



Walleye growth declines following zebra mussel and *Bythotrephes* invasion

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Abstract Invasive species represent a threat to aquatic ecosystems globally; however, impacts can be heterogeneous across systems. Documented impacts of invasive zebra mussels (*Dreissena polymorpha*) and spiny water fleas (*Bythotrephes cederstroemii*; hereafter *Bythotrephes*) on native fishes are variable and context dependent across locations and time periods. Here, we use a hierarchical Bayesian analysis of a 35-year dataset on two fish species from 9 lakes to demonstrate that early life growth of ecologically

important fishes are influenced by these aquatic invasive species. Walleye (*Sander vitreus*) in their first year of life grew more slowly in the presence of either invader after correcting for temperature (measured by degree days), and were on average 12 or 14% smaller at the end of their first summer following invasion by *Bythotrephes* or zebra mussels, respectively. Yellow perch (*Perca flavescens*) growth was less affected by invasion. Yellow perch on average grew more slowly in their first year of life following invasion by zebra mussels, although this effect was not statistically distinguishable from zero. Early life growth of both walleye and yellow perch was less tightly coupled to degree days in invaded systems, as

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demonstrated by increased variance surrounding the degree day-length relationship. Smaller first-year size is related to walleye survival and recruitment to later life stages and has important implications for lake food webs and fisheries management. Future research quantifying effects of zebra mussels and *Bythotrephes* on other population-level processes and across a wider gradient of lake types is needed to understand the mechanisms driving observed changes in walleye growth.

Keywords Walleye · Yellow perch · Zebra mussel · Spiny water flea · Indirect effects · Food web · Growth · Lake · Impacts · Historical data · Fisheries

Introduction

Zebra mussels (*Dreissena polymorpha*) and spiny water fleas (*Bythotrephes cederstroemi*; Korovchinsky and Arnott 2019; hereafter *Bythotrephes*) are aquatic invasive species (AIS) that transform freshwater ecosystems. Zebra mussels are filter feeders that reduce pelagic primary production and increase water clarity (Macisaac 1996; Strayer et al. 1999; Karatayev et al. 2002). They also indirectly affect zooplankton biomass, size structure, and community composition (Pace et al. 1998; Idrisi et al. 2001; Higgins and Vander Zanden 2010). At the same time, zebra mussels can increase benthic primary production and biomass of some benthic invertebrates by shunting nutrients into benthic zones and providing additional structure (Vanderploeg et al. 2001; Hecky et al. 2004; Higgins and Vander Zanden 2010). *Bythotrephes* are predatory zooplankters that also reduce native zooplankton biomass and can shift zooplankton community composition to prey species that are suboptimal for fish via both direct predation and indirect effects (Yan and Pawson 1997; Hoffman et al. 2001; Barbiero and Tuchman 2004; Fernandez et al. 2009; Rennie et al. 2011; Kerfoot et al. 2016). These changes in the zooplankton community can decrease water clarity via a trophic cascade (Walsh et al. 2016), although effects on phytoplankton communities vary among lakes (Strecker et al. 2006, 2011).

Despite their documented effects on lower trophic levels and ecosystem functioning, the effects of zebra mussels and *Bythotrephes* on higher trophic levels

such as fish are less well known and appear to vary among systems and species (Strayer et al. 2004; Higgins and Vander Zanden 2010). Fish species and life stages that rely on pelagic energy sources are often negatively affected by zebra mussels, while those that rely on benthic/littoral resources often respond positively in terms of growth and abundance (e.g., Strayer et al. 2004; Guiliano 2011; Kaemingk et al. 2012; but see McNickle et al. 2006; Lumb et al. 2007; Nalepa et al. 2009). The eponymous spine of the *Bythotrephes* can make them difficult to ingest for many planktivorous fishes. Fish above a certain size may consume *Bythotrephes*, although the spines can cause internal damage and can lead to learned avoidance (Barnhisel and Kerfoot 2004; Compton and Kerfoot 2004).

Walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) are economically and ecologically important fish species in North America, and the ecosystem changes associated with zebra mussel and *Bythotrephes* invasions may affect first year growth and survival of these fishes. Both walleye and yellow perch rely on zooplankton prey for a portion of their first year of life before switching to benthic macroinvertebrates and then fish (Wu and Culver 1992; Mittelbach and Persson 1998; Galarowicz et al. 2006). If native zooplankton become limited due to the presence of either AIS, walleye and yellow perch may switch to alternative food sources if they are large enough to make that shift (Wu and Culver 1992; Gopalan et al. 1998) or continue to persist on pelagic resources (Bremigan et al. 2003; Truemper et al. 2006). In either case, their growth may be affected. Growth of these fishes during the first year is critical to survival to later life stages, because larger individuals are less likely to succumb to size-selective predation (Nielsen 1980; Roswell 2011) and have access to a more diverse prey base (Wu and Culver 1992).

The impacts of zebra mussels and/or *Bythotrephes* on first year walleye or yellow perch growth are inconsistent in both direction and magnitude across studies to date. Zooplankton declines were associated with decreased age-0 yellow perch growth in lakes containing *Bythotrephes* (Staples et al. 2017). Zebra mussels caused reduced larval perch growth in mesocosms (Mavrin and Strel'nikova 2011), whereas in natural systems (e.g. Lake Oneida, New York) there are conflicting reports of either increased (Mayer et al. 2000) or unchanged (Idrisi et al. 2001) growth following zebra mussel establishment. Walleye

biomass dropped by approximately half post-zebra mussel invasion in Lake Oneida (Irwin et al. 2008), while no effect of zebra mussels on age-0 growth of any species including yellow perch and walleye was observed in Lake Erie (Trometer and Busch 1999). Length-specific differences in growth and condition of yellow perch and walleye in zebra mussel infested lakes have also been documented, with larger individuals growing faster, suggesting impacts of zebra mussels on fishes may vary with fish life stage (Mavrin and Strel'nikova 2011; Nienhuis et al. 2014).

