



Pelagic forage versus abiotic factors as drivers of walleye growth in northern Wisconsin lakes

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With 3 figures and 1 table

Abstract: Understanding ecological relationships among fishes and their environments are important for informing management policies. We conducted a statewide assessment of cisco (*Coregonus artedii*) in inland lakes of Wisconsin to better understand the status of this pelagic, coldwater forage fish. We then used long-term (2005–2014), standardized walleye (*Sander vitreus*) survey data from the Ceded Territory of Wisconsin (CTWI) to test for the influence of cisco (present, extirpated, or never present) and several abiotic factors on walleye growth trajectories described using sex-specific asymptotic lengths (L_{∞}), Brody growth coefficients (K), and time in years required to attain common length limits used to manage harvest of walleye in the recreational fishery (381 and 457 mm). Despite being top predators in many north-temperate waters, walleye growth was highly variable among lakes, suggesting that forage base and abiotic factors may be important drivers. Growth characteristics of 160 CTWI walleye populations revealed that females reached greatest L_{∞} in lakes with cisco compared to those where cisco were never present or those lakes where cisco have been extirpated; however, differences were not statistically significant. Male walleye L_{∞} did not differ based on cisco presence. Brody growth coefficients (K) for female walleye were positively correlated with growing degree days and Secchi depth; K for males was positively correlated with Secchi depth. Average time to attain 381 and 457 mm were lowest in lakes where cisco have been extirpated. Our results suggest that cooler water temperatures

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and lower water clarity may be more important drivers of walleye maximum growth potential in northern Wisconsin lakes than the presence of cisco.

Keywords: abiotic, cisco, *Coregonus artedii*, growth, *Sander vitreus*, walleye

Introduction

Fish growth rates and maximum growth potential are regulated by population, community, and ecosystem conditions (e.g., water temperature, consumption rates, diet composition, prey energy content, individual diet specialization) (Kitchell et al., 1977; Hanson et al., 1997). Thus, differences in fish growth patterns among lakes and across regions can be used to identify drivers of change and variability and to sustainably manage exploited stocks. Explaining fish growth patterns becomes more complex when considering warming water temperatures (Hansen et al., 2017), habitat loss (Schindler et al., 2000; Sass et al., 2006; Gaeta et al., 2011; Gaeta et al., 2014), tradeoffs between survival and optimizing growth (Werner & Hall, 1988; Walters & Juanes, 1993), prey availability and associated energy content (Holling, 1959a; 1959b; Hodgson & Kitchell, 1987; Hanson et al., 1997), density-dependence (Diana et al., 1991; Sass & Kitchell, 2005; Venturelli et al., 2010; Gilbert & Sass, 2016), and activity costs (Ahrenstorff et al., 2009; Kaufman et al., 2006). Changes in food web dynamics as a function of various levels of species-specific angler exploitation or stocking can also influence individual fish growth rates and maximum growth potential through various positive and negative feedback loops (Kitchell, 1992).

Cisco (*Coregonus artedii*) are a pelagic, coldwater fish whose range substantially overlaps with the native range of walleye (*Sander vitreus*) (Lee et al., 1980). Although walleye consume a diversity of prey items (Becker, 1983; Lyons, 1987), they are typically considered piscivores and readily consume cisco in lakes where the species coexist (Becker, 1983; Henderson et al., 2004; Krueger & Hrabik, 2005; Kaufman et al., 2009). According to Kaufman et al. (2009), female walleye asymptotic lengths were greater in Ontario lakes with cisco compared to lakes where yellow perch (*Perca flavescens*) was the primary forage. Walleye growth efficiencies were also higher and ingestion and activity rates were lower in lakes with cisco (Henderson et al., 2004; Kaufman et al., 2006). Because many cisco populations have been extirpated in the southern extent of their native range (Honsey et al., 2016) and extirpations are expanding northward due to lake warming and land use change (Jacobson et al., 2008; 2010; 2012), the loss of this potentially important pelagic forage species may have negative effects on walleye growth, fecundity, condition, and survival.

Walleye growth can be highly variable among populations due to differences in latitude and associated growing degree days (Quist et al., 2003; Venturelli et al., 2010), prey availability (Henderson et al., 2004; Kaufman et al., 2009), and lake productivity (Ryder, 1965; Sass et al., 2004; Sass & Kitchell, 2005). Thermal regimes can largely regulate fish growth, but growth can also differ among populations in close geographic proximity, particularly when lake characteristics are highly heterogeneous across a region (Boisclair & Leggett, 1989a; Venturelli et al., 2010). Growth is more than just a function of thermal conditions and is dictated by the interactions of temperature, consumption rates, prey energy content, and prey size, ultimately leading to growth as a result of surplus energy acquired minus

metabolic, gonadal investment, and activity costs (Kitchell et al., 1977; Hanson et al., 1997; Henderson et al., 2004). Thus, prey type and associated energy content are also primary determinants of fish growth (Paloheimo & Dickie, 1966; Fry, 1971; Kitchell et al., 1977; Boisclair & Leggett, 1989b; Henderson et al., 2004; Kaufman et al., 2009).

Optimal foraging theory principles maintain that fish should select a diet (if available) that maximizes energetic gain (Hodgson & Kitchell, 1987), while minimizing handling costs and predation risk (Schoener, 1971; Werner & Hall, 1988; Mittelbach, 1981; Walters & Juanes, 1993; Walters et al., 2000). However, multiple factors affect the prey selection process and realized prey choice does not always reflect an optimal diet for growth. Several studies have closely related feeding strategies to density and type of prey (Fox, 1989; Floeter & Temming, 2003; Carruthers et al., 2005; Ahrenstorff et al., 2009). Other studies have shown that fish will abandon consuming highly abundant prey when more energetically profitable prey is available (Hodgson & Kitchell, 1987; Lankford & Targett, 1997).

Although growth is dependent on consumption rates, prey characteristics, and environmental variables, differences in system-specific walleye abundance have also been shown to affect individual growth rates (e.g., density-dependence; Sass et al., 2004; Sass & Kitchell, 2005; Venturelli et al., 2010; Pedersen et al., 2017). Walleye density can be highly variable among lakes, and previous research suggested that walleye growth was poorly related to



Fig. 1. Location of Ceded Territory of Wisconsin walleye (*Sander vitreus*) lakes with cisco (*Coregonus artedii*) present (grey circles with black outline), cisco extirpated (black circles), and cisco never present (white circles with black outline).

density in northern Wisconsin lakes (Sass et al., 2004; Sass & Kitchell, 2005; Pedersen et al., 2017), but growth was more strongly related to density in Ontario and Quebec lakes (Ventur-elli et al., 2010). According to Sass and Kitchell (2005), density-independent, surrogate measures of lake productivity (pH, the morphoedaphic index, maximum depth, conductivity) were better predictors of walleye growth.

Walleye are ecologically, economically, and culturally important in the Ceded Territory of Wisconsin (CTWI; about the northern third of the state) and climate change has the potential to reduce critical coldwater habitat for pelagic forage fishes important to walleye (Figure 1). In conjunction with several other lake-specific abiotic factors, we simultaneously tested whether sex-specific Brody growth coefficients (K) and asymptotic lengths (L_{∞}) estimated from von Bertalanffy growth models differed among CTWI walleye populations in lakes where cisco were present, were extirpated, and have never been present. We also tested whether average time to reach minimum length limits (381 and 457 mm) commonly used to manage harvest in the recreational walleye fishery differed among the three lake-types. Comparisons of von Bertalanffy growth parameters were specifically used to test for differences because we were interested in generalized juvenile walleye growth (K), maximum growth potential (L_{∞}), and time to reach common minimum length limits among walleye populations based on cisco presence. Our selection of abiotic factor covariates to test were aimed to represent the diversity of lakes found in the CTWI (Magnuson et al., 2006), and based on data availability and known abiotic factors influencing CTWI walleye growth (Sass et al., 2004; Sass & Kitchell, 2005; Pedersen et al., 2017).

Methods

Data

The CTWI encompasses about the northern third of the state and has about 850 walleye lakes (Figure 1). In the mid-1980's, Chippewa Native American off-reservation fishing, hunting, and gathering rights were affirmed in federal court and a spring walleye spear fishery was reinstated in the CTWI (U.S. Department of the Interior, 1991). As a result, walleye have been subjected to a joint tribal spear and recreational angling fishery since the late-1980s (U.S. Department of the Interior, 1991). Because of the joint fishery, an extensive, standardized walleye monitoring program has been conducted on CTWI lakes including annual creel surveys, mark-recapture population estimates, and collection of length, weight, and age information since 1990 (Hansen et al., 1991; Beard et al., 1997). We used walleye data collected during 2005–2014 in our analyses.

The Wisconsin Department of Natural Resources (WDNR) has estimated adult walleye (sexually mature or ≥ 381 mm in total length) abundance annually on about 20–30 lakes selected at random in addition to 12 “trend” lakes sampled every three years in the CTWI using mark-recapture (detailed methodology and justification for the adult walleye population estimates can be found in Beard et al. (1997) and Hansen et al. (2000)). In association with the population estimates, total length, weight, sex, and aging structures (5 fish per 10 mm length increment per sex) are also collected from adult walleye. Scales are removed from walleye < 508 mm and dorsal spines are collected from fish ≥ 508 mm for age estimation.

