INFLUENCE OF PREY TYPE AND ENVIRONMENT ON LAKE TROUT (*SALVELINUS NAMAYCUSH)* ACTIVITY, MERCURY DYNAMICS, AND LIFE HISTORIES

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Alexander John Ross

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Supervisor: Dr. Michael Rennie
Committee Members: Dr. Erin Dunlop, Dr. Brian Shuter
External Examiner: Dr. Jake Vander Zanden

ABSTRACT

Understanding food web structure in lentic ecosystems is a requirement for determining pathways and rates of energy flow, yet predator-prey interactions can be highly dynamic across space (i.e., between- and within-lakes) and time (e.g., diel daily cycles, seasonal). Differences in prey availability can influence predator life history traits and behaviours, though life histories can also vary across environmental gradients. Metabolic theory predicts that variation in prey and habitat availability affects metabolic rates by modifications to active behaviours, though the precise conditions controlling variation in activity have rarely been empirically assessed. Further, the relative influence of activity via food web structure (compared with environmental characteristics) on life history traits and contaminant dynamics remain poorly understood. Here, I integrate information regarding both prey availability and environmental factors to gain novel insights into their combined effects on Lake Trout activity, contaminant accumulation and life histories. Using stationary hydroacoustics, I directly observed higher activity in planktivorous Lake Trout populations that exhibited sustained day-night swimming and higher active metabolism, which contrasted with piscivorous populations that had distinct day-night behavioural shifts, including nighttime rest. Planktivorous Lake Trout maintained faster, more complex swimming paths, exhibited higher oxygen consumption, and were more frequently observed in suboptimal oxythermal conditions than piscivorous Lake Trout. Secondly, Lake Trout mercury (Hg) concentrations were affected by prey availability but not according to classical contaminant food chain length theory; rather, Hg accumulation slopes against body size were more shallow when *Mysis* *diluviana* was present than when they were absent, independent of overall food chain length. Increasing dissolved organic carbon concentrations (DOC) were also positively associated with Lake Trout Hg, and the combined use of prey availability and DOC proved essential for predicting whether Lake Trout Hg concentrations exceeded Canadian consumption guidelines for a given size. Lastly, life history traits in Lake Trout were best explained by models combining both food web structure and environmental variables; adult length and size-at-maturity generally increased with greater prey availability, while environmental variables such as lake size and total phosphorus were key for describing trait variation within categories of prey availability. These findings provide empirical, field-validated support that prey availability can play as important of a role as environmental characteristics in shaping the life history traits of predatory fishes, like Lake Trout, through effects on activity, metabolic rates, and foraging opportunities.

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CHAPTER 1

General Introduction

Food web structure plays an important role in determining how energy flows through populations, communities, and ecosystems (Lindeman 1942, Polis and Strong 1996, McMeans et al. 2015). In aquatic ecosystems, food webs are highly structured, encompassing numerous direct and indirect interactions. These interactions can affect organismal growth (Barneche and Allen 2018), individual movement rates (Cruz-Font et al. 2019), energy coupling from distinct habitats (McCann et al. 2005), and overall ecosystem productivity (Vander Zanden and Vadeboncoeur 2002). While lake ecosystems may appear static and self-contained, they are highly dynamic, with fluctuating connectance strength and niche overlap between predators and prey across both space and time (McCann et al. 2005, McMeans et al. 2015). Habitat selection by organisms, from microbes to fish, is critically influenced by temperature, light, and oxygen (Wetzel 2001) yet each of these factors varies annually, seasonally, daily, and even sub-daily (i.e., minutes to hours), influencing realized food web interactions within a given lake.

The metabolic theory of ecology (MTE; Brown et al. 2004) offers a useful framework for understanding how lake ecosystems, and particularly fish, respond to spatiotemporal dynamics. The MTE suggests organisms' metabolic rates, primarily driven by body size and temperature, energetically link them to the ecological characteristics of their environment (Brown et al. 2004). This relationship between ecological characteristics and energy flow follows bioenergetic principles, where energy availability (which provides the capacity for growth) is generally balanced by the amount of energy an individual can ingest relative to the energy it expends in acquiring it (e.g., Kitchell et al. 1977; Stewart et al. 1983). Given that metabolism scales consistently with body size and temperature across lakes (Robinson et al. 1983), any changes in fish metabolic rates are most likely driven by variation in energy availability (i.e., prey availability) across lakes.

Active metabolism in freshwater fishes can account for up to half of their total energy expenditures, with foraging-related movement comprising the majority of this cost (Boisclair and Leggett 1989a, Rowan and Rasmussen 1996, Rennie et al. 2005, 2012). Consistent with the MTE, prey availability—both in density and energetic quality—is suggested to regulate activity by modifying the movement required for fish to forage to satiation (Giacomini 2013, Barneche and Allen 2018). While all energy acquired prior to satiation primarily supports maintenance metabolism (Schindler and Eby 1997), it stands to reason that post-satiation fish can attribute surplus energy to somatic and gonadal growth. While empirical and theoretical studies indicate that activity likely exerts a significant metabolic influence on the life history traits of fish (Sherwood et al. 2002a, Rennie et al. 2005, 2012, Cruz-Font et al. 2019), direct field-validated observations of activity as it relates to prey availability and environmental factors remain rare. As habitat use and foraging dynamics—including prey handling (pursuit, capture, ingestion, digestion) and attack rates (reactive distance, predator and prey speeds, capture success)—will vary based on prey availability (Wootton et al. 2021, Cherif et al. 2024), it stands to reason that population-level activity rates are driven by the availability of prey. Further, energy allocated to activity in the pursuit of prey should also directly relate to the life history patterns of consumers (Johansson and Leonardsson 1998, Turesson and Brönmark 2007, Ahrens et al. 2012).

Lake Trout (*Salvelinus namaycush*) are a stenothermic glacial relict that occur across broad geographic and environmental gradients in lakes of Canada and the northern United States (Scott and Crossman 1973, McDermid et al. 2010). In North America where they are native, they inhabit lakes varying in size from 8.0 to 8 million ha, maximum lake depths between 12 m and 600 m, and environmental gradients spanning ultra-oligotrophic to eutrophic lakes as well as along a clear to brown water clarity gradient (Hansen et al. 2021). Lake Trout have extremely flexible life history strategies as evidenced by wide variation in maturation size (length at 50% maturity, 208 mm – 660 mm), early growth rates (ω, 33 mm/yr – 237 mm/yr), adult size (average length, 225 mm – 824 mm; asymptotic length, 343 mm – 1200 mm) and population biomass (0.004 – 14 kg/ha; Kidd et al. 2014; Hansen et al. 2021). Lake Trout have specific habitat requirements bounded by physiological constraints of 15°C and 4 mg/L of dissolved oxygen (Plumb and Blanchfield 2009), which in all but arctic regions generally limit their summer habitat occupancy to pelagic habitat when lakes are thermally stratified (Blanchfield et al. 2009, Guzzo and Blanchfield 2017). As generalist predators, Lake Trout are thought to optimize foraging by selecting prey and habitats that maximize energy gains and minimize losses (e.g., in ways that follow the MTE). During fall, winter, and spring (a period where water temperatures are low and Lake Trout growth rates are generally slow; Morbey et al. 2010), they forage across the entire lake with access to littoral prey fishes (Guzzo et al. 2017, Gallagher et al. 2019). During summer, thermal stratification mostly prevents access to these littoral prey items and forces Lake Trout to choose between foraging in thermally suitable habitats that hold lower quality prey (e.g., zooplankton, macroinvertebrates if pelagic fish are not available) or making brief, physiologically taxing forays into lake littoral areas for higher value prey (like minnows; Dolson et al. 2009, Guzzo and Blanchfield 2017). When thermal conditions restrict Lake Trout to pelagic waters, they typically favour pelagic prey fishes that share similar oxythermal habitats (i.e., coregonids; *Coregonus artedi*, *C. clupeoformix*, *Prosopium cylindraceum*), followed by *Mysis diluviana* (Trippel and Beamish 1993), with zooplankton dominating diets when these other items are not available (Martin 1952). The post-glacial distribution of Lake Trout is closely linked to the post-glacial distribution of relict prey species, like coregonids and *Mysis*, resulting in generally consistent species and predator-prey associations across their geographic range (Dadswell 1974, Ridgway et al. 2017, 2022).

With extensive variation in both environmental factors and prey interactions across spatiotemporal scales, Lake Trout could serve as an ideal model for examining whether activity varies according to principles consistent with the MTE. While a substantial body of literature documents how certain aspects of Lake Trout ecology are affected by both prey size and identity and environmental factors separately, knowledge gaps remain as few (if any) studies have considered both environmental and prey communities together. Studies examining environmental drivers suggest that larger, more productive lakes that experience cooler annual water temperatures (i.e., more northern lakes) favour life history strategies leading to later maturation and larger growth (Shuter et al. 1998, McDermid et al. 2010, Wilson et al. 2019). Additionally, theoretical and empirical work suggests that smaller predator prey mass ratios for Lake Trout reduce activity costs, enhance growth rates and shift maturation reaction norms to older ages (Pazzia et al. 2002; Giacomini et al. 2013; Shuter et al. 2016; Cruz-Font et al. 2019). Despite these insights, uncertainties remain about how environmental and prey-based factors interact to shape activity rates and life histories across the species' geographic range. Further, given the suggested links between metabolic demands and contaminant dynamics (Trudel and Rasmussen 2006), understanding how activity differences drive contaminant concentrations is crucial for this culturally, economically, and nutritionally important species.

The overarching goal for this thesis was to understand how prey availability and environmental factors together influence Lake Trout ecology, enabling broad scale comparisons across lakes typical of their range (i.e., lakes with common food web types spanning wide environmental gradients). My specific objectives were to:

1) Directly observe *in situ* swimming activity with a novel stationary hydroacoustic platform to determine if Lake Trout activity is related to spatiotemporal variation in prey availability and environmental factors;
2) Re-assess drivers of Lake Trout mercury dynamics by incorporating a more nuanced view of prey availability compared to classic food chain length models (e.g., Rasmussen et al. 1990; Cabana et al. 1994), while also

evaluating how bottom-up, environmental conditions influence predicted mercury concentrations;

3) Test the relative importance of environmental factors and prey community structure, both independently and in combination, on shaping Lake Trout life history traits in ways that are consistent with the MTE.

To meet these goals, each objective (i.e., chapter) followed a consistent experimental design. Prey availability was classified using a categorical Lake Class system, following a modified version described in Rasmussen et al. (1990), Cabana et al. (1994), Vander Zanden and Rasmussen (1996) and Vander Zanden et al. (1999). Lake Classes were categorized by pelagic prey structure: Class 1 lakes contained only pelagic zooplankton, Class 1.5 lakes included *Mysis* but not pelagic prey fish, Class 2 lakes had pelagic prey fish but not *Mysis*, and Class 3 lakes featured both pelagic prey fish and *Mysis*. Selection of environmental variables was tailored to each objective, depending on the specific biological response variables under investigation.

CHAPTER 2

The impact of food web structure on Lake Trout activity rate

Abstract

Accurately measured fish activity rates are essential for understanding both the energetic costs and foraging strategies of aquatic predators like Lake Trout (*Salvelinus namaycush*). While metabolic theory predicts that Lake Trout activity and metabolism should decrease with increasing prey community complexity, direct field-based observations on wild, free-swimming fish with which to test this theory are scarce. Using a novel stationary hydroacoustic approach across distinct food web structures, I directly observed how Lake Trout activity responds to variation in both prey availability and environmental conditions. Activity was highest in lakes without pelagic prey fishes, where Lake Trout maintained consistent swimming speeds day and night and swam in more convoluted paths compared to lakes with pelagic prey fishes. Further, nearly 50% of Lake Trout detections from planktivorous populations were observed in thermal conditions exceeding literature-defined physiological thresholds. In contrast, lake with pelagic prey fish had similar daytime swimming behaviours as lakes without pelagic prey fishes, but had significantly lower nighttime swimming speeds, generally swam in more linear paths, and were significantly less likely to be observed in suboptimal oxythermal environments. Consequently, Lake Trout in lakes without prey fishes had much higher levels of active metabolism. The results of this study demonstrate that activity is directly measurable using stationary hydroacoustic applications, and that both swimming

behaviour and metabolic rates estimated from direct observation of movement are modified by prey communities in ways consistent with predictions from metabolic theory.

Introduction

Food web structure defines the boundaries for interactions between predators and prey. Realized interactions between predators and prey largely depend on the presence and availability of suitable for each (McCann et al. 2005), and in dynamic ecosystems, such as those experiencing seasonality, habitat overlap between predators and prey can vary dramatically in time (Pyke et al. 1997, Ahrens et al. 2012). Consequently, at the population level, differences in prey availability can lead to fluctuations in predator behaviour (Rennie et al. 2005, Guzzo et al. 2017, Cruz-Font et al. 2019), life history traits (Pazzia et al. 2002, Giacomini et al. 2013), and contaminant bioaccumulation (Rasmussen et al. 1990, Cabana et al. 1994, Ross *Chapter 3*). Variation in these traits typically results from differences in predator-prey mass ratios and prey quality (Boisclair and Leggett 1989b, 1989c, Shuter et al. 2016), whereby access to large, energy dense prey items leads to higher growth rates and delayed maturity (Kerr 1971a, Shuter et al. 2016). These traits are directly influenced by the consumptive benefits of foraging on energy-rich versus energy-poor prey, though it is also likely that shifts in absolute consumer activity rates, which are often linked to foraging behaviour, influence conversion efficiency and the movement required for the maintenance of metabolic demands (Kerr 1971a, Rennie et al. 2005).

Movement plays a critical role in the energy budget of freshwater fish, with active metabolism accounting for up to 50% of energy expenditures (Boisclair and Leggett 1989a, Rowan and Rasmussen 1996, Rennie et al. 2005, 2012). Theory suggests that prey availability — in relation to body size, resource density and energetic quality —

regulates activity by adjusting the movement needed to forage to satiation (Giacomini 2013, Barneche and Allen 2018). After satiation, fish can rest and allocate surplus energy to either somatic or gonadal tissue growth, while all energy acquired prior to satiation primarily supports maintenance metabolism (Schindler and Eby 1997). Foraging dynamics, such as prey handling time (pursuing, subduing, ingesting, digesting prey) and attack rates (reactive distances, predator and prey speeds, capture success) vary with prey type and availability (Brose 2010), and can be divergent in both absolute (i.e., prey community presence/absence among lakes) and relative terms (i.e., diurnal or seasonal availability). Prey density may also influence foraging behaviour through density dependent mechanisms. When resource density is high, activity rates may decrease as less movement is needed to locate prey; whereas at low densities, activity rates may increase as predators move between patches to find sufficient prey (Ahrens et al. 2012). Although studies stress the importance of considering activity as an explicit metabolic cost in the life history dynamics of freshwater fish (Sherwood et al. 2002a, Rennie et al. 2005, 2012, Cruz-Font et al. 2019), direct measurements of activity in wild, free-swimming fish are exceedingly rare. Much of our understanding stems from laboratory populations exposed to various environmental conditions (Cruz-Font et al. 2016, Reeve et al. 2024), direct observation via SCUBA or snorkel surveys (Rennie et al. 2005), muscle metabolite or radioisotopic proxies (e.g., lactate dehydrogenase; Rowan and Rasmussen 1996, Pazzia et al. 2002, Sherwood et al. 2002a, 2002b, Rennie et al. 2005a), and short-term biotelemetry tracking focusing on small proportions of individuals from larger populations (Cruz-Font et al. 2019, Hlina et al. 2024). Currently, no empirical evidence directly links observed predator activity to prey characteristics when prey availability differs across space and time.

The stenothermic glacial relict, Lake Trout (*Salvelinus namaycush*), exhibits varied life histories (Hansen et al. 2021) and occupies a diverse range of geographic and environmental gradients across lakes in Canada and the northern United States (McDermid et al. 2010), making it an ideal species to test how variation in spatial and temporal prey availability affects activity. Lake Trout often co-occur with predictable coldwater relict prey communities, such as *Mysis diluviana* (hereafter, *Mysis*) and/or/nor coregonids (Dadswell 1974), whose presence or absence may modify Lake Trout behaviour based on access to preferred prey. As generalist predators, Lake Trout are thought to optimize foraging by selecting prey and habitats that maximize energy gains and minimize losses. During fall, winter, and spring, they forage across the entire lake, accessing larger prey items or denser prey aggregations (i.e., prey fish schools, planktonic aggregations) in both littoral and pelagic habitats (Blanchfield et al. 2009, Guzzo et al. 2017) . However, during summer when Lake Trout aim to maximize consumption and growth (Morbey et al. 2010, Wilkins and Marsden 2021), thermal stratification creates a dilemma in lakes where littoral areas become too warm, forcing Lake Trout to choose between foraging in thermally suitable areas with potentially lower quality prey (e.g. foraging on deepwater zooplankton in lakes without pelagic prey fishes or *Mysis*) or making brief, physiologically taxing forays into warmer littoral waters for higher value prey (like minnows; Dolson et al. 2009, Guzzo and Blanchfield 2017). Additionally, diurnal availability of taxa that undergo diel migrations (e.g., zooplankton, *Mysis* and *Chaoborus*, coregonids) may further alter the availability of certain prey items, and therefore, Lake Trout foraging behaviour (Hrabik et al. 2006).

When restricted to pelagic waters during stratification, access of Lake Trout to prey follows a preferential hierarchy that provides a categorical assessment of prey identity and habitat, and, indirectly, predator-prey mass ratios. Specifically, Lake Trout show a consistent dietary preference in order of prey trophic position, favouring pelagic prey fishes (typically coregonids; *Coregonus artedi, C. clupeaformis*, *Prosopium cylindraceum*) followed by *Mysis* (Trippel and Beamish 1993), with zooplankton dominating diets when higher-preference taxa are absent (Martin 1952). A previously developed Lake Class system for Lake Trout formalized this order of preference, for the purposes of examining associations between food web structure and contaminant dynamics (Rasmussen et al. 1990), demonstrating that contaminant bioaccumulation and biomagnification increased with prey food chain length.

I propose that applying a similar categorization system could also aid in describing the influence of prey community structure on Lake Trout activity. Under the previously proposed Lake Class categorization, all lakes had pelagic zooplankton at the base of the food chain (Rasmussen et al. 1990a); lakes where this was the only coldwater pelagic prey present in the system were categorized as Class 1 lakes. Class 2 lakes had pelagic prey fishes as coldwater pelagic prey (but no *Mysis*), and Class 3 lakes had both *Mysis* and pelagic prey fishes available. However, Lake Trout also occupy lakes where *Mysis* are the sole pelagic prey item (apart from zooplankton) and coldwater prey fish are absent, a category of lakes not previously considered. Given that each Lake Class represents an increase in food chain length (and thus reduced predator-prey mass ratios), it follows that the presence of *Mysis* without pelagic prey fish is a category intermediate between Class 1 and Class 2 lakes. As such, I propose a new Lake Class—Class 1.5—to capture this previously undescribed scenario of food chain length.

To better understand the effects of prey community structure on the activity rates of wild, free-swimming Lake Trout, I directly observed swimming activity in 12 lakes across these four distinct Lake Classes using a stationary up-looking hydroacoustic platform. I hypothesized that three main variables were likely to affect Lake Trout activity; 1) Lake Class, as a reflection of prey availability/identity and predator-prey mass ratios (and therefore foraging efficiency), 2) diurnal period, corresponding to daily prey aggregations associated with fish schooling and invertebrate diel migration patterns, and 3) prey concentrations (i.e. acoustic S_v and prey fish density), as swimming behaviour may vary with resource density. Given that many Lake Trout lakes within their range have defined prey communities, a Lake Class perspective on activity determinants and constraints could support future assessment and management of Lake Trout and their food webs.

Methods

Study design, site selection, and environmental sampling

To investigate the impact of prey availability on the *in situ* swimming behaviour of Lake Trout, I conducted a study using an up-looking, stationary hydroacoustic platform deployed in pelagic ecosystems across 12 lakes in Algonquin Provincial Park (n = 2) and the International Institute of Sustainable Development Experimental Lakes Area (IISD ELA; n = 10). Surveys were conducted during 2019, 2021 and 2022 after surface water temperatures exceeded 16°C and lakes had thermally stratified. In all lakes, Lake Trout were the dominant pelagic piscivore, while the pelagic prey communities varied in terms of prey availability following taxonomic prey classification groups of Class 1, 1.5, 2, and 3 (see introduction for Lake Class descriptions; Table 2 - 1). During each survey, oxythermal conditions were assessed by vertical temperature and dissolved oxygen profiles at one-meter intervals from surface waters to the bottom sediments using a ProSolo Digital Water Quality Meter (YSI, Ohio, USA).

Hydroacoustic data collection and processing

Hydroacoustic surveys were conducted in each study lake using an EK80 Wideband Transceiver (WBT) and 120 kHz split-beam Simrad transducer (Kongsberg Maritime, Norway) operating at its center frequency in continuous wave (CW) mode. The transducer was mounted facing upwards on a ~70 lb stainless steel mooring platform which was lowered from a small outboard research vessel to the lake bottom. The acoustic unit was powered from shore with a solar-charged 12 V, 800 amp-hour battery bank and contained an acoustic processor running EK80 software (i.e., a computer), the WBT, and a 170 m transducer cable leading from the WBT to the transducer. Deployment locations were chosen to represent the deepest point of each study lake that was within

~125 m from shore that had adequate cardinal orientation for solar charging of the battery bank. Once deployed, data were recorded continuously (i.e., 24 hr/day) for seven to ten days. Lake-specific echosounder parameters for depth-averaged water temperature were used to inform calibration coefficients within the EK80 software (Table 2 - 2). Lake-specific acoustic ping rates were modified based on depth of deployment to ensure that return echoes were received prior to the unit sending out another ping. The acoustic system was calibrated at least twice annually during the period of data collection using a standard 23 mm copper calibration sphere and the EK80 calibration wizard.

All raw hydroacoustic data were processed using Echoview software to translate acoustic detections into single target fish tracks and prey density estimates (version 13.0, Echoview Software Pty. Lld., Australia). Near- and far-field acoustic exclusion zones were created to account for non-uniformity in wavefronts close to the transducer face and at the surface to account for entrained air from surface waters at maximum transducer range. Following the consensus-based freshwater standard-operating-procedure for acoustic data analysis (Parker-Stetter et al. 2009), the nearfield exclusion zone for all study lakes was calculated and set at 2 m from the transducer. To determine the far-field exclusion zones for each lake, a set of Echoview operators were used on acoustic backscatter data (S_v). First, an ‘XxY statistic’ operand with a maximum 3 rows by 7 ping statistic was used to increase the intensity of surface echoes. The ‘Best Bottom Candidate Line Pick’ was applied to the XxY statistic, followed by a “Span Gaps” operand and a “Smoothing Filter”. Finally, a 0.2 m offset was added to each far-field exclusion line before the entire line was manually examined and edited for areas not well represented by the automated line pick. It was also at this point that bad data regions were identified within the water column and isolated from further analysis (e.g., areas with spurious noise). Although system noise was low throughout all deployments (evident through daily passive-mode recordings; acoustic "listening"), each Echoview processing template included Background Noise Removal and Impulse Noise Removal operands for between-lake consistency.

To isolate fish targets from acoustic backscatter (S_v), I first applied a threshold of -75 dB to the S_v data. Next, I used Echoview's "School Detection" algorithm on the remaining S_v. This step was required to eliminate cases of target coincidence (multiple fish within a single sampling volume) and fish schooling (See Appendix 2.A, Table A. 1 for school detection parameter settings). A School Region Bitmap was then used to mask all volume targets within the region, with all bitmapped regions being classified as "no data". We used Echoview's "Single Target Detection – Split Beam (method 2)" on TS data to identify individual fish as they encountered the beam, then applied Echoview's Fish Track detection algorithm to assess fish size and behaviour on targets identified in the previous step (i.e., fish swimming speed, detection depth, tortuosity). Fish Tracks were created using default Echoview parameters with the following exceptions: "minimum number of single targets in a track" was set at 5, "minimum number of pings in track" was set at 5, and the "maximum gap between single targets" was set to 2. Fish track regions were exported, and fish length (mm) was estimated using mean Fish Track TS (dB) and Love's (1971) equation.

Acoustic targets were classified as Lake Trout by pairing acoustic detection depth with known habitat preferences of the fish community of the lake with historical fishery-independent size-structure data. When lakes are thermally stratified during summer (corresponding to when my surveys were conducted), Lake Trout are typically found in pelagic waters < 15°C. By contrast, two other commonly-encountered large-bodied species in my survey lakes generally prefer warmer temperatures; White Sucker (*Catostomus commersoni*), present in all my survey lakes, have a much higher preferred temperature than Lake Trout (23.4°C compared to 10°C; Hasnain et al. 2018) and separate from Lake Trout in range by occupying more shallow, near-surface waters (Shuter et al. 2023), including depths commonly included in my far-field acoustic exclusion zones. Northern Pike (*Esox lucius*) also have much warmer preferred thermal habitat (20.7°C; Hasnain et al. 2018) and are typically oriented to epilimnetic littoral waters during the summer (Scott and Crossman 1973, Pierce 2012), an area within the lake that my up-looking hydroacoustics did not assess. Burbot (*Lota lota*) were also present in four of my study lakes, though they occur at low relative densities compared to Lake Trout (Rennie *unpublished data*), are bottom-oriented (Scott and Crossman 1973), and perform "diel bank migration" where diel migration to warmer temperatures occurs by horizontal swimming up contours rather than through the water column (Cott et al. 2015); it is unlikely that Burbot could be observed in up-looking surveys with a 2 m exclusion zone. Finally, fish targets were filtered using Lake Trout size structure data from lake-specific historical catch records. Fish tracks were classified as Lake Trout if their estimated acoustic length fell between the 5th quantile fork length and the maximum fork length of Lake Trout previously handled for that specific lake (Table 2 - 3). My choice to use the 5th quantile provides high confidence that we are not confusing Lake Trout targets with those possibly attributed to Cisco, which occurred in six of my lakes and share similar preferred summertime pelagic habitats as Lake Trout; the 95th quantile fork length for Cisco in ELA study lakes is 197mm (Rennie *unpublished data*), and the maximum fork length for Opeongo and Smoke Lake Cisco is 149mm and 197mm, respectively (Vascotto 2006), all considerably lower than the 5th Lake Trout quantile (Table 2 - 3).

The influence of prey assemblage on Lake Trout swimming behaviour was acoustically assessed in two ways: 1) as prey fish density estimates and 2) as non-fish prey concentrations (i.e., acoustic S_v from non-fish targets; large-bodied pelagic invertebrates). Prey fish densities (#/m^3) were estimated by scaling volume backscattering coefficients (s_v in m^2/m^3; linearized acoustic S_v) with the mean backscattering cross section (σ_{bs} in m^2) for each lake during both day and night. Prey fish were identified in single target echograms, using the same methods as above, as fish tracks with TS between -40 dB and -60 dB (e.g., fish between ~ 20 to 180 mm). To estimate the contribution of non-fish prey concentrations, all non-fish echoes were isolated by removing the contribution of fish tracks (determined from S_v echograms as described above) through a series of Echoview operands. Following a process similar to Rudstam et al. (2008), fish echoes were identified and removed by applying a 7 x 7 maximum dilation filter on TS data to reduce the influence of weaker TS values surrounding fish targets. To isolate non-fish echoes (i.e., large-bodied pelagic invertebrates, rather than smaller-bodied zooplankton) a “fish region” bitmap was created from the dilated filter data and a -60 dB minimum TS threshold. A complimentary “non-fish region” bitmap was then created to remove all fish echoes. The non-fish region bitmap was then applied to S_v data with a -60 dB maximum threshold to create a relative metric for large-bodied invertebrate prey concentrations (see Appendix 2.A, Figure A. *1* for example echogram demonstrating various echogram quantities). To account for diurnal differences in prey distribution, day/night periods within each echogram were categorized by sunset and sunrise times for geographic lake centers using the “suncalc” R package (Thieurmel and Elmarhraoui 2022).

Despite its limitations in detecting smaller zooplankton, using a 120 kHz transducer for assessing “non-fish prey” is an accepted method for resolving the presence and relative density of large zooplankton and macroinvertebrates such as *Mysis* and *Chaoborus*. Knudsen et al. (2006) demonstrated that non-fish backscattering at this frequency is dominated by *Chaoborus* with zooplankton contributing minimally to the observed signal. Similarly, Rudstam et al. (2008) showed distinct scattering patterns for *Mysis*, underscoring the frequency’s ability to differentiate these taxa from background zooplankton based on a multi-frequency assessment. Diel vertical migration patterns—characteristic of both zooplankton and larger macroinvertebrates—were readily observed across all echograms within this study, supporting the utility of a 120 kHz assessment for non-fish prey. Thus, despite excluding smaller zooplankton, the 120 kHz frequency provides meaningful insights into larger zooplankton and macroinvertebrate dynamics relevant to ecosystem studies.

To determine the optimal sized region for integrating prey S_v, reflecting the volume of water that Lake Trout targets likely interacted with, I created a "prey influence" region for each Lake Trout detection. For each lake, I defined a vertical prey range based on the 25th and 75th quantiles of Lake Trout detection depths. I set the horizontal extent, or elementary distance sampling unit (EDSU) using a semivariance analysis on the non-fish prey S_v object. Modelling prey S_v estimates at 30 second time intervals over periods from 30 seconds to five minutes, prey S_v variability began to stabilize after two minutes (Appendix 2.A, Figure A. 2). Consequently, the final "prey influence" cell size was defined as the nearest two-minute EDSU for each Lake Trout fish track, encompassing the 25th to 75th quantiles of detection depths specific for each lake.

Testing for differences in swimming behaviours

To assess differences in Lake Trout swimming speeds across Lake Classes, I assembled a linear mixed effect model using the lme4 package in R (Bates et al. 2015). The full model prior to any optimization was:

$$SwimSpeed \sim lakeClass * diurnalPeriod * preyS_v * \ preyFishDensity + (1|lakeID) \text{ [Eq.1]}$$

Where *SwimSpeed* is observed acoustic swimming speeds in body lengths per second, and fixed effects are: lakeClass, representing prey communities categorized by Lake

Class, diurnalPeriod indicating day and nighttime detections; preyS_v, corresponding to acoustic concentrations of large-bodied pelagic invertebrates; and preyFishDensity, reporting prey fish density (#/m^3). lakeID represented distinct survey lakes as an additive random effect. Additionally, prey S_v was Z-score scaled to center all observations, and my response variable, swimming speed, was converted to body lengths per second (bls) to normalize swimming speed and $\log_{10}$ transformed. The full model (Eq. 1) also included all subordinate interaction terms and main effects.

Covariate multicollinearity was first assessed for fixed effect predictor variables, revealing a strong, significant positive correlation between prey fish density and non-fish prey S_v ($r = 0.19$, df = 1176, $p < 0.0001$). A random forest model using the "randomForestSRC" package (Ishwaran and Kogalur 2023) was then used to choose the most important covariate for modelling Lake Trout swimming speeds, following advice by Feld et al. (2016). Non-fish prey S_v was retained as the model covariate because of a considerably higher variable importance score compared to prey fish density. Further, non-fish prey S_v proved to be a better covariate for this model as it had a much longer gradient length, was normally distributed and was not zero-inflated. Collectively, these attributes of non-fish prey S_v led to its inclusion as a covariate despite some of the limitations of using a 120 kHz frequency for assess smaller targets where sound scattering is more variable (see detailed explanation above) . This resulted in an optimized full model of:

$$SwimSpeed \sim lakeClass * diurnalPeriod * preyS_v + (preyS_v | lakeID) \qquad \text{[Eq. 2]}$$

The final model was determined using stepwise term deletion from the full model, first through optimizing model random effects in the full model (lake being modelled as a random intercept or as a random slope with prey S_v), and then refining model fixed effects. Likelihood ratio tests between nested models determined the appropriate final model as:

$$SwimSpeed_{log10} \sim lakeClass * diurnalPeriod + preyS_v + (preyS_v|lakeID)$$ [Eq. 3]

Finally, model assumptions were tested visually using residual vs. fitted plots and Q-Q plots. Variable significance in mixed effects models were assessed with a Type III Satterthwaite approximation for Sums of Squares, and pairwise significance was assessed using post-hoc Tukey tests from the “emmeans” R package (Lenth, 2023). All post-hoc *p*-values were corrected for multiple tests using standard Bonferroni adjustments.

To assess differences in the frequency of swimming behaviours across Lake Classes, I used a chi-square test of frequencies. Following metabolically-relevant behaviours estimated in Cruz-Font et al. (2016), raw swimming speed (meters/sec) was categorized as “burst” when speeds were > 0.57 m/s, “active” when > 0.17 m/s but < 0.57 m/s, and “resting” when < 0.17 m/s. A Levene’s test was used to assess raw swimming speed variation across lake classes.

Tortuosity (i.e., ‘sinuosity’ of a fish track) was modelled using a gamma-distributed generalized linear mixed effect model (GLMM) as the data were considerably right skewed. For each Lake Trout detection, a tortuosity value was calculated as the sum of all detections within a fish track divided by the linear distance from the first to last target in the track. Tortuosity scales from a value of 1 (representing a perfectly straight fish track) to infinity, with higher values describing more meandrous/sinuous tracks through the acoustic beam. To standardize tortuosity values across Lake Classes, fish tracks were removed if they contained less than six single targets and if observations lasted longer than 20 seconds in the beam (as 20 seconds was the maximum observation length for fish tracks in Class 1 lakes). Furthermore, only “active” and “burst” swimming behaviours were retained in tortuosity analyses (see above) so that the final tortuosity dataset represented individuals interacting within their prey field rather than those solely at rest. A random forest modelling approach was again used to determine the appropriate GLMM model covariate structure. Three possible covariates – time in beam (i.e., observation time), prey S_v and prey fish density – along with categorical variables for Lake Class and diurnal period – were included within a fully parameterized random forest model. Model results indicated that time in beam was overwhelmingly more important than the other two possible covariates (Variable importance, VIMP; time in beam = 0.14, prey S_v = 0.05, prey fish density = 0.004) and was therefore the only covariate retained. This left a full model of:

$$Tortuosity \sim lakeClass * diurnalPeriod * TimeInBeam + (TimeInBeam|lakeID)$$

[Eq. 4]

Where Tortuosity was a unitless measure of swim track convolutedness, lakeClass representing categorical prey structure, diurnalPeriod indicating day or night detections, and TimeInBeam relating to the duration (in seconds) a fish remained within the acoustic beam. The full model (Eq. 1) also included all subordinate interaction terms and main effects.

The final GLMM model was determined through stepwise variable deletion using likelihood ratio tests comparing nested models, first by optimizing random effects in the full model and then optimizing fixed effects. The three-way main-effect interaction among Lake Class, diurnal period and time in beam was statistically significant, so the full model was retained. The R package *glmmTMB* (Brooks et al. 2017) was used to assess Lake Trout tortuosity, model assumptions were assessed using the *DHARMa* package (Hartig 2022), and model significance was assessed using Type III Sums of Squares.

Testing for differences in Lake Trout exposure to sub-optimal oxythermal environments

To investigate how prey availability affects Lake Trout exposure to suboptimal, and metabolically challenging oxythermal conditions, I used a series of generalized linear mixed effect logistic regressions. Lake Trout prefer temperatures around 12°C (Hasnain et al. 2018) and are rarely found in waters > 15°C (Plumb and Blanchfield 2009, Raby et al. 2020). Similarly, Lake Trout performance declines at dissolved oxygen concentrations < 6 mg/L (Evans 2007) and individuals are rarely present in water < 4 mg/L dissolved oxygen (Plumb and Blanchfield 2009). Thus, four separate models were assembled to test how Lake Classes influence environmental exposures with a "stressed" vs. "non-stressed" binary distinction. Each Lake Trout acoustic detection was paired with oxythermal water profile data recorded during the survey period. Categories of suboptimal oxythermal exposure were classified as (1) those where water temperatures were between 12 and 15°C, and (2), those where dissolved oxygen concentrations between 4 and 6 mg/L. Categories where apparent physiological limits were exceeded were for detections that occurred in habitats where (3) water exceeded 15°C, and (4), dissolved oxygen fell below 4 mg/L. Models were run using glmmTMB (Brooks et al. 2017). Unlike previous analyses, Lake Class was treated as a continuous integer in this analysis reflecting relative food chain length amongst Lake Classes (i.e., predictors in this analysis were coded as 1, 2, 3, 4 rather than 1, 1.5, 2, 3) to allow for the fitting of a generalized logistic model. LakeID was included as a random intercept. Model assumptions were evaluated using residual vs fitted plots and assessing the goodness of model fit with a Pearson's $\chi 2$ residuals significance test.

Metabolic assessment of swimming behaviour

Oxygen consumption was estimated for each fish track to investigate the metabolic consequences of activity differences among Lake Classes. Metabolic output was estimated as the oxygen consumption (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) associated with each fish track encountering the hydroacoustic beam. Oxygen consumption was estimated from fish track swimming speeds (in cm/s^{-1}) using a Lake Trout specific regression equation (Cruz-Font et al. 2016). A linear mixed-effect model was used to test for differences in Lake Classes and diurnal periods, with a random intercept of lakeID to control for within-Lake Class differences among lakes. Model optimization retained the interaction term of Lake Class with diurnal period within the final model structure. Assessment of model assumptions, significance testing and post-hoc analysis was identical to methods used for assessing differences in swimming speeds (see Methods Section 3, above).

All statistical analyses and visualizations were conducted in R 4.1.2 (R Core Team 2023).

Results

Swimming activity differences across food web types

Hydroacoustic surveys indicated that Lake Trout swimming speeds were significantly different between Lake Classes, but that these differences depended on diurnal period (Figure 2 - 1; Table 2 - 4). Though daytime swimming speeds were similar across all Lake Classes, mean Class 2 and Class 3 nighttime speeds were 0.19 bls^{-1} and 0.24 bls^{-1} lower than their average daytime swimming speed, respectively. By contrast, nighttime Class 1 Lake Trout swimming speed was on average 0.41 bls^{-1} higher than Class 3 at night. Between Class 1 and Class 1.5, there were no differences in day or nighttime swimming speeds (Table 2 - 5). Though prey S_v was marginally non-significant ($F_{1,13.95} = 4.57$, $p = 0.051$), swimming speeds were negatively related to large-bodied invertebrate prey concentrations across all Lake Classes and diurnal periods (Figure 2 - 1; Table 2 - 4).

Lake Class influenced variability in Lake Trout swimming behaviours, with narrow movement rate distributions in Class 1 and 1.5 lakes where individuals maintained one general swimming mode during both day and night periods (Figure 2 - 2). In contrast, Class 2 and especially Class 3 lakes had broader movement rate distributions (Levene's Test: $F_3 = 12.366$, $p < 0.0001$). This increase in variability reflects shifts in “active” compared to “resting” swimming behaviours across Lake Classes (Figure 2 - 3). The frequency of “burst”, “active”, and “resting” swimming was significantly different across Lake Classes (Chi-square test; $\chi^2 = 151.67$, df = 6, $p < 0.0001$), with progressively higher occurrences of “rest” swimming with each successive Lake Class (Figure 2 - 3). Amongst Lake Classes, Class 1 Lake Trout rested in only 9% of all detections, increasing to 23% in Class 1.5 lakes. Conversely, Class 2 Lake Trout were at rest in more than one-third of all detections, while Class 3 individual were at rest 69% of the time (Table 2 - 6). “Burst” swimming remained mostly consistent across Lake Classes (range: 2.1 – 3.6%).

