a]		29				147	52			1[b]		13	1[b]	85		
Great Mountain	4		23					20							40		
Gullrock	7		16														
Johnnie	13		7		4		128	114	11		2		24	18	167		
Kelly #27	3		23														
Laundrie	5		28					100					43				
Makobe	11	1	64			9					227	72	173		103	1	
Marina	10	2	1	11						5			25				
Matagamasi	9		28		4	2	89	82		19			62	34			
Nelson	7		43			4		70					115	1			
Paradise	11		48		3	1	136	112			112		68				
Peter	12		9		5		99	81					5	1	130		
Rawson	5		116					97					58				
Silvester	4		4					75					60				
Tyson	11		14		1		66	56	5				36	15	203		
Wavy	3		13							44							
White Oak	8		21											68	12		
White Pine	8		91			6							35				
Wolf	4		24					76					26				

[a]Species richness increases with the presence of NORDIC nets and is therefore higher than the species richness value used in analyses

[b]Species was only caught in NORDIC nets (and not in BsM nets) in the listed lake

Species codes: brook trout (**bt**), lake trout (**lt**), aurora trout (**at**, northern pike (**np**), burbot (**br**), rock bass (**rb**), smallmouth bass (**smb**), largemouth bass (**lmb**), walleye (**wal**), lake whitefish (**lw**), longnose sucker (**lns**), white sucker (**ws**), brown bullhead (**bb**), cisco (**cis**), brook stickleback (**bs**), slimy sculpin (**ss**)

Table SI-4b List of fish species (by Ontario fish species code) in both NORDIC and BsM nets by lake. Species richness values indicated by #. Three # values differ from fish species richness values used in modelling (see Table SI-2) because species richness used in modelling was calculated using only BsM nets to remain consistent across all lakes.

		Littoral prey													
Lake	**#**	**nrd**	**fsd**	**lc**	**gs**	**cs**	**bns**	**bnm**	**fhm**	**cc**	**pd**	**ps**	**yp**	**id**	**lp**
Bell	12[a]				1					10		1[b]	205		3
Bowland	4												20		
Brodill	4											12	516		
Chief	7									17	1	17	302	11	
Colin Scott	1														
Davis	5				16								368		
Dewdney	4												5		
Donald	3												4		
Elboga	8[a]			196	165						58				
Florence	8				57	39				6		18	100		
Fraleck	7											2	15		
George	12[a]						32	14		1		15	54		
Great Mountain	4											9			
Gullrock	7	129	128		106	923		136	53						
Johnnie	13				1			15				7	45		
Kelly #27	3	1											691		
Laundrie	5									2			150		
Makobe	11			954							9			1	
Marina	10			8	3	7						13	819		
Matagamasi	9												146		
Nelson	7					7							578		
Paradise	11			15		6						12	28		
Peter	12				2			28				37	9		1
Rawson	5											5	1		
Silvester	4												9		
Tyson	11				7							8	61		
Wavy	3												1235		
White Oak	8	5			10			1				1	141		
White Pine	8				24	7				7	39		294		
Wolf	4												25		

[a]Species richness increases with the presence of NORDIC nets and is therefore higher than the species richness value used for modelling

[b]Species was only caught in NORDIC nets (and not in BsM nets) in the listed lake

Species codes: northern redbelly dace (**nrd**), finescale dace (**fsd**), lake chub (**lc**), golden shiner (**gs**), common shiner (**cs**), blacknose shiner (**bns**), bluntnose minnow (**bnm**), fathead minnow (**fhm**), creek chub (**cc**), pearl dace (**pd**), pumpkinseed (**ps**), yellow perch (**yp**), iowa darter (**id**), logperch (**lp**)

Table SI-5 Water chemistry variable loadings of the top three principal components extracted from the principal component analysis. All three principal components were included as candidate predictors in modelling. Bolded values indicate dominant variables (loading of ≥ 0.3).

Variable	PC1	PC2	PC3
Historical pH	**-0.435**	0.104	0.054
Contemporary pH	**-0.452**	-0.139	0.062
log Secchi	0.131	**-0.461**	-0.055
log Chloride	-0.122	**0.335**	-0.068
Sulphate	-0.022	**-0.362**	0.264
log Alkalinity	**-0.483**	0.011	0.034
DOC	-0.182	**0.482**	-0.019
Reactive silicate	0.051	0.213	0.248
log TP	-0.087	-0.179	0.03
Ca	**-0.444**	-0.031	0.128
log Al	0.246	**0.426**	-0.168
log Cu	0.064	0.121	**0.649**
log Ni	0.186	0.087	**0.621**
Eigenvalue	3.557	3.258	2.046
Variance Explained (%)	27	25	16
Sum Variance Explained (%)	27	52	68