The context-dependent impacts of zebra mussels and *Bythotrephes* on fish growth are common in studies of invasive species impacts (Parker et al. 1999). If the effects of zebra mussels and *Bythotrephes* on fish really differ among systems, identifying characteristics associated with resilient versus vulnerable populations will be critical for prioritizing invasive species prevention efforts, managing fisheries, and predicting the effects of invasion in uninvaded lakes. Generalizability can be achieved by moving beyond single system case studies to examining impacts across multiple locations and over longer, management-relevant time frames. Here, we evaluated changes in first year growth of walleye and yellow perch pre- and post-invasion in lakes invaded by zebra mussels and/or *Bythotrephes*. We examined data from 9 lakes sampled over 35 years to estimate AIS impacts at management-relevant spatial and temporal scales. To correct for temperature effects on fish growth, we standardized growth by degree days (cumulative daily temperatures $> 5^{\circ}\text{C}$) and tested for differences in the temperature-standardized rates of growth. We hypothesized that young of year growth of both yellow perch and walleye would be slower in invaded systems due to decreased availability of suitably sized zooplankton resources.

Methods

Study lakes

We examined walleye and yellow perch growth rates in nine lakes in Minnesota, USA (Fig. 1), ranging in area from 6500 to 309,000 ha and maximum depths from 5 to 64 m (Table 1). These lakes are important economic, cultural, and ecological resources in the state (MN DNR 1997), accounting for 33% of

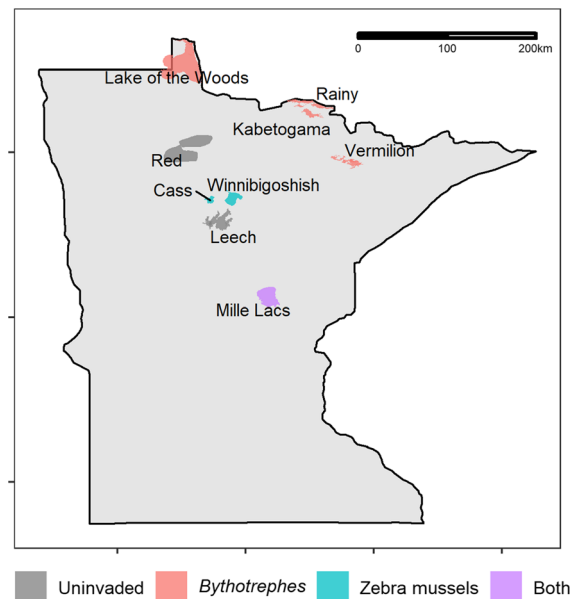


Fig. 1 Study lake locations colored by the invasion status during this study

Minnesota's walleye harvest (Jacobson 2004) and contributing significantly to the \$2.4 billion spent each year on fishing in Minnesota (U.S. Department of the Interior et al. 2011). Our study lakes vary in invasion status and timing (Table 1); zebra mussels are present in two lakes, *Bythotrephes* are present in four lakes, both species are present in one lake, and two lakes were uninvaded at the time of study. For this study, we consider timing of invasion as the year zebra mussel adults were discovered or two years after the discovery of *Bythotrephes*, which corresponds to the lag documented between discovery of *Bythotrephes* and impacts on the zooplankton community (Staples et al. 2017). Zebra mussel veligers were found in Leech Lake in 2016 and Red Lake in 2018, but no adults were confirmed as of 2018 and thus we considered these lakes uninvaded for the time period of this study. Lake Vermilion has two discrete basins (East and West), which are connected by a relatively small channel (1 km long and ~ 100 m wide at its narrowest location). *Bythotrephes* were discovered in East Vermilion in 2015 and were not documented in West Vermilion until 2018, therefore, we split Lake Vermilion into East and West basins for analysis and considered West Vermilion uninvaded for this study. Significant declines in total zooplankton biomass have been documented in each of the study lakes invaded by

Table 1 Characteristics of study lakes, invasion year by zebra mussels (ZM) and *Bythotrephes* (Bytho.), and age-0 walleye (WAE) and yellow perch (YEP) samples used in this analysis

Lake	Area (ha)	Max depth (m)	Median Secchi depth (m)	Invasion year (species)	# YEP sampled	# WAE sampled	# years sampled	August 15 median degree day value (range)
Cass	6458	37	3.4	2014 (ZM)	11,246	1371	29	1424 (1185–1789)
Kabetogama	9727	24	2.4	2007 (Bytho.)	39,036	13,687	34	1358 (1086–1640)
Lake of the Woods ^a	309,276	64	1.1	2007 (Bytho.)	17,129	4752	27	1257 (950–1513)
Leech	44,641	46	2.7		14,104	5209	31	1478 (1248–1820)
Mille Lacs	51,891	13	3.1	2005 (ZM), 2009 (Bytho.)	9579	1555	14	1514 (1276–1913)
Rainy ^a	85,065	49	2.4	2006 (Bytho.)	38,290	6189	30	1373 (1059–1667)
Upper Red	48,297	5	0.8		12,530	8711	35	1459 (1163–1758)
Vermilion (East)	11,400	23	2.4	2015 (Bytho.)	12,787	2488	34	1254 (1010–1553)
Vermilion (West)	4599	15	3.1		13,945	555	34	1254 (1010–1553)
Winnibigoshish	22,853	21	3.1	2014 (ZM)	8337	5495	34	1450 (1219–1763)

^a Lake of the Woods and Rainy Lake are border lakes, only a portion of which are in Minnesota, USA

August 15 degree day value is based on air temperatures and calculated using a base of 5 °C

Bythotrephes. Cladocerans and cyclopoid copepods were impacted the most, with the zooplankton shifting to a community dominated by calanoid copepods (Kerfoot et al. 2016; Hirsch, unpublished data). Decreasing trends in total zooplankton biomass have also been detected in each of the study lakes invaded by zebra mussels, with parallel declines among all zooplankton taxa in these communities (Hirsch, unpublished data).

