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Complete List of Authors:	<p>Pedersen, Eric; University of Wisconsin Madison, Center for Limnology Goto, Daisuke; University of Wisconsin-Madison, Center for Limnology Gaeta, Jereme W.; Utah State University, Watershed Sciences and the Ecology Center Hansen, Gretchen; Wisconsin Department of Natural Resources, Science Services; Minnesota Department of Natural Resources, Fisheries and Wildlife Sass, Greg; Wisconsin Department of Natural Resources, Escanaba Lake Research Station Vander Zanden, M. Jake; University of Wisconsin - Madison Cichosz, Thomas; Wisconsin Department of Natural Resources, Fisheries Management Rypel, Andrew; Wisconsin Department of Natural Resources and University of Wisconsin Center for Limnology,</p>
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Long-term growth trends in northern Wisconsin walleye populations under changing biotic and abiotic conditions

Eric J. Pedersen^{1*}, Daisuke Goto^{1,4}, Jereme W. Gaeta^{1,5}, Gretchen J.A. Hansen^{2,6}, Greg G. Sass³, M. Jake Vander Zanden¹, Thomas A. Cichosz², Andrew L. Rypel^{1,2}

¹Center for Limnology, University of Wisconsin-Madison, 680 North Park Street, Madison, Wisconsin 53706 USA

²Wisconsin Department of Natural Resources, Bureau of Science Services, 2801 Progress Road, Madison, Wisconsin 53716 USA

³Escanaba Lake Research Station, Wisconsin Department of Natural Resources, 3110 Trout Lake Station Drive, Boulder Junction, Wisconsin 54512, USA

⁴Present address: Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Room 3055, Toronto, Ontario M5S 3B2, Canada

⁵Present address: Department of Watershed Sciences and the Ecology Center, Utah State University, 5210 Old Main Hill, Logan, UT 84322 USA

⁶Present address: Minnesota Department of Natural Resources, Fisheries Research, 500 Lafayette Road, Saint Paul MN, 55155 USA

*Corresponding author: eric.pedersen@wisc.edu

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Abstract

Walleye (*Sander vitreus*) populations are declining in Wisconsin and neighboring regions, motivating broader interest in walleye biology amidst ecological change. In fishes, growth integrates variation in ecological drivers and provides a signal of changing ecological conditions. We used a 23-year dataset of length-at-age from 353 walleye populations across Wisconsin to test whether walleye growth rates changed over time and what ecological factors best predicted these changes. Using hierarchical models, we tested whether spatio-temporal variation in walleye growth was related to adult walleye density (density-dependent effects), water temperature, and largemouth bass (*Micropterus salmoides*) catch per unit effort (predator/competitor effects). The average length of young walleye increased over time, and as a result, time to reach harvestable size declined significantly. In contrast, average lengths of older walleye have remained relatively constant over time. Juvenile walleye length-at-age was positively correlated with largemouth bass CPUE and surface water temperatures, but negatively correlated with adult walleye density. Our finding of widespread and long-term changes in walleye growth rates provides additional insights into how inland fisheries are responding to environmental change.

Introduction

Understanding variation in and drivers of growth rates is fundamental to fish conservation and management (Campana and Thorrold 2001; Conover and Munch 2002). In fishes, growth rates reflect metabolic processes and understanding what factors affect growth is critical to understanding how fish populations will change over time (Brandt et al. 1992; Clarke and Johnston 1999; Haag and Rypel 2011). Growth rates determine body size (Angilletta et al. 2004), which in turn affects a wide array of life history traits including fecundity, longevity, and juvenile survivorship (Blueweiss et al. 1978; Conover and Present 1990; Winemiller and Rose 1992). Studies have shown that growth rates can be highly plastic, as growth depends on the amount of energy available from food, the rate at which organisms metabolize that energy, and the allocation of net resources to somatic growth or reproduction, all of which can respond to environmental factors (Lorenzen 2016).

Temporal studies of fish growth are critical to understanding environmental drivers and shifts to freshwater ecosystems (King et al. 1999; Morrongiello et al. 2011; Nguyen et al. 2015). For example, growth can change over time in response to water temperature (Black 2009; Magnuson et al. 1979; Rypel 2009), abundance of prey (Gaeta et al. 2014; Sass et al. 2006; Venturelli et al. 2010; Winemiller 1990), and changing fish densities (Venturelli et al. 2010). As fish growth is tightly coupled to other life history traits, such as natural mortality, changes in growth may substantially alter population dynamics and affect how many fish can be sustainably harvested (Lester et al. 2014). Further, changes in growth can alter effective fishing mortality, as many recreational fisheries rely on size limits to reduce harvest, and faster or slower growth rates can change the fraction of fish protected by these limits. Nevertheless, long-term studies of fish growth are uncommon (Berkeley et al. 2004; Blanck and Lamouroux 2007; Rypel 2012).

Our study focuses on variation in growth rates in northern Wisconsin walleye (*Sander vitreus*) stocks. Walleye are native to the mid- and high-latitudes of North America. The species is of high

commercial, recreational, and cultural value, which has led to extensive research and management efforts. For example, walleye are generally considered the most valuable species in Canada's inland waters (Post et al. 2016; Scott and Crossman 1973). In Wisconsin USA, walleye are native to large rivers and drainage lakes; however, natural distributions are obscured by a long history of stocking (Becker 1983). In Wisconsin, naturally reproducing walleye populations persist primarily in large drainage lakes (typically > 200 ha) with cool epilimnetic temperatures (Becker 1983; Hansen et al. 2015b; Hansen et al. 2016).

Management of walleye in Wisconsin has been complex, especially over the last 30 years. Following affirmation of off-reservation Native American hunting, fishing, and gathering treaty rights in 1985, a tribal spring spear fishery for walleye was reinstated in the Ceded Territory of Wisconsin (~northern 1/3 of the state) (Nesper 2002). Following this change, the Wisconsin Department of Natural Resources (WDNR) in collaboration with the Great Lakes Indian Fish and Wildlife Commission initiated a regional walleye management and monitoring program. "The current management system utilizes statewide bag and size limits and abundance based spearing harvest quotas on individual lakes in order to not exceed a defined "limit reference point" (Hansen 1989; Hansen et al. 1991). The limit reference point is designed to ensure that harvest does not exceed 35% of the adult walleye population in more than 1 in 40 lake-years (Hansen et al. 1991). The management system has generally been effective at maintaining regional adult walleye density targets at about 7.5 adults•ha⁻¹ over time in lakes with naturally reproducing populations. Recently, walleye recruitment and adult densities have been declining in lakes across the Ceded Territory, coincident with increasing water temperatures (Winslow et al. 2015) and largemouth bass (*Micropterus salmoides*) abundances (Hansen et al. 2015c; Hansen et al. 2016). It is unknown the extent to which changes in these drivers may be affecting walleye growth in Wisconsin lakes, and how this may affect long-term management.

To better understand options for walleye management in the midst of population declines, a regional synthesis of walleye growth is needed. It is largely unknown whether walleye growth patterns

have changed over time during the period of recruitment and abundance declines (but see Wagner et al. 2007 for multi-state trends in ages 2-4), and if it has, what drivers are responsible. Such questions are increasingly pertinent to fisheries management as the declines have stimulated renewed interest in better understanding ecological dynamics of walleye, including potential management options to assist in this emerging challenge (Hansen et al. 2015c; Hansen et al. 2016). Because growth rates are linked to size structure, production rates, and time necessary to reach harvestable size, understanding walleye growth is essential for future management.

Here, we analyze length-at-age estimates for 353 Wisconsin walleye populations sampled from 1990 to 2012. The primary goal of our study was to test for spatial and temporal trends in walleye growth rates. To accomplish this goal, we developed hierarchical linear models of walleye growth that explicitly incorporate spatio-temporal variation and estimate the effects of a suite of ecological predictor variables. In addition to describing spatio-temporal trends, we evaluated three potential drivers of growth relevant to the conservation and management of walleye: 1) intraspecific density-dependence; 2) water temperature; and 3) interspecific interactions with largemouth bass. We show that walleye are growing faster at young ages, and that this increase is related to declines in walleye abundance and increases in water temperature and largemouth bass CPUE. We illustrate the effect of these changes on the dynamics of the fishery by showing that the average time for a fish to enter the fishery has declined by over a year across the 20+ year time series.

Materials and methods

Walleye growth data

We used walleye length-at-age data collected by the Wisconsin Department of Natural Resources (WDNR) during 1990-2012. The WDNR conducted annual field surveys of walleye stocks in northern

Wisconsin lakes, which are generally selected by a stratified random sampling design (mean number of lakes sampled per year = 23, range = 7–37), although lake selection occasionally deviated from the stratified random approach because of special circumstances. In each survey year, individual fish (mean fish per lake = 162, range = 30–1095) were collected during spring spawning using fyke-nets and total length (TL, mm) was measured.

Fish age was estimated using hard structures collected from a subset of fish in each 10-mm length increment bin. Scales were used to age individuals smaller than < 508 mm (TL) and a combination of scales and spines were used to age individuals ≥ 508 mm (TL). Age estimations were made by two experienced WDNR staff and disagreements between age assignments were typically handled by either a third independent reader or a concert read between the two initial readers. Although dorsal spines are considered more accurate for aging older walleye (Kocovsky and Carline 2000), both spines and scales were collected for different lakes, and which structure was used to age a given fish was not always recorded. To determine if changes in the proportion of different aging structures over time accounted for any observed changes in the length-age relationship, we conducted sensitivity tests using only records where the aging structures were known unambiguously (see Supplemental Material), which indicated that our results were not sensitive to the choice of aging structure.

Length-at-age data were filtered to eliminate missing age or TL data. We excluded all fish older than age-16, as aging error increases in older fish (Isermann et al. 2003) and few fish of these ages were present. We also excluded stocks with fewer than 5 year classes or total sample sizes of fewer than 30 fish in any lake-year combination. Because the sex of the majority of the fish in the data set were not identified, we pooled male and female fish. Our final data set consisted of 97,445 individual fish with TL and age data representing 353 populations and 601 lake-year combinations during 1990-2012.

Extrinsic drivers of walleye growth

Adult population size for walleye stocks were estimated using standard mark-recapture methods (Beard et al. 1997; Hansen et al. 1991). As part of spring walleye surveys, fish were collected via fyke-netting (1219 × 1828 mm with 19 mm mesh size). Netting continued until 10% of the previous population estimate was marked. Netted fish were marked with fin clips and then released. The recapture sample was collected using AC or pulsed-DC electroshocking of the entire shoreline of each lake during peak spawning (Beard et al. 1997; Hansen et al. 1991). A population estimate was then calculated using the Chapman modification of the Peterson method, and converted to density by dividing the population estimate by the lake surface area as defined in the Wisconsin Registry of Waterbodies.

The growing degree day (GDD) metric is a heat accumulation measure (Chezik et al. 2013). We used modeled daily water temperatures (1980-2012) for Wisconsin lakes with a record of fisheries data (model fully described in Read et al. 2014). Using these daily estimates, annual estimates of GDD were estimated for each lake year as:

$$GDD = \sum_1^n \text{Daily average surface temp} - 5$$

where n is the number of days in which daily average surface temperatures exceeded 5°C. A base temperature of 5°C was used based on previous research (Chezik et al. 2013; Hansen et al. 2016; Rypel and David 2017). To give a more stable estimate of the average environment experienced by fish during their entire lives in a given lake, we used GDD averaged over the 5 years prior to the year a given lake was sampled.

We used catch-per-unit-effort (CPUE) to index largemouth bass relative abundances. Largemouth bass CPUEs were estimated by WDNR biologists during standardized early summer (April and May)

surveys of littoral fish communities using boom-mounted AC boat electrofishing. CPUE data (catch • km⁻¹) were used in all modeling exercises. Largemouth bass CPUE data were available from 1995 onwards.

To visualize spatial structure in our drivers (walleye density, largemouth bass CPUE, and GDD) we averaged each driver across all years within each lake, then fit smooth regression curves estimating how each driver or summary statistic changed across the landscape, using a generalized additive model with a two-dimensional thin-plate spline smoother (Wood 2006).

Hierarchical modeling

We used hierarchical linear models to address two questions: 1) Are there spatial or temporal trends in walleye length-at-age?; and 2) What proportion of spatiotemporal variability in walleye growth is explained by three extrinsic drivers of interest to the ecology and management of Wisconsin walleye (i.e., adult walleye density, GDD, and largemouth bass relative abundance)? All models were fit using the lme4 package (ver. 1.17, Bates et al. 2014) in R (ver. 3.2.4 R Core Team 2015). We used a power-law relationship between length and age as the functional form for the growth function, as it is a flexible model that can approximate a wide range of other growth models, and often fits observed growth patterns well in the absence of strong asymptotic behaviour (Katsanevakis and Maravelias 2008; Lorenzen 2016), which we did not observe in the range of ages in the dataset.

For a single stock at a given time, length-at-age denotes the functional relationship describing average TL of fish at a given age (A): $L \sim f(A)$. For our walleye data, for any given year in any lake, the natural log of walleye TL ($\ln(L)$) increased approximately linearly with the natural log of age ($\ln(A)$). We therefore modeled $f(A)$ as a power function and TL of individual i ($L_{i,j,t}$) in lake j and year t :

$$\ln(L_{i,j,t}) = \alpha_{j,t} + \beta_{j,t} \cdot (\ln(A_i) - \ln(5.2)) + \epsilon_{i,j,t} \quad (1a)$$

$$\begin{pmatrix} \alpha_{jt} \\ \beta_{jt} \end{pmatrix} \sim MVN \left(\begin{pmatrix} \alpha_0 \\ \beta_0 \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \rho\sigma_\alpha\sigma_\beta \\ \rho\sigma_\alpha\sigma_\beta & \sigma_\beta^2 \end{pmatrix} \right) \quad (1b)$$

$$\epsilon_{i,j,t} \sim N(0, \sigma_{indiv}) \quad (1c)$$

153

154 Where A_i is age of fish i and the intercepts ($\alpha_{j,t}$) and slopes ($\beta_{j,t}$) are modelled as lake- and year-specific
 155 multivariate normal (MVN) distributed variables (equation (1b)), with overall means α_0 and β_0 , standard
 156 deviations σ_α and σ_β and between-term correlation of ρ . The term $\ln(5.2)$ represents the mean of the
 157 natural log of age across the whole dataset and is used to center age around zero. We centered ages to
 158 improve interpretability of the intercept; under this parameterization, the intercept corresponds to the
 159 length of an average aged fish. The ($\epsilon_{i,j,t}$) term represents variation in the length of individual fish at a
 160 given age and lake-year, drawn from a normal distribution with a mean of 0 and a standard distribution
 161 (σ_{indiv}) estimated across the whole dataset. This hierarchical approach allows the age-length relationship
 162 to vary over time and across the region, while still drawing parameter estimates from different lakes
 163 closer to one another, reducing the variability of parameter estimates for lakes with small amounts of data
 164 (Thorson and Minto 2015).

165 We tested for three forms of length-at-age variability:

166 1. *Temporal variation alone*: slopes or intercepts assumed only to vary over time, not among lakes:

$$167 \quad \alpha_{j,t} = \alpha_t, \beta_{j,t} = \beta_t.$$

168 2. *Spatial variation alone*: slopes or intercepts treated as a random effect varying among lakes (with the
 169 same lake in different years having the same length-at-age): $\alpha_{j,t} = \alpha_j, \beta_{j,t} = \beta_j$.

170 3. *Spatio-temporal variation*: each slope or intercept assumed to vary as a random effect for each lake in
 171 each year. This corresponds to the full model specified in equation (1).

172

We compared how well each model captured variation in the age-length relationship by comparing model AIC and R^2 for individual fish (calculated as one minus the ratio of variance of the model residuals to the variance of log-lengths for all fish in the study).

We also calculated four ecologically meaningful summary statistics for the best fitting of the above models to visualize how growth of walleye changed over time and space: 1) geometric mean TL of age-3 (young fish); 2) geometric mean TL of age-8 fish; 3) geometric mean TL of age-12 (older) fish; and 4) predicted age when individuals reach 381 mm (i.e., age when first harvestable). We used the best-fitting hierarchical model to estimate the geometric means of age-3, -8, and -12 fish in each lake and each year, then calculated the arithmetic mean and standard deviation of these means among lakes in each year. We estimated the age when first harvestable for each lake in each year as:

$$A_{H,j,t} = (\ln(381 \text{ mm}) - \alpha_{j,t} + \beta_{j,t} \cdot \mu_A) / \beta_{j,t}. \quad (2)$$

We also estimated a relative index of sexual maturity to determine if the age of walleye sexual maturity was changing at a rate comparable to observed changes in age of when first harvestable, using information from the survey on the number of fish of each age and length group that were actively spawning at the time of each survey. See the Supplemental Material for details on this index.

Models with temporal trends and extrinsic drivers

To test for factors best predicting differences in length-at-age, we incorporated our three predictor variables (adult walleye density, largemouth bass relative abundance, and GDD) as linear fixed effects into the random effects model. We also included survey year as a linear fixed effect, to test whether there was any significant long-term trend in the length-age relationship not explained by our predictors. Because we did not have predictor data for every lake in every year, this portion of our analysis was restricted to lake-years where we had complete data on all three predictors (192 lake-year combinations in

135 lakes), which also limited the analysis to changes after 1995, as largemouth bass data were missing prior to this. The full model was:

$$\ln(L_{i,j,t}) = \alpha_{j,t} + \beta_{j,t} \cdot (\ln(A_i) - \ln(5.2 \text{ y})) + \epsilon_{i,j,t} \quad (3a)$$

$$\begin{pmatrix} \alpha_{j,t} \\ \beta_{j,t} \end{pmatrix} \sim \text{MVN} \left(\begin{pmatrix} \alpha_0 + a_W \cdot W_{j,t} + a_B \cdot B_{j,t} + a_G \cdot G_{j,t} + a_D \cdot D_t \\ \beta_0 + b_W \cdot W_{j,t} + b_B \cdot B_{j,t} + b_G \cdot G_{j,t} + b_D \cdot D_t \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \rho\sigma_\alpha\sigma_\beta \\ \rho\sigma_\alpha\sigma_\beta & \sigma_\beta^2 \end{pmatrix} \right) \quad (3b)$$

$$\epsilon_{i,j,t} \sim N(0, \sigma_{\text{indiv}}) \quad (3c)$$

The a and b parameters in equation (3b) represent the effects on the intercept and slope (respectively) of changing walleye density (a_W and b_W), largemouth bass CPUE (a_B and b_B), GDD (a_G and b_G), and the decadal trend (a_D and b_D). To improve interpretability, we natural log-transformed GDD, adult walleye density, and largemouth bass CPUE, and centered and scaled the resultant values by subtracting the mean value of the predictor and dividing by the standard deviation (see Table 1 for these values). Prior to transforming largemouth bass CPUE, we added the minimum non-zero CPUE (0.025 fish per hour) observed to all values to account for locations with zero observed largemouth bass. We transformed time, measured in years, into decades before or after the year 2000, by subtracting 2000 from all values and dividing by 10 ($D_t = (\text{Year}_t - 2000) \cdot 10^{-1}$). Therefore, the global intercept (α_0) and slope (β_0) described the age-length relationship of a lake in the year 2000 with an average ln-adult walleye density, ln-largemouth bass CPUE, and ln-GDD.

To test which predictor variables best explained inter-lake-year variability in the age-length relationship, we fit a series of models of increasing complexity (Table 3), by setting different sets of the a and b parameters in equation (3) to zero. We fit models using maximum likelihood to ensure models with different fixed effects had equivalent likelihoods (Bates et al. 2015) and compared models via AIC. Within each model, we calculated 95% confidence intervals for estimated fixed effect parameters using a parametric bootstrap procedure and percentile intervals (Bates et al. 2015).

Interpreting the effect of drivers on the age-length relationship

We used a set of scenarios to illustrate how regional variation and temporal change in the predictor variables may have affected length-at-age in walleye populations across northern Wisconsin. We examined four scenarios including: 1) average adult walleye density (using the geometric mean) and largemouth bass CPUE, representing an average lake; 2) below average largemouth bass CPUE and walleye adult density (with abundances of both species at one standard deviation below their geometric mean); 3) below average largemouth bass CPUE and above average adult walleye density (abundance set at one standard deviation below and above their geometric mean, respectively); and 4) above average largemouth bass CPUE and below average adult density of walleye. We used parametric bootstrapping to estimate the mean and standard deviation of predictions for each of our statistics under each scenario.

We used a simplified form of a hierarchical R^2 measure (Gelman and Pardoe 2006) to estimate the amount of variance of the random effects (i.e. the among-lake variability in the age-length relationship itself) that each model with predictors explained. We calculated among-lake-year variance of the random effect fitted for each parameter (intercept or slope) as well as the derived statistics we previously calculated (mean length of age 3,8, and 12-year old fish, and age when first harvestable) x in the absence of any predictors (hereafter, $\sigma_{x,null}^2$) using equation (1). For a given model y , we then calculated residual variance in the random effect for that parameter after accounting for the fixed effects in a given model ($\sigma_{x,y}^2$). An R^2 for each model and parameter was calculated as:

$$R_{x,y}^2 = 1 - \frac{\sigma_{x,y}^2}{\sigma_{x,null}^2} \quad (4)$$

Environmental predictors of length-at-age

Although our analysis focused on how temporal predictors (GDD, largemouth bass density and walleye density) predicted age-at-length, lakes in the Ceded Territory of Wisconsin also vary substantially in

physical characteristics. To test whether physical lake characteristics were able to predict any of the residual variation in length-at-age, we took the geometric mean within each lake of the ratio of observed lengths to lengths predicted based only on fixed effects for age-3 and age-12 fish. We then regressed these residuals against four lake traits: lake area, conductivity, and shoreline development factor (defined as the ratio between observed lake perimeter divided by the perimeter expected if the lake was a circle with the same area (Wetzel 2001)) which were derived from the WDNR SWIMS database, and average Secchi depth (derived from satellite observations; see Torbick et al. (2013) for methodology). We chose these four predictors as they incorporate information about available habitat (area and development) and available food resources and productivity (Secchi depth and conductivity) (Soranno et al. 1999; Webster et al. 1996), they best predicted variation in walleye recruitment in prior studies (Hansen et al. 2015a), and we had this information for almost all lakes in our study.

