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ORIGINAL PAPER

Spiny water flea invasion alters fish mercury bioaccumulation rates

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Abstract *Bythotrephes cederströemi* are a predatory cladoceran zooplankter that have invaded numerous inland lakes in North America, many of which are stratified and support offshore fishes like Cisco (*Coregonus artedi*). While changes in zooplankton community composition following *Bythotrephes* invasion predict an increase in Cisco mercury concentrations (Hg), this phenomenon was not detected from a survey evaluating temporal changes in Cisco Hg across a broad range of lakes varying in the presence or absence of *Bythotrephes*. Here, we compare temporal changes in Cisco bioaccumulation slopes (i.e., slopes of relationships between Cisco Hg and trophic position) from lakes experiencing *Bythotrephes* invasion over the study period to those already invaded (as a reference) over similar time periods. Our results show that bioaccumulation slopes after *Bythotrephes* invasion either changed direction entirely (from positive to negative relationships) or decreased in elevation relative to those prior to invasion. No such pattern was observed in previously invaded reference lakes. Reductions in Cisco bioaccumulation slopes and/or intercepts following *Bythotrephes* invasion suggest that conversion efficiency (and therefore growth) of Cisco increased after invasion (i.e., less Hg accumulates in fish at an equivalent trophic position after vs. before invasion). Back-calculated Cisco growth rates and size-at-age from a second complimentary study were greater in the presence of *Bythotrephes* than without, further supporting the hypothesis that changes in Hg bioaccumulation are likely due to increased conversion efficiency among invaded populations. These findings highlight the potential importance of foraging energetics over and above shifts in trophic position in modifying fish contaminant concentrations.

Keywords Methylmercury · Aquatic invasive species · Stable isotopes · Trophic position · Biomagnification · Coregonidae

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Introduction

Human exposure to mercury (Hg) from wild-caught fish is a major concern globally; many provincial and state agencies publish regularly-updated consumption guidelines for wild-caught fish, with Hg being the main contaminant of concern for inland populations (e.g., Government of Ontario 2023; Minnesota Department of Health 2023). Concerns over high Hg levels in commercially caught fish have closed multimillion dollar inland fisheries for years (Jansen 2021). Fish accumulate methylmercury (MeHg; much more toxic than elemental Hg), which in humans and other vertebrates is a powerful neurotoxin, causing disability and death in humans at unsafe exposure levels (Broussard et al. 2002; Aschner 2002; Mosa and Duffin 2017). Approximately ¼ of all fish caught by anglers are retained, presumably for consumption (Fisheries and Oceans Canada 2019). Further, rural communities and First Nations rely heavily on fish from inland lakes as a source of nutrition (Marushka et al. 2021). As such, understanding what factors affect fish Hg is of significant interest to both policy makers and consumers.

Though a large and growing body of literature exists regarding factors that impact fish Hg (and therefore human exposure), very little is known regarding the potential impacts of lower- and mid-trophic invasive species on consumer fish Hg (Eagles-Smith et al. 2018). Generally, factors such as pH (Qian et al. 2001; Ikingura and Akagi 2003), dissolved organic carbon (Cope et al. 1990; Suns and Hitchin 1990; Driscoll et al. 1995), influx from wetlands (Greenfield et al. 2001) and sediment MeHg (Rennie et al. 2005) are strongly correlated with MeHg concentrations in aquatic organisms. Literature showing that contaminants (including Hg) increase with trophic level has been used to suggest that the addition of novel mid-trophic species consumed by fish may elevate the trophic position (and therefore contaminant concentrations) of higher-trophic fish and other organisms (Rasmussen et al. 1990; Cabana et al. 1994; Vander Zanden and Rasmussen 1996). Elevated trophic position of fish may also result from community-level impacts of mid-trophic invasions, rather than via direct predation of invasives per se (Rennie et al. 2011). Broadly, invasive species are speculated to have major impacts on Hg biomagnification, and are commonly cited as a cause for concern regarding fish Hg dynamics in ecosystems (e.g., Azim et al. 2011; Gandhi et al. 2014; Nanini-Costa et al. 2016; Gerig et al. 2019; Brown et al. 2022).

Despite this broad speculation, the impacts of species invasion impacts on fish Hg have been identified as a critical information gap (Eagles-Smith et al. 2018). Further, studies that have sought to explicitly evaluate the impacts of mid-trophic invaders (i.e. either invertebrates or lower-trophic prey fish) on higher-trophic consumers (i.e. fish) have almost exclusively demonstrated no impacts on the Hg concentrations of these higher-trophic consumers (Johnston et al. 2003; Hogan et al. 2007; Thomas et al. 2016; Prestie et al. 2019; Barst et al. 2020; Jurajda et al. 2020) or observed declines in consumer Hg (Rennie et al. 2010). Exceptionally, increased Hg concentrations in Lake Simcoe Lake Whitefish (*Coregonus clupearformis*) were observed following invasions of dreissenid mussels and spiny water flea (*Bythotrephes cederströemi*, *Bythotrephes* hereafter; Korovchinsky and Arnott 2019), but similar impacts were not observed in other benthic or planktivorous fishes over the same time period (Gewurtz et al. 2011).

A frequently proposed mechanism for the inability to detect changes in consumer Hg following mid-trophic invasions is increased conversion efficiency in consumer or competitor species in the presence of invaders (Johnston et al. 2003; Swanson et al. 2003; Rennie et al. 2011; Johnson et al. 2014), but this process has yet to be demonstrated empirically. A potential increase in conversion efficiency—often inaccurately described as 'growth dilution' (Trudel and Rasmussen 2006)—could result from increased feeding and/or processing efficiency of native fishes in the presence of invading prey species, either through reduced energy allocated to food acquisition or feeding on more energy dense prey. In turn, these processes would facilitate greater biomass accumulation (growth) per unit food consumed, and Hg concentrations in tissues would decrease as a result (Trudel and Rasmussen 2006; Ward et al. 2010).

Contaminant accumulation in organisms is a sum of several processes and depends on several factors, including concentrations at the base of the food chain, concentrations in prey/assimilation efficiencies, metabolic processes that affect contaminant accumulation, and consumer trophic position (Kidd et al. 2012). Patterns in the relationships between organism contaminant concentrations (Hg in particular) with trophic position have been employed to provide insight into the relative contribution of these processes on food web Hg accumulation. Specifically, changes in the intercept of this relationship would indicate changes in the contaminant at the base of the food web, whereas changes in trophic position which represent the lengthening/shortening of food chains, or increases/decreases in slope (Kidd et al. 2012; Lavoie et al. 2013) should reflect changes in conversion, growth or trophic transfer efficiency (e.g., altering the amount of Hg accumulated per trophic position).

A model system for testing these relationships between mid-trophic invasions on contaminant levels of higher-level consumers are Cisco (*Coregonus artedi*) lakes invaded by *Bythotrephes*. *Bythotrephes* are a broadly-distributed invasive species in North America. Introduced to the Laurentian Great Lakes in the mid-1980s (Bur et al. 1986), they spread rapidly into inland lakes throughout Canada and the United States (Sprules et al. 1990). A large, predatory cladoceran, *Bythotrephes* consume zooplankton at higher rates than they are produced, causing rapid declines in zooplankton diversity and biomass following establishment (Yan et al. 2002; Barbiero and Tuchman 2004; Kerfoot et al. 2016). Common impacts on invaded lakes include substantial reductions in microcrustacean biomass (particularly cladocerans and cyclopoid copepods), resulting in decreased prey availability for other zooplanktivores (Yan et al. 2002; North et al. 2013; Kerfoot et al. 2016; Gillis and Walsh 2017). *Bythotrephes* consumption can even exceed that of native zooplanktivorous fishes (Bunnell et al. 2011). While the early growth rates of percids appears to decline in the presence of *Bythotrephes* (Hansen et al. 2020; Gartshore and Rennie 2023), the impacts of *Bythotrephes* on the growth of larger-bodied planktivores remains unknown. Cisco are a broadly-distributed planktivorous fish in Canada which are known to include *Bythotrephes* in their diets preferentially over other zooplankton (Coulas et al. 1998).

