

# Do lake-specific characteristics mediate the temporal relationship between walleye growth and warming water temperatures?

Danielle L. Massie, Gretchen J.A. Hansen, Yan Li, Greg G. Sass, and Tyler Wagner

**Abstract:** Walleye (*Sander vitreus*) population declines have been linked to climate change, but it is unclear how the growth of this cool-water species may be affected by warming water temperatures. Because warming rates vary among lakes, it is uncertain whether lake characteristics may mediate the temperature effects on walleye growth or may vary as a result of differences in lake habitat or productivity. In this study, we (i) quantified walleye annual growth from 1983 to 2015 in 61 lakes in midwestern United States; (ii) estimated the relationship between annual early life growth ( $\omega$ ; mm·year<sup>-1</sup>) and water growing degree days (GDD); and (iii) identified lake characteristics affecting  $\log_e(\omega)$ -GDD relationships. On average,  $\omega$  estimates significantly increased with increasing GDD; however, this relationship varied in direction and magnitude among lakes. We estimated an 84% posterior probability of a negative effect of water clarity on the  $\log_e(\omega)$ -GDD relationship, suggesting that water clarity may mediate the effect of warming water temperatures by affecting the magnitude and direction of the  $\log_e(\omega)$ -GDD relationship. Our results provide insights into the conservation of cool-water species in a changing environment and identify lakes characteristics in which walleye growth may be more resilient to climate change.

**Résumé :** Les déclin des populations de doré jaune (*Sander vitreus*) ont été reliés aux changements climatiques, mais l'incidence du réchauffement des températures de l'eau sur la croissance de cette espèce d'eau froide n'est pas bien établie. Comme les taux de réchauffement varient d'un lac à l'autre, il se pourrait que les caractéristiques du lac modulent les effets de la température, des effets qui pourraient quant à eux varier en fonction des habitats ou de la productivité des lacs. Nous avons (i) quantifié la croissance annuelle des dorés jaunes dans 61 lacs du Midwest des États-Unis de 1983 à 2015, (ii) estimé la relation entre la croissance annuelle au début de la vie ( $\omega$ ; mm·année<sup>-1</sup>) et les degrés-jours de croissance (DJC) et (iii) cerné des caractéristiques des lacs qui ont une incidence sur la relation  $\log_e(\omega)$ -DJC. En moyenne, les estimations de  $\omega$  augmentent de manière significative parallèlement à l'augmentation des DJC; toutefois, la direction et la magnitude de cette relation varient d'un lac à l'autre. Nous estimons une probabilité a posteriori de 84 % d'un effet négatif de la clarté de l'eau sur la relation  $\log_e(\omega)$ -DJC, ce qui indiquerait que la clarté de l'eau pourrait moduler l'effet de la hausse des températures de l'eau en modifiant la magnitude et la direction de la relation  $\log_e(\omega)$ -DJC. Nos résultats fournissent de nouveaux renseignements utiles pour la conservation d'espèces d'eau froide dans un milieu changeant et relèvent des caractéristiques de lacs dans lesquels la croissance des dorés jaunes pourrait être plus résiliente dans un contexte de changements climatiques. [Traduit par la Rédaction]

## Introduction

A critical component to managing fish populations is understanding how and why individual vital rates (e.g., mortality, growth, and recruitment) fluctuate through time (McClelland et al. 2012). For example, fish populations may shift over time due to changes in management regulations (Myers et al. 2008), water temperature (Black 2009), and prey abundance (Forney 1977). Individual fish vital rates also vary spatially (Helser and Lai 2004; Midway et al. 2016; Massie et al. 2018) because many of the ecological drivers affecting fish populations act across broad spatial extents (e.g., land use and climate change; Mantyka-Pringle et al. 2015). Therefore, understanding the variability and drivers

of fish vital rates across multiple scales (i.e., temporal and spatial) is important for informing management and conservation decisions (Pedersen et al. 2018; Li et al. 2018). For example, identifying spatial and temporal drivers could help forecast how vital rates may change under future environmental conditions. In particular, quantifying the spatiotemporal variability of growth is important because growth rates are an integrated measure of ecological success of organisms (i.e., health and wellbeing, stress, and prey availability; Rypel 2011; Quist et al. 2012; Li et al. 2018).

Water temperature is a primary driver of the growth of fishes because it influences metabolic activity, food consumption, and activity level (Jobling 1981, 1997; Brett 1979; Kitchell et al. 1977). When water temperatures warm, growth rates should initially

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increase as fish energy and food consumption increase (Jobling 1997; Kitchell et al. 1977; Neuheimer et al. 2011; Madenjian et al. 2018). However, as temperatures increase above the metabolic thermal optimum temperature (assuming that food consumption has not changed), growth rates should eventually start to decline (Kitchell et al. 1977; Neuheimer et al. 2011). Therefore, as global water temperatures continue to rise due to the direct and indirect effects of climate change (Poff et al. 2002; O'Reilly et al. 2015), fish will require more food to meet higher metabolic costs or growth will be negatively affected (Kitchell et al. 1977). In fact, it is well documented that lake water temperatures are sensitive to increases in climate-driven changes in air temperatures (Woolway et al. 2019, 2020). However, the relationship between air temperatures and lake temperatures varies based on morphometry and the ecological context of individual lakes (Winslow et al. 2015; Woolway and Merchant 2017).

We expect the negative impacts of temperature on growth to be more prominent in cold- and cool-water fish species than in warm-water species since their species' specific optimum is lower. In fact, some temperate marine species have already demonstrated negative effects of warming water temperatures on growth (Thresher et al. 2007; Neuheimer et al. 2011). Less is known about the potential effects of warming water temperatures on the growth of inland fishes. However, one study found that juvenile walleye (*Sander vitreus*) growth was positively correlated with warmer water temperatures in Wisconsin lakes after accounting for density-dependent effects of conspecifics and largemouth bass (*Micropterus salmoides*) (Pedersen et al. 2018). In addition, a lake's thermal response to climate change may differ due to physical lake-specific characteristics (Read et al. 2014). For example, lake size, depth, and water clarity affect lake temperature responses to climate change. This suggests that certain lake characteristics may mediate the effects of climate change on the growth for some inland fish populations. In addition, growth responses to temperature might vary due to differences in prey availability, habitat area, and population densities (Sass et al. 2006; Venturelli et al. 2010). Identifying lake characteristics that mediate the effects of climatic stress on growth may help inform management decisions and identify locations to focus conservation efforts.

Here, we describe the spatiotemporal relationship between walleye growth and water temperature for inland lakes in Minnesota and Wisconsin, USA. Walleye are a cool-water species native to the lakes and rivers of Canada and the northern USA (Quist et al. 2003). As an apex predator, walleye play a vital role in aquatic food chains (Van Zuiden and Sharma 2016). Additionally, the species is highly prized and of cultural importance for its recreational, subsistence, and commercial fisheries in the Laurentian Great Lakes region and contributes millions of dollars annually to the area's economy (Hansen et al. 1991; Pandit et al. 2013).

Walleye populations in some locations in the Laurentian Great Lakes region have been or are projected to be negatively affected by environmental stressors, including Lake Erie (Pandit et al. 2013), lakes in Ontario, Canada (Van Zuiden and Sharma 2016), and the Ceded Territory of Wisconsin (Hansen et al. 2015; Rypel et al. 2018; Embke et al. 2019). Walleye population declines in the region have been associated with poor natural recruitment in some locations (Hansen et al. 2018). Many studies implicate climate change (and competition with other species) to be an important direct or indirect contributor to regional declines in recruitment and abundance (Van Zuiden and Sharma 2016; Hansen et al. 2018). However, it is unclear whether warming temperatures may be affecting the growth of walleye in inland lakes, especially in the Laurentian Great Lakes region, where lakes are found to be warming

faster than the global average (O'Reilly et al. 2015). In addition, it is likely that the effects of warming water temperatures on growth varies across the region because these lakes exhibit a high level of heterogeneity in surface area, depth, productivity, and community composition and span a latitudinal gradient that results in thermally diverse lakes. Therefore, the objectives of our study were to (i) quantify the spatial and temporal variability of walleye growth in a subset of Minnesota and Wisconsin inland lakes; (ii) quantify the relationship between annual early life growth rate ( $\omega$ ; Gallucci and Quinn 1979) and water temperature; and (iii) identify lake characteristics (i.e., lake depth, area, water clarity, and average water temperature) that may influence the lake-specific  $\omega$ -water temperature relationships.

## Materials and methods

### Length-at-age and predictor data

Walleye length-at-age data (total length (mm) and age (years)) were collated from the Minnesota and Wisconsin Departments of Natural Resources for 1520 inland lakes in Minnesota and 374 lakes in Wisconsin. Length-at-age data were sampled across a range of years (1962–2018) using multiple gear types. Because the goal of our project was to quantify the temporal relationship between walleye growth and water temperature, the data were filtered to only include lakes with at least 10 years of length-at-age data. We choose lakes with at least 10 years of data because studies of fish populations (and their habitats) with less than 10 years of data likely have low statistical power to detect a temporal trend (Wagner et al. 2009). Four lakes were missing data on covariates (see below) and were also excluded. Our final dataset consisted of 304 222 walleye lengths-at-age from 61 lakes sampled during 1983–2018 (2196 lake-years). Fish were aged using a variety of hard structures, including otoliths (20%), fin spines (11%), scales (9%), cleithrum, fin rays, and opercles (<1% combined). For the majority of the samples (60%), the aging structure was unknown. However, it is likely that many of these samples were aged using scales, spines, or otoliths based on a poll of natural resources agencies (Maceina et al. 2007). Although the accuracy of ages may vary depending on the structure used for ageing, it is unlikely that any systematic biases existed in this dataset that would affect our inferences as demonstrated by Pedersen et al. (2018). Rather, the uncertainty in aging structures used added an additional source of variation and may serve to make our estimates conservative, given that our ability to detect effects may be lower with this added source of variation.

Lake water temperatures were indexed using water temperature growing degree days (GDD, °C-days). GDD is a time-based integral of heat available for growth (Chezik et al. 2014) and has been shown to be a strong predictor of walleye growth. Annual GDD estimates were calculated from simulated daily lake surface temperatures during 1980–2015 generated using a thermodynamic model of 10 744 lakes located in the upper midwestern USA (Winslow et al. 2017). GDD estimates calculated with a base temperature of 5 °C were used because this base temperature is recommended for describing the growth of temperate fish species (Chezik et al. 2014) and has successfully described the length of the walleye growing season (Uphoff et al. 2013). A preliminary model showed that GDD, on average, significantly increased over time for the lakes used in our analysis — with a mean annual GDD increase of ~16% per year (see online Supplementary material, Fig. S1<sup>1</sup>). Additionally, all lakes showed a ≥85% posterior probability of increasing GDD estimates over time. These results support our hypothesis that GDD increases may result in changes in walleye growth. Information on lake characteristics, including maximum lake depth (m), average water clarity as

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2020-169>.

indexed by Secchi depth (m), and lake area (km<sup>2</sup>), were from Winslow et al. (2017) (Supplementary Table S2<sup>1</sup>). Lake-specific mean GDD values were calculated by taking the average GDD across all years for each lake (Supplementary Table S1<sup>1</sup>).

**Statistical modeling**

**Spatiotemporal variability of walleye growth**

To estimate the relationship between walleye growth and GDD, we first required estimates of annual walleye somatic growth for each lake. These annual growth estimates were obtained using a spatiotemporal von Bertalanffy growth model (Li et al. 2018) fitted to a time series of walleye length-at-age data. In this model the traditional von Bertalanffy growth equation was incorporated into a Bayesian hierarchical modeling framework (eq. 1) as follows:

$$(1) \quad \begin{aligned} TL_{ijy} &= L_{\infty yj} \{1 - \exp[-K_{jy}(t_{ijy} - t_{0jy})]\} + \epsilon_{ijy} & \epsilon_{ijy} &\sim N(0, \sigma^2) \\ \begin{bmatrix} \ln L_{\infty, y+1, j} \\ \ln K_{y+1, j} \\ t_{0, y+1, j} \end{bmatrix} &\sim \text{MVN} \left[ \begin{pmatrix} \ln L_{\infty, y, j} \\ \ln K_{y, j} \\ t_{0, y, j} \end{pmatrix}, \hat{\Sigma} \right] \\ \begin{bmatrix} \ln L_{\infty, y=1, j} \\ \ln K_{y=1, j} \\ t_{0, y=1, j} \end{bmatrix} &\sim \text{MVN} \left[ \begin{pmatrix} \ln \bar{L}_{\infty} \\ \ln \bar{K} \\ \bar{t}_0 \end{pmatrix}, \Sigma \right] \end{aligned}$$

where  $TL_{ijy}$  is the total length for fish  $i$  from lake  $j$  in year  $y$ , and  $t_{ijy}$  is the observed age for fish  $i$  from lake  $j$  in year  $y$ .  $L_{\infty}$  refers to the asymptotic length or theoretical maximum average length, and  $K$  is the Brody growth coefficient. This coefficient describes how quickly mean lengths-at-age approach  $L_{\infty}$ .  $t_0$  is the hypothetical age (years) when length is equal to 0. The growth parameters ( $L_{\infty}$ ,  $K$ , and  $t_0$ ) were estimated for every lake and year and thus were assumed to vary temporally and spatially.  $L_{\infty}$  and  $K$  were estimated

on the  $\log_e$  scale to reduce scale differences between parameters and improve convergence. All three growth parameters followed a multivariate normal distribution (MVN) and were modeled using a random-walk process. Specifically,  $\bar{L}_{\infty}$ ,  $\bar{K}$ , and  $\bar{t}_0$  are the lake-average parameters for year = 1, and future years are modeled using a one-step random walk prior, with a scaled inverse-Wishart prior on the covariances ( $\Sigma$  and  $\hat{\Sigma}$ ; Gelman and Hill 2007). The residual error term,  $\epsilon_{ijy}$ , was assumed to come from a normal distribution with a mean of 0 and a variance  $\sigma^2$ . The product of the posterior distributions for  $L_{\infty}$  and  $K$  were used to derive a posterior distribution for  $\omega$ , which is the slope of the growth curve near its origin and represents early life growth rate (mm·year<sup>-1</sup>; Gallucci and Quinn 1979). The highest posterior density for early life growth ( $\omega$ ; hereinafter also referred to as the “growth coefficient”) in each lake and year was used in subsequent analyses.

**Estimating the  $\log_e(\omega)$ -GDD relationships and the effects of lake characteristics**

To estimate the overall relationship between  $\log_e$  annual walleye growth estimates ( $\omega_{jy}$ ) and GDD, we first fit a varying intercept, varying slope model without covariates on the varying parameters (e.g., eq. 2 without covariates on the varying slopes and intercepts). Next, to estimate the effect of lake characteristics on the lake-specific intercepts and slopes, we fitted the same model with the addition of lake characteristic covariates (see Supplementary Table S1<sup>1</sup> for lake-specific predictor information).  $\log_e$ -transformed highest posterior density estimates of annual growth coefficients,  $\omega_{jy}$ , that were estimated in eq. 1 were modeled as a function of GDD in lake  $j$  and year  $y$  (eq. 2). The varying intercept, varying slope model used to quantify the  $\log_e(\omega)$ -GDD relationship and the effects of lake characteristics was as follows:

$$(2) \quad \begin{aligned} \log_e(\omega)_i &\sim N[\alpha_{j(i)} + \beta_{j(i)} \times \text{GDD}_i, \sigma^2] \\ \begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} &\sim \text{MVN} \left[ \begin{pmatrix} \mu_{\alpha} + \gamma_{\alpha 1} \times \text{depth}_j + \gamma_{\alpha 2} \times \text{area}_j + \gamma_{\alpha 3} \times \text{clarity}_j + \gamma_{\alpha 4} \times \overline{\text{GDD}}_j \\ \mu_{\beta} + \gamma_{\beta 1} \times \text{depth}_j + \gamma_{\beta 2} \times \text{area}_j + \gamma_{\beta 3} \times \text{clarity}_j + \gamma_{\beta 4} \times \overline{\text{GDD}}_j \end{pmatrix}, \Sigma \right] \end{aligned}$$

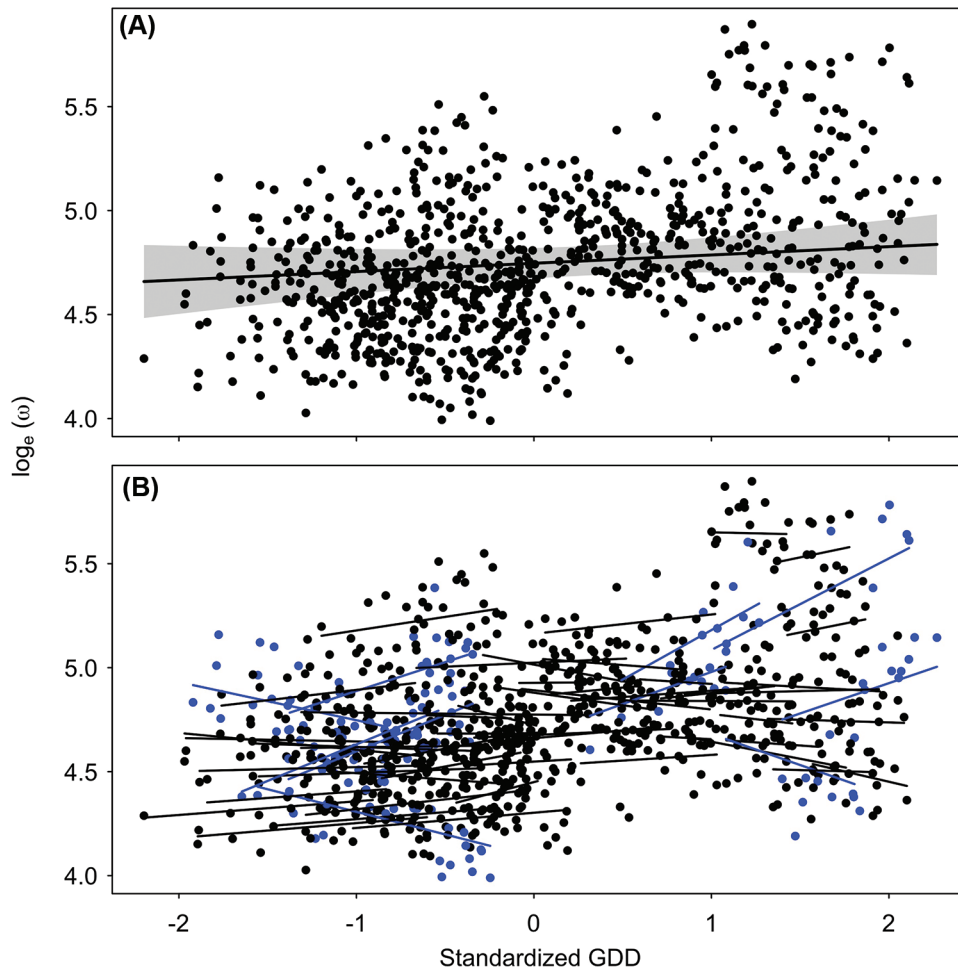
where the subscript “ $j(i)$ ” indicates that observation  $i$  of  $\log_e(\omega)$  belongs to lake  $j$ . To account for the cumulative temperature experienced over the period of most rapid growth for walleye (i.e., prior to maturation or age 6; Malison and Held 1996; Quist and Isermann 2017), we set  $\text{GDD}_i$  as the average of GDD estimates from the year of each observation  $i$  and the 5 years prior (hereinafter referred to as a 6-year lag). Thus, the GDD for every lake and in every year represents the thermal environment experienced by fish in each lake over the 6-year time period prior to being sampled. Although the 6-year time lag makes biological sense, our inferences were not sensitive to this cut-off, as we found no differences when using 5-, 6-, or 8-year GDD lag models (Supplementary Table S2<sup>1</sup>).

The parameters  $\alpha_j$  and  $\beta_j$  are the lake-specific intercepts (i.e., average growth coefficients;  $\omega$ ) and slopes (i.e., the  $\log_e(\omega)$ -GDD relationship), respectively. These lake-specific intercepts and slopes were assumed to come from an MVN and were modeled as a function of lake-level predictors (i.e., depth = maximum lake depth, area = lake area, clarity = average water clarity as indexed by Secchi disk depth, and  $\overline{\text{GDD}}$  = lake-specific mean water GDD). Lake-specific intercepts are described by the grand mean intercept ( $\mu_{\alpha}$ ) and the relationship between average  $\log_e(\omega)$  and the lake-level predictors that are characterized by the estimated parameters  $\gamma_{\alpha 1-4}$ . Similarly, lake-specific slopes are described by grand mean slope ( $\mu_{\beta}$ ) and the relationship between the  $\log_e(\omega)$ -

GDD slope and the lake-level predictors that are characterized by the estimated parameters  $\gamma_{\alpha 1-4}$ . All covariates were standardized (mean = 0, SD = 1) prior to analysis, and lake area was  $\log_e$ -transformed to reduce scale differences among lakes. Annual growth estimates after 2015 were excluded from the analysis because GDD estimates were not available for those years. In addition, years without length-at-age data were removed prior to fitting eq. 2. Although these years without length-at-age data are still able to be estimated with the spatiotemporal growth model (eq. 1), those estimates largely reflect the lake-specific average growth across all years and thus would likely dilute temporal effects investigated in the  $\log_e(\omega)$ -GDD model (eq. 2). Diffuse normal priors were used for all slope and intercept parameters ( $\mu_x \sim N[0, 1000]$ ,  $\gamma_x \sim N[0, 1000]$ ), a uniform prior was used for the residual standard deviation ( $\sigma \sim U[0, 100]$ ), and a scaled inverse-Wishart prior was used for the covariance.

We identified important relationships by evaluating whether or not the 90% credible interval of the estimated effects overlapped with zero. Additionally, we calculated the posterior probability that effects of covariates (on the lake-specific intercepts and slopes) were in the direction (i.e., positive or negative) of the posterior mean (Filstrup et al. 2014). This approach lacks an arbitrary cutoff level of significance (i.e., whether or not the 90% credible interval overlaps zero) and allows for a simple representation of uncertainty in the posterior distributions of parameter estimates,

**Fig. 1.** Relationship between walleye (*Sander vitreus*) annual early life growth estimates ( $\log_e(\omega)$ ) and growing degree days (GDD) in 61 inland lakes in Minnesota and Wisconsin sampled from 1983 to 2015. The black dots show the annual  $\log_e(\omega)$  estimates from the spatiotemporal model (eq. 1) with the corresponding annual GDD value. Plot A illustrates the grand mean relationship between  $\log_e(\omega)$  and GDD for a lake with average lake characteristics. The black line is the posterior mean, and the shaded area is the associated 90% credible region. Plot B shows the lake-specific  $\log_e(\omega)$ –GDD relationships for the 61 lakes (lines represent posterior means), where the length of the horizontal line shows the range of GDD values for each lake. The lake-specific slopes blue represent the relationships where the 90% credible interval did not overlap zero. The lake-specific 90% credible intervals were excluded to ease interpretation.



which is a more objective means to determine potential biological significance (Filstrup et al. 2014).

Models were fit using the JAGS version 3.3.0 software (Plummer 2017) called from the programming environment R (R Core Team 2016) via the R2jags package (Su and Yajima 2012). Three Markov chains were run with different starting values. The chains for the spatiotemporal growth model (eq. 1) were run for 500 000 iterations, 190 000 of which were discarded as burn-in. Posterior estimates were additionally thinned by taking every 10th sample, which provided 93 000 total MCMC samples used to characterize the posterior distribution. Chains for the K–GDD models (eq. 2) were run for 10 000 iterations with 5000 burn-in, and posterior estimates were not thinned. This resulted in a total of 15 000 MCMC samples used to characterize the posterior distribution. Model convergence was visually assessed through posterior distribution trace plots and using Brooks–Gelman–Rubin statistic ( $\hat{R}$ ), with values  $< 1.1$  indicating convergence.

## Results

### Spatiotemporal variability of walleye growth

Lake-specific length-at-age sample sizes ranged from 187 to 42 188, with a mean of 3714 samples per lake. Total lengths and

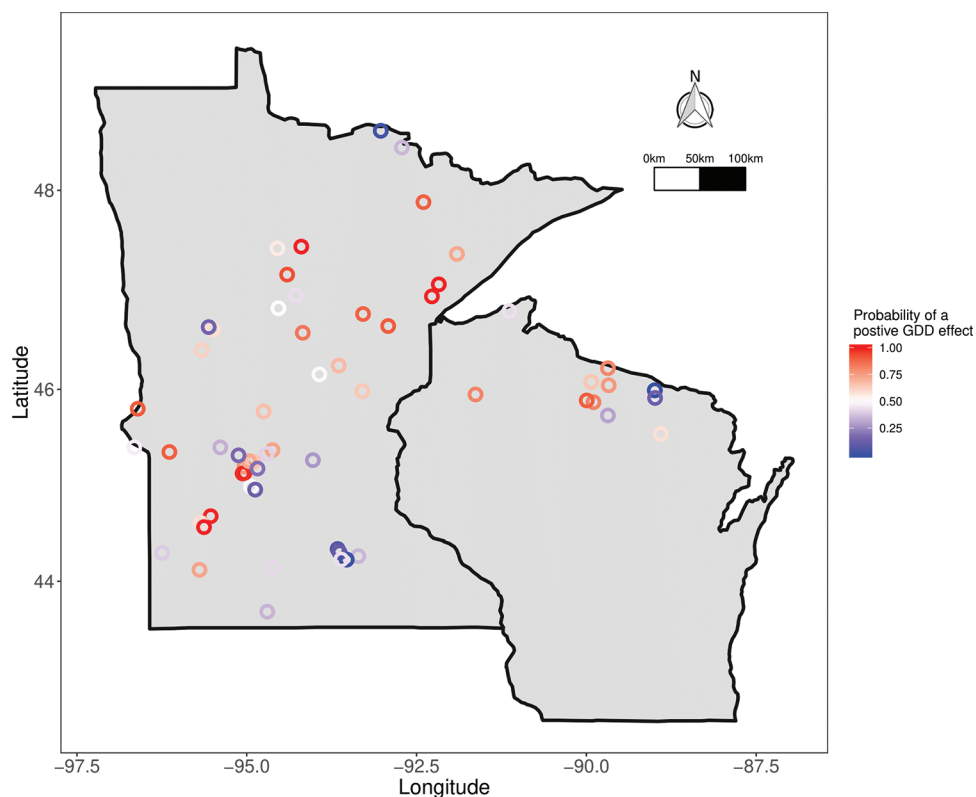
ages ranged from 8 to 800 mm and from 0 to 27 years, respectively. Within-lake growth trajectories varied substantially across years (see Supplementary Fig. S2<sup>1</sup> for an example lake). Specifically, growth coefficients were found to vary substantially among lakes and across years ( $\omega$  range = 54 to 396 mm·year<sup>-1</sup>; Supplementary Fig. S3<sup>1</sup>). Within-lake temporal variation in growth coefficients also varied among lakes. For example, growth coefficients ranged from 59 to 130 mm·year<sup>-1</sup> for lake 5, and from 140 to 258 mm·year<sup>-1</sup> for lake 50 (Supplementary Fig. S3<sup>1</sup>).

### $\log_e(\omega)$ –GDD relationships and the effects of lake characteristics

In the varying intercept, varying slope model without lake covariates, the estimated grand mean intercept ( $\hat{\mu}_\alpha$ ) and slope ( $\hat{\mu}_\beta$ ) of the  $\log_e(\omega)$ –GDD relationship were 4.72 and 0.06, respectively. The 90% credible interval of the grand mean slope estimate slightly overlapped zero (90% CI:  $-0.0006, 0.11$ ), but had a 95% posterior probability of a positive effect.

For a lake with average characteristics, walleye growth ( $\log_e(\omega)$ ) did not significantly increase with increasing GDD (the  $\log_e(\omega)$ –GDD relationship ( $\hat{\mu}_\beta$ ) was 0.040 and 90% CI:  $-0.025, 0.10$ ; Fig. 1A). However, this relationship varied in direction and magnitude among the 61 lakes (Fig. 1B). Estimated lake-specific slopes ranged from  $-0.30$  to  $0.48$ . We found 57% of lakes were estimated to have

**Fig. 2.** Map of 61 inland lakes in Minnesota and Wisconsin, where the colour of the point indicates the posterior probability that the lake-specific walleye (*Sander vitreus*)  $\log_e(\omega)$ –GDD relationship was positive over the years 1983–2015.



**Table 1.** Posterior mean parameter estimates and 90% credible intervals (CI) from a varying intercept, varying slope model investigating annual growing degree days (GDD) effects on walleye (*Sander vitreus*) early life growth  $\omega$  estimates for 61 Minnesota and Wisconsin lakes during 1983–2015.