Data collection and collation

Age-0 walleye and yellow perch were collected from 1983 to 2018 by shoreline seining as part of the Minnesota Department of Natural Resources standardized large lakes monitoring program (Wingate and Schupp 1984). A 30-m long, 2-m deep, 6.4-mm bar mesh bag seine was used with a fixed pole seining technique, where one brail is fixed on shore while the other begins perpendicular to shore and is pulled toward shore in a sweeping motion while keeping the net taut. Seining began in 1983 for several lakes and was conducted annually with some exceptions (Table 1). An average of 13 stations (range 6–23

stations) were sampled in each lake during each sampling year. The same stations within each lake were typically sampled weekly, from mid-July to mid-August. All fishes were identified and enumerated. Walleye and yellow perch total length (TL) was measured to the nearest mm. To verify that only age-0 individuals were used in subsequent analyses, the data were quality checked by plotting length-frequency histograms for each species by lake, year, and week (nested within year). Data considered out of range of age-0 cohorts (either erroneous data or suspected age-1 + individuals) were removed. The remaining age-0 walleye and yellow perch individual lengths were corrected for growing degree days, as described below, allowing for standardized comparisons.

To account for differences in age-0 fish length due to differences in temperature, we calculated cumulative degree days with a 5 °C base (Chezik et al. 2013) for each sample date in each lake. Because we lacked water temperature data for the time period of analysis, we used air temperature as a proxy for surface water temperature when calculating degree days (Honsey et al. 2019). We acquired daily air temperature data for degree day calculation from NCEP North American

Regional Reanalysis (NARR) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at <https://www.esrl.noaa.gov/psd/>. Grid resolution for NARR data is approximately 0.3° (32 km) at the lowest latitude. Lake-specific daily air temperatures were extracted using the geoknife package (Read et al. 2015) in R version 3.5.1 (R Core Team 2018) with lake centroids as inputs. Degree day values were centered by subtracting the mean degree day value for each species to improve model convergence.

Statistical analysis

We used Bayesian hierarchical linear models to evaluate the effects of invasion on first year growth of walleye and yellow perch. We fit separate models for walleye and yellow perch. For each species, the model was as follows:

$$\begin{aligned}
 y_i &\sim N(\alpha_{j(i)} + \beta_{j(i)} \cdot DD_i + \eta_{k(i)}, \sigma_j^2), \\
 &\text{for } i = 1 \dots n \text{ observations} \\
 \eta_k &\sim N(0, \sigma_\eta^2) \text{ for } k = 1 \dots K \text{ lakes} \\
 \begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} &\sim MVN\left(\begin{pmatrix} \gamma_0^\alpha + \gamma_1^\alpha \cdot Z_{1j} + \gamma_2^\alpha \cdot Z_{2j} \\ \gamma_0^\beta + \gamma_1^\beta \cdot Z_{1j} + \gamma_2^\beta \cdot Z_{2j} \end{pmatrix}, \Sigma\right), \\
 &\text{for } j = 1 \dots J \text{ lake-years} \\
 \log(\sigma_j) &\sim N(\gamma_0^\sigma + \gamma_1^\sigma \cdot Z_{1j} + \gamma_2^\sigma \cdot Z_{2j}, \omega^2), \\
 &\text{for } j = 1 \dots J \text{ lake-years}
 \end{aligned}$$

where y_i is an individual fish length (mm) for observation i (for a given lake-year), α_j and β_j are the intercepts and slopes that describe the relationship between first year length and degree days (DD_i) on the day of sample for lake-year j , and σ_j^2 is the residual variance, which was also allowed to vary by lake-year j . Specifically, the residual standard deviations, σ_j , are assumed to follow a log-normal distribution with a linear predictor equal to $\gamma_0^\sigma + \gamma_1^\sigma \cdot Z_{1j} + \gamma_2^\sigma \cdot Z_{2j}$ and a conditional variance ω^2 . Degree days were standardized by subtracting the mean and dividing by the standard deviation prior to analysis. We assumed a linear relationship between fish length and degree days accumulated to that date (Neuheimer and Taggart 2007; Staples et al. 2017). The lake-year specific intercepts, slopes, and residual standard deviations were modeled as a function of invasion status of each lake-year, where $Z_1 = 1$ if a lake-year was invaded by

the *Bythotrephes*, $Z_2 = 1$ if a lake-year was invaded by zebra mussels. If Z_1 and Z_2 both equaled 1, then a lake-year was invaded by both *Bythotrephes* and zebra mussels and if Z_1 and Z_2 both equaled zero then a lake-year was not invaded. The parameters γ_n^x describe the effects of invasion status on the lake-year specific intercepts, slopes, and residual standard deviations. The parameter η_k is a lake random effect, assumed to be normally distributed with a mean of zero and variance σ_η^2 . We modeled the variance–covariance matrix (Σ) of the multivariate normal distribution for the varying slopes and intercepts using the scaled inverse-Wishart distribution (Gelman and Hill 2007). Diffuse normal priors were used for γ_n^x , and diffuse uniform priors were used for σ_η and ω . We ran three parallel Markov chains beginning each chain with random starting values. Each chain was run for 60,000 iterations, from which the first 30,000 were discarded. Each chain was thinned to 10,000 samples, resulting in a total of 30,000 samples used to summarize the posterior distributions. Convergence was assessed visually through inspection of trace plots and quantitatively using the Brooks–Gelman–Rubin statistic (Brooks and Gelman 1997). Models were fit by calling the program JAGS (Plummer 2003) using the jagsUI package (Kellner 2018) in R (R Core Team 2018). Data and R code are available at the University of Minnesota’s digital conservancy data repository (<https://hdl.handle.net/11299/208865>).