Drivers of Lake Trout tortuosity (i.e., how convoluted their swimming path was) were complex, as the most adequate model suggested a significant three-way interaction between Lake Class, invertebrate prey concentrations, and the time in which an individual was in the acoustic beam (Table 2 - 7). Nevertheless, certain patterns emerged (Figure 2 - 4). Model-adjusted mean tortuosity estimates, centered on the covariate of time in the acoustic beam and accounting for both day and night observations, indicate a decrease in mean tortuosity as prey communities became more complex. For a Class 1 fish spending ~7.5 seconds within the acoustic beam (covariate mean), it's swimming path was 50.5% more tortuous than a Class 1.5 fish, and approximately 67% more tortuous than Class 2 and Class 3 fish. Tortuosity was generally higher during the day, however there were Lake Class specific diurnal differences that also varied depending on how long a Lake Trout was observed in the acoustic beam. For example, there were apparent similarities in tortuosity patterns for lakes with and without *Mysis*; nighttime tortuosity in Class 1 and 2 lakes (no *Mysis*) was significantly higher with more time spent in the acoustic beam, whereas tortuosity remined low in lakes with *Mysis* (Class 1.5 and 3) and was independent of the time an individual was detected within the acoustic beam (Figure 2 - 4).

Food-web mediated exposure to sub-optimal oxythermal environments

Lake Trout exposure to sub-optimal oxythermal conditions decreased as lake food webs increased in complexity (Figure 2 - 5). Lake Trout in planktonic food webs (Class 1 and 1.5) were detected in water temperatures exceeding the 15°C literature-defined physiological threshold in over 50% of all acoustic detections (Figure 2 - 5.A) and were significantly more likely to be detected in water temperatures between 12 and 15°C (Figure 2 - 5.B; Table 2 - 8). While acoustic detections in hypoxic environments were rare in Class 1 and 1.5 lakes, they did occur, whereas no fish were detected in hypoxic conditions when pelagic prey fish were present (i.e., Class 2 or Class 3; Figure 2 - 5.C, 5.D). By contrast, almost one quarter of all Class 1 acoustic detections occurred in waters with dissolved oxygen content between 4 – 6 mg/L (Figure 2 - 5.D), resulting in significantly higher odds for Lake Trout experiencing hypoxic conditions in planktonic food webs compared to those inhabiting more complex prey assemblages (Table 2 - 8). While available habitat was more restricted in Class 1 and 1.5 lakes because of smaller lake volumes available between the 12 and 15°C isotherms and 4 to 6 mg/L oxyclines, there was "ideal" habitat available to Lake Trout in all survey lakes (Appendix 2.A, Table A. 2).

Metabolic consequences of prey availability

Behavioural differences among Lake Classes led to significantly lower levels of estimated oxygen consumption in Class 2 and Class 3 lakes during the night compared to during the day (Figure 2 - 6; Type III approximation linear mixed effect model, lakeClass:dayNight $F_{3,36.59} = 46.59$, $p < 0.0001$). Class 2 nighttime oxygen consumption decreased nearly 3-fold compared with daytime estimates, from 668.81 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ during the day to 210.65 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ at night, and Class 3 decreased from 676.81 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ during the day to 191.03 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ at night. Active metabolism was statistically equivalent for Class 1 and 1.5 Lake Trout both day and night, though median Class 1.5 nighttime oxygen consumption was nearly half that of Class 1 nighttime metabolism. By contrast, daytime oxygen consumption remained consistent across all Lake Classes, averaging 553.37 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (range: 330.27 – 691.65).

Discussion

Using a novel application of hydroacoustic technology in lake ecosystems, patterns of Lake Trout swimming activity observed directly in my study are consistent with predications based in metabolic theory (e.g. Brown et al. 2004, Giacomini et al. 2013); both clearly show that Lake Trout activity and metabolic rates are driven by prey availability. Importantly, diurnal period, prey concentrations, and time duration of acoustic tracks all modified aspects of the response of Lake Trout swimming behaviour across the range of prey availability examined here. In thermally stratified lakes without pelagic prey fishes (Class 1 and Class 1.5), Lake Trout swimming behaviour was generally consistent during both day and night. Relative to Class 2 and 3 lakes where behavioural variation was much broader, planktivory resulted in behaviours dominated by metabolically active swimming styles, higher absolute nighttime swimming speeds, generally higher track tortuosity and increased exposure to suboptimal oxythermal conditions. Unsurprisingly, elevated activity, particularly at night, led to higher rates of oxygen consumption and active metabolism for individuals in Class 1 and Class 1.5 lakes.

In this study, I demonstrated the potential of stationary hydroacoustics as an innovative approach for directly observing the behaviour of wild, free-swimming fish. Accurately estimating fish behaviour and activity in natural environments has presented a challenge for fisheries biology (Cooke et al. 2016, Brownscombe et al. 2022), yet accurate measurements of these quantities are critical for understanding fish ecology and managing fish stocks. Various existing methods for assessing activity (e.g., short-term sensor/telemetric observations, enzymatic proxies, contaminant-bioenergetic models) offer insight into bioenergetic processes, but often lack field validation and fail to directly integrate environmental factors that drive behaviour, energy use, and metabolic rates (e.g., prey availability, thermal environments, diurnal cycles). This new approach captures quantitative movement data across entire populations, as well as *in situ* covariates, which were critical in revealing the behavioural patterns linked to Lake Trout activity and metabolic rates. For example, I found that prey availability influenced Lake Trout activity independently from Lake Class and diurnal periods, with fish swimming faster when prey densities were low, a behaviour that is likely to increase encounter rates with more abundant, energy-rich prey (Johansson and Leonardsson 1998, Turesson and Brönmark 2007, Ahrens et al. 2012). Further, direct observations across different Lake Classes indicated a marked decrease in median swimming tortuosity—by 50% from Class 1 to Class 1.5, and by approximately 67% in both Class 2 and 3 lakes relative to Class 1—and revealed that swimming paths were influenced by both the time of day and swimming speed/behaviour (as approximated by observation time within the acoustic beam). As more tortuous swimming patterns are assumed to be more energetically costly (Webb 1975, Benhamou 1992, Krohn and Boisclair 1994), this could further influence the various energetic costs of planktivory for Lake Trout. Finally, by pairing real-time observations of fish activity with real-time environmental conditions (e.g., water temperature and dissolved oxygen), this methodology identified instances where fish remained active even outside their assumed physiological limits, highlighting potentially additional metabolic costs of foraging in suboptimal environments for Lake Trout in Class 1 and 1.5 lakes. Stationary hydroacoustics made it possible to directly assess how fish respond to environmental conditions, bridging a critical gap between optimal foraging theory (Pyke et al. 1997), metabolic theory (Brown et al. 2004, Giacomini et al. 2013) and observational ecology. Improved activity estimates derived from observed ecological responses could ultimately be used to make more informed and accurate bioenergetic models.

Diurnal period played a crucial role in shaping Lake Trout behaviour across the different prey community types I assessed. Swimming speed, tortuosity, and oxygen consumption estimates all exhibited significant interactions between diurnal period and Lake Class, with Class 1 and 1.5 fish maintaining consistent daytime behaviours into the night, while fish activity in Class 2, and especially Class 3, significantly decreased after dark. As visual feeders (Keyler et al. 2019), Lake Trout are believed to display increased daytime foraging and activity rates, particularly during crepuscular periods when low light conditions and prey migratory behaviours likely improve prey accessibility (Milne et al. 2005, Dunlop et al. 2010, Cruz-Font et al. 2019). While I was unable to isolate dawn and dusk periods from my hydroacoustic data due to limited detections during these short observational windows, clear day/night patterns between Class 1 and 1.5 compared to Class 2 and 3 indicate a timing component where Lake Trout across all lakes appear to optimize foraging during the most advantageous periods for prey capture (where “day” includes crepuscular times). In smaller inland lakes, such as those in my study, it seems likely that the higher proportion of Class 1 and 1.5 active nighttime swimming is associated with the need to subsidize daytime foraging with additional nighttime foraging as the energy density (ED) associated with a planktivorous invertebrate diet (e.g., zooplankton, *Mysis* and Chaoborous) is considerably less than that of piscivorous prey items (e.g., ~ 2600 J.g zooplankton/macroinvertebrate ED compared to ~6000 J.g fish ED; Cumminns and Wuycheck 1971, Fernandez et al. 2009, Rennie et al. 2012). In Class 1 and 1.5 lakes, energetic shortfalls are probably associated with inefficient prey conversion, stemming from elevated activity levels and the lower energy density associated with a planktivorous diet.

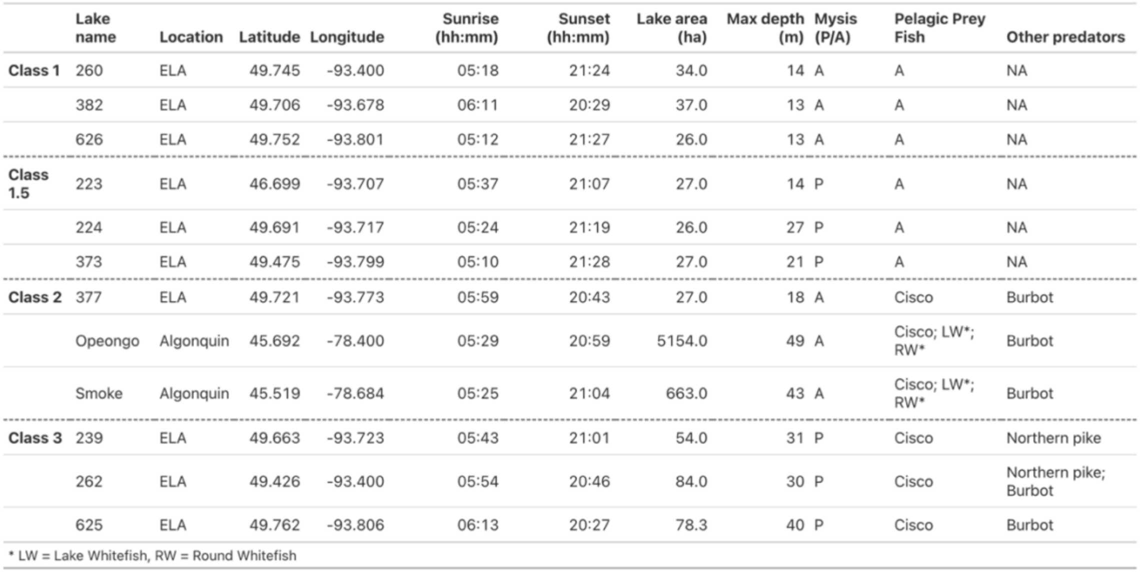
Relying on planktivory as a main foraging style poses distinct metabolic challenges for Lake Trout**.** In Class 1 and 1.5 lakes, where planktivory dominates, higher active metabolic rates reflect the sustained daily swimming behaviours required to maintain energetic efficiency. For instance, mean nighttime model-predicted active metabolism (estimated oxygen consumption) for Class 1 Lake Trout was an order of magnitude higher compared to Class 3 fish. Extended across a full summer stratification period, these elevated metabolic demands may leave planktivorous Lake Trout in an energy deficit, which is only likely to intensify as climate change prolongs open-water stratified periods (Guzzo and Blanchfield 2017). Secondly, the differential oxythermal conditions experienced by planktivorous (Class 1 and 1.5) and piscivorous (Class 2 and 3) Lake Trout populations likely put planktivores at an added energetic disadvantage. For poikilotherms like Lake Trout, standard metabolic rates rise with temperature, which poses challenges for species when behavioural needs conflict with their thermal preferences. In Class 1 and 1.5 lakes, Lake Trout spent nearly half their time in waters above 15°C — temperatures beyond their supposed thermal optimum (Plumb and Blanchfield 2009, Hasnain et al. 2010) and which would represent further increases from baseline metabolic rates. Additionally, planktivorous Lake Trout (Class 1 and 1.5) were observed in hypoxic regions, while fish in Class 2 and 3 lakes avoided these areas altogether. Although Class 1 lakes were the shallowest of all Lake Classes (Deployment depth ~ Lake class ANOVA; $F_{3,8} = 4.07$, $p = 0.050$; Class 1:Class3 TukeyHSD $p = 0.038$, all other pairwise groups $p > 0.05$), regions of normoxia were available in all lakes (Appendix 2.A, Table A. 2) indicating that Class 1 and 1.5 Lake Trout actively chose hypoxic regions even when normoxic water were available. Prolonged exposure to hypoxia reduces the aerobic scope of fish by limiting oxygen availability (Claireaux and Chabot 2016). This can lead to increased gill ventilation rates and slower digestion, both of which raise metabolic demands, and ultimately can lead to reduced growth, recruitment, and activity levels (Evans 2007, Zhang et al. 2010).

The presence of *Mysis* had little impact on the swimming behaviour of Lake Trout in Class 1.5 compared to those in Class 1 lakes. However, notable behavioural shifts occurred from Class 2 to Class 3, with Lake Trout observed at rest nearly twice as often (36% in Class 2 compared to 69% in Class 3), resulting in broader distributions of swimming speeds in Class 3 lakes. Additionally, swimming tracks in Class 3 lakes were more linear, particularly at night. This suggests that *Mysis*, alongside pelagic prey fish, may indirectly benefit Lake Trout energy budgets by reducing lake-wide predator-prey mass ratios. Although *Mysis* comprise only a minor portion of Class 3 Lake Trout diets (Trippel and Beamish 1993), their availability to pelagic prey fishes likely enhances the conversion efficiency of pelagic prey fish, and indirectly the conversion efficiency of Lake Trout.

To manage inland Lake Trout stocks effectively, resource managers should consider behavioural differences among populations, including the activity differences I observed across Lake Classes. Fishery-independent surveys assume that catch-per-unit-effort (CPUE) is proportional to density of fish in a body of water (Hilborn and Walters 1992). Ideally, CPUE would correlate precisely with species abundance; however, studies regularly show that this relationship varies (Harley et al. 2001, Dassow et al. 2019, Lester et al. 2021, Mosley et al. 2022). To account for this, managers often apply catchability coefficients to survey data to adjust CPUE to best reflect population abundances. For example, Lake Trout biomass estimates improve when the catchability coefficient is scaled by the mean weight of Lake Trout within a population (Lester et al. 2021). My findings suggest that Lake Trout catchability estimates should also consider activity related to food web assemblages. Further to this point, the provincial fish management program for Ontario, Canada assesses Lake Trout populations by overnight sets of passive collection gear (e.g., gillnets; Sandstorm et al. 2013), a diurnal period which I have shown large differences in swimming speeds among Lake Classes. Consequently, it is reasonable to expect that encounter rates with passive collection gear will vary with Lake Class-specific swimming speeds; primarily planktonic individuals in Class 1 and 1.5 lakes swim faster at night than those piscivorous individuals in Class 2 and 3 lakes, likely leading to higher gear encounter rates among planktonic populations. Without correcting for these activity-related encounter rates, this could lead to overestimating standing biomass in planktivorous Lake Trout populations, which could in turn lead to the risk of setting harvest rates much higher than the maximum sustainable yield for these populations would allow. While swimming speed primarily influences potential gear encounter rates, gillnet contact and retention may also be affected by distinct swimming behaviours associated with different Lake Classes, as factors like sampling gear type and location, fish behaviour, and density dependence can all impact contact and retention (Olin et al. 2004, Prchalová et al. 2008, 2011, DuFour et al. 2019, Giacomini et al. 2020). Although the effect of swimming tortuosity on gillnet contact and retention has not been tested, investigating these differences seem warranted. Angular gillnet encounters, that would be more common at night, particularly in lakes without *Mysis* (Class 1 and 2), could lead to varied retention rates, with further implications for the assumption of catch rate and fish abundance proportionality.

The modified presence/absence Lake Class approach for describing lake food webs described here provides a simple yet effective way to integrate Lake Trout behaviour into fisheries management. In Ontario alone, there are over 2,000 Lake Trout lakes designated for management that span more than 12° latitude (Muir et al. 2021). Managing resources across such a vast geographic area necessitates easily accessible indicators that capture ecological differences between populations, particularly those relative to abundance estimates. While trophic position models that quantify omnivory and direct food web interactions via stable isotopes (e.g., Vander Zanden and Rasmussen 1996) may provide more detailed insights into population-specific predator-prey dynamics, my coarse application of Lake Classes across 12 different lakes in Ontario highlights the significant influence of planktivory and piscivory on Lake Trout activity rates and energy budgets. Given that activity can constitute 30% to 50% of a fish's overall energy budget (Boisclair and Leggett 1989d, Rennie et al. 2005), and that swimming speeds and activity rates influence fish life history traits (Giacomini et al. 2013, Cruz-Font et al. 2019), it is incumbent to further explore how Lake Classes can enhance our understanding of Lake Trout ecology, building on the results reported here.

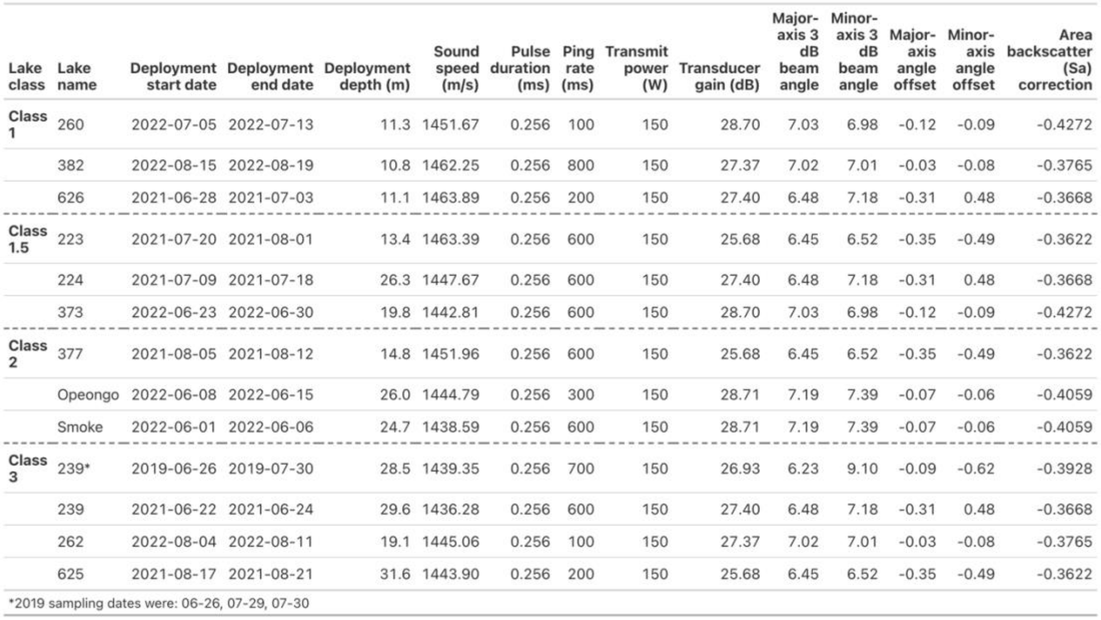
Table 2 - 1. Geographic, physical, and biological information for all acoustic survey lakes. Sunrise and sunset times are the median sunrise/sunset time during the survey period. Mysis and pelagic prey fish presence and absence are denoted by "P" and "A", respectively. Lake trout are the primary predatory species in each study lake, but in certain cases co-occur with other predatory fishes.



	Lake name	Location	Latitude	Longitude	Sunrise (hh:mm)	Sunset (hh:mm)	Lake area (ha)	Max depth (m)	Mysis (P/A)	Pelagic Prey Fish	Other predators
Class 1	260	ELA	49.745	-93.400	05:18	21:24	34.0	14	A	A	NA
	382	ELA	49.706	-93.678	06:11	20:29	37.0	13	A	A	NA
	626	ELA	49.752	-93.801	05:12	21:27	26.0	13	A	A	NA
Class 1.5	223	ELA	46.699	-93.707	05:37	21:07	27.0	14	P	A	NA
	224	ELA	49.691	-93.717	05:24	21:19	26.0	27	P	A	NA
	373	ELA	49.475	-93.799	05:10	21:28	27.0	21	P	A	NA
Class 2	377	ELA	49.721	-93.773	05:59	20:43	27.0	18	A	Cisco	Burbot
	Opeongo	Algonquin	45.692	-78.400	05:29	20:59	5154.0	49	A	Cisco; LW*; RW*	Burbot
	Smoke	Algonquin	45.519	-78.684	05:25	21:04	663.0	43	A	Cisco; LW*; RW*	Burbot
Class 3	239	ELA	49.663	-93.723	05:43	21:01	54.0	31	P	Cisco	Northern pike
	262	ELA	49.426	-93.400	05:54	20:46	84.0	30	P	Cisco	Northern pike; Burbot
	625	ELA	49.762	-93.806	06:13	20:27	78.3	40	P	Cisco	Burbot

* LW = Lake Whitefish, RW = Round Whitefish

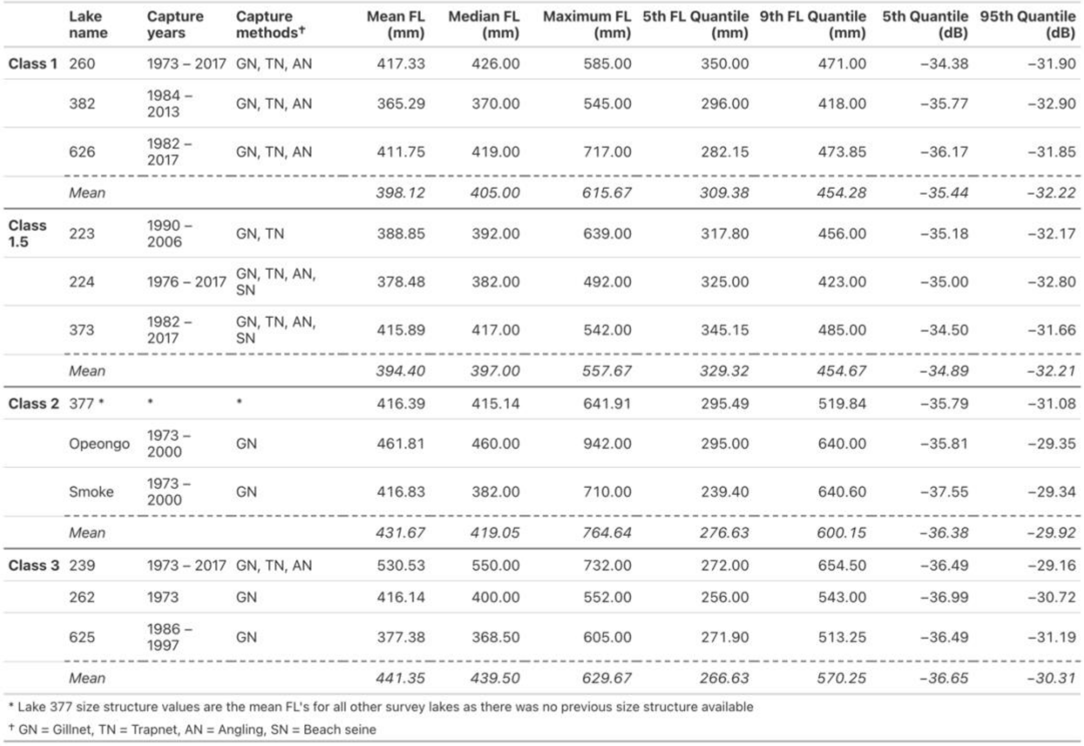
Table 2 - 2. Acoustic deployment information, recording settings, and calibration parameters for all hydroacoustic surveys. Lake 239 survey data has been aggregated over the two summers of surveys.



Lake class	Lake name	Deployment start date	Deployment end date	Deployment depth (m)	Sound speed (m/s)	Pulse duration (ms)	Ping rate (ms)	Transmit power (W)	Transducer gain (dB)	Major-axis 3 dB beam angle	Minor-axis 3 dB beam angle	Major-axis angle offset	Minor-axis angle offset	Area backscatter (Sa) correction
Class 1	260	2022-07-05	2022-07-13	11.3	1451.67	0.256	100	150	28.70	7.03	6.98	-0.12	-0.09	-0.4272
	382	2022-08-15	2022-08-19	10.8	1462.25	0.256	800	150	27.37	7.02	7.01	-0.03	-0.08	-0.3765
	626	2021-06-28	2021-07-03	11.1	1463.89	0.256	200	150	27.40	6.48	7.18	-0.31	0.48	-0.3668
Class 1.5	223	2021-07-20	2021-08-01	13.4	1463.39	0.256	600	150	25.68	6.45	6.52	-0.35	-0.49	-0.3622
	224	2021-07-09	2021-07-18	26.3	1447.67	0.256	600	150	27.40	6.48	7.18	-0.31	0.48	-0.3668
	373	2022-06-23	2022-06-30	19.8	1442.81	0.256	600	150	28.70	7.03	6.98	-0.12	-0.09	-0.4272
Class 2	377	2021-08-05	2021-08-12	14.8	1451.96	0.256	600	150	25.68	6.45	6.52	-0.35	-0.49	-0.3622
	Opeongo	2022-06-08	2022-06-15	26.0	1444.79	0.256	300	150	28.71	7.19	7.39	-0.07	-0.06	-0.4059
	Smoke	2022-06-01	2022-06-06	24.7	1438.59	0.256	600	150	28.71	7.19	7.39	-0.07	-0.06	-0.4059
Class 3	239*	2019-06-26	2019-07-30	28.5	1439.35	0.256	700	150	26.93	6.23	9.10	-0.09	-0.62	-0.3928
	239	2021-06-22	2021-06-24	29.6	1436.28	0.256	600	150	27.40	6.48	7.18	-0.31	0.48	-0.3668
	262	2022-08-04	2022-08-11	19.1	1445.06	0.256	100	150	27.37	7.02	7.01	-0.03	-0.08	-0.3765
	625	2021-08-17	2021-08-21	31.6	1443.90	0.256	200	150	25.68	6.45	6.52	-0.35	-0.49	-0.3622

*2019 sampling dates were: 06-26, 07-29, 07-30

Table 2 - 3. Lake trout size structure from long-term data collection in IISD-ELA and Algonquin Provincial Park lakes. All lengths are reported as fork length (FL), and quantile target strengths (dB) were calculated using lake-specific sound speed (see Table 2).

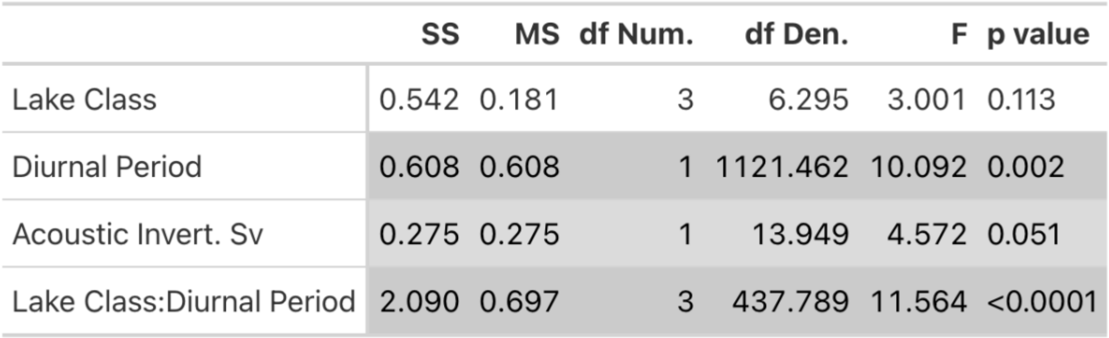


	Lake name	Capture years	Capture methods†	Mean FL (mm)	Median FL (mm)	Maximum FL (mm)	5th FL Quantile (mm)	9th FL Quantile (mm)	5th Quantile (dB)	95th Quantile (dB)
Class 1	260	1973 – 2017	GN, TN, AN	417.33	426.00	585.00	350.00	471.00	−34.38	−31.90
	382	1984 – 2013	GN, TN, AN	365.29	370.00	545.00	296.00	418.00	−35.77	−32.90
	626	1982 – 2017	GN, TN, AN	411.75	419.00	717.00	282.15	473.85	−36.17	−31.85
	Mean			*398.12*	*405.00*	*615.67*	*309.38*	*454.28*	*−35.44*	*−32.22*
Class 1.5	223	1990 – 2006	GN, TN	388.85	392.00	639.00	317.80	456.00	−35.18	−32.17
	224	1976 – 2017	GN, TN, AN, SN	378.48	382.00	492.00	325.00	423.00	−35.00	−32.80
	373	1982 – 2017	GN, TN, AN, SN	415.89	417.00	542.00	345.15	485.00	−34.50	−31.66
	Mean			*394.40*	*397.00*	*557.67*	*329.32*	*454.67*	*−34.89*	*−32.21*
Class 2	377 *	*	*	416.39	415.14	641.91	295.49	519.84	−35.79	−31.08
	Opeongo	1973 – 2000	GN	461.81	460.00	942.00	295.00	640.00	−35.81	−29.35
	Smoke	1973 – 2000	GN	416.83	382.00	710.00	239.40	640.60	−37.55	−29.34
	Mean			*431.67*	*419.05*	*764.64*	*276.63*	*600.15*	*−36.38*	*−29.92*
Class 3	239	1973 – 2017	GN, TN, AN	530.53	550.00	732.00	272.00	654.50	−36.49	−29.16
	262	1973	GN	416.14	400.00	552.00	256.00	543.00	−36.99	−30.72
	625	1986 – 1997	GN	377.38	368.50	605.00	271.90	513.25	−36.49	−31.19
	Mean			*441.35*	*439.50*	*629.67*	*266.63*	*570.25*	*−36.65*	*−30.31*

* Lake 377 size structure values are the mean FL's for all other survey lakes as there was no previous size structure available

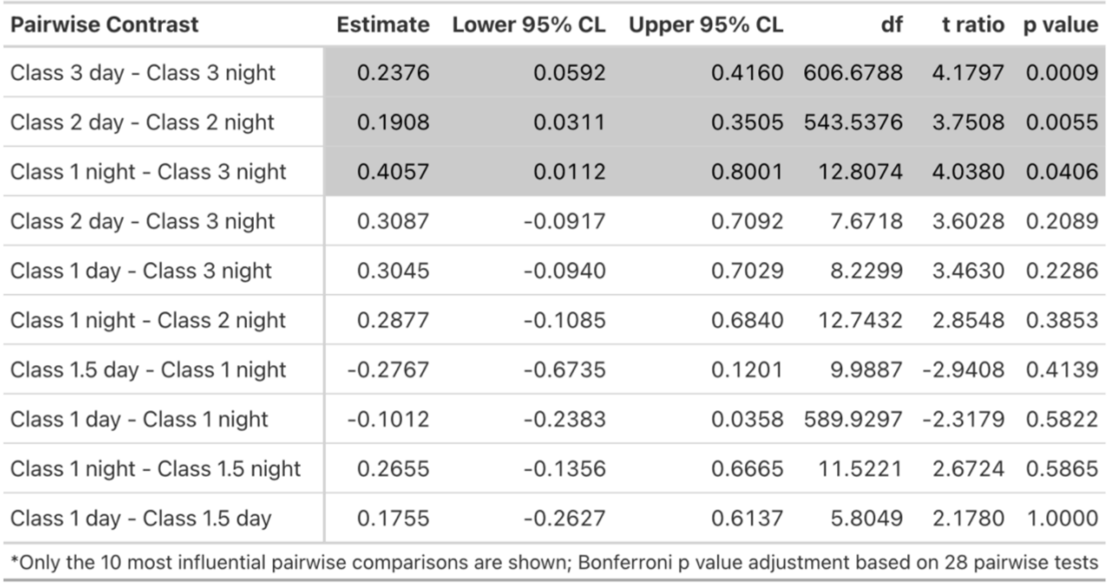
† GN = Gillnet, TN = Trapnet, AN = Angling, SN = Beach seine

Table 2 - 4. ANOVA results for Lake Trout swimming speeds between diurnal periods (day and night) across four prey-specific Lake Classes (Class 1, no Mysis or pelagic prey fishes; Class 1.5, Mysis present but no pelagic prey fishes; Class 2, Mysis absent but pelagic prey fishes present; Class 3, Mysis and pelagic prey fishes present). An estimate of acoustic invertebrate concentrations (Acoustic Invert. Sv) was scaled and included as a covariate. Table rows highlighted in dark grey are statistically significant (alpha < 0.05), while those highlighted in light grey were significant at alpha < 0.10.



	SS	MS	df Num.	df Den.	F	p value
Lake Class	0.542	0.181	3	6.295	3.001	0.113
Diurnal Period	0.608	0.608	1	1121.462	10.092	0.002
Acoustic Invert. Sv	0.275	0.275	1	13.949	4.572	0.051
Lake Class:Diurnal Period	2.090	0.697	3	437.789	11.564	<0.0001

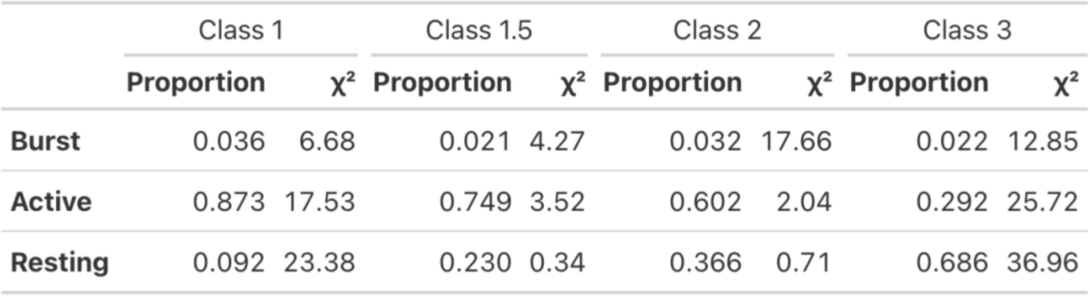
Table 2 - 5. Pairwise swimming speed differences (in body lengths per second) for all levels of Lake Class and diurnal periods. Tukey pairwise contrasts were compared using Sattherthwaite approximation, and p-*values were adjusted using a Bonferroni correction for multiple tests. Pairwise comparisons with different swimming speeds are highlighted in grey (alpha < 0.05).*



Pairwise Contrast	**Estimate**	**Lower 95% CL**	**Upper 95% CL**	**df**	**t ratio**	**p value**
Class 3 day - Class 3 night	0.2376	0.0592	0.4160	606.6788	4.1797	0.0009
Class 2 day - Class 2 night	0.1908	0.0311	0.3505	543.5376	3.7508	0.0055
Class 1 night - Class 3 night	0.4057	0.0112	0.8001	12.8074	4.0380	0.0406
Class 2 day - Class 3 night	0.3087	-0.0917	0.7092	7.6718	3.6028	0.2089
Class 1 day - Class 3 night	0.3045	-0.0940	0.7029	8.2299	3.4630	0.2286
Class 1 night - Class 2 night	0.2877	-0.1085	0.6840	12.7432	2.8548	0.3853
Class 1.5 day - Class 1 night	-0.2767	-0.6735	0.1201	9.9887	-2.9408	0.4139
Class 1 day - Class 1 night	-0.1012	-0.2383	0.0358	589.9297	-2.3179	0.5822
Class 1 night - Class 1.5 night	0.2655	-0.1356	0.6665	11.5221	2.6724	0.5865
Class 1 day - Class 1.5 day	0.1755	-0.2627	0.6137	5.8049	2.1780	1.0000

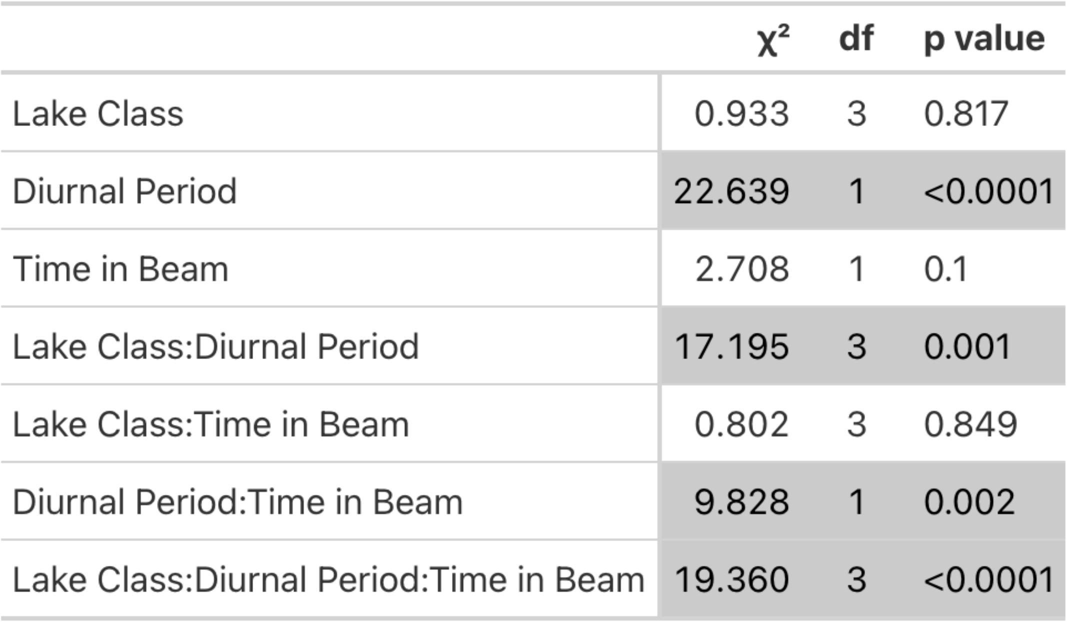
*Only the 10 most influential pairwise comparisons are shown; Bonferroni p value adjustment based on 28 pairwise tests

Table 2 - 6. Chi-square summary statistics for Lake Trout swimming behaviour across four unique Lake Classes; where Burst speeds > 0.57 m/s, Active speeds 0.17 – 0.57 m/s and Resting speeds were < 0.17 m/s. Proportion represents the relative number of one swimming behaviour compared to all others within the Lake Class, and χ^2 are distinct chi-square statistics for each variable combination. χ^2 values closer to zero indicate observed frequencies of swimming behaviours close to those that would be expected, whereas values much larger than zero indicate substantial departure from expectations.