Parameter	Estimate (90% CI)	Post. prob.
<b>Effects on the <math>\log_e(\omega)</math>–GDD relationship</b>		
Grand mean slope ( $\mu_\beta$ )	0.040 (–0.025, 0.100)	0.85
Effect of lake depth on slope ( $\gamma_{\beta 1}$ )	0.030 (–0.060, 0.120)	0.72
Effect of lake area on slope ( $\gamma_{\beta 2}$ )	–0.003 (–0.070, 0.060)	0.53
Effect of Secchi disk depth on slope ( $\gamma_{\beta 3}$ )	–0.060 (–0.150, 0.040)	0.84
Effect of mean GDD on slope ( $\gamma_{\beta 4}$ )	–0.030 (–0.120, 0.050)	0.73
<b>Effects on the <math>\log_e</math> average growth coefficient (<math>\omega</math>)</b>		
Grand mean intercept ( $\mu_\alpha$ )	4.750 (4.670, 4.820)	1.00
Effect of lake depth on intercept ( $\gamma_{\alpha 1}$ )	–0.080 (–0.170, 0.017)	0.92
Effect of lake area on intercept ( $\gamma_{\alpha 2}$ )	0.150 (0.080, 0.230)	1.00
Effect of Secchi disk depth on intercept ( $\gamma_{\alpha 3}$ )	0.002 (–0.110, 0.100)	0.51
Effect of mean GDD on intercept ( $\gamma_{\alpha 4}$ )	0.100 (–0.003, 0.200)	0.95

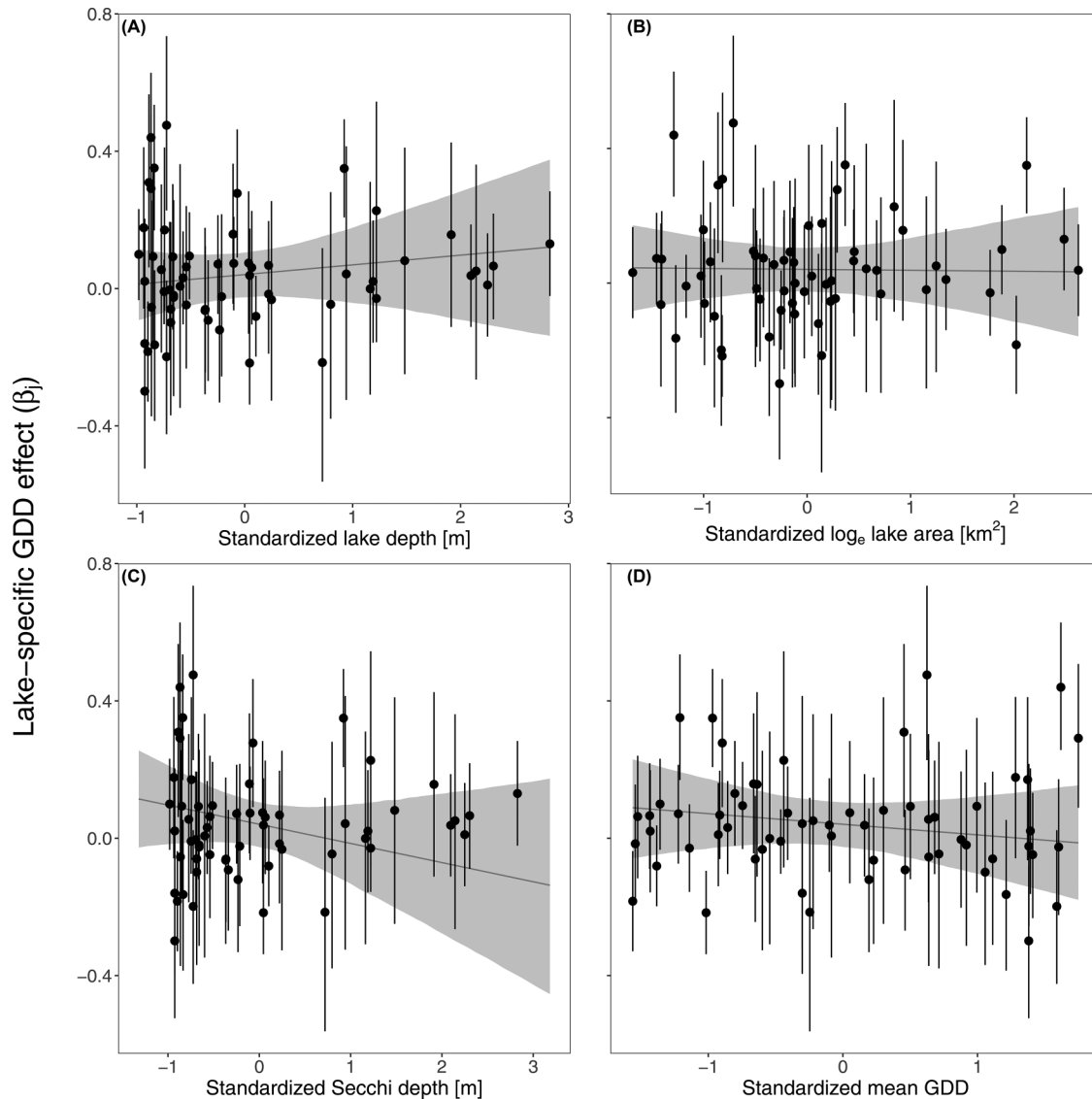
**Note:** Parameter = parameter estimated from eq. 2; Estimate (90% CI) = estimated posterior mean and associated 90% credible interval; Post. prob. = posterior probability that the estimated effect is in the same direction as the posterior mean (either positive or negative).

$\log_e(\omega)$  increase with increasing GDD, and seven of these positive relationships were significant (Fig. 1B). Across all lakes, 24 lakes were estimated with a  $\geq 70\%$  posterior probability of a positive  $\log_e(\omega)$ –GDD relationship. These lakes with strong positive slopes were evenly distributed across the study area (Fig. 2), suggesting that physical lake characteristics, rather than regional climate patterns, may be driving some of the heterogeneity of this relationship among lakes.

The 90% credible intervals for all predictor variables on the lake-specific  $\log_e(\omega)$ –GDD relationships overlapped with zero (Table 1; Fig. 3). Lake water clarity (Secchi disk depth) had the highest

posterior probability of an effect, and this effect was negative (posterior probability = 0.84; Fig. 3C), suggesting that increased GDD was more likely to reduce walleye growth in clear lakes than in turbid lakes. Lake characteristics were correlated with lake-specific average  $\log_e(\omega)$  estimates (i.e.,  $\hat{\alpha}_i$ ; lake-specific intercepts). The effects of lake area, water clarity, and mean water GDD were all positive (Figs. 4B, 4C, and 4D), meaning that walleye growth was fastest in larger, clearer, and warmer lakes. Water clarity and mean GDD 90% credible intervals overlapped with zero (Table 1); however, the posterior probability of a positive effect of mean GDD on lake average  $\log_e(\omega)$  was 0.95. Lake average

**Fig. 3.** The effects of lake-specific covariates, (A) lake depth (m), (B) lake area (km<sup>2</sup>), (C) Secchi disk depth (m), and (D) mean growing degree days (GDD), on the lake-specific slopes of the walleye (*Sander vitreus*)  $\log_e(\omega)$ -GDD relationship for 61 Minnesota and Wisconsin lakes during 1983–2015. Black dots are the posterior mean estimates of the lake-specific slopes of the  $\log_e(\omega)$ -GDD relationship. The vertical bars show the estimated 90% credible interval for the lake-specific slope estimates, and the black horizontal line shows the fitted relationship between the lake-specific slope estimates and the given lake characteristic. The shaded region is the 90% credible interval of the hierarchical regression fitted line.



