

# Fish growth and degree-days II: selecting a base temperature for an among-population study

Kyle A. Chezik, Nigel P. Lester, and Paul A. Venturelli

**Abstract:** The degree-day (DD) is a method of describing the thermal opportunity for growth and development and is becoming increasingly popular when comparing fish growth over large spatial scales (e.g., counter-gradient growth). Temperatures too cold to permit growth are excluded in the DD equation by incorporating a lower temperature threshold ( $T_o$ ). However, there is no convention for choosing  $T_o$ , and unknown is the effect of an incorrect  $T_o$  on how growth is perceived. We simulate data to demonstrate how an incorrect  $T_o$  may lead to differences in temperature-corrected growth rates among populations. These differences increase with the error in  $T_o$  and the thermal range among simulated populations. We then show the same relationships in an analysis of length-at-age data from 81 walleye (*Sander vitreus*) populations in North America. Together, our results demonstrate that differences in temperature-corrected growth rates among populations can be a statistical artifact rather than a biological phenomenon, especially when populations are distributed over a large thermal gradient.

**Résumé :** La méthode des degrés-jour (DJ), utilisée pour décrire les possibilités de croissance et de développement selon la température, est de plus en plus employée pour comparer la croissance des poissons sur de grandes étendues (p. ex. croissance à contre-gradient). Les températures trop basses pour permettre la croissance sont exclues de l'équation des DJ en incorporant un seuil de température minimum ( $T_o$ ). Il n'existe toutefois aucune convention sur le choix de la valeur de  $T_o$ , et l'effet d'une  $T_o$  incorrecte sur la perception de la croissance est inconnu. Nous simulons des données afin de démontrer comment une  $T_o$  incorrecte peut mener à des différences entre populations sur le plan des taux de croissance corrigés pour la température. Plus l'erreur associée à  $T_o$  et la fourchette de températures pour les populations simulées sont grandes, plus ces différences sont importantes. Nous démontrons ensuite l'existence des mêmes relations dans une analyse de données de longueur selon l'âge pour 81 populations de dorés jaunes (*Sander vitreus*) en Amérique du Nord. Collectivement, nos résultats démontrent que des différences entre populations sur le plan des taux de croissance corrigés pour la température peuvent être des artefacts statistiques plutôt que le produit d'un phénomène biologique, particulièrement dans le cas de populations réparties le long d'un important gradient thermique. [Traduit par la Rédaction]

## Introduction

Fish growth scales with temperature and is bound by upper and lower thermal limits (Brett 1969; Fry 1971). The temperature that optimizes growth falls between these thermal extremes and varies by species (Hasnain et al. 2013) and consumption rates (Jobling 1994). Therefore, the amount of time that is spent both within the thermal limits of growth and near the thermal optimum (e.g., as a result of the annual temperature cycle) defines the thermal opportunity for growth.

Because there are many life history and fitness advantages to optimizing growth, isolated populations may show physiological or behavioral adaptations to their local environments (but see Angilletta 2009). Thermal adaptation results in among-population differences in observed growth even after correcting for differences in thermal opportunity. This phenomenon is often referred to as counter-gradient growth (CGG) compensation, where populations living in colder environments grow faster than would be expected given how temperature is known (or thought) to affect their growth (Conover and Present 1990).

The standard test for CGG involves common garden experiments in which individuals are sampled over some thermal gra-

dient and are then grown together under standard conditions (e.g., Rypel 2012a). An increasingly popular (but less rigorous) alternative is to test for CGG by observing growth in the field, correcting for the thermal opportunity for growth, and then regressing corrected growth against latitude (e.g., Power and McKinley 1997; Conover et al. 2009; Chavarie et al. 2010). A positive relationship is considered evidence for CGG. The degree-day ( $DD_{T_o}$ ; °C-day) is often used to test for apparent CGG (e.g., Table 1) because it is an index of the thermal opportunity for growth. DD calculations incorporate a lower temperature threