

# Environmental and food web determinants of Lake Trout mercury concentrations in Ontario lakes

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## Abstract

Prey composition and availability is considered a primary predictor of lake trout (*Salvelinus namaycush*) mercury (Hg) concentrations. Evidence from other freshwater fishes suggests that environmental and landscape factors likely also contribute to fish Hg dynamics, yet comprehensive, contemporary assessments for lake trout from boreal and north-temperate lakes are lacking. Here, we reassess the importance of prey characteristics using both previously published and contemporary data, incorporating additional variables and model complexity to better understand factors influencing Hg dynamics of Ontario lake trout. Our analyses indicate that (1) lake trout Hg concentrations are primarily associated with individual body size, (2) high dissolved organic carbon (DOC) concentrations elevate Hg for fish of a given size, and (3) a coarse categorization of food chain length, specifically the presence of *Mysis diluviana*, informs Hg biomagnification slopes. 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. Drivers of lake trout Hg levels in boreal and north-temperate lakes closely match those reported to affect other fishes in the region, regardless of feeding, thermal, and habitat strategies.

**Key words:** biomagnification, bioaccumulation, food web, dissolved organic matter, trophic efficiency, predator–prey interactions

## 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. Hg toxicity has been linked to a wide variety of neural impairments and syndromes in children and adults, including decreased motor system function, neurological impairment, compromised immunity, and reproductive health issues (Zahir et al. 2005; Kim et al. 2016). As such, understanding what controls fish Hg dynamics and being able to easily predict under what scenarios contaminated fish may be present is essential in the development of effective public health policy and advice. 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, while recognizing the critical importance of wild-caught fish to food security and nutritional, cultural, and community well-being, particularly for Indigenous communities. One such consumption guideline is Health Canada's safe guideline limit of 0.5 parts per million or  $\mu\text{g}_{\text{Hg}}/\text{g}_{\text{fish}}$  wet weight 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, it is important to continually re-assess and test the circumstances that may result in unacceptable or sub-optimal risk-benefit trade-offs for consuming fish.

Hg 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 (see Lavoie et al. 2013). Despite Hg emission reductions, persistently high yet variable 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).

Prey contamination was originally considered the primary route for accumulation of Hg and other contaminants of

concern in fish (Thomann 1981). It was under this premise that seminal research on lake trout (*Salvelinus namaycush*) contaminant dynamics in Ontario lakes were investigated, initially from work by Rasmussen et al. (1990) predicting lake trout polychlorinated biphenyl (PCB) concentrations across lakes varying in food chain length, 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 food chain length; 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) as well as pelagic prey fishes present. With each increase in Lake Class (i.e., pelagic food chain length), lake trout contaminants (PCBs and Hg) increased 1–4 fold from one Lake Class to the next (Rasmussen et al. 1990; Cabana et al. 1994). While landscape and body size predictors were included within a subset of these 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 food web complexity and established a quantitative link between lake trout trophic position and Hg (Vander Zanden and Rasmussen 1996; Garcia and Carignan 2005; Swanson and Kidd 2010; Johnston et al. 2022). Meta-analyses and reviews published since have also highlighted the central role of food chains as a determinant of Hg concentrations in predatory fishes (Kidd et al. 2012; Lavoie et al. 2013).

Other research highlights demographic, morphometric, and metabolic processes as modifiers of fish contaminants, particularly in relation to Hg (Gewurtz et al. 2011a, 2011b; Chen et al. 2018; Lescord et al. 2018b; Thomas et al. 2020). 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 abiotic factors, such as watershed and lake physicochemical properties, can also modify fish Hg concentrations (Finley et al. 2016; Lescord et al. 2018a, 2019; Sumner et al. 2020; Thomas et al. 2020; Moslemi-Aqdam et al. 2023). 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 also having higher bacterial methylation potential associated with an 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 mat-

ter associated with high levels of DOC (Tsui and Finlay 2011; French et al. 2014; Braaten et al. 2018). Lake pH, surface area, primary productivity (often assessed as total phosphorus or chlorophyll-*a* concentrations), forestry operations, forest fire activity, and latitude have all additionally been shown to affect Hg under specific scenarios (Table 1). Given the numerous factors influencing fish Hg concentrations, incorporating landscape, climate, and physicochemical variables has been useful when describing Hg dynamics in certain freshwater fishes—such as walleye *Sander vitreus*, northern pike *Esox lucius*, and white sucker *Catostomus commersonii* (Finley et al. 2016; Chen et al. 2018; Lescord et al. 2019; Sumner et al. 2020; Thomas et al. 2020).

This perspective paper aims to provide a contemporary re-examination of the factors driving Hg accumulation in lake trout, a top predator in tens of thousands of North American lakes, and a common food fish across their range. The current effort starts with a re-assessment of seminal work by Cabana et al. (1994) that demonstrated a role of food chain length in shaping consumer Hg dynamics (via the lake trout food chain length Lake Class system), followed by models that provide successively more explicit considerations of other contributing drivers of contaminant accumulation. While the lake trout Lake Class system provides an important starting point for characterizing broadscale contaminant risks that affect fish and those who consume them, much more has been learned since these original papers were published in terms of what variables modify Hg concentrations of freshwater fishes (e.g., Lescord et al. 2019; Thomas et al. 2020; Johnston et al. 2022), and new statistical tools and improved computational power now allow for more complex analyses of landscape determinants on contaminant dynamics (e.g., Thomas et al. 2020; Harrow-Lyle et al. 2023; Lepak et al. 2023). Despite these insights from other species and advances in analytical power, there remains a need for a more comprehensive evaluation of what variables are useful in predicting lake trout Hg concentrations and variability across the landscape, within the context of previous research highlighting the importance of food chain length (i.e., Rasmussen et al. 1990 and Cabana et al. 1994).