Results

After processing lake data as specified in the methods, our data set consisted of 353 lakes during 1990-2012, with an average of 26 lakes y^{-1} (Fig. 1A, black line). One hundred and forty-six of those lake-years had data for the full complement of predictors (adult walleye density, largemouth bass CPUE, and GDD), for an average of 10 lakes y^{-1} (Fig. 1A, grey line). Number of fish sampled per lake declined throughout the study period, from 220 walleye lake $^{-1}$ in 1990 to 120 walleye lake $^{-1}$ in 2012, with similar catches per year in the whole complement of lakes and lakes with predictor data (Fig. 1B). The age structure of fish caught also stayed relatively consistent, with a slight decline in the numbers of age 1-5 and age 6-10 fish caught per lake over time, and relatively constant (but low) number of older (age-11+) fish caught (Fig. 1C). However, the median TL of walleye increased from start to end of the study period (Fig. 1D).

Walleye growth rates changed substantially during 1990-2012 (Fig. 2A). Generally, young fish were larger at later periods in the time series, whereas length at age of the oldest fish did not change. The

best-fitting random effects model explaining the growth curves included both spatial and temporal variation in intercepts (i.e., length at mean age, $\ln(5.2 \text{ years})$) and slopes (Table 2, model 3). This model explained 88% of the individual-level variation in $\ln(\text{TL})$ (a linear regression of $\ln(\text{TL})$ on $\ln(\text{age})$ only explained 78% of the variation in $\ln(\text{TL})$), and had a ΔAIC of -9471 relative to the next-best fitting model, which included only spatial variation in the model parameters. This model fit the observed age-length relationship well across the bulk of the data, although the model did overestimate lengths of the oldest fish by approximately 5% (Supplemental Fig. S3). On average, fish grew at roughly the square root of age (mean intercept corresponding to the average length of an average-aged fish) $\alpha_0 = 6.0$; slope $\beta_0 = 0.48$). However, there was considerable variation in relationships across lake-years with $\alpha_{j,t}$ and $\beta_{j,t}$ ranging from 5.8-6.3 (sd = 0.1) and 0.14-0.95 (sd = 0.11), respectively, and slopes and intercepts were correlated among lake-years, with a correlation of 0.45 between random effects. Age-3 fish were on average about 50 mm longer in 2012 compared to 1990 (Fig. 2B), age-8 fish were on average 25 mm longer (Fig. 2C), and TLs of age-12 fish were roughly the same (Fig. 2D). Average age when walleye became harvestable ($\geq 381 \text{ mm}$) declined by more than a full year over the study period (Fig. 2E), from more than 5 years to less than 4 years. Our relative index of timing of sexual maturity also declined across the course of the study, but by less than half a year (Supplemental Fig. S4).

Walleye lengths were also spatially structured for all ages of fish; age 3, 8, and 12 fish (Fig. 3A-C) were larger in the east and west compared to lakes at the center of the Ceded Territory. Larger length-at-age of young fish meant that walleye reached harvestable lengths almost two years earlier in eastern and western lakes compared to the center of the Ceded Territory (Fig. 3D).

All three drivers also varied substantially over space and time. Average adult walleye density declined over time (Fig. 4A), and was greatest in lakes in more north central longitudes of the Ceded Territory (Fig. 4B). Largemouth bass CPUE increased from 1995 until the mid-2000's (Fig. 4C), and was greatest in western Ceded Territory lakes, lowest in the mid-longitude Ceded Territory lakes, and modest

287 in eastern Ceded Territory lakes (Fig. 4D). Surface water temperatures, as indexed by GDD, were
288 increasing since 1990 (Fig. 4E) and the warmest lakes were found in the southern portion of the Ceded
289 Territory (Fig. 4F). Although predictors varied in correlated patterns over time and across the region,
290 they did include independent information; largemouth bass CPUE and adult walleye density had a
291 Pearson correlation of -0.5 across lake-years, largemouth bass CPUE and GDD had a correlation of 0.41,
292 and adult walleye density and GDD had a correlation of -0.36.

293 Two models best explained spatio-temporal variation in length-at-age, differing by only 1 AIC units
294 and explaining very similar amounts of variation in population statistics (Table 3). The top two models
295 included a linear temporal trend (representing growth trends unexplained by other drivers), largemouth
296 bass relative abundance, and adult walleye density as drivers, and only differed by including or excluding
297 GDD as a driver. After accounting for the effects of largemouth bass CPUE and adult walleye density,
298 including GDD only slightly improved model fit. However, we kept GDD in the final model (Table 3,
299 model 8) to show what the potential range of temperature effects on growth might be when holding
300 species densities fixed. Coefficients for the best fit model are given in Table 4.

301 Our final model explained (using equation (4)) 48% of among-stock variation in length-at-age
302 intercepts and 25% of variation in slopes (Table 3, model 8). Ultimately, our model explained 51% of the
303 variation in TL of age-3 fish, 33% of the variance of age-8 fish, 19% of the variation in age-12 fish, and
304 54% of the variation in age at which walleye become harvestable. Our final model revealed that
305 largemouth bass CPUE and adult walleye density have opposing relationships with walleye growth (Fig.
306 5); intercepts were higher and slopes were lower in lakes with greater largemouth bass relative
307 abundances, whereas the reverse was true in lakes with greater adult walleye densities. This meant that
308 young walleye in high bass, low walleye lakes were growing faster, so that age-3 and age-8 were
309 expected to be 8% larger compared to lakes with average bass and walleye density (Fig. 6A&B).
310 However, these growth rates dropped off in older fish, such that age-12 fish were only expected to be 4%

larger in high-bass, low-walleye lakes (Fig. 6C). Higher GDDs were predicted to have a similar effect to largemouth bass abundance, although the estimates for this effect were weaker and more variable than largemouth bass effects (Fig. 5). After accounting for effects of changing GDD and walleye and largemouth bass abundance metrics, there was no remaining temporal pattern in the intercept, but the slope declined at a rate of $0.03 \cdot \text{decade}^{-1}$ (Fig. 5). This implies that, if bass and walleye densities and water temperature did not change over the study period in a given lake, this model predicts that age-3 fish would still be ~4% larger at the end of the study than at the start (Fig. 6A), whereas age-8 and age-12 fish would be about 3% and 7% smaller, respectively (Fig. 6B&C). The model further predicts that walleye should be reaching harvestable length about 1 year earlier at the end of the study compared to the beginning, all else being equal (Fig. 6). The temporal trend accentuated the effect of higher adult walleye densities and largemouth bass relative abundances on age-3 fish (Fig. 6A), but acted to reduce the effect on age-8 (Fig. 6B) and age-12 fish (Fig. 6C).