As part of a statewide effort to assess the status of cisco populations in all Wisconsin lakes with historical presence of the species, we sampled 114 CTWI lakes during summer (2011–2014) following stratification (Figure 1). To determine if cisco were present, we used an experimental vertical gillnet sampling design with a combination of seven mesh sizes (9.5, 12.7, 19.1, 25.4, 31.8, 38.1, 44.5 mm bar mesh) distributed among five nets varying from 1.8–3.1 m in width. All nets had the capacity to sample pelagic lake habitats down to a maximum depth of 30.5 m, which covered the entire water column in all lakes sampled except for one (Trout Lake, Vilas County, 36 m maximum depth). During sampling, all five nets were connected in a line and suspended from the surface to the bottom in the deepest basin(s) of each lake. At a minimum, vertical gillnets were set for 24–48 h (1–2 net nights) to detect cisco in lakes with simple bathymetry (i.e., lakes with one deep basin). If no cisco were captured during the first 24 h, sampling continued for an additional 24 h to improve the probability of detection. Lakes with complex bathymetry (i.e., multiple deep sub-basins separated by shallower water of ≤ 9 m) were sampled with one net night of effort per deep basin. No repeat sampling was conducted in sub-basins where cisco were not captured. At each sample site, we also recorded GPS coordinates (DMS format) and conducted water temperature/dissolved oxygen profiles prior to setting nets. We identified all fish captured (including non-cisco bycatch) to species and recorded total length (TL [mm]). Mesh size and depth of capture within the vertical gillnet was recorded for each fish. We assumed that cisco were extirpated in a particular lake where historic records indicated they previously occurred (John Lyons, Wisconsin Department of Natural Resources, unpublished data), but our sampling failed to detect any specimens.

Growth modeling and analysis

We used the Beverton-Holt (Beverton & Holt, 1957) parameterization of the von Bertalanffy growth model (von Bertalanffy, 1938) within a hierarchical Bayesian framework to describe walleye growth. The hierarchical framework allowed us to not only estimate parameters for all fish, but more importantly, to explicitly estimate growth parameters for walleye populations within each lake. Reliable lake-specific growth models are able to be estimated based on the Bayesian property of sharing statistical strength, whereby low information (sample size) groups combine their information with that of the grand mean (all groups), which results in estimates shrunk toward the overall model fit (Kéry 2010). We retained only lakes with ≥ 5 samples over the sampling period (2004–2014), where a sample comprised an individual fish that was collected for length and age information. Lake-specific parameters were then modeled with lake-level covariates to draw inference on and compare walleye growth variability among lakes. The von Bertalanffy observation-level (level-1) model was expressed as:

$$y_{ij} = L_{\infty j} (1 - e^{-K_j(t_{ij} - t_{0j})}) + \varepsilon_{ij}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$
(Eq. 1)

In equation 1, y_{ij} is the total length (mm) for fish i from lake j , and t_{ij} is the estimated age from fish i from lake j . $L_{\infty j}$, K_j , and t_{0j} are the three von Bertalanffy model parameters for lake j that represent the asymptotic length, Brody growth coefficient, and the predicted fish length at

time 0, respectively. Specifically, $L_{\infty j}$ represents maximum mean length attained by fish in lake j and K_j describes how quickly length-at-age approaches $L_{\infty j}$. We assumed that the natural log of these parameters came from a multivariate normal distribution with a population mean μ and variance–covariance Σ . The μ contains the population-average estimates for the three von Bertalanffy parameters, which describe the growth model across all lakes. ε_{ij} is the residual error, which is assumed to be independent and identically distributed as $N(0, \sigma^2)$. Model fitting was improved by adopting the Kimura (2008) approach of using the logarithmic scale to estimate parameters (please note that 10 is added to t_0 because negative t_0 are not biologically possible, even though it may be negative, when estimated on the log-scale). Finally, we modeled males and females separately because walleye growth is sexually dimorphic (Sass, 2001; Henderson et al., 2003; Midway et al., 2015).

The second level of the model was added to model the lake-specific von Bertalanffy parameters ($L_{\infty j}$ and K_j) against lake-level covariates. Level 2 was expressed as:

$$\begin{pmatrix} K_j \\ L_{\infty j} \\ t_{0j} \end{pmatrix} \sim MVN \left(\begin{pmatrix} \gamma_0^K + \gamma_1^K Z_1 + \gamma_2^K Z_2 + \gamma_3^K Z_3 + \gamma_4^K Z_4 + \gamma_5^K Z_5 + \gamma_6^K Z_6 \\ \gamma_0^{L_{\infty}} + \gamma_1^{L_{\infty}} Z_1 + \gamma_2^{L_{\infty}} Z_2 + \gamma_3^{L_{\infty}} Z_3 + \gamma_4^{L_{\infty}} Z_4 + \gamma_5^{L_{\infty}} Z_5 + \gamma_6^{L_{\infty}} Z_6 \\ \bar{t}_0 \end{pmatrix}, \Sigma \right),$$

for $j = 1, \dots, J$

(Eq. 2)