For lake trout populations in Ontario's boreal and north-temperate lakes, we demonstrate that both body size and physicochemical landscape variables—particularly DOC concentrations—play key roles in determining Hg concentrations. Linear mixed-effect modeling indicated that while body size is the strongest predictor of lake trout Hg concentrations, lake DOC concentrations dictate whether a lake trout of a given size is likely to exceed Hg contaminant consumption guidelines. Notably, even relatively small-bodied lake trout from high-DOC lakes are likely to have Hg concentrations above these thresholds. Our updated lake trout Hg contamination model also reinforces the value of incorporating simple, categorical designations of food chain length (i.e., Lake Class) to describe Hg bioaccumulation slopes. Specifically, our revised Lake Class categories revealed that the presence of *Mysis* was associated with shallower lake trout Hg accumulation slopes regardless of whether pelagic prey fishes are present or absent, likely due to higher growth rates and prey conversion efficiency in the presence of *Mysis*. Below, we

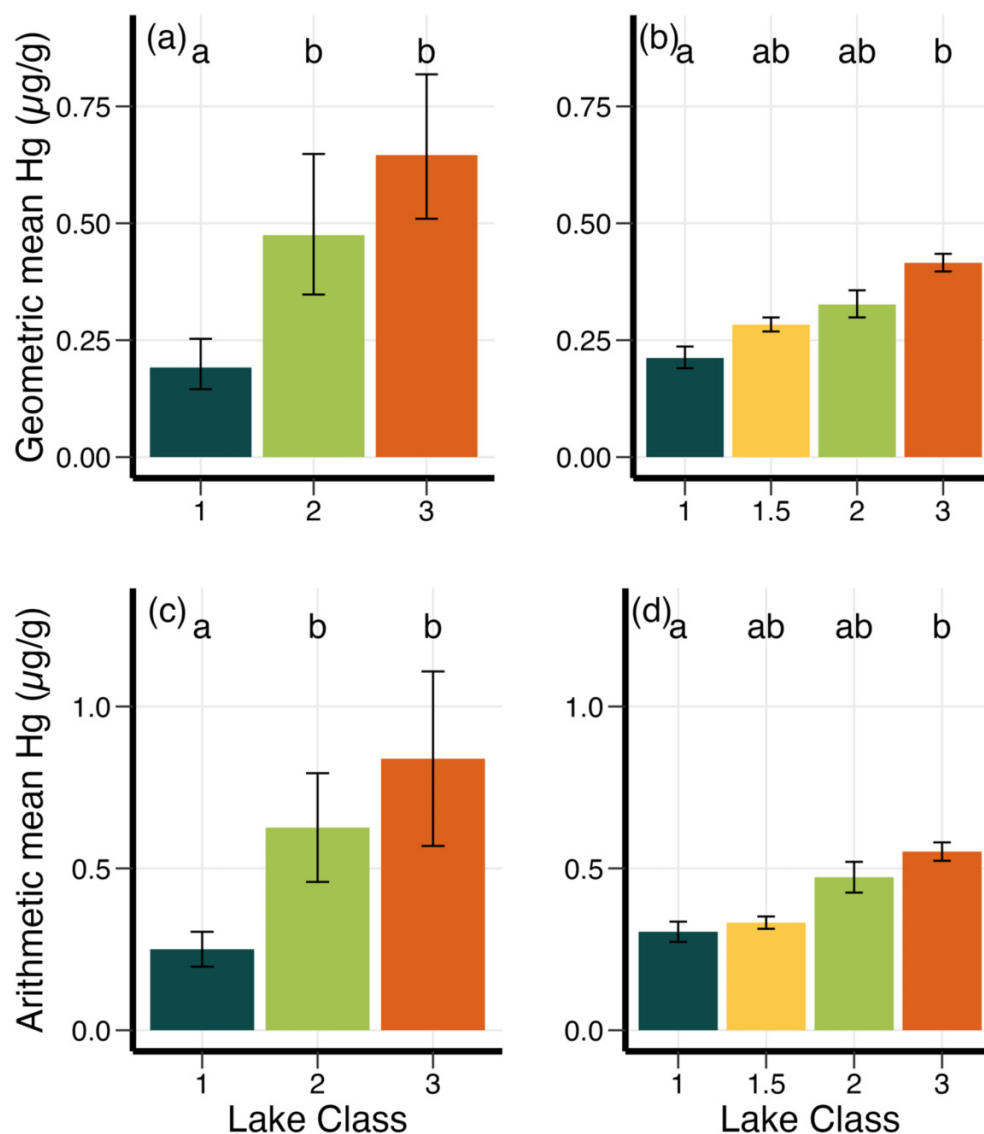
**Table 1.** Predictions of lake trout Hg dynamics in the presence of independent landscape and physicochemical variables.

Variable type	Proposed lake trout effect mechanism	Assessment variable	Landscape characteristic	Predicted lake trout [Hg]	References
<b>Trophic complexity</b>	Extension of food chain length (FCL) promotes consumer Hg biomagnification	FCL	High FCL	+	1–3
<b>Body size</b>	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	$\delta N$ isotopes Length	High $\delta N$ Larger body size	+	4–9
<b>Dissolved organic matter (DOM)</b>	Lake trout Hg exposure will be influenced by watershed processes governing Hg availability	Weight Age	Older age		
	Hg can readily complex with DOM, and methylation potential increases concomitantly with [DOM] and wetland presence, though;	Dissolved organic carbon (DOC)	High DOC	+ or –	10–17
	Some studies suggest high DOC actually reduces methylation, particularly in acidic environments (ref. 12,13), thereby altering Hg availability to fish (ref. 14)	Watershed characteristics	High % connected wetland/lake area		
<b>Productivity</b>	Relative [Hg]'s of all food web compartments concentrate/dilute based on available biomass	Water clarity	High secchi		
	Lake trout activity should scale with ecosystem productivity, affecting growth efficiency and Hg “dilution”	Total phosphorus (TP)	High TP	–	20–22
<b>Acidity</b>	Low pH can limit ecosystem productivity, thereby concentrating Hg in remaining biomass	Chl- <i>a</i>	High Chl- <i>a</i>		
	High concentrations of H <sup>+</sup> ions compete with DOC for Hg complexation	pH	Low pH	+	13–15, 18,19
<b>Lake size</b>	Lake pH helps explain [Hg] in other fish species				
	Waterbody size affects limnetic oxythermal conditions, where warmer and shallower lakes have higher methylation potential	Surface area	Small lake	+	23–24
<b>Watershed disturbance</b>		Maximum depth	Shallow lake		
	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
<b>Latitude</b>	Particulate Hg is released during forest combustion and can be redposited on landscapes, and subsequently methylated				
	More northerly lakes should stay relatively cooler than southern lakes, reducing methylation potential, though;	Latitude	Northern range edge	+ or –	32
<b>Sex</b>	In northern lakes, fish growth rates should also be slower, excretion will be reduced making Hg growth dilution less likely				
	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				

**Note:** 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 an increase (+) or decrease (–) in lake trout Hg concentrations.