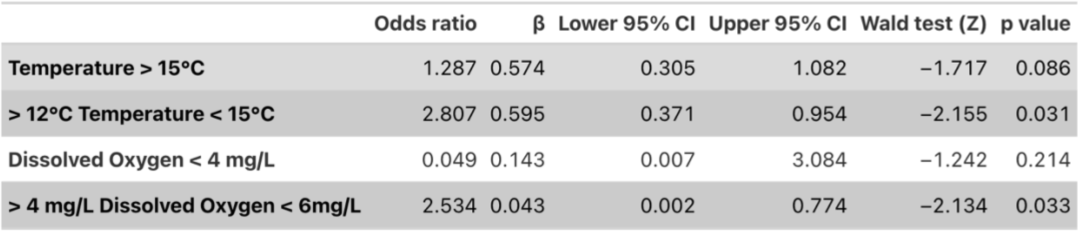
	Class 1		Class 1.5		Class 2		Class 3	
	Proportion	**χ^2**	**Proportion**	**χ^2**	**Proportion**	**χ^2**	**Proportion**	**χ^2**
Burst	0.036	6.68	0.021	4.27	0.032	17.66	0.022	12.85
Active	0.873	17.53	0.749	3.52	0.602	2.04	0.292	25.72
Resting	0.092	23.38	0.230	0.34	0.366	0.71	0.686	36.96

Table 2 - 7: Fish track tortuosity differences across Lake Classes (Class 1, 1.5, 2, 3), diurnal period (day, night), and length of time within the acoustic beam (seconds). Significance was assessed through Type III Sums of Squares approximation, with statistically significant variables (alpha < 0.05) highlighted in grey.



	χ^2	df	p value
Lake Class	0.933	3	0.817
Diurnal Period	22.639	1	<0.0001
Time in Beam	2.708	1	0.1
Lake Class:Diurnal Period	17.195	3	0.001
Lake Class:Time in Beam	0.802	3	0.849
Diurnal Period:Time in Beam	9.828	1	0.002
Lake Class:Diurnal Period:Time in Beam	19.360	3	<0.0001

Table 2 - 8. Odds ratio and parameter estimates for generalized linear mixed effect logistic regression models testing the effect of Lake Class on exposure to various types of oxythermal stress. Cases where prey availability significantly affects Lake Trout exposure to sub-optimal environmental conditions are highlighted in dark grey (alpha < 0.05), and instances with higher estimate variability but still strong directional effects are highlighted in light grey (alpha < 0.10).



	Odds ratio	β	Lower 95% CI	Upper 95% CI	Wald test (Z)	p value
Temperature > 15°C	1.287	0.574	0.305	1.082	−1.717	0.086
> 12°C Temperature < 15°C	2.807	0.595	0.371	0.954	−2.155	0.031
Dissolved Oxygen < 4 mg/L	0.049	0.143	0.007	3.084	−1.242	0.214
> 4 mg/L Dissolved Oxygen < 6mg/L	2.534	0.043	0.002	0.774	−2.134	0.033

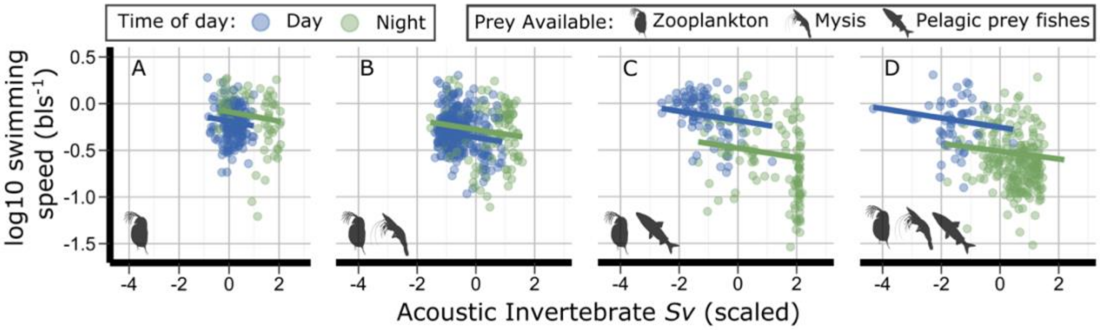


Figure 2 - 1. Comparison of Lake Trout swimming speeds (body lengths per second) across four food web types varying and a gradient of acoustic prey concentrations (S_v). Food webs are categorized as A) Class 1 where zooplankton are the only pelagic prey item available, B) Class 1.5 where *Mysis* are present, C) Class 2 where pelagic prey fish are present, and D) Class 3 where both *Mysis* and pelagic prey fish are present. The log-linear relationship between scaled invertebrate S_v and swimming speed is represented for each Lake Class across Day (blue points and line) and Night (green points and line) diurnal periods.

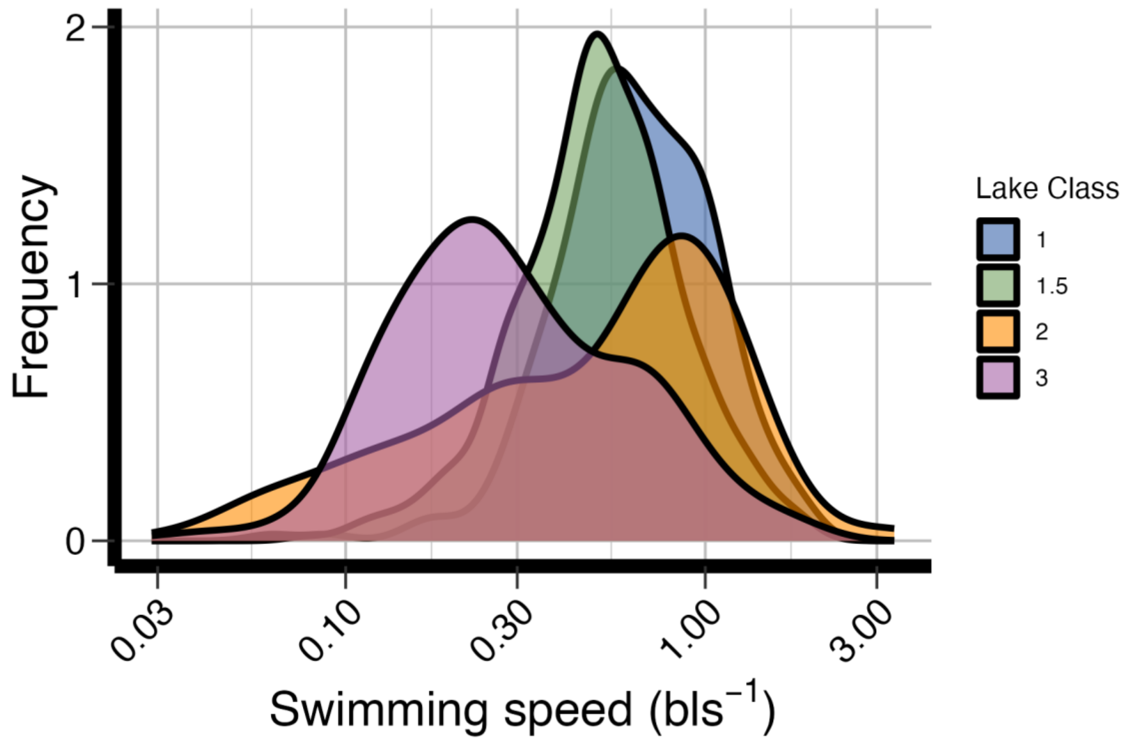


Figure 2 - 2. Lake trout swimming speed frequency distributions for Class 1 (no pelagic prey except zooplankton), Class 1.5 (*Mysis* present), Class 2 (pelagic prey fishes present), and Class 3 (*Mysis* and pelagic prey fishes present) lakes.

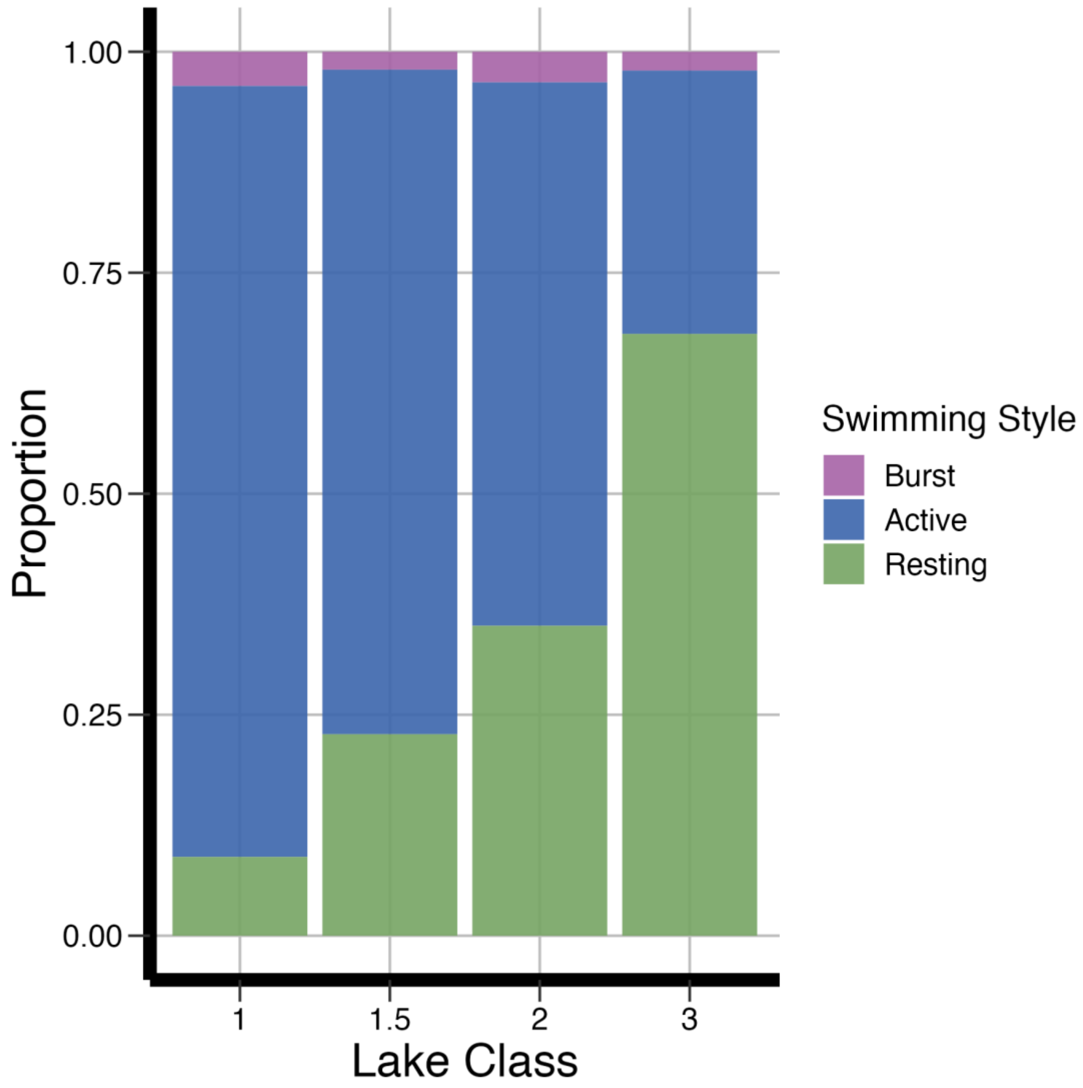


Figure 2 - 3. Proportion of Lake Class swimming speeds categorized as “Burst” (> 0.57 m/s), “Active” (< 0.57 but > 0.17 m/s), and “Rest” (< 0.17 m/s) across Class 1 (no pelagic prey except zooplankton), Class 1.5 (*Mysis* present), Class 2 (pelagic prey fishes present), and Class 3 (*Mysis* and pelagic prey fishes present) lakes.

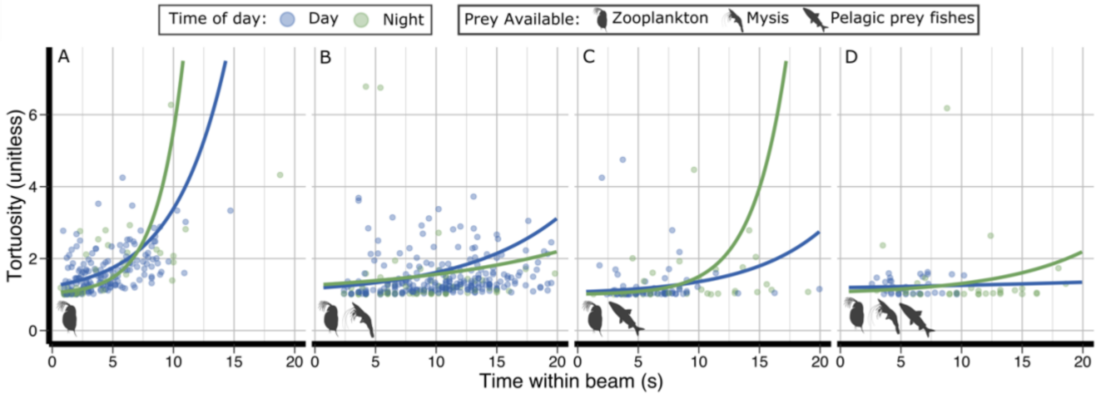


Figure 2 - 4. Fish track tortuosity (i.e., swimming path "convolutedness") across Lake Classes and diurnal period, while controlling for the time an individual spent travelling through the acoustic beam. Food webs are classified as (A) Class 1 where no pelagic prey except zooplankton were present, (B) Class 1.5 where Mysis were present, (C) Class 2 with no Mysis but pelagic prey fishes present, and (D) Class 3 where both Mysis and pelagic prey fishes were present. Solid coloured lines are the fitted relationship for day (blue) and night (green) from a gamma-distributed GLMM.

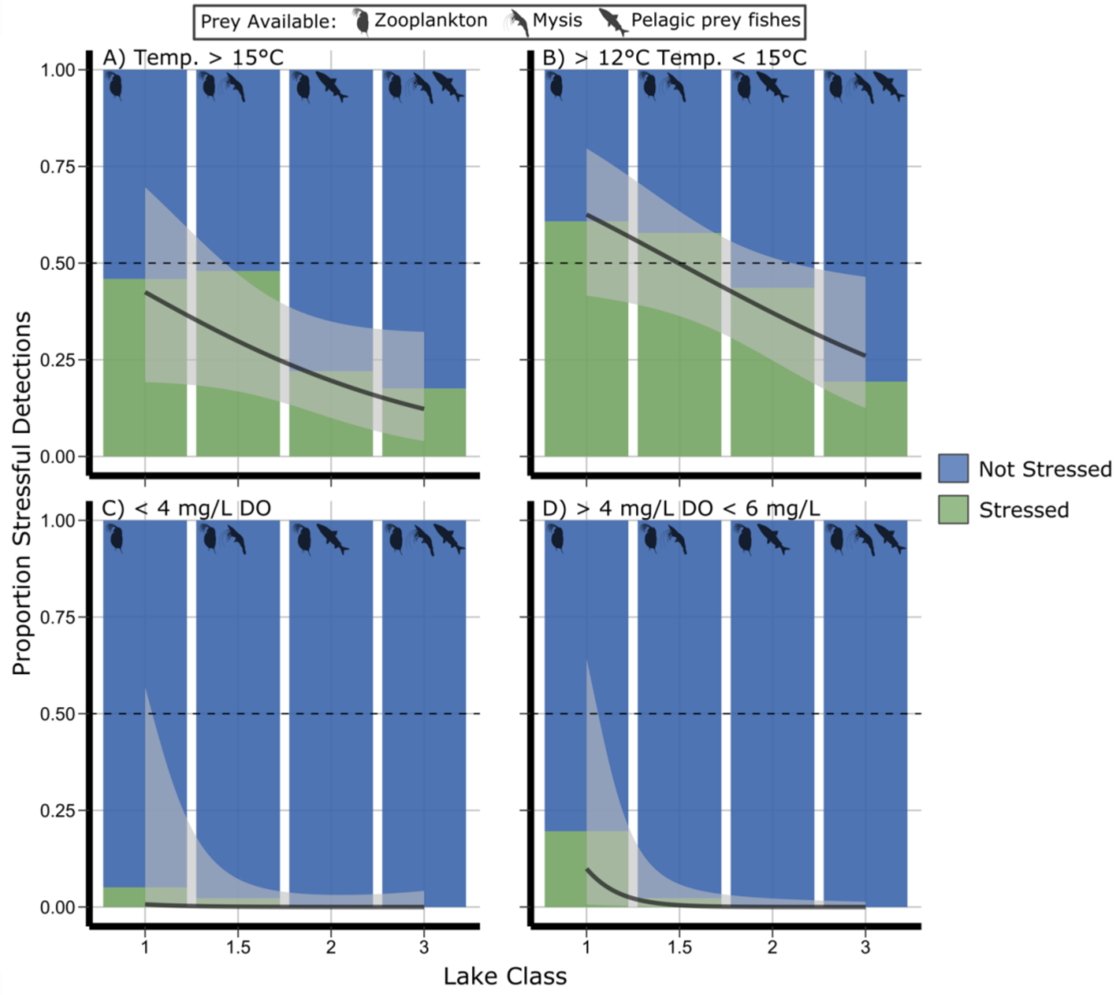


Figure 2 - 5. Binary categorization of whether Lake Trout acoustic detections were in stressful (green bars) or non-stressful oxythermal environments (blue bars). Water temperatures > 15°C are considered above that of Lake Trout thermal tolerances (A), whereas temperatures > 12°C are above literature defined thermal optima (B). Similarly, dissolved oxygen concentrations < 4 mg/L are considered below Lake Trout physiological tolerances (C) and performance decreases < 6 mg/L (D). The predicted logistic relationship across Lake Classes is represented by the black line, and 95% confidence limits are outlined in grey.

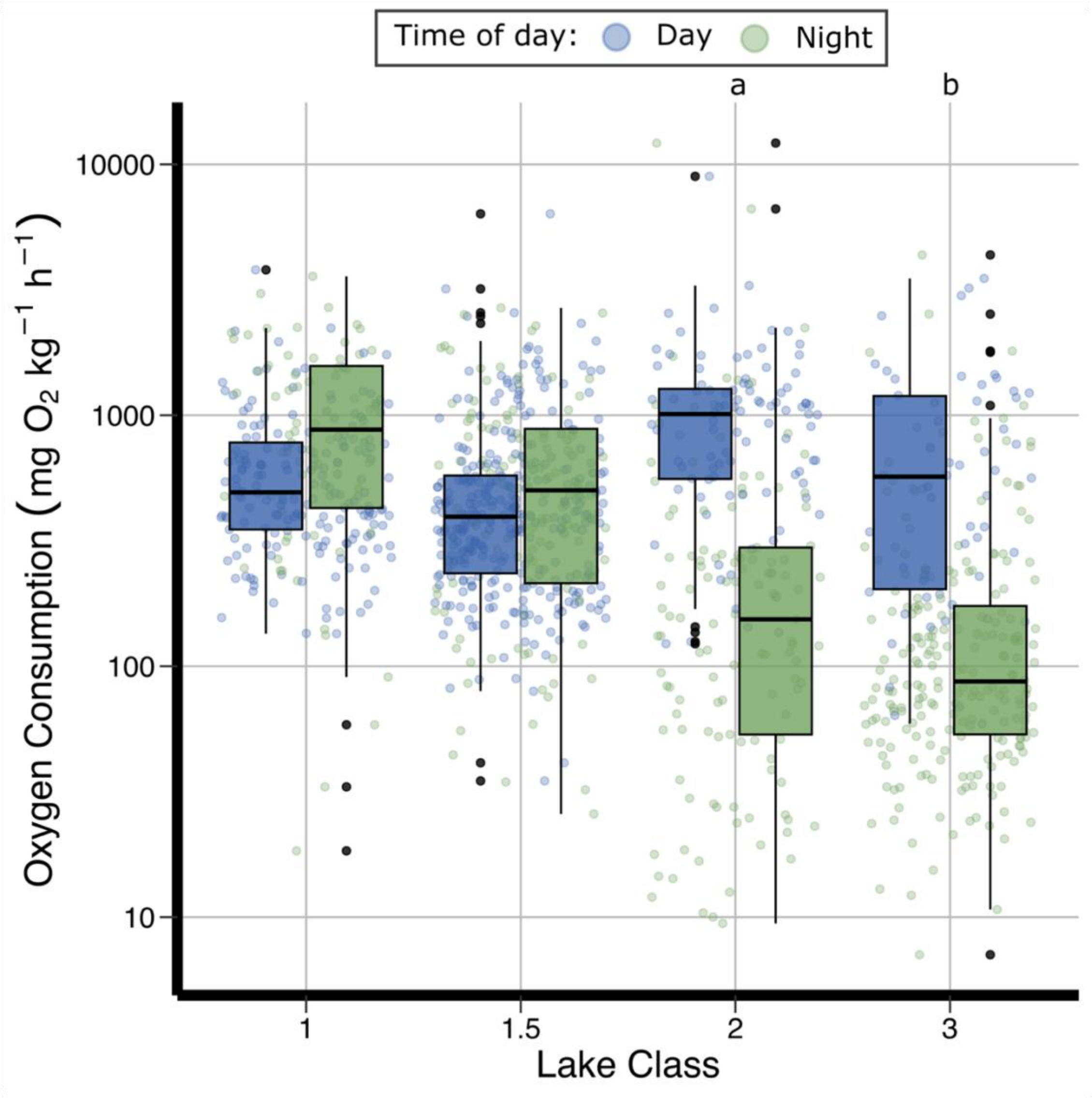
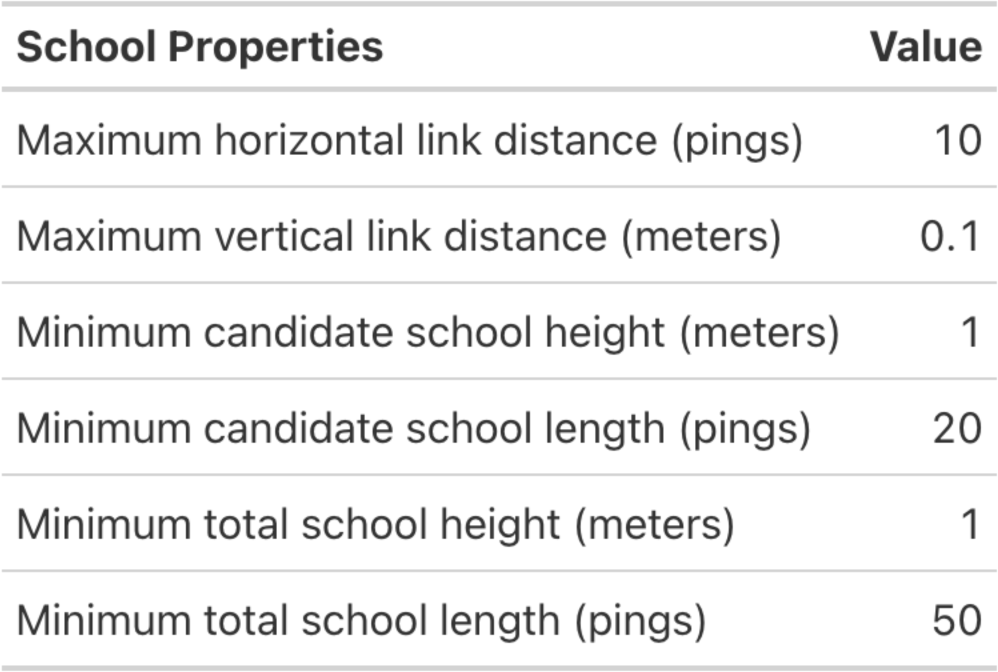


Figure 2 - 6. Estimated metabolic demand for Lake Trout assessed across Class 1 (only pelagic zooplankton), Class 1.5 (*Mysis* present), Class 2 (pelagic prey fishes present) and Class 3 lakes (both *Mysis* and pelagic prey fishes). Oxygen consumption was derived from the log10-log10 relationship between oxygen consumption and Lake Trout swimming speed ($cm{\cdot}s^{-1}$) from Cruz-Font et al. (2016). Significant Lake Class and diurnal periods pairwise differences are indicated by letters 'a' and 'b; absence of letters indicates no significant difference. Blue and green points represent all raw oxygen consumption estimates, jittered within Lake Class for clarity. Boxplot distributions indicate Lake Class medians (thick horizontal bar), interquartile ranges (box edges), and 1.5*interquartile ranges (whiskers), while outlying values are shown as black points.

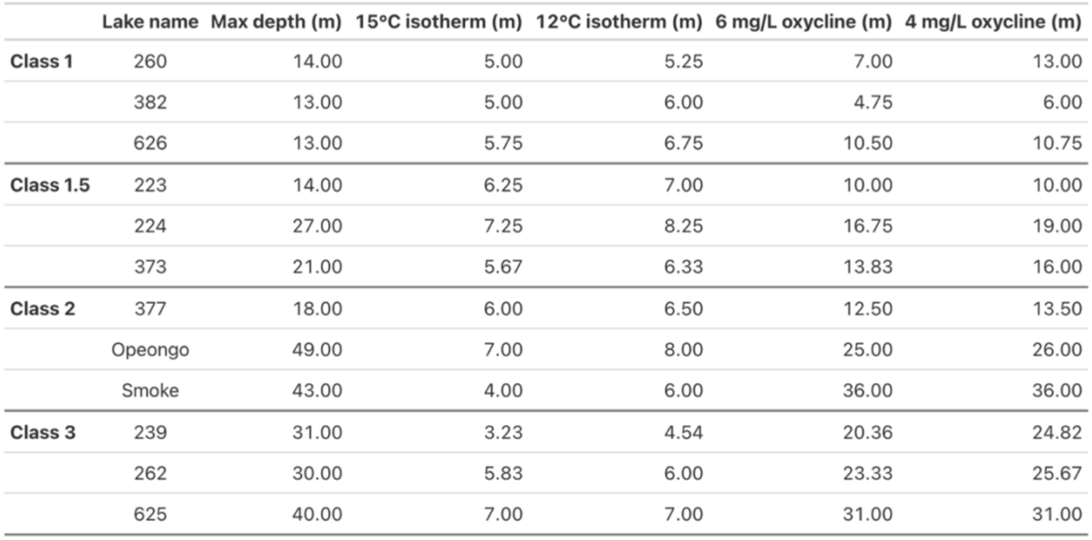
Appendix 2

Appendix 2.A, Table A. 1: Echoview School Detection operand parameter settings for classifying fish schools

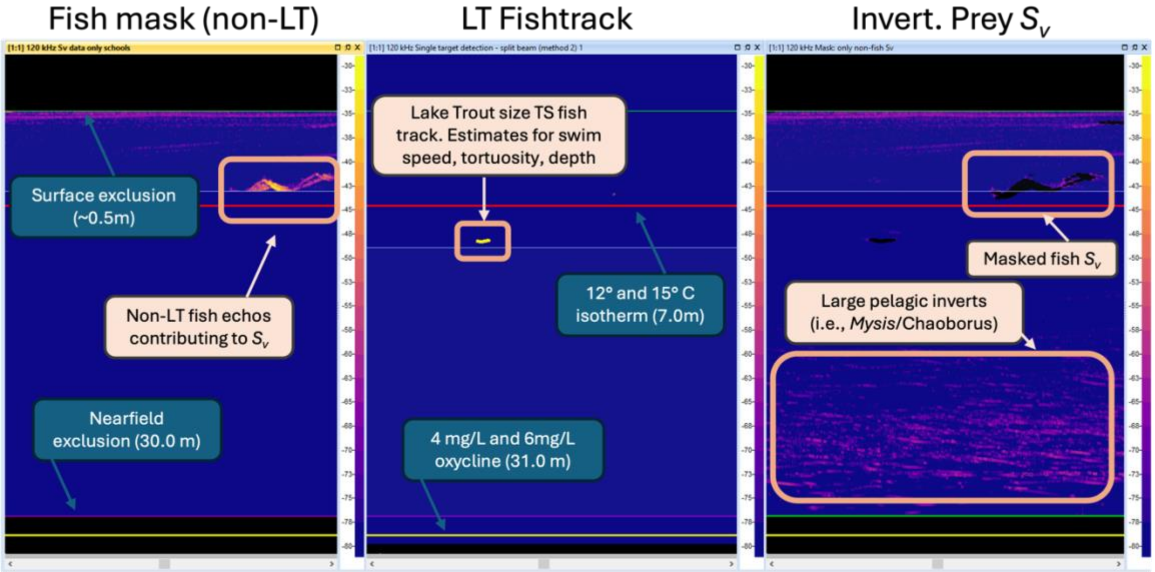


School Properties	Value
Maximum horizontal link distance (pings)	10
Maximum vertical link distance (meters)	0.1
Minimum candidate school height (meters)	1
Minimum candidate school length (pings)	20
Minimum total school height (meters)	1
Minimum total school length (pings)	50

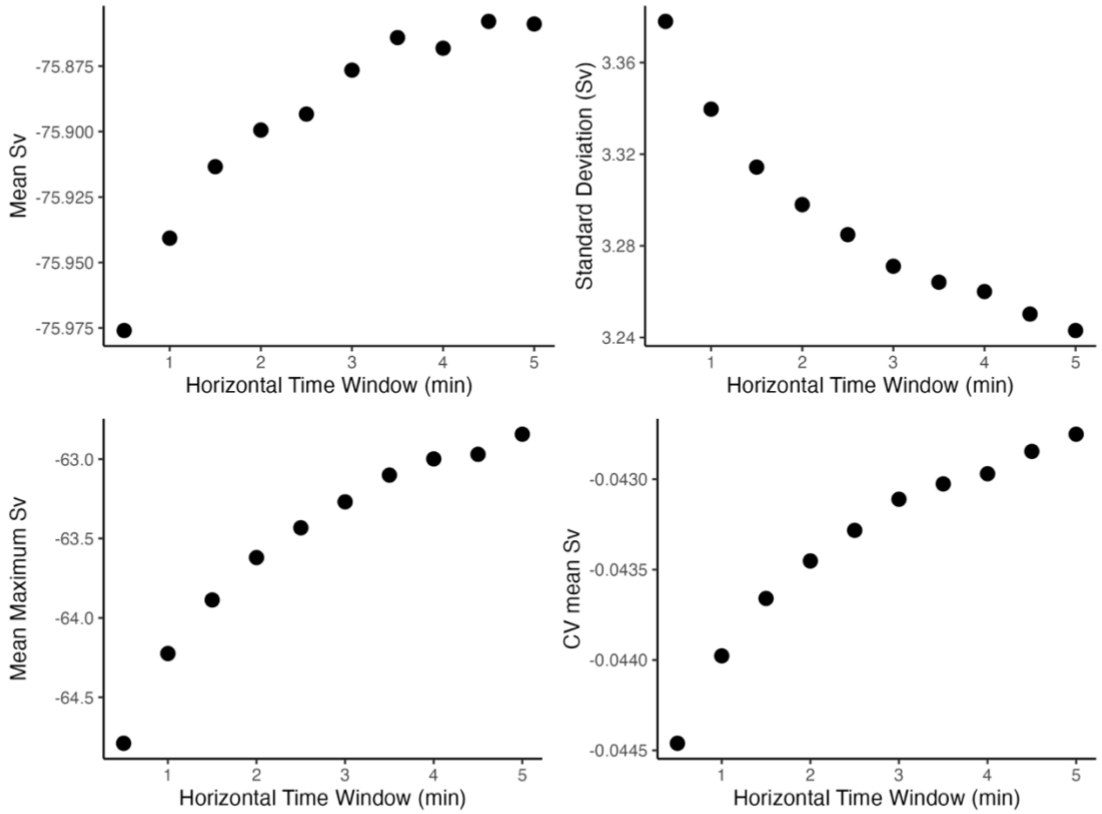
Appendix 2.A, Table A. 2. Lake-specific summaries defining the “ideal” oxythermal habitat envelope for Lake Trout. The top of this habitat envelope is typically marked by depths at the 12 or 15°C isotherm, while dissolved oxygen concentrations of 4 mg/L or 6 mg/L generally set the lower boundary (Plumb and Blanchfield 2009).



	Lake name	Max depth (m)	15°C isotherm (m)	12°C isotherm (m)	6 mg/L oxycline (m)	4 mg/L oxycline (m)
Class 1	260	14.00	5.00	5.25	7.00	13.00
	382	13.00	5.00	6.00	4.75	6.00
	626	13.00	5.75	6.75	10.50	10.75
Class 1.5	223	14.00	6.25	7.00	10.00	10.00
	224	27.00	7.25	8.25	16.75	19.00
	373	21.00	5.67	6.33	13.83	16.00
Class 2	377	18.00	6.00	6.50	12.50	13.50
	Opeongo	49.00	7.00	8.00	25.00	26.00
	Smoke	43.00	4.00	6.00	36.00	36.00
Class 3	239	31.00	3.23	4.54	20.36	24.82
	262	30.00	5.83	6.00	23.33	25.67
	625	40.00	7.00	7.00	31.00	31.00



Appendix 2.A, Figure A. 1: Example L625 (max depth = 40 m) echogram at the beginning of night as *Mysis* are ascending in the water column. The platform was deployed in 32m of water, leading to a nearfield exclusion of 30 m. This was a calm night, so the surface exclusion (farfield) was just below surface waters. To demonstrate available habitat, the 12°C and 15°C isotherms are shown by the red line (same depth, 7 m in this instance), and the 4 mg/L and 6 mg/L oxyclines are shown by the yellow line (also the same depth in this case, and also below the nearfield exclusion). The three panels describe the different steps and quantities acquired from the acoustic data. The left panel shows fish volume backscattering (S_v) for volume targets larger than Lake Trout (which was dynamic for each lake, based on LT size structure) but smaller than -60 dB (my fish cutoff). The middle-panel shows target strength (TS) single detections that remained after masking out fish volume targets from step 1 (left-side panel). With the remaining single targets, Fishtracks were created, from which estimates of swimming speed, tortuosity, and observation depth were created. Finally, the right-side plot shows all non-fish backscattering (all black regions represent fish/biota > - 60 dB). The remaining S_v is attributable to large pelagic invertebrates like *Mysis* or *Chaoborus spp.*.



Appendix 2.A, Figure A. 2. Prey S_v semivariance analysis that was used to determine the optimal horizontal EDSU window for assessing prey concentrations. For analytical cell sizes, I used two-minute EDSUs, which reflected variance asymptotes near two minutes for the different variables that were assessed.

CHAPTER 3

From Top to Bottom: Revisiting the role of pelagic food web structure on Lake Trout mercury concentrations

Abstract

Food web and trophic complexity are considered primary predictors of Lake Trout (*Salvelinus namaycush*) mercury (Hg) concentrations. However, several other well-documented environmental and landscape factors may also contribute, yet comprehensive assessments of Lake Trout Hg dynamics and associated public health risks are lacking. Here, I reassess the importance of trophic complexity in both previously published and contemporary data, incorporating additional model complexity to better understand the Hg concentration dynamics of Ontario Lake Trout. In contrast to previous assertions that trophic complexity alone can sufficiently predict Lake Trout Hg, my analysis indicates a relatively small role for trophic complexity, mainly as an interacting factor with individual body size and lake dissolved organic carbon (DOC) concentrations. The inclusion of DOC was vital for assessing human consumption risk, as Lake Trout in high DOC lakes were more likely to exceed Hg guidelines at sizes often harvested by anglers. This reassessment refocuses the putative importance of food chain length on Lake Trout Hg through the lens of both physiological factors (i.e., conversion efficiency) and bottom-up landscape processes (e.g., DOC-regulated Hg supply).

Introduction

Human mercury (Hg) exposure is normally determined by diet, primarily through the consumption of fish. Even at low but persistent Hg exposure levels, Hg can negatively affect nearly every organ within the human body, and Hg toxicity has been linked to a wide variety of neural impairments and syndromes in children and adults — decreased motor system function, compromised immunity and reproductive concerns, among others (Zahir et al. 2005, Kim et al. 2016). As such, understanding what controls fish Hg dynamics and being able to predict under what scenarios contaminated fish should be avoided is essential for effective public health policy. An important aspect of this policy is risk management through consumption advisories for wild fish, published both regionally and nationally to safeguard against the over-consumption of contaminated fish. For example, Health Canada's safe guideline limits mercury at 0.5 parts per million or $\mu g_{Hg}/g_{fish}$ for most commercial fish (Canadian Food Inspection Agency 1998). Risk management through such guidelines depends on reliable knowledge of fish Hg levels. Since inter- and intraspecific variation in fish Hg concentrations is high and our current understanding of what drives fish Hg accumulation across large spatial gradients is incomplete, it is incumbent to continually re-assess the circumstances that may increase risks for humans consuming fish.

Mercury emissions increased markedly in the 20th century with coal-fired power production globally diffusing inorganic Hg through long-range atmospheric transport and deposition. In the aquatic environment, inorganic Hg readily transforms into its toxic form, methylmercury (MeHg), which can accumulate and biomagnify through food webs (Lavoie et al. 2013). Despite Hg emission reductions, persistently high MeHg concentrations remain in watersheds and the biota found within them, even in seemingly remote areas because of long-range atmospheric deposition, extended water residence times, and ecosystem-mediated Hg cycling (Tang et al. 2013, Branfireun et al. 2020, Pilote et al. 2024). Along with Hg poisoning in humans, high Hg concentrations in fish can alter individual behaviour, change spawning time, and reduce reproductive success (Hammerschmidt et al. 2002, Berntssen et al. 2003).

It has long been considered that contaminated prey is the primary route for accumulation of Hg and other contaminants of concern in fish (Thomann 1981)**.** It was under this premise that seminal work on Lake Trout (*Salvelinus namaycush*) contaminant dynamics was investigated, initially from work by Rasmussen et al. (1990) predicting Lake Trout polychlorinated biphenyl (PCB) concentrations across lakes varying in food chain length (i.e., trophic complexity), followed shortly thereafter by Cabana et al. (1994) predicting Lake Trout Hg concentrations on the same basis. In both of these works, lakes were categorically assigned to one of three Lake Classes based on pelagic trophic complexity; specifically, the presence of pelagic prey items — Class 1 lakes, which had no pelagic prey other than zooplankton; Class 2 lakes, which had pelagic prey fishes like Coregonids present, and Class 3 lakes, which had *Mysis diluviana* (*Mysis* hereafter) and pelagic prey fishes present. With each increase in Lake Class (i.e., pelagic trophic complexity or food chain length), Lake Trout contaminants (PCBs and Hg) increased 1 to 4 fold from the previous Lake Class (Rasmussen et al. 1990b, Cabana et al.

1994). While landscape predictors were included within a subset of analyses, the main result communicated to readers of these two studies was the categorical increase of contaminants with increasing Lake Class. Further work using nitrogen stable isotopes supported findings of contaminant biomagnification with increasing prey availability and established a quantitative link between Lake Trout trophic position and Hg (Vander Zanden and Rasmussen 1996, Garcia and Carignan 2005). Furthermore, meta-analyses and reviews published since have also highlighted the central role of trophic complexity as a determinant of Hg concentrations in predatory fishes (Kidd et al. 2012, Lavoie et al. 2013).

While trophic dynamics are often emphasized as driving contaminant dynamics, other research highlights demographic, biotic and abiotic variables as modifiers of fish contaminants, particularly in relation to Hg (Gewurtz et al. 2011a, 2011b). Age and/or body size specifically serve as key demographic and morphometric predictors of fish Hg burden (Somers and Jackson 1993, Stafford and Haines 2001, Power et al. 2002, Trudel and Rasmussen 2006, Johnston et al. 2022). As fish approach asymptotic size, they tend to eat larger and more contaminated prey items, which in combination with longer lifespans leads to high accumulation of slow-to-eliminate contaminants like Hg. Additionally, larger fish display higher metabolic costs (and hence, poor growth efficiency) compared with relatively younger, smaller, and faster growing individuals (Trudel and Rasmussen 2006, Jenssen et al. 2010, Johnston et al. 2022).