We used this model to test whether the parameters relating degree days to fish length (γ_n^x) differed as a function of invasion status. We assessed significance of group differences by calculating differences between parameters in each of 10,000 samples from the posterior distributions. We then evaluated whether the 90% credible interval of differences between coefficients contained zero. Additionally, we predicted fish lengths across a range of degree day values to compare predicted lengths among individual lake-years as well as for invaded and uninvaded lakes in general, while accounting for uncertainty in all parameters. Walleye and yellow perch lengths were predicted for the observed range of degree day values as a function of invasion status using 10,000 samples from the posterior distributions of parameter estimates. We also calculated the posterior probability that walleye and yellow perch in invaded systems were smaller than those in uninvaded systems as a function

of degree days. Because end-of-season length is particularly important for overwinter survival, we also predicted lengths for each invasion status at 1400 degree days, the median degree day value across all lake years for August 15. Finally, we predicted lake- and year-specific length on August 15 based on the median degree day value for that date in each lake to account for differences in temperature among lakes and years and their influence on end of summer length. For each of these analyses, we predicted fish length across 10,000 samples from the posterior distribution; summary statistics such as mean, probabilities, and credible intervals are summarized from this distribution of estimates. We calculated differences in predicted length between invasion status, lakes, and lake-years based on differences in predicted lengths across the 10,000 samples, and assess significance based on whether the 90% credible intervals of the differences in predicted lengths contained zero.

Results

We collated 50,012 walleye and 176,983 yellow perch individual fish lengths collected between mid-June and early September from 1983 to 2018. Walleye ranged from 15 to 162 mm at the time of capture (median = 64 mm). Yellow perch ranged from 10 to 80 mm at the time of capture (median = 38 mm). Cumulative degree days varied among lakes and years (Figure S1). Lake Vermilion was on average the coldest lake (range [median] end of year degree days 1423–2172 [1816]), while Mille Lacs was on average the warmest lake (1791–2571 [2178]).

Walleye

Age-0 walleye were smaller at mid-summer when zebra mussels were present (Fig. 2; intercept). Walleye lengths at mid-summer—were 6.5 mm (9.2%) smaller on average than in uninvaded systems (Table 2). On average, age-0 walleye grew more slowly per degree day increase when zebra mussels were present (Fig. 2; slope). On average walleye grew 4.02 mm less per standardized degree day or 19% slower growth when zebra mussels were present, although the 90% credible interval of this difference included zero (Table 2). Additionally, walleye exhibited higher variability in growth per degree day when

zebra mussels were present (Fig. 2; SD) with a mean difference of 0.15 (6.6% more variable; Table 2).

Age-0 walleye growth was also reduced in systems invaded by *Bythotrephes* (Fig. 2). The presence of *Bythotrephes* was associated with a 9 mm (12.8%) reduction in mid-summer length (intercept) and a reduced growth rate of 1.99 mm per standardized degree day or 9.6% slower growth (slope; Table 2). In contrast to zebra mussels, *Bythotrephes* presence was not associated with any difference in the variability of walleye growth per degree day (Table 2; SD, median difference is – 0.05 or 2% less variable, 90% credible interval included zero).

Together, the differences in intercepts and slopes relating degree days to age-0 walleye length resulted in diverging walleye lengths in invaded versus uninvaded lake-years over the course of the growing season (Fig. 3a). As degree days accumulated within a year, the magnitude of the differences between age-0 walleye length in invaded lakes compared to uninvaded lakes increased, with the largest differences in Mille Lacs, where *Bythotrephes* and zebra mussels co-occurred (Fig. 3b). Walleye in the presence of *Bythotrephes* were highly likely (posterior probability approaching 1) to be smaller than walleye from uninvaded lake-years across a wide range of degree day values (Fig. 3c). Uncertainty in the response of walleye growth was highest for zebra mussels (Fig. 3c). At low degree day values, walleye from zebra mussel invaded systems were unlikely to be smaller than walleye from uninvaded systems, but by the end of the summer the posterior probability of walleye in invaded lakes being smaller than those in uninvaded lakes approached 1.0 (Fig. 3c).

By mid-August, age-0 walleye in lakes containing zebra mussels were on average 18 mm (14%) smaller than walleye in uninvaded lakes (Fig. 4). Walleye in lakes containing *Bythotrephes* were 15 mm (12%) smaller, and walleye in lakes containing both AIS were on average 32 mm (25%) smaller than walleye in uninvaded lakes. Uncertainty in these estimates and high variability in growth rates resulted in wide ranges of predicted end of season walleye lengths. Despite this variability, the 90% credible interval of estimated differences for each category of invaded lakes did not contain zero. Still, walleye length varied substantially among lakes and years, with mid-August lengths varying by more than 50 mm even within uninvaded lakes (Figure S2). Within invaded lakes, walleye were