References: (1) Rasmussen et al. (1990); (2) Cabana et al. (1994); (3) Vander Zanden and Rasmussen (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. (1992); (13) Kidd et al. (2012); (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) Qian et al. (2001); (20) Kidd et al. (1999); (21) Kidd et al. (2012); (22) Trudel and Rasmussen (2006); (23) Bodaly 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).

**Fig. 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.



detail the progression of our models, from those parameterized solely with food chain length information to our final machine-learning informed mixed-effect model.

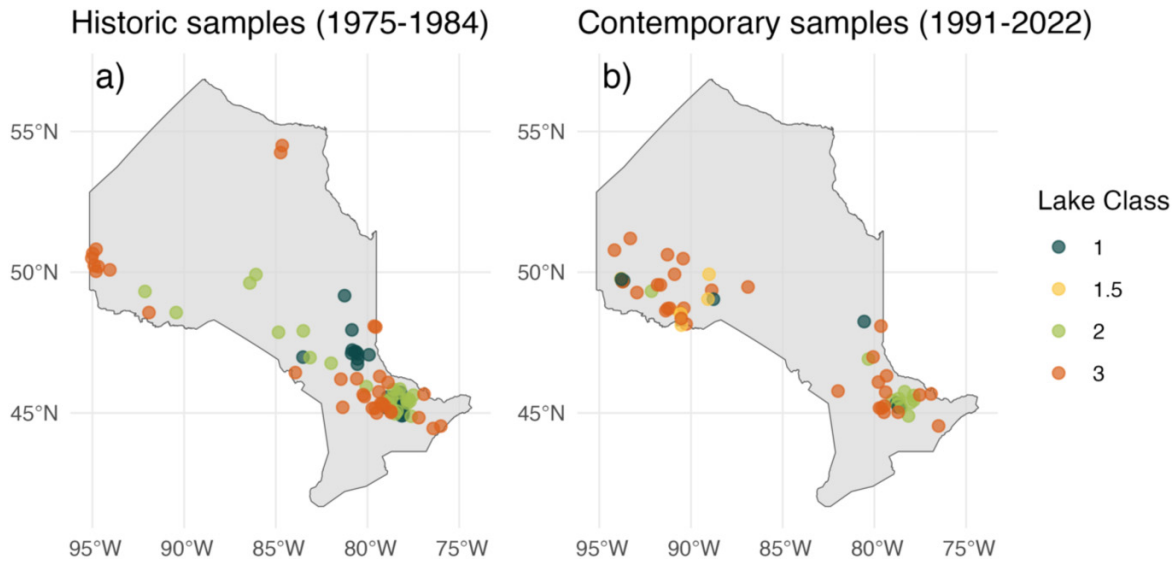
## Revisiting the use of food web lake classes to estimate lake trout mercury contamination—the case for including a body size metric

Biomagnification describes the process by which higher trophic levels and top consumers accumulate more Hg than primary producers and lower trophic consumers, with biomagnification generally increasing as food chain length 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 boreal and north-temperate Ontario lakes were separated into three Lake Classes based on the presence of pelagic prey items, and mean Hg concentrations of lakes among Lake Classes were compared using fish collected between 1975 and 1984 (Table S.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 (Figs. 1a and 1c). However, re-analysis of



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



the Cabana data using one-way ANOVA to confirm their main communicated result of increasing Hg with increasing Lake Classes revealed that pairwise differences between all Lake Classes were not detected despite overall model significance ( $F_{[2,93]} = 21.56$ ,  $p < 0.0001$ ;  $R^2 = 0.32$ ). Though Tukey HSD tests identified Class 1 lakes as having significantly lower mean Hg concentrations than either Class 2 or Class 3 lakes, 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,  $p = 0.29$ ).

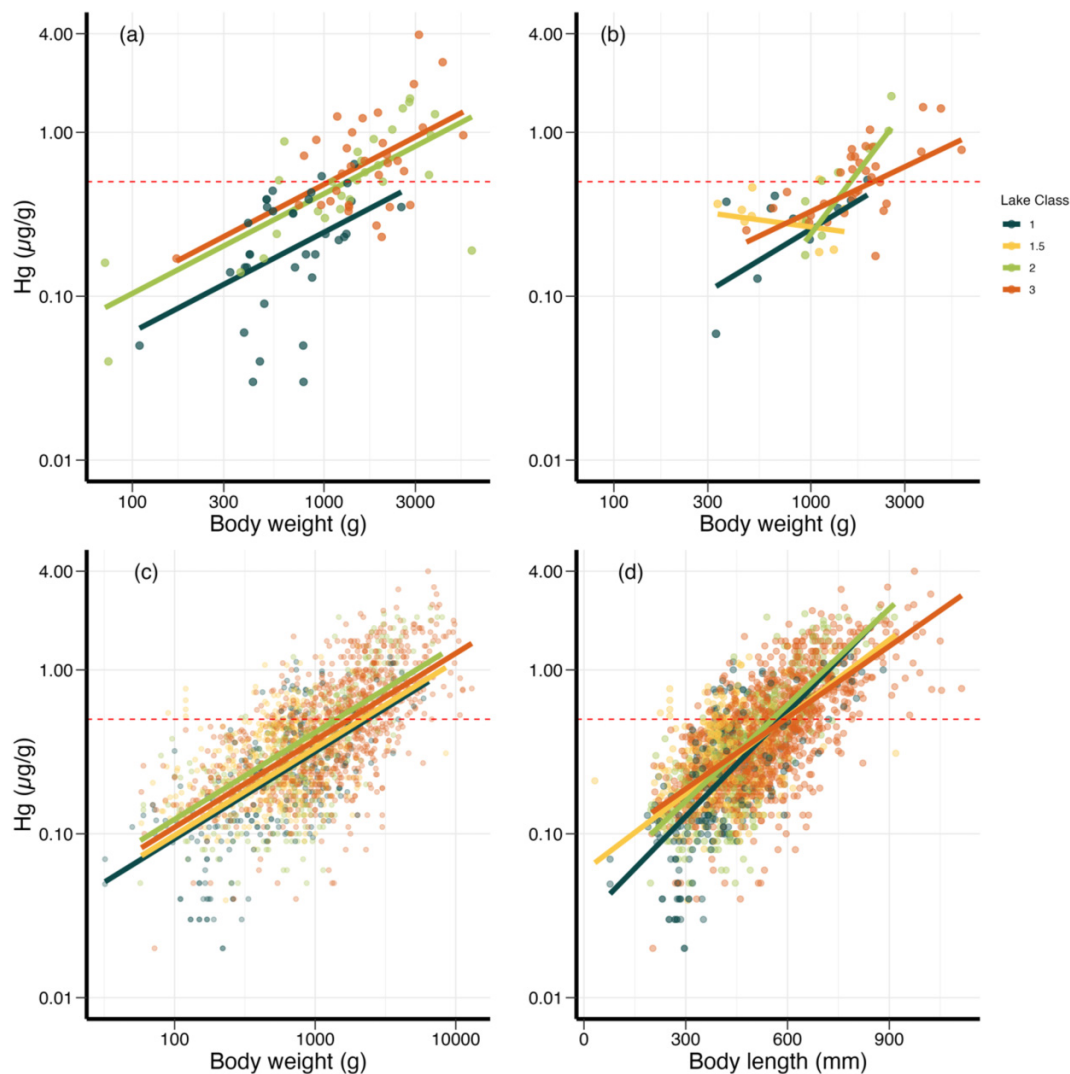
To compare this result with an independent and contemporary dataset (SI.1—Dataset Descriptions), another set of 64 lakes covering a similar geographic range but with samples collected between 1991 and 2022 was assembled (Fig. 2, Table S.2). A new Lake Class, Class 1.5, was also introduced, describing 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 mean lake trout Hg concentrations with the contemporary data set (ANOVA,  $F_{[3,59]} = 5.12$ ,  $p = 0.003$ ,  $R^2 = 0.21$ ), though significant pairwise differences in mean Hg concentrations were only detected between Class 1 and Class 3 lakes (Figs. 1b and 1d).