Landscape-level factors, such as watershed and lake physicochemical properties, can also modify fish Hg concentrations. High dissolved organic carbon (DOC) concentrations typically correspond with higher fish Hg concentrations (Lavoie et al. 2019) due to Hg's ability to complex with DOC, and lakes with high DOC typically having higher bacterial methylation potential associated with the increased presence of wetlands and anoxic conditions (Ravichandran 2004). However, at DOC concentrations greater than ~8 – 10 mg/L there is also some evidence that MeHg transfer efficiency (i.e., biomagnification) can decrease with changes in the composition of organic matter associated with high levels of DOC (Tsui and Finlay 2011, French et al. 2014, Braaten et al. 2018). Lake surface area, pH, productivity (often assessed as total phosphorus or chlorophyll-*a*), forestry operations, forest fire activity, and latitude have all additionally been shown to affect Hg under specific scenarios (Table 3 - 1). Given that watershed and fish Hg dynamics can be affected by many variables beyond food chain length, predictions of Hg among lakes should also include these other potentially compounding factors.

This perspective paper aims to re-examine the models and theories that emphasize the role of food chain length in shaping consumer Hg dynamics, with a more explicit quantitative consideration of other contributing drivers of contaminant accumulation than previously described. The current effort focusses on Lake Trout, a top predator in tens of thousands of North American lakes, and a common food-fish across their range (Scott and Crossman 1973). The Lake Class system describing associations between food chain length and contaminants of Lake Trout proposed by Rasmussen et al. (1990) provides an important starting point for characterizing broadscale contaminant risks that affect fish and those who consume them. However, much more has been learned in regards to other potential covariates since these original papers were published in terms of what can modify Lake Trout Hg concentrations, and new statistical tools and improved computational power now allow for more complex analyses. Despite these advances in analytical power, there has not been a comprehensive re-assessment of what variables are useful in estimating Lake Trout Hg across the landscape in over 30 years. Starting with a reassessment of the Lake Class system using both previously published and contemporary data, I explore how including extra layers of variable and model complexity helps inform Lake Trout Hg dynamics beyond using simple models of food chain length. Using my more recent data, I go on to show important interactions between food web structure, landscape variables, and body size for predicting Hg concentrations for Lake Trout in Ontario, Canada lakes. The benefits of using a Lake Class system, along with other easily acquired habitat information, are obvious — if Hg contamination dynamics can be better understood across large spatial scales, then lakes fulfilling specific criteria can be targeted for further testing, and management decisions can be guided that promote the sustainability of fish populations while ensuring public health.

Revisiting the use of food web Lake Classes to estimate Lake Trout mercury contamination – the case for including a body size metric

Biomagnification describes the process by which higher trophic levels and top consumers accumulate more Hg than primary producers and lower trophic consumers, with biomagnification increasing as trophic complexity increases (Phillips et al. 1980). Under this theory, Cabana et al. (1994) assessed Lake Trout Hg dynamics across a prey community gradient of increasing pelagic food chain length to test whether distinct Lake Classes could predict Lake Trout Hg levels. Ninety-six Ontario lakes were separated into three Lake Classes based on the presence of pelagic prey items, and Hg concentrations among Lake Classes were compared using fish collected between 1975 and 1984 (Appendix 3.B - Table B. 1; Class 1, no pelagic prey other than zooplankton; Class 2, pelagic prey fishes present; Class 3, *Mysis* and pelagic prey fishes present; See Cabana et al. (1994) for full methodology). As predicted, mean Class 1 Lake Trout Hg concentrations were lower than those in Class 2 and Class 3 lakes, and there was some visual evidence that Class 3 Lake Trout Hg concentrations were higher than those from Class 2 lakes (Figure 3 - 1.a, 1.c). However, upon re-analyzing the Cabana data using a one-way ANOVA to confirm their main communicated result of increasing Hg with increasing Lake Classes, broad differences between all Lake Classes were not detected despite model significance ($F_{2,93} = 21.56$, $p < 0.0001$). Lake Class explained 32% of the variance in Lake Trout Hg concentrations, with Tukey HSD tests identifying Class 1 lakes as having significantly lower Hg concentrations than either Class 2 or Class 3 lakes. However, there was no difference between lakes that had pelagic prey fish compared to those with pelagic prey fish and *Mysis* (Class 1 – 2, $p = < 0.00001$; Class 1 – 3, $p = < 0.00001$; Class 2 – 3, $p = 0.29$).

To compare this result with an independent and contemporary dataset (Appendix 3.A – Dataset description), another set of lakes covering a similar geographic range but with samples collected between 1991 and 2022 was assembled (Figure 3 - 2, Appendix 3.B - Table B. 2). A new Lake Class, Class 1.5, was also introduced, describing lakes where *Mysis* were available to Lake Trout but pelagic prey fishes were absent. *Mysis* only lakes appear to be an omission in previous Lake Class studies, given their importance in the original Lake Class definitions (i.e., as the key component separating Class 2 and 3 lakes). According to prevailing food web theory, we anticipated Class 1.5 Lake Trout Hg concentrations to be intermediate between those of Class 1 and Class 2 lakes. Similar to Cabana et al. (1994), we found a significant effect of Lake Class on Lake Trout Hg concentrations with the contemporary data set (ANOVA, $F_{3,59} = 5.12$, $p = 0.003$, $R^2 = 0.21$), though only Class 1 and Class 3 Hg concentrations were significantly different from each other again (Figure 3 - 1.b, 1.d).

By and large, neither the data from Cabana et al. (1994) nor the contemporary dataset support the role of using categorical food chain length alone as a predictor of Lake Trout Hg. The narrative put forward by Cabana et al. (1994) assumes sequential increases in Hg with the inclusion of each new pelagic prey item in the food web from Class 1 to Class 3, which was not observed. Critically, when using Lake Class as the lone model predictor, body size was unaccounted for. Yet, other Lake Trout Hg models, including an analysis in Cabana et al. (1994), have demonstrated body size as an important modifier of Lake Trout Hg concentrations (Somers and Jackson 1993, Futter 1994, Stafford et al. 2014). Within both datasets, one-way ANOVAs where mean body weight was used as a response variable in place of mean Hg concentrations reveal nearly identical results as those of Lake Trout Hg (Mean body weight ~ Lake Class

ANOVA, Cabana data: $F_{2,93} = 12.46$, $p < 0.0001$, $R^2 = 0.21$; contemporary data: $F_{3,59} = 9.46$, $p < 0.0001$, $R^2 = 0.27$; Appendix 3.B - Figure B. 1). Similar statistical outcomes between response variables of mean Hg and mean body weight across Lake Classes indicate that any significant result of Hg concentrations between Lake Classes may be spurious, or at the very least simply masking the role of body size as the main driver of Lake Trout Hg concentrations. Lake Trout typically reach larger sizes when they have access to bigger prey, such as in Class 3 lakes (Shuter et al. 2005, 2016), and since there is a general positive relationships between body size and Hg concentrations in fish, Lake Trout in these lakes are more likely to have elevated Hg levels due to their larger size.

To address the potential dependency of body size on Lake Trout Hg concentrations across Lake Classes, it can be easily included as a model covariate. Cabana et al. (1994) did attempt to account for body size by using mean weight within a multiple regression, though in doing so they erroneously included Lake Class—a distinctively categorical variable—as a continuous variable. Their multiple regression also included mean body weight and maximum lake depth, though lake depth was ultimately excluded from the final model (citing issues with collinearity, though those issues were not justified or explained). With mean body weight included, the model reported by Cabana et al. (1994) was highly significant (model $R^2 = 0.56$; t-tests on predictors $p < 0.0001$) though no follow-up analyses or visualizations provided any description of the relative role of body weight compared to Lake Class in explaining Lake Trout Hg. Consequently, I reanalyzed the Cabana et al. (1994) data using their multiple regression approach and found that mean body weight was overwhelmingly more important than Lake Class when describing Hg concentrations (partial variance explained; mean body weight = 46.5%, continuous Lake Class = 7.0%). While the authors describe that "much" of the between lake differences in Lake Trout Hg concentrations stemmed from differences in food chain length, my re-analysis of their data strongly suggest that mean body weight was actually the main driver of Lake Trout Hg in their dataset.

To confirm that 1) multiple regression was an acceptable approach, and that 2) Lake Trout Hg concentrations were largely driven by body size, we re-analyzed the Cabana and contemporary datasets using Analysis of Covariance (ANCOVA), treating Lake Class as a categorical variable and mean weight as a covariate. After confirming ANCOVA assumptions (residual normality, variance heteroscedasticity, presence of interaction between covariate and categorical predictor), a reanalysis of Cabana's data confirmed the outsized role of mean body weight on Hg concentrations (log body weight $F_{1,92} = 94.97$, partial variance explained = 46.5%, $p < 0.0001$) compared to Lake Class (Lake Class $F_{2,92} = 8.04$, partial variance explained = 8.0 %, $p = 0.0006$; Figure 3 - 3.a). ANCOVA performed similarly to multiple regression (despite the treatment of Lake Class as a continuous variable), and both approaches explained a higher amount of overall variance than the simple Lake Class ANOVA presented previously (i.e., my ANOVA analysis of Cabana et al. (1994) data based solely on Lake Class, $R^2 = 0.32$; Cabana et al. (1994) reported Multiple Regression, $R^2 = 0.56$; my ANCOVA of Cabana et al. (1994) data, $R^2 = 0.54$). To test if the significant improvement of model fit from the inclusion of body size and application of ANCOVA could be replicated, we applied

ANCOVA to my contemporary dataset of mean fish weights. In initial model assessments, one Class 2 lake — Kimball Lake — was removed from the dataset because of extreme values in a residuals vs. leverage diagnostic plot. Further, a significant interaction was identified when testing for an interaction between the covariate and categorical predictor, precluding the use of ANCOVA (a significant interaction was also present when the aforementioned outlier was included). Assessing the model with an interaction term, body weight was again the main driver of Lake Trout Hg concentrations, though variation in Lake Class slopes revealed unexpected Hg dynamics, including a negative relationship between Hg and mean body weight of Class 1.5 fish (Figure 3 - 3.b and Table 3 - 2). Different statistical conclusions between the two datasets, as well as potential shortcomings associated with reducing body weight and Hg to lake-wide means in the Cabana et al. (1994) assessment indicate that the approaches taken to date, using only categorical food chain length and a body size metric, are likely inadequate for predicting Lake Trout Hg across large spatial scales.

The influence of body size on Lake Trout Hg dynamics – moving from populations to individuals

To investigate the degree to which allometric relationships between individual body size and Hg concentrations within Lake Classes provide better support than population-level means for the hypothesis that Lake Classes structure Lake Trout Hg, linear mixed-effect models were used. Individual observations did not exist within the Cabana et al. (1994) dataset that was publicly available, and linear mixed effects modelling approaches using maximum likelihood were rare and not a widely adopted statistical approach at the time. However, to better elicit underlying variance explained by Lake Class, a mixed-effects approach could be applied with the contemporary dataset, allowing for potential random variance in the relationship between fish body size and Hg among lakes to be captured. With contemporary data, comparisons of fish Hg with body weight compared to fish Hg with body length can also be made. Only body weight was reported for historic data, though body length has generally been the typical covariate being used in studies of fish Hg wishing to control for fish size (e.g., Somers and Jackson 1993, Johnston et al. 2022), and is the metric most commonly reported in contaminant consumption guidelines (Canadian Food Inspection Agency 1998, MNR 2016).

Model structure was determined using likelihood ratio tests, first optimizing for the inclusion of random effects (as either random slopes or intercepts) and then fixed effects. The full model prior to any optimization included the interaction between body size (weight or length) and Lake Class along with random covariate slopes and intercepts for unique lakes within Lake Classes. After determining the final model structure, model assumptions were verified using histograms of residuals, plots of residual vs. fitted values, Q-Q plots, and testing for a non-significant correlation between model residual and fitted values. Type III Satterthwaitte approximation for Sum of Squares were used to assess significance of fixed effects, and marginal R^2 values of the fixed effects were used to describe model fit from the *MuMIn* R package (Barton 2023). All linear mixed effect models were conducted using *lme4* and *lmertest* R packages and R version 4.1.2 (Kuznetsova et al. 2017, Bates 2018).

When using body weight as a covariate, model parsimony was found with the additive effect of Lake Class and individual body weight, and incorporating lake as a random slope with body weight (Eq. 1):

$$\log[Hg] \sim {}_{log}bodyWeight + lakeClass + ({}_{log}bodyWeight|lakeID) \qquad \text{(Eq. 1)}$$

With individual body weight included as a covariate, predicted increases in Lake Trout Hg with increasing Lake Class were not observed (Figure 3 - 3.c). Similar to previous ANCOVA approaches that used population means, the presence of individual body weight overwhelmed the effect of Lake Class on Hg concentrations (Table 3 - 2). Allometric scaling between individual body weight and Hg showed no differences between Lake Classes, demonstrating a clear log-linear relationship between individual body mass and Hg concentrations.

When body length was used as a covariate (as opposed to body weight), a possible role for Lake Classes became apparent (Figure 3 - 3.d). Following model selection, the best model included the interaction term between Lake Class and body length, along with lake modelled as a random slope with body length:

$$\log[Hg] \sim bodyLength * lakeClass + (bodyLength|lakeID) \qquad \text{(Eq. 2)}$$

Based on fitted relationships across Lake Classes, Hg concentrations of an average sized Lake Trout (~500 mm, where relationships describing the Hg-body length relationship for each Lake Class intersect) should be similar amongst individuals from different Lake

Classes (Figure 3 - 3.d). However, the significant interaction between Lake Class and body length ($F_{3,73} = 5.57$, $p = 0.0017$) revealed ontogenetic differences in Hg contamination, where small and large individuals occupying different Lake Classes exhibited distinct Hg dynamics (Figure 3 - 3.d). Specifically, Class 1 and 2 lakes had steeper Hg slopes than Class 1.5 and 3 lakes. Thus, at small sizes, Class 1 and 2 Lake Trout (where *Mysis* were absent) had lower Hg concentrations compared to Class 1.5 and 3 individuals (both with *Mysis* present), whereas at larger sizes, Lake Trout in Class 1 and 2 lakes had higher Hg than Class 1.5 and 3 at a given length.

Despite using more sophisticated models, expected sequential increases in Lake Trout Hg concentrations with increasing Lake Classes were not observed, suggesting that strictly top-down model structures considering only food web structure with body size may overlook other important physiological and landscape processes**.** The Cabana model posits that large adult Class 3 Lake Trout Hg concentrations should be higher than those of individuals from any other Lake Classes. However, at large body lengths, my linear mixed-effects model estimates that Class 3 Lake Trout would actually have lower Hg concentrations than individuals of the same size from any other Lake Class. Further, when considering just planktivorous Lake Trout populations (Class 1 and Class 1.5), Hg accumulation slopes were shallower in lakes where *Mysis* were present*,* despite having a longer relative food chain.

Mysis are a preferred prey for both juvenile Lake Trout as well as other pelagic prey fishes (France and Steedman 1996). As such, their presence may modulate Hg concentrations differently for juvenile versus adult Lake Trout (Figure 3 - 3.d). Higher juvenile Lake Trout Hg concentrations in lakes with *Mysis* (Class 1.5 and 3) may in part be due to consuming a more contaminated prey base, as *Mysis* MeHg concentrations are typically more than double that of both pelagic zooplankton and *Chaoborus* spp. (Back et al. 2003, Chételat et al. 2013, Brown et al. 2022). Conversely, *Mysis* appear to confer a metabolic advantage to Lake Trout at adult life stages. Biomass size spectra theory and examinations of predator-prey mass ratios both suggest there are metabolic and energetic efficiencies gained when larger prey are made available to predators (i.e., predator-prey ratios are small; Giacomini et al. 2013, Shuter et al. 2016, Sprules and Barth 2016). Further, Hg biomagnification intensifies at low predator growth rates and high activity rates, conditions that are expected when predator-prey mass ratios are large (Trudel and Rasmussen 2006).

While biotic mechanisms likely explain Hg biomagnification through food webs, they disregard the potential controls to the supply of Hg to lakes (Table 3 - 1). Ultimately, ecosystem processes influence the bottom-up availability of Hg to aquatic ecosystems (Branfireun et al. 2020) and must be considered when understanding context-dependent differences in Lake Trout Hg burdens, which are explored in detail below.

What's missing? A lakescape assessment of Lake Trout Hg concentrations

I present two complementary yet independent statistical methods to understand how physicochemical and landscape attributes contribute to reported relationships between body size and food chain length with Lake Trout Hg concentrations. Multivariate statistics have commonly been used to assess interconnected relationships between multiple variables that cannot be assessed using traditional univariate approaches (James and McCulloch 1990). However, traditional multivariate statistics (e.g., Principal Components Analysis (PCA), Redundancy Analysis, Correspondence Analysis) only allow predictions to be made at the population level. Alternatively, recent advancements in machine learning have led to the emergence of more computationally-demanding statistical tools that can determine patterns and trends in complex, individual-level data, but can also facilitate predictions that scale from individuals to ecosystems (Pichler and Hartig 2023). I therefore selected Principal Components Analysis (PCA) and Random Forest (RF) algorithms as alternative but complimentary methods for assessing biotic and abiotic variables with the greatest influence on Lake Trout Hg concentrations. Concordant predictors from both methods can then be used in further modelling efforts to estimate Hg contamination risk across the lakescape (Feld et al. 2016). Using these two methods was also useful for comparing multivariate approaches that differ in how data is handled; PCA uses a data-reductionist approach, where mean values are required for each input variable (which precludes the use of individual body size as a metric, and as demonstrated above, predicting fish Hg using population mean body sizes can be misleading). Conversely, RF uses all individual observations and can handle many predictor variables (including those that are non-linear) without the fear of over-parameterizing the final model (Prasad et al. 2006).

Based on the fundamental differences between these two approaches, data used for PCA and RF were handled slightly differently. PCA was performed using a subset of available physicochemical variables. PCA can describe relationships between interacting and collinear variables, but also faces many of the same assumptions and limitations of univariate linear models (i.e., sufficient observation-to-predictor ratios, requirements of data to be linear and normally distributed, handling of missing observations; James and McCulloch 1990, Feld et al. 2016). To avoid over-parameterizing the PCA, only mean Lake Trout body length (mm), maximum lake depth (m), lake surface area (ha), total dissolved phosphorus (TDP; µg/L), pH, dissolved organic carbon (DOC; mg/L) and latitude were included as variables based on *a priori* assumptions of their roles modifying Lake Trout Hg dynamics (Table 3 - 1). Five lakes (L448, Big Salmon, Opeongo, Sherborne, Smoke) had some combination of variables that were not reported (DOC, TDP, pH, surface area, and max depth). In these cases, mean Lake Class values were imputed for missing data (final PCA sample size; Class 1 = 9, Class 1.5 = 10, Class 2 = 10, Class 3 = 30). Lake Class was not formerly included as a variable within the PCA, but 95% confidence ellipses around lake scores on the first two axes were plotted for each Lake Class to indicate potential associations between PCA variables and Lake Classes. All variables were Z-score standardized, and PCA was performed using the *vegan* package in R (Oksanen et al. 2022).

By contrast, random forest (RF) can overcome some of the limitations of more traditional multivariate analyses like PCA. RF is a flexible machine learning algorithm that can use non-parametric data, large amounts of predictors, and both categorical and continuous predictor variables (Feld et al. 2016). Further, it can effectively analyze observations with missing, non-linear or complex relationships (Breiman 2001, Tang and Ishwaran 2017). As such, the RF model was built using the same set of lakes used in PCA but with additional physicochemical, lake morphometric, and individual-level Lake Trout variables (see Figure 3 - 5). The RF model assessed 5000 different “tree” combinations, each with the possibility of up to seven variables split at each node (*via* guidance from package creators to set variable splits to the number of total model variables divided by three). Variable importance (VIMP), a relative measure of variable significance, was reported for each variable within the model. Models were built in R using the *randomForestSRC* and *ggRandomForests* packages (Ehrlinger 2022, Ishwaren and Kogalur 2023), and model fit was described with overall model R^2 and the out-of-bag error rate.

Results of the PCA suggest a strong association between Lake Trout Hg, body size and ecosystem productivity metrics, and secondarily an association between DOC and Lake Trout [Hg] that is modified across a latitudinal and lake size gradient (Figure 3 - 4). PC axis 1 explained 41% of the overall model variation and primarily described an association between mean Lake Trout Hg and mean body size, which was also the dominant association detected when using univariate methods. Larger and more productive, nutrient-rich lakes typically produce larger Lake Trout (Shuter et al. 1998, McDermid et al. 2010, Lester et al. 2021), while my analysis suggests these larger fish should also harbour higher Hg concentrations (e.g., Figure 3 - 3). PC axis 2, explaining an additional 25% of the PCA, associates high Hg concentrations with geographic and lake morphology variables (maximum depth and surface area) that ultimately affect lentic DOC concentrations (Ross et al. *in review*). In other words, smaller, darker, and more northern lakes were associated with higher Lake Trout Hg concentrations. Positive associations between latitude and Hg biomagnification have also been observed elsewhere (Lavoie et al. 2013). Lake Classes tend to increase along Axis 1 (i.e., mean length), but with no clear separation based on 95% confidence ellipses, again emphasizing the limited ability to independently predict Lake Trout Hg concentrations in the absence of other factors.

My RF model further confirmed the predominant influence of Lake Trout body size on Hg concentrations, while emphasizing that ecosystem variables can modify Hg dynamics (similar conclusions to the PCA but based on individual body size compared to population means; Figure 3 - 5). Multiple methods and both datasets in the current analysis indicate that body size (measured either as length or weight) plays a key role in modulating Lake Trout Hg concentrations (Figure 3 - 3, 4, 5), findings that are also supported by a large body of literature (e.g., Somers and Jackson 1993, Stafford and Haines 2001, Johnston et al. 2022). Moreover, between the two body size metrics considered here, RF indicated body length as a more useful predictor than body weight, particularly at small and large body sizes (Appendix 3.B - Figure B. 2.a, B. 2.b). Length may provide better estimates of Hg concentrations for very slowly eliminated contaminants like Hg (Madenjian et al. 2012) because it represents lifetime skeletal growth, which is always positive and is strongly correlated with fish age. In contrast, body weight can fluctuate with changes in growth rates, productivity, and metabolic activity (Trudel and Rasmussen 2006). The next six most important RF variables were all related to lake physicochemical characteristics (latitude, surface area, DOC, longitude, maximum depth, conductivity). While body size presumably is linked to Hg bioaccumulation over time, lake physicochemical characteristics may control the baseline supply of Hg to aquatic biota and influence biomagnification. Latitude and lake size (surface area and maximum depth) are strongly related to lentic DOC concentrations (Sobek et al. 2007, Toming et al. 2020), while DOC itself is typically correlated with MeHg availability (Lavoie et al. 2019, Branfireun et al. 2020). As aquatic biota respond rapidly to Hg availability (Paterson et al. 1998, Blanchfield et al. 2022), the RF model clearly shows it is necessary to also account for the conditions controlling the bottom-up availability of Hg to Lake Trout, regardless of how Hg bioaccumulates in Lake Trout over time. Finally, Lake Class as a stand-alone categorical variable only displays a modest variable importance, falling below that of physicochemical variables and body size metrics.

Despite being inherently different statistical methods, both PCA and RF independently highlight the importance of ecosystem variables alongside body size in altering Lake Trout Hg concentrations. While my analysis indicates that Lake Class alone does not appear to be useful for independently describing Lake Trout Hg dynamics as previously reported (Cabana et al. 1994), it reveals that a basic understanding of food chain length (i.e., Lake Class) still remains valuable for several reasons. Specifically, (1) Lake Class acts as a proxy for understanding how generalized predator-prey mass ratios can affect life history traits, which in turn modify Hg concentrations via growth efficiency

(Trudel and Rasmussen 2006, Shuter et al. 2016), and (2) Lake Class allows for a categorization of contaminant risks across broad landscape scales based on coarse, yet easily assessed, prey community characteristics once environmental and allometric drivers are accounted for. For these reasons, a model parametrized with body size, ecosystem variables, and my proposed four-tiered Lake Class system can be assembled for predicting size-specific Lake Trout Hg concentrations across Ontario lakes.

Developing an ecosystem model for Lake Trout Hg concentrations

To provide a more comprehensive prediction of Lake Trout Hg dynamics, important ecosystem variables identified in PCA and RF models were added to the linear mixed-effects model of Lake Trout Hg accumulation that described an interaction between Lake Classes and fish body length. Ecosystem variables were included as additive covariates under the assumption that they primarily modulate Hg supply and availability at the base of the food chain (e.g., Table 3 - 1; Kidd et al. 2012). Lake surface area and maximum depth are highly correlated (Oliver et al. 2016), so only surface area was retained because of a higher variable importance score in the RF analysis, leaving a full LMM of:

$$\log[Hg] \sim bodyLength * lakeClass + DOC + surfaceArea + latitude + longitude + \ (bodyLength|lakeID)$$

(Eq. 3)

Model diagnostics, significance, and fit were all assessed identically to earlier LMMs in the analysis. Latitude and longitude were removed in a step-wise fashion due to high variable collinearity identified with variance inflation factors > 2 (Zuur et al. 2010). Further, a likelihood ratio test on the now reduced model (i.e., model without latitude and longitude) indicated that lake surface area was no longer informative (i.e., $p > 0.05$), and as such it was dropped to create a parsimonious final model of:

$$\log[Hg] \sim bodyLength * lakeClass + DOC + \ (bodyLength|lakeID)$$

(Eq. 4)

Compared to Eq. 2, including the additive effect of DOC substantially improved the model fit, resulting in a model $R^2 = 0.59$ compared to $R^2 = 0.49$ when only the interaction between Lake Class and individual body size was considered (Table 3 - 2). Consistent with the model without DOC included (Eq. 2), the interaction between Lake Class and body size was significant ($F_{3,65.22} = 5.97$, $p = 0.0012$). DOC was also significant ($F_{1,74.24} = 35.39$, $p < 0.0001$), contributing 6.4% of the explained variance, which was second only to the outsized role of body length in structuring Hg concentrations (body length accounted for 88% of the explained variance; body length x Lake Class interaction accounted for 3.2%).

This DOC-informed mixed model can be used to explore conditions under which Lake Trout are likely to experience elevated Hg contamination. Using model coefficients (Table 3 - 2), Lake Trout Hg concentrations were estimated across Lake Classes and gradients of observed Lake Trout body sizes and DOC concentrations from my contemporary data set (*Figure 3 - 6*). Model predictions and visualizations continue to support body size being the primary determinant of Hg concentrations, though lake DOC concentrations play an important role determining whether Lake Trout of a given size are contaminated below or above the Canadian Hg consumption guidelines of 0.5 $\mu g_{Hg}/g_{fish}$. For example, a 500 mm Lake Trout in a median DOC lake (~4.3 mg/L) from any Lake Class is predicted to have Hg concentrations below that of the national guidelines (*Figure 3 - 6*, middle panel). However, as DOC increases to 12.4 mg/L (the maximum observed DOC concentration in my sample lakes), a 500 mm Lake Trout is predicted to accumulate nearly double the acceptable Hg concentration in its tissues across all Lake Classes, elevating median sized Lake Trout above safe consumption levels (*Figure 3 - 6*, right panel). In clear, low DOC lakes, Lake Trout Hg contamination is not likely to be of concern, except for the very largest fish (*Figure 3 - 6*, left panel). However, in darker, high DOC lakes, even smaller Lake Trout are subject to significant Hg contamination, posing potential public health risks for human consumption (*Figure 3 - 6*, right panel). Furthermore, the significant interaction between body length and Lake Class again emphasizes how prey availability might affect predator conversion efficiency, particularly at the smallest and largest body sizes. For example, a 750 mm, Class 3 Lake Trout from the lowest modelled DOC lake (*Figure 3 - 6*, left panel) would not be subject to a consumption advisory, though same-sized individuals from Class 1 or 2 may have nearly twice as much Hg and would be above national consumption guidelines.

To better understand Lake Trout Hg dynamics, I have shown that predictive models must consider the influence of environmental drivers and their impact on MeHg availability at the base of food webs. Being stenothermic, Lake Trout habitat occupancy and foraging is primarily constrained by the presence of suitable oxythermal conditions; conditions that are directly affected by variability in physicochemical and landscape variables, and conditions that can also affect both fish growth rates and exposure to environmental Hg (e.g., Shuter et al. 1998, Shuter et al. 2016, and as reviewed in Table 3 - 1). Furthermore, these variables can influence the timing and severity of oxythermal habitat restrictions during summer stratification, when Lake Trout are attempting to maximize annual energy acquisition for growth and reproduction (Morbey et al. 2010, Wilkins and Marsden 2021). In my contemporary dataset of 64 lakes, conditions varied widely in surface area (16 to 34518 ha), maximum depth (12 to 186 m), total dissolved phosphorus levels (2.6 to 39.6 µg/L) and DOC concentrations (1.7 to 12.35 mg/L). I have shown that DOC must be accounted for to understand Lake Trout Hg dynamics across Ontario lakes (*Figure 3 - 6*), and other work has demonstrated the importance of lake size and ecosystem productivity controlling Lake Trout life history traits and growth rates (Shuter et al. 1998, McDermid et al. 2010, Ross *Chapter 4*). Collectively, dynamics modulating Lake Trout growth rates and Hg accumulation are surely linked, as growth and conversion efficiency are tightly associated with how Hg bioaccumulates within individuals (i.e., Hg 'growth dilution'; Trudel and Rasmussen 2006). An advantage to my ecosystem-based risk approach is that my model has identified DOC as the key environmental variable explaining Lake Trout Hg dynamics of those considered here.

Most regional and provincial water monitoring agencies already collect DOC samples, which provides the potential for targeted verification of fish Hg levels, and possible updates to risk assessment guidelines where reported DOC concentrations (or lake colour) along with standard fish body lengths could provide a more nuanced and specific assessment of risk to fishers than current length-based approaches.

Despite regional decreases in atmospheric Hg deposition (Tang et al. 2013), ongoing environmental change in many regions appears to be shifting lakes towards greater DOC concentrations (lake 'browning', Solomon et al. 2015), which my analysis suggests has the potential to amplify future Lake Trout Hg concentrations given the general close coupling of DOC concentrations and Hg availability as indicated here and elsewhere (Lavoie et al. 2019, though see Tsui and Finlay 2011; French et al. 2014; Braaten et al. 2018). Higher DOC loads typically increase methylation rates of existing Hg pools (Eckley and Hintelmann 2006), but will also change the light climate and oxythermal environments of lakes in potentially detrimental ways as they relate to stenothermic salmonids (Jane et al. 2024). Increased DOC can lead to higher surface temperatures, more intense and longer periods of thermal stratification, and increased duration and extent of hypoxic bottom waters (Solomon et al. 2015). The indirect effects of lake brownification largely mirror those of climate change, which have previously been shown to alter Lake Trout behaviour, growth, activity, and body condition by reductions in suitable seasonal habitat availability and energy acquisition, especially in Class 1 and 1.5 lakes which lack offshore prey fish (Guzzo et al. 2017). Ongoing environmental change within the current distribution of Lake Trout lakes is predicted to lead to both darker and warmer lakes (Magnuson et al. 2000, Evans et al. 2005, Vuorenmaa et al. 2006, Meyer-Jacob et al. 2019, Sharma et al. 2019) which should yield smaller Lake Trout due to the metabolic consequences of inhabiting increasingly high-temperature, hypoxic waters (Ohlberger 2013, but see Solokas et al. 2023 and Warne et al. 2024). While my model predicts that relatively smaller Lake Trout have lower Hg concentrations (e.g., *Figure 3 - 6*), the challenges of existing in warmer, oxygen-depleted environments should reduce prey conversion efficiency via increased metabolic costs and could lead to Hg concentrating within muscle tissues (Trudel and Rasmussen, 2006).

Summary and Conclusions

Through various iterations of data and model complexity, I show that understanding Lake Trout Hg dynamics requires an examination of both the top-down food web characteristics impacting traits like body size, as well as the bottom-up drivers that facilitate Hg availability (e.g., DOC). Multiple lines of evidence suggest that body size is the most important variable when predicting Lake Trout Hg, though ultimate determinations of Hg burden depend on ecosystem properties and energetic efficiencies conveyed by the presence of certain prey. Cabana et al. (1994) originally suggested that Lake Trout Hg should increase with increasing food chain length, and while my assessment here indicates that Lake Class does not predict Hg concentrations as Cabana et al. (1994) suggested, a coarse understanding of prey communities can still be useful, particularly when predicting Hg concentrations from the smallest and largest individuals within a population. Further, my integrated ecosystem approach encourages reconsidering the use of models containing just trophic position (e.g., δN^{15} trophic models) and body size that are common within the literature (e.g. Vander Zanden and Rasmussen 1996, Swanson and Kidd 2010, Drouillard et al. 2024). Isotopic trophic relationships with Hg are arguably a continuous-scale extension of the original Rasmussen and Cabana Lake Class system, and while including information regarding body size and composition provides overwhelmingly more information than models containing solely trophic position, they do not explicitly account for ecosystem-level processes that modulate the supply of Hg into lakes.

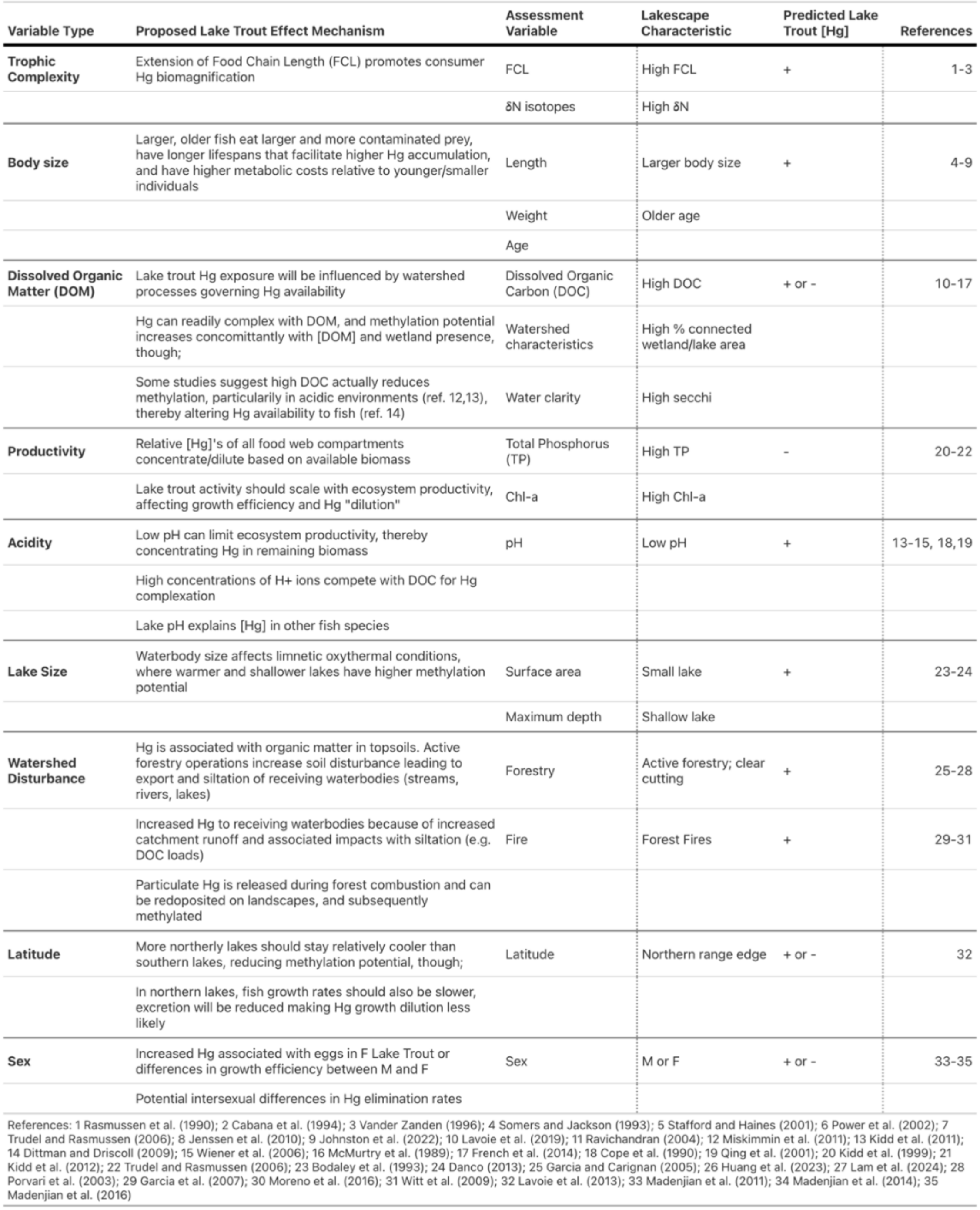
Important dynamics between prey community size-structure with Lake Trout body size and Hg has been noted in the past (Somers and Jackson 1993, Trudel and Rasmussen 2006, Shuter et al. 2016), and my results contribute to the notion that predator energetics play an important role when determining realized Hg contamination (Trudel and Rasmussen 2006). Notably, the interaction between body length and Lake Class observed here highlights a potentially important role for *Mysis* in Lake Trout Hg accumulation dynamics, with improved conversion efficiency for larger harvestable-sized individuals and by facilitating Hg growth dilution through access to higher quality prey (at least in lakes where *Mysis* are native, like those in my analysis). In lakes where *Mysis* are present, Lake Trout growth efficiency — and growth efficiency of pelagic prey fishes if present — is maintained through having an abundant invertebrate prey source with optimal oxythermal habitat similar to that as Lake Trout, ultimately reducing the foraging activity required to reach satiation (Giacomini et al. 2013), as well as providing an efficient and rapid transition between invertivorous and piscivorous feeding modes

(Lester et al. 2020). Consequently, *Mysis* appear to be a key modifier of Lake Trout metabolic requirements, allowing for surplus energy not being allocated to active metabolism to instead be allocated to growth and reproduction, thereby diluting Hg concentrations. To test the importance of *Mysis* presence on Lake Trout energy allocation and acquisition directly (and therefore Hg accumulation rates), estimates of Lake Trout consumption, activity and growth rates contrasted among the Lake Classes outlined here are required. Future studies using a combination of hydroacoustic and biotelemetric measurements of activity, movement and oxythermal habitat use, along with updated bioenergetic models, could provide further insight into the different slopes associated with unique lake classes that appear to separate on the basis of the presence or absence of *Mysis*.