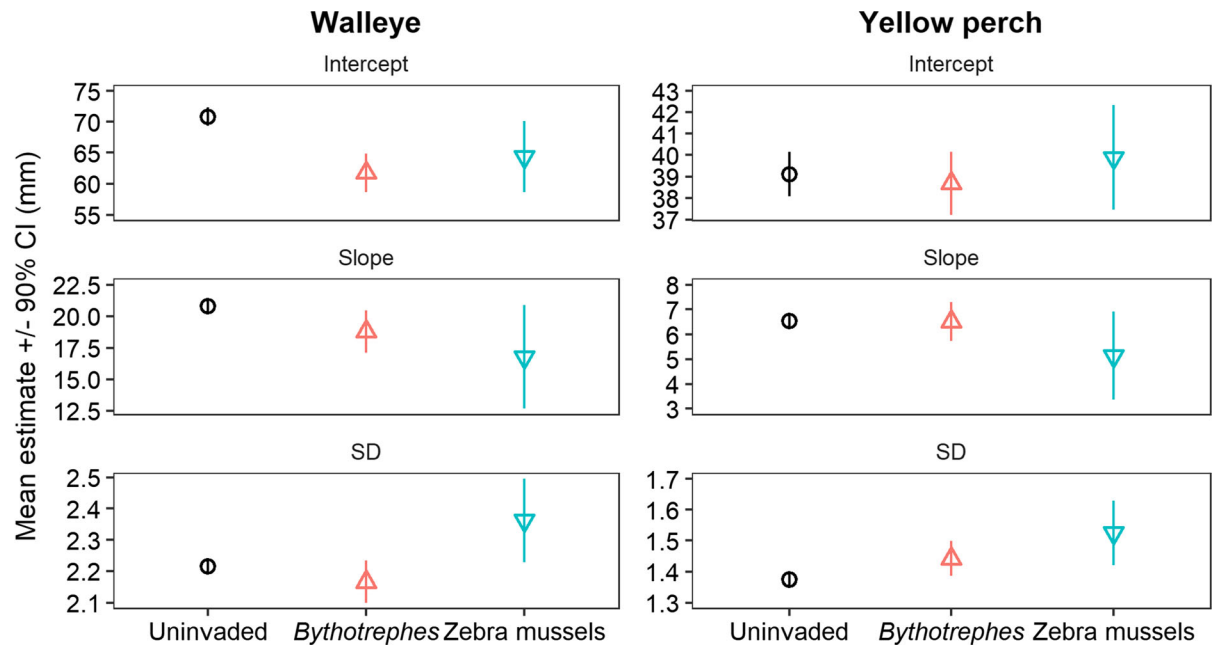


Fig. 2 Estimated intercept, slope, and standard deviations (SD) of the relationship between degree days and fish length for walleye (left) and yellow perch (right) as a function of invasion status. Points are mean estimates; lines are 90% credible intervals (CI)

Table 2 Estimated (mean and 90% credible interval) of intercepts (γ_n^α), slopes (γ_n^β), and standard deviations (SDs; γ_n^σ) from the model relating age-0 fish length to standardized degree days

Invasion category	Coefficient	Mean (90% CI)	Difference from uninvaded (90% CI)
Walleye			
Uninvaded	Intercept	70.82 (69.35, 72.28)	–
<i>Bythotrephes</i>	Intercept	61.75 (58.65, 64.85)	– 9.07 (– 12.22, – 5.95) ^a
Zebra mussels	Intercept	64.34 (58.61, 70.09)	– 6.48 (– 12.22, – 0.73) ^a
Uninvaded	Slope	20.78 (20.15, 21.43)	–
<i>Bythotrephes</i>	Slope	18.78 (17.11, 20.44)	– 2.00 (– 3.78, – 0.23) ^a
Zebra mussels	Slope	16.76 (12.66, 20.87)	– 4.02 (– 8.15, 0.10)
Uninvaded	SD	2.22 (2.19, 2.24)	–
<i>Bythotrephes</i>	SD	2.17 (2.10, 2.23)	– 0.05 (– 0.12, 0.02)
Zebra mussels	SD	2.36 (2.23, 2.50)	0.15 (0.01, 0.28) ^a
Yellow perch			
Uninvaded	Intercept	39.10 (38.06, 40.14)	–
<i>Bythotrephes</i>	Intercept	38.69 (37.22, 40.15)	– 0.41 (– 1.58, 0.77)
Zebra mussels	Intercept	39.88 (37.47, 42.32)	0.77 (– 1.49, 3.07)
Uninvaded	Slope	6.54 (6.25, 6.83)	–
<i>Bythotrephes</i>	Slope	6.52 (5.74, 7.30)	– 0.02 (– 0.85, 0.80)
Zebra mussels	Slope	5.13 (3.37, 6.90)	– 1.41 (– 3.18, 0.38)
Uninvaded	SD	1.37 (1.35, 1.39)	–
<i>Bythotrephes</i>	SD	1.44 (1.39, 1.50)	0.07 (0.01, 0.13) ^a
Zebra mussels	SD	1.52 (1.42, 1.63)	0.15 (0.05, 0.26) ^a

Also shown are estimated differences (mean and 90% credible interval) from uninvaded systems as a function of invasion status

^aCredible interval does not include zero

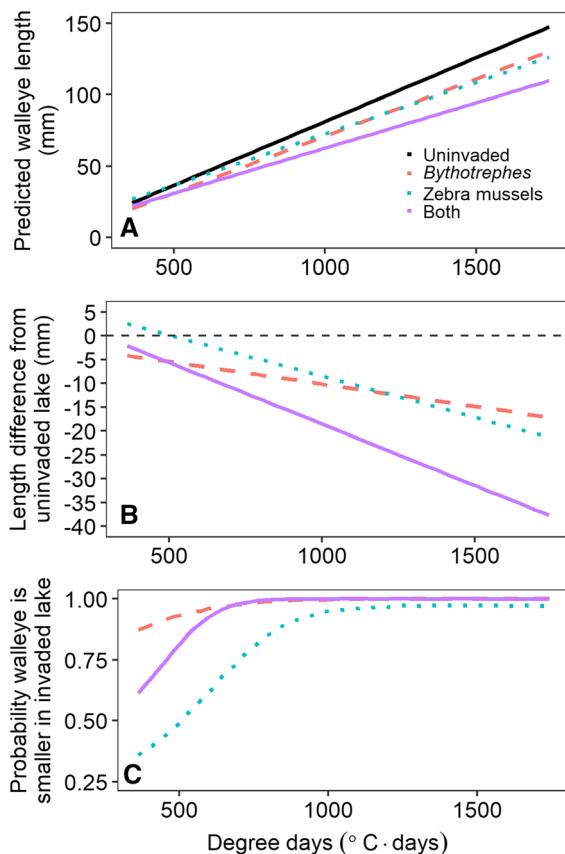


Fig. 3 Differences in age-0 walleye length metrics depend on degree days. **a** Predicted walleye length as a function of invasion status, **b** difference in length compared to uninvaded systems; and **c** posterior probabilities that walleye were smaller in invaded lake-years compared to uninvaded lake-years across a range of degree day values (base 5 °C). Colors represent invasion status

smaller when zebra mussels were present compared to uninvaded years in every case, while the lake- and year-specific effects of *Bythotrephes* were much more variable (Figure S3). Lake-specific model fits are shown in Figure S4.

