Biol Invasions (2023) 25:2643–2658
https://doi.org/10.1007/s10530-023-03065-9

ORIGINAL PAPER

Decline of young-of-year walleye (*Sander vitreus*) growth due to *Bythotrephes* impacts predicted from bioenergetic principles

Danni J. Gartshore · Michael D. Rennie

Received: 22 April 2022 / Accepted: 29 March 2023 / Published online: 12 April 2023

Abstract Invasive species are a major threat to ecosystem structure and function. For example, *Bythotrephes cederströmii* (*Bythotrephes* hereafter) invasions have significantly reduced native zooplankton density and biomass, resulting in competitive interactions with zooplanktivorous fishes. Young of year (YOY) walleye (*Sander vitreus*) are initially zooplanktivorous and have recently been shown to display reduced growth in *Bythotrephes*-invaded lakes. Here, we combined a bioenergetics model for larval walleye with changes in the zooplankton community following *Bythotrephes* invasion and predicted reduced larval walleye growth in the presence of *Bythotrephes*, supporting field observations. The model predicted greater negative impacts on larval walleye growth in oligotrophic compared with mesotrophic lakes, though reduced growth was only significant under oligotrophic conditions. Under *Bythotrephes* invasion, net energy available to growth over the simulated period was often observed to be negative (indicating mass loss). These combined results from the model suggest that *Bythotrephes* invasion could potentially lead to walleye recruitment failure, especially in low nutrient environments. This result was insensitive to differences in annual mean water temperatures ranging from 18.5 to 23.5 °C. As YOY growth, survival, and recruitment are ultimately linked to adult abundance and sustainability of managed stocks, our results highlight the potential impacts of *Bythotrephes* on the sustainability of walleye populations in boreal lakes.

Keywords Invasive species · Larvae · Percidae · Prey density · Year-class strength · Zooplankton

Introduction

The growth and survival of early life stages of fishes, especially during the first month of life, are major limiting factors to fish recruitment and may determine year-class strength (Venturelli et al. 2010; Grote et al. 2018; May et al. 2020). Mortality is often greatest in early life stages of fish, where factors such as predation, temperature, and prey availability are important predictors of larval fish survival (Hoxmeier et al. 2006). Prey availability is considered to be one of the most critical factors to larval fish survival, as inadequate food supply may lead to death and/or slower growth rates, along with decreased swimming speed, thus increasing the risk predation (Jonas and Wahl 1998). For predatory fish like walleye (*Sander vitreus*) which are initially planktivorous, faster growing larvae will reach larger sizes sooner,

D. J. Gartshore (✉) · M. D. Rennie
Department of Biology, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada
e-mail: dgartsho@lakeheadu.ca

M. D. Rennie
IISD Experimental Lakes Area, Suite 325, 111 Lombard Avenue, Winnipeg, MB R3B 0T4, Canada

making ontogenetic diet shifts to benthivory and piscivory earlier. These more rapidly growing individuals, making earlier transitions in diet show selective advantages via increased survival in their first year versus their slower-growing counterparts (Bergenius et al. 2002; May et al. 2020). Larval walleye growth rates (and therefore mortality through to their first year of life) ultimately influence future recruitment of fish populations, and therefore the sustainability of fisheries (Anderson 1988; Post and Evans 1989; Grote et al. 2018). Bioenergetics models can be used to describe the energy and growth budget of fishes, where energetic costs for metabolism, waste loss, and growth can be balanced against the energy consumed from the available prey field (Deslauriers et al. 2017). Understanding how prey availability affects larval growth (and mortality) is therefore critical for identifying recruitment bottlenecks at a particular life stage and represents a critical consideration for informed fisheries management decisions.

Studies have shown that invasive species, particularly *Bythotrephes cederströmii* (hereafter *Bythotrephes*), significantly impact the zooplankton communities of lakes they have invaded (Dumitru et al. 2001; Yan et al. 2002; Boudreau and Yan 2003; Pangle et al. 2007). *Bythotrephes* are a large, predatory cladoceran, and are known to consume zooplankton at higher rates than they are produced, causing rapid decreases in zooplankton diversity and biomass following establishment (Yan et al. 2002; Barbiero and Tuchman 2004; Kerfoot et al. 2016). In some lakes invaded by *Bythotrephes,* microcrustacean biomass (particularly cladocerans and cyclopoid copepods) was reduced by 40–90%, resulting in decreased prey availability for other zooplanktivores (Yan et al. 2002; Kerfoot et al. 2016; Gillis and Walsh 2017; Rantala et al. 2022). Further, *Bythotrephes* can consume more zooplankton than some native zooplanktivores, including larval stages of fishes of economically and culturally significance, such as walleye (Bunnell et al. 2011). Reductions in zooplankton prey availability due to *Bythotrephes* invasion might therefore lead to reductions in the growth, survival, and recruitment rates of other zooplanktivores, including fishes.

Walleye are an important freshwater fish, representing 26% of all fish caught recreationally and 35% of all fish caught commercially in Canada, contributing $7.9 billion to local economies (Fisheries and Oceans Canada 2019a, 2019b). For iteroparous species of fishes and other vertebrates, higher rates of larval recruitment success should lead to more sustainable populations (Shelton and Mangel 2011). However, the response of young-of-year (YOY) walleye survival in relation to invasive species impacts on planktivore communities is largely unknown. *Bythotrephes* is not likely a prey item for YOY walleye during their zooplanktivorous phase, as YOY fishes tend to adopt an aversion behaviour to *Bythotrephes* due to the difficulty of ingesting their long spine (Barnhisel 1991a, b; Compton and Kerfoot 2004). As zooplanktivores, larval walleye diet typically consists of calanoid copepods, cyclopoid copepods, and *Daphnia spp.* (Graham and Sprules 1992). In Minnesota lakes, YOY walleye size was reported as smaller in *Bythotrephes*-invaded lakes compared to non-invaded populations once walleye sizes were corrected for temperature variation that may influence growth (Hansen et al. 2020). As *Bythotrephes* invasions appear to reduce zooplankton abundance, potentially limiting prey availability to zooplanktivores (Rantala et al. 2022), one might predict a decrease in larval fish (i.e., walleye) prey consumption, leading to slower growth, but this potential link between reduced growth and zooplankton prey abundance has only been speculated (Hansen et al. 2020) and not demonstrated experimentally or theoretically.

Other stressors such as climate change may compound the potential negative impacts of species invasions on fish growth. Temperature plays a critical role in the growth of ectothermic aquatic species, particularly regarding temperature dependent metabolic processes (Kitchell et al. 1977). Walleye metabolic rate, food consumption, and growth are known to increase with temperature up to a thermal optimum (Kitchell et al. 1977; Galarowicz and Wahl 2003). Mean annual water temperature varies between lakes and is predicted to increase by 5 °C for most northern temperate lakes by the end of the twenty-first century due to increased greenhouse gas emissions (Maberly et al. 2020). As food consumption demands vary with temperature, it is important to consider the relationship between *Bythotrephes*-induced decreases in prey availability and larval walleye growth across latitudes, and in the case of increasing water temperatures due to climate change.

Our overall objective in this study was to use a bioenergetics approach to evaluate whether changes in the zooplankton community expected due to

Bythotrephes invasions could provide a mechanistic explanation for observed slower growth of larval walleye in *Bythotrephes*-invaded lakes as observed elsewhere (Hansen et al. 2020). Specifically, we aimed to combine information from three different sources to determine this linkage: a characterization of key zooplankton taxa known to be consumed by larval walleye in lakes with and without *Bythotrephes* present, functional response models to predict the consumption of key zooplankton taxa by larval walleye, and a bioenergetics model for larval walleye that uses consumption from the functional response model to predict growth. Using this approach, we sought to determine whether the direction and magnitude of differences in larval walleye growth between lakes with and without *Bythotrephes* predicted solely by the structure of the zooplankton communities they encounter there, were of similar direction and magnitude to observed differences in larval walleye growth between lakes with and without *Bythotrephes* as reported elsewhere. In order to account for potential differences in trophic state of lakes subjected to invasion, which is known to affect the species richness and functional diversity of zooplankton (Barnett and Beisner 2007), we compared these predicted impacts in both mesotrophic and oligotrophic lakes, which represents a range of lake productivity, as well as the range of habitats suitable for both walleye and *Bythotrephes* occupancy (Johnson et al. 1977; Sorensen and Branstrator 2017). Furthermore, metabolic demands are temperature dependent; therefore, we conducted a sensitivity analysis to evaluate the consistency of our findings in both colder, northern lakes as well as in warmer, more southern latitudes.