My results also clearly highlight the importance of DOC as a modifier of Lake Trout Hg. With Hg concentrations shifting additively with increasing DOC concentrations, my results suggest that any Hg contaminant models that consider only food web effects without also accounting for environmental factors have the potential to misrepresent Hg bioaccumulation. My study shows that a failure to account for the role of DOC could also have public health consequences, where even small fish inhabiting high DOC lakes are at risk of being above Canadian contaminant guidelines. Ensuring that DOC is included in predictive models of Lake Trout Hg (and potentially other stenothermic salmonids inhabiting lakes, like the Brook Trout, *Salvelinus fontinalis*) will be increasingly important in a world of both warming and browning lakes. Lake Trout are common across lakes in the northern regions of North America, which is coincidentally where increases in Hg biomagnification (Lavoie et al. 2013), brownification (Ross et al. *in review*), and warming (Sharma et al. 2019) are occurring at rates higher than anywhere else on the continent. As such, Lake Trout Hg may be insensitive to regional decreases in Hg deposition (Tang et al. 2013, Weiss-Penzias et al. 2016, Blanchfield et al. 2022, Pilote et al. 2024). To better forecast future Hg estimates, physicochemical variables that reflect our rapidly changing environment and that are also known to impact fish Hg concentrations must be included in models to better predict Hg contaminant dynamics under future scenarios.

Here, I show that variables associated with landscape (e.g., DOC), physiological and ecological processes (e.g., factors related to food conversion efficiency) are all needed to properly assess Hg contamination risk for Lake Trout and the people who consume them. My analysis suggests that contaminant advisories based on older/historic fish Hg data likely require updating given rapid decadal changes in lake surface temperatures with climate warming (O' Reilly et al. 2015) and the darkening of lakes with increasing DOC concentrations (Imtiazy et al. 2020). Following further validation, my proposed model may provide a means of updating contaminant guidelines based on regional water quality and existing food web structure information, which would be easier and more cost effective to sample than multi-day campaigns to capture fish. Eating fish is the primary mechanism of Hg poisoning in humans, and as such, understanding what controls Hg dynamics of a common food-fish, like Lake Trout, is imperative. Here, I show that Hg risk can be conservatively estimated using three easily assessed quantities – 1) the body length of a Lake Trout likely to be captured and consumed by anglers, 2) the DOC concentration of a lake, and 3) the presence and absence of two key prey items (*Mysis* and pelagic prey fishes). I also demonstrate that Lake Trout Hg concentrations are better assessed when using individual, rather than population-level data; Hg concentrations are highly variable both between and within populations and reducing lake-specific dynamics to a single value does not adequately describe Hg dynamics across lakes.

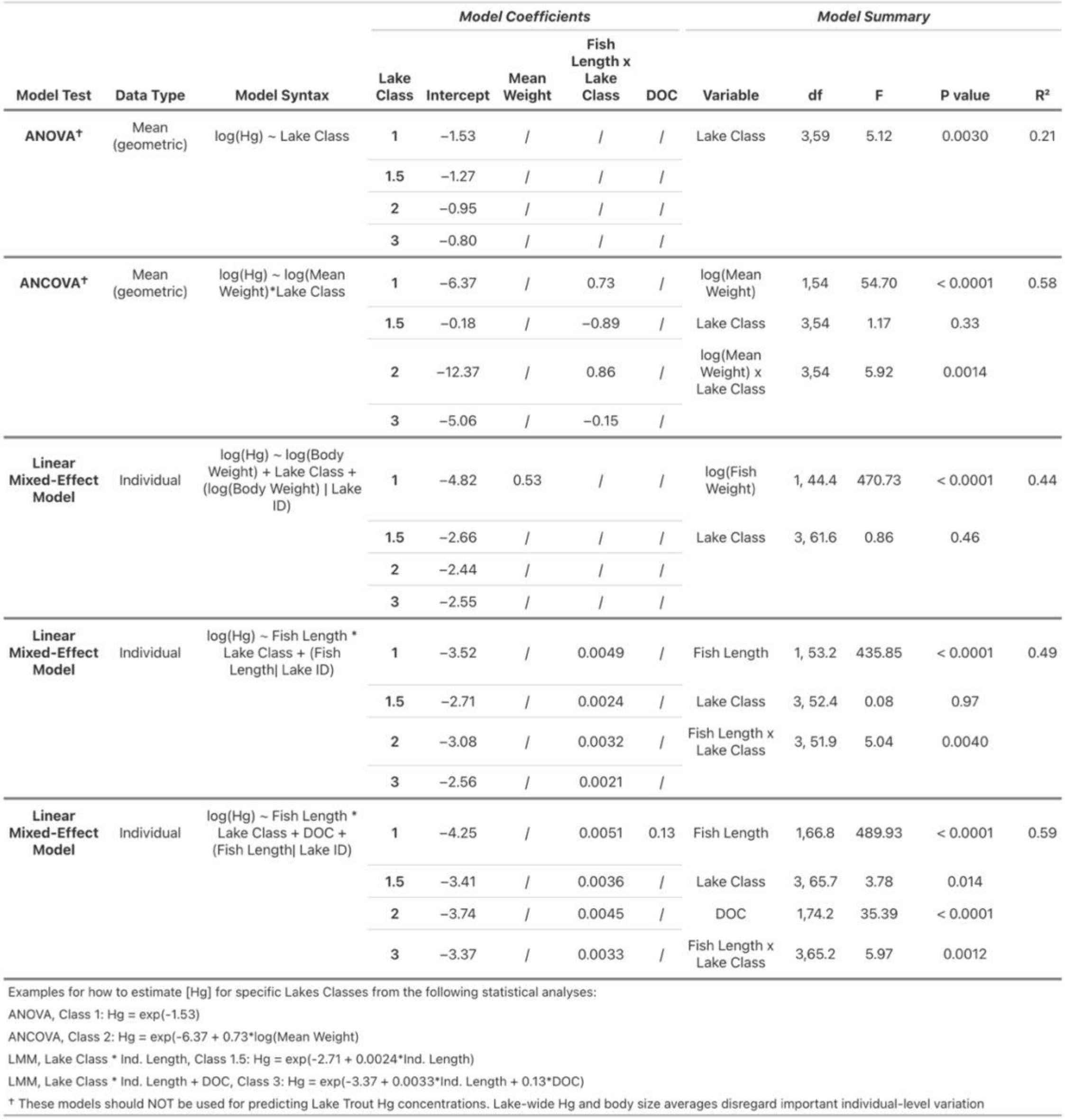
Table 3 - 1. Predictions of Lake Trout Hg dynamics in the presence of independent landscape and physicochemical variables. Mechanisms are described by the common assessment variable for a given attribute, and predictions are made based on whether the variable is likely to cause on increase (+) or decrease (-) in Lake Trout Hg concentrations.



Variable Type	Proposed Lake Trout Effect Mechanism	Assessment Variable	Lakescape Characteristic	Predicted Lake Trout [Hg]	References
Trophic Complexity	Extension of Food Chain Length (FCL) promotes consumer Hg biomagnification	FCL	High FCL	+	1-3
		δN isotopes	High δN		
Body size	Larger, older fish eat larger and more contaminated prey, have longer lifespans that facilitate higher Hg accumulation, and have higher metabolic costs relative to younger/smaller individuals	Length	Larger body size	+	4-9
		Weight	Older age		
		Age			
Dissolved Organic Matter (DOM)	Lake trout Hg exposure will be influenced by watershed processes governing Hg availability	Dissolved Organic Carbon (DOC)	High DOC	+ or -	10-17
	Hg can readily complex with DOM, and methylation potential increases concomittantly with [DOM] and wetland presence, though;	Watershed characteristics	High % connected wetland/lake area		
	Some studies suggest high DOC actually reduces methylation, particularily in acidic environments (ref. 12,13), thereby altering Hg availability to fish (ref. 14)	Water clarity	High secchi		
Productivity	Relative [Hg]'s of all food web compartments concentrate/dilute based on available biomass	Total Phosphorus (TP)	High TP	-	20-22
	Lake trout activity should scale with ecosystem productivity, affecting growth efficiency and Hg "dilution"	Chl-a	High Chl-a		
Acidity	Low pH can limit ecosystem productivity, thereby concentrating Hg in remaining biomass	pH	Low pH	+	13-15, 18,19
	High concentrations of H+ ions compete with DOC for Hg complexation				
	Lake pH explains [Hg] in other fish species				
Lake Size	Waterbody size affects limnetic oxythermal conditions, where warmer and shallower lakes have higher methylation potential	Surface area	Small lake	+	23-24
		Maximum depth	Shallow lake		
Watershed Disturbance	Hg is associated with organic matter in topsoils. Active forestry operations increase soil disturbance leading to export and siltation of receiving waterbodies (streams, rivers, lakes)	Forestry	Active forestry; clear cutting	+	25-28
	Increased Hg to receiving waterbodies because of increased catchment runoff and associated impacts with siltation (e.g. DOC loads)	Fire	Forest Fires	+	29-31
	Particulate Hg is released during forest combustion and can be redoposited on landscapes, and subsequently methylated				
Latitude	More northerly lakes should stay relatively cooler than southern lakes, reducing methylation potential, though;	Latitude	Northern range edge	+ or -	32
	In northern lakes, fish growth rates should also be slower, excretion will be reduced making Hg growth dilution less likely				
Sex	Increased Hg associated with eggs in F Lake Trout or differences in growth efficiency between M and F	Sex	M or F	+ or -	33-35
	Potential intersexual differences in Hg elimination rates				

References: 1 Rasmussen et al. (1990); 2 Cabana et al. (1994); 3 Vander Zanden (1996); 4 Somers and Jackson (1993); 5 Stafford and Haines (2001); 6 Power et al. (2002); 7 Trudel and Rasmussen (2006); 8 Jenssen et al. (2010); 9 Johnston et al. (2022); 10 Lavoie et al. (2019); 11 Ravichandran (2004); 12 Miskimmin et al. (2011); 13 Kidd et al. (2011); 14 Dittman and Driscoll (2009); 15 Wiener et al. (2006); 16 McMurtry et al. (1989); 17 French et al. (2014); 18 Cope et al. (1990); 19 Qing et al. (2001); 20 Kidd et al. (1999); 21 Kidd et al. (2012); 22 Trudel and Rasmussen (2006); 23 Bodaley et al. (1993); 24 Danco (2013); 25 Garcia and Carignan (2005); 26 Huang et al. (2023); 27 Lam et al. (2024); 28 Porvari et al. (2003); 29 Garcia et al. (2007); 30 Moreno et al. (2016); 31 Witt et al. (2009); 32 Lavoie et al. (2013); 33 Madenjian et al. (2011); 34 Madenjian et al. (2014); 35 Madenjian et al. (2016)

Table 3 - 2. Model coefficients and summaries for the various statistical approaches for predicting Lake Trout Hg from the contemporary dataset (i.e., no summaries provided for Cabana et al. (1994) models). Only model coefficients necessary for estimating Hg concentrations for a given model are presented.



			Model Coefficients					*Model Summary*				
Model Test	**Data Type**	**Model Syntax**	**Lake Class**	**Intercept**	**Mean Weight**	**Fish Length x Lake Class**	**DOC**	**Variable**	**df**	**F**	**P value**	**R²**
ANOVA†	Mean (geometric)	log(Hg) ~ Lake Class	**1**	−1.53	/	/	/	Lake Class	3,59	5.12	0.0030	0.21
			1.5	−1.27	/	/	/					
			2	−0.95	/	/	/					
			3	−0.80	/	/	/					
ANCOVA†	Mean (geometric)	log(Hg) ~ log(Mean Weight)*Lake Class	**1**	−6.37	/	0.73	/	log(Mean Weight)	1,54	54.70	< 0.0001	0.58
			1.5	−0.18	/	−0.89	/	Lake Class	3,54	1.17	0.33	
			2	−12.37	/	0.86	/	log(Mean Weight) x Lake Class	3,54	5.92	0.0014	
			3	−5.06	/	−0.15	/					
Linear Mixed-Effect Model	Individual	log(Hg) ~ log(Body Weight) + Lake Class + (log(Body Weight) | Lake ID)	**1**	−4.82	0.53	/	/	log(Fish Weight)	1, 44.4	470.73	< 0.0001	0.44
			1.5	−2.66	/	/	/	Lake Class	3, 61.6	0.86	0.46	
			2	−2.44	/	/	/					
			3	−2.55	/	/	/					
Linear Mixed-Effect Model	Individual	log(Hg) ~ Fish Length * Lake Class + (Fish Length| Lake ID)	**1**	−3.52	/	0.0049	/	Fish Length	1, 53.2	435.85	< 0.0001	0.49
			1.5	−2.71	/	0.0024	/	Lake Class	3, 52.4	0.08	0.97	
			2	−3.08	/	0.0032	/	Fish Length x Lake Class	3, 51.9	5.04	0.0040	
			3	−2.56	/	0.0021	/					
Linear Mixed-Effect Model	Individual	log(Hg) ~ Fish Length * Lake Class + DOC + (Fish Length| Lake ID)	**1**	−4.25	/	0.0051	0.13	Fish Length	1,66.8	489.93	< 0.0001	0.59
			1.5	−3.41	/	0.0036	/	Lake Class	3, 65.7	3.78	0.014	
			2	−3.74	/	0.0045	/	DOC	1,74.2	35.39	< 0.0001	
			3	−3.37	/	0.0033	/	Fish Length x Lake Class	3,65.2	5.97	0.0012	

Examples for how to estimate [Hg] for specific Lakes Classes from the following statistical analyses:

ANOVA, Class 1: Hg = exp(-1.53)

ANCOVA, Class 2: Hg = exp(-6.37 + 0.73*log(Mean Weight)

LMM, Lake Class * Ind. Length, Class 1.5: Hg = exp(-2.71 + 0.0024*Ind. Length)

LMM, Lake Class * Ind. Length + DOC, Class 3: Hg = exp(-3.37 + 0.0033*Ind. Length + 0.13*DOC)

† These models should NOT be used for predicting Lake Trout Hg concentrations. Lake-wide Hg and body size averages disregard important individual-level variation

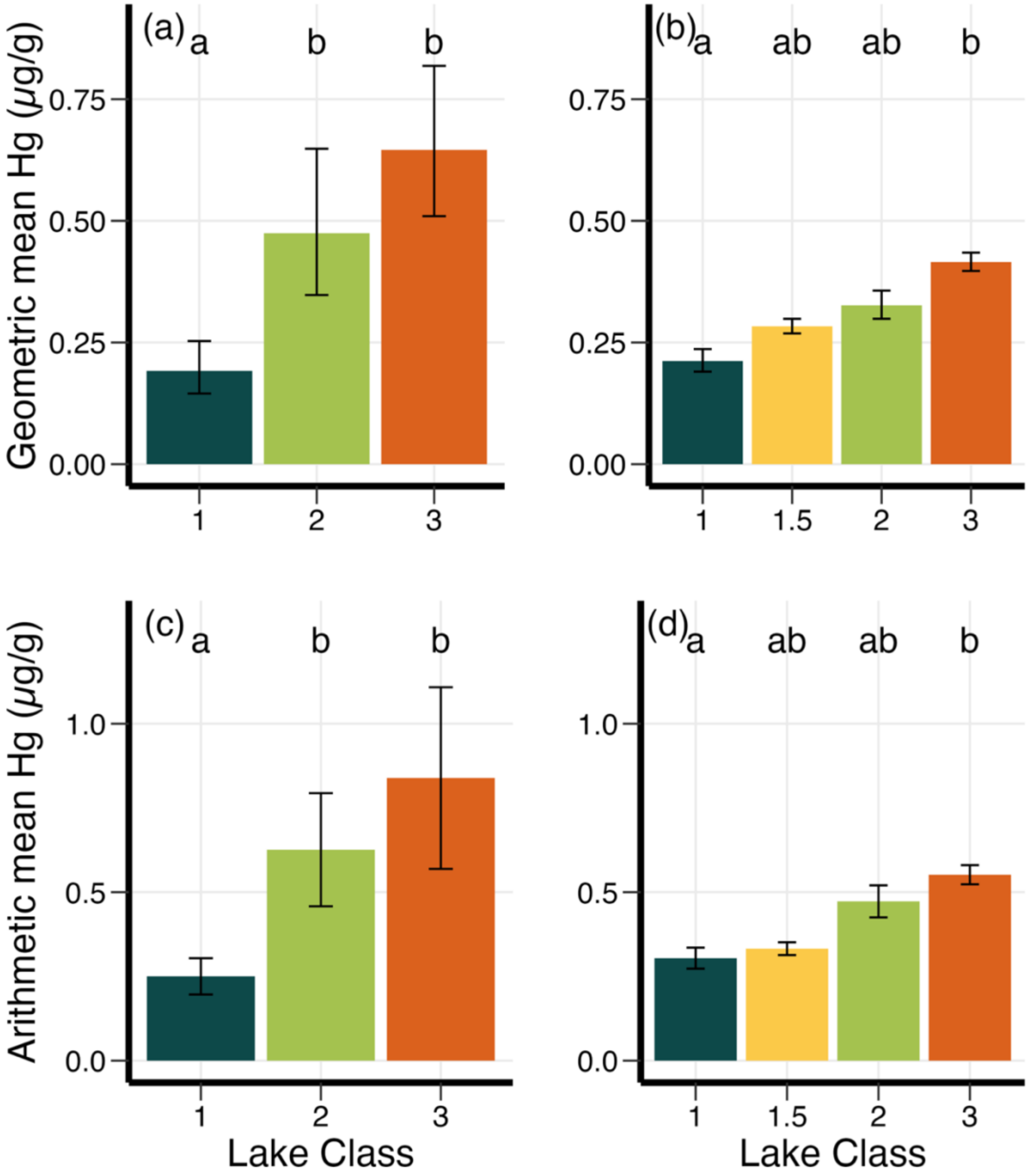


Figure 3 - 1. Comparison of mean geometric (a, b) and arithmetic (c, d) Hg concentrations between different Lake Classes from the Cabana (a,c) and contemporary (b,d) datasets. Common letters between Lake Classes within a given panel represent Lake Classes where mean Hg concentrations are statistically equivalent from a Tukey HSD test. Error bars represent 95% confidence intervals. Lake Classes describe Lake Trout pelagic prey communities, where Class 1 only have pelagic zooplankton, Class 1.5 contain *Mysis* but no pelagic prey fishes, Class 2 have pelagic prey fishes but no *Mysis*, and Class 3 contain both *Mysis* and pelagic prey fishes.

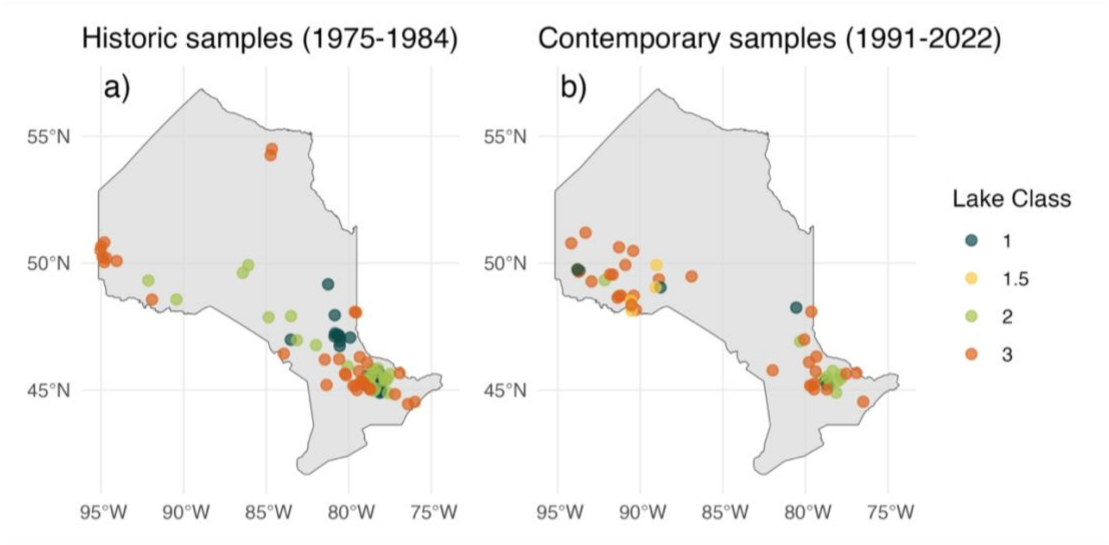


Figure 3 - 2. Survey lakes across the Province of Ontario, Canada from a) Cabana et al. (1994), and b) those compiled for this study.

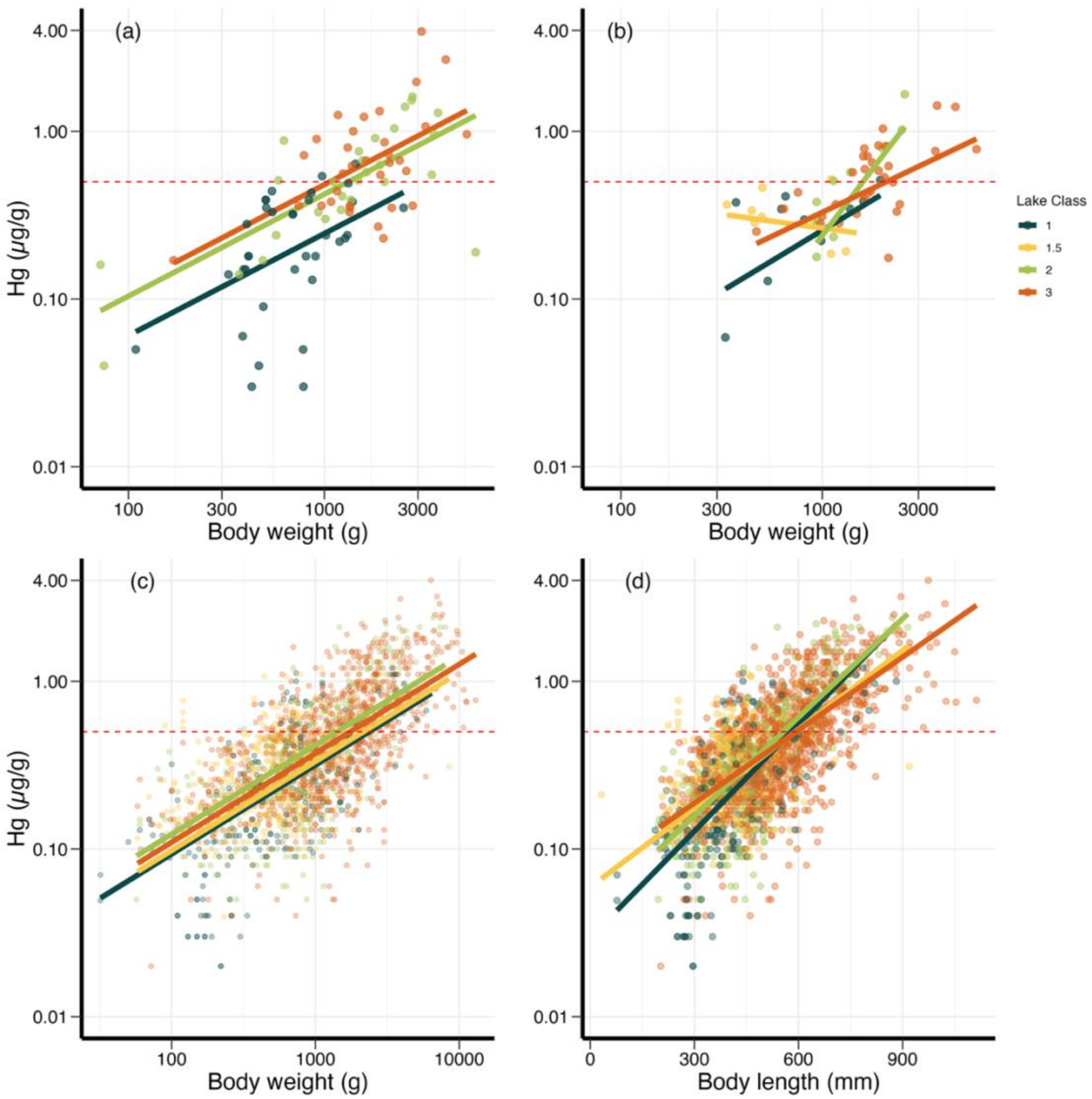


Figure 3 - 3. Predictions of Lake Trout Hg concentrations across different Lake Classes when body size is included as a model covariate: (a) a reassessment of Cabana et al. (1994) data using ANCOVA where mean body weight was used as a covariate with discrete Lake Classes as treatment groups; (b) an attempt at using ANCOVA for the contemporary dataset with mean body weight as a covariate, (c) individual body weight as a covariate in a linear mixed-effect model, and (d) individual body length as a model covariate in a linear mixed-effect model. For all panels, solid lines represent predictions from model coefficients, and the dotted red line indicates the Canadian Hg consumptions guideline (0.5 ppm Hg). Note, log axes on all y-axes and x-axes in panels a-c.

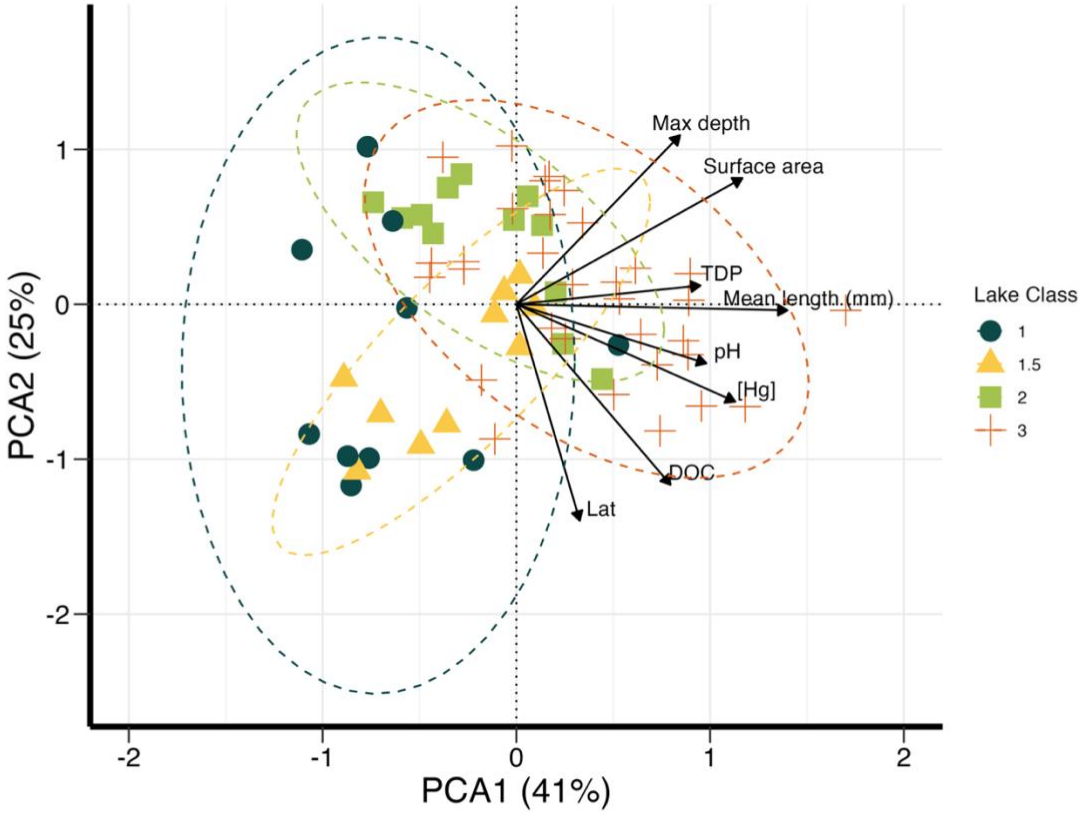


Figure 3 - 4. Principal Component Analysis (PCA) of environmental and landscape variables, mean body length (mm) and total Lake Trout Hg concentrations ([Hg]) within the contemporary dataset. Lake Classes are identified by point shape, and colour with 95% confidence ellipses identified by the dashed coloured lines. TDP = Total Dissolved Phosphorus, Lat = Latitude, DOC = Dissolved Organic Carbon.

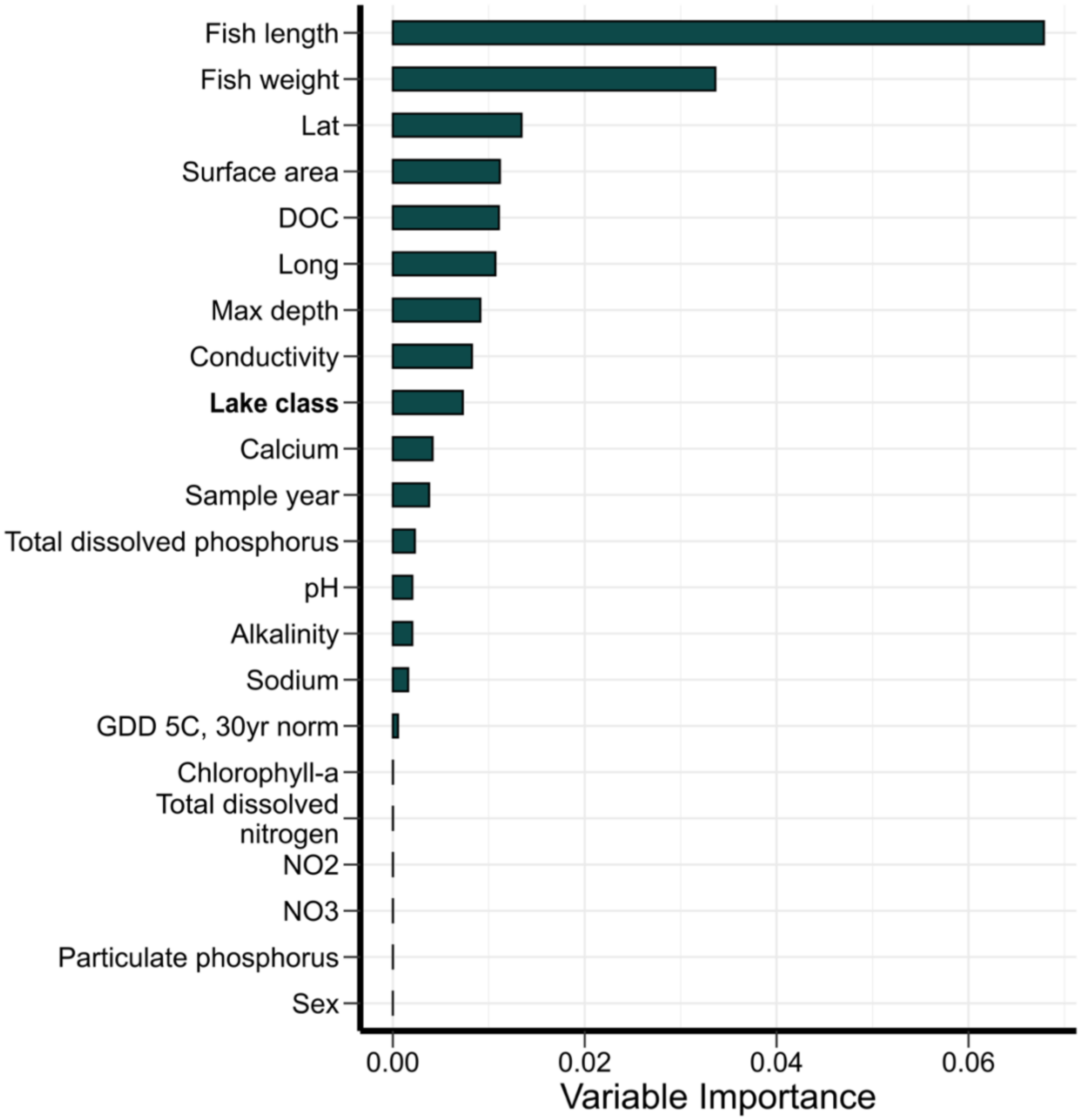


Figure 3 - 5. Random forest analysis of Lake Trout Hg concentrations from contemporary data. Variable importance from the extensive set of physicochemical and body size predictors were included, and relative importance is assessed in descending order of importance. Model performance was high (R^2 = 0.72; model variance out-of-bag performance error = 0.049). Lake Class is bolded to emphasize its relative independent contribution when predicting Lake Trout Hg concentrations.

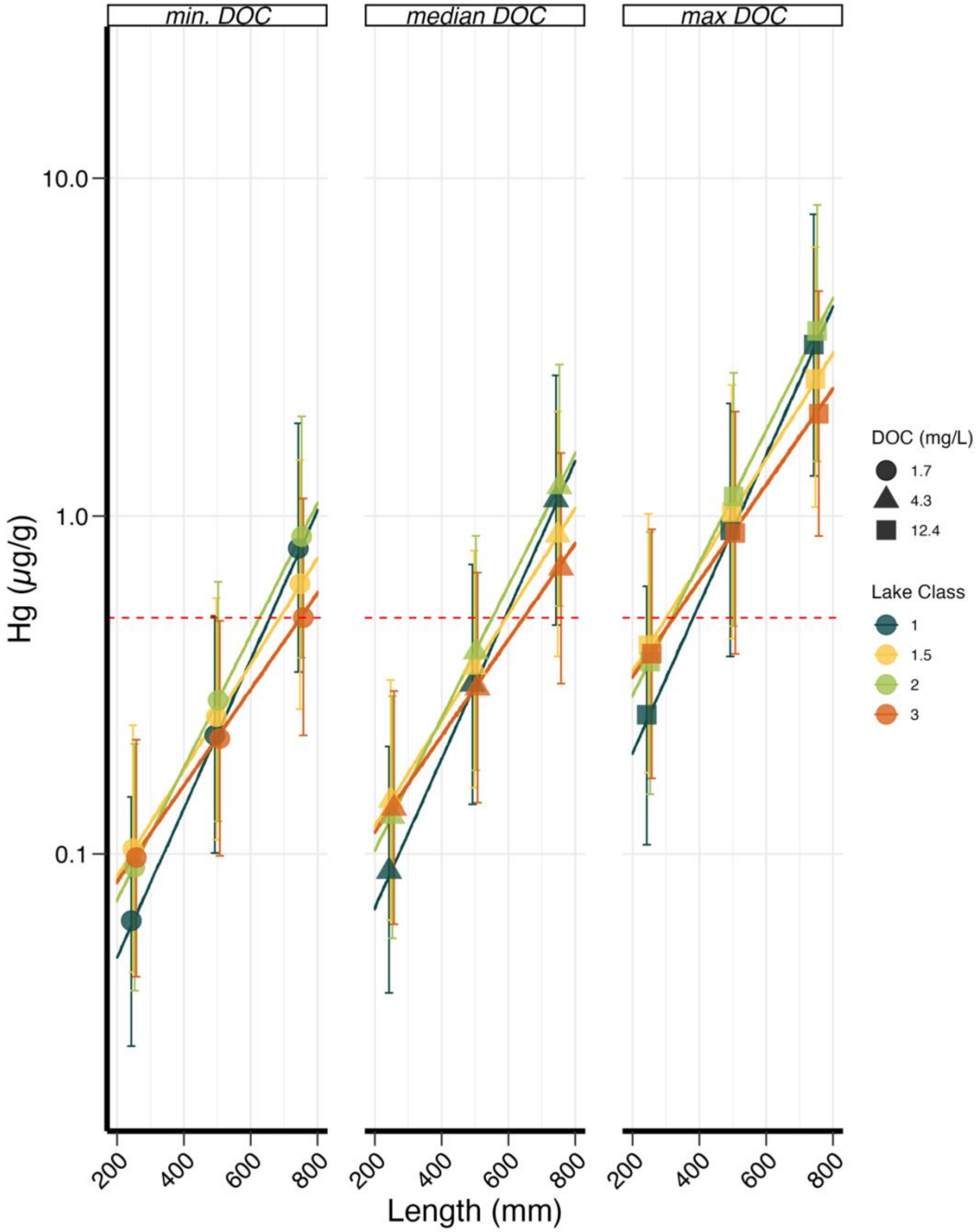


Figure 3 - 6. The influence of DOC, body size (calculated with individual total length) and Lake Class on Lake Trout Hg concentrations. Panels represent the minimum (1.7 mg/L), median (4.3 mg/L) and maximum (12.4 mg/L) observed DOC concentrations, with data points representing small (250 mm), medium (500 mm) and large (750mm) fish. Error bars represent the 95% confidence intervals from the mean, with solid lines indicating predictions from model coefficients. The horizontal dashed red line indicates the Canadian Hg consumption guideline of 0.5 ppm.

Appendix 3.A

Dataset Descriptions

Cabana et al. (1994) dataset

To reassess the original findings that posit pelagic prey availability (i.e., lake class) drives Lake Trout Hg biomagnification, I transposed Table 1 observations for the three separate lake classes (Cabana et al. 1994). Complete methodology can be found in the original paper, but in brief, Lake Trout from 96 Ontario lakes were sampled between 1975 and 1984. Data were accessed from the Ontario Ministry of Environment (MOE) Sports Fish Contaminants Monitoring Program, and geometric mean body weight and Hg concentrations were calculated for each study lake. Physicochemical and lake morphological characteristics were accessed from a variety of provincial monitoring programs. Lake classes were based on the presence and absence of pelagic prey items, namely *Mysis diluviana* (hereafter, *Mysis*) and pelagic prey fishes (smelt, ciscoes, lake and round whitefish, alewife, and nine-spine stickleback). *Mysis* presence/absence was assessed by 1) the Dadswell (1974) monograph of *Mysis* distributions across Ontario, and 2) the maximum extent of glacial lakes where *Mysis* were assumed to be present within those boundaries. All statistical analyses were conducted on Lake Trout means (Hg and weight), and independent variables were log-transformed to meet the assumptions of linear models, except for pH.

Contemporary dataset

I assembled a contemporary dataset with Lake Trout Hg, body size, habitat variables, and lake classes to reassess conclusions in Cabana et al. (1994). Further, this contemporary dataset was used to evaluate how increased model and variable complexity could help explain Lake Trout Hg concentrations across Ontario lakes. Sixty-four lakes covering a similar geographic range to those of Cabana et al. (1994) were chosen with Hg and body sizes sampled between 1991 and 2002. Lake Trout Hg and body size measurements were acquired from the Fish Contaminants Monitoring

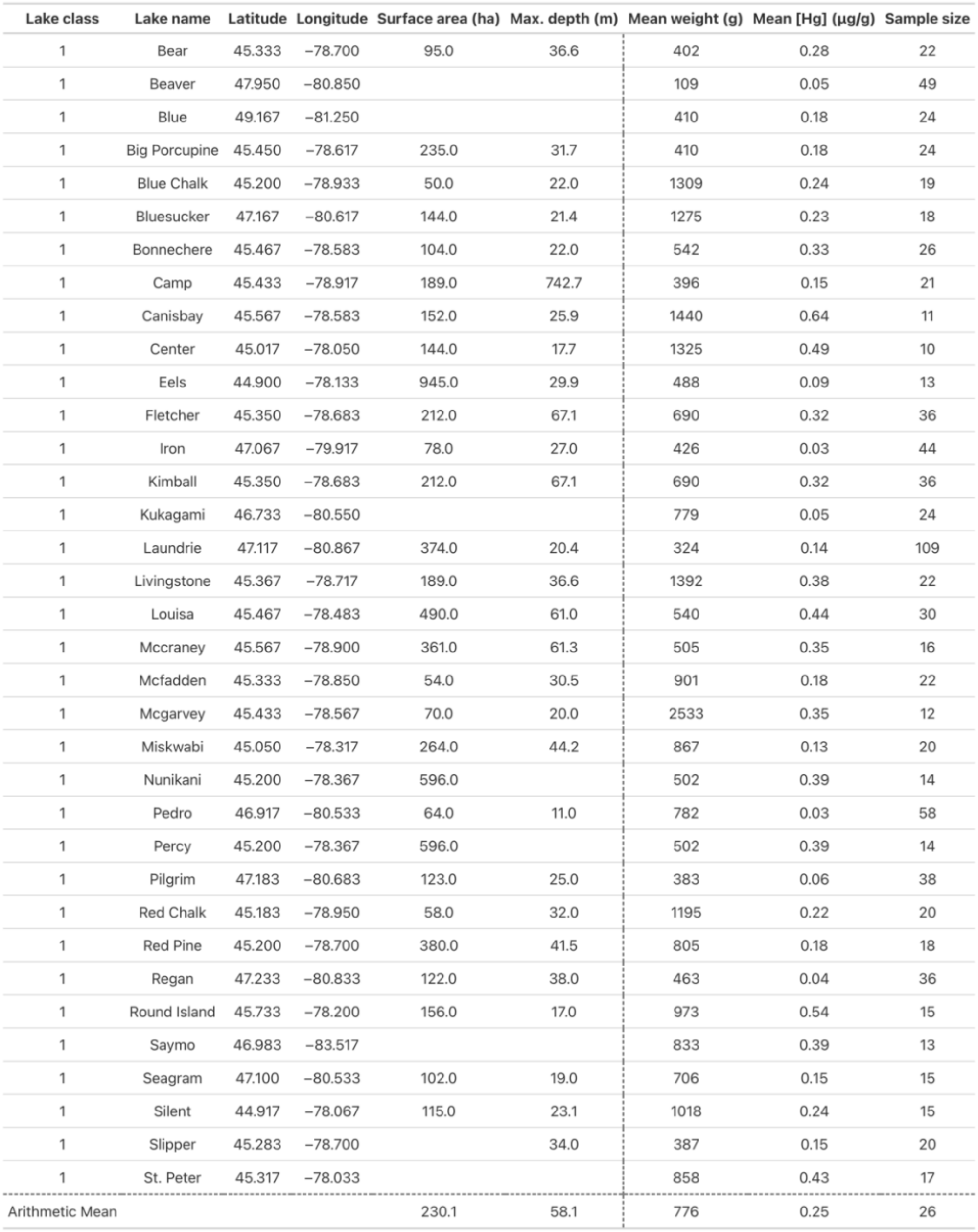
Program administered by the Ontario Ministry of Environment, Conservation, and Parks (MECP, formerly MOE), and long-term data records from the International Institute of Sustainable Development, Experimental Lakes Area (IISD-ELA). In both data sets, Lake Trout dry weight methylmercury concentrations (µg/g) were assumed from reported total Hg concentrations, as greater than 95% of Hg in predatory fish is considered to be in the form of methylmercury (Bloom 1992, Sumner et al. 2020). Total Hg concentrations from the MECP Fish Contaminants dataset were analyzed by vapor-flameless atomic absorption spectrophotometry, with complete methodology detailed in the supplementary information of Bhavsar et al. (2010). IISD-ELA Hg samples were analyzed. All Hg observations are associated with individual fork length (mm) and round body weight (g) measurements from when fish were sampled.

Lake classes were identical to those of Cabana et al. (1994), apart from a new Class 1.5 lake class where pelagic prey fishes were absent but *Mysis* was present. Importantly, pelagic prey communities were only classified using true, verified presences. Data sources categorizing confirmed presences included database records from the IISD-ELA, the Dadswell *Mysis* monograph (1974), physical catch records or diet items collected between 2007 and 2019 from the Broadscale Monitoring Program run by Ontario's Ministry of Natural Resources and Forestry (MNRF), targeted night-time *Mysis* sampling by the author during summer and fall 2020, technical reports from the Coldwater Lakes Experimental fishery (MNRF) and Algonquin Provincial Park describing *Mysis* distributions and presence (Ridgway et al. 2017), as well as observations from Rasmussen et al. (1990) where prey communities were assessed by confirmed, not assumed, presence.

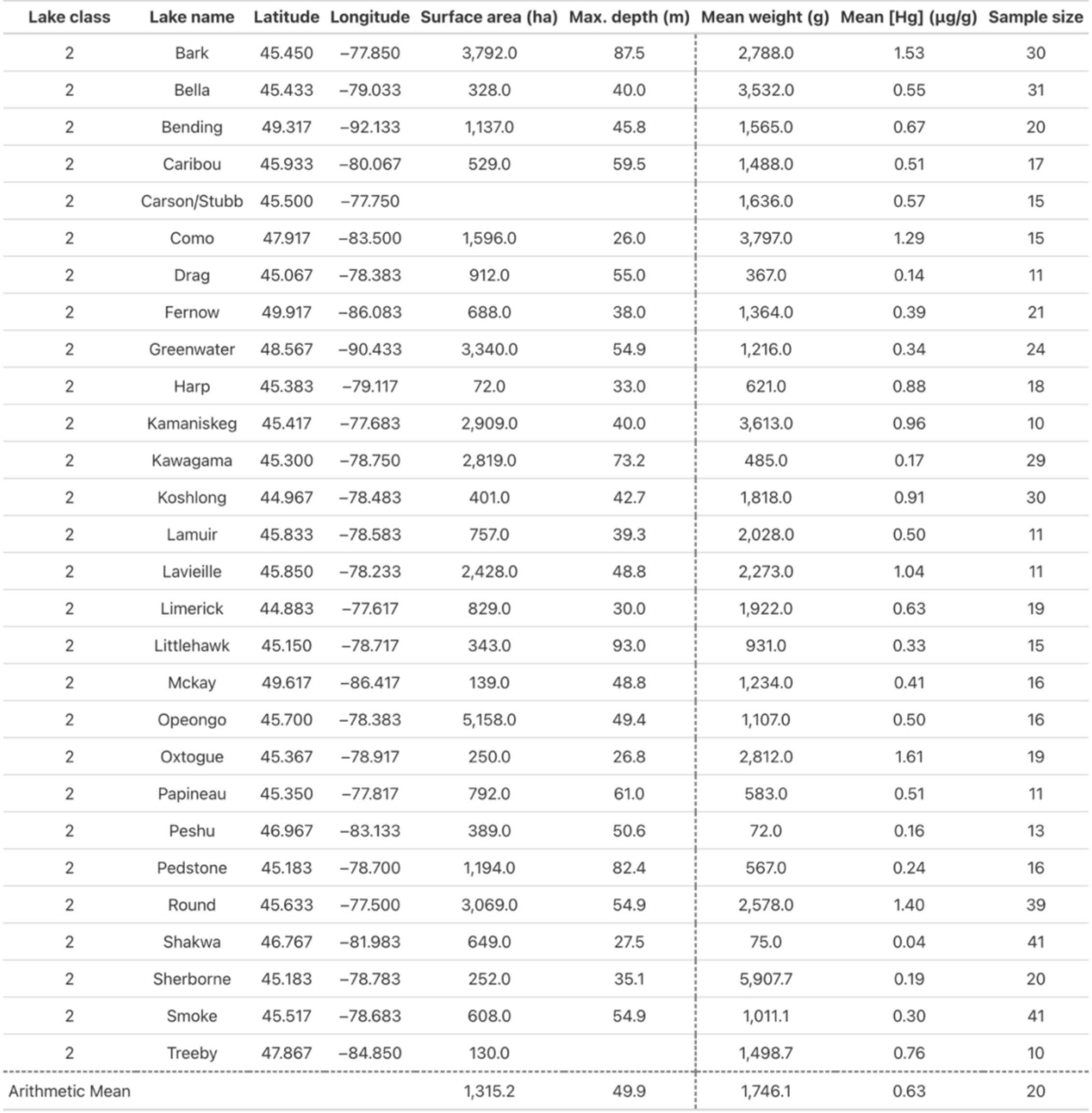
Physicochemical and lake morphological variables were acquired from the Broadscale Monitoring Program (MNRF) and IISD-ELA's long-term monitoring database. Mean water chemistry values were used in cases where multiple lake-years of data existed.

Appendix 3.B

Appendix 3.B - Table B. 1. Geographic and lake morphometric characteristics from Cabana et al. (1994) lakes across three distinct Lake Classes. Only zooplankton are available as pelagic prey in Class 1 lakes, pelagic prey fishes (i.e. Coregonids) are present in Class 2 lakes and both *Mysis* and pelagic prey fishes are present in Class 3 lakes. Arithmetic mean Lake Trout weight, and Hg concentrations are provided for each lake and Lake Class, along with the number of Hg samples that were analyzed (sample size).



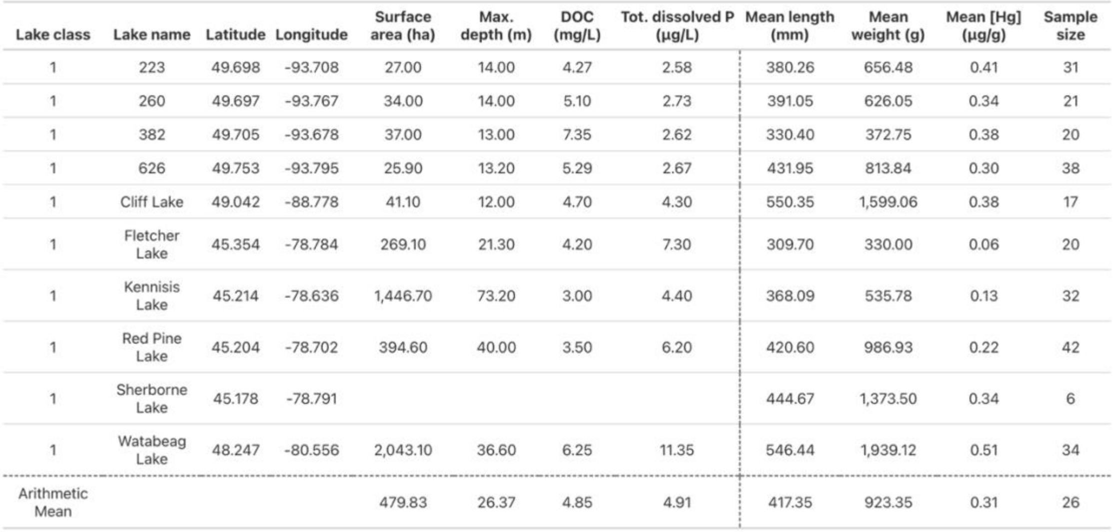
Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
1	Bear	45.333	−78.700	95.0	36.6	402	0.28	22
1	Beaver	47.950	−80.850			109	0.05	49
1	Blue	49.167	−81.250			410	0.18	24
1	Big Porcupine	45.450	−78.617	235.0	31.7	410	0.18	24
1	Blue Chalk	45.200	−78.933	50.0	22.0	1309	0.24	19
1	Bluesucker	47.167	−80.617	144.0	21.4	1275	0.23	18
1	Bonnechere	45.467	−78.583	104.0	22.0	542	0.33	26
1	Camp	45.433	−78.917	189.0	742.7	396	0.15	21
1	Canisbay	45.567	−78.583	152.0	25.9	1440	0.64	11
1	Center	45.017	−78.050	144.0	17.7	1325	0.49	10
1	Eels	44.900	−78.133	945.0	29.9	488	0.09	13
1	Fletcher	45.350	−78.683	212.0	67.1	690	0.32	36
1	Iron	47.067	−79.917	78.0	27.0	426	0.03	44
1	Kimball	45.350	−78.683	212.0	67.1	690	0.32	36
1	Kukagami	46.733	−80.550			779	0.05	24
1	Laundrie	47.117	−80.867	374.0	20.4	324	0.14	109
1	Livingstone	45.367	−78.717	189.0	36.6	1392	0.38	22
1	Louisa	45.467	−78.483	490.0	61.0	540	0.44	30
1	Mccraney	45.567	−78.900	361.0	61.3	505	0.35	16
1	Mcfadden	45.333	−78.850	54.0	30.5	901	0.18	22
1	Mcgarvey	45.433	−78.567	70.0	20.0	2533	0.35	12
1	Miskwabi	45.050	−78.317	264.0	44.2	867	0.13	20
1	Nunikani	45.200	−78.367	596.0		502	0.39	14
1	Pedro	46.917	−80.533	64.0	11.0	782	0.03	58
1	Percy	45.200	−78.367	596.0		502	0.39	14
1	Pilgrim	47.183	−80.683	123.0	25.0	383	0.06	38
1	Red Chalk	45.183	−78.950	58.0	32.0	1195	0.22	20
1	Red Pine	45.200	−78.700	380.0	41.5	805	0.18	18
1	Regan	47.233	−80.833	122.0	38.0	463	0.04	36
1	Round Island	45.733	−78.200	156.0	17.0	973	0.54	15
1	Saymo	46.983	−83.517			833	0.39	13
1	Seagram	47.100	−80.533	102.0	19.0	706	0.15	15
1	Silent	44.917	−78.067	115.0	23.1	1018	0.24	15
1	Slipper	45.283	−78.700		34.0	387	0.15	20
1	St. Peter	45.317	−78.033			858	0.43	17
Arithmetic Mean				230.1	58.1	776	0.25	26



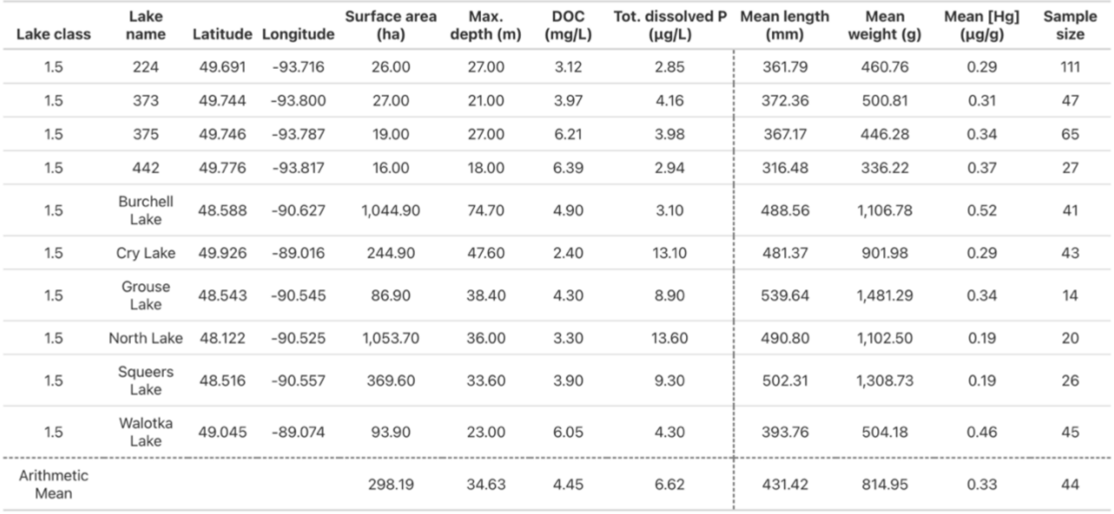
Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
2	Bark	45.450	−77.850	3,792.0	87.5	2,788.0	1.53	30
2	Bella	45.433	−79.033	328.0	40.0	3,532.0	0.55	31
2	Bending	49.317	−92.133	1,137.0	45.8	1,565.0	0.67	20
2	Caribou	45.933	−80.067	529.0	59.5	1,488.0	0.51	17
2	Carson/Stubb	45.500	−77.750			1,636.0	0.57	15
2	Como	47.917	−83.500	1,596.0	26.0	3,797.0	1.29	15
2	Drag	45.067	−78.383	912.0	55.0	367.0	0.14	11
2	Fernow	49.917	−86.083	688.0	38.0	1,364.0	0.39	21
2	Greenwater	48.567	−90.433	3,340.0	54.9	1,216.0	0.34	24
2	Harp	45.383	−79.117	72.0	33.0	621.0	0.88	18
2	Kamaniskeg	45.417	−77.683	2,909.0	40.0	3,613.0	0.96	10
2	Kawagama	45.300	−78.750	2,819.0	73.2	485.0	0.17	29
2	Koshlong	44.967	−78.483	401.0	42.7	1,818.0	0.91	30
2	Lamuir	45.833	−78.583	757.0	39.3	2,028.0	0.50	11
2	Lavieille	45.850	−78.233	2,428.0	48.8	2,273.0	1.04	11
2	Limerick	44.883	−77.617	829.0	30.0	1,922.0	0.63	19
2	Littlehawk	45.150	−78.717	343.0	93.0	931.0	0.33	15
2	Mckay	49.617	−86.417	139.0	48.8	1,234.0	0.41	16
2	Opeongo	45.700	−78.383	5,158.0	49.4	1,107.0	0.50	16
2	Oxtogue	45.367	−78.917	250.0	26.8	2,812.0	1.61	19
2	Papineau	45.350	−77.817	792.0	61.0	583.0	0.51	11
2	Peshu	46.967	−83.133	389.0	50.6	72.0	0.16	13
2	Pedstone	45.183	−78.700	1,194.0	82.4	567.0	0.24	16
2	Round	45.633	−77.500	3,069.0	54.9	2,578.0	1.40	39
2	Shakwa	46.767	−81.983	649.0	27.5	75.0	0.04	41
2	Sherborne	45.183	−78.783	252.0	35.1	5,907.7	0.19	20
2	Smoke	45.517	−78.683	608.0	54.9	1,011.1	0.30	41
2	Treeby	47.867	−84.850	130.0		1,498.7	0.76	10
Arithmetic Mean				1,315.2	49.9	1,746.1	0.63	20

Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
3	Aegean	50.817	−94.800	482.0	59.0	1,913.0	1.32	18
3	Bear	46.200	−81.450	683.0	36.6	2,001.0	0.23	16
3	Bernard	45.750	−79.383	2,058.0	47.9	2,423.0	0.67	32
3	Boshkung	45.067	−78.733	716.0	71.1	1,161.0	0.44	20
3	Charleston	44.533	−76.000	2,519.0	91.5	966.0	0.36	15
3	Delaney	50.083	−94.050	1,282.0	81.4	1,880.0	0.27	31
3	Eden	50.667	−94.983	489.0	24.6	1,343.0	0.33	39
3	Fairy	45.333	−79.183	712.0	69.5	4,163.0	2.68	28
3	Gillies	45.200	−81.350	228.0	34.0	170.0	0.17	16
3	Gooseneck	50.033	−94.800	172.0	29.9	2,126.0	0.73	31
3	Hawley	54.500	−84.650	1,235.0	54.0	1,081.0	0.38	15
3	Joseph	45.167	−79.733	4,268.0	90.0	2,205.0	0.35	25
3	Kioshkokwi	46.083	−78.883	1,127.0	45.8	1,173.0	1.25	10
3	Lake Of Bays	45.250	−79.067	6,105.0	53.0	3,280.0	1.07	58
3	Larder	48.083	−79.633	3,704.0	33.5	1,351.0	0.35	10
3	Loughborough	44.450	−76.417	10,166.0	34.0	2,821.0	0.36	26
3	Mazinaw	44.833	−77.200	1,572.0	135.0	1,591.0	1.22	21
3	Mccarroll	46.433	−83.933	198.0	33.6	1,242.0	0.56	12
3	Miskokway	45.650	−80.233	238.0	41.2	787.0	0.72	28
3	Muskoka	45.000	−79.500	12,215.0	66.5	2,947.0	1.97	83
3	Muskrat	45.667	−76.917	1,202.0	64.0	2,617.0	0.58	19
3	Quetico	48.567	−91.917	42.6	61.0	1,632.0	0.67	17
3	Raven	48.050	−79.550	617.0	46.9	1,381.0	0.62	12
3	Rosseau	45.167	−79.583	6,374.0	90.0	2,027.0	0.86	44
3	Snook	50.200	−94.683	263.0	37.2	1,316.0	0.80	71
3	Sutton	54.250	−84.733	3,764.0	82.0	1,403.0	1.00	15
3	Trout	45.583	−80.167	290.0	37.2	1,349.0	0.36	21
3	Trout	46.300	−79.333	1,675.0	69.2	5,331.0	0.96	22
3	Trout	46.217	−80.583	930.0	36.6	1,932.0	0.55	11
3	Trout	50.233	−94.900	110.0	34.8	2,152.0	0.65	16
3	Twelve Mile	45.017	−78.717	337.0	27.5	740.0	0.36	20
3	Vernon	45.333	−79.283	1,506.0	37.5	3,129.0	3.94	36
3	Wilson	50.500	−95.033	312.0	42.7	912.0	0.90	13
Arithmetic Mean				2,048.2	54.5	1,895.3	0.84	26

Appendix 3.B - Table B. 2. Geographic and physicochemical characteristics from contemporary study lakes across four distinct Lake Classes. Only zooplankton are available as pelagic prey in Class 1 lakes, *Mysis* are present in Class 1.5, pelagic prey fishes (i.e. coregonids) are present in Class 2 lakes and both *Mysis* and pelagic prey fishes are present in Class 3 lakes. Arithmetic mean Lake Trout length, weight, and Hg concentrations are provided for each lake and Lake Class, along with the number of Hg samples that were analyzed (sample size).



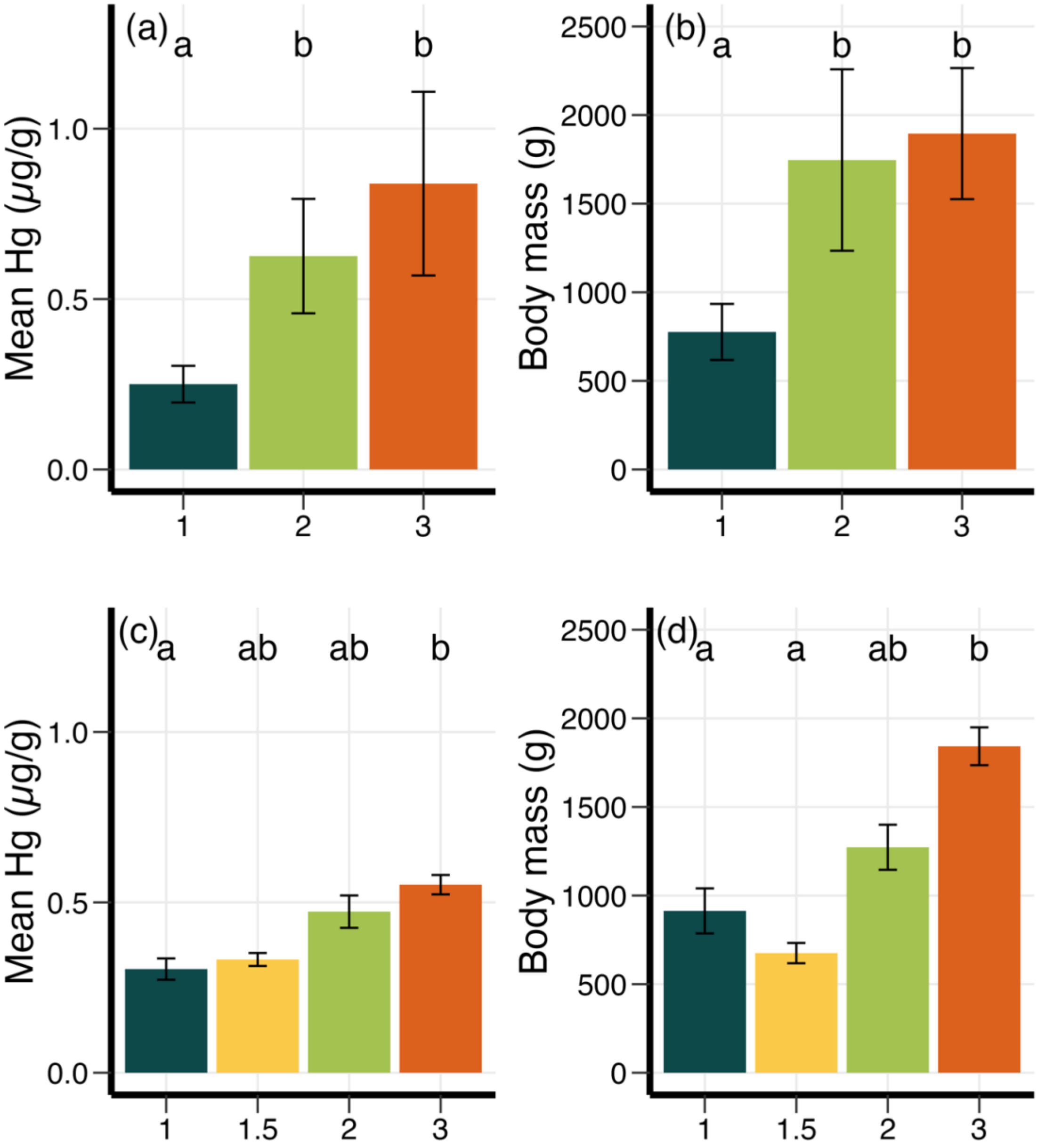
Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	DOC (mg/L)	Tot. dissolved P (µg/L)	Mean length (mm)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
1	223	49.698	-93.708	27.00	14.00	4.27	2.58	380.26	656.48	0.41	31
1	260	49.697	-93.767	34.00	14.00	5.10	2.73	391.05	626.05	0.34	21
1	382	49.705	-93.678	37.00	13.00	7.35	2.62	330.40	372.75	0.38	20
1	626	49.753	-93.795	25.90	13.20	5.29	2.67	431.95	813.84	0.30	38
1	Cliff Lake	49.042	-88.778	41.10	12.00	4.70	4.30	550.35	1,599.06	0.38	17
1	Fletcher Lake	45.354	-78.784	269.10	21.30	4.20	7.30	309.70	330.00	0.06	20
1	Kennisis Lake	45.214	-78.636	1,446.70	73.20	3.00	4.40	368.09	535.78	0.13	32
1	Red Pine Lake	45.204	-78.702	394.60	40.00	3.50	6.20	420.60	986.93	0.22	42
1	Sherborne Lake	45.178	-78.791					444.67	1,373.50	0.34	6
1	Watabeag Lake	48.247	-80.556	2,043.10	36.60	6.25	11.35	546.44	1,939.12	0.51	34
Arithmetic Mean				479.83	26.37	4.85	4.91	417.35	923.35	0.31	26



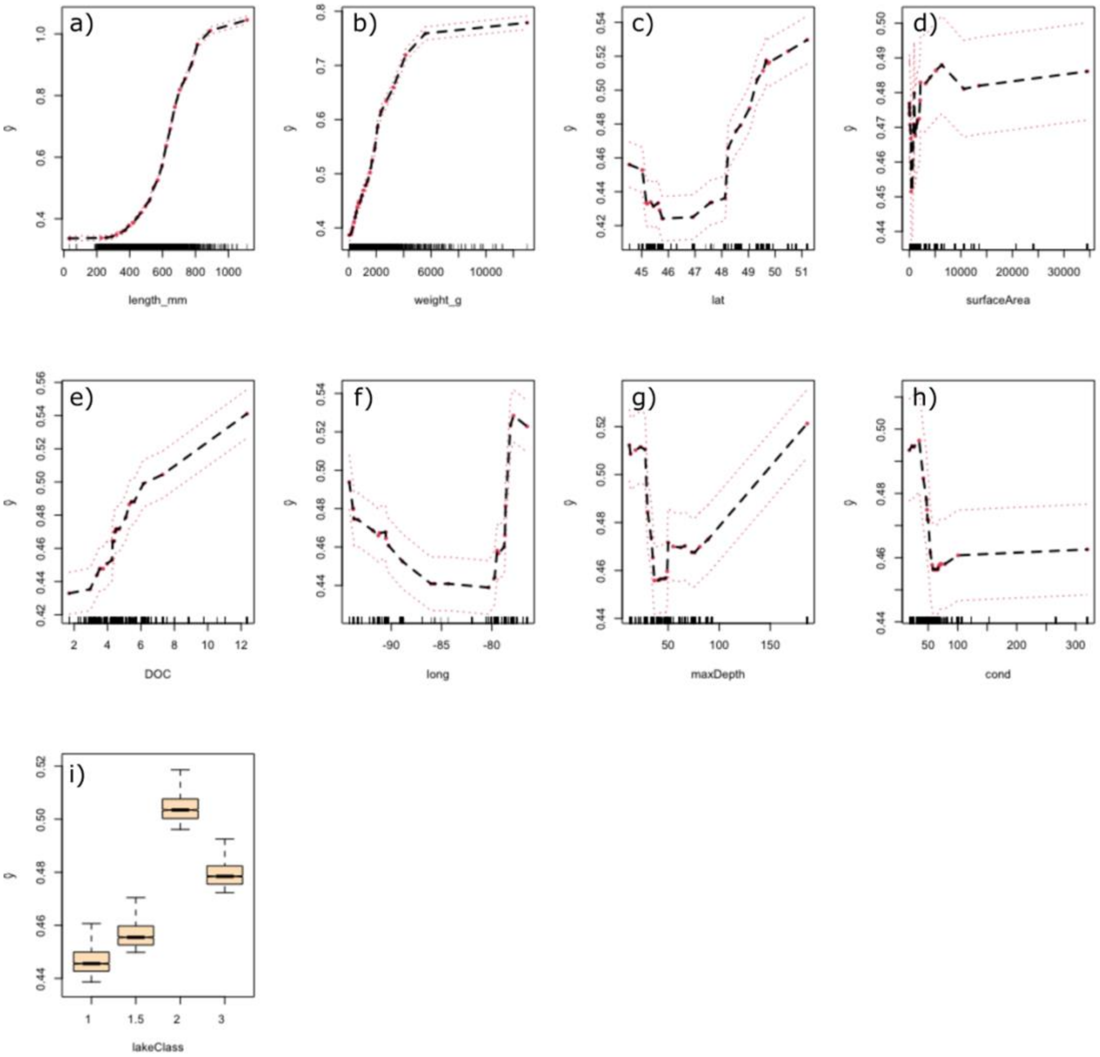
Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	DOC (mg/L)	Tot. dissolved P (µg/L)	Mean length (mm)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
1.5	224	49.691	-93.716	26.00	27.00	3.12	2.85	361.79	460.76	0.29	111
1.5	373	49.744	-93.800	27.00	21.00	3.97	4.16	372.36	500.81	0.31	47
1.5	375	49.746	-93.787	19.00	27.00	6.21	3.98	367.17	446.28	0.34	65
1.5	442	49.776	-93.817	16.00	18.00	6.39	2.94	316.48	336.22	0.37	27
1.5	Burchell Lake	48.588	-90.627	1,044.90	74.70	4.90	3.10	488.56	1,106.78	0.52	41
1.5	Cry Lake	49.926	-89.016	244.90	47.60	2.40	13.10	481.37	901.98	0.29	43
1.5	Grouse Lake	48.543	-90.545	86.90	38.40	4.30	8.90	539.64	1,481.29	0.34	14
1.5	North Lake	48.122	-90.525	1,053.70	36.00	3.30	13.60	490.80	1,102.50	0.19	20
1.5	Squeers Lake	48.516	-90.557	369.60	33.60	3.90	9.30	502.31	1,308.73	0.19	26
1.5	Walotka Lake	49.045	-89.074	93.90	23.00	6.05	4.30	393.76	504.18	0.46	45
Arithmetic Mean				298.19	34.63	4.45	6.62	431.42	814.95	0.33	44

Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	DOC (mg/L)	Tot. dissolved P (µg/L)	Mean length (mm)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
2	Aylen Lake	45.618	-77.856	2,104.60	67.10	3.45	3.85	560.58	2,110.77	0.82	48
2	Bark Lake	45.455	-77.849	4,024.40	87.50	4.80	7.05	467.13	1,138.04	0.51	23
2	Bella Lake	45.444	-79.031	356.90	36.60	2.70	7.20	498.55	1,136.68	0.23	31
2	Bending Lake	49.326	-92.153	1,147.10	45.80	8.00	5.90	615.80	1,973.00	0.80	10
2	Eels Lake	44.895	-78.140	942.00	29.90	4.80	7.30	574.55	2,480.91	1.02	11
2	Emerald Lake	46.916	-80.323	581.00	48.80	2.25	3.40	451.56	936.52	0.18	50
2	Kawagama Lake	45.299	-78.753	3,149.90	77.00	3.20	3.60	467.35	937.30	0.38	37
2	Kimball Lake	45.342	-78.676	216.50	67.10	3.30	5.50	340.67	347.48	0.26	21
2	McKenzie Lake	45.365	-78.020	313.50	27.40	5.75	6.25	622.78	2,565.33	1.66	9
2	Opeongo Lake	45.756	-78.353	5,154.20	49.40			516.39	1,376.86	0.57	51
2	Redstone Lake	45.184	-78.536	1,178.20	80.50	3.80	4.60	409.62	949.90	0.29	40
2	Smoke Lake	45.510	-78.681	663.10	43.30			444.92	940.19	0.28	26
Arithmetic Mean				1,652.62	55.03	4.20	5.46	497.49	1,407.75	0.58	30

Lake class	Lake name	Latitude	Longitude	Surface area (ha)	Max. depth (m)	DOC (mg/L)	Tot. dissolved P (µg/L)	Mean length (mm)	Mean weight (g)	Mean [Hg] (µg/g)	Sample size
3	239	49.663	-93.723	54.00	30.00	6.48	3.10	559.60	1,675.70	0.71	20
3	468	49.679	-93.736	301.00	29.00			404.57	756.83	0.43	28
3	Arrow Lake	48.159	-90.265	3,234.40	54.90	2.95	5.05	553.78	1,624.02	0.39	45
3	Big Salmon Lake	44.538	-76.500	148.20	42.40			463.79	980.00	0.28	14
3	Black Sturgeon Lake	49.358	-88.872	4,874.40	52.40	11.05	6.35	730.21	3,713.96	1.42	28
3	Carling Lake	50.622	-91.280	1,555.60	40.90	12.35	11.60	600.06	1,902.67	0.58	18
3	Clear (Watt) Lake	46.098	-79.781	264.70	40.00	4.40	7.00	361.06	470.72	0.25	36
3	Crystal Lake	48.708	-91.278	623.90	47.00	2.60	4.90	504.00	1,212.10	0.28	30
3	Eva Lake	48.717	-91.160	1,726.20	54.90	7.30	12.65	600.64	2,247.40	0.50	25
3	Indian Lake	49.548	-91.666	4,000.10	36.00	5.30	8.95	792.80	5,828.00	0.78	5
3	Kashabowie Lake	48.719	-90.394	2,163.30	35.00	10.55	8.65	554.00	1,597.00	0.71	2
3	Lake Bernard	45.739	-79.385	2,088.70	47.90	3.37	10.87	587.86	2,423.43	0.37	7
3	Lake Joseph	45.174	-79.724	5,167.10	92.00	2.96	5.65	510.23	1,478.81	0.32	69
3	Lake Manitou	45.778	-81.983	10,588.40	49.10	4.30	5.20	602.91	2,130.16	0.18	32
3	Lake Muskoka	45.024	-79.477	12,036.00	66.50	4.30	7.50	527.48	1,625.04	0.60	25
3	Lake Rosseau	45.174	-79.598	6,297.40	89.00	3.80	5.52	493.22	1,415.69	0.57	58
3	Lake Temagami	46.989	-80.070	20,714.10	75.90	2.95	4.80	574.41	2,343.40	0.33	68
3	Larder Lake	48.085	-79.642	3,711.10	33.50	5.70	8.30	419.52	643.87	0.34	67
3	Long Lake	49.475	-86.891	13,498.60	186.10	9.75	10.65	762.24	4,577.49	1.40	37
3	Longlegged Lake	50.784	-94.175	6,760.30	35.40	8.85	19.60	596.27	1,997.41	1.04	22
3	Lower Manitou Lake	49.278	-92.948	8,871.70	81.00	5.30	5.95	568.40	1,739.32	0.44	25
3	Mameigwess Lake	49.551	-91.825	5,242.00	50.00	2.90	5.25	563.65	2,032.40	0.53	65
3	Muskrat Lake	45.675	-76.908	1,215.40	64.00	6.90	39.60	501.71	1,684.90	0.43	21
3	Pickerel Lake	48.634	-91.372	5,355.70	74.70	6.60	6.75	578.00	1,768.12	0.65	25
3	Round Lake	45.641	-77.529	2,969.70	54.90	5.75	7.65	663.74	3,639.31	0.76	35
3	Savant Lake	50.482	-90.427	12,524.00	53.00	7.55	6.00	599.60	2,058.40	0.81	10
3	Skeleton Lake	45.251	-79.453	2,115.00	61.00	1.70	2.70	504.42	1,166.58	0.37	38
3	Sturgeon Lake	49.927	-90.897	24,047.80	93.00	6.05	6.50	599.13	1,898.73	0.82	15
3	Titmarsh Lake	48.355	-90.530	968.30	49.40	6.15	5.70	544.68	1,616.04	0.79	76
3	Trout Lake	51.199	-93.309	34,518.20	47.30	4.50	5.50	677.64	2,918.21	0.92	39
3	Trout Lake	46.319	-79.337	1,884.70	69.20	3.10	5.10	519.51	1,420.84	0.35	43
3	Twelve Mile Lake	45.025	-78.705	355.20	27.50	3.30	5.35	455.69	999.31	0.31	32
Arithmetic Mean				6,246.10	58.22	5.63	8.28	561.71	1,987.06	0.58	33



Appendix 3.B - Figure B. 1. Comparison between arithmetic mean Hg concentrations and mean body mass across Lake Classes for historic Cabana et al. (1994) data (panels a, b) and contemporary data (c,d). Letters above bars represent Tukey HSD pairwise differences from one-way ANOVA, and error bars represent 95% confidence intervals of the mean.



Appendix 3.B - Figure B. 2. Random Forest partial dependence plots outlining independent estimates of predictor variables (x-axis) on mean Lake Trout Hg concentrations (y-axis).

Chapter 4

Prey structure and environmental characteristics jointly describe Lake Trout (*Salvelinus namaycush*) life history traits

Abstract

Lake trout, a widely distributed pelagic predator, show diverse life histories across their native range. While environmental factors, like lake size and productivity, are known to influence these traits, the role of prey availability as a driver of life histories is less well understood, and its combined impact with environmental factors remains uncertain. To address this knowledge gap, Lake Trout life history traits were examined across 49 lakes from four categorical Lake Classes, differentiated by the presence or absence of *Mysis diluviana* and pelagic prey fishes. Prey structure, measured by Lake Class, explained more model variance in life history traits compared to environmental factors alone (15.4% vs. 12.3% variance explained). However, combining Lake Class with lake-specific environmental factors collectively explained 35.4% of variation in life history traits, highlighting the value of considering the influence of both factors together. In general, piscivorous Lake Trout (Class 2 and 3) mature later and are larger in size than planktivorous Lake Trout (Class 1 and 1.5), though lake size and total phosphorus concentrations were important predictors of life history within Lake Classes. This was particularly the case when lakes fell at the extreme ends of environmental distributions, such as the smallest or largest lakes within a Lake Class. This study presents a framework for understanding Lake Trout life history in relation to two key pelagic prey items, *Mysis* and Coregonids, along with easily accessed lake-specific environmental variables to help

better evaluate potential changes of sensitive Lake Trout populations in the face of environmental change.