Yellow perch

Contrary to our expectation, age-0 yellow perch were not consistently smaller in lakes with zebra mussels or *Bythotrephes*, although lengths were more variable in invaded systems. The presence of zebra mussels was not associated with differences in yellow perch length at mid-summer (Fig. 2; intercept), the estimated intercept was 0.77 mm (1.9%) greater and the 90%

credible interval included zero (Table 2). On average, age-0 yellow perch grew 1.4 mm (22%) more slowly per degree day increase when zebra mussels were present (Fig. 2; slope), although the 90% credible interval of this difference included zero (Table 2). Yellow perch exhibited 11% higher variability in growth per degree day when zebra mussels were present (Fig. 2; Table 2; SD).

The presence of *Bythotrephes* did not affect yellow perch length at mid-summer (Fig. 2; intercept). The intercept of the relationship between degree days and yellow perch length was 0.41 mm (1%) smaller, and the 90% credible interval included zero (Table 2). Yellow perch growth per degree day increase was also unaffected by the presence of *Bythotrephes* (mean difference in slope was -0.02 mm/standardized degree day or 0.2% slower growth and the 90% credible interval included zero; Table 2). Yellow perch growth per degree day was 5% more variable in the presence of *Bythotrephes* (Fig. 2; Table 2; SD).

Yellow perch lengths in lakes invaded by zebra mussels diverged slightly from those in uninvaded lakes and lakes invaded by *Bythotrephes* over the course of the growing season (Fig. 5a). As degree days accumulated, the magnitude of the differences between age-0 yellow perch total length in zebra mussel infested lakes compared to uninvaded lakes increased, although differences were generally small (Fig. 5b). The posterior probability of yellow perch being smaller in lakes with zebra mussels or both zebra mussels and *Bythotrephes* increased as degree days accumulated, but never exceeded 0.8 (Fig. 5c).

No differences in age-0 yellow perch lengths were detectable in mid-August (Fig. 6). Yellow perch in the presence of *Bythotrephes* were 1.5 mm (3%) larger than those in uninvaded lakes. Yellow perch in the presence of zebra mussels or both AIS were on average 3 and 4 mm (6%) smaller, respectively, than yellow perch in uninvaded systems. In all cases, the 90% credible interval of estimated differences for each category of invaded lakes included zero. As was the case with walleye, yellow perch total length varied substantially among lakes and years, with end of season length varying by up to 40 mm even within uninvaded lakes (Figure S5). Within invaded lakes, yellow perch were smaller in years invaded by zebra mussels in one of the three invaded lakes, while year-specific effects of *Bythotrephes* were highly variable

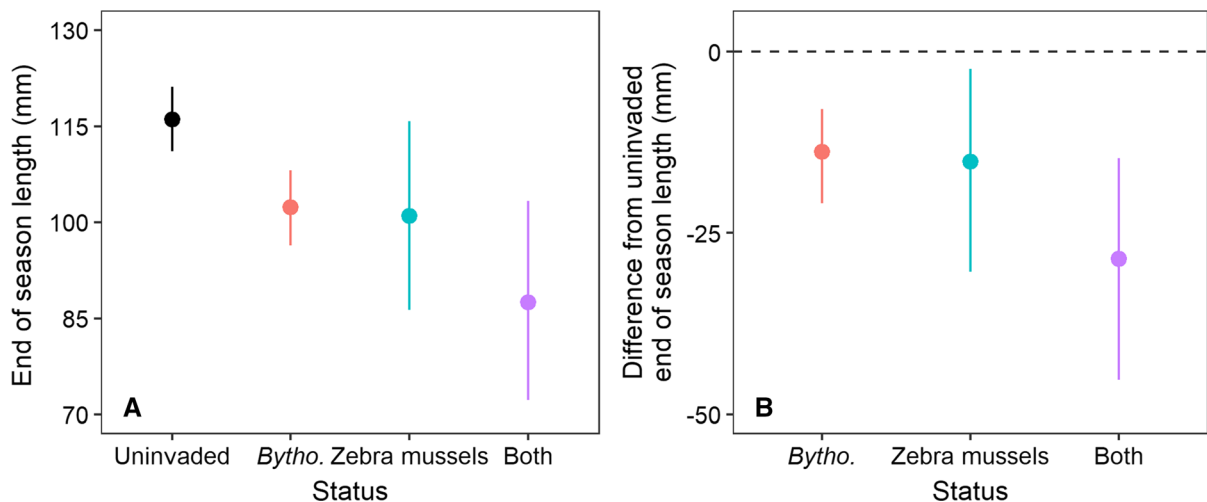


Fig. 4 **a** Predicted age-0 walleye length and **b** difference in predicted walleye length at 1400 degree days as a function of invasion status. Points represent mean estimates, bars represent 90% credible intervals

(Figure S6). Lake specific model fits are shown in Figure S7.

Discussion

Documented impacts of invasive zebra mussels and *Bythotrephes* on fish are variable across locations and time periods. Here, we use a 35-year dataset from 9 lakes to demonstrate that early life growth of an important top predator, walleye, is influenced by these aquatic invasive species. The magnitude of the estimated effects of each AIS on first year walleye growth were remarkably similar. Walleye were smaller at mid-summer and grew more slowly throughout the growing season in the presence of each species, resulting in mid-August lengths that were 15 and 18 mm (12 and 14%) smaller in lakes containing *Bythotrephes* and zebra mussels, respectively, compared to uninvaded systems. Growth responses varied among lakes, years, and individuals, and suggest some degree of decoupling of growth from temperature in systems invaded by zebra mussels.