The purpose of this study was to understand how the impacts of *Bythotrephes* establishment affect both the growth and mercury concentrations of Cisco. To do this, we combined results of two separate, previously unpublished but complementary studies. First, comparing both archived and contemporary tissue collections, we evaluated changes in bioaccumulation slopes among Ontario Cisco populations which had experienced *Bythotrephes* invasion with those where zooplankton communities were stable (i.e., *Bythotrephes* were established and present over the entire study period; Fig. 1). Stable isotopes of nitrogen ($\delta^{15}N$) scale positively with trophic position (by approximately 3.4‰; Minagawa and Wada 1984), allowing this chemical tracer to be used as a proxy for trophic position. Second, we compared individual Cisco growth among lakes in which *Bythotrephes* were well established with those where they were absent (Fig. 1) to determine whether changes in Hg concentrations/bioaccumulation patterns in Cisco documented in the tissue comparison study could be explained by changes in conversion efficiency.

Methods

Field sampling- tissue comparisons

Frozen, historical Cisco carcasses from all lakes (except Lake Simcoe) were from sampling performed during a 1995 survey of Cisco (Coulas et al. 1998) and were obtained from the Ontario Ministry of Natural Resources and Forestry (OMNRF) Algonquin Fisheries Assessment Unit and the Great Lakes Institute for Environmental Research at the University of Windsor. Contemporary samples from lakes sampled by Coulas et al. (1998) were obtained in 2006 using a series of gillnets targeting hypolimnetic coregonid species (Rennie et al. 2010). Of the lakes included in the Coulas et al. (1998) survey, no historical carcasses were available for Lake Joseph. Additionally, *Bythotrephes* were found in Young Lake only one year prior to sampling in 2006 and was deemed unlikely to reflect any impact of *Bythotrephes* after such a short period of time. Both lakes were excluded from the current study. Lengths and weights of all fish were recorded in the field within 8 h of collection. Cisco were collected from Lake Simcoe during 1983 and 2009 as part of a depth-stratified index netting program (Rennie et al. 2013). Samples from Lake Simcoe in 2006 were obtained from the Offshore Benthic Index Netting program run by the OMNRF Lake Simcoe Fisheries Assessment Unit.

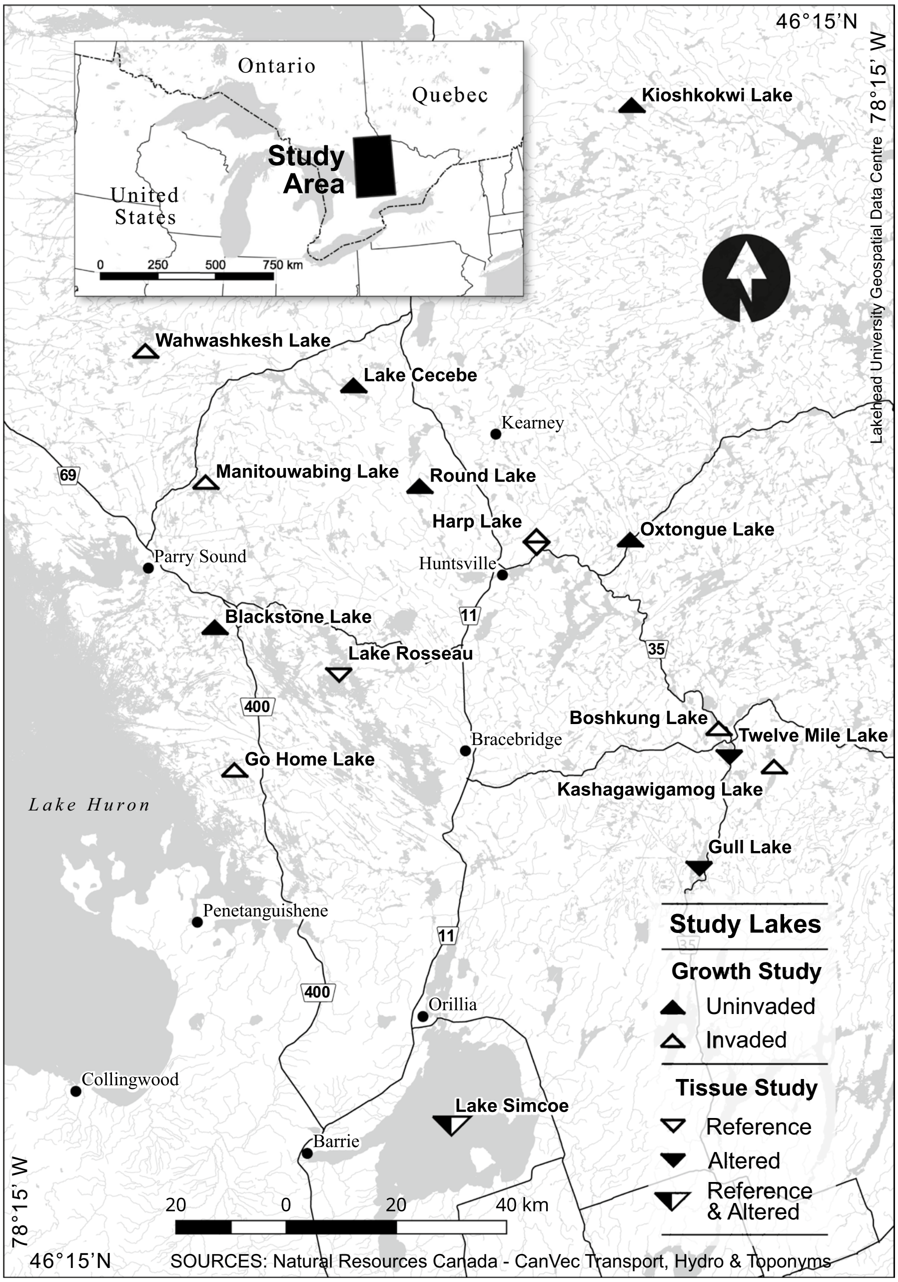

Fig. 1 Location of lakes included in study. Note symbols for Harp Lake indicating inclusion in both studies, and colouring for Lake Simcoe indicating its use in both reference and altered categories (utilizing different time periods; see text)

Experimental design- tissue comparisons

Lakes in our tissue comparison analysis were divided into two categories based on sampling dates relative to the reported dates of *Bythotrephes* detection (Table 1). 'Altered' lakes were defined as those invaded by *Bythotrephes* in the interim between the two sampling periods, resulting in an alteration of the native zooplankton community. Reference lakes in this study were defined as those where *Bythotrephes* were already well established in the lake at both first and last sampling (i.e., no alteration in the zooplankton community by *Bythotrephes*; Coulas et al. 1998, Rennie et al. 2013). Because we had tissue samples from fish at three time periods from Lake Simcoe, we examined both altered and reference states for this lake, over two different time periods (Table 1).