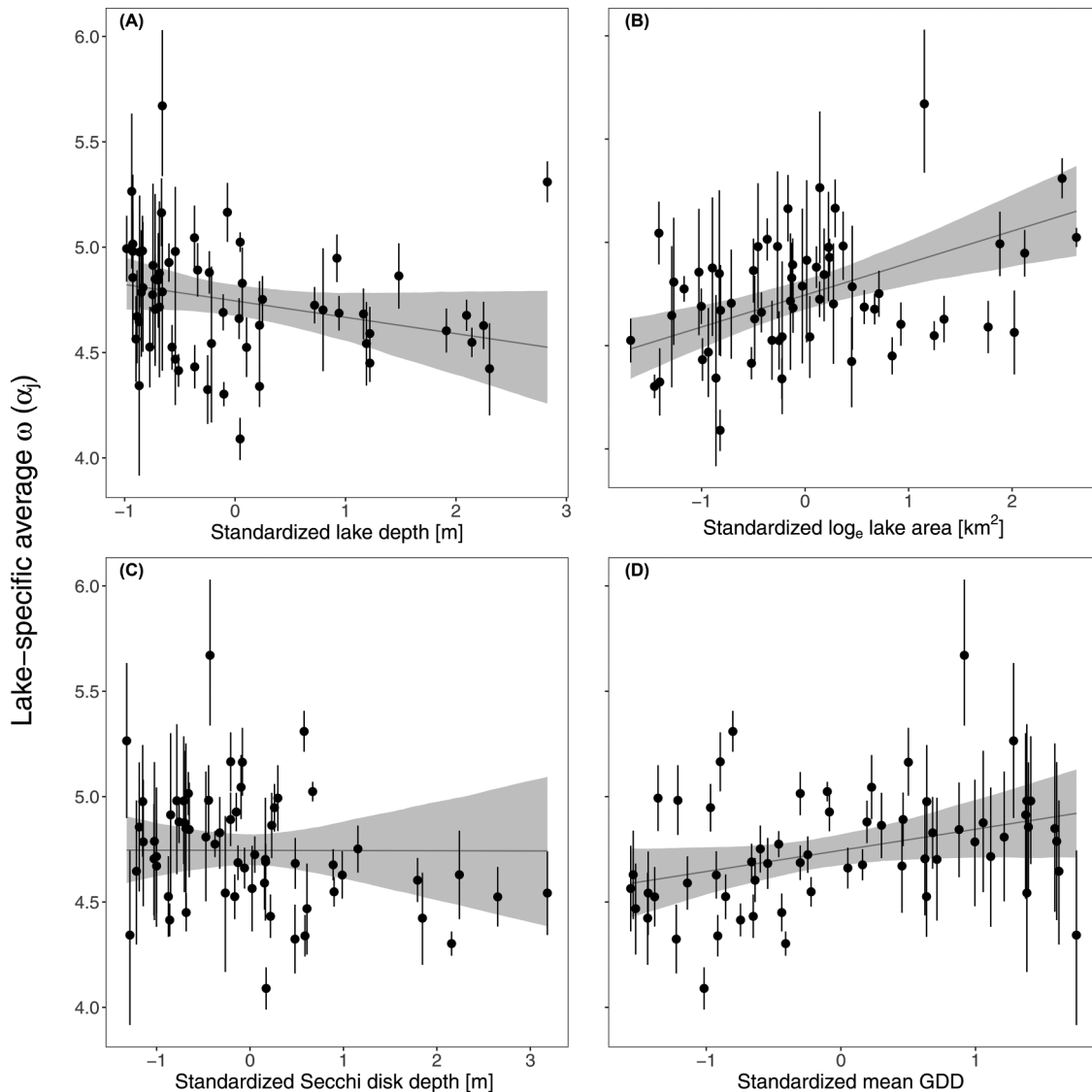
$\log_e(\omega)$  significantly increased with increasing lake surface area. Although the 90% credible interval overlapped with zero, the posterior probability of a negative lake depth effect was 0.92 (Fig. 4A).

To quantify and visualize the biological significance of the model parameter estimates, we selected the predictor variable that had the largest effect size on the varying slopes and varying intercepts and predicted  $\omega$  across a range of GDD (Supplementary Table S1<sup>1</sup> lists the GDD values for lakes in this study). The predictor variables evaluated were Secchi disk depth and lake area for the varying slopes and varying intercepts, respectively. We predicted  $\omega$  for lakes with Secchi disk depth and lake area values that corresponded to the 5th, 50th, and 95th percentiles of lakes included in the analysis while holding all other predictors at their average values in the dataset. These percentiles were chosen to provide a contrast across a range of water clarity and lake sizes.

Lake area positively affected lake-specific intercepts and did not influence the varying slopes. As such, as lake area increases the average  $\omega$  increases, but the  $\omega$ -GDD relationship remains relatively unchanged (Figs. 5A–5C). For example, predicted  $\omega$  is 94 mm·year<sup>-1</sup> in a 0.80 km<sup>2</sup> lake but is 161 mm·year<sup>-1</sup> in a 197 km<sup>2</sup> lake at an average GDD value. In contrast, Secchi disk depth had a 0.84 posterior probability of a negative effect on the  $\log_e(\omega)$ -GDD relationship and no effect on the varying intercepts. Therefore, as Secchi disk depth increases from 0.8 to 7.6 m, we predict a shift from a slightly positive  $\omega$ -GDD relationship to a negative relationship  $\omega$ -GDD (Figs. 5D–5F). At the maximum GDD observed in our dataset, the predicted  $\omega$  for a lake with a Secchi disk depth of 0.8 m was 152 mm·year<sup>-1</sup>; however, for a lake with a Secchi disk depth of 7.6 m, the predicted early life growth rate decreased to 101 mm·year<sup>-1</sup>.

The posterior predictive distributions were summarized in Fig. 6 to show the posterior probability that a lake with a surface area of

**Fig. 4.** The effects of lake-specific covariates, (A) lake depth (m), (B) lake area (km<sup>2</sup>), (C) Secchi disk depth (m), and (D) mean growing degree days (GDD), on the lake-specific intercepts (or the average log<sub>e</sub>( $\omega$ ) estimates) for walleye (*Sander vitreus*) in 61 Minnesota and Wisconsin lake during 1983–2015. Black dots are the posterior mean estimates of the lake-specific intercepts. The vertical bars show the estimated 90% credible interval for the lake-specific intercepts, and the black horizontal line shows the fitted relationship between the lake-specific intercepts and the given lake characteristic. The shaded region is the 90% credible interval of the hierarchical regression fitted line.



197 or 6.0 km<sup>2</sup> has an estimated  $\omega$  that is larger than the estimated  $\omega$  in a smaller lake with a surface area of 0.8 km<sup>2</sup> (Fig. 6A). This was also done for Secchi disk depth (Fig. 6B). For a large lake, the mean (across all GDD values) posterior probability of a larger lake (197 km<sup>2</sup>) having a greater  $\omega$  compared with a smaller lake (0.8 km<sup>2</sup>) was 0.95, whereas this probability was 0.81 for a moderate-sized lake (6.0 km<sup>2</sup>). In contrast, and because Secchi disk depth affects the slope of the  $\omega$ -GDD relationship, a clearer lake (7.6 m Secchi disk depth) has a 0.79 posterior probability of having an  $\omega$  greater than that of a turbid lake (0.8 m) at low GDD conditions, but only a 0.19 posterior probability of being greater under high GDD conditions. A similar pattern was observed for a lake with moderate clarity (1.6 m), but the effect was not as pronounced — with a posterior probability of having a larger  $\omega$  declining from 0.69 to 0.28.

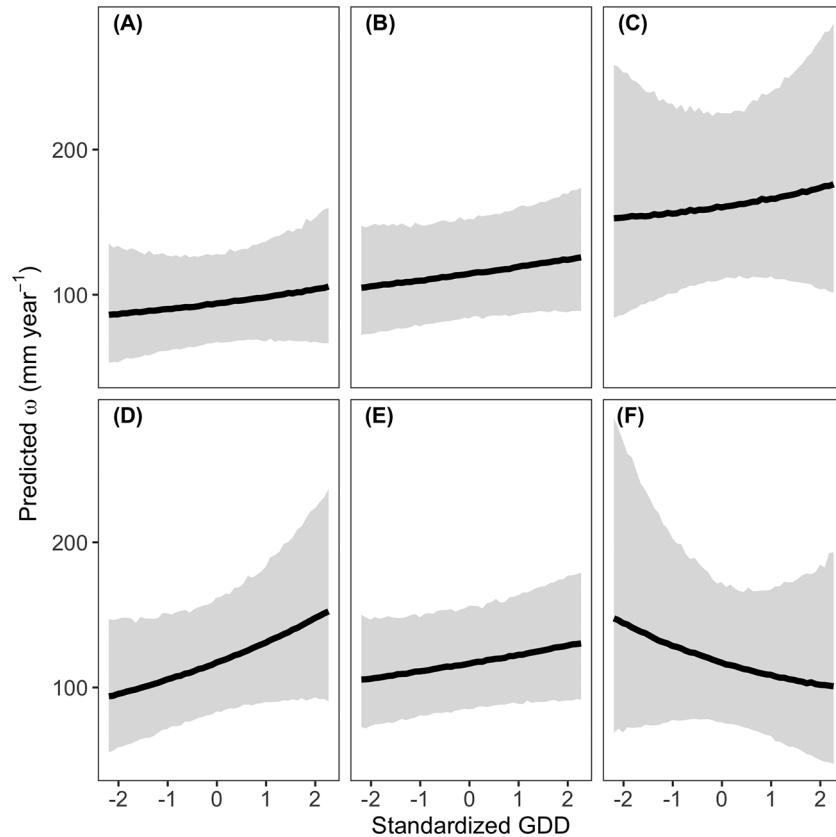
Finally, the predictor effects were summarized in terms of  $\omega$  effect size. Specifically, the posterior probability that the walleye

growth rate in a clear lake (7.6 m Secchi disk depth) was greater than a prespecified growth rate compared with a turbid lake (0.8 m Secchi disk depth) across a range of GDD was examined. This can be useful to visualize because the difference in early growth rate that might be considered biologically meaningful may be context-dependent. For example, the posterior probability that the difference in early life growth rate between a clear and turbid lake was greater than 10 mm·year<sup>-1</sup> is 0.73 under low GDD conditions and 0.16 at high GDD conditions (Fig. 7). The posterior probability that growth rate in a clear lake was greater than that of a turbid lake, regardless of effect size, never got above 0.5 once GDD approached the average GDD in the dataset. See Supplementary Fig. S4<sup>1</sup> for lake surface area.

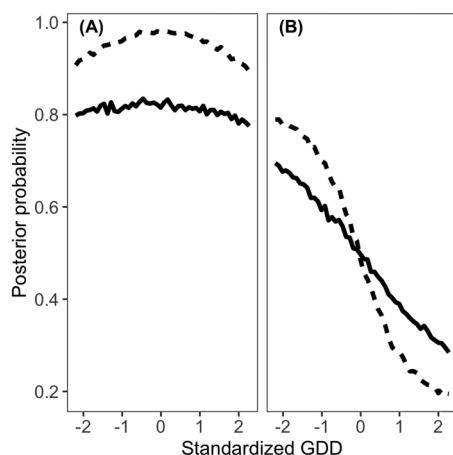
### Discussion

Understanding whether warming water temperatures, associated with climate change-induced increases in air temperatures,

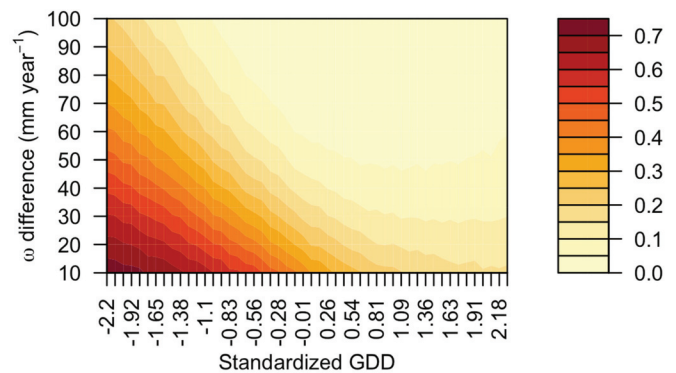
**Fig. 5.** Predicted  $\omega$  ( $\text{mm}\cdot\text{year}^{-1}$ ) as a function of growing degree days (GDD) for lakes with surface areas of 0.80, 6.0, and 197  $\text{km}^2$  (A–C, respectively) and for lakes with Secchi disk transparency of 0.8, 1.6, and 7.6 m (D–F, respectively). Lake surface area and Secchi disk depth values correspond to the 5th, 50th, and 95th percentiles of lakes included in the analysis. Solid line is predicted posterior mean, and shaded region is 95% prediction interval. All other predictors in the model were held at their mean values.



**Fig. 6.** Posterior probability that (A) a lake with a surface area of 197  $\text{km}^2$  (dashed line) and 6.0  $\text{km}^2$  (solid line) has an estimated  $\omega$  ( $\text{mm}\cdot\text{year}^{-1}$ ) that is larger than a lake with a surface area of 0.8  $\text{km}^2$  and (B) a lake with a Secchi disk depth of 7.6 m (dashed line) and 1.6 m (solid line) has an estimated  $\omega$  that is larger than a lake with a Secchi disk depth of 0.8 m, across a range of growing degree days (GDD). Lake surface area and Secchi disk depth values correspond to the 5th, 50th, and 95th percentiles of lakes included in the analysis.



**Fig. 7.** The posterior probability that the difference in  $\omega$  ( $\text{mm}\cdot\text{year}^{-1}$ ) between a clear lake (7.6 m Secchi disk depth) and turbid lake (0.8 m Secchi disk depth) is greater than  $\omega$  values ranging from 10 to 100  $\text{mm}\cdot\text{year}^{-1}$  (y axis), across a range of growing degree days (GDD; x axis). Secchi disk depth values correspond to the 5th and 95th percentiles of lakes included in the analysis.



may be altering the demographics of cool-water fish species is important for informing conservation and climate adaptation management decisions. Information on how growth will be altered is especially important because growth is a function of water temperature and is an integrated metric for assessing the health and



success of a population (Kitchell 1977; Rypel 2011). Walleye populations are predicted to be negatively affected by warming water temperatures (Van Zuiden and Sharma 2016; Hansen et al. 2018). However, we found that, on average, walleye growth coefficients significantly increased with increasing GDD. Our results are consistent with findings from Pedersen et al. (2018), where the growth of juvenile walleye was positively correlated with temporal increases in surface water temperatures. Slight water temperature increases generally increase fish energy and consumption, which is beneficial to growth (Kitchell 1977; Neuheimer et al. 2011). However, as water temperatures continue to rise (Poff et al. 2002; O'Reilly et al. 2015), temperatures can surpass a species' thermal maximum limit, resulting in growth slowing or decreasing due to increased metabolic demands (Kitchell 1977; Dutta 1994; Neuheimer et al. 2011). Our results suggest that the thermal conditions walleyes are exposed to in most lakes in our study are still on the ascending limb of the growth–temperature response curve (Neuheimer et al. 2011). However, for walleye — whose thermal optimal temperature for growth is 21 °C (Lester 2004) — continued increases in water temperatures could result in negative effects on growth if food consumption is not increased enough to meet metabolic demands. In addition, as temperatures warm to a point where growth is hindered (i.e., if populations are on the descending limb of the growth–temperature response curve), the direction and magnitude of the effects of abiotic (e.g., water clarity, as investigated herein) and biotic factors (e.g., competition or prey availability) that may mediate the temperature–growth relationship will likely change. This suggests using empirical relationships that exist under current thermal conditions to forecast growth conditions under warmer thermal regimes should be done with caution.

Twenty-four lakes were estimated with a strong positive  $\log_e(\omega)$ –GDD relationship (i.e.,  $\geq 70\%$  posterior probability), and few lakes were estimated with a strong negative  $\log_e(\omega)$ –GDD relationship (i.e., three lakes). Interestingly, most of the lakes with negative  $\log_e(\omega)$ –GDD relationships (Fig. 1) were on average cooler, indicating that factors other than temperature may be more important determinants of walleye growth in these lakes, such as competition with other species (Johnson and Hale 1977; Van Zuiden and Sharma 2016; Hansen et al. 2018) or density dependence (Sass and Kitchell 2005; Pedersen et al. 2018). Additionally, we did not find lake-specific slopes to cluster in certain geographic regions based on slope direction (Fig. 2). For example, lakes with high probabilities of a positive effect of GDD on growth were found throughout the study area. This suggests that lake-specific biotic and abiotic conditions, and not just regional climate, are likely important factors influencing walleye growth across the landscape. Understanding the relative roles of these abiotic and biotic interactions in determining growth rates, and whether these interactions will change under future environmental conditions, is an important area of future research.

Water clarity was found to influence the  $\log_e(\omega)$ –GDD relationship. We estimated a relatively high posterior probability (i.e., 84%) of a negative effect of water clarity on the  $\log_e(\omega)$ –GDD relationship. Importantly, this effect indicates a shift in how early life growth responds to GDD as lake water clarity increases. In particular, growth in turbid lakes is predicted to increase with increasing GDD; however, the magnitude of this positive effect decreases and eventually switches to a negative relationship as water clarity increases — leading to reduced growth rates at higher levels of water clarity (i.e., a shift from a positive to a negative  $\log_e(\omega)$ –GDD relationship with increasing water clarity). Walleye prefer low light conditions for feeding, and walleye production is maximized in moderately turbid, cool-water conditions (e.g., Secchi depths of 1–3 m; Ryder 1977; Lester 2004). Positive responses of growth to increased temperatures in more turbid waters may reflect the greater feeding efficiency of walleye relative to other species in low light conditions. Additionally, water

clarity is almost as important as air temperature in determining how waterbodies respond to climate change because it regulates how heat is partitioned throughout the water column (Rose et al. 2016). In turbid lakes, heat is trapped closer to the surface, and since walleye prefer to feed in shallow habitats (Ryder 1977), this could help explain why the effect of GDD on growth would be positive in turbid lakes. Water clarity is changing in lakes throughout North America due to changes in nutrient loading, precipitation regimes, and dreissenid mussel (*Dreissena polymorpha* and *Dreissena bugensis*) invasions. Although the direction and magnitude of clarity changes varies across the landscape of lakes (Higgins and Vander Zanden 2010; Lottig et al. 2014; Oliver et al. 2017; Lisi and Hein 2019), such changes are likely to influence walleye growth, with potentially complex interactions between clarity and temperature change (Lester et al. 2004; Geisler et al. 2016; Hansen et al. 2019). Therefore, the trend of water clarity (either increasing or decreasing) combined with other abiotic and biotic facts, might play a role in how walleye growth is affected by a warming climate in the future.

In addition to physical lake characteristic drivers, the  $\log_e(\omega)$ –GDD relationship is also likely influenced by biotic factors not investigated in this study. For example, temperature increases will shift community structure through potentially altering the abundance of species present in a lake and through the range expansions of native and non-native competing, predator, or prey species (Sharma et al. 2007; Rypel et al. 2019). These shifts in food web dynamics could benefit or hinder walleye growth depending on the species introduced. The Great Lakes region has already shown evidence that warming temperatures are causing species range shifts, which are negatively affecting walleye populations. For example, largemouth bass population increases in Wisconsin lakes has been linked to walleye recruitment being less resilient to climatic stress in lakes with high bass densities (Hansen et al. 2018). Similarly, smallmouth bass (*Micropterus dolomieu*) are expected to expand their range across Ontario, Canada, and this will likely further intensify the climate-induced lowering of walleye abundances in co-occurring lakes (Van Zuiden and Sharma 2016). In addition to species range shifts, changes in light availability and nutrient content associated with climate change can affect lake productivity (Vincent 2009). The amount of productivity within a given lake directly affects the amount of food available for fish (Yusoff and McNabb 1989; Moyle and Cech 1996). Therefore, changes in lake productivity can alter food web dynamics, which directly affects fish growth rates (Yusoff and McNabb 1989; Vincent 2009). For example, walleye growth has been shown to be less in lakes with lower lake productivity (Rudstram 1996; Sass and Kitchell 2005). Future studies may want to consider biotic factors, such as shifting community structures, lake productivity changes, or density-dependent interactions, that likely also affect how walleye growth is influenced by warming water temperatures.

In addition to water clarity, average growth coefficients were found to be influenced by other lake characteristics. We estimated that lake depth negatively influenced average growth coefficients. There are several potential mechanisms that could result in lower growth rates in deep lakes. For example, deeper lakes are often cooler and less productive (Stoll et al. 2008). Lake area was positively correlated with average  $\omega$  estimates. Other studies have also found walleye abundance and recruitment to be greater in larger lakes (Nate et al. 2000; Hansen et al. 2018), although the exact mechanisms are uncertain. Perhaps because ecosystem size is often positively related to species diversity, walleye in larger lakes have access to a more expansive prey selection and thus more available prey. These larger lakes may also offer more diverse thermal and foraging habitats. Lastly, our results show that average  $\omega$  estimates were lower in lakes with higher average GDD, potentially indicating that walleye in these warmer lakes incur increased metabolic costs resulting in less energy allocated towards somatic growth (Kitchell 1977; Dutta 1994; Neuheimer et al. 2011). However, as previously mentioned,

biotic conditions (that we were unable to quantify in our study) are also likely important in determining lake average walleye growth rates.

Understanding the effects of warming water temperatures on the growth of fishes is critical for developing climate adaptation strategies for ecologically and socio-economically important fishes. Because the effects of warming water temperatures on vital rates, such as individual growth rates, will not be homogeneous across the landscape, understanding what factors might mediate climate effects and therefore affect a population's sensitivity to climate change is critical. In our study, we quantified the spatiotemporal variability of walleye growth during 1983–2015 in 61 lakes in Minnesota and Wisconsin. We found that annual walleye growth coefficients, on average, significantly increased with increasing water temperature. However, the lake-specific slopes of the  $\log_e(\omega)$ –GDD relationship varied in direction and magnitude, which supported our expectation that physical lake characteristics may be mediators of these relationships. Of the lake characteristics explored, we found water clarity to be an important mediator of the effect of warming temperatures potentially through effects of modifying a lake's thermal and foraging conditions. These results provide insights into how cool-water species are being affected by warming waters and identify lakes in which abiotic conditions may allow walleye growth to be more resilient to climatic stress.

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