Introduction

Variation in fish life history traits stems from individuals attempting to optimize fitness within a suite of local constraints (Charnov 1993). Within a given species, population size- and age-structure, growth rates, maturation schedules, and recruitment can vary dramatically (Blanck and Lamouroux 2007, Thorson et al. 2017). Understanding the conditions that control the extent of this variation is necessary for understanding population vital rates, predicting resiliency to changing environmental conditions, and for ensuring the sustainability of taxa facing anthropogenic activities (e.g., harvest, development, climate change). This is increasingly important for freshwater fishes, which are important culturally and economically, vital for local food security and sovereignty, and identified as the second most threatened group of vertebrates globally after amphibians (Darwall and Freyhof 2016).

Environmental factors are well known determinants of freshwater fish life history traits. Across isolated populations, seasonal temperatures and lengths, ecosystem productivity, and human disturbance are among several factors known to modify life histories. For example, life history traits across North America and Europe follow latitudinal clines, with fish at northern range edges typically growing more slowly prior to maturation, experiencing later maturity, longer lives, larger sizes, lower annual mortality rates and higher overall fecundity than fish at Southern range edges (Heibo et al. 2005, McDermid et al. 2010, Venturelli et al. 2010, McMeans et al. 2016). In more productive environments, fish often exhibit life history strategies that favour delayed maturity, increased somatic growth, lower mortality and higher fecundity (Winemiller and Rose 1992, Evans et al. 1996). Also, growth rates, maximum size, and fecundity are typically lower in darker lakes (or where dissolved organic carbon (DOC) concentrations are high; Benoît et al. 2016; Craig et al. 2017).

Prey community assemblages can also modify predator life history traits and strategies of freshwater fishes. Predator growth and maturation traits are influenced by factors such as prey availability, predator-prey mass ratios, and prey quality (Boisclair and Leggett 1989b, 1989c, Shuter et al. 2016). Prey handling time (pursuing, subduing, ingesting, and digesting prey) and attack rates (reactive distances, predator and prey speeds, capture success) vary with prey availability and composition (Brose 2010). When larger prey are available, activity levels are often reduced (Pazzia et al. 2002; Sherwood et al. 2002b; Rennie et al. 2005; Kaufman et al. 2006, Ross et al. *Chapter 2*), and maturity is delayed, typically resulting in larger adult body sizes (Dunlop et al. 2005, Kaufman et al. 2009, Shuter et al. 2016, Kennedy et al. 2018). Further, predator-prey interactions shift seasonally and ontogenetically. As ectotherms, fish rely on suitable thermal conditions, often making optimal prey seasonally unavailable due to differential thermal preferences between predator and prey (Durant et al. 2007, Guzzo et al. 2017). Ontogenetic bottlenecks can also result from limits the availability of prey of the size required to allow for further growth (Pazzia et al. 2002, Sherwood et al. 2002a).

Lake Trout *Salvelinus namaycush* are a model species known to respond to variation in both the environment as well as prey community structure. As with other freshwater species, larger lake surface area, higher total dissolved solids (a proxy for total phosphorus and primary productivity) and individuals inhabiting cooler climates and water temperatures typically mature at larger sizes and later in life (Shuter et al. 1998, McDermid et al. 2010, Wilson et al. 2019), and early growth rates can be lower in lakes with high DOC (Benoît et al. 2016). Other work has shown that smaller predator-prey mass ratios in Lake Trout lead to lower activity costs, reduced foraging rates and reductions in the amount of time spent in inhospitable oxythermal environments, all resulting in larger growth potential (i.e., larger maximum sizes and size-at-maturity), higher overall fecundity, and reduced metabolic costs (Pazzia et al. 2002; Giacomini et al. 2013; Shuter et al. 2016; Cruz-Font et al. 2019, Ross *Chapter 2*). Despite this body of knowledge, the way in which these two factors—environmental drivers and prey community assemblages—interact when considering life history outcomes of consumer species (including Lake Trout) remains unknown.

In this study, I test the relative importance of environmental factors and prey community structure, both independently and in combination, in shaping the life history traits of Lake Trout, a glacial relict species distributed widely through Canada and the northern United States. Lake Trout show considerable intraspecific life history variation (Hansen et al. 2021) and span wide geographic and environmental gradients (McDermid et al. 2010). Across their entire post-glacial range, they typically co-occur within a predictable community of pelagic prey (i.e., with or without other glacial relict species such as *Mysis diluviana* and Coregonids). As coldwater stenotherms, Lake Trout are mainly restricted to a habitat envelope defined by hypolimnetic dissolved oxygen concentrations greater than 4—6 mg/L and epilimnetic waters cooler than ~15ºC (Plumb and Blanchfield 2009). Thus, during summer thermal stratification when Lake Trout are focused on maximizing both somatic and reproductive growth (Morbey et al. 2010, Wilkins and Marsden 2021), they often experience truncated food chain lengths (Shipley et al. 2023) associated with oxy-thermal habitat constraints (Guzzo et al. 2017). The magnitude of these constraints likely varies in response to both the environmental conditions and pelagic prey communities present across different lakes (McDermid et al. 2010, Hansen et al. 2021). To understand how this between-lake variation in both environment and prey availability affects consumer life history traits, I categorized Lake Trout food webs using a modified version of a conceptual Lake Class model originally proposed by Rasmussen et al. (1990).

To determine the influence of both Lake Classes (i.e., categorical food web classifications, see methods) and environmental factors on Lake Trout life history traits, I first investigated these relationships separately. Results of environmental drivers of Lake Trout life history were considered separate from Lake Class to compare to previously reported findings that considered environmental drivers only (e.g., Shuter et al. 1998; Mcdermid et al. 2010; Hansen et al. 2021). Next, life history traits were compared across distinct Lake Classes on the same dataset (not considering environmental drivers). In the absence of any previous analysis using this approach, and given that successive Lake Classes are categorized by discrete increases in prey size-structure and food chain length, I hypothesized sequential step-wise differences in life history traits from one Lake Class to the next. Specifically, I expected individuals from simple food webs to exhibit faster pre-maturation traits (e.g., early growth rates and standardized juvenile lengths), leading to smaller maximum sizes and early maturation, whereas individuals from more complex food webs were predicted to show higher post-maturation growth (e.g., larger asymptotic and maximum sizes and delayed maturation) relative to individuals from simple food webs. Finally, using this same dataset, I investigated whether combining both environmental variables and food web structure (i.e., Lake Class) enhanced the variation in observed Lake Trout life histories compared to either suite of variables alone.

Methods

Lake Selection and Sampling

Lake Trout and environmental data were summarized from five different databases across 49 lakes in Ontario, Canada (Appendix 4.A - Table A. *1*). Data were sourced from the Ontario Ministry of Natural Resources (including populations from the Broadscale Monitoring Program, Harkness Laboratory for Fisheries Research, the Coldwater Lakes Experimental Watershed, and a National Lake Trout database) as well as the IISD Experimental Lakes Area (ELA; sampling methodology for all programs described below). Lakes were categorically assigned to food web classes using a system modified from one originally proposed by Rasmussen et al. (1990). The original Lake Class system was designed to describe differences in bioaccumulation and biomagnification of contaminants with increasing pelagic prey availability. In Class 1 lakes, only pelagic zooplankton were available to Lake Trout; Class 2 lakes had offshore forage fish (Coregonids and Rainbow Smelt, *Osmerus mordax*); and Class 3 lakes were categorized when both pelagic prey fishes and *Mysis diluviana* (hereafter *Mysis*) were present. For this study, I used the same three categories but introduced an intermediate Lake Class—Class 1.5—where *Mysis* were present but pelagic prey fishes were absent. The original Lake Class system was useful for describing differences in Lake Trout PCB (Rasmussen et al. 1990a) and Hg concentrations (Cabana et al. 1994). Despite being based on predictable differences in prey size structure, and work following this demonstrating the role of prey size structure on consumer life history traits (Pazzia et al. 2002; Giacomini et al. 2013; Shuter et al. 2016; Cruz-Font et al. 2019), the Lake Class model has yet to be explicitly tested for its ability to explain variation in Lake Trout life history traits.

Prey assemblages were classified to Lake Classes using only true, verified presences of *Mysis* and pelagic prey fishes. Data sources categorizing confirmed prey species presence included: IISD-ELA long-term database records; a monograph on post-glacial fish and invertebrate distributions in Canada (Dadswell 1974); Ontario Broadscale Monitoring Program (BsM) data, including Pelagic prey fish catch records (i.e, Cisco, Whitefish, Rainbow Smelt) and Lake Trout stomach examinations that contained *Mysis* or pelagic prey fishes; targeted night-time *Mysis* sampling by the author during summer and fall 2020; technical reports from the Coldwater Lakes Experimental fishery and Algonquin Provincial Park describing *Mysis* presence (France and Steedman 1996, Ridgway et al. 2017); and observations from Rasmussen et al. (1990) where prey communities were assessed by observation, rather than assumed based on other data (e.g. projected extents of glacial lake inundation).

Fish Sampling and Environmental Data Compilation

Among all sampling programs, Lake Trout fork length, weight and age were used to calculate life history traits. Sex was not considered in analyses as Lake Trout are not morphometrically dimorphic (McDermid et al. 2010). Age was primarily estimated using otoliths, though fin rays (particularly for ELA samples) were also used. Scale ages were only used for fish less than eight years of estimated age. Fin rays and otolith ages are not biased for slow-growing stenothermic fishes (Muir et al. 2008) and scale-ages in Lake Trout are generally biased only at ages greater than eight (Dubois and Lagueux 1968, Casselman 1983). In any lake where scale ages were used, alternative ageing structures (either fin rays or otoliths for 8+ fish) were also used (Appendix 4.A - Table A. *1*), ensuring my ability to characterize size-at-age for older/larger fish. All fish sampling programs were compliant with animal care and scientific collection permits at the time of collection, where required.

Broadscale Monitoring Program (BsM)

The Broadscale Monitoring Program is administered by the Ontario Ministry of Natural Resources (MNR) and has collected extensive data on fish populations across Ontario, Canada lakes since 2008. Data from 28 BsM lakes were used (Appendix 4.A - Table A. *1*), where samples were collected with experimental gillnets consisting of eight randomly stitched panels of 38, 51, 64, 76, 89, 102, 114, and 127 mm stretched mesh. Gillnets were systematically oriented at randomly selected locations across pre-determined depth-strata and left to soak overnight, whereby the effort (number of nets) was dictated by the area represented by each depth strata in the lake. All fish species captured were identified and measured for length and weight. Lake Trout otoliths and stomachs were removed for age analysis and prey diet information, respectively. Ages were interpreted by a consistent group of trained MNR staff at the provincial fish aging laboratory. Full details of BsM sampling and aging procedures are available in the program manual (Sandstorm et al. 2013).

IISD Experimental Lakes Area (ELA)

Long-term Lake Trout data were compiled from 11 ELA lakes (Appendix 4.A - Table A. *1*). Fish were primarily captured using trap nets during spring and fall to characterize the broader fish community. Fall surveys were augmented with short-set (i.e. non-lethal) gillnetting to specifically target Lake Trout. During spring and fall surveys, two to four trap nets were deployed for four to six weeks. Two styles of trap net were used, one with a center lead positioned perpendicular to shore and the other without a central lead where one trap net wing was tied roughly parallel to shore to capture fish travelling in a specific direction (Rennie et al. 2019). Catch was assessed multiple times each week by emptying traps before redeployment; catch was placed and held in bins filled with fresh lake water, and was enumerated and measured. Fall gillnet surveys were conducted at night with 38 mm gill nets and targeted Lake Trout spawning shoals with short-set (~20 min) sampling. As with trap net catches, fish captured in gill nets were placed into bins of fresh lake water; after nets were re-set, fish were transported to holding pens where they remained overnight until they could be processed the next morning. Angling during fall was also used in very rare cases as a supplementary capture method. After capture, Lake Trout were measured for length and weight. Over all capture methods, the leading 2-3 pectoral fin rays were cut as close to the insertion of the body as possible and taken for age analysis. Fin ray sections were dried, epoxied, cross-sectioned and finally mounted on microscope slides for age interpretation (Mills and Chalanchuk 2004). Fin rays were the primary Lake Trout aging structure from ELA lakes due to the necessity of non-lethal sampling to facilitate ongoing population estimates not influenced by capture mortality. Lake Trout were live-released following sampling for all ELA lakes included in this study.

Coldwater Lakes Experimental Watershed

Between 1991 and 1998, Lake Trout were collected from four lakes at the Coldwater Lakes Experimental Watershed (Appendix 4.A - Table A. *1*). Fish were captured in September and October using a combination of gill netting, trap netting and angling. Short set gill nets (~20 mins) with 38 mm mesh and 100 m long gangs were used to capture Lake Trout near spawning shoals. Trap nets with 64mm mesh and 26 m leads were set perpendicular to shore and checked daily for catch throughout the fall season (i.e, early September to late October). Pelvic and pectoral fin clips as well as otoliths were used for aging analysis; no details were available regarding aging structure preparation and interpretation, though it was assumed that standard Ontario MNR methods were used, which would prioritize otoliths as the primary ageing structure over fin rays on fish captured lethally, but fin rays on fish that were subsequently released back into the lake (see Mann 2004).

Algonquin Provincial Park Lakes/Harkness Laboratory for Fisheries Research

Only two lakes from Algonquin Provincial Park were used in this analysis, and their collection methods differed (Appendix 4.A - Table A. *1*). For Smoke Lake, 17 lake-years of data were collected between 1978 and 2003 using a combination of Spring Littoral Index Netting (SLIN) and Summer Profundal Index Netting (SPIN), both standardized sampling methods used by the Ontario MNR. Briefly, SLIN sampling used short-set gill nets (~90 mins) within littoral areas of lakes after ice-out and prior to water temperatures eclipsing 13°C. Three gangs of 91.4 m gill nets with varying sized mesh were used (38, 54, and 61 mm). Gill nets were oriented perpendicular to shore and set between 2.5 m to 60 m in depth depending on overall lake depth (Hicks 1999). SPIN was used to assess Lake Trout > 300 mm during summer months when surface waters were greater than 18°C. One SPIN gill net gang was 64 m long by 1.8 m high, with eight 8.0 m long panels of 57, 64, 70, 76, 89, 102, 114, and 127 mm stretch grill nets. In Smoke Lake, SPIN nets were set for two hours across seven depth strata (2—10 m, 10—20 m, 20—30 m, 30—40 m, 40—60 m) and nets were randomly oriented within each stratum (Sandstrom and Lester 2009). A combination of scales (only ages < 8) and otoliths were used to estimate Smoke Lake age structure. Lake Trout from Lake Opeongo were exclusively captured by angling during the open-water season from the long running Lake Opeongo Creel Survey (see Shuter et al. 1987 for survey methods and motivations). Creel samples were limited to between 1990 and 2016 as these were the data made available, and ages were interpreted using only otoliths. Age interpretation from all Algonquin Park lakes followed MNR standard methods (Mann 2004).

National Lake Trout Database

Five additional lakes from the Ontario portion of the National Lake Trout Database were included, based on data in recent Lake Charr book chapter (Lester et al. 2021). Capture details for these data were not described, noting only that they were acquired from a long-term harvest monitoring program (Marshall 1996), and an earlier Ontario monitoring program predating the current BsM program. These historical monitoring data were likely captured using SLIN and SPIN protocols, as described above.

Environmental Predictors

I summarized water chemistry (TDP and DOC) and lake surface area from records associated with each respective fish sampling program (Appendix 4.A - Table A. *1*). For lakes with multiple years of water chemistry data, I averaged values across the years when fish data were collected. A 30-year Cumulative Growing Degree Days above 5°C (cGDD5) norm was calculated for each lake by acquiring daily air temperature between 1991 to 2021 from the nearest Environment and Climate Change Canada weather station using the R package *weathercan* (Lazerte and Albers 2018). Daily growing degree days were then calculated by:

$$(Eq. 1) \qquad DD = \left(\frac{T_{Max} + T_{Min}}{2}\right) - 5$$

where T_{Max} and T_{Min} were daily maximum and minimum air temperatures, respectively, with a base threshold of 5°C. Base 5 was chosen as this value has been a recommended value for studies of fish growth from temperate to arctic lakes (Chezik et al. 2014). In cases where daily mean temperature was less than or equal to 5, daily DD value was set to zero. Daily growing degree days were then summed within the calendar year to estimate an annual cumulative growing degree day, which was then averaged across the 30-year period of 1991 to 2021 to obtain a single value for each lake.

Lake Trout Life History Traits

I used the Galluci-Quinn parameterization of the von Bertalanffy (VB) growth model to estimate asymptotic fork length (L_∞), the Brody growth coefficient (K), and early growth rate (Omega, ω) for each study population (Gallucci and Quinn 1979). The Galluci-Quinn parameterization of this model allows for cross-lake comparisons of pre-maturation growth rates, predicted by ω, and post-maturation energy allocation through adult body size predictions (i.e., L_∞ or asymptotic length). The VB parameter t_0, which describes the theoretical age at which a fish has a length of zero, was fixed at zero for all lakes. Using a fixed intercept reduces bias in fish captured across multiple months within a given year and using various fish-capture techniques. Setting t_0 to zero for Lake Trout and other coldwater stenotherms has been shown to improve model fit, particularly when pre-maturity data are limited (Shuter et al. 1998, Beauchamp et al. 2004). Although biphasic growth models provide a better representation of lifetime growth by separating pre- and post-maturation growth rates and energy allocations (Lester et al. 2004), they require a substantial amount of data to parameterize both growth phases. By using VB growth models, I was able to include 12 additional lake populations across the four Lake Classes in the final analyses than had I used biphasic models. Furthermore, when data quantity was sufficient, life history parameters estimated from VB and biphasic models were significantly correlated (Appendix 4.B - Figure B. *1*), which suggests that data produced from either growth models should exhibit similar patterns in relation to predictor variables (e.g., Lake Classes, environmental variables), comparing across equivalent parameters from each model formulation.

Using the VB parameters ω and L_∞, I calculated length at 50% maturity with an equation derived for Lake Trout across the same study region (Shuter et al. 1998):

(*Eq. 2*) $L_{m50} = 1.56 * \ \omega^{0.257} * \ \ L_\infty^{0.665}$

To provide an independent estimate of pre- and post-maturation growth phases apart from VB model estimates (in an attempt to validate modelled values using empirical data), I compared juvenile and adult fork lengths in a standard fashion between Lake Classes. Based on length-at-maturity estimates (Eq. 2), length-at-age-three fish across all lakes were assumed to represent a juvenile life stage, allocating all surplus energy towards somatic growth. Thus, I selected observed mean length-at-age-three was used as an independent index of immature growth across all populations. Post-maturation growth was assessed as maximum length, which was defined as the 95th quartile fork length from a given population.

Finally, I estimated the instantaneous mortality rate (*Z*) for each lake. Chapman-Robson catch-curves, where annual survival (*S*) assessed from the descending limb of a catch curve, was applied to catch-at-age data to estimate *Z*. Following advice from Smith et al. (2012), a Hoenig correction was applied to reduce bias and overdispersion. Catch-curves were analyzed using the *chapmanRobson* function from the *FSA* package in R (Ogle et al. 2023), which follows equation 2 in (Smith et al. 2012).

Statistical Analyses

A multiple linear regression approach was used to assess the response of Lake Trout life history traits to lake-specific environmental variables (lake surface area, mean total dissolved phosphorus, mean DOC, cGDD5 30-year norm). Given the additive nature of environmental variables on Lake Trout life history traits previously described in the literature (Shuter et al. 1998, McDermid et al. 2010) and relatively limited sample size for the current study (n = 49 lakes) relative to my number of predictors (n = 4), each model considered only additive terms for each environmental variable (i.e., no interaction terms included). All assumptions for linear models were confirmed using diagnostic plots of model residuals vs. fitted values, residual quantile-quantile plots and Cook's distances to check for outliers. To improve model fit, all predictor variables were

$\log_{10}$ transformed to reduce predictor gradient lengths and improve model residuals. Response variables (i.e., each life history trait) were kept as untransformed, raw values.

One-way Analyses of Variance (ANOVA) were used to 1) investigate potential differences in environmental variables between Lake Classes, and 2) assess the degree to which Lake Trout life history traits varied among Lake Classes (i.e., prey availability). Assumptions of linear models were confirmed for each response variable using Anderson-Darling normality tests and Levene's tests for homogeneity of variance and by observing diagnostic plots of model residuals. Models assessing the effect of Lake Class on lake-specific environmental factors (i.e., lake size, TDP, DOC, cGDD5) were $\log_{10}$ transformed to conform to model assumptions, whereas models assessing life history traits were conducted on raw, untransformed data. In cases where ANOVA was determined to be significant (at an alpha of $p < 0.05$), Tukey's HSD tests were conducted to test for significant pairwise differences between Lake Classes.

I used a multivariate Redundancy Analysis (RDA) to evaluate the independent and combined effects of both lake-level environmental predictors (i.e., lake surface area, mean total dissolved phosphorus, mean DOC, cGDD5 30-year norm) and prey availability (i.e., Lake Classes) on Lake Trout life history traits. RDA is well-suited for assessing potential shifts in collective life histories as it first models the proportion of total variance explained by all response variables and then relates this to the proportion explained by linear combinations of predictor variables. Input data for RDA need to be complete, though there were certain instances of lakes having one or more missing values for environmental predictor variables (see NA's in Appendix 4.A - Table A. *1*). For missing data, I imputed the dataset mean for each variable as needed. The proportion of lakes requiring imputed values never exceeded a quarter of the total sample size within any Lake Class (Class 1: 2/9, Class 1.5: 1/13, Class 2: 1/5, Class 3: 3/19), and with the exception of one missing lake surface area value, all missing values were for DOC or TDP concentrations. All variables were Z-score standardized, and RDA was performed using the *vegan* packing in R (Oksanen et al. 2022). RDA scores were evaluated with Scaling == 2 to assess differences in life history traits rather than the environmental predictors. Follow-up variance partitioning allowed for a direct comparison of the adjusted R^2 values for environmental predictors (TDP, DOC, Lake Area, CGDD5), Lake Classes (Class 1 → Class 3), and their interactive effects. Model, axis, and variable significance were tested using ANOVA-like permutation tests, with an alpha set to 0.05. Triplots were used to visually describe relationships between Lake Classes, environmental predictors, and life history traits.

All statistical analyses were conducted using functions in *Base-R* (R Core Team 2023, version 4.4). Data curation and visualizations were prepared using *dplyr and ggplot2* from the *tidyverse* (Wickham et al. 2019).

Results

Environmental variables modified Lake Trout life history traits as expected based on existing literature. Multiple regression models for all life history variables examined, except those for length-at-age-three and instantaneous mortality (*Z*) were significant, with environmental traits explaining between 38% and 73% of the observed variation in life history traits (Appendix 4.A - Table A. 2). Among the environmental variables tested, $\log_{10}$-transformed lake surface area was the strongest predictor of Lake Trout life history traits (Table 4 - 1). Pre-maturation growth (ω) was higher in smaller lakes, and post-maturation growth traits (length-at-maturity, asymptotic length, and maximum length) all increased with increasing lake surface areas (Table 4 - 1). While the full model for length-at-age-three was not significant (Appendix 4.A - Table A. 2), beta coefficients indicated significant decreases in the size of three year old fish with increasing lake size (similar to patterns observed for ω), while age three fish length also appeared to increase with increasing lake DOC (Table 4 - 1). Neither cumulative growing degree days nor total dissolved phosphorus concentrations affected Lake Trout life history traits in the lakes I assessed using multiple regression.

Lake Class alone also explained certain Lake Trout life history traits, though variability across all response variables was high (Table 4 - 2, Figure 4 - 1). Lake Trout matured at larger lengths in lakes with pelagic prey fish present (i.e., Class 2 and 3) but significant differences were observed only between Class 1.5 and Class 3 lakes (Figure 4 - 1.a; Tukey HSD Class 1.5—Class 3 $p = 0.0048$). While median asymptotic lengths appeared to be higher in Class 2 and Class 3 lakes compared to Class 1 and 1.5 lakes, these differences were not statistically significant (Figure 4 - 1.b). However, an alternative, model-independent assessment of maximum growth potential showed that the maximum length (95% quantile length) of Lake Trout increased with Lake Class, with Class 3 lakes having ~40% higher maximum lengths than Class 1 and Class 1.5 lakes (Figure 4 - 1.c; TukeyHSD Class 1—Class 3 $p < 0.0001$, Class 1.5—Class 3 $p < 0.0001$, all other pairwise interactions p > 0.05). Considering pre-maturation growth traits, early growth rates (*ω*) were significantly higher in planktivorous Lake Trout populations (i.e., Class 1 and Class 1.5) compared to Class 2 and Class 3 lakes (Figure 4 - 1.d). Length-at-age-three, another indicator of pre-maturation development relevant to my Lake Trout populations, was not significantly different among Lake Classes but showed a similar pattern to *ω*, with the largest age three fish being found in Class 1 lakes and the smallest in Class 2 and Class 3 lakes (Figure 4 - 1.e). Instantaneous mortality rates were equivalent across Lake Classes (Figure 4 - 1.f).

Both lake size and cumulative growing degree days above 5°C (cGDD5) differed among Lake Classes. Class 3 lakes were significantly larger by surface area than both Class 1 and 1.5 lakes (ANOVA, $F_{3,45} = 12.1$, $p < 0.0001$; TukeyHSD Class 1 vs. 3 $p = 0.0003$, Class 1.5 vs. 3 $p < 0.0001$, all other pairwise comparisons p > 0.05). Additionally, the 30-year average climate norm of Class 1 and 2 lakes was greater than in Class 1.5 lakes (Tukey HSD Class 1 vs 1.5 $p = 0.011$, Class 1.5 to 2 $p = 0.0008$, with Class 3 lakes showing intermediate values (Class 2 vs. 3 $p = 0.025$, all other pairwise comparisons p > 0.05). No significant differences among Lake Classes were observed for DOC or TDP (Appendix 4.A - Figure A. 1)

Variation in Lake Trout life history traits were best explained by combining Lake Class assemblages with environmental characteristics than by using either factor alone (Figure 4 - 2). RDA Axis 1 explained a significant amount of variation in all traits ($F = 23.18$, $p = 0.001$, $R^2 = 0.31$), primarily contrasting planktivorous (Class 1 and Class 1.5 lakes) and piscivorous (Class 2 and Class 3) populations. Piscivorous (Class 2 and 3) Lake

Trout generally exhibited larger post-maturation growth traits (L_∞, length-at-maturity, maximum length) which were also associated with larger and more productive lakes (higher TDP). Within Lake Classes, lake size and productivity (e.g., TDP) were useful for understanding trait variation; for example, a Class 2 population from a small lake (~ -0.5 on RDA1) had smaller post-maturation growth traits—more similar to Class 1 and 1.5 lakes—compared to populations from larger Class 2 lakes (~ 1.0 on RDA1; Figure 4 - 2). In contrast, faster pre-maturation growth traits (ω and length-at-age-three) were linked to smaller, less productive lakes; often associated with Class 1 and Class 1.5 lakes (Figure 4 - 2). The second RDA Axis also explained significant differences in life history traits (F = 8.81, p = 0.012, R^2 = 0.12; Figure 4 - 2), suggesting a possible influence of latitude, where lakes with high cGDD5, common to the species' southern range were negatively correlated with higher DOC concentrations, which, are more typical of northern Ontario lakes.

Variance partitioning further revealed the usefulness of considering both Lake Class and environmental traits together (Figure 4 - 3). Individually, Lake Class alone accounted for 15.4% of the model variance, while environmental predictors alone accounted for 12.3%. When combined, an additional 7.7% of variance is explained over and above the independent contributions of either environment or Lake Class alone. Lake Class, lake size, and total phosphorus independently explained variation across collective life history traits when using RDA (Lake Class: F = 6.89, p = 0.001; lake size: F = 7.78, p = 0.001 total phosphorus: F = 2.86, p = 0.045; all other terms p > 0.05), though a triplot of the entire RDA suggests that life history traits of Lake Trout are best explained when Lake Class, lake surface area, and productivity are considered together (Figure 4 - 3).

Discussion

Among the lakes included in the current study, ranging over 5 degrees in latitude and 5 orders of magnitude in lake size, Lake Class (i.e. food web structure) had a greater independent influence on Lake Trout life history traits (15.4% variance explained) than environmental factors (12.3%); when considered together Lake Class and lake-specific environmental characteristics collectively explained 35.4% of the variance in life history traits, explaining more variance in Lake Trout life history traits than either factor individually. In lakes with pelagic prey fish (Class 2 and 3), Lake Trout matured at larger sizes, reached greater asymptotic and maximum lengths, and grew more slowly before maturity compared to planktivorous populations. Predicted changes in life history traits from one Lake Class to the next, when only considering food web structure as a predictor, however, were not observed. Instead, RDA revealed that variation between adjacent Lake Classes was largely driven by environmental conditions within each Lake Class. For instance, Lake Trout in larger and more productive Class 1 and Class 1.5 lakes matured at larger sizes and reached greater asymptotic and maximum lengths than those in smaller and less productive lakes of the same classes, while smaller, less productive Class 2 and 3 lakes showed higher juvenile growth rates, similar to planktivorous Class 1 or 1.5 lakes. Based on these results, my analysis suggests that Lake Trout life histories in Ontario lakes can be relatively well described using two easily accessed pieces of information – lake specific environmental variables (lake size and TDP, in particular) and the presence/absence of two key Lake Trout prey items (Coregonids and *Mysis*).

Lake Class likely acts as an initial filter for Lake Trout life history traits, where generalized predator-prey mass ratios (PPMR) for each Lake Class place firm limits on the scope for growth based on prey availability (e.g., Sherwood et al. 2002a; Iles and Rasmussen 2005; Kaufman et al. 2009), regardless of environmental conditions. When PPMR are sufficiently low, such as in Class 2 and 3 lakes, life history strategies favour larger and later maturing fish (Shuter et al. 2016) and lower activity rates (Giacomini et al. 2013, Ross *Chapter 2*), likely through improvements to prey conversion efficiency and growth efficiency (Kerr 1971b, Shuter et al. 2016, Cruz-Font et al. 2019). Consequently, in planktivorous Class 1 and Class 1.5 lakes, life history traits characterized by smaller adult sizes and faster juvenile growth are likely a result of incurring higher metabolic costs than in piscivorous populations from a combination of 1) the cumulative effort required to locate and consume many small prey items, 2) lower digestible prey matter in planktivorous diets (high PPMR) relative to those with piscivorous prey (low PPMR), and, 3) increased metabolic costs associated with foraging in suboptimal oxythermal environments that are more common to lakes with higher PPMR's (Martin 1952; Pazzia et al. 2002; Sherwood et al. 2002; Guzzo et al. 2017, Ross *Chapter 2*).

The findings in the current study generally support predictions on life history responses to PPMR's, though *Mysis* presence had a smaller than expected effect on Lake Trout life history traits. Using the same categorical Lake Class system, *Mysis* presence lowered mercury biomagnification slopes for Class 1.5 and Class 3 Lake Trout (*Chapter 3*) and was associated with decreased activity and metabolic rates in lakes with piscivorous prey (Class 3 compared to Class 2; *Chapter 2*). In both cases, these effects were likely driven by *Mysis* providing higher amounts of energy per unit prey compared to zooplankton or other pelagic invertebrates (Pazzia et al. 2002), and reducing foraging activity required for satiation (Giacomini et al. 2013, Cruz-Font et al. 2019). Yet, *Mysis* presence did not have a similar effect on Lake Trout life history traits, suggesting that a simple presence/absence measure may overlook important factors like *Mysis* size and density, or the degree of Lake Trout omnivory, for the possible modification of life history traits. Lacking more detailed *Mysis* data, lake depth may be a useful proxy for *Mysis* life histories, as deeper lakes can support larger *Mysis* populations (both in body size and density) that exhibit more diverse migratory behaviours (Stockwell et al. 2020, Ridgway et al. 2022). Indeed, the inclusion of lake size (positively corelated with lake depth; Fee et al. 1996) alongside *Mysis* presence/absence in my RDA showed that Class 1.5 and Class 3 Lake Trout in larger lakes—where *Mysis* populations are likely more complex—displayed life history traits associated with larger, later-maturing fish, consistent with theory on reductions in PPMR. Although *Mysis* are recognized as a keystone species, there remain significant gaps in our knowledge of their ecology and distribution; further research on their roles is aquatic food webs is required.

While univariate approaches, both in this study and others (Shuter et al. 1998, McDermid et al. 2010) demonstrate that lake surface area modifies Lake Trout life histories, multivariate variance partitioning revealed that this effect is strongly linked to food web structure. Lake surface area is correlated with characteristics that are important not only to Lake Trout ecology but also to the ecology and availability of key prey items (Ridgway et al. 2022). Larger lakes are typically deeper, provide larger habitat volumes, offer increased suitable oxythermal habitat, and commonly have more complex shorelines/shapes that enhance littoral-pelagic food web coupling (Dolson et al. 2009, McMeans et al. 2016, Kangosjärvi et al. 2024, Hlina et al. 2024). For salmonids, these characteristics can be associated with increased richness of other pelagic fishes, reduced omnivory, less reliance on littoral and invertebrate prey, and a greater reliance on key pelagic prey fishes—particularly Cisco and Whitefish (Eloranta et al. 2015, McMeans et al. 2016, Cordero and Jackson 2021). These characteristics generally support life history strategies favouring delayed maturation in exchange for larger adult growth (Shuter et al. 1998, McMeans et al. 2016, Hansen et al. 2021). In my study, the effect of lake size within a given Lake Class was particularly important for interpreting life history traits in the smallest or largest lakes of a given class; individuals in the largest Class 1 lake exhibited life history traits similar to those in Class 2 and Class 3 lakes, and vice versa. Without considering the combined influence of lake size and food web structure, such traits might be misclassified or viewed as anomalies.

The three remaining environmental variables tested—total phosphorus, climate norms, and DOC—showed less support for directly influencing Lake Trout life history traits in this lake set. However, these variables may gain importance with ongoing environmental change. Total dissolved solids, a proxy for productivity, has previously been associated with larger Lake Trout maximum sizes and greater pre-maturation growth in Southern Ontario Lake Trout populations (Shuter et al. 1998, McDermid et al. 2010). While my analyses yielded mixed responses to total dissolved phosphorus concentrations (i.e., no significant univariate effect but a significant multivariate effect), the role of phosphorus in shaping Lake Trout life history traits could strengthen under future environmental shifts. Although cultural eutrophication remains a global concern, many north-temperate and boreal lakes are now experiencing “oligotrophication” because of changes in atmospheric deposition, weathering rates, and changing climatic conditions (Huser et al. 2018, Isles et al. 2018, 2023, Carleton and Washington 2021). If sustained, oligotrophication may reduce Lake Trout size-structure and lead to delayed maturation schedules.

In addition to changes in total phosphorus concentrations, Ontario lakes are both warming because of elevated air temperatures and “browning” due to increased DOC. Warmer spring and summer temperatures can reduce Lake Trout’s use of littoral habitat, decrease nearshore habitat coupling, and shift reliance away from nearshore prey fish despite stable nearshore prey populations (Tunney et al. 2014, Guzzo et al. 2017). This behavioural shift has resulted in lower Lake Trout growth rates and poorer condition factors during warmer years (Tunney et al. 2014, Guzzo et al. 2017). As such, sustained warming might be particularly detrimental to planktivorous Lake Trout populations (i.e., Class 1 and 1.5), where further separation from littoral resource subsidies is likely (Dolson et al. 2009, Guzzo et al. 2017). Additionally, increasing DOC in Ontario lakes (Ross et al. *in review*) is expected to affect the oxythermal habitat and productivity of coldwater fishes (Jane et al. 2024); the combined effects of concurrent warming and browning, however, are uncertain. Increased warming and higher DOC may concentrate warmer water temperatures in shallower epilimnions, creating deeper thermoclines with the potential to increase suitable Lake Trout oxythermal habitat, or, hypolimnetic deoxygenation rates might outpace any gains from shallower epilimnions leading to habitat reductions. Evidence from 28 temperate lakes in Northeastern United States suggests the latter, with habitat volumes for stenothermic salmonids declining, especially in shallower lakes with even just moderate DOC concentrations (Jane et al. 2024). As such, concurrent warming and browning in Ontario lakes may further disadvantage Lake Trout, particularly in smaller, shallower Class 1 and 1.5 Lakes.

This current analysis demonstrates the importance of both food web assemblages and environmental factors as being important determinants of Lake Trout life history traits, though some variation remains unexplained. Previous studies indicate that angling mortality affects Lake Trout growth rates, size-structure, and age at maturity (Chu et al. 2016, Wilson et al. 2019). Unfortunately, cohesive angling data were unavailable for the lakes in this study, though some variation, particularly in instantaneous mortality estimates, may reflect between-lake differences in exploitation rates. While maximum sustainable fishing effort for Lake Trout populations decreases with increasing lake size (Lester et al. 2021), sustained harvest pressure in small inland lakes with small population sizes can substantially reduce adult size-structure, abundance and biomass (Gunn and Sein 2000, Lenker et al. 2016). Thus, Class 1 and 1.5 lakes, which are generally smaller than Class 2 and 3 lakes, may be more susceptible to increased mortality and shifts in population size-structure when open to angling.

In conclusion, this study presents a framework for understanding Lake Trout life history in relation to two key pelagic prey items, *Mysis* and Coregonids, along with easily accessed environmental variables. Class 1 and 1.5 Lake Trout exhibited faster early growth rates, matured at smaller sizes, and remained smaller throughout their lives, especially in small lakes. Although climate norms, phosphorus, and DOC had minimal influence on life history traits, their potential effects on Lake Trout, particularly in smaller Class 1 and 1.5 lakes, should be considered, as these lakes are more vulnerable to warming, browning, changes in productivity, and high angling pressure.

Table 4 - 1. Model coefficients from multiple linear regressions assessing individual life history traits as a function of environmental factors. The model was run on log$_{10}$ transformed data, so "Intercept" is the value when all other predictor variables are at 0. Variables highlighted in grey were statistically significant at alpha < 0.05. TDP = Total dissolved phosphorus, cGDD5 30-yr norm = 30-year norm for cumulative growing degree days above 5ºC, DOC = dissolved organic carbon.

Life History Trait	**Predictor Variable (log$_{10}$)**	**Estimate (β)**	**Standard Error**	***t*-value**	***p*-value**
Length-at-maturity	Intercept	229.32	483.57	0.47	0.64
	Surface area	20.68	6.58	3.15	0.0033
	TDP	20.81	32.14	0.65	0.52
	cGDD5 30-yr norm	8.30	148.51	0.06	0.96
	DOC	46.27	28.91	1.60	0.12
Asymptotic length	Intercept	-825.22	923.06	-0.89	0.38
	Surface area	91.33	12.55	7.28	< 0.0001
	TDP	60.01	61.35	0.98	0.33
	cGDD5 30-yr norm	338.80	283.47	1.20	0.24
	DOC	29.52	55.19	0.54	0.60
Maximum length	Intercept	1387.57	989.84	1.40	0.17
	Surface area	88.73	13.68	6.48	< 0.0001
	TDP	6.84	65.52	0.10	0.92
	cGDD5 30-yr norm	-349.18	304.15	-1.15	0.26
	DOC	106.47	59.88	1.78	0.084
ω **(Omega)**	Intercept	501.00	445.69	1.12	0.27
	Surface area	-25.04	6.06	-4.13	0.0002
	TDP	-17.17	29.62	-0.58	0.57
	cGDD5 30-yr norm	-102.67	136.87	-0.75	0.46
	DOC	45.71	26.65	1.72	0.095
Length-at-age 3	Intercept	454.78	692.70	0.66	0.52
	Surface area	-21.14	9.95	-2.12	0.042
	TDP	10.64	48.28	0.22	0.83
	cGDD5 30-yr norm	-61.62	212.84	-0.29	0.77
	DOC	96.80	46.66	2.07	0.046
Z **(Instantaneous Mortality)**	Intercept	-1.06	1.01	-1.06	0.30
	Surface area	-0.01	0.01	-0.55	0.59
	TDP	0.08	0.07	1.16	0.25
	cGDD5 30-yr norm	0.38	0.31	1.22	0.23
	DOC	-0.02	0.06	-0.38	0.70

Table 4 - 2. One-way ANOVA model summaries for individual life history traits as response variables and Lake Class as a predictor variable. Rows highlighted in light grey were significant at alpha < 0.1, and dark grey are models where alpha < 0.05.