Table 1 Lakes under study for temporal Cisco tissue comparisons

Category	Lake	Surface area (ha)	Z_{max} (m)	First sampling (historical)	Year *Bythotrephes* detected	Last sampling (contemporary)
Altered	Gull Lake	996	49.1	1995	2003	2006
	Twelve Mile Lake	337	27.5	1995	2003	2006
	Lake Simcoe*	72,500	41.5	1983	1993	2006
Reference	Harp Lake	72	37.5	1995	1993	2006
	Lake Rosseau	6,374	90.0	1995	1989	2006
	Lake Simcoe*	72,500	41.5	2006	1993	2009

Altered lakes are those where *Bythotrephes cederströemi* invaded in the interim between first and last sampling. Reference lakes are those where *Bythotrephes* were present during the entire time period

*Lake Simcoe appears under two categories due to the relation of timing of sampling with the time of *Bythotrephes* invasion. See text for details

Tissue sampling

Fish were sampled for tissues from either fresh specimens in the field within 8 h of collection, or from archived carcasses when partially thawed. Tissues for mercury and stable isotope analyses were taken below the dorsal fin and above the lateral line. Two small pieces of tissue were removed from the carcass of the fish, carefully excluding bone and skin. Each tissue sample was placed in a labelled whirl pack for later analysis and frozen at −20 °C.

Tissue analyses

Mercury analyses for fish were conducted by two laboratories. A subset of contemporary Hg concentrations across all lakes was analyzed by the Sportfish Contaminant Section of the Ontario Ministry of Environment, Conservation and Parks (MECP) using cold-vapour flameless atomic absorption spectroscopy. Details regarding MECP methods and quality assurance/quality control are outlined in detail elsewhere (French et al. 2006; Choy et al. 2008; Goulet et al. 2008). Most other samples (including all archived historical samples) were analyzed on a Milestone DMA-80 direct mercury analyzer following EPA method 7473 SW-846 at the University of Toronto Mississauga. Between 0.1 and 0.2 g (wet mass) of thawed fish muscle tissue was weighed into nickel boats and loaded onto the analyzer. Mean estimates of NRC reference material DORM-2 ranged between 4.51 and 4.75 mg g^{-1} in each of 11 runs conducted during the study (based on 25 determinations total), and 4.66 mg g^{-1} averaged over all runs, which was well within the 95% confidence limits reported by NRC (4.64 ± 0.26 mg g^{-1}). Duplicate samples of tissues were not significantly different (paired t-test, $t_{40} = 1.16$, $P_{\text{two-tailed}} = 0.25$), indicating good repeatability of results using this method. Subsets of tissues analyzed using both the DM-80 and MECP methods were also not statistically different (paired t-test, $t_{45} = 0.7$, $P_{\text{two-tailed}} = 0.49$; Rennie et al. 2010), indicating good agreement between both laboratories.

Tissues for stable isotope analyses were weighed, dried for 24 h at 60 °C to constant weight and reweighed to determine water content. Samples were then ground to powder with a mortar and pestle. Between 0.2 and 0.4 mg of dried tissue was weighed into tin capsules, placed into trays and sent for analysis of both $\delta^{15}N$ and $\delta^{13}C$. Samples were analyzed at the laboratories of Isotope Tracer Technologies Inc. (Waterloo, Ontario) on a Delta continuous flow stable isotope mass spectrometer (Micromass) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108). The laboratory reported analytical error of $\delta^{13}C$ and $\delta^{15}N$ determinations at 0.2‰ and 0.3‰ respectively. One in every 20 samples was run in duplicate. For $\delta^{15}N$, the mean difference between paired samples was approximately 0.2‰ (paired t-test, $t_{12} = 3.64$, $P_{\text{two-tailed}} = 0.003$), which was within the reported analytical error of the instrument for this analyte. Duplicate samples were not significantly different for $\delta^{13}C$ (paired t-test, $t_{12} = -1.315$, $P_{\text{two-tailed}} = 0.2$).

Field sampling- growth comparisons

Ageing structures were available only for a subset of populations used for mercury and stable isotope analyses. Therefore, results from a second study were used to compare Cisco growth rates based on back-calculations between invaded and non-invaded lakes (James 2010). Sampling for this study was conducted in 2007 on several lakes, one of which was also included in the effort comparing Cisco tissues over time (Harp Lake; Table 2). Fish were captured from each lake using bottom set NORDIC nets (Morgan and Snucins 2005) during June and July. Nets were set just below the thermocline and perpendicular to the shore contour between 1700 and 1800 h and retrieved the next day after 12 h of fishing. Fishing sites within lakes were selected at random from a numbered grid overlaid on the bottom contour related to the thermocline depth on the day of sampling. In lakes larger than 1000 ha, sampling was restricted to regions of the lake that were readily accessible by boat. These methods were used until 40–50 individual Cisco were captured from each lake (between 2 and 8 sets per lake; see James 2010 for additional detail). Captured fish were identified, measured (total length), weighed (round weight, g) and sexed based on the identification of gonads upon dissection. Cisco scales were taken anterior to the dorsal fin and above the lateral line for assignment of ages to annuli (see below).

Experimental design- growth comparisons

Lakes were divided into those that were previously invaded by *Bythotrephes* and those that were not (or invaded only in the year of fish sampling). For three lakes classified as uninvaded, surveys of the zooplankton community in 2006 failed to detect *Bythotrephes*. However, *Bythotrephes* were detected in these lakes in 2007 when fish were captured. Given their absence in a survey year immediately prior to Cisco collections, and the low densities of *Bythotrephes* observed during Cisco collections (James 2010), it was assumed that back-calculated growth patterns of these individuals represented their growth trajectory in the absence of *Bythotrephes* (or during a period where *Bythotrephes* densities were so low as to avoid detection and unlikely to have significant ecosystem-level impacts).

Interpretation of ageing structures and back calculations

Acetate imprints of scales were made from 6–8 clean, non-regenerated scales for each fish. Of these, one clear scale imprint from each fish was magnified and digitized (4008 × 2706 dpi) using a camera mounted

Table 2 Lakes under study for contemporary back-calculated Cisco growth comparisons

Category	Lake	Surface area (ha)	Z_{max} (m)	Year invaded
Uninvaded	Blackstone	516	58.0	–
	Cecebe*	1130	82.4	2007
	Kioshkokwi	1127	24.4	–
	Oxtongue*	249	32.0	2007
	Round*	190	21.0	2007
Invaded	Boshkung	716	71.1	2003
	Go Home	487	30.0	1993
	Harp	72	37.5	1993
	Kashagawigamog	818	39.7	1991
	Manitouwabing	1010	33.6	2000
	Wahwashkesh	1720	45.4	2000

Lakes indicated as either invaded or uninvaded at the time of sampling, and date of invasion is reported. Lakes where *Bythotrephes* were detected in the year of sampling are marked with an asterisk (*) and were classified as uninvaded for the purposes of analyses of back-calculated growth (see text)

[*] *Bythotrephes* not detected when lakes were sampled in 2006 (James 2010)

onto a Leica dissecting scope. Magnification was recorded for each image taken. Scale age and growth interpretations were made using the Calcified Structure Age-Growth Extraction Software, or CSAGES (Casselman and Scott 2000; modified to use Age-Area, version 2008). Age was interpreted from the scale image produced at a known magnification (typically 40X) for each fish by enumerating the number of 'checks' in the circuli that were associated with annuli (Appendix S1, Figure S1). Scale age, along with a rank-based measure of confidence (1 = low, 9 = high) was recorded for each fish. To reduce age interpretation errors, each scale image was interpreted by the same reader a minimum of three times. Plots of length-at-age were also used to identify obvious outliers which were then re-interpreted.