In equation 2, γ_{0-5}^K and $\gamma_{0-5}^{L_{\infty}}$ are the coefficients for the intercept (subscript 0) and effect of the covariate Z_{1-5} (i.e., slope; subscripts 1–5). Parameter t_0 was not of biological interest to us, thus we did not seek to evaluate covariates for a relationship with t_0 . Covariates examined (see Table 1) were lake surface area (Z_1), conductivity (surrogate measure of lake productivity, Webster et al. [1996]; Soranno et al. [1999]; Sass and Kitchell [2005]; Z_2), growing degree days (GDD) (modeled values of water temperature degree days with a base temperature of 5 °C, Hansen et al. [2017]; Z_3), mean Secchi disc transparency (Z_4), and cisco presence (where Z_5 represents cisco extirpated, Z_6 represents cisco never present, and reference levels represents cisco present). Lake surface area, conductivity, and mean Secchi disc transparency data were acquired from the WDNR Surface Water Integrated Monitoring System (SWIMS) database (a WDNR repository of chemical, biological, and limnological data on Wisconsin’s waters). All covariates except cisco presence were continuous data and were log transformed and standardized (scaled to mean of 0 and standard deviation of 1) before model fitting. This transformation helped with model fitting and also allowed the effect of covariates to be interpreted with all other covariates at their mean value. To avoid multicollinearity, we examined correlations among all covariates using Spearman’s rank correlation coefficients before including them in the model. All covariates were retained as none were strongly correlated (Spearman’s $\rho < 0.4$ for all pairwise correlations). All continuous covariates were averaged to provide a single value for each lake. Cisco was treated as a categorical variable that included three levels; lakes with cisco, lakes where cisco have been extirpated, and lakes where cisco have never been present. Cisco was also treated as a categorical variable because our vertical gillnet assessments were aimed to evaluate status (presence/absence) and cisco gillnet catch per unit effort has been shown to be highly variable within lakes and over time (Ahrenstorff et al., 2013). Non-cisco, alternative forage species (e.g., yellow perch) presence/absence or catch per unit effort influences on walleye growth were not evaluated because

Table 1. Posterior means (with 95% credible intervals in parentheses) of covariate effects on Brody growth coefficient (K) and asymptotic length (L_{∞}) of male and female walleye (*Sander vitreus*) in Ceded Territory of Wisconsin lakes, 2005–2014. Bold values indicate significant covariate effects (where significance is interpreted as the 95% credible interval not overlapping 0). Results are from two separate sex-specific models. Values below the covariates of lake area, conductivity, growing degree days, and Secchi depth represent the mean and range of values observed from the 160 lakes used in our analysis.

Covariate	Model term	Female K	Female L_{∞}	Male K	Male L_{∞}
Lake area 365, 20–5377	Z1	–0.03 (–0.1, 0.05)	0.003 (–0.04, 0.04)	–0.01 (–0.08, 0.06)	–0.01 (–0.05, 0.02)
Conductivity 104, 18–523	Z2	0.07 (–0.02, 0.15)	–0.009 (–0.05, 0.03)	0.05 (–0.02, 0.13)	–0.004 (–0.04, 0.03)
Growing degree days 2553, 2216–3045	Z3	0.15 (0.6, 0.24)	–0.05 (–0.1, –0.0001)	0.06 (–0.02, 0.14)	0.03 (–0.01, 0.06)
Secchi depth 2.8, 0.7–9.5	Z4	0.2 (0.11, 0.29)	–0.09 (–0.13, –0.04)	0.08 (0.003, 0.16)	0.01 (–0.03, 0.05)
Cisco present	Reference	0.11 (0.09, 0.13)	847 (770, 934)	0.16 (0.13, 0.19)	582 (539, 631)
Cisco extirpated	Z5	0.13 (0.1, 0.17)	789 (685, 909)	0.16 (0.13, 0.21)	590 (524, 660)
Cisco never present	Z6	0.12 (0.09, 0.14)	821 (737, 918)	0.17 (0.14, 0.21)	589 (539, 643)

non-cisco bycatch was low. Adult walleye density was not tested as a lake-level covariate because walleye growth has been shown to be weakly density-dependent in CTWI lakes (Sass et al., 2004; Sass & Kitchell, 2005; Pedersen et al., 2017).

For all models, prior probability distributions for σ , μ , and Σ were diffuse with a uniform distribution given to σ , a normal distribution given to μ , and a scaled inverse-Wishert distribution given to Σ (Gelman & Hill, 2007). We ran three concurrent Markov chains beginning each chain with a different value. From 100,000 iterations, the first 40,000 iterations of each chain were discarded as burn-in. We then thinned the remaining chains by retaining every third value. This resulted in a total of 60,000 values for analysis. Posterior distributions were assessed for convergence visually and with the Brooks–Gelman–Rubin statistic, \hat{R} , where any values <1.1 indicated convergence. JAGS analyses were run using the rjags package (Plummer, 2013), run from within R software (R Core Team, 2016). Finally, significance of any model effects (e.g., parameter or factor level) were interpreted as the 95% credible interval for the posterior distribution not overlapping 0 (in the case of a parameter) or the 95% credible intervals not overlapping between two factor levels (in the case of a multiple comparisons of groups).

Time to reach minimum lengths

Using estimates of $L_{\infty j}$ and K_j , we estimated time required for walleyes of each sex to attain lengths of 381 (t_{381}) and 457mm (t_{457}) for each lake type using the formula provided by Ogle & Isermann (2017):

$$L_{ij} = L_r + (L_{\infty j} - L_r)[1 - e^{-K_j(t - t_{rj})}] \quad (\text{Eq. 3})$$

where L_{ij} = expected or mean length of walleyes in lake j at time or age t and t_r = time required for walleyes in lake j to reach a specified length (either 381 or 457mm). We selected these lengths for comparison because they represent two minimum length limits commonly used to regulate recreational angler harvest of walleye within the CTWI. Mean t_{381} and t_{457} and associated 95% confidence intervals were calculated based on cisco presence; lack of overlap between the 95% confidence intervals was used to determine statistical differences in mean t_{381} and t_{457} among lake types.

Results

Growth modeling and analysis

Walleye growth metrics varied by sex and the presence of cisco. The number of lakes included in female and male analyses were 160 and 158, respectively. Lake-type was dominated by lakes where cisco were never present ($n = 117$ and 116 lakes for females and males). Holding all continuous covariates at their means, female walleye K in lakes with cisco present (the reference level in the model) was estimated to be 0.11 (95% credible interval [95% CI] = 0.09–0.13), while mean L_{∞} was 847mm (95% CI = 770–934) (Table 1). In lakes with cisco extirpated or never present, estimates of mean K were slightly higher and estimates of mean L_{∞} were slightly lower (Table 1). Mean female L_{∞} was greatest in lakes with cisco present and was nearly 60 mm greater than in lakes where cisco have been extirpated, but this difference was not statistically significant (Figure 2). Male walleye had a larger mean K than female walleye (about 0.16 for all lake types), and smaller mean L_{∞} , which ranged from 582–590 mm depending on cisco presence/absence (Table 1).

Among the continuous covariates examined for female walleye, GDD and Secchi depth showed a significant, positive relationship with K and a negative relationship with L_{∞} (Table 1; Figure 3). The only significant effect correlated with male walleye growth was Secchi depth, being positively correlated with K (Table 1, Figure 3).

Time to minimum length

Estimates of t_{381} and t_{457} differed among lake-types, with walleye in lakes where cisco have been extirpated attaining these lengths in the shortest period of time. On average, females reached 381 mm in 3.7 years and 457 mm in 5.3 years in lakes where cisco were extirpated, whereas males reached these lengths in 4.6 and 7.3 years, respectively. Females in lakes with

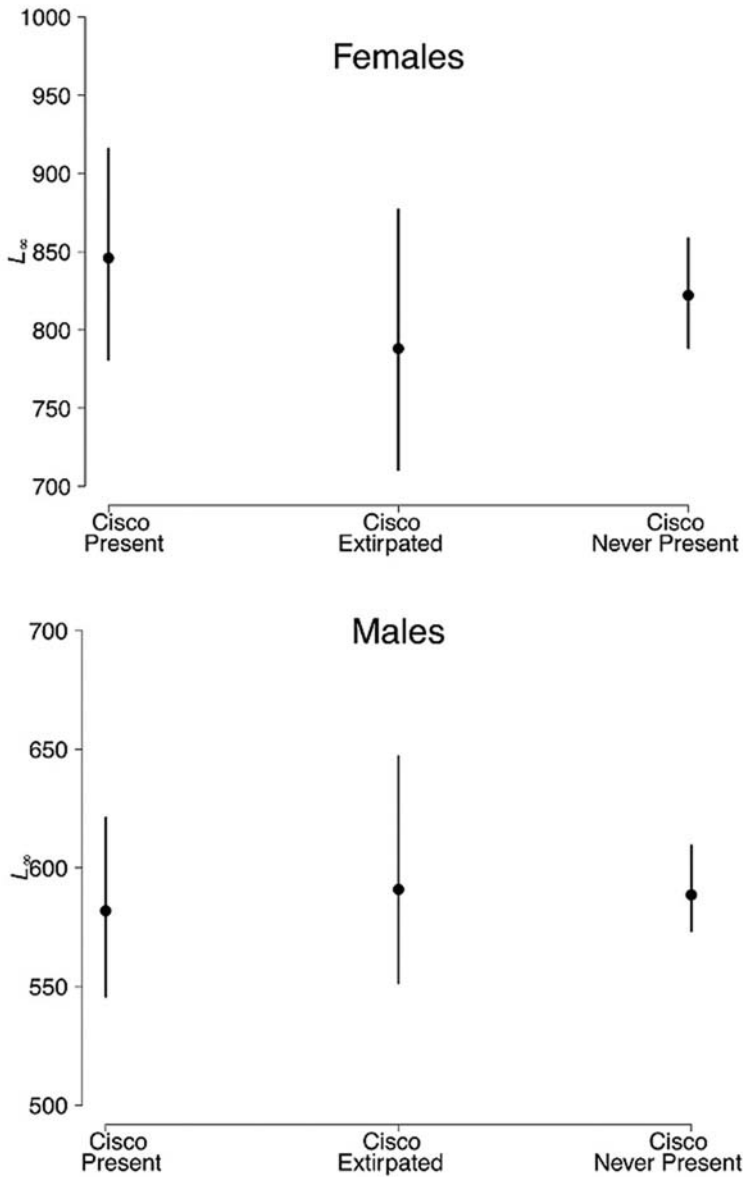


Fig. 2. Posterior mean female (top panel) and male (bottom panel) walleye (*Sander vitreus*) asymptotic length (L_{∞}) among Ceded Territory of Wisconsin lakes with cisco (*Coregonus artedii*) present, extirpated, and never present during 2005–2014. Vertical bars represent the 95% credible intervals about the mean.