As such, neither the data from Cabana et al. (1994) nor our contemporary dataset support categorical food chain length alone as a primary determinant of lake trout Hg. The theory put forward by Cabana et al. (1994) assumes stepwise lake trout Hg increases with the inclusion of each new pelagic prey item in the food web from Class 1 to Class 3, independent of body size, which was not observed. Yet, other lake trout Hg models, including an analysis reported 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). Indeed, applying one-way ANOVAs to mean body weight as a response variable in place of mean Hg concentrations reveal nearly identical results as those of lake trout Hg for both datasets (Mean body weight ~ Lake Class ANOVA, Cabana data:  $F_{[2,93]} = 12.46$ ,  $p < 0.0001$ ,  $R^2 = 0.21$ ; contemporary data:  $F_{[3,59]} = 9.46$ ,  $p < 0.0001$ ,  $R^2 = 0.27$ ; SI Fig. S1). Similar statistical outcomes between mean Hg and mean body weight response variables across Lake Classes indicate that any significant result of Hg concentrations between Lake Classes may be misinterpreted, simply reflecting 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 relationship 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, we reanalyzed both the historic Cabana et al. dataset and our independent dataset using an Analysis of covariance (ANCOVA). After confirming ANCOVA assumptions (residual normality, variance homoscedasticity, absence of interaction between covariate and categorical predictor), a reanalysis of Cabana's data confirmed that mean body weight was a significantly more important predictor of mean lake trout Hg concentrations compared to Lake Class (log body weight  $F_{[1,92]} = 94.97$ , partial variance explained = 46.5%,  $p < 0.0001$ ; Lake Class  $F_{[2,92]} = 8.04$ , partial variance explained = 8.0%,  $p = 0.0006$ ; Fig. 3a). To test if the significant improvement of model fit from including body size could be replicated, we applied ANCOVA to our 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 versus leverage diagnostic plot. Further, a

**Fig. 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.



significant interaction was identified when testing for an interaction between the covariate and categorical predictor, precluding the ability to examine the effect of Lake Class across the gradient of body weight (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 (Fig. 3b and Table 2). Different statistical conclusions between the two datasets based on the interaction (or lack thereof) between Lake Class and body size, as well as potential shortcomings associated with reducing body weight and Hg observations to lake-wide population

means as in the Cabana et al. (1994) assessment indicate that the approaches taken to date may be inadequate for best describing either intra- or inter-lake variation in lake trout Hg.

### The influence of body size on lake trout Hg dynamics—moving from populations to individuals

To investigate if 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 applied to the contemporary

**Table 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).

Model test	Data type	Model syntax	Model coefficients					Model summary				
			Lake class	Intercept	Mean weight	Fish length × Lake class	DOC	Variable	df	F	p value	R <sup>2</sup>
ANOVA <sup>†</sup>	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	/	/	/					
ANCOVA <sup>†</sup>	Mean (geometric)	log(Hg) ~ log(mean weight)*lake class	3	− 0.80	/	/	/					
			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	
Linear mixed-effect model	Individual	log(Hg) ~ log(body weight) + lake class + (log(body weight)   Lake ID)	2	− 12.37	/	0.86	/	log(mean weight) × lake class	3,54	5.92	0.0014	
			3	− 5.06	/	− 0.15	/					
			1	− 4.82	0.53	/	/	log(fish weight)	1, 44.4	470.73	< 0.0001	0.44
Linear mixed-effect model	Individual	log(Hg) ~ fish length * lake class + (fish length  Lake ID)	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 × lake class	3, 51.9	5.04	0.0015	
Linear mixed-effect model	Individual	log(Hg) ~ fish length * lake class + DOC + (fish length  Lake ID)	3	− 2.56	/	0.0021	/					
			1	− 4.25	/	0.0051	0.13	Fish length	1,67.19	493.50	< 0.0001	0.59
			1.5	− 3.41	/	0.0036	/	Lake class	3, 65.64	3.73	0.015	
Linear mixed-effect model	Individual	log(Hg) ~ fish length * lake class + DOC + (fish length  Lake ID)	2	− 3.74	/	0.0045	/	DOC	1,73.5	35.52	< 0.0001	
			3	− 3.37	/	0.0033	/	Fish length × lake class	3,65.59	6.00	0.0011	

**Note:** Only model coefficients necessary for estimating Hg concentrations for a given model are presented. 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:  $Hg = \exp(-6.37 + 0.73 \cdot \log(\text{Mean Weight}))$ , LMM, Lake Class \* Ind. Length, Class 1.5:  $Hg = \exp(-2.71 + 0.0024 \cdot \text{Ind. Length})$ , LMM, Lake Class \* Ind. Length + DOC, Class 3:  $Hg = \exp(-3.37 + 0.0033 \cdot \text{Ind. Length} + 0.13 \cdot \text{DOC})$ . DOC, dissolved organic carbon.

<sup>†</sup>These models should NOT be used for predicting lake trout Hg concentrations. Lake-wide Hg and body size averages disregard important individual-level variation.

dataset, allowing for potential random variance in the relationship between fish body size and Hg among lakes to be accounted for when considering the overall relationship within and among Lake Classes (individual observations of fish size were not reported in the Cabana et al. (1994) publication, and could not be analyzed similarly). Comparisons of fish Hg with different metrics of body size (i.e., body weight and body length) can also be made. Only body weight was reported for the Cabana et al. 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).

Mixed-effect 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 initial full model prior to any optimization included the interaction between body size (weight or length) and Lake Class, along with random slopes and intercepts of lake trout Hg with the covariate (body size) for unique lakes within Lake Classes. After finalizing model structure, model assumptions were verified using histograms of residuals, plots of residual versus fitted values, Q-Q plots, and by testing for a non-significant correlation between model residual and fitted values. A Type III Satterthwaite ANOVA was 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 (Bartoń 2025). Restricted maximum likelihood was used for assessing the final model, though traditional maximum likelihood methods were used for optimizing fixed effects during model selection. 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).

With individual body weight included as a covariate, the predicted increases in lake trout Hg associated with higher Lake Classes were not observed. Model parsimony was found with the independent effect of Lake Class and individual body weight, and incorporating lake as a random slope with body weight (eq. 1):

$$(1) \quad \log[Hg] \sim_{\log} bodyWeight + lakeClass + (_{\log} bodyWeight | lakeID)$$

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 2; Fig. 3c). Allometric scaling between individual body weight and Hg revealed 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 (Fig. 3d). 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:

$$(2) \quad \log[Hg] \sim bodyLength * lakeClass + (bodyLength | lakeID)$$

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 (Fig. 3d). 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 (Fig. 3d). 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 (where Mysis were present), whereas at larger sizes, lake trout in Class 1 and 2 lakes had higher Hg than Class 1.5 and 3 lakes at a given length.

Despite using more sophisticated models, expected step-wise increases in lake trout Hg concentrations with increasing Lake Class were not observed, suggesting that strictly top-down model structures considering only food chain length with body size are insufficient. 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, our linear mixed-effects model estimates that Class 3 lake trout would actually have lower Hg concentrations than individuals of the same size from any Class 1 or 2 lakes. Further, when considering strictly 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 web.

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 (Fig. 3d). 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 typically are 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. Mysis % lipid content is generally much higher than that of zooplankton (Paterson et al. 2022), and 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). Unfortunately, the data necessary to fit robust growth models for lake trout populations across different Lake Classes—particularly those with and without Mysis—are unavailable for our study, preventing a



direct quantification of the energetic and biomagnification benefits associated with improved predator–prey mass ratios. However, in a whole-lake acidification experiment where *Myxosoma* and other lake trout prey were extirpated, lake trout body condition declined significantly (Mills et al. 1987, 2000), and has yet to recover despite lake chemical recovery and the return of all other pre-acidification prey species (Rennie, unpublished data).

While biotic mechanisms likely explain lake trout Hg bioaccumulation through prey type and availability, they disregard the potential controls to the supply of Hg to lakes at the base of the food web (Table 1). Ultimately, broader ecosystem-level processes influence the bottom-up availability of Hg to aquatic ecosystems (Branfireun et al. 2020), and given their importance for describing Hg concentrations in other freshwater fishes (Lescord et al. 2019; Sumner et al. 2020; Thomas et al. 2020), must be considered when examining patterns of lake trout Hg concentrations among lakes with varying food web complexity as described above.

## What's missing? A lakescape assessment of lake trout Hg concentrations

We present two complimentary 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, and 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 (Pichler and Hartig 2023). We therefore selected PCA and random forest (RF) algorithms as alternative but complementary 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 are also useful for comparing multivariate approaches that differ in how data are 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 can incorporate all individual body size observations and can handle many predictor variables (including those that are nonlinear) without the fear of over-parameterizing the final model (Prasad et al. 2006).

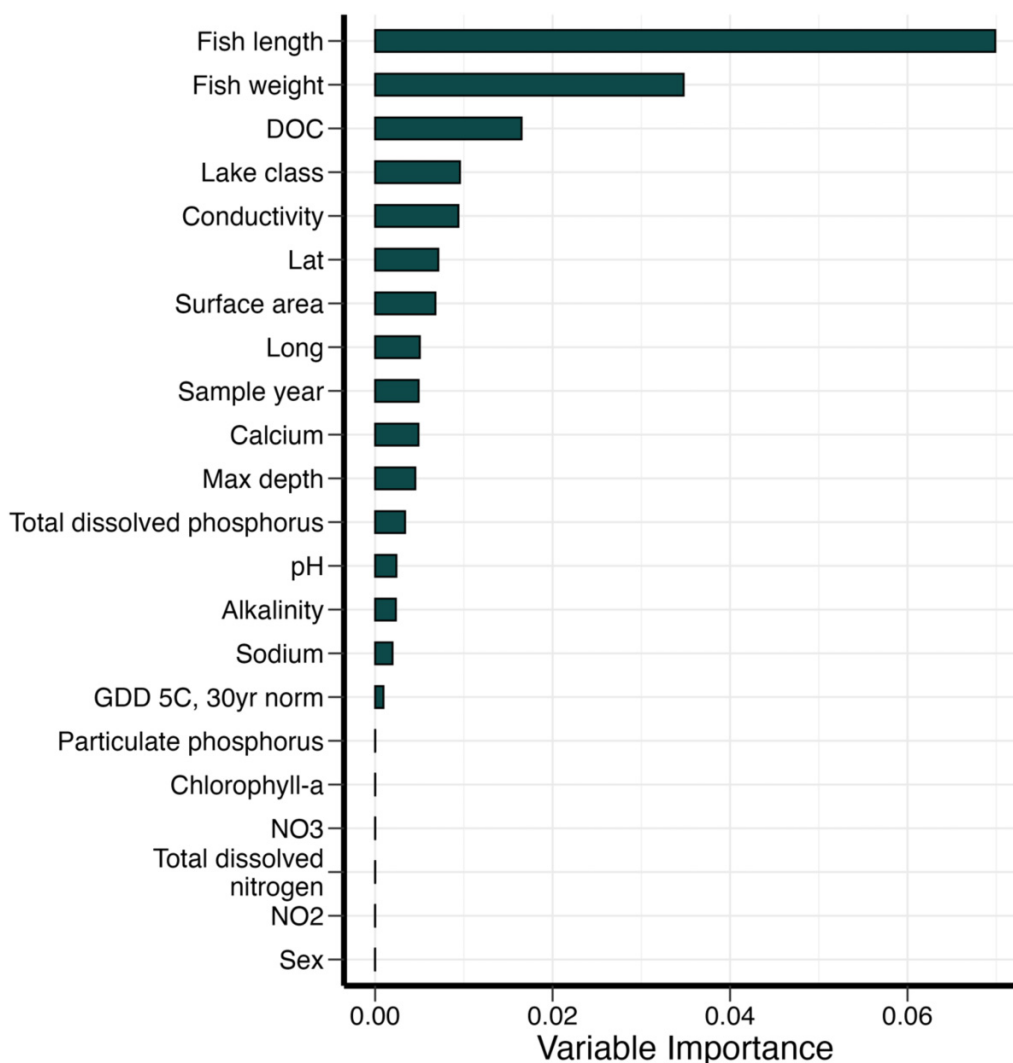
Based on the fundamental differences between these two approaches, data used for PCA and RF were handled slightly differently. PCA was performed using a subset of available physicochemical variables. PCA can describe relationships

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;  $\mu\text{g/L}$ ), pH, dissolved organic carbon (DOC;  $\text{mg/L}$ ) and latitude were included as variables based on a priori assumptions of their roles modifying lake trout Hg dynamics (see Table 1). Water chemistry data were collected from long-term sampling programs conducted by the Ontario Ministry of Natural Resources and IISD-Experimental Lakes Area between May and June of a given year, and mean chemistry values were applied across multiple sample years (SI.1—Dataset Descriptions; Table S.3). Four lakes (Big Salmon, Class 3; Opeongo, Class 2; Sherborne, Class 1; Smoke, Class 2) had some combination of variables that were not reported (DOC, TDP, and pH). For each instance of a missing value, the dataset mean for that variable was imputed (imputed DOC, TDP, and pH  $n = 4$ ; imputed values in Class 1  $n = 1$ , Class 2  $n = 2$ , and Class 3  $n = 1$ ). 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, 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, nonlinear or complex relationships (Breiman 2001; Tang and Ishwaran 2017). As such, the RF model was built using the same set of lakes and water chemistry data used in PCA but with additional physicochemical, lake morphometric, and individual-level lake trout variables (see Fig. 4 for additional variables relative to those included for PCA). 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, 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, and model fit was described with overall model  $R^2$  and the out-of-bag error rate (Ehrlinger 2022; Ishwaran and Kogalur 2023).

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 (Fig. 5). PC axis 1 explained 40% 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

**Fig. 4.** 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 ( $R^2 = 0.71$ ; model variance out-of-bag performance error = 0.051).

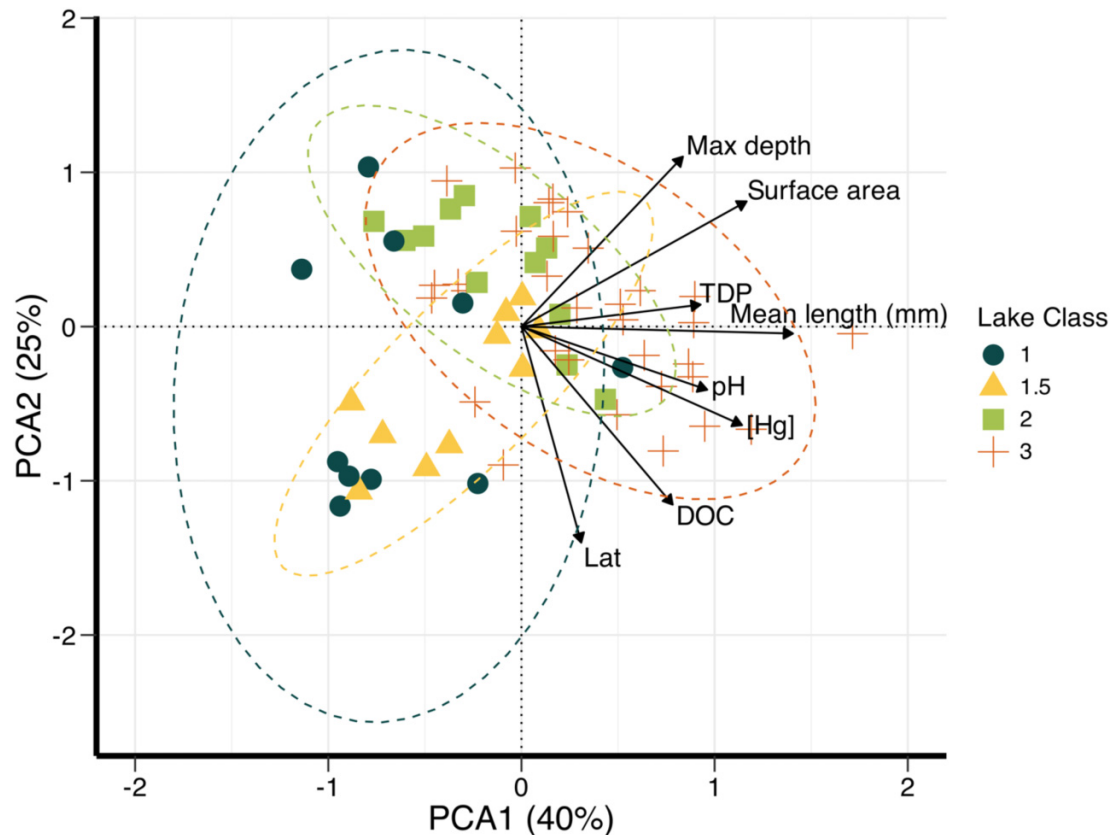


produce larger lake trout (Shuter et al. 1998; McDermid et al. 2010; Lester et al. 2021); our analysis suggests that these larger fish from large, productive lakes likely also harbour higher Hg concentrations (e.g., Fig. 3 body size relationship). PC axis 2, explaining an additional 25% of the PCA, relates high mean Hg concentrations to geographic and lake morphology variables (maximum depth and surface area), which are known to affect lentic DOC concentrations (Sobek et al. 2007; Toming et al. 2020). In other words, smaller, darker, and more northern lakes were associated with higher lake trout Hg concentrations. Globally, food web Hg biomagnification is positively associated with latitude (see Lavoie et al. 2013), while increased DOC in more northern lakes has also been associated with higher Hg concentrations walleye and Northern pike (Thomas et al. 2020). 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 poor ability to independently predict lake trout Hg concentrations

on the basis of Lake Class at the population level (i.e., using lake means).