Where differences among interpretations of a single image were found, scales were re-examined and the calcified structure age (CSA) of the highest-ranked interpretation was included in the analysis (Casselman 1987; Casselman and Scott 2000). Additionally, a random selection of 10% of our initial CSA interpretations was compared with that of a duplicate, clear scale imprint from the same fish. Examination of duplicate structures indicated good precision and repeatability; of 56 structures examined in duplicate, only 7 were found to disagree with the age assignment of the first read (12.5%), and only one was off by more than one year (1.7%), which was outside the age range examined in this study (age determined as either 6 or 8 years). Where there was incongruence between interpretations, both scales were re-examined and the determination of the highest-ranked interpretation was used.

To quantify scale growth, measurements were made along the anterior portion of the magnified scale image. A 120° sector was found to best fit the anterior area of Cisco scales. This encompassed the triangular portion from the origin to the dorsal anterolateral and ventral anterolateral lobes (Appendix S1, Figure S1). The most distal circulus associated with each annulus was digitized across this sector. This digitized arc made it possible to calculate the radial lengths from the origin to each annulus for each degree. The mean of these 120 radial measurements was calculated and used to estimate scale size and growth. These multiple measurements could be considered as a surrogate measurement of area, which is much more precise for estimating scale growth than is a single linear measurement, which is normally used when measuring and estimating calcified structure size (Casselman 1987). Cumulative growth was estimated for each year of life, using these mean radial lengths at each annuli. Back calculation of total length-at-scale age for each fish was then estimated from the relationship between scale size and body size (total length), calculated as

$$L_x = \left[\left(L_c - L_0\right)/SR_c\right] * SR_x + L_0 \tag{1}$$

where, with this intercept method, L_x is the body length (as total length) age x, L_c is the body length at capture, L_0 is fish length at the first appearance of the scale, SR_c is the scale radius at capture, and SR_x is the measured scale radius at age x. Body length at the first appearance of scales for Cisco (L_0) was assumed to be 31.5 mm (Hoagman 1970).

To ensure that the back-calculated growth of fish in designated invaded lakes reflected growth during the period where *Bythotrephes* were impacting ecosystems, we only included estimated length at age (L_x) for year classes of fish hatched after the reported date of invasion.

Statistical analyses

Cisco Hg concentrations were analyzed based on wet tissue mass. Archived samples held by OMNRF were evaluated for water content loss, so that unusually high Hg concentrations could be corrected for water content losses, if necessary. We examined water content as a function of lake and time (before, after invasion) using a two-factor fixed effects ANOVA. All statistical analyses and graphs were done using R (version 4.1.2, R Core Team 2021). Water content outliers were identified in residual plots using this model; two fish from Harp Lake in 1995, two fish from Lake Rosseau in 2006 and one fish from Harp Lake in 2006 had water content values between 54 and 71%. However, Hg concentrations were not exceptionally high for these fish compared to others of similar body size, so we did not adjust Hg concentrations in these fish. Low water content was found in 8 of 29 Cisco samples from Lake Simcoe in 1983 with high Hg concentrations; for these samples, Hg measured as concentrations per unit dry mass were adjusted to reflect the mean water content of fish from uncorrected samples (73%). Linear regression between water content with fish size was also evaluated to determine whether changes in water content (via differences in fish size over time) might play a role in shaping our reported results.

We initially evaluated changes in several attributes of Cisco and their tissues over time using a linear mixed effects modelling framework, using the *lme4* package in R. We modelled response variables (base 10 logarithm of Hg concentrations, and untransformed measures of total length, δ^{15}N, δ^{13}C) as a function of lake type (altered, reference) time (historical, contemporary) and their interaction with lake as a random effect, as follows:

$$\text{Response} \sim \text{lake type} * \text{time} + (1|\text{Lake}) \tag{2}$$

Lake was included as a random additive effect primarily to control for among-lake differences that could not otherwise be accounted for in our models, including geographic and/or geological differences in isotopic baselines and Hg deposition/availability among lakes. Significance of fixed effects were estimated using the *lmerTest* package in R, which uses Sattherwaite approximations of degrees of freedom to generate tests for significance. Plots of residuals vs. predicted values and histograms of residuals confirmed that assumptions of heterogeneity of variance and normality were met. We generated 95% confidence intervals around predicted responses for both altered and reference lakes from mixed effects models, using the *bootMer* package in R over 999 simulated values, from which we extracted the 0.025 and 0.975 quantiles.

Second, bioaccumulation of Hg for individual lakes was assessed by examining changes in the slopes of $\log_{10}$(Hg) of Cisco tissue as a function of tissue δ^{15}N for each individual lake using tests of homogeneity of slopes. Where slopes were not different, we used ANCOVA to test for changes in fish Hg with δ^{15}N as a covariate. Fish Hg was $\log_{10}$-transformed in all analyses to satisfy assumptions of normality and linearity with fish size. As body size often scales positively with both fish Hg concentrations and δ^{15}N, relationships between Cisco $\log_{10}$(Hg) and δ^{15}N with body size (total length) were also estimated and reported to help evaluate the degree to which patterns in bioaccumulation might be an artefact of changes in body size (Appendix S1, Tables S1, S2; Figures S2, S3).

Differences in growth (slopes of total length vs. age) were also evaluated for Cisco. Most inland Cisco populations tend to mature by age 4 (Shuter et al. 2005); indeed, initial plots of our data indicated that the size at age of fish began to become non-linear by age 5. However, $\log_{10}$-transformation of age, treated as a continuous variable, provided linear fits across the age range of fish in our study (up to and including age 5).

We therefore fit mixed effects models to back-calculated total lengths of Cisco, with the interaction between $\log_{10}$(Age) and invasion status (binary variable, invaded or non-invaded) as fixed effects, with lake as an additive random intercept and individual fish ID as random slope with $\log_{10}$(Age):

$$\begin{aligned}\text{Total length} &\sim \text{invasion status} * \log_{10}(\text{Age}) \\ &\quad + \left(\log_{10}(\text{Age})|\text{fish}\right) + (1|\text{Lake})\end{aligned} \tag{3}$$

The significance of fixed effects and tests of assumptions were carried out as described above. Significance was assessed compared to an accepted error rate of 0.05 for each test.