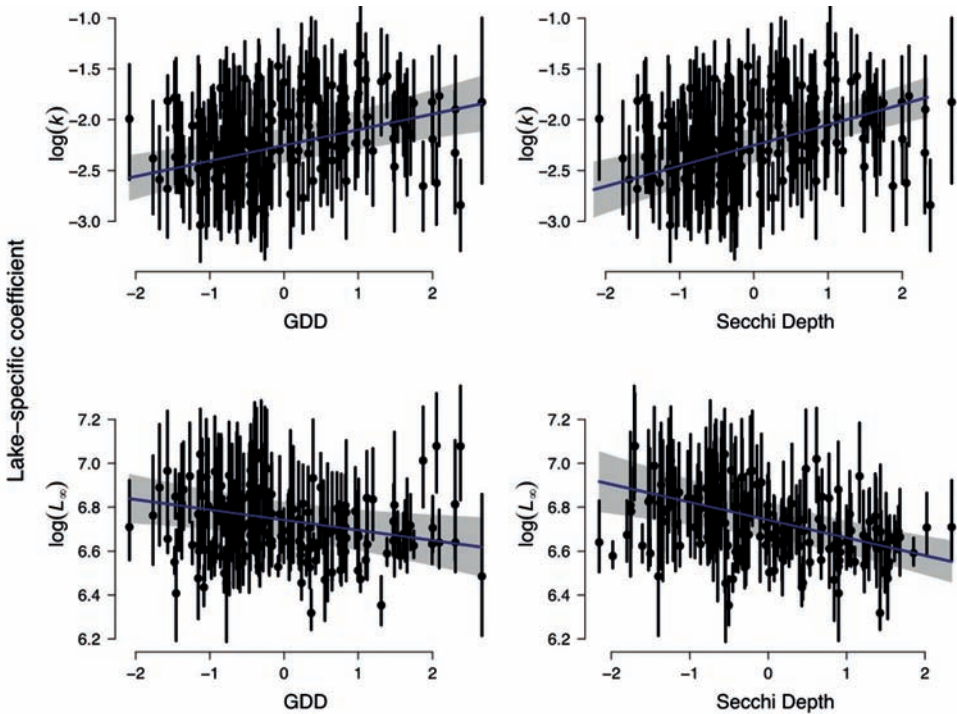


Fig. 3. Relationships between lake-level predictors (modeled growing degree days and Secchi depth) and lake-level growth parameters (estimates of K and L_{∞}) for female walleye (*Sander vitreus*) in Ceded Territory of Wisconsin lakes during 2005–2014. Solid points are posterior means and vertical lines are 90% credible intervals. The thick blue line represents the hierarchical regression line and gray shading is the 90% credible region.

cisco present required about 0.2 years longer to reach both critical lengths, and in lakes where cisco were never present, females required 0.5 years longer to reach both critical lengths compared to lakes where cisco had been extirpated. In lakes with cisco present, male walleye reached 381 mm at nearly the same time ($t_{381} = 4.7$ years) as in lakes where cisco were extirpated; however, t_{457} was significantly greater ($t_{457} = 7.7$) in lakes where cisco were present. In lakes where cisco were never present, males needed 5.0 years to reach 381 mm and 7.9 years to reach 457 mm, representing differences of 0.4 and 0.6 years compared to lakes where cisco were extirpated.

Discussion

Our results suggested that variation in the maximum growth potential of female walleye in northern Wisconsin lakes is better explained by abiotic factors such as GDD and water clarity than the presence of cisco. Nevertheless, mean female walleye L_{∞} was highest in lakes with cisco present than mean L_{∞} for lakes where cisco have been extirpated or were never present.

Our results suggest that cisco extirpation may result in an erosion of up to about 60 mm of L_{∞} for females on average, which represented a greater difference in female L_{∞} (37 mm) than that observed by Kaufman et al. (2009) for Ontario lakes with and without cisco. Male walleye K and L_{∞} were relatively unrelated to presence of cisco. This result is not surprising given that male walleye have shorter life spans and growth is sexually dimorphic favoring females due to sex-specific differences in energy allocation (Henderson & Nepszy, 1994; Henderson et al., 1996; Sass, 2001; Henderson & Morgan, 2002; Henderson et al., 2003; Sass & Kitchell, 2005). In the CTWI, male walleye live to about age-10 and grow to a maximum length of about 600 mm (Sass, 2001; Sass & Kitchell, 2005). Thus, cisco may be less important for the growth potential of smaller, shorter-lived males (particularly due to gape limitation in lakes with larger sized cisco), but somewhat beneficial (albeit variable) for female walleye to reach maximum growth potential where the two species coexist. In our study, water temperature and water clarity were better predictors of walleye growth potential compared to the presence/absence of cisco in CTWI lakes.