Methods

Zooplankton biomass

To assess how larval walleye growth rate might change due to the impacts of *Bythotrephes* invasion on zooplankton community structure, we first determined zooplankton densities and basic water chemistry parameters from 265 lakes, both invaded and non-invaded by *Bythotrephes*, across Northern Ontario and Minnesota. Zooplankton densities were available from four mesotrophic *Bythotrephes*-invaded lakes in Minnesota (MN DNR Large Lakes Monitoring Program 2020 [Unpublished raw data]), as well as 34 mesotrophic (33 non-invaded and one invaded) and 227 oligotrophic lakes (188 non-invaded and 39 invaded) in Ontario (Arnott 2021 [Unpublished raw data]). These lakes were separated by invasion status and nutrient status/trophic state (categorized as either oligotrophic, 5–12 µg/L total phosphorus [TP], or mesotrophic 12–24 µg/L TP), based on the Trophic State Index (TSI) of Carlson (1977). For the purpose of this study, and to match groupings employed by functional response curves and available energy density estimates for modelling purposes (McDonnell and Roth 2014), we assumed larval walleye consume exclusively preferred zooplankton, classified broadly as *Daphnia spp.*, calanoid and cyclopoid copepods (Houde 1967).

We simulated larval walleye growth under four different conditions: non-invaded mesotrophic lakes (NM), non-invaded oligotrophic lakes (NO), invaded mesotrophic lakes (IM), and invaded oligotrophic lakes (IO). Zooplankton biomass (µg/L) was estimated from densities (individuals/L) using taxa-specific length-mass regressions reported elsewhere (McDonnell and Roth 2014). To determine if zooplankton densities differed between treatments, we used a bootstrap procedure with 1000 iterations and compared 95% bootstrapped confidence intervals for mean zooplankton densities for each zooplankton taxa considered (*Daphnia spp.*, calanoid and cyclopoid copepods).

Bioenergetics model

We used a bioenergetics model to determine larval walleye growth rates over the first three weeks (21 days) of life, comparing results from representative zooplankton community composition in *Bythotrephes*-invaded lakes and non-invaded lakes. We chose a three week model to simulate the period over which a walleye are typically zooplanktivorous and when zooplankton density is especially important for larval walleye survival (Graham and Sprules 1992; Hoxmeier et al. 2004). At first feeding, walleye typically weigh 0.0040–0.0055 g (Mathias and Li 1982; Malison and Held 1996), so each treatment was run at both these weights as the initial masses for a walleye larva to capture a range of initial larvae sizes. Growth (*G*) was then determined through a daily energy budget equation (Deslauriers et al. 2017) using bioenergetic parameters from Johnston 1999 (Table 1):

$$G_t = C_{r,t} - R_t - F_t - U_t - SDA_t \tag{1}$$

where growth (G; J·g^{-1}·day^{-1}) is the difference between realized consumption ($C_{r,t}$, J·g^{-1}·day^{-1}) and energy losses (the sum of R_t, F_t, U_t, and SDA_t). Losses are characterized as respiration (R_t, J·g^{-1}·day^{-1}), egestion (F_t, J·g^{-1}·day^{-1}), excretion (U_t, J·g^{-1}·day^{-1}), and specific dynamic action (SDA_t, J·g^{-1}·day^{-1}). Each of these metabolic parameters can be further broken down into functions (Eqs. 4–16) dependent on mass (g), prey density (µg/L wet mass), and temperature (°C). We simulated daily temperature (T) using a water temperature curve in Trudel et al. (2000) from Lake Simcoe, ON based on the Julian day (J) using Eq. (2) to represent a typical larval walleye environment in temperate lakes during the first three weeks of their life (Julian day 135 to 155).

$$T = 4.0 + 18.5 \cdot e^{-(J-207)^2/70^2} \tag{2}$$

The resulting growth (G_t; J·g^{-1}·day^{-1}) was then applied to the initial mass (M_t) and energy density of a larval walleye (E_{pred}; 3349 J·g^{-1}; Madon and Culver 1993) using Eq. (3) and input as the mass for the proceeding time-step (M_{t+1}) for the duration of the simulation, as:

$$M_{t+1} = M_t + \frac{G_t \cdot M_t}{E_{pred}} \tag{3}$$

The above model was run for the four treatments of prey availability described previously. If at any

Table 1 Bioenergetic parameter estimates used in this study from Johnston 1999, and D90 parameters from McDonnell and Roth 2014

Symbol	Description	Value
Consumption		
CA	Intercept for maximum consumption	0.51
CB	Slope for maximum consumption	−0.42
CTO	Optimum temperature for consumption (°C)	25
CTM	Maximum temperature for consumption (°C)	28
CQ	Slope for temperature dependence of consumption	2.3
Respiration		
RA	Intercept for maximum standard respiration	0.056
RB	Slope for maximum standard respiration	−0.22
RTO	Optimum temperature for standard respiration	27
RTM	Maximum temperature for standard respiration	32
RQ	Slope for temperature dependence of respiration	2.1
ACT	Activity coefficient	1.0
SDA	Specific dynamic action coefficient	0.15
Waste losses		
FA	Intercept for proportion of consumed food egested	0.428
FB	Coefficient for egestion vs. temperature	−0.222
FG	Coefficient for egestion vs. feeding level	0.631
UA	Intercept for proportion of consumed food excreted	0.0292
UB	Coefficient for excretion vs. temperature	0.58
UG	Coefficient for excretion vs. feeding level	−0.299
D90 estimation		
Ca_1	Baseline calanoid shape parameter	8.55
Ca_2	Modifying calanoid shape parameter	−6.226
Cy_1	Cyclopoid D90 value at length 0	1.11×10^5
Cy_2	Cyclopoid shape parameter	1.167
Da_1	Peak value of *Daphnia* curve	4323.9
Da_2	*Daphnia* shape parameter	38.033

time step the mass dropped to 0 g, the larva was considered deceased. Final length, and total growth (J) between treatments were compared to determine how changes in prey availability due to *Bythotrephes* invasion impact larval walleye growth rates.

Consumption

Prey-specific realized consumption, or the energy input contributed to the specific consumption rate ($C_{j,t}$; g·g^{-1}·day^{-1}) of each prey item (*j*) was based on a multispecies type II functional response model for larval walleye (McDonnell and Roth 2014):

$$C_{j,t} = \frac{C_{max,t} * (\frac{9P_{j,t}}{D90_{j,L}})}{1 + \sum_{j=1}^{n}(\frac{9P_{j,t}}{D90_{j,L}})} \tag{4}$$

where $P_{j,t}$ is the environmental prey density (μg·L^{-1} wet mass) for prey type *j* at time *t*, and $D90_{j,L}$ is the prey density at which 90% of the maximum consumption rate ($C_{\max}$) can be achieved for a walleye at length L (in mm). C_{max} (Eq. 5; g of prey·g of fish^{-1}·day^{-1}) is a function of consumer mass, M_t (g), with parameter estimates of the intercept (CA) and slope (CB) from Johnston 1999.

$$C_{max} = CA * M_t^{CB} \tag{5}$$

Lastly, $P_{j,t}$ is multiplied by 9 so that $D90_{j,L}$ reflects the prey density in which consumption is 90% of C_{max}. We assumed that larval walleye consumed exclusively their preferred prey of calanoid copepods, cyclopoid copepods, and *Daphnia spp.*, whose proportions changed based on larval walleye length (L_t) due to gape limitation (Fig. 1; Houde 1967; Graham and Sprules 1992). The proportions of larvae diet consisted of cyclopoids until they reached 11 mm, then a mix of calanoid and cyclopoids until 16 mm where *Daphnia* began to be the dominant prey item (Fig. 1; Graham and Sprules 1992; McDonnell and Roth 2014). We calculated $D90_{\mathrm{j,L}}$ using equations below and parameters (Table 1) reported by McDonnell and Roth 2014:

$$D90_{cyclopoid,L} = \frac{cy_1 \cdot e^{-cy_2 \cdot L_t}}{1 - \left(\frac{cy_1}{1.367} \cdot 10^5\right) + \left(\frac{cy_1}{1.367} \cdot 10^5\right) \cdot e^{-cy_2 \cdot L_t}} \tag{6}$$

$$D90_{calanoid,L} = \left\{ ca_1 \left[ca_2 \left(\frac{L_t - 16}{|L_t - 16|} \right) \right] \right\} \cdot (L_t - 16)^2 + 6.757 \tag{7}$$

$$D90_{daphnia,L} = da_1 \cdot e^{\left[-\frac{(L_t-16)^2}{da_2}\right]} + 2.788 \tag{8}$$

Due to gape-limitation, larval walleye may not be capable of consuming larger zooplankton or benthos until they reach larger sizes (Johnston and Mathias 1994). To account for poor capture success at small body sizes, we used a walleye capture success (K_t) function using constants a_v (338.45) and b_v (−0.16) derived from laboratory studies on larval walleye