Results

Controlling for among-lake differences, we found a significant interaction ($t_{268.3} = 4.79$, $P < 0.0001$) between time period (historical, contemporary) and lake type (altered, reference) for $\log_{10}$-transformed Cisco Hg. Cisco mercury concentrations tended to be lower after *Bythotrephes* invasion in altered lakes but were unchanged in the continued presence of *Bythotrephes* (reference lakes; Fig. 2A). We also found a significant interaction between time period and lake type for total length ($t_{268.9} = 6.9$, $P < 0.0001$), indicating that fish length increased over time in reference lakes, but decreased in altered lakes (Fig. 2B). There was also significant interaction for δ^{15}N between time and lake type ($t_{267.1} = -8.3$, $P < 0.0001$). However, in contrast to both body size and Hg concentrations, mean δ^{15}N declined in reference lakes, but increased slightly in altered lakes (Fig. 2C). Finally, there was a significant interaction

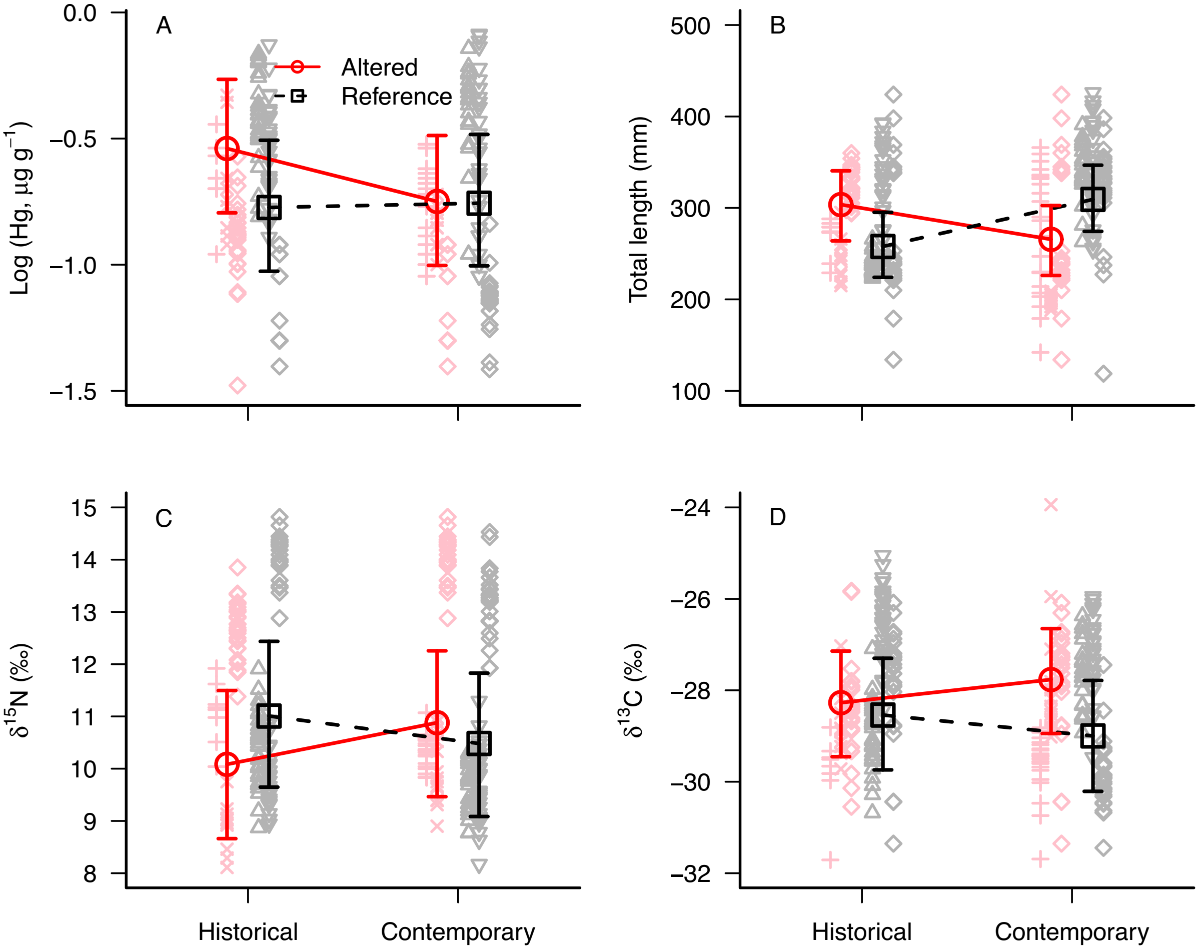

Fig. 2 Predicted means of main effects from mixed effects models (controlling for among-lake differences) representing mean responses of Cisco (A, $\log_{10}$-transformed Hg; B, total length; C, $\delta^{15}N$ and D, $\delta^{13}C$) over time (historic vs. contemporary) for altered lakes (those invaded by *Bythorephes* between historic and contemporary time periods) and reference lakes (those where *Bythotrephes* were already established). Error bars are 95% bootstrapped prediction intervals from mixed effects models. Individual observations are indicated as faded symbols. Altered lakes: Gull Lake, vertical cross; Twelve Mile Lake, ex mark; Lake Simcoe (1983–2006), diamond; Reference lakes: Harp Lake, triangle; Lake Rosseau, inverted triangle; Lake Simcoe (2006–2009), diamond. Means and individual lake data in each time period are slightly offset to avoid overlap

for $\delta^{13}C$ ($t_{267.4}$ = -3.5, $P = 0.0005$), with a slight shift towards more positive values in altered lakes, and a slight decrease in reference lakes (Fig. 2D). Patterns in mean shifts for individual lakes generally followed the pattern predicted by mixed effects models (Table 3).

Water content was consistently lower in contemporary samples than in archived carcasses (3% on average, $F_{1,213} = 186$, $P < 0.0001$), but differences varied over time among lakes, ranging from 1 to 5% (significant interaction; $F_{4,213} = 14.7$, $P < 0.0001$). Water content differences over time were lower by 4–5% in reference lakes, but only by 1–3% in altered lakes. Water content in Cisco muscle tissues decreased with body size (slope = 0.00019% per mm total length; $F_{1,221} = 50$, $P < 0.0001$). Given this pattern, all else being equal, increases in fish size would be expected to lead to increases in fish Hg concentrations; by contrast, larger fish in reference lakes did not have higher Hg concentrations.

Differences were observed in Hg bioaccumulation between time periods for altered lakes (experiencing

Table 3 Means of Cisco length, Hg concentrations, and δ^{13}C and δ^{15}N isotopes between historical and contemporary time periods in lakes where *Bythotrephes* invaded between time periods (altered) and lakes where *Bythotrephes* were present in both time periods (reference)

Category	Lake	Total length (mm)		Hg (µg/g)		δ^{15}N (‰)		δ^{13}C (‰)	
		< 1996	2006	< 1996	2006	< 1996	2006	< 1996	2006
Altered	Gull Lake	268 (7.7) *8*	280 (13.5) *24*	0.23 (0.03)	0.18 (0.01)	11.1 (0.20)	10.4 (0.06)	−29.8 (0.30)	−29.6 (0.13)
	Twelve Mile Lake	246 (7.1) *11*	200 (1.5) *16*	0.22 (0.04)	0.15 (0.01)	8.9 (0.14)	10.1 (0.17)	−28.8 (0.22)	−27.9 (0.33)
	Lake Simcoe[1]	329 (3.3) *28*	272 (11.0) *46*	0.14 (0.01)	0.07 (0.004)	12.7 (0.01)	14.0 (0.07)	−28.4 (0.19)	−27.9 (0.20)
Reference	Harp Lake	237 (1.8) *32*	339 (6.8) *21*	0.41 (0.03)	0.42 (0.03)	10.4 (0.12)	9.6 (0.11)	-28.9 (0.13)	−27.6 (0.16)
	Lake Rosseau	322 (8.3) *30*	333 (9.8) *30*	0.31 (0.02)	0.36 (0.04)	9.7 (0.10)	9.7 (0.13)	−26.5 (0.14)	−27.2 (0.16)
		2006	2009	2006	2009	2006	2009	2006	2009
	Lake Simcoe[1]	272 (11.0) *46*	322 (9.8) *30*	0.07 (0.004)	0.07 (0.003)	14.0 (0.07)	13.2 (0.11)	−27.9 (0.20)	−29.8 (0.13)