Diet effects on walleye growth

Kaufman et al. (2006; 2009) found that female walleye L_{∞} in Ontario lakes were greatest when cisco were present compared to lakes with yellow perch as the primary forage base. Furthermore, Kaufman et al. (2009) observed that interactions between walleye and cisco (based on diet composition) were most prevalent during fall, which corresponds with movements of cisco from pelagic to inshore habitats for spawning (Becker, 1983). Our findings suggested that female walleye maximum growth potential was about 25 mm greater on average in CTWI lakes with cisco present compared to lakes with cisco never present, although this difference was not statistically significant. Reduced importance of cisco for walleye growth potential in CTWI lakes compared to Kaufman et al. (2006; 2009) may be due to the increased diversity of prey available in CTWI lakes versus those in Canadian shield lakes as freshwater fish species diversity declines with increasing latitude, especially above 40° N (Rohde et al., 1993; Rohde, 1999). For example, Krueger and Hrabik (2005) found cisco, various cyprinids, rainbow smelt (*Osmerus mordax*), and yellow perch to be the dominant prey in the diets of walleye caught in Fence Lake, Wisconsin and Frey et al. (2003) found invasive rusty crayfish (*Orconectes rusticus*), mayflies, and yellow perch to dominate the diets of Big Crooked Lake, Wisconsin walleye. Wisconsin walleye diets are diverse and largely dictated by prey availability; prey items observed in walleye diets excluding those mentioned above have included darters, Diptera larvae, entomostracans, caddisfly larvae, bullhead (*Ameiurus* spp.), common carp (*Cyprinus carpio*), and black crappie (*Pomoxis nigromaculatus*) (Becker, 1983; Lyons, 1987). Although cisco presence/absence was a weak driver of walleye growth potential in CTWI lakes, some of the variability in female L_{∞} in cisco lakes may also be attributed to walleye and/or cisco size-structure (i.e., walleye gape limitation) and abundance differences of the individual cisco populations themselves (Kaufman et al., 2009, Ahrenstorff et al., 2013).

Cisco require specific oxythermal habitat (cold, oxygenated) and are generally found in lakes > 10 m in depth (Jacobson et al., 2008; 2010). Of Wisconsin's ~15,000 lakes, only 202 lakes have a historical record of cisco, with most occurring in the CTWI (John Lyons,

Wisconsin Department of Natural Resources, unpublished data). Out of the CTWI's ~850 walleye lakes, only 114 had a historical record of cisco. Cisco oxythermal habitat in Wisconsin lakes has been characterized by water temperature in the water column at dissolved oxygen of $\geq 6 \text{ mg L}^{-1}$ (TDO6) and by the vertical extent of the water column within which water temperature is $\leq 22.8 \text{ }^\circ\text{C}$ and dissolved oxygen is $\geq 6 \text{ mg L}^{-1}$ (cisco layer thickness, CLT) (Lyons et al., 2017). Potentially stressful oxythermal habitat conditions for cisco in Wisconsin lakes have been identified using the benchmarks of TDO6 = $22.8 \text{ }^\circ\text{C}$ and CLT = 1 m, where cisco relative abundances were greater in lakes with lower values of TDO6 and higher values of CLT (Lyons et al. 2017). Values of TDO6 above and CLT below the benchmarks were generally characteristic of lakes with remnant or extirpated cisco populations (Lyons et al. 2017). Differences in forage base types among lakes may explain differences in the walleye growth potential we observed. In CTWI lakes without cisco, walleye growth is likely driven by a littoral-based food web consisting of a number of fish and invertebrate prey species and overall more productive, shallow lake conditions (lower water clarity). In contrast, the forage base for walleye in lakes with cisco is likely more pelagic based, strongly influenced by benthic-pelagic coupling, and lower in prey species diversity (Schindler & Scheuerell, 2002). Therefore, walleye growth potential may be more compromised by the extirpation of cisco in these pelagic-based food webs due to the lack of alternative prey and unproductive nature of the lakes (higher water clarity). Additionally, lake conditions – including some of those captured in our abiotic predictors – may influence cisco population dynamics and limit the amount of available cisco resources for walleye. Kaufman et al. (2009) suggested that lakes with higher proportions of larger cisco ($\geq 300 \text{ mm}$) resulted in an energetic bottleneck for walleye due to gape limitation.