The mechanisms through which zebra mussels and *Bythotrephes* affect walleye early life growth likely differ. Walleye rely on zooplankton prey for a portion of their first year of life (Wu and Culver 1992; Mittelbach and Persson 1998; Galarowicz et al. 2006), so AIS-induced changes in zooplankton prey

resources are likely to impact walleye at this life stage. *Bythotrephes* reduce zooplankton biomass (Boudreau and Yan 2003; Barbiero and Tuchman 2004; Kerfoot et al. 2016), change community composition (Strecker et al. 2006; Bunnell et al. 2012), and alter behavior (Pangle and Peacor 2006; Pangle et al. 2007) including vertical migration patterns (Bourdeau et al. 2015). Zebra mussels also influence zooplankton biomass, size structure, and community composition (Macisaac 1996; Pace et al. 1998; Idrisi et al. 2001; Higgins and Vander Zanden 2010) indirectly by reducing phytoplankton biomass and community composition as well as directly by consuming micro-zooplankton (e.g., Kissman 2010). In both cases, lack of access to preferred zooplankton prey on which walleye rely in their early life could explain our finding that walleye were smaller at mid-summer in the presence of either AIS. However, we also observed continued negative effects throughout the growing season when *Bythotrephes* were present, even after walleye were capable of shifting to other prey resources. Walleye grew 19% more slowly per degree day increase when zebra mussels were present, although variability in this response means that results were not statistically distinguishable from zero. These changes could indicate that littoral resources do not compensate for reduced energy flow to the pelagic food web in lakes invaded by either species. *Bythotrephes* may sequester energy if planktivorous prey fishes are unable to consume them (Barnhisel and

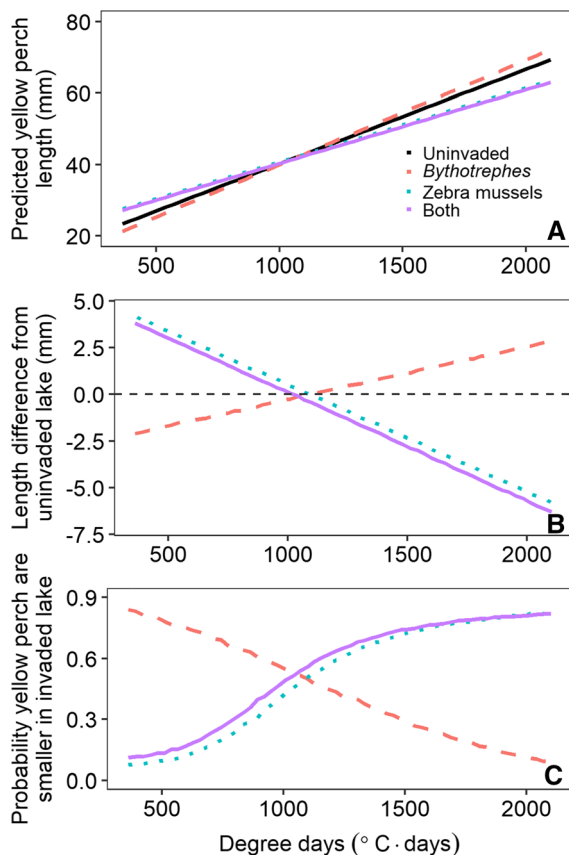


Fig. 5 Differences in age-0 yellow perch length metrics depend on degree days. **a** Predicted yellow perch length as a function of invasion status, **b** difference in length compared to uninvaded systems; and **c** posterior probabilities that yellow perch were smaller in invaded lake-years compared to uninvaded lake-years across a range of degree day values (base 5 °C). Colors represent invasion status

Kerfoot 2004; Compton and Kerfoot 2004) and because their production cannot compensate for the loss of production from native zooplankton declines (Kerfoot et al. 2016). Zebra mussels reduce pelagic production and increase benthic invertebrate biomass and production (Gergs et al. 2009; Burlakova et al. 2012; Karatayev et al. 2015). Fish that are able to access these increased benthic prey resources are expected to be more resilient to zebra mussel invasion (Higgins and Vander Zanden 2010), although fish growth response depends on the abundance and energy density of available prey pre- and post-invasion (McNickle et al. 2006; Lumb et al. 2007; Nalepa et al. 2009; Herbst et al. 2013). The observed variability in the response of walleye growth to zebra

mussels suggests differences in the capacity of fish to access this increased benthic production. Additionally, increased water clarity associated with zebra mussels can reduce walleye production (Geisler et al. 2016), and walleye in lakes with high water clarity rely more heavily on pelagic energy sources due to their preference for low light conditions (Tunney et al. 2018), potentially explaining lower growth of age-0 walleye associated with zebra mussels.

Interestingly, although both walleye and yellow perch rely on zooplankton prey for portions of their first year of life, estimated effects of either AIS on yellow perch growth were not distinguishable from zero. The lack of response of yellow perch growth was unexpected, given the documented negative effects of *Bythotrephes* on yellow perch growth in a subset of our study lakes and years chosen to minimize the confounding influences of a rainbow smelt invasion and a change in lake level management (Staples et al. 2017). Yellow perch are more of a foraging generalist compared to walleye (Graeb et al. 2005; Weber et al. 2010); thus, it is possible that yellow perch are able to shift to alternative prey items more easily when favored prey items become limited. For example, selective predation by *Bythotrephes* results in a shift in zooplankton community composition towards prey items that are more difficult to capture and ingest (Kerfoot et al. 2016). Yellow perch might be buffered from the negative effects of these changes because they can consume these less preferred prey items sooner and more easily than walleye. Yellow perch growth also did not respond negatively to zebra mussel invasion, similar to other studies (Mayer et al. 2000; Idrisi et al. 2001), again suggesting that yellow perch are capable of accessing alternative resources as food webs shift in the presence of AIS (Mitchell et al. 1996).