Lake-level predictors (lake area, shoreline development factor, Secchi depth, and conductivity) did not explain a substantial fraction of the remaining variation in age-3 fish (Fig. 7 A-D). However, residual length in age-12 fish decreased slightly with Secchi depth (Fig. 7G), and increased with conductivity (Fig. 7H), although neither predictor explained more than a small fraction of the residual variation.

Discussion

Growth rates of walleye varied widely through time and across the Ceded Territory of Wisconsin. Over the study period, walleye have been consistently growing faster at young ages, whereas growth rates of older fish have shown much smaller increases. Increases in growth rates were correlated with increases in bass relative abundance and surface water temperatures and declines in adult walleye densities. We also found substantial longitudinal variation in walleye growth, with the fastest growth rates occurring in

the eastern and western portions of the Ceded Territory, in locations with high average largemouth bass relative abundances and surface temperatures and low adult walleye abundances.

Drivers of growth variation in young walleye

Our analyses imply that growth rates of young walleye are density-dependent, a similar pattern documented by Sass et al. (2004) and Sass and Kitchell (2005) using Wisconsin walleye data from 1977-1999, and in Ontario and Quebec, documented by Venturelli et al. (2010). Density-dependence in resource acquisition often results in compensatory effects on fish growth (Lorenzen and Enberg 2002). However, the pattern of our and other studies of walleye growth, where young fish grow more slowly when adult densities are high but the growth rates of older fish are unaffected, differs from the prediction of simple single-resource competition growth models (Walters and Post 1993), where resource competition affects growth rates at all sizes by decreasing the asymptotic size parameter. This discrepancy could be explained if prey competition in walleye was size-asymmetric, with larger walleye either having access to more desirable foraging territories or being able to eat a wider range of resources, such that older walleye become less resource limited. This implies that walleye stocks may not be as prone to stunting as other Wisconsin piscivores such as northern pike (*Esox lucius*) (Margenau et al. 1998).

Over the last two decades, Wisconsin lakes have warmed, with statewide epilimnetic water temperatures in lakes rising by ~ 2.1 GDD y^{-1} (Read et al. 2014; Winslow et al. 2015). This increase in temperature is significant for walleye populations and may be responsible for reduced walleye recruitment and increased densities of largemouth bass (Hansen et al. 2016). There are a few potential mechanisms that might create the observed positive relationship between temperature and juvenile growth. First, walleye may simply grow faster in warmer waters; optimal temperature for walleye growth

ranges from 22 °C (Smith and Koenst 1975), to 26 °C (Hokanson and Koenst 1986), and northern Wisconsin lakes are frequently below these temperatures. Further, GDD also measures the length of growing season, so walleye have more time at optimal temperatures to grow in high GDD lakes. Second, prey for juvenile walleye may occur at greater densities in warmer lakes, reducing food limitation. Whatever the mechanism, however, our results indicate that increasing temperatures are only weakly predictive of walleye growth after accounting for largemouth bass relative abundances and adult walleye densities. This may mean that temperatures in the observed range of variation may have a weak effect on growth, or that temperature has a stronger, but nonlinear effect that our data did not have the power to detect. GDD may have been more predictive if we had used individual-level lifetime average GDD (Venturelli et al. 2010) instead of rolling 5-year mean GDD as a predictor. However, these two metrics were highly correlated in our data (Pearson's $r=0.98$), so the effect would not change substantially. Further, walleye and bass densities would also have been fluctuating over an individual walleye's lifetime, so the effects of all three drivers would be subject to similar errors.

The positive correlation between largemouth bass relative abundance and growth of young walleye is perhaps our most puzzling finding, as the direct and indirect ecological links between largemouth bass and walleye remain unclear. There are a few possible mechanisms that may be driving this relationship. First, largemouth bass may selectively prey on juvenile walleye (Fayram et al. 2005). This could promote faster growth among surviving walleye due to reduced competition or selection for faster growing individuals (Langerhans et al. 2004; Metcalfe and Monaghan 2001). However, there is presently little evidence of largemouth bass predation on walleye in Wisconsin (Kelling et al. 2016). Second, largemouth bass could be competing with walleye for limited habitat and food resources, as their adult diets overlap substantially in Wisconsin lakes (Kelling et al. 2016). Increased competition might reduce survival or growth of older walleye, which in turn could reduce intra-specific competitive effects on younger walleye. Third, if juvenile walleye compete with other small fish such as yellow perch (*Perca*

flavescens) or small centrarchids, largemouth bass predation on these competitors may free up resources for juvenile walleye. Finally, there may be no direct mechanism; walleye growth and largemouth bass CPUE could both be increasing in response to an unmeasured common driver, such as changes in angler harvest or mean lake temperature patterns (Hansen et al. 2015d; Rypel et al. 2015; Rypel et al. 2016). Determining which of these mechanisms is responsible for this relationship will require either experimental manipulation of largemouth bass or walleye abundances or more detailed observations of size-specific walleye-largemouth bass interactions.