In lakes with cisco, this forage species may be required by walleye to achieve maximum growth potential due to bioenergetic constraints on growth at larger body sizes. As can be observed in the von Bertalanffy growth relationship, fish growth asymptotes at older ages and lengths due to increased metabolic costs associated with being larger. That is, energy required to satisfy routine metabolic costs increases with body size; surplus energy acquisition above standard metabolic costs is then required for somatic growth and to produce gonads (Hanson et al., 1997). Given that the energy density of cisco (as derived from bloater [*Coregonus hoyi*]) is likely about 25–100% greater than that of yellow perch (Kitchell et al., 1977; Pothoven et al., 2012), the additional energy provided by cisco likely drives the ability of female walleye to reach greater L_∞ in lakes where this forage species is present compared to lakes where they have been extirpated. As suggested by Kaufman et al. (2009), increased consumption rates on alternative non-cisco prey is likely required to achieve greater female walleye L_∞ in lakes without cisco.

Our results indicated that cisco may be unimportant to juvenile and younger age classes of walleye based on the time required to reach t_{381} and t_{457} in CTWI lakes. Time required for walleye to reach these commonly used minimum length limits in the recreational fishery were shortest in lakes where cisco have been extirpated. Although Kaufman et al. (2009) observed cisco in diets of walleye as small as 175 mm, our results suggested that cisco may be less important for early walleye growth in the CTWI (Lyons, 1987). Given that cisco extirpations are occurring at the southern extent of their range and moving northward, these occurrences may weakly influence early growth of walleye due to prolonged cisco recruitment failure and a lack of smaller-sized individuals.

Covariate effects on walleye growth

Within lakes, water clarity and GDD influenced sex-specific walleye K and maximum growth potential. Water clarity may be important for walleye growth and production because it influences the amount of thermal-optical habitat available (Lester et al., 2004). Because water clarity in some north-temperate lakes has increased over time due to climate change (Rose et al., 2016) and reduced nutrient loading, our results suggest that these water clarity changes may have had a positive effect on K at the expense of maximum growth potential. Nevertheless, continued water clarity increases exceeding 2 m Secchi disc transparency may be detrimental to walleye growth and production (Lester et al., 2004).

Modeled GDD were positively correlated with K for females and negatively correlated with female L_{∞} . Immature walleye growth rates have been shown to be density-dependent when evaluated using GDD, particularly when juvenile densities were low (Venturelli et al., 2010). Growing degree days and corresponding water temperatures have increased in northern Wisconsin lakes over time and walleye natural recruitment is predicted to decline as a consequence (Hansen et al., 2015; 2017). Therefore, female K may be positively correlated with GDD due to a relaxation of density-dependent constraints on juvenile growth and/or more favorable temperatures for growth (Venturelli et al., 2010). Likewise, female L_{∞} may be negatively correlated with GDD because rapid growth early in life generally results in lower maximum growth potential (Gallucci & Quinn, 1979). Moreover, Pedersen et al. (2017) found that juvenile walleye growth rates have increased over time in CTWI lakes with a corresponding decline in maximum length. Future scenarios of climate change have predicted extirpations of walleye populations in CTWI lakes with corresponding increases in largemouth bass (*Micropterus salmoides*) abundances due to increasing cumulative growing degree days over time (Hansen et al., 2017). As such, we may also expect a corresponding negative influence on walleye growth potential as a result of water temperatures being elevated beyond those optimal for growth (22° C for adult walleye, 25° C for juvenile walleye) in the future (Kitchell et al., 1977; Madon & Culver, 1993; Hansen et al., 2016).

Management implications

Two primary management implications can be derived from our study based on known extirpations of cisco and those predicted by lake warming and land use change in the future; cisco conservation and walleye angler expectations. Because cisco require specific oxythermal habitat and the availability of this habitat is declining over time due to excess nutrient loading and lake warming (Jacobson et al., 2008; 2010), cisco conservation efforts may still be important to maintain maximum walleye growth potential, fecundity, condition, and survival for anglers in lakes where walleye and cisco coexist. Despite the observed variability, our results still suggested that female walleye L_{∞} may be compromised by about 60 mm on average when cisco are extirpated from a lake. Although slowing or reversing lake warming in the short-term is unlikely, reduced nutrient loading can be achieved through management actions to maintain oxythermal habitat critically needed by cisco. A better understanding of potential genetic stock differentiation among remaining cisco populations may also aid in conservation

efforts should some cisco stocks be genetically more tolerant to degradations in oxythermal habitat.

Our results also have implications for walleye anglers and their expectations. Given current trends of increasing water temperature and clarity (Hansen et al., 2017; Rose et al., 2016), trophy walleye anglers may expect the length of maximum-sized individuals to decline in lakes over time regardless of cisco presence/absence (Pedersen et al., 2017). For harvest-oriented walleye anglers, the presence/absence of cisco appears less important than water temperature and water clarity for affecting the time it takes for walleye to reach harvestable size. Therefore, walleye in lakes where cisco have been extirpated should still recruit to the recreational fishery more rapidly than walleye in lakes with cisco and in lakes where cisco have never been present.

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