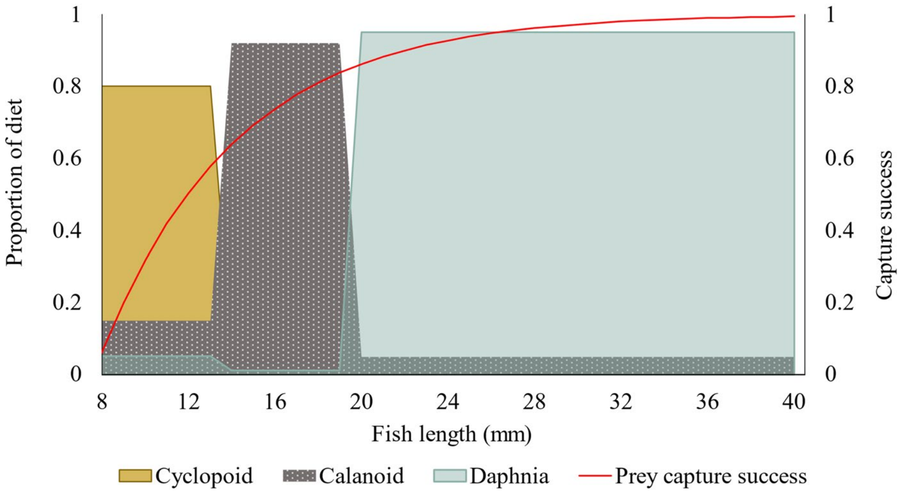

Fig. 1 Diet proportions for the first 40 days of feeding for a larval walleye (*Sander vitreus)* based on length assuming cyclopoid (yellow), calanoid (grey dotted), and *Daphnia* (blue) are the exclusive prey items along with the prey capture success (red line). Data from Johnston and Mathias (1994)

length and zooplankton capture success (Johnston and Mathias 1994):

$$K_t = \frac{100 - \left[a_v \cdot e^{(b_v \cdot L_t)}\right]}{100} \tag{9}$$

Total realized consumption ($C_{r,t}$, J·g^{-1}.day^{-1}) for inclusion in Eq. (1) was then calculated by summing the specific consumption rates of each prey item ($C_{j,t}$, Eq. 4) at each time step using Eq. (10), scaling consumption for capture success (Eq. 9) and converting to units of energy, where $E_{prey,j}$ is the energy density of the respective prey item ($E_{copepods} = 2100$ J·g^{-1}, $E_{Daphnia} = 2600$ J·g^{-1}, McDonnell and Roth 2014):

$$C_{r,t} = \sum\nolimits_{j=1}^{n} (C_{j,t} * K_t * E_{prey,j}) \tag{10}$$

Metabolic costs

To account for costs associated with metabolism from Eq. 1, we used a respiration function which is a mass and temperature-dependent model with an activity multiplier from Deslauriers et al. (2017):

$$R_t = RA \cdot M_t^{RB} \cdot F(T) \cdot ACT \tag{11}$$

$$F(T) = V^X \cdot e^{(X \cdot (1-V))} \tag{12}$$

where,

$$V = (RTM - T)/(RTM - RTO) \tag{13}$$

$$X = (Z^2 \cdot (1 + (1 + \frac{40}{Y})^{0.5})^2)/400 \tag{14}$$

$$Z = ln(RQ) \cdot (RTM - RTO) \tag{15}$$

$$Y = ln(RQ) \cdot (RTM - RTO + 2) \tag{16}$$

where RA is the intercept for maximum standard respiration (g O_2 ·g^{-1}·day^{-1}), RB is the slope for maximum standard respiration, RQ is the slope for temperature dependent respiration, and RTM and RTO are the maximum and optimal temperatures (°C) for standard respiration. We included an activity multiplier (ACT) to account for energy lost to active metabolism which was set to a constant value of 1 (unitless) to remain consistent with other larval walleye bioenergetic models in the literature (Kitchell et al. 1977; Johnston 1999). Egestion (F_t), excretion (U_t), and assimilated energy (SDA_t) costs from Eq. 1 in this study are equivalent to model 4 from Deslauriers et al. (2017) which are functions of consumption rates and temperature.

As the sample size for lake types were unequal, and that for *Bythotrephes*-invaded mesotrophic lakes ($n = 5$) was much smaller than other treatments (i.e., NM $n = 33$, NO $n = 188$, and IO $n = 39$), we used bootstrapping with 1000 iterations to estimate mean larval walleye growth estimates (i.e., length [mm] and growth as units of energy [J]) for the four trophic-invasion treatments (IM, NM, NO, IO). To evaluate the effect of *Bythotrephes* invasion on the growth of larval walleye, we compared 95% bootstrapped confidence intervals of mean larval walleye length and growth estimates between treatments. We calculated bias-corrected and accelerated bootstrap (BCa) 95% confidence intervals when the distribution of mean growth estimates in a treatment were not normally distributed. Bootstrapping is an appropriate resampling method that allows for a characterization of a population of lakes of each category type, particularly when applied to small sample sizes (Dwivedi et al. 2017), and additionally provides an opportunity to report variation in larval walleye growth across varying zooplankton densities, both among and between treatments.

Temperature sensitivity analysis

To assess the sensitivity of the model to temperature, we simulated two temperature regimes, one using the output of Eq. (2), and another with 5°C higher mean annual temperature by altering Eq. (2) to become Eq. (17) below (Fig. 2).

$$T = 4.0 + 23.5 \cdot e^{-(J-207)^2/70^2} \tag{17}$$

The higher daily temperature regime was chosen to represent the projected increase in temperate lake surface water temperatures as predicted by climate change (Maberly et al. 2020), but because it also provides a representation of walleye growth at more southern latitudes. This warmer temperature regime was used an input for separate bioenergetics models using the same zooplankton density estimates, modelling, and bootstrapping methods as above. We

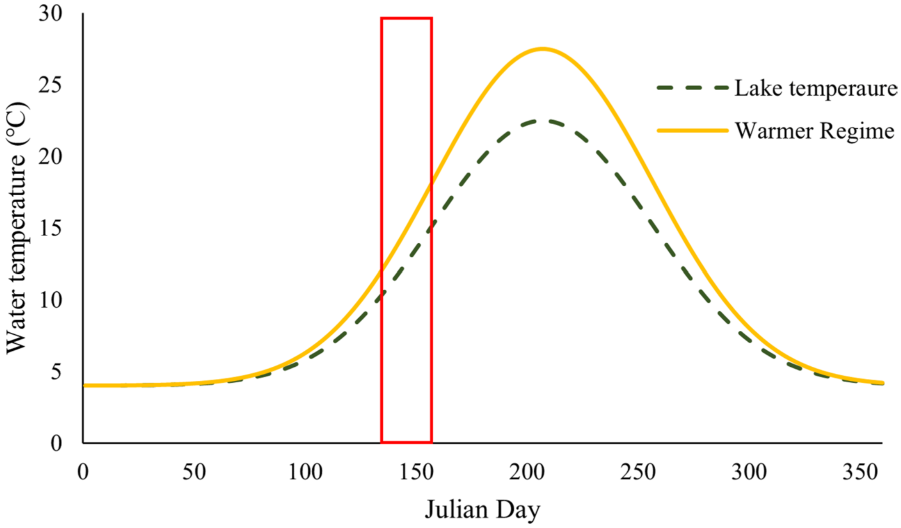

Fig. 2 Lake temperature used for temperature dependent functions of the bioenergetic modelling, estimated from a temperature curve of Lake Simcoe water temperatures based on the Julian day (Trudel et al. 2000). A warmer temperature regime (solid yellow line) was used in a sensitivity analysis to represent lake temperatures towards the end of the twenty-first century as warmer lake surface temperatures are predicted by Maberly et al. (2020). The area highlighted with a red box indicates the Julian days (135–155) and temperatures used for model simulations in this study

compared 95% bootstrapped confidence intervals of the mean final length (mm) between warm and cool temperature regimes to evaluate differences.

Results

Zooplankton biomass

Using the entire set of 265 lakes, biomass of the three taxa (Calanoid, cyclopoid and *Daphnia*) varied both between and within treatments (Fig. 3). Though the bootstrapped means of biomass in invaded mesotrophic lakes appeared lower than in non-invaded mesotrophic lakes, the 95% confidence intervals between treatments overlapped for each of the three taxa, indicating no significant difference of means (Fig. 3). In contrast, mean biomass of each of the three zooplankton taxa was significantly lower in the invaded oligotrophic treatment compared to the non-invaded oligotrophic treatment. There were no significant differences in mean biomass for each of the three taxa between the non-invaded mesotrophic and non-invaded oligotrophic treatments, or between the invaded treatments.