One standard error of the mean is presented (in brackets). Sample sizes (italics) are reported under total length means only but are the same for all measured parameters

[1] Lake Simcoe appears under two categories due to the relation of timing of sampling with the time of *Bythotrephes* invasion. See text for details

Bythotrephes invasion), and these patterns were distinct from those observed in reference lakes. In altered lakes, bioaccumulation slopes were marginally but significantly different for both Gull and 12-Mile lakes, switching from positive historically to negative or null after the establishment of *Bythotrephes* (Fig. 3A, C; Table 4). In Lake Simcoe, while slopes of Hg bioaccumulation were similar before and after *Bythotrephes* invasion, the elevation of the relationship declined significantly (Fig. 3E; Table 4). Among all three altered lakes, Cisco above a particular trophic level (corresponding to δ^{15}N of 9‰ in 12 Mile, 10.5‰ in Gull, and at all δ^{15}N in Lake Simcoe) had lower Hg concentrations after the arrival of *Bythotrephes* (Fig. 3). In reference lakes, where *Bythotrephes* were present in both time periods considered, there was either no difference in bioaccumulation slopes or intercepts between years (Harp Lake, Lake Rosseau; Fig. 3B, D; Table 4), or the intercept of the relationship actually increased compared to historical samples (as opposed to a decrease observed in altered lakes; Fig. 3F; Table 4).

Further examination of Cisco Hg concentrations and δ^{15}N with body size were consistent with patterns revealed in mixed effects models and bioaccumulation; generally, across Cisco body sizes sampled, Hg concentrations in each lake tended to decrease after *Bythotrephes* invasion, despite increases in δ^{15}N. By contrast, both Cisco Hg and δ^{15}N tended to decrease in reference lakes or show no difference with body size (Appendix S1, Figure S2, S3; Table S2, S3).

Linear mixed effects models applied to back-calculated Cisco length-at-age (controlling for among-individual and among-lake differences) demonstrated a significant interaction between invasion status and $\log_{10}$ age ($t_{383.1} = -9.1$, $P < 0.0001$); the slope of the line fit to back-calculated lengths at age was steeper for invaded than non-invaded lakes, indicating more rapid growth rates and larger size at age of Cisco in lakes in which *Bythotrephes* had established (Fig. 4).

Discussion

The patterns observed across our two datasets—reduced Cisco Hg bioaccumulation in lakes following *Bythotrephes* establishment and increased growth rates of Cisco in *Bythotrephes*-invaded lakes—provides the first direct evidence we know of that increased conversion efficiency following species invasions can explain negligible or reduced concentrations in fish contaminants following invasions

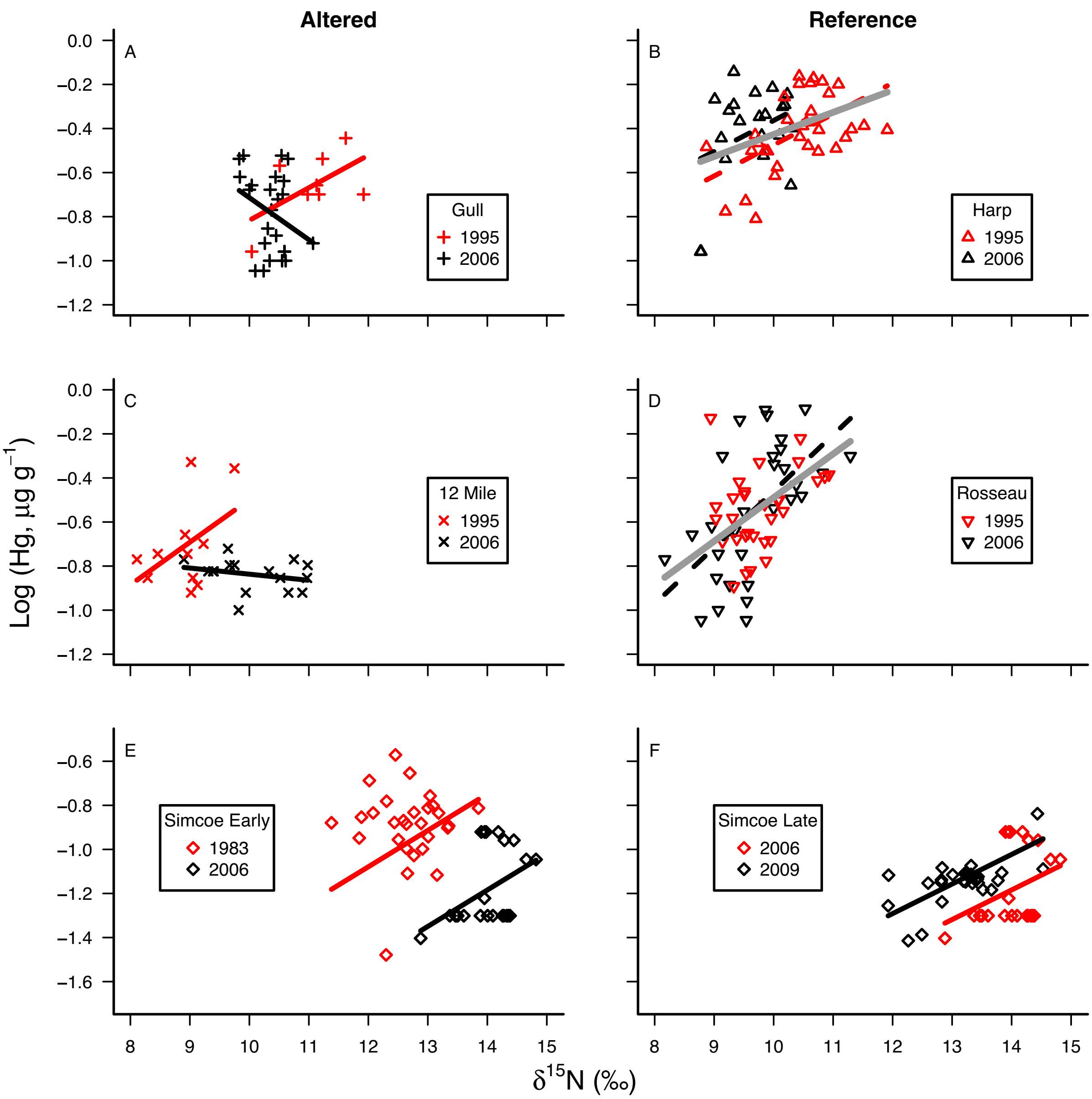

Fig. 3 Cisco bioaccumulation slopes (relationships between $\log_{10}$-transformed Hg concentrations and $\delta^{15}N$ isotopic values) for altered lakes (those invaded by *Bythorephes* between historic and contemporary time periods; left panels) and reference lakes (those where *Bythotrephes* were already established; right panels). Red symbols and lines represent relationships during historical time periods, and black lines/symbols represent relationships during contemporary time periods. Grey lines show relationships across all years, where relevant. Dashed lines in Panel B show fits for ANCOVA model (see Table 4). Dashed line in Panel D shows fit for the 2006 year only (see Table 4). Note differences in y-axis ranges in panels E, F

observed elsewhere in the literature. Controlling for among-lake variation, Cisco Hg concentrations declined after *Bythotrephes* established, despite increases in trophic position (as indicated by $\delta^{15}N$ values), opposite the predicted pattern of increased Hg with longer food chains (Cabana et al. 1994). Among altered lakes, Cisco Hg concentrations at a similar trophic position were lower after *Bythotrephes*