Our 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; Fig. 4). 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 (Figs. 3–5), 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 lake trout body length as a more useful predictor than body weight, particularly at small and large body sizes (Figs. S.2.a and S.2.b). Length may provide better estimates of Hg concentrations for very slowly eliminated contaminants like Hg (Madenjian et al. 2012) because it

**Fig. 5.** 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.



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). In our survey of Ontario lakes, DOC was the third most important variable for predicting lake trout Hg levels, outperforming Lake Class by 74%. The next three most important variables in the RF were related to lake physicochemical characteristics (conductivity, latitude, and surface area). DOC concentrations are often correlated with aqueous MeHg availability (Lavoie et al. 2019; Branfireun et al. 2020) and are also linked to latitude and lake size (Sobek et al. 2007; Toming et al. 2020). While latitude and surface area may indirectly determine DOC concentrations, and therefore Hg availability (Thomas et al. 2020), they may also indirectly influence Hg bioaccumulation by driving variation in temperature-dependent growth rates of stenothermic fish like lake trout (McDermid et al. 2010). While body size presumably is linked to Hg bioaccumulation over time, lake physicochemical characteristics (i.e., DOC, latitude, and surface area) likely modulate the baseline supply of Hg to aquatic biota, ultimately influencing biomagnification. Given the rapid response of aquatic organisms to Hg availability (Paterson et al. 1998; Blanchfield et al. 2022), our RF model underscores the necessity of accounting for bottom-up ecosystem controls on Hg

supply to lake trout, in addition to understanding how body size affects bioaccumulation processes.

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 our analysis indicates that Lake Class alone does not appear capable of independently describing lake trout Hg dynamics, it reveals that a basic understanding of food chain length (i.e., Lake Class) remains a valuable consideration for at least two reasons. First, our analysis shows that Lake Class acts as a proxy for understanding how generalized predator–prey mass ratios can affect life history traits; in our analysis, the presence or absence of *Mysis* altered the bioaccumulation slopes of lake trout. This is supported by literature demonstrating how predator–prey mass ratios can modify Hg concentrations via growth efficiency (Trudel and Rasmussen 2006; Shuter et al. 2016). Second, 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 our 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 description of lake trout Hg dynamics, important ecosystem variables identified in PCA and RF models were added to the linear mixed-effect model of lake trout Hg accumulation which described the interaction between Lake Class 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 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, resulting in a full linear mixed-effects model of:

$$(3) \quad \log[Hg] \sim \text{bodyLength} * \text{lakeClass} + \text{DOC} + \text{surfaceArea} \\ + \text{latitude} + \text{longitude} + (\text{bodyLength} | \text{lakeID})$$

Model diagnostics, significance, and fit were all assessed as described previously. Despite high variable importance in the RF analysis, latitude and longitude were removed from the model due to high variable collinearity (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, and as such was removed to create a parsimonious final model of:

$$(4) \quad \log[Hg] \sim \text{bodyLength} * \text{lakeClass} \\ + \text{DOC} + (\text{bodyLength} | \text{lakeID})$$

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 2). Consistent with the model where DOC was not included (i.e., eq. 2), the interaction between Lake Class and body size was significant ( $F_{[3,65.59]} = 5.99$ ,  $p = 0.0011$ ). In the present model, DOC was significant ( $F_{[1,73.49]} = 35.52$ ,  $p < 0.0001$ ), 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  $\times$  Lake Class interaction accounted for 3.2%). Model residuals were normally distributed (Fig. S.3), although there was some indication that modelled Hg concentrations were slightly overestimated at low observed Hg levels and underestimated at high Hg levels (Fig. S.4).

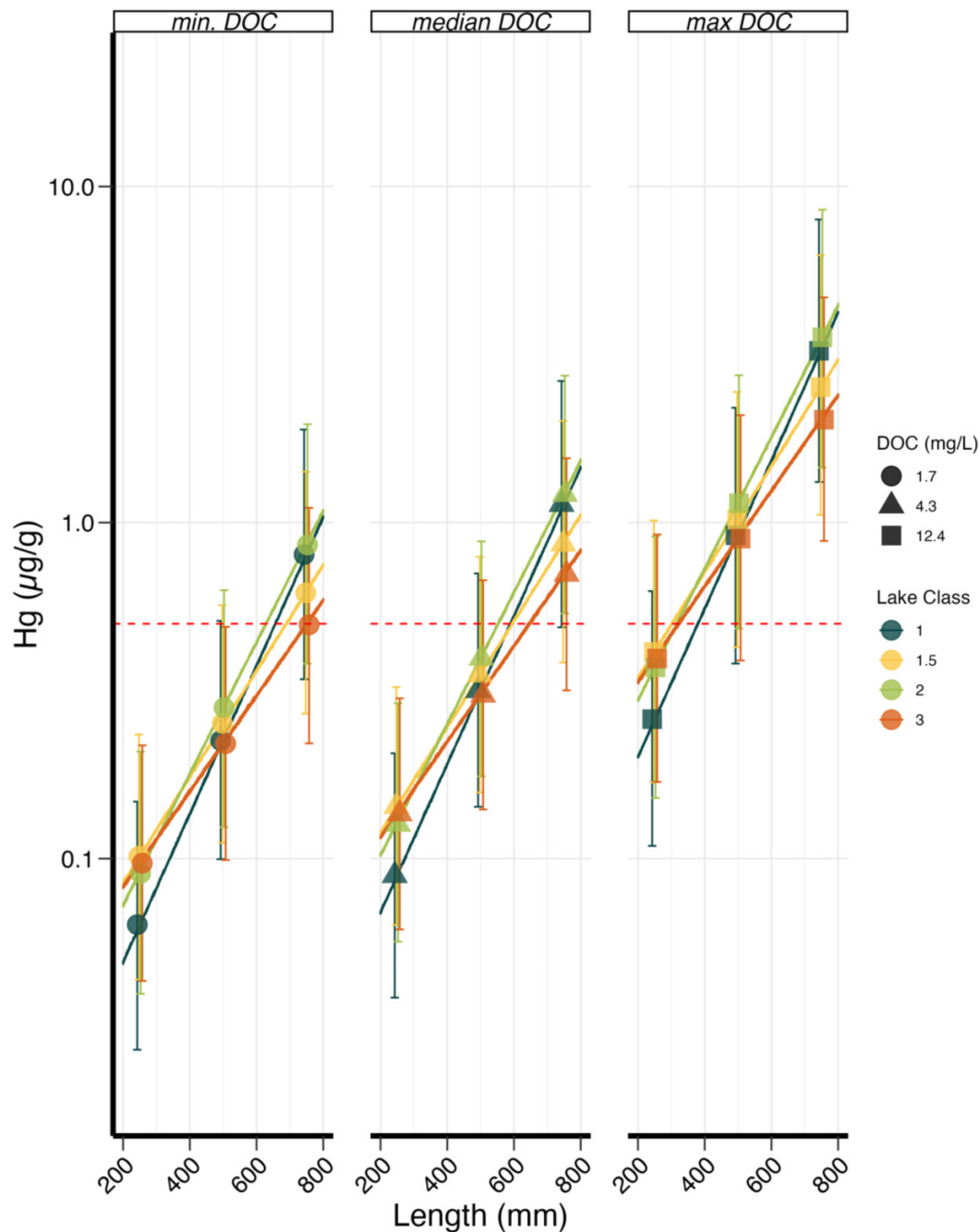
This DOC-informed mixed model can be used to explore conditions under which lake trout from Ontario lakes are likely to experience elevated Hg contamination. Using model coefficients (Table 2), lake trout Hg concentrations were estimated across Lake Classes and gradients of observed lake trout body sizes and DOC concentrations from our contemporary data set (Fig. 6). Model predictions and visualizations continue to support body size being the primary determinant of Hg concentrations, though it is clear that 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  $0.5 \mu\text{gHg/g}_{\text{fish}}$ . For example, a 500 mm lake trout in a median DOC lake ( $\sim 4.3 \text{ mg/L}$ ) from any Lake Class is predicted to have Hg concentrations below that of the national guidelines (Fig. 6, middle panel). However, as DOC increases to  $12.4 \text{ mg/L}$  (the maximum observed DOC concentration in our 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 (Fig. 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 (Fig. 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 (Fig. 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 DOC lake (Fig. 6, left panel) would not be subject to a consumption advisory, though same-sized individuals from a low DOC Class 1 or 2 lake may have nearly twice as much Hg and would be above national consumption guidelines.