Larval walleye growth

Our larval walleye model predicted faster growth rates under non-invaded conditions compared to invaded conditions in both mesotrophic and oligotrophic lakes, with the non-invaded mesotrophic conditions providing the fastest larval growth (0.82 mm/day). Based on 95% bootstrapped confidence intervals, mean final larval walleye length under the invaded-oligotrophic treatment was significantly smaller than mean larval length under the non-invaded oligotrophic, and the non-invaded mesotrophic treatments for both small (0.0040 g or 9.31 mm) and large (0.0055 g or 10.30 mm) initial larvae sizes (Fig. 4a). However, there was high variation within the mean final length and total growth of both large and small initial sized larvae under the invaded mesotrophic treatment, which did not differ significantly from any of the other treatments (Fig. 4).

The model allowed a diet shift in zooplankton type depending on length in which the first shift occurred from feeding exclusively on cyclopoids to a mix of calanoids and cyclopoids at 11 mm in fish length. In the invaded oligotrophic treatment (both initial sizes), larval walleye on average did not successfully grow above the size with which this

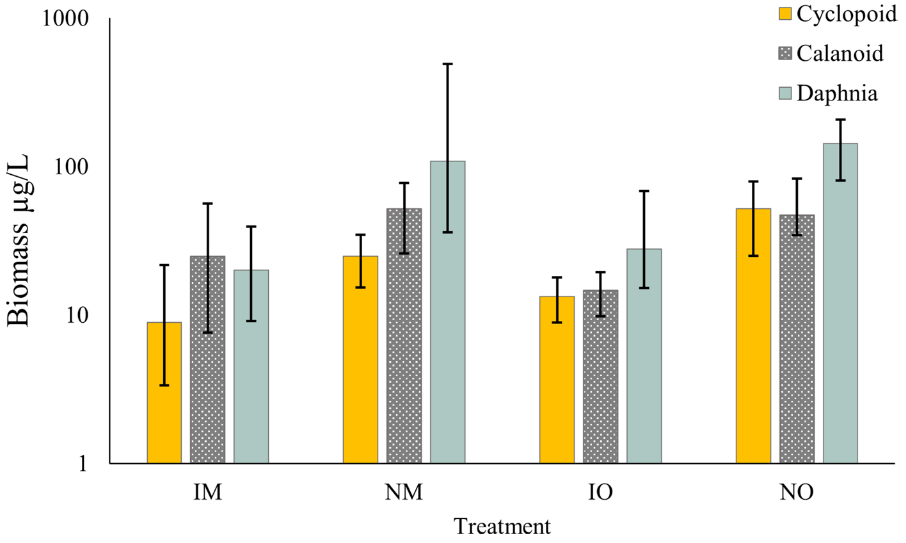

Fig. 3 Bar plot of the zooplankton biomass (µg/L) estimates for three taxa (cyclopoid, calanoid, and *Daphnia spp.*) on a log-scale for each *Bythotrephes* invasion and trophic status treatment (non-invaded oligotrophic [NO], invaded oligotrophic [IO], non-invaded mesotrophic [NM], and invaded mesotrophic [IM]). Zooplankton biomass estimates were based on zooplankton abundance estimates from 265 invaded and non-invaded lakes of Northern Ontario (Arnott 2021 [Unpublished raw data]) and Northern Minnesota (MN DNR Large Lakes Monitoring Program 2020 [Unpublished raw data]). Error bars represent bootstrapped 95% confidence intervals

diet shift could be achieved (≥ 11 mm). Notably, small initial sized larval walleye rarely grew above 11 mm under any treatment (Fig. 4a). Overall, with *Bythotrephes* present, the final walleye larvae length after 21 days was on average 35.03% and 37.43% shorter than in non-invaded mesotrophic and non-invaded oligotrophic systems, respectively.

Larval walleye successfully grew in all treatments, however in the invaded oligotrophic treatment after 21 days, both initial sized larvae had negligible growth and in some cases a net loss of energy (Fig. 4b). The same was true of small initial sized larvae in the invaded mesotrophic treatment (Fig. 4b). The lower limit of the 95% bootstrapped confidence intervals for total larval growth under the invaded mesotrophic conditions were −8.54 J and −9.80 J for large and small initial sized larvae respectively, and −3.46 J for small initial sized larvae under the invaded oligotrophic treatment. As with final length, energy accumulated as growth in larval walleye in the presence of *Bythotrephes* was significantly lower than in non-invaded systems for oligotrophic systems only; while the pattern in means was similar in mesotrophic lakes, the large error in walleye growth from invaded systems overlapped with those in non-invaded systems.

Temperature sensitivity analysis

Modelled larval walleye were only slightly sensitive to water temperature; within treatments, 95% bootstrapped confidence intervals overlapped between cool and warm mean temperatures for both initial larval walleye sizes (Fig. 5), As a result, the growth patterns in response to *Bythotrephes*-induced decreases in prey availability remained the same when exposed to warmer temperatures as under the original temperature regime (Figs. 4, 5). Specifically, both large and small initial sized larvae reached larger final lengths in the non-invaded oligotrophic and non-invaded mesotrophic treatments compared to the invaded oligotrophic treatment under warmer temperatures, but only significantly so in oligotrophic lakes (Fig. 5).

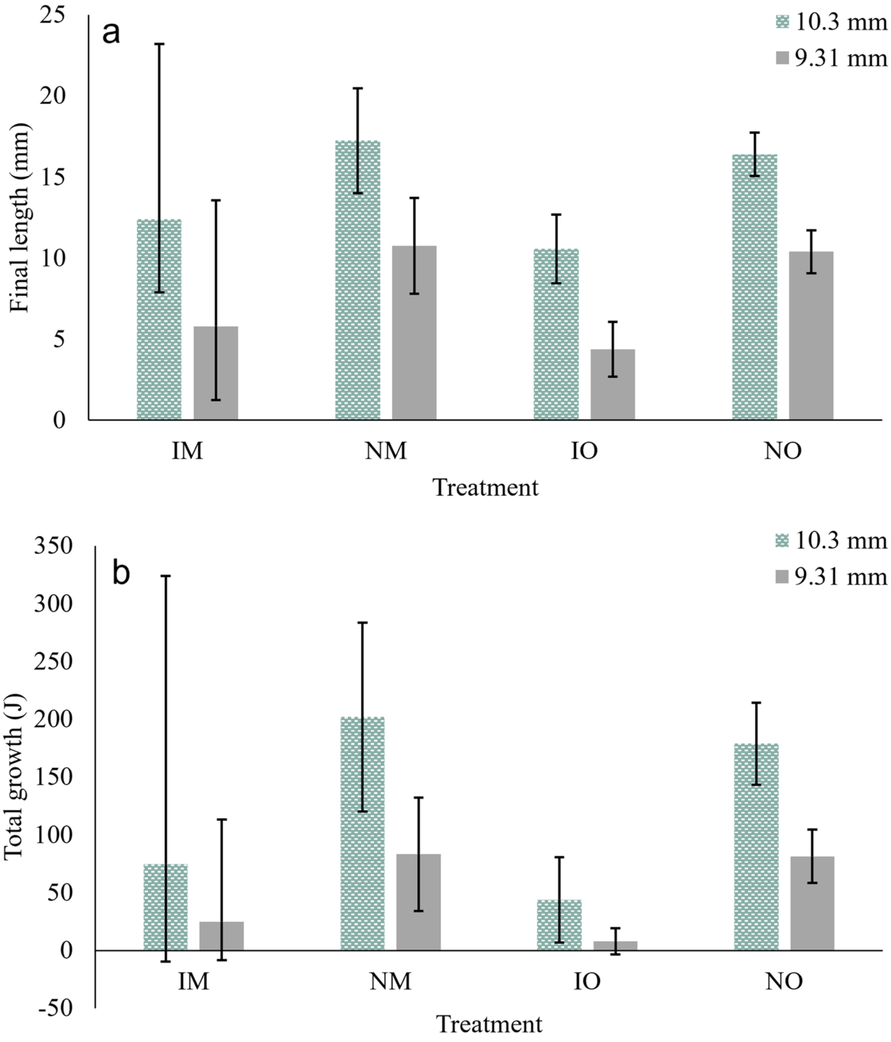

Fig. 4 Results of the bioenergetics model in this study showing **a** final length (mm) of larval walleye (*Sander vitreus;* initial length of either 10.30 mm or 9.31 mm), and **b** total growth (J) of larval walleye with consumption varying based on zooplankton abundance treatments for 21 days: Invaded with *Bythotrephes* and mesotrophic (IM), invaded and oligotrophic (IO), not invaded and mesotrophic (NM), and not invaded and oligotrophic (NO). Error bars represent bootstrapped 95% confidence intervals