Changes in the density of age-0 fish can also cause changes in growth via density dependent processes (e.g., Rose et al. 2001, Irwin et al. 2009). The abundance of age-0 yellow perch in Lake Erie increased following zebra mussel invasion (Trometer and Busch 1999), and yellow perch densities were also high in Rainy and Kabetogama lakes in the invaded years for which growth was reduced as reported in Staples et al. (2017). The presence of dreissenid mussels has been associated with yellow perch recruitment failures in Lake Michigan (Marsden and Robillard 2004), which would be expected to result in

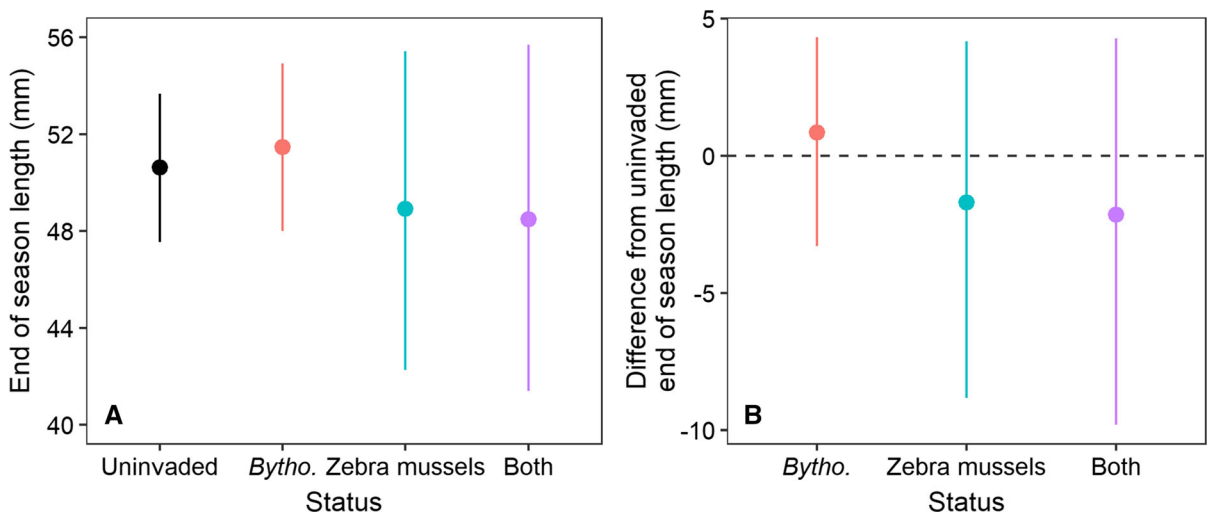


Fig. 6 **a** Predicted age-0 yellow perch length and **b** Difference in predicted yellow perch length at 1400 degree days as a function of invasion status. Points represent mean estimates, bars represent 90% credible intervals

increased growth if density dependence was an important driver of growth (Headley and Lauer 2008). Furthermore, walleye and yellow perch interact, and first year abundance and growth rates of each are intimately connected (e.g., Maloney and Johnson 1957; Rudstam et al. 1996; Rutherford et al. 1999; Pierce et al. 2006; Dembkowski et al. 2017). Abundant walleye populations can limit yellow perch recruitment, resulting in fast growth of age-0 yellow perch and slow growth of age-0 walleye. Conversely, low density walleye populations allow for abundant yellow perch, slow yellow perch growth, and fast walleye growth. We did not examine changes in age-0 fish abundance associated with invasion due to lack of data on age-0 fish densities. Future research examining effects of AIS on early life growth and abundance of fishes across a broader gradient of lakes may help elucidate mechanisms and understand differences among species and lakes.

Reduced growth rates resulting in smaller end of season length for age-0 walleye may have important implications for walleye fisheries. Slow growth during early life of fishes is associated with higher mortality due to increased predation (Houde 1987, 2008; Rose et al. 1999), lower energy reserves leading to lower winter survival (Post and Prankevicus 1987; Johnson and Evans 1991; Post et al. 1998), and later access to energetically profitable prey items (Wu and Culver 1992). These impacts on early life survival can impact eventual recruitment to later life stages and to the

fishery (Anderson 1988; Sogard 1997). Walleye size at the end of their first growing season is a good predictor of recruitment to later life stages in Lake Oneida (Forney 1974, 1976, 1977), Lake Mendota (Madenjian and Carpenter 1991), and in some South Dakota lakes (Grote et al. 2018), but not in Lake Erie (Madenjian et al. 1996). These differences could be due to differences in the relative importance of cannibalism in each system, which in turn is a function of the abundance of age-0 walleye relative to other prey sources, and winter duration (Forney 1976; Madenjian et al. 1996). Furthermore, age-0 piscivores can be an important prey item for larger fish (Chevalier 1973; Forney 1974; Ahrenstorff unpublished data), and the 12 and 14% reductions in walleye length associated with *Bythotrephes* and zebra mussels, respectively, translate to reductions in weight of 31 and 35% if weight is approximated as a cube function of length (Froese 2006).

Understanding how ecosystem-level effects of strongly interacting invasive species are transmitted through food webs to influence fish populations is challenging. Invasion ecology as a discipline has been criticized for a lack of generalizability and quantitative assessments of comparable invaded and uninvaded systems (Parker et al. 1999; Hulme et al. 2013). Among-system differences in impacts could be a result of spurious results reflecting a statistical or sampling artifact (Hulme et al. 2013) or can reflect real heterogeneity in impacts due to complex interacting

drivers of change and indirect effects (White et al. 2006; Brown et al. 2011; Strecker et al. 2011). We combined data across lakes and years to quantify effects of zebra mussels and *Bythotrephes* on walleye and yellow perch early life growth using statistical models that explicitly account for variability and uncertainty and are generalizable across lakes. At the same time, our statistical approach can estimate lake- and year-specific effects that may be useful for developing lake-specific management plans. Our results suggest that zebra mussels and *Bythotrephes* can influence walleye through indirect pathways, although the mechanisms of such effects are unknown. Of course, these lakes are subject to other stressors including climate change, nutrient pollution, and harvest (Ormerod et al. 2010; Carpenter et al. 2011), all of which have the potential to influence fish populations via numerous pathways. We detected biologically significant effects of AIS on early life growth of a top predator fish in spite of the existence of these potentially confounding factors. Continued long-term monitoring of fish populations and lake ecosystems will be critical for testing whether similar effects are observed in other time periods and other lakes, and for understanding the mechanisms through which invasive species and other stressors influence fish and aquatic food webs.

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