To better understand lake trout Hg dynamics, we have shown that predictive models must consider the influence of environmental drivers and their impact on MeHg availability at the base of food webs as well as food chain length and body size. 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, 2016, and as reviewed in Table 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 our contemporary dataset of 64 lakes, conditions varied widely in surface area (16–34 518 ha), maximum depth (12–186 m), total dissolved phosphorus levels ( $2.6\text{--}39.6 \mu\text{g/L}$ ), and DOC concentrations ( $1.7\text{--}12.35 \text{ mg/L}$ ). We have shown that DOC must be accounted for to understand lake trout Hg dynamics across Ontario lakes (Fig. 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). 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). While latitude, DOC and pH have been shown as determinants of walleye, Northern pike, and white sucker Hg concentrations (Sumner et al. 2020; Thomas et al. 2020), our ecosystem-based approach and model selection identified DOC as the key environmental variable explaining lake trout Hg dynamics of the



**Fig. 6.** The influence of dissolved organic carbon (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 (750 mm) 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.



variables considered here. Most regional and provincial water monitoring agencies already collect DOC samples, which provides the potential for targeted sampling efforts to validate predictions of our model, and potentially provide information for further development of lake trout consumption guidelines for lakes where DOC concentrations (or lake colour) and standard fish body lengths are known. In cases where DOC data are unavailable, a model excluding DOC

but incorporating latitude still provides a useful, albeit less predictive, approach for describing lake trout Hg dynamics across Ontario lakes (SI.2; Figs. S.5, S.6).

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 our 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 determinantal 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 our model predicts that relatively smaller lake trout have lower Hg concentrations, this may be counteracted by the effects of increasing DOC (e.g., Fig. 6). Additionally, the challenges of existing in warmer, oxygen-depleted environments are predicted to reduce prey conversion efficiency via increased metabolic costs and could lead to Hg further concentrating within muscle tissues (Trudel and Rasmussen 2006).

## Summary and conclusions

Through various iterations of data and model complexity, we show that understanding lake trout Hg dynamics in lakes typical of Ontario boreal and north-temperate ecosystems 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 (i.e., 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 proposed that lake trout Hg should increase with increasing food chain length, and while our assessment here indicates that Lake Class does not predict Hg concentrations as Cabana et al. (1994) suggested, a coarse categorization of prey communities is still useful (particularly *Mysis* presence), especially when predicting Hg concentrations from the smallest and largest individuals within a population. Size-corrected trophic position contaminant models for fishes from inland lakes provide valuable insights into how diet influences both consumer life history traits and contaminant dynamics (Swanson and Kidd 2010; Johnston et al. 2022; Drouillard et al. 2024); however, our study and the work of others emphasizes the importance

of considering environmental determinants of aqueous Hg–DOC in the case of lake trout—especially in small inland lakes like those examined here. With DOC concentrations being identified as an important determinant of lake trout Hg concentrations, future studies could assess the temporal importance of changing DOC concentrations on Hg dynamics of specific lake trout populations, while also forecasting how future brownification is likely to affect Hg concentrations going forward.

Here, we show that lake trout Hg risk in Ontario lakes 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). We 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. With further targeted field validation of our model, this ecosystem-scale framework may provide a means of updating contaminant guidelines based on regional water quality data and existing food web structure information which may be easier and more cost effective to sample than multi-day campaigns to capture fish. Consumption guidelines are generally based on fish length because it is an easily measurable characteristic for anglers. Similarly, our analysis suggests that a practical recommendation for anglers—aligned with current Health Canada guidelines—would be to consider the nutritional and health trade-offs from consuming lake trout from darker, tea-stained lakes, where Hg concentrations are more likely to exceed advisory thresholds. Lastly, our findings on the drivers of lake trout Hg dynamics from boreal and north-temperate lakes align closely with those observed in other freshwater fishes from this region despite diverse feeding strategies, thermal preferences and habitat use among the different species (e.g., Walleye, Northern Pike, White Sucker; Sumner et al. 2020; Thomas et al. 2020).

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### Data availability

All data and R code necessary to replicate the analyses and visualizations within the manuscript are housed in a Dryad repository that can be found at <https://doi.org/10.5061/dryad.0gb5mkm96>.

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Formal analysis: AJR

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Supervision: MDR

Visualization: AJR

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Writing – review & editing: MG, SPB, MDR

### Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2024-0197>.

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