Table 4 Statistical results of Cisco bioaccumulation patterns (i.e., relationship between Cisco Hg and δ^{15}N, shown in Fig. 3) across time periods in lakes where *Bythotrephes* invaded between time periods (Altered) and lakes where *Bythotrephes* were present in both time periods (Reference)

Category	Lake	Test for homogeneity of slopes	ANCOVA	Linear regression
Altered	Gull Lake	$F_{1,28}=4.4$, $P=0.045$ (+1995, -2006)		
	Twelve Mile Lake	$F_{1,23}=4.7$, $P=0.041$ (+1995, -2006)		
	Lake Simcoe[1]	$F_{1,33}=0.007$, $P=0.93$	$F_{1,34}=26.9$, $P<0.0001$ (1983 > 2009)	
Reference	Harp Lake	$F_{1,49}=0.4$, $P=0.6$	$F_{1,50}=3.93$, $P=0.053$ (1995 < 2006)	$F_{1,51}=8.8$, $P=0.005$ (positive slope)
	Lake Rosseau	$F_{1,56}=2.6$, $P=0.11$	$F_{1,57}=0.14$, $P=0.7$	$F_{1,58}=18.6$, $P<0.0001$ (positive slope)[2]
	Lake Simcoe[1]	$F_{1,33}=0.33$, $P=0.57$	$F_{1,34}=7.8$, $P=0.009$ (2006 < 2009)	

[1] Lake Simcoe appears under two categories due to the relation of timing of sampling with the time of *Bythotrephes* invasion. See text for details

[2] Only the slope for 2006 was significant when considered individually; $F_{1,19}=8.6$, $P=0.008$

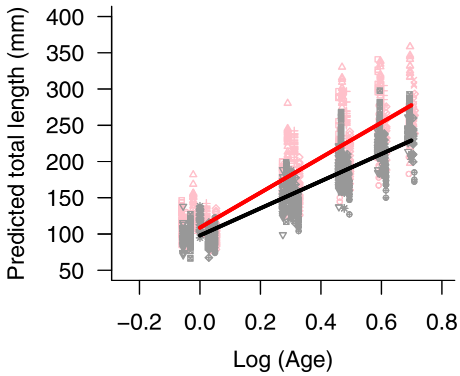

Fig. 4 Comparison of predicted back-calculated growth rates (size in total length at $\log_{10}$-transformed age) from mixed effects models (controlling for among-lake and among-individual differences) between *Bythotrephes* invaded (pink symbols, red line) and non-invaded lakes (grey symbols, black line). Invaded lakes: Square = Boshkung, circle = Go Home, triangle = Harp, vertical cross = Kashagawigamog, ex mark = Manitouwabing, diamond = Wahwashkesh. Non-invaded lakes: Inverted triangle = Blackstone, hashed square = Ceceebe, star = Kioshkokwi, hashed diamond = Oxtongue, hashed circle = Round. Symbols for each lake are offset slightly at each age

invasion, either across all trophic levels as observed in Lake Simcoe (lower intercept), or above a certain trophic threshold (δ^{15}N of 9–10.5‰) due to shallower bioaccumulation slopes observed in Gull and 12 Mile lakes after invasion. By contrast, Hg and δ^{15}N values in reference lakes were relatively unchanged, where bioaccumulation relationships across time periods were either explained by a common relationship, or actually showed higher Cisco Hg concentrations at a given trophic position, opposite the pattern observed in altered lakes. Furthermore, patterns observed in Cisco Hg and δ^{15}N did not simply reflect changes in body size between time periods. These observations, combined with the higher individual growth rates observed among *Bythotrephes*-invaded lakes suggests that reduced Cisco Hg at or above a given trophic position following *Bythotrephes* establishment was due to increased conversion efficiency, as reflected by more rapidly growing Cisco in lakes where *Bythotrephes* had become well established.

The long list of studies to date that have examined fish Hg concentrations following species invasions and found little to no effect have often invoked the concept of growth altering fish Hg to explain their results (e.g., Johnston et al. 2003; Hogan et al. 2007; Barst et al. 2020), but our study is one of the very few to explicitly evaluate the potential impact of invasive species on fish growth in modulating fish Hg concentrations. While 'growth dilution' is commonly invoked as an explanatory factor in reduced fish Hg in the literature, studies clearly demonstrating evidence for increased conversion efficiency leading to reduced fish Hg concentrations are infrequent (Trudel and Rasmussen 2006), and actual empirical demonstrations of the process are similarly scarce (see Ward et al. 2010 as a rare example). Though our study considered different sets of lakes in our evaluations of growth and bioaccumulation (with the exception of Harp Lake), the sum of evidence across both datasets suggests that this same process (i.e., increased conversion efficiency) is likely responsible for reduced or negligible increases in Cisco Hg concentrations following *Bythotrephes* invasion.

Our study also provides some of the only direct evidence of invasive species promoting growth rates of native fishes, which runs counter to the existing narrative (and observations) presented for many other native organisms experiencing non-native species invasions (e.g., Hansen et al. 2020). As two rare exceptions, growth rates of native Walleye were observed to increase over a period where Rainbow Smelt (*Osmerus mordax*) invaded Lake Winnipeg (Johnston et al. 2012), and the intentional introduction of non-native Cisco to Lake Opeongo resulted in a more rapid growth rate of Lake Trout (*Salvelinus namaycush*), at least initially (Matuszek et al. 1990). By contrast, zebra mussels on the Great Lakes and elsewhere have been implicated in reduced adult growth rates of Lake Whitefish (Pothoven et al. 2001; Rennie et al. 2009; Fera et al. 2015), likely due to reductions in foraging efficiency (Rennie et al. 2012). Elsewhere, both Dreissenids and *Bythotrephes* invasion have been shown to reduce early (young-of-year) growth rates of Walleye and Yellow Perch (*Perca flavescens*, Hansen et al. 2020), where the mechanism for negative impacts is likely due to competition for shared zooplankton resources (Gartshore and Rennie 2023). Whether similar impacts on early growth in other primarily zooplanktivorous species, like Cisco, are also apparent remains to be evaluated directly. Though our study demonstrates that age 1 Cisco in invaded populations were actually larger than those from non-invaded populations, these results are based on back-calculated size at age, and therefore represent the growth rates of only those individuals that survived their first year. Slow young-of-year growth in other species is associated with high rates of overwinter mortality (Post and Evans 1989; Johnson and Evans 1991). Understanding impacts of early growth on YOY recruitment as well as potential impacts on adult population size (via recruitment) are both required to further understand the potential impact of *Bythotrephes* invasion on other species of zooplanktivorous juvenile fishes, including Cisco.

Recognizing these uncertainties, if survival of YOY Cisco or other planktivorous fishes are impaired by *Bythotrephes*, then reduced recruitment could lead to lower planktivore densities and declines in population abundance following invasion, suggesting that observed increases in Cisco growth could actually result from competitive release. Among our populations sampled in 2007, the relative abundance (catch per unit effort) of planktivorous fishes (including Cisco) was negatively related to *Bythotrephes* densities, though Cisco relative abundance alone was not (Appendix S1, Figure S4). Regardless of the mechanism for increased growth after *Bythotrephes* invasion (competitive release versus increased foraging/handling and growth efficiency), the ultimate outcome on Cisco Hg bioaccumulation would be the same. To resolve this issue definitively, demographics of Cisco/planktivore communities in response to *Bythotrephes* invasion and estimates of planktivore YOY size and overwinter survival are required.

Our data indicate that observed reductions in Cisco Hg concentrations are not simply due to reductions of Hg at the base of the food web (e.g., reductions in Hg deposition or methylation rates), as reductions in the regional deposition of Hg would be reflected in a decline in biomaccumulation intercepts for our reference lakes over time (which were not observed). There is evidence of regional declines in Hg deposition in North America (Engstrom and Swain 1997; Brigham et al. 2021), where coal-fired power generation has declined and increased emissions regulations have helped to mitigate the release of Hg to the atmosphere (Zhang et al. 2016). Further, reductions in sulphate due to emissions reductions enacted in the 1980s to control acid rain deposition have also lowered lake sulphate concentrations (Nopmongcol et al. 2019), which enhances Hg methylation and fish Hg concentrations; indeed, reduced sulphate deposition has been attributed to reductions in fish Hg concentrations observed elsewhere in North America (Drevnick et al. 2007). However, there was either no significant difference in the elevation of bioaccumulation relationships between years in our reference lakes, or intercepts actually increased over time, suggesting that changes in Hg deposition and/or mobilization in this region were minimal over the time period of study. Supporting this observation, another study reported no temporal change in Cisco Hg concentrations from lakes in this region, but dramatic declines in more northern regions (Rennie et al. 2010).

Further, our data indicate that reductions in Cisco Hg concentrations are not simply an artefact of reduced food chain length. Controlling for among-lake differences, Cisco trophic position actually increased following *Bythotrephes* invasion (as predicted), which on its own would imply an increase in Cisco Hg concentrations (Cabana et al. 1994; Rennie et al. 2011). Compared with other large native invertebrate predators, the trophic position of *Bythotrephes* is similar to native *Leptodora kindtii*, but lower than *Mysis diluviana* or *Chaoborus spp.* (Foster and Sprules 2010). Further, the establishment of *Bythotrephes* appears to have little effect on the trophic position of other invertebrate predators (Foster and Sprules 2010). By contrast, changes in communities of non-predatory zooplankton following *Bythotrephes* invasions have led to zooplankton communities with a higher mean trophic position generally (Rennie et al. 2011), which could also explain the increased δ^{15}N among Cisco experiencing invasion.

Finally, differences in water content cannot explain the patterns we observed in Cisco Hg. First, Hg concentrations of fish with unusually low water content observations were corrected based on average water content values. Second, over all lakes, water content was actually greater in archived (historical) samples, which, all else being equal, would be expected to result in lower Cisco Hg historically compared to contemporary samples. This pattern was only observed in invaded lakes, which had a small reduction in water content between time periods (but larger reduction in Hg over time), compared with reference lakes, which had a greater reduction in water content but no change in Cisco Hg. Additionally, water content decreased with fish size in our study, indicating that larger fish should have higher mercury concentrations due simply to reduced water content (i.e., less dilution by water). By contrast, we observed the opposite–contemporary vs. historical Hg concentrations for reference populations of Cisco were similar, despite the larger body size of contemporary Cisco in these populations.

The observed increase in conversion efficiency of Cisco is likely facilitated in part by direct predation of adult Cisco on *Bythotrephes*. The increase in Cisco δ^{15}N after *Bythotrephes* establishment provides some evidence of feeding on *Bythotrephes* by Cisco, assuming that other invertebrate predators (e.g., *Mysis*, *Chaoborus spp.*) with higher δ^{15}N than *Bythotrephes* (Foster and Sprules 2010) did not previously make up a large proportion of Cisco diets, as they can elsewhere (Trippel and Beamish 1993; Ahrenstorff et al. 2013). *Bythotrephes* are common in Cisco diets when they are present (Coulas et al. 1998; Young et al. 2009; Gatch et al. 2021), and Cisco selectively feed on *Bythorephes* (Coulas et al. 1998). Supporting this finding, the prevalence of *Bythorephes* in Cisco diets increased with increasing *Bythotrephes* densities in our lakes sampled during 2007 (Appendix S1, Figure S5). *Bythotrephes* abundance is patchy both in time (Kelly et al. 2013) and space (Jansen et al. 2017) which can facilitate increased foraging efficiency for predators. If Cisco forage on *Bythotrephes* patches when they are abundant during summer months (e.g., Young et al. 2009), it may promote growth at times of year when fish also tend to accumulate most of their somatic mass (Honsey et al. 2023). In addition, *Bythotrephes* represent a larger-bodied particle compared with smaller native zooplankters, and may therefore also result in reduced handling times and higher foraging efficiency (e.g., Giacomini et al. 2013; Shuter et al. 2016).

Though speculative, our results also suggest increased reliance on benthic resources among *Bythotrephes*-invaded Cisco populations, as predicted δ^{13}C values from our mixed effects model were slightly less negative following *Bythotrephes* establishment. A significant shift towards more benthic resources in Lake Simcoe Cisco following *Bythotrephes* invasion has been reported previously (Rennie et al. 2013), but our study is the first we know of to indicate a broader pattern across several invaded ecosystems. Though we lack baseline data for most of our lakes, the treatment of 'lake' in our statistical models as a random effect controls for baseline isotopic differences among lakes, assuming that lake-specific baselines are temporally more similar than among-lake differences. In the one lake for which isotopic baseline data were available through time (Lake Simcoe), no clear differences in pelagic zooplankton or profundal benthos $\delta^{13}C$ or $\delta^{15}N$ values were apparent between the time periods corresponding to those used in this study (Rennie et al. 2013). Though not documented in our study lakes to any significant degree (Coulas et al. 1998; James 2010), benthic feeding has been observed elsewhere in Cisco (e.g., Trippel and Beamish 1993) and can be an important determinant in their carbon isotopic signatures (Grow et al. 2022). As reductions in zooplankton biomass (Yan et al. 2002; Barbiero and Tuchman 2004; Kerfoot et al. 2016) and production (Strecker and Arnott 2008) are commonly reported responses to *Bythotrephes* invasion, a shift in resource use for these typically pelagic feeding fishes to alternative energy sources is not unexpected.

While our results provide a mechanistic explanation for previous studies indicating no influence of invasive *Bythotrephes* on fish mercury concentrations, they raise further questions as to the degree to which observed growth increases in Cisco are density-dependent and possibly due to a reduction in YOY overwinter survival as suggested for percids (Hansen et al. 2020; Gartshore and Rennie 2023), versus facilitated by *Bythotrephes* as patchy, abundant prey. We recommend future analyses of long-term datasets across broad geographical regions where *Bythotrephes* continue to spread that can also consider changes in the abundance of both fish and their prey across invasion events. While the impacts of *Bythotrephes* on Cisco Hg concentrations reported here may be considered to alleviate concerns over human consumption of this particular species, an overall reduction in Cisco/planktivore abundance in response to *Bythotrephes* invasion could be of equal or greater concern, given their importance as prey to other sport fish species (e.g., Kaufman et al. 2009; Kennedy et al. 2018).

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Author contribution MDR, SEA and LAHJ conceived the study. LAHJ and MDR conducted field work, organized samples for analysis, gathered and analyzed data. LAHJ processed and aged fish. JMC provided expertise and training in fish ageing techniques. WGS, DOH, SEA and JMC provided supervisory support. MDR wrote the first draft of the manuscript. All authors reviewed and provided edits on the submitted version of the manuscript.

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Data availability Data are available upon reasonable request from the corresponding author.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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