Life History Trait	***F*-value**	**Degrees of freedom**	***p*-value**	R^2
Length-at-maturity	5.00	3,45	0.004	0.25
Asymptotic length	2.80	3,45	0.051	0.51
Maximum length	14.64	3,44	< 0.0001	0.5
ω (Omega)	4.84	3,45	0.005	0.24
Length-at-age 3	2.12	3,37	0.11	0.15
Z	0.75	3,44	0.53	0.05

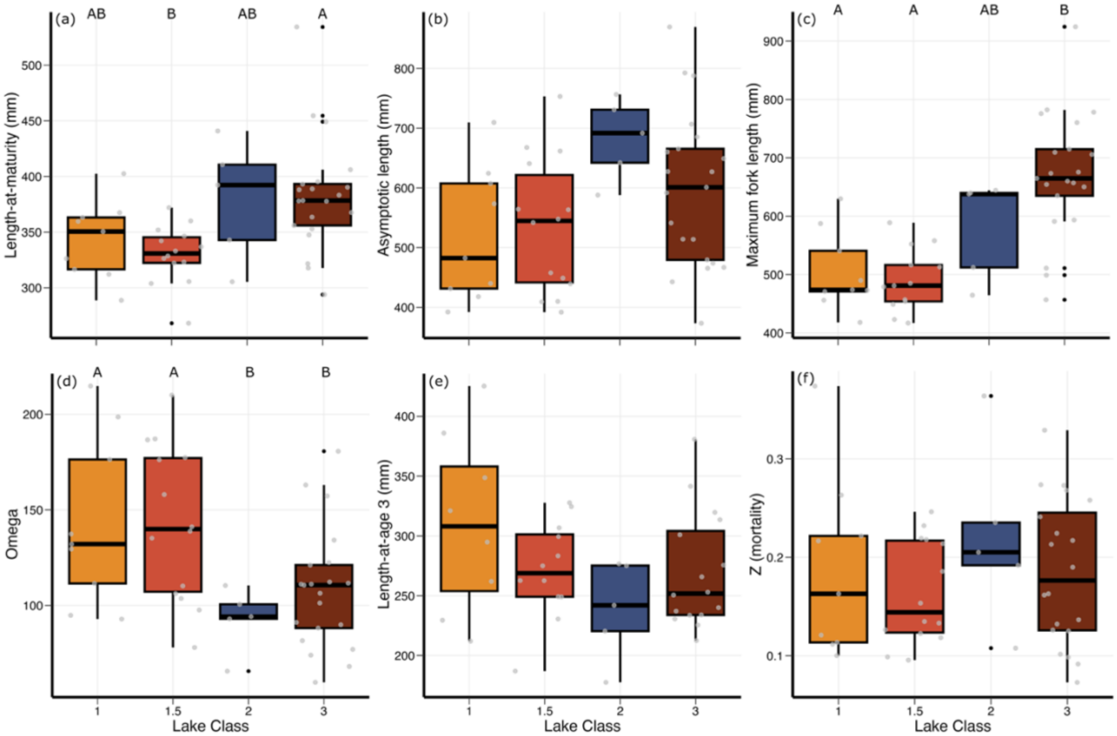


Figure 4 - 1. Lake Trout life history traits for distinct Lake Classes (Class 1, no pelagic prey available; Class 1.5, *Mysis* present; Class 2, pelagic prey fishes present; Class 3, both *Mysis* and pelagic prey fishes present). Boxplot distributions indicate Lake Class medians (thick horizontal bar), interquartile ranges (box edges), and 1.5*interquartile ranges (whiskers), while outlying values are shown as black points. Grey jittered points indicate lake specific life history observations. Within a given panel, Lake Classes with shared capitalized letters are not significantly different from each other; models with $p > 0.05$ have no pairwise comparisons.

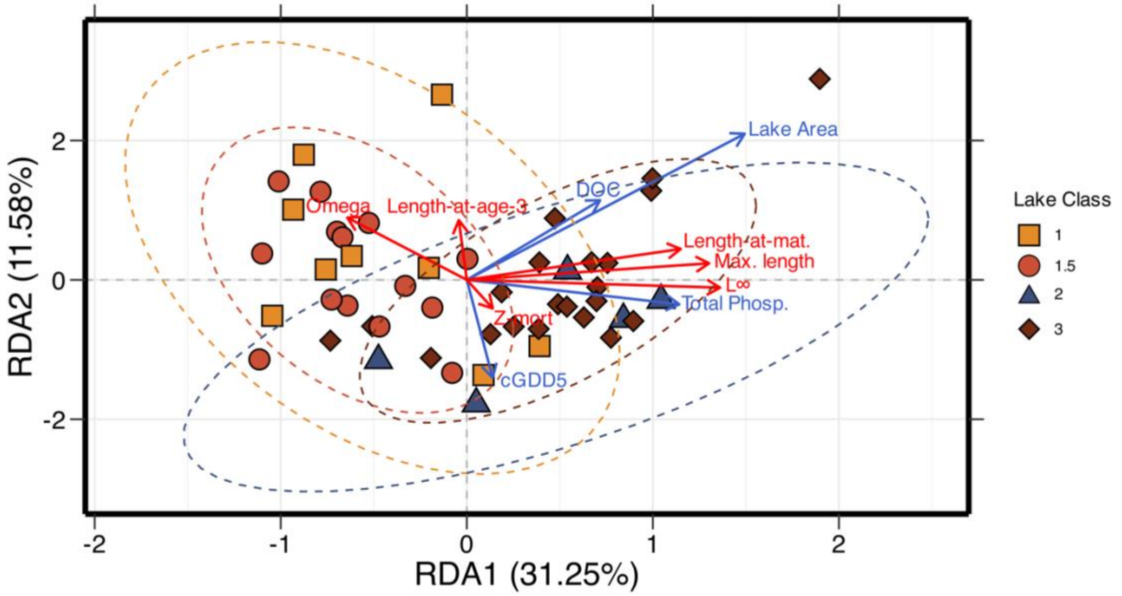
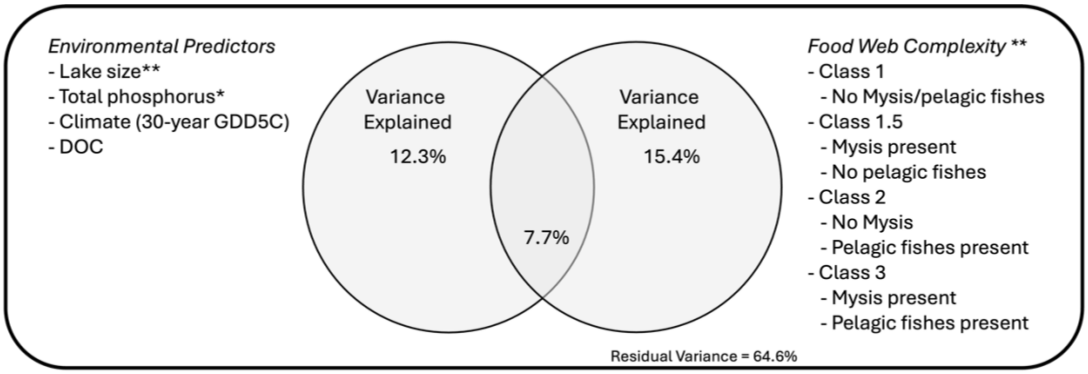


Figure 4 - 2. RDA triplot of Lake Trout life history traits (red arrows and text) and environmental predictor variables (blue arrows and texts) mapped onto Lake Class RDA scores (symbols and colours as indicated in figure legend). Lake Classes are grouped by 95% confidence intervals within dashed-line ellipses.

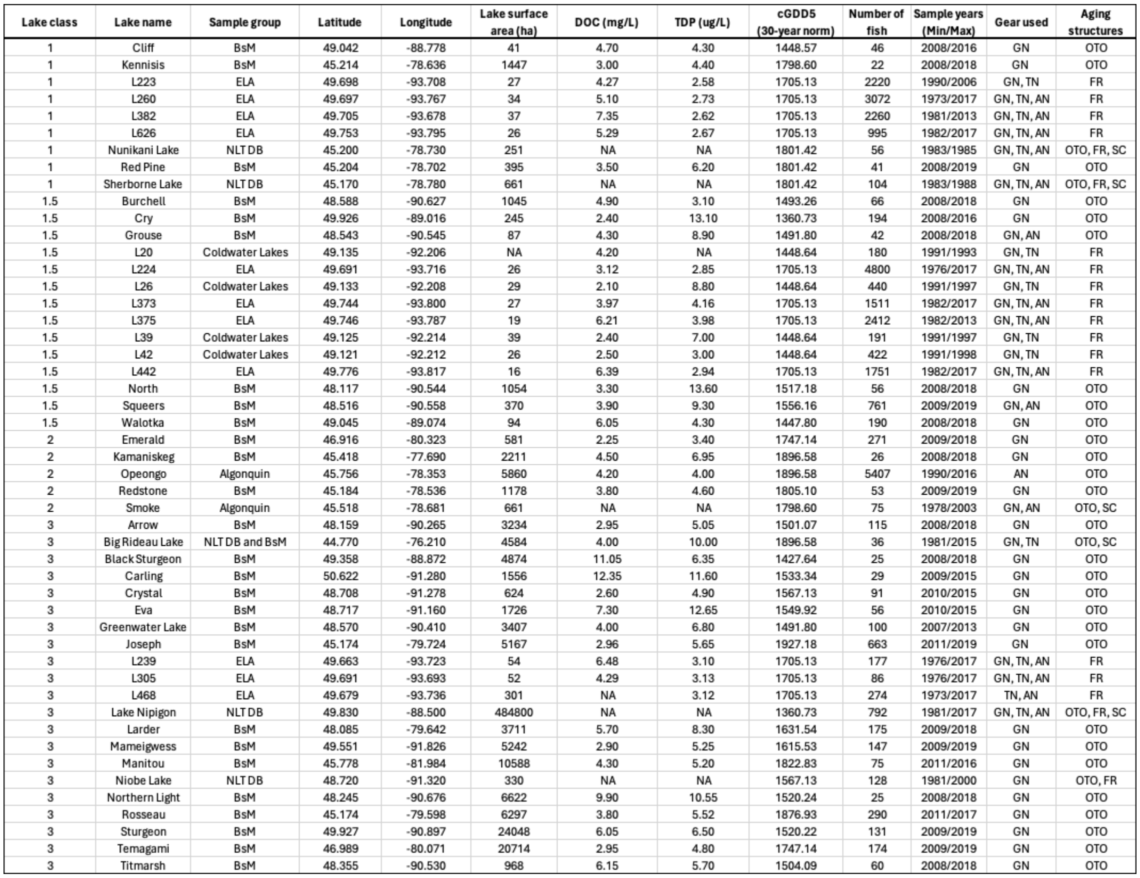


Permutation tests for reduced models: ** = p<0.01; *=p<0.05

Figure 4 - 3. RDA variance partitioning of the independent and combined effects of environmental predictors (left circle) and Lake Class (right circle) on Lake Trout life history traits. The overlapping area, representing ~7,7% of overall model variance, indicates the combined effects of both environmental predictors and Lake Class. Significant predictor variables are denoted with asterisks, while non-significant predictors are not marked.

Appendix 4.A – Supplementary Model Results

Appendix 4.A - Table A. 1. Summary of survey lakes, locations, environmental characteristics, and fish sample size used for life history analyses.



Lake class	Lake name	Sample group	Latitude	Longitude	Lake surface area (ha)	DOC (mg/L)	TDP (ug/L)	cGDD5 (30-year norm)	Number of fish	Sample years (Min/Max)	Gear used	Aging structures
1	Cliff	BsM	49.042	-88.778	41	4.70	4.30	1448.57	46	2008/2016	GN	OTO
1	Kennisis	BsM	45.214	-78.636	1447	3.00	4.40	1798.60	22	2008/2018	GN	OTO
1	L223	ELA	49.698	-93.708	27	4.27	2.58	1705.13	2220	1990/2006	GN, TN	FR
1	L260	ELA	49.697	-93.767	34	5.10	2.73	1705.13	3072	1973/2017	GN, TN, AN	FR
1	L382	ELA	49.705	-93.678	37	7.35	2.62	1705.13	2260	1981/2013	GN, TN, AN	FR
1	L626	ELA	49.753	-93.795	26	5.29	2.67	1705.13	995	1982/2017	GN, TN, AN	FR
1	Nunikani Lake	NLT DB	45.200	-78.730	251	NA	NA	1801.42	56	1983/1985	GN, TN, AN	OTO, FR, SC
1	Red Pine	BsM	45.204	-78.702	395	3.50	6.20	1801.42	41	2008/2019	GN	OTO
1	Sherborne Lake	NLT DB	45.170	-78.780	661	NA	NA	1801.42	104	1983/1988	GN, TN, AN	OTO, FR, SC
1.5	Burchell	BsM	48.588	-90.627	1045	4.90	3.10	1493.26	66	2008/2018	GN	OTO
1.5	Cry	BsM	49.926	-89.016	245	2.40	13.10	1360.73	194	2008/2016	GN	OTO
1.5	Grouse	BsM	48.543	-90.545	87	4.30	8.90	1491.80	42	2008/2018	GN, AN	OTO
1.5	L20	Coldwater Lakes	49.135	-92.206	NA	4.20	NA	1448.64	180	1991/1993	GN, TN	FR
1.5	L224	ELA	49.691	-93.716	26	3.12	2.85	1705.13	4800	1976/2017	GN, TN, AN	FR
1.5	L26	Coldwater Lakes	49.133	-92.208	29	2.10	8.80	1448.64	440	1991/1997	GN, TN	FR
1.5	L373	ELA	49.744	-93.800	27	3.97	4.16	1705.13	1511	1982/2017	GN, TN, AN	FR
1.5	L375	ELA	49.746	-93.787	19	6.21	3.98	1705.13	2412	1982/2013	GN, TN, AN	FR
1.5	L39	Coldwater Lakes	49.125	-92.214	39	2.40	7.00	1448.64	191	1991/1997	GN, TN	FR
1.5	L42	Coldwater Lakes	49.121	-92.212	26	2.50	3.00	1448.64	422	1991/1998	GN, TN	FR
1.5	L442	ELA	49.776	-93.817	16	6.39	2.94	1705.13	1751	1982/2017	GN, TN, AN	FR
1.5	North	BsM	48.117	-90.544	1054	3.30	13.60	1517.18	56	2008/2018	GN	OTO
1.5	Squeers	BsM	48.516	-90.558	370	3.90	9.30	1556.16	761	2009/2019	GN, AN	OTO
1.5	Walotka	BsM	49.045	-89.074	94	6.05	4.30	1447.80	190	2008/2018	GN	OTO
2	Emerald	BsM	46.916	-80.323	581	2.25	3.40	1747.14	271	2009/2018	GN	OTO
2	Kamaniskeg	BsM	45.418	-77.690	2211	4.50	6.95	1896.58	26	2008/2018	GN	OTO
2	Opeongo	Algonquin	45.756	-78.353	5860	4.20	4.00	1896.58	5407	1990/2016	AN	OTO
2	Redstone	BsM	45.184	-78.536	1178	3.80	4.60	1805.10	53	2009/2019	GN	OTO
2	Smoke	Algonquin	45.518	-78.681	661	NA	NA	1798.60	75	1978/2003	GN, AN	OTO, SC
3	Arrow	BsM	48.159	-90.265	3234	2.95	5.05	1501.07	115	2008/2018	GN	OTO
3	Big Rideau Lake	NLT DB and BsM	44.770	-76.210	4584	4.00	10.00	1896.58	36	1981/2015	GN, TN	OTO, SC
3	Black Sturgeon	BsM	49.358	-88.872	4874	11.05	6.35	1427.64	25	2008/2018	GN	OTO
3	Carling	BsM	50.622	-91.280	1556	12.35	11.60	1533.34	29	2009/2015	GN	OTO
3	Crystal	BsM	48.708	-91.278	624	2.60	4.90	1567.13	91	2010/2015	GN	OTO
3	Eva	BsM	48.717	-91.160	1726	7.30	12.65	1549.92	56	2010/2015	GN	OTO
3	Greenwater Lake	BsM	48.570	-90.410	3407	4.00	6.80	1491.80	100	2007/2013	GN	OTO
3	Joseph	BsM	45.174	-79.724	5167	2.96	5.65	1927.18	663	2011/2019	GN	OTO
3	L239	ELA	49.663	-93.723	54	6.48	3.10	1705.13	177	1976/2017	GN, TN, AN	FR
3	L305	ELA	49.691	-93.693	52	4.29	3.13	1705.13	86	1976/2017	GN, TN, AN	FR
3	L468	ELA	49.679	-93.736	301	NA	3.12	1705.13	274	1973/2017	TN, AN	FR
3	Lake Nipigon	NLT DB	49.830	-88.500	484800	NA	NA	1360.73	792	1981/2017	GN, TN, AN	OTO, FR, SC
3	Larder	BsM	48.085	-79.642	3711	5.70	8.30	1631.54	175	2009/2018	GN	OTO
3	Mameigwess	BsM	49.551	-91.826	5242	2.90	5.25	1615.53	147	2009/2019	GN	OTO
3	Manitou	BsM	45.778	-81.984	10588	4.30	5.20	1822.83	75	2011/2016	GN	OTO
3	Niobe Lake	NLT DB	48.720	-91.320	330	NA	NA	1567.13	128	1981/2000	GN	OTO, FR
3	Northern Light	BsM	48.245	-90.676	6622	9.90	10.55	1520.24	25	2008/2018	GN	OTO
3	Rosseau	BsM	45.174	-79.598	6297	3.80	5.52	1876.93	290	2011/2017	GN	OTO
3	Sturgeon	BsM	49.927	-90.897	24048	6.05	6.50	1520.22	131	2009/2019	GN	OTO
3	Temagami	BsM	46.989	-80.071	20714	2.95	4.80	1747.14	174	2009/2019	GN	OTO
3	Titmarsh	BsM	48.355	-90.530	968	6.15	5.70	1504.09	60	2008/2018	GN	OTO

Notes:

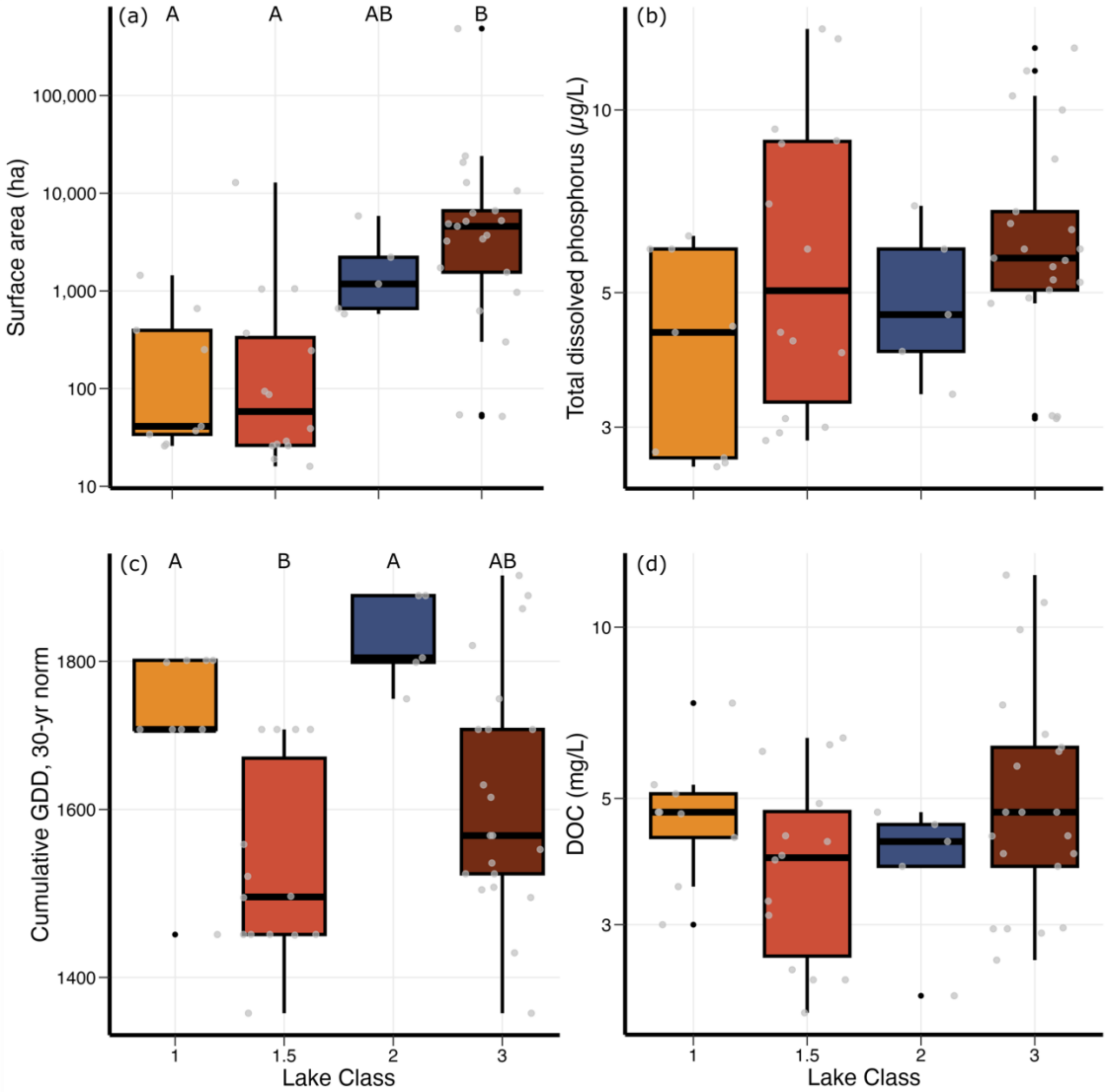
Sample groups: BsM, Broadscale Monitoring Program; ELA, IISD-Experimental Lakes Area; NLT DB, National Lake Trout Database

Gear used: AN, angling; GN, gillnet; TN, trapnet

Aging structures: SC, scale; FR, pelvic or pectoral fin ray; OTO, otolith

Appendix 4.A - Table A. 2. Multiple regression model summaries for life history traits as a function of environmental variables ($\log_{10}$ surface area, $\log_{10}$ TDP, $\log_{10}$ cGGD5 30-yr norm, $\log_{10}$ DOC).

Life History Trait	**Degrees of freedom**	***F*-value**	***p*-value**	**Model R^2**
Length-at-maturity	4,37	5.64	0.0012	0.38
Asymptotic length	4,37	24.78	<0.00001	0.73
Maximum length	4,36	17.27	<0.00001	0.66
Omega	4,37	8.45	<0.00001	0.48
Length-at-age 3	4,31	2.54	0.060	—
Z	4,36	0.53	0.71	—

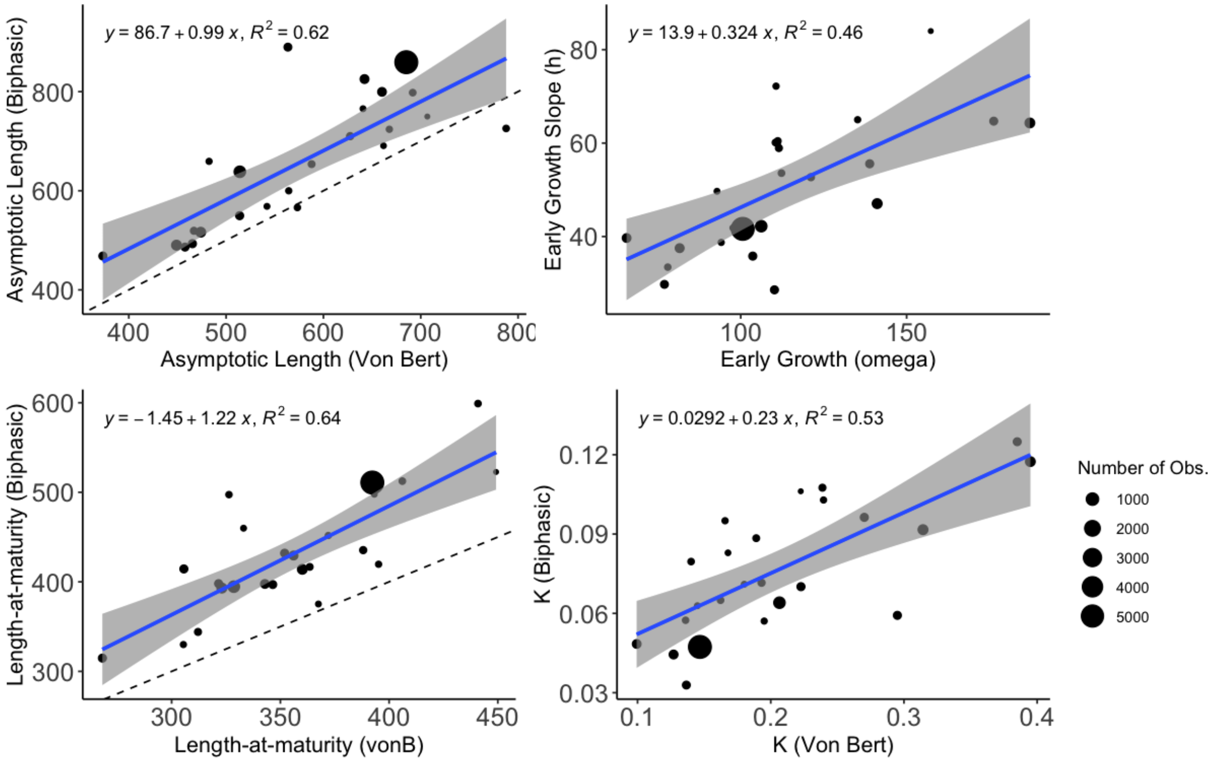


Appendix 4.A - Figure A. 1. Distributions of environmental variables for each Lake Class. Boxplot distributions indicate Lake Class medians (thick horizontal bar), interquartile ranges (box edges), and 1.5*interquartile ranges (whiskers), while outlying values are shown as black points. Grey jittered points indicate lake specific life history observations. Shared capitalized letters among Lake Classes within a given panel represent Lake Classes where life history traits are statistically equivalent from a Tukey HSD test.

Appendix 4.B - Comparing von Bertalanffy (VB) and biphasic growth models

Biphasic growth models better describe the lifetime growth of Lake Trout by explicitly separating juvenile and adult growth phases. However, during my assessment of Lake Trout life history traits, I found that many biphasic models could not be fit to existing data because of sparce juvenile and/or adult observations. Alternatively, VB growth models typically require less data, providing a simpler yet still robust way of estimating life history traits.

To evaluate the agreement between biphasic and VB growth models, I created models for a subset of 33 lakes across four Lake Classes where there was adequate data to estimate biphasic growth. Although not all parameters from the two models allow for direct comparisons (i.e., early growth from biphasic is the slope coefficient of the juvenile growth phase, whereas Omega is a relative growth rate towards asymptotic size), simple linear regressions between similar parameters indicates good agreement between the two modelling approaches (Figure A.1).



Appendix 4.B - Figure B. 1: Comparison of complimentary biphasic (y-axes) and von Bertalanffy (x-axes) growth model parameters. All comparisons were positively associated and statistically significant ($p < 0.05$). Number of observations (i.e., sampled individuals within a population) was not an important predictor of model fit.

CHAPTER 5

General Conclusions

This thesis provides compelling evidence, through field-validated empirical support, that a coarse classification of food chain length (i.e., Lake Class) alongside environmental factors is useful for describing the active metabolism of Lake Trout in Ontario lakes. Further, I demonstrate that active metabolic differences associated with distinct prey fields among lakes influence Lake Trout mercury (Hg) concentrations, but in a more complex fashion than previously-proposed food chain length contaminant models (e.g., Rasmussen et al. 1990b; Cabana et al. 1994), and that life history traits observed across Lake Classes align with predictions from the metabolic theory of ecology.

While Lake Class and diurnal period were sufficient to predict Lake Trout activity rates and behaviours among lakes, Lake Class alone was insufficient to fully explain Hg contamination dynamics and life history variation. In both cases, models were improved by adding environmental variables alongside prey structure. Accounting for lake-specific dissolved organic carbon (DOC) concentrations was critical in assessing human consumption risk from exposure to Lake Trout Hg, as fish in high DOC lakes were more likely to exceed Hg consumption guidelines at harvestable sizes. For life history traits, incorporating lake size and productivity (e.g., total phosphorus) along with Lake Class improved explained model variance by constraining within-Lake Class trait variation. Collectively, this work strongly supports the theory that predators are metabolically linked to their environment by the available prey and habitats they encounter. Moreover, by using simple, accessible metrics of prey availability (i.e., four-stage Lake Class rather than more intensive and costly methods like stable isotope analyses) alongside other easily assessed information (e.g., lake size, diel cycles, DOC), Lake Trout populations can be effectively characterized across broad geographic regions like Ontario.

In Chapter 2, I introduced a novel method using a stationary hydroacoustic platform to empirically assess activity in pelagic ecosystems, allowing for an *in situ* examination of how wild, free-swimming Lake Trout activity responds to prey availability and diurnal cycles. In thermally stratified lakes lacking pelagic prey fish (Class 1 and Class 1.5), Lake Trout maintained consistent swimming behaviour day and night. Compared to Class 2 and 3 lakes where behaviour was more variable, planktivorous Lake Trout displayed more metabolically active swimming styles, including higher nighttime speeds, increased track tortuosity, and frequent exposure to suboptimal oxythermal conditions. This elevated activity led to nighttime oxygen consumption rates (i.e., active metabolism) that were an order of magnitude higher than those in Class 2 and 3 lakes. *Mysis* presence generally did not affect swimming behaviour from Class 1 to 1.5 lakes, despite moderate decreases in swimming speeds and a 14% increase in Class 1.5 resting behaviours. However, the presence of *Mysis* in Class 3 lakes was associated with a near doubling in resting behaviours relative to Class 2. *Mysis* presence likely confers indirect energetic benefits in Class 3 lakes by enhancing coregonid growth efficiency (the primary prey for Class 3 Lake Trout), thereby boosting Lake Trout growth efficiency through trophic cascades.

This work addressed a clear need in fisheries biology, by providing a method to quantitatively observe fine-scale free-swimming fish activity in natural lake environments. While similar approaches have been used in marine and Great Lakes environments to assess fish abundance (De Robertis et al. 2017, Elliott et al. 2021, Grow et al. 2024), this study is the first to demonstrate the effectiveness of up-looking stationary hydroacoustics in shallower inland lakes, where acoustic search volumes are typically smaller. The results of this work also have important implications for fisheries management. Assessment programs such as the Ontario Broadscale Management Program (Sandstorm et al. 2013), which monitor fish populations using passive capture gear, assume uniform movement, and thus uniform gear encounter rates, among a given species across lakes. This study challenges that assumption, revealing that prey-mediated differences in nighttime activity could bias population biomass estimates when encounter rates are assumed to be equal. My work strongly suggests that Lake Trout in different prey environments will exhibit varying gear encounter rates, and suggests that catchability coefficients can likely be calibrated based on the presence or absence of key prey species. Furthermore, this method can also be adapted to observe a multitude of other fine-scale behaviours of interest in aquatic ecosystems, including targeted activity observations for other fishes, diel vertical migration patterns, habitat-specific behaviours around structures that aggregate fish (e.g., deep chlorophyll layers, lake-mounts, spawning shoals), or observations within lake littoral zones using horizontal hydroacoustic deployments, all opening new avenues for understanding interactions between fish and their environments.

Given the observed differences in Lake Trout activity across a modified four-stage Lake Class system (Chapter 2), which indicated higher active metabolic rates in planktivorous populations, it seemed prudent to re-evaluate how Hg dynamics are influenced by prey availability within this framework. *In Chapter 3*, I showed that food web structure (i.e., Lake Class) does affect Lake Trout Hg dynamics, but not as originally proposed by Cabana et al. (1994). Rather, Lake Class interacts with body length, in a way that suggests that *Mysis* may play a role in moderating Hg accumulation in Lake Trout. Specifically, lakes in Classes 1.5 and 3, where *Mysis* is present, had lower Lake Trout Hg accumulation slopes than lakes without *Mysis*. This pattern likely reflects the energy-dense alternative to zooplankton represented by *Mysis* in Class 1.5 lakes (Cumminns and Wuycheck 1971, Fernandez et al. 2009, Rennie et al. 2012) for supporting Lake Trout growth efficiency directly, while in Class 3 lakes, *Mysis* presence may enhance growth efficiency primarily in offshore prey fish like coregonids, the primary prey for Lake Trout. These potential improvements in growth efficiency in Class 1.5 and 3 populations could help reduce relative Hg burdens. My results also emphasize the importance of dissolved organic carbon (DOC) as a modifier of Hg levels, as Lake Trout of harvestable size in high-DOC lakes were more likely to exceed Hg consumption guidelines.

Human exposure to mercury primarily occurs through fish consumption, making this work timely as we seek to refine our understanding of the substantial variation in fish Hg dynamics across aquatic ecosystems. For Ontario lakes, I demonstrate that Lake Trout Hg concentrations can be reliably estimated using three readily measured factors: *Mysis* and coregonid presence, Lake Trout population size structure, and lake DOC concentrations (which can also be inferred from secchi depth, latitude, and lake depth; Ross et al., *in review*). While these estimates are not substitutes for direct Hg testing of fish flesh, they offer a valuable predictive tool for managing consumption risks. This work also has important implications in the context of environmental change. As lakes globally experience both warming and browning (i.e., DOC enrichment; Solomon et al. 2015; Jane et al. 2024), Hg concentrations may rise from a combination of elevated temperatures reducing fish growth efficiency, and increases in DOC concentrations increasing Hg availability within ecosystems (Lavoie et al. 2019)

Given the influence of prey availability and environmental factors on Lake Trout activity (Chapter 2) and Hg dynamics (Chapter 3), I expected that life history traits should shift concomitantly across Lake Classes, consistent with metabolic theory. *In Chapter 4*, using an independent dataset from previous efforts (e.g., Shuter et al. 1998, 2016; McDermid et al. 2010), I show that Lake Trout life history traits shifted as expected; larger lake sizes, higher phosphorus levels, and a progression through Lake Classes (i.e., from high to low predator-prey mass ratios) favour larger, later-maturing fish. However, the variance explained by life history models significantly improved when considering the joint effects of prey structure and environmental factors. Together, considering Lake Class with environmental factors explained ~20% of explained model variance, with Lake Class structuring broad patterns in life history traits (e.g., fast Class 1 juvenile growth rates, slow Class 3 juvenile growth rates) and lake size and phosphorus improving estimates of trait variation within each Lake Class (e.g., small Class 3 lakes had relatively smaller maximum sizes than larger Class 3 lakes). This pattern provides support for the metabolic theory of ecology, which emphasizes resource (i.e., prey availability) and temperature-related (i.e., lake size) drivers as being important determinants of life history trait variation (Brown et al. 2004).

Understanding life history variation is critical for conserving, managing, and sustaining resilience in aquatic ecosystems. Identifying the factors that drive trait variation enables management efforts to focus on key landscape variables important to species management. Here, I showed that Lake Trout life history traits were shaped by ecosystem dynamics, particularly through prey interactions driven by habitat availability and predator-prey overlap. Notably, three key variables—*Mysis* and coregonid presence, lake size and total phosphorus—were effective indicators of Lake Trout life history patterns across Ontario lakes. Integrating this information allows fish management to occur within an ecosystem context. While thorough population assessments remain essential for validating ecosystem models and collecting vital rates (e.g., age-structure, sex ratios), leveraging information on environmental covariates, including categorical prey assemblages, offer a cost- and effort-effective approach to estimating population size structure and managing fish in less studied or remote populations.

A central aspect to the experimental design of this thesis was the deliberate use of a simple categorization of food chain length (i.e., Lake Classes) to represent prey availability and approximate predator-prey mass ratios. This approach offers the advantage of broad generalizability across the geographic range of Lake Trout in Ontario. Due to shared glacial histories, elevational gradients and lake morphometry, Lake Trout populations often coexist with pelagic prey communities composed of other glacial relict species, such as *Mysis* or coregonids (Dadswell 1974); across Ontario there is a well-distributed patchwork of Lake Classes across latitudinal gradients (see Chapter 2, Figure 2). However, the main limitation of this approach is a lack of specificity, as specific food web dynamics, such as prey size structure or biomass, food chain omnivory, or the degree of habitat coupling between pelagic and other lake regions, are not recognized. Despite these limitations, my results demonstrate predictable changes in Lake Trout ecology—spanning activity, contaminant dynamics, and life history traits—using this simple food web categorization along with a few key environmental variables. Thus, while this “noisy” and non-specific metric of prey availability may sacrifice precision, it offers valuable generalizability, making it a robust framework for broader Lake Trout management. This approach could also serve as a baseline for more population-specific studies aimed at clarifying underlying mechanisms or thresholds for ecological change. For example, stable isotope information could be used to better describe feeding relationships among habitats, while incorporating prey-specific information on size-structure or density would better capture energy flow within aquatic communities.

Given that each of my three data chapters highlights how prey availability influences Lake Trout metabolic rates, the next step is to apply bioenergetic models across Lake Classes to parse the relative effects of consumption and activity on active metabolism. These models will aim to 1) estimate differences in consumption and growth efficiency based on lake-specific prey food web structure, and 2) compare model-estimated activity rates with those observed using hydroacoustics (*Chapter 2*). By integrating a mercury mass balance model (e.g., Trudel and Rasmussen 2006) with a standard Lake Trout bioenergetics model (e.g., Stewart et al. 1983), I can estimate prey consumption using a contaminant tracer approach and further estimate activity levels specific to each Lake Class. This will allow me to assess relative differences in growth rate, with predictions that growth efficiency should improve (a) with inclusion of *Mysis* and (b) generally across Lake Classes as predicted in Chapter 3 (Hg dynamics) and Chapter 4 (life history strategies). Additionally, comparing model-generated activity estimates with direct hydroacoustic observations will provide a valuable comparison, given the known methodological constraints of current bioenergetic models for predicting activity (Stewart et al. 1983, Rennie et al. 2005).

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