Discussion

Using a simple bioenergetic and functional response modelling framework, we predicted lower growth rates of larval walleye based solely on changes in prey (zooplankton) biomass associated with *Bythotrephes* invasions. In oligotrophic lakes, our models predicted an average 37% reduction in body length at the end of their first three weeks compared to the non-invaded oligotrophic lakes. For invaded mesotrophic lakes, our models predicted body length to be 35% shorter compared to non-invaded mesotrophic lakes, though predictions were highly variable. These reductions in length relative to invasion status are generally consistent with a recent field study that reported declines in age-0 walleye length at the end of their first summer in lakes invaded by *Bythotrephes* compared to non-invaded systems (Hansen et al. 2020). The magnitude of our predicted declines were greater than those observed in the field, corrected for GDD (12.8% smaller; Hansen et al. 2020). These differences could be due to the high variation we observed in invaded mesotrophic lakes as well as additional factors that are not accounted for in our model. For example, although we considered lake trophic state, other lake characteristics such as depth and clarity are known to influence the growth of walleye which were not included in this study (Massie et al. 2021). Additionally, predation on YOY walleye may also limit growth, as predation can select against rapid growth (Biro et al. 2006). Furthermore, in invaded oligotrophic lakes, our models predicted larval walleye of

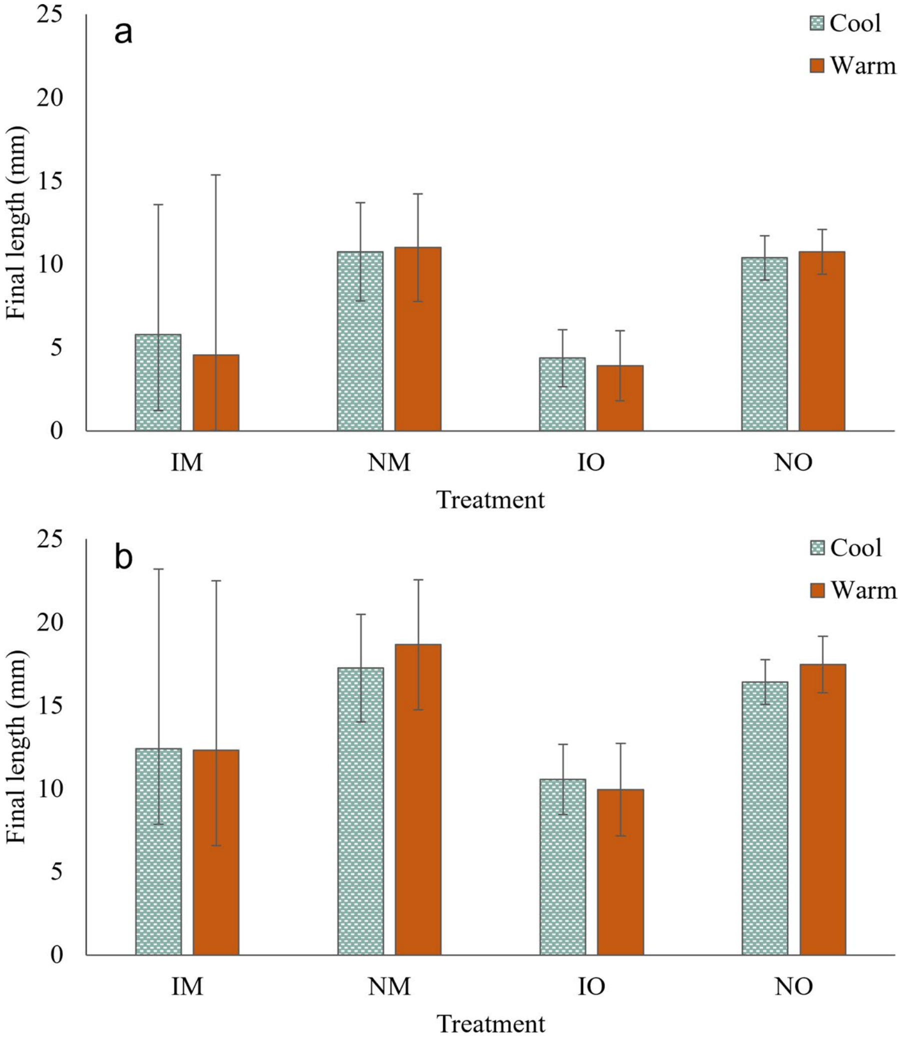

Fig. 5 Sensitivity analysis of daily water temperature using either typical/cool water temperatures (blue pattern bars), or mean annual water temperature increased by 5℃ (solid orange bars) on the growth of larval walleye (*Sander vitreus*) estimated through a bioenergetics model showing the final length (mm) of larval walleye (initial length of either 9.31 mm [a] or 10.3 mm [b]) with consumption varying based on zooplankton biomass treatments (estimated from 265 lakes) for 21 days: non-*Bythotrephes*-invaded mesotrophic (NM), invaded mesotrophic (IM), non-invaded oligotrophic (NO), and invaded oligotrophic (IO). Error bars represent bootstrapped 95% confidence intervals

both initial sizes could not survive on available zooplankton alone, suggesting that lakes below a certain trophic status might be more vulnerable to recruitment failure following *Bythotrephes* establishment.

Our findings provide evidence that food limitation due to zooplankton community changes resulting from the predatory impacts *Bythotrephes* is a likely mechanism for YOY walleye growth declines observed elsewhere. Our modelling exercise shows that these differences in YOY walleye growth patterns between lakes with and without *Bythotrephes* result directly from the distribution of zooplankton taxa biomass in lakes where *Bythotrephes* are established. This supports speculation in the literature that *Bythotrephes*-related changes in zooplankton abundance and community composition may be responsible for YOY walleye growth; both May et al. (2020) and Hansen et al. (2020) observed reduced walleye growth rate in the presence of *Bythotrephes*, and concluded these reductions were due to reduced zooplankton abundances over their study period. In this study, we observed reduced larval walleye growth in both oligotrophic conditions and mesotrophic conditions despite the fact that changes in prey biomass among the mesotrophic lakes supporting our modelling efforts were not significant at the 0.05 level (presumably due to small sample sizes of lakes representing the mesotrophic-invaded category); however, it is worth noting that the mean abundance for all three zooplankton taxa were visually lower in mesotrophic invaded lakes, which is supported by findings elsewhere in the literature (Dumitru et al. 2001;

Boudreau and Yan 2003; Strecker and Arnott 2008; Kerfoot et al. 2016).

Differences observed in the final size achieved by larval walleye in our simulations likely have significant implications for understanding walleye recruitment and population growth rates in *Bythotrephes*-invaded lakes, which may ultimately impact the long-term sustainability of these populations. Walleye can grow to ~ 15 to 25 mm within their first three weeks of feeding (Moore et al. 1994; Dabrowski et al. 2000), and this occurred for large initial sized larvae in both non-invaded treatments and the invaded mesotrophic treatment. However, this large final size was never achieved for small initial-sized larvae in any treatment, nor for large or small initial sized larvae in the oligotrophic invaded treatment. Slow larval walleye growth was likely due to an insufficient availability of cyclopoids early in life, resulting in insufficient growth to reach the length-dependent diet shifts to calanoids at 11 mm or the more energy dense *Daphnia* at 16 mm (McDonnell and Roth 2014). Because gape is dependent on fish length, decreased growth due to low prey availability delays the timing of diet shifts of larval walleye to larger, more energy dense prey. Decreased growth during the first three weeks of life also implies that ontogenetic diet shifts to benthic invertebrates, and ultimately, piscivory later in their first year of growth are also likely to be delayed (Uphoff et al. 2019). Delayed diet shifts are likely energetically detrimental, as larval walleye are confined to consuming less energy-dense prey items (zooplankton) for a longer period, ultimately with negative impacts on growth potential to the end of their first year. Importantly, small end of year size is known to result in greater overwinter mortality (Post and Evans 1989; Grote et al. 2018), suggesting walleye populations that exhibit smaller sizes at first feeding that appear to grow slower in *Bythotrephes*-invaded lakes are at an even higher risk of overwinter mortality.

Beyond overwinter mortality, cascading impacts of delayed YOY growth can impact other life history outcomes, including time to reproduction. Maturity of walleye is typically defined by a length at maturation relationship (Ma et al. 2021), and walleye age at maturation depends on growth rate/time to reach the length at maturity (Venturelli et al. 2010). Delayed maturation can act to reduce the proportion of spawning fish in the population, with negative impacts on future recruitment (Rowe and Thorpe 1990). Future studies that continue building this bioenergetics approach could extend the modelling period to also incorporate length-dependent diet shifts to benthic invertebrates and piscivory, which may ultimately demonstrate how *Bythotrephes* invasions impact the timing of diet shifts and the total growth of not just larval walleye, but ultimately growth and development into both YOY and juvenile stages.

Although our study found that prey availability in lakes invaded by *Bythotrephes* results in an energetic deficiency for larval walleye*,* walleye persist in many invaded oligotrophic lakes such as Lake Michigan (TP = 7–12 μg/L) and Lake Ontario (TP = 5.9 μg/L; Bunnell et al. 2011; Wang et al. 2012; Zorn et al. 2020), and invaded mesotrophic lakes such as Lake Winnipeg (TP = 15–20 μg/L; Bunting et al. 2016; Jansen et al. 2017). The reason our model may predict an such a great energy deficiency for larval walleye in oligotrophic lakes may be due to our inability to account for seasonal variation in zooplankton densities among our lakes. Like many datasets that trade off sampling effort across space against temporal detail, the lakes used in this study were based on one sampling event per lake (excluding the four lakes in Minnesota which were based on monthly events), at some point between May–August (Ross, personal communication). By contrast, first feeding in walleye typically occurs in spring (modelled here during the month of May or on Julian day 135–155). Therefore, our prey availability estimates may not necessarily coincide with the communities present at first larval walleye first feeding (spring) and may reflect densities later in the summer when native zooplankton are more impacted by *Bythotrephes* (Kerfoot et al. 2016; Stein et al. 2017). A more accurate representation of prey availability would be daily prey density estimates for the month of the simulation (late spring); unfortunately, daily zooplankton density estimates are rare for most lake ecosystems, as are early spring data immediately after ice off for most lakes of the size and region being considered here, due mainly to logistical reasons. Another potential issue may arise from the zooplankton taxa selected for prey availability estimates, as we included only prey preferred by larval walleye. It is possible prey alternatives may be consumed by larval walleye when preferred prey are not readily available. As an example, during their zooplanktivorous phase, larval walleye are known to consume *Chaoborus* larvae (Mathias and Li 1982), and some small benthic invertebrates such as chironomids (Galarowicz et al. 2006; Hoxmeier et al. 2006), neither of which are typically consumed by *Bythotrephes* (Foster and Sprules 2010; Jokela et al. 2017). While chironomids and/or *Chaoborus* could be diet items for larval walleye in *Bythotrephes*-invaded lakes where native zooplankton may be not readily available, their ability to be included in diets will still be limited by gape, as both are much larger than the zooplankton diet items considered here. Additionally, we made the simplifying assumption in this modelling exercise that activity was negligible (e.g., essentially included in basal metabolism), other studies have shown that this assumption is unrealistic, including for larval walleye (Madon and Culver 1993). Based on our findings, it is reasonable to expect that including increased activity in the metabolic costs of larval walleye would only exacerbate the patterns of growth declines and reduced survival observed here.

Recognizing these potential limitations, we believe our findings are important as they still provide a mechanistic framework through mathematical models, explicitly linking the connection between prey availability and walleye growth in wild populations. Future efforts may be improved by encouraging monitoring agencies to better emphasize early spring zooplankton community characterizations and undertake newer studies evaluating walleye diets from across a broader field of potential prey items. As such data and studies become available, our study can provide an important methodological framework for testing hypotheses linking prey availability to larval walleye growth.

The impact of *Bythotrephes* on larval walleye growth was greatest in oligotrophic lakes in our study, identifying them as potentially most vulnerable to *Bythotrephes* invasion. To determine the management implications of this finding, we examined publicly available survey data from lakes across the province of Ontario, Canada (Ontario Biodiversity Council 2021), and classified them according to trophic state as described previously using reported TP data (see methods). This lake database was then cross-referenced for lakes that had been sampled for walleye presence using the Broad Scale Monitoring (BSM) program, intended to represent the state of sport fisheries in Ontario (Ontario Ministry of Natural Resources and Forestry 2020a). Across 524 surveyed lakes which had been evaluated by both programs, we found that most lakes were classified as either oligotrophic (61.6%) or mesotrophic (19.3%). Of those lakes, walleye were present in 36.8% of oligotrophic lakes surveyed and 64.4% of mesotrophic lakes surveyed (Fig. 6). For lakes that support walleye, 91% fall into the mesotrophic to oligotrophic categories. Based on these survey data, our results suggest that among lakes identified and surveyed as important sport fisheries for provincial monitoring, the majority (91%) of walleye populations across Ontario may be vulnerable to reduced growth, and, in the case of oligotrophic

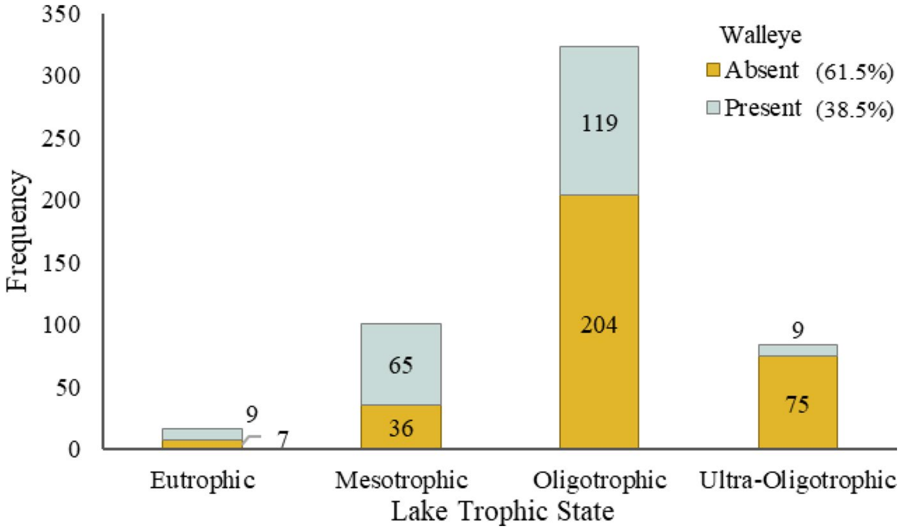

Fig. 6 Distribution of walleye (*Sander vitreus*) among 524 surveyed lakes in Ontario, Canada, classified by lake trophic state based on the total phosphorus of the trophic state index (Carlson 1977). Walleye presence data are from Ontario Ministry of Natural Resources and Forestry (2020), and TP data are from the Ontario Biodiversity Council (2021)

lakes, potentially recruitment failure, if invaded by *Bythotrephes*.

The compounding effects of both climate change and invasive species have been predicted to be the key drivers in biodiversity loss (Mainka and Howard 2010). Our temperature sensitivity analysis results suggest that the impacts of *Bythotrephes* invasion were similar under contemporary and warming climates. The response to temperature may have been insensitive because although the warmer temperature regime had an average annual temperature 5 °C higher than the contemporary regime, the average daily temperature among the 21-day simulation differed by only 2.33 °C between the two temperature regimes. Another important caveat of this simulation under warmer temperatures is that we do not have zooplankton data available from lakes with and without *Bythotrephes* at latitudes that experience a gaussian maximum of 23.5 °C. As such, our results should be interpreted primarily on the basis of how changes in temperature affect the scaling of maximum consumption and metabolism in the larval bioenergetics model.

As surface water temperatures are predicted to increase by 5 °C by the end of the twenty-first century (Maberly et al. 2020), YOY walleye that have previously been observed to have slower growth (Hansen et al. 2020) may be at higher risk of mortality with increasing temperature due to additional factors we could not account for in our model. Increased water temperatures due to climate change will influence not just zooplankton community composition, but also influence the phenological timing of plankton in lakes and optical thermal habitat for all aquatic species (Kraemer et al. 2021; Matsuzaki et al. 2021), a factor known to be important in walleye yield (Lester et al. 2004; Geisler et al. 2016). Although the number of waterbodies within the habitable temperature range for *Bythotrephes* are predicted to decrease with temperature in the next few decades (Walsh et al. 2020), climate change may shift some waterbodies into a suitable temperature range which could trigger "sleeper populations" of *Bythotrephes* to become highly abundant, likely impacting the prey availability for zooplanktivores in those systems (Walsh et al. 2016; Spear et al. 2021). As demonstrated here, predicting the impacts of *Bythotrephes* on the growth of fishes requires a holistic approach given that temperature strongly influences ecological processes, including planktonic community composition. Further research is suggested to expand on this study by evaluating the impacts of *Bythotrephes* on the growth of larval walleye under a broader range of climate scenarios that consider *Bythotrephes* densities and prey availability (community composition) as they fluctuate with temperature (Walsh et al. 2016).

This study aimed to determine if a change in zooplankton biomass due to *Bythotrephes* invasion could impact the growth rates of larval walleye. Our results suggest that walleye in less productive/oligotrophic lakes may be particularly at risk to *Bythotrephes* invasion, where zooplankton biomass post-invasion may be insufficient to sustain larval walleye growth. In more productive/mesotrophic lakes, larval walleye growth was slower in invaded lakes, but not significantly. Bioenergetics models have been used in the past to determine changes in fish growth due to invasive species (Johnston 1999; McDonnell and Roth 2014), but this is the first we know of to apply bioenergetics models in the evaluation of the impacts of *Bythotrephes* invasions on larval walleye specifically. Importantly, we have linked observed decreases in growth rate of YOY walleye found in Hansen et al. (2020) to the decreased prey availability in *Bythotrephes*-invaded lakes, expanding our knowledge on the impacts of invasive species to freshwater fisheries.

Acknowledgements The authors would like to thank Shelley Arnott for providing zooplankton abundance estimates from various lakes in Northern Ontario generated through the Canadian Aquatic Invasive Species Network (CAISN). The authors would also like to thank the Minnesota Department of Natural Resources Large Lakes Monitoring Program for providing zooplankton abundance estimates from various lakes in Northern Minnesota. Comments from two anonymous reviewers helped improve both the readability and scope of the manuscript. This work was supported by grants from the Quetico Foundation, the Rainy Lakes Fishery Trust, NSERC Discovery, the Canada Research Chair program and Lakehead University.

Author's contribution Both authors contributed to the design and conception of the study. DG preformed data preparation, analysis, and prepared the first draft of the manuscript. MR provided support to automate results generation, provided comments and edits on subsequent versions of the manuscript and approved the final manuscript.

Data availability Lake total phosphorus data are publicly available from The Ontario Biodiversity Council (https://sobr.ca/indicator/water-quality-inland-lakes/) and walleye presence data are available from the Land Information Ontario repository (https://geohub.lio.gov.on.ca/datasets/lio::aquatic-resource-area-survey-point/about). Zooplankton biomass estimates and bioenergetic model output data are available from the Knowledge Network for Biocomplexity (https://knb.ecoinformatics.org/view/urn%3Auuid%3Aea68a408-8a33-4f2d-a0a3-8b0d848d11b6). All other data and parameters used in models are available in the source literature referenced in the body text of the manuscript.

Declarations

Conflict of interest The authors declare that they have no competing interests.

References

Anderson JT (1988) A review of size dependant survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Sci 8:55–66. https://doi.org/10.2960/j.v8.a6

Barbiero RP, Tuchman ML (2004) Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. Can J Fish Aquat Sci 61:2111–2125. https://doi.org/10.1139/F04-149

Barnett A, Beisner BE (2007) Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. Ecology 88:1675–1686. https://doi.org/10.1890/06-1056.1

Barnhisel DR (1991a) The caudal appendage of the cladoceran *Bythotrephes cederstroemi* as defense against young fish. J Plankton Res 13:529–537. https://doi.org/10.1093/plankt/13.3.529

Barnhisel DR (1991b) Zooplankton spine induces aversion in small fish predators. Oecologia 88:444–450. https://doi.org/10.1007/BF00317591

Bergenius MA, Meekan MG, Robertson DR, McCormick M (2002) Larval growth predicts the recruitment success of a coral reef fish. Oecologia 131:521–525. https://doi.org/10.1007/s00442-002-0918-4

Biro PA, Abrahams MV, Post JR, Parkinson EA (2006) Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. J Anim Ecol 75:1165–1171. https://doi.org/10.1111/j.1365-2656.2006.01137.x

Boudreau S, Yan ND (2003) The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. Can J Fish Aquat Sci 60:1307–1313. https://doi.org/10.1139/f03-111

Bunnell DB, Davis BM, Warner DM et al (2011) Planktivory in the changing Lake Huron zooplankton community: *Bythotrephes* consumption exceeds that of *Mysis* and fish. Freshw Biol 56:1281–1296. https://doi.org/10.1111/j.1365-2427.2010.02568.x

Bunting L, Leavitt PR, Simpson GL et al (2016) Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture. Limnol Oceanogr 61:2090–2107. https://doi.org/10.1002/lno.10355

Carlson RE (1977) A trophic state index for lakes. Limnol Oceanogr 22:361–369. https://doi.org/10.4319/lo.1977.22.2.0361

Compton JA, Kerfoot CW (2004) Colonizing inland lakes: Consequences of YOY fish ingesting the spiny cladoceran (*Bythotrephes cederstroemi*). J Great Lakes Res 30:315–326. https://doi.org/10.1016/S0380-1330(04)70394-9

Dabrowski K, Czesny S, Kolkovski S et al (2000) Intensive culture of walleye larvae Produced out of season and during regular season spawning. N Am J Aquac 62:219–224. https://doi.org/10.1577/1548-8454(2000)062%3c0219:icowlp%3e2.3.co;2

Deslauriers D, Chipps SR, Breck JE et al (2017) Fish bioenergetics 4.0: an R-based modeling application. Fisheries 42:586–596. https://doi.org/10.1080/03632415.2017.1377558

Dumitru C, Sprules GW, Yan ND (2001) Impact of *Bythotrephes longimanus* on zooplankton assemblages of Harp Lake, Canada: an assessment based on predator consumption and prey production. Freshw Biol 46:241–251. https://doi.org/10.1046/j.1365-2427.2001.00649.x

Dwivedi AK, Mallawaarachchi I, Alvarado LA (2017) Analysis of small sample size studies using nonparametric bootstrap test with pooled resampling method. Stat Med 36:2187–2205. https://doi.org/10.1002/sim.7263

Fisheries and Oceans Canada (2019a) Survey of Recreational Fishing in Canada, 2015

Fisheries and Oceans Canada (2019b) Freshwater Landings. https://www.dfo-mpo.gc.ca/stats/commercial/land-debarq/freshwater-eaudouce/2019b-eng.htm

Foster SE, Sprules GW (2010) Effects of *Bythotrephes* on the trophic position of native macroinvertebrates. Can J Fish Aquat Sci 67:58–69. https://doi.org/10.1139/F09-164

Galarowicz TL, Adams JA, Wahl DH (2006) The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. Can J Fish Aquat Sci 63:1722–1733. https://doi.org/10.1139/F06-073

Galarowicz TL, Wahl DH (2003) Differences in growth, consumption, and metabolism among walleyes from different latitudes. Trans Am Fish Soc 132:425–437. https://doi.org/10.1577/1548-8659(2003)132%3c0425:digcam%3e2.0.co;2

Geisler ME, Rennie MD, Gillis DM, Higgins SN (2016) A predictive model for water clarity following dreissenid invasion. Biol Invasions 18:1989–2006. https://doi.org/10.1007/s10530-016-1146-x

Gillis MK, Walsh MR (2017) Rapid evolution mitigates the ecological consequences of an invasive species (*Bythotrephes longimanus*) in lakes in Wisconsin. Proc R Soc B Biol Sci. https://doi.org/10.1098/rspb.2017.0814

Graham DM, Sprules GW (1992) Size and species selection of zooplankton by larval and juvenile walleye (*Stizostedion vitreum vitreum*) in Oneida Lake, New York. Can J Zool 70:2059–2067. https://doi.org/10.1139/z92-277

Grote JD, Wuellner MR, Blackwell BG, Lucchesi DO (2018) Evaluation of potential overwinter mortality of age-0 walleye and appropriate age-1 sampling gear. J Fish Wildl Manag 9:65–74. https://doi.org/10.3996/082017-JFWM-062

Hansen GJA, Ahrenstorff TD, Bethke BJ et al (2020) Walleye growth declines following zebra mussel and *Bythotrephes* invasion. Biol Invasions 22:1481–1495. https://doi.org/10.1007/s10530-020-02198-5

Houde ED (1967) Food of Pelagic Young of the Walleye, *Stizostedion vitreum vitreum*, in Oneida Lake, New York. Trans Am Fish Soc 96:17–24. https://doi.org/10.1577/1548-8659(1967)96[17:fopyot]2.0.co;2

Hoxmeier JH, Wahl DH, Hooe ML, Pierce CL (2004) Growth and survival of larval walleyes in response to prey availability. Trans Am Fish Soc 133:45–54. https://doi.org/10.1577/t01-082

Hoxmeier JH, Wahl DH, Brooks RC, Heidinger RC (2006) Growth and survival of age-0 walleye (*Sander vitreus*): interactions among walleye size, prey availability, predation, and abiotic factors. Can J Fish Aquat Sci 63:2173–2182. https://doi.org/10.1139/F06-087

Jansen W, Gill G, Hann B (2017) Rapid geographic expansion of spiny water flea (*Bythotrephes longimanus*) in Manitoba, Canada, 2009–2015. Aquat Invasions 12:287–297. https://doi.org/10.3391/ai.2017.12.3.03

Johnson MG, Leach JH, Minns CK, Olver CH (1977) Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and smallmouth bass (*Micropterus dolomieui*). J Fish Res Board Canada 34:1592–1601. https://doi.org/10.1139/f77-224