Drivers of growth variation in older walleye

Although older (age-8 and 12) fish did show substantial inter-lake variation in size, this variation did not change substantially over time or track variation in growth rates of young fish, nor was it predictable from fish densities or climatic variation. Given that these older and larger fish are the preferred target for anglers, this implies that these factors may not be dependable predictors of fishing quality. There are at least four possible explanations for why our model does not effectively capture variation in older fish. First, it may be an issue of abundances of older fish, and therefore low sample sizes: in the vast majority of lakes, most fish caught were young, and therefore our model will give more weight to coefficient estimates that explain variation in the size of young fish. Second, as the length of older fish will integrate variation in environmental conditions across many years, we may not have measured the relevant drivers across long enough time scales to detect their effect on growth. Our results showing that some of the residual variation in length of age-12 fish was correlated to mean conductivity and Secchi depth may indicate that longer-term trends in food availability or water condition may affect the growth of older fish. Third, as fish tend to shift energy allocation from growth to reproduction as they age (Lorenzen 2016), variation in food availability from competition may be reducing reproductive output in high walleye density lakes, rather than slowing growth. Finally, other factors besides our measured ones may be more important in driving variation in older fish. We did observe that walleye were slightly

larger in high conductivity, shallow-Secchi depth lakes. As conductivity and Secchi depth are indicators of lake productivity (Soranno et al. 1999; Webster et al. 1996), this may indicate that unmeasured food availability may enhance growth in older walleye. However, this effect was not substantial. The most plausible unmeasured driver that might affect the length of older fish is fishing pressure. If larger fish are typically favored for harvest, fish of any given age should be smaller in heavily fished lakes. We do not have information on harvest rates at the same spatial resolution of our current data, though this is an important avenue for future research.

Management implications

From a management standpoint, one of the most important effects of these changes is that the time to reach harvestable size has decreased, suggesting that the vulnerability of the population is increasing. Minimum length limits were set in Wisconsin in part to ensure that walleye were able to reproduce at least once prior to being vulnerable to harvest. If minimum length limits remain the same, even though time to harvestable size is decreasing, walleye are spending less time safe from exploitation. Our maturation index indicated that walleye are becoming sexually mature sooner, but the reduction in this index has not been as substantial as the decline in time to reach harvestable size, which implies that these stocks may be becoming increasingly vulnerable to harvest. We note, however, that our maturation timing estimates should be viewed as a coarse estimate of timing of sexual maturity, as we were not able to distinguish between male and female maturation rates. Female walleye mature later and at larger sizes than males (Margenau et al. 1998), and changes in female maturation rates would have more significant effects on long term population dynamics than changes in male maturation rates.

If time to sexual maturity has not decreased at the same rate as time to harvestable length, this would reduce the amount of time each walleye had to spawn before being vulnerable to harvest. Walleye

recruitment has been declining in Wisconsin lakes more rapidly than adult abundances (Hansen et al. 2015c), and greater fishing mortality may exacerbate this trend. Further, this trend could ultimately mask larger declines in walleye abundance as fish are entering the fishery sooner, even though total walleye numbers are generally in decline (Hansen et al. 2015c). We recommend more intensive studies to determine how sex-specific maturation rates vary across the state, and that our observed changes in growth rates be incorporated into future regional models of walleye dynamics (Tsehaye et al. 2016) to determine what consequences they might have for the fishery.

We documented a significant shift in the growth rates of walleye in the Ceded Territory of Wisconsin. Younger walleye grew faster in recent years, and this pattern is concordant with reduced adult walleye densities, increased GDDs, and increased largemouth bass relative abundances. One of the major effects of this change on the fishery is that walleye are now entering the fishery at a faster rate than before, which may lead to increasing per-capita mortality rates on mature fish as populations decline. Understanding the drivers and implications of the observed changes in walleye growth will require more research, and perhaps experimentation. However, our finding of enhanced younger walleye growth rates in the midst of declining young-of-year and adult numbers is important as this pattern may serve as a more general barometer of declining walleye populations in other nearby regions. Based on our results, we expect that juvenile walleye are likely growing faster in other nearby regions, especially those undergoing similar declines in walleye numbers. We suggest that changing growth rates of younger walleye may serve as a potential indicator for other walleye fisheries declines.

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Tables

Table 1: Geometric means and standard deviations of drivers, used in standardization for modelling.

Driver	Geometric mean	Geometric standard deviation
Walleye density	2.10 fish per acre	2.29 fish per acre
Largemouth bass CPUE	1.57 fish per hour	11.1 fish per hour
GDD	2480 °c · day	1.1 °c · day

Table 2. Terms and model fits of tested random effects for among-lake variation in walleye (*Sander vitreus*) growth rates in the Ceded Territory of Wisconsin during 1990-2012.

Effects vary among:	ΔAIC	R ² of lengths of individual fish
1. years only	46059	0.80
2. lakes only	9471	0.87
3. lake-years	0	0.88

Table 3. Walleye (*Sander vitreus*) growth model specification, fit, and hierarchical variance explained for tested fixed effect models for the Ceded Territory of Wisconsin during 1990-2012. The model column indicates which predictor variables were included in the model: D_t = temporal trend (measured in decades), $G_{j,t}$ = GDD in year t in lake j , $B_{j,t}$ = bass CPUE in year t in lake j , and $W_{j,t}$ = walleye density in year t in lake j . R^2 values calculated using equation (4), and indicate the fraction of lake-year scale variation of that parameter or summary statistic explained by the fixed effects in each model.

Model	R ² intercept	R ² slope	R ² age-3 fish	R ² age-8 fish	R ² age-12 fish	R ² harvestable age	ΔAIC
1. D_t	0.05	0.14	0.08	0.01	0	0.09	111
2. $D_t, G_{j,t}$	0.13	0.21	0.20	0.04	0	0.19	93
3. $D_t, W_{j,t}$	0.36	0.18	0.39	0.26	0.13	0.41	38
4. $D_t, B_{j,t}$	0.36	0.22	0.39	0.24	0.15	0.43	34
5. $D_t, B_{j,t}, G_{j,t}$	0.38	0.25	0.41	0.24	0.15	0.44	31
6. $D_t, W_{j,t}, G_{j,t}$	0.38	0.22	0.42	0.26	0.13	0.43	31
7. $D_t, W_{j,t}, B_{j,t}$	0.48	0.23	0.50	0.33	0.18	0.54	1
8. $D_t, W_{j,t}, B_{j,t}, G_{j,t}$	0.48	0.25	0.51	0.33	0.19	0.54	0

Table 4: Coefficient estimates from best fitting hierarchical model (parameter names are as in equation (1)).