Johnston TA (1999) Factors affecting food consumption and growth of walleye, *Stizostedion vitreum*, larvae in culture ponds. Hydrobiologia 400:129–140. https://doi.org/10.1023/A:1003755115000

Johnston TA, Mathias JA (1994) Feeding ecology of walleye, *Stizostedion vitreum*, larvae: effects of body size, zooplankton abundance, and zooplankton community composition. Can J Fish Aquat Sci 51:2077–2089. https://doi.org/10.1139/f94-210

Jokela A, Arnott SE, Beisner BE (2017) Biotic resistance of impact: a native predator (*Chaoborus*) influences the impact of an invasive predator (*Bythotrephes*) in temperate lakes. Biol Invasions 19:1495–1515. https://doi.org/10.1007/s10530-017-1374-8

Jonas JL, Wahl DH (1998) Relative importance of direct and indirect effects of starvation for young walleyes. Trans Am Fish Soc 127:192–205. https://doi.org/10.1577/1548-8659(1998)127%3c0192:riodai%3e2.0.co;2

Kerfoot CW, Hobmeier MM, Yousef F et al (2016) A plague of waterfleas (*Bythotrephes*): impacts on microcrustacean community structure, seasonal biomass, and secondary production in a large inland-lake complex. Biol Invasions 18:1121–1145. https://doi.org/10.1007/s10530-015-1050-9

Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). J Fish Res Board Canada 34:1922–1935. https://doi.org/10.1139/f77-258

Kraemer BM, Pilla RM, Woolway RI et al (2021) Climate change drives widespread shifts in lake thermal habitat. Nat Clim Chang 11:521–529. https://doi.org/10.1038/s41558-021-01060-3

Lester NP, Dextrase AJ, Kushneriuk RS et al (2004) Light and temperature: key factors affecting walleye abundance and production. Trans Am Fish Soc 133:588–605. https://doi.org/10.1577/t02-111.1

Ma Q, Jiao Y, Zhou C, Ren Y (2021) Sexual and spatio-temporal variation of Lake Erie Walleye growth and maturity: a consequence of multiple impacting factors. Aquac Fish 6:400–413. https://doi.org/10.1016/j.aaf.2020.06.010

Maberly SC, O'Donnell RA, Woolway RI et al (2020) Global lake thermal regions shift under climate change. Nat Commun. https://doi.org/10.1038/s41467-020-15108-z

Madon SP, Culver DA (1993) Bioenergetics model for larval and juvenile walleyes: an in situ approach with experimental ponds. Trans Am Fish Soc 122:797–813. https://doi.org/10.1577/1548-8659(1993)122%3c0797:bmflaj%3e2.3.co;2

Mainka SA, Howard GW (2010) Climate change and invasive species: double jeopardy. Integr Zool 5:102–111

Malison JA, Held JA (1996) Reproductive biology and spawning. In: Summerfelt RC (ed) Walleye culture manual. North Central Regional Aquaculture Center Publications Office, Iowa State University, Ames, pp 11–18

Massie DL, Hansen GJA, Li Y et al (2021) Do lake-specific characteristics mediate the temporal relationship between walleye growth and warming water temperatures? Can J Fish Aquat Sci 78:913–923. https://doi.org/10.1139/cjfas-2020-0169

Mathias JA, Li S (1982) Feeding habits of walleye larvae and juveniles: comparative laboratory and field studies. Trans Am Fish Soc 111:722–735. https://doi.org/10.1577/1548-8659(1982)111%3c722:fhowla%3e2.0.co;2

Matsuzaki SIS, Lathrop RC, Carpenter SR et al (2021) Climate and food web effects on the spring clear-water phase in two north-temperate eutrophic lakes. Limnol Oceanogr 66:30–46. https://doi.org/10.1002/lno.11584

May CJ, Ludsin SA, Glover DC, Marschall EA (2020) The influence of larval growth rate on juvenile recruitment in Lake Erie walleye (*Sander vitreus*). Can J Fish Aquat Sci 77:548–555. https://doi.org/10.1139/cjfas-2019-0059

McDonnell KN, Roth BM (2014) Evaluating the effect of pelagic zooplankton community composition and density on larval walleye (*Sander vitreus*) growth with a bioenergetic-based foraging model. Can J Fish Aquat Sci 71:1039–1049. https://doi.org/10.1139/cjfas-2013-0498

Moore A, Prange M, Bristow B, Summerfelt R (1994) Influence of stocking densities on walleye fry viability in experimental and production tanks. Prog Fish-Cult 56:192–201. https://doi.org/10.1577/1548-8640(1994)056%3c0194:IOSDOW%3e2.3.CO;2

Ontario Biodiversity Council (2021) State of Ontario's Biodiversity. http://ontariobiodiversitycouncil.ca/sobr. Accessed 5 Apr 2022

Ontario Ministry of Natural Resources and Forestry (2020) Aquatic Resource Area Survey Point. https://geohub.lio.gov.on.ca/datasets/lio::aquatic-resource-area-survey-point/about

Pangle KL, Peacor SD, Johannsson OE (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88:402–412. https://doi.org/10.1890/06-0768

Post JR, Evans DO (1989) Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*):

laboratory, in situ enclosure, and field experiments. Can J Fish Aquat Sci 46:1958–1968. https://doi.org/10.1139/f89-246

Rantala HM, Branstrator DK, Hirsch JK et al (2022) Simultaneous invasion decouples zebra mussels and water clarity. Commun Biol. https://doi.org/10.1038/s42003-022-04355-z

Rowe DK, Thorpe JE (1990) Suppression of maturation in male Atlantic salmon (*Salmo salar L.*) parr by reduction in feeding and growth during spring months. Aquaculture 86:291–313. https://doi.org/10.1016/0044-8486(90)90121-3

Shelton AO, Mangel M (2011) Fluctuations of fish populations and the magnifying effects of fishing. Proc Natl Acad Sci U S A 108:7075–7080. https://doi.org/10.1073/pnas.1100334108

Sorensen ML, Branstrator DK (2017) The North American invasive zooplanktivore *Bythotrephes longimanus* is less hypoxia-tolerant than the native *Leptodora kindtii*. Can J Fish Aquat Sci 74:824–832. https://doi.org/10.1139/cjfas-2016-0188

Spear MJ, Walsh JR, Ricciardi A, Jake Vander Zanden M (2021) The Invasion ecology of sleeper populations: prevalence, persistence, and abrupt shifts. Bioscience 71:357–369. https://doi.org/10.1093/biosci/biaa168

Stein SR, Roswell CR, Pothoven SA, Höök TO (2017) Diets and growth of age-0 walleye in a recently recovered population. J Great Lakes Res 43:100–107. https://doi.org/10.1016/j.jglr.2017.03.019

Strecker AL, Arnott SE (2008) Invasive predator, *Bythotrephes*, has varied effects on ecosystem function in freshwater lakes. Ecosystems 11:490–503. https://doi.org/10.1007/s10021-008-9137-0

Trudel M, Tremblay A, Schetagne R, Rasmussen JB (2000) Estimating food consumption rates of fish using a mercury mass balance model. Can J Fish Aquat Sci 57:414–428. https://doi.org/10.1139/f99-262

Uphoff CS, Schoenebeck CW, Koupal KD et al (2019) Age-0 walleye *Sander vitreus* display length-dependent diet shift to piscivory. J Freshw Ecol 34:27–36. https://doi.org/10.1080/02705060.2018.1529637

Venturelli PA, Lester NP, Marshall TR, Shuter BJ (2010) Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. Can J Fish Aquat Sci 67:1057–1067. https://doi.org/10.1139/F10-041

Walsh JR, Munoz SE, Van Der Zanden MJ (2016) Outbreak of an undetected invasive species triggered by a climate anomaly. Ecosphere. https://doi.org/10.1002/ecs2.1628

Walsh JR, Hansen GJA, Read JS, Vander Zanden MJ (2020) Comparing models using air and water temperature to forecast an aquatic invasive species response to climate change. Ecosphere. https://doi.org/10.1002/ecs2.3137

Wang HY, Einhouse DW, Fielder DG et al (2012) Maternal and stock effects on egg-size variation among walleye *Sander vitreus* stocks from the Great Lakes region. J Great Lakes Res 38:477–489. https://doi.org/10.1016/j.jglr.2012.06.002

Yan ND, Girard R, Boudreau S (2002) An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. Ecol Lett 5:481–485. https://doi.org/10.1046/j.1461-0248.2002.00348.x

Zorn TG, Hayes DB, McCullough DE, Watson NM (2020) Crustacean zooplankton available for larval walleyes in a Lake Michigan embayment. J Great Lakes Res. https://doi.org/10.1016/j.jglr.2020.06.017