Parameter	Coefficient	Estimate	Standard error
Global intercept	α_0	6.0	0.008
Global slope	β_0	0.47	0.008
Effect of walleye density on the intercept	a_W	-0.039	0.006
Effect of largemouth bass CPUE on the intercept	a_B	0.36	0.006
Effect of GDD on the intercept	a_G	0.010	0.01
Decadal trend in the intercept	a_D	-0.006	0.01
Effect of walleye density on the slope	b_W	0.0072	0.006
Effect of largemouth bass CPUE on the slope	b_B	-0.015	0.006
Effect of GDD on the slope	b_G	-0.019	0.01
Decadal trend in the slope	b_D	-0.027	0.01
Standard deviation of the intercept random effect	σ_α	0.069	-
Standard deviation of the slope random effect	σ_β	0.068	-
Correlation between slope and intercept estimates	ρ	-0.05	-
Standard deviation of residual log-lengths	σ_{indiv}	0.11	-

Figures

Figure 1: Time series of walleye (*Sander vitreus*) sampling effort and average walleye population characteristics for Ceded Territory of Wisconsin lakes during 1990-2012 (black lines) and lakes with available predictor data (grey lines). A) Number of walleye lakes sampled per year. B) Average number of walleye caught per lake. C) Number of fish caught by age group in each year. Top lines: 1-5-year-old fish; middle lines: 6-10 year old fish; bottom line: 11+ year old fish. D) Median total length of walleye in each year (thick lines) and yearly interquartile ranges of TL (thin lines).

Figure 2: A) Trends in walleye (*Sander vitreus*) length at age over time (5-year intervals) in the Ceded Territory of Wisconsin during 1990-2012. Vertical filled regions are probability densities of the lengths of fish of each age in a given group of years. Lines are a log-log linear regression fit to the age-length relationship for each year group to illustrate growth trends. B-D) Trends in total length (TL) of walleye over time based on hierarchical model estimates. Points represent across lake-averages of estimated geometric mean length at age ± 1 SD. Black lines indicate the best fit linear regression of mean TL on year ± 2 SE, to illustrate average trends. B) TL of age-3 fish. C) TL of age-8 fish. D) TL of age-12 fish. E) Trend in mean age when walleye are first harvestable (≥ 381 mm). Age when first harvestable calculated using equation (2). Points and lines are as in B-D.

Figure 3: Maps of average walleye (*Sander vitreus*) stock size characteristics across the Ceded Territory of Wisconsin during 1990-2012. Each grey point represents a lake. Colors represent an estimate of the mean value of each characteristic at a given point in the landscape modelled using a generalized additive model. Light colors indicate higher average values and dark colors represent lower values. A) Average length of age-3 walleye. B) Average length of age-8 walleye. C) Average length of age-12 walleye. D) Average age when walleye are first harvestable.

Figure 4: Temporal and spatial trends in predictor variables: adult walleye (*Sander vitreus*) density (A&B), largemouth bass (*Micropterus salmoides*) CPUE (C&D), and growing degree days calculated from surface water temperature models (E&F). For the time series (A,C,E), points and lines represent means ± 1 std. dev. of the predictor across all lakes observed in the year. For the maps (B, D, F), points indicate individual lakes, and colors represent an estimate of the mean value of each characteristic at a given point in the landscape modelled using a generalized additive model.

Figure 5: Estimates (points) ± 2 SE (vertical lines) of effect sizes of predictors on the intercept (top) and slope (bottom) of the walleye (*Sander vitreus*) length-at-age relationship. Dashed horizontal line indicates a zero effect size. Note that these parameter estimates are unitless, as they correspond to exponents when equation (3) is back-transformed into the original units of age and length. Intercept terms will affect age-at-length multiplicatively; a difference of one in the intercept between two lakes corresponds to all fish in the lake with the greater intercept being e times larger at each age. The slope terms will affect how non-linear the growth curve is; more negative values correspond to growth rates that increase more slowly with age.

Figure 6: Estimated demographic effects on A) mean total length (TL) of age-3 walleye (*Sander vitreus*). B) mean TL of age-12 walleye and C) mean age when fish are first harvestable (≥ 381 mm) under four alternate scenarios in three years (1990, 2000, and 2010). Scenarios are as described in the Methods. Points indicate mean estimates and vertical lines indicate 95% parametric bootstrap percentile confidence intervals using the best fit model. Each observed lake-year was classified into one of the scenarios by whether the sum of squared bass and walleye deviations from zero was greater or less than 2. If the sum of squared deviations was less than 2, it was classified as having mean bass and walleye, otherwise it was classified based on the signs of the deviation from average for bass and walleye.

Figure 7: Relationship between unexplained length and lake-level environmental characteristics. Points indicate the geometric mean ratio of observed to predicted length for each lake in the study. Lines with grey ribbons indicate the best fit linear relationship and its 95% CI between each unexplained length and each environmental characteristic. Top row: relationships between unexplained length in age-3 fish and environmental predictors. Bottom row: relationships between unexplained length in age-12 fish and environmental predictors. All predictors are plotted on a log-scale.

mean length of
age-12 fish (mm)

mean age when first
harvestable (years)

parameter estimate (unitless)

intercept

slope

<https://mc.manuscriptcentral.com/cjfas-pubs>
decade $\ln(\text{bass CPUE})$ $\ln(\text{GDD})$ $\ln(\text{walleye density})$

coefficient

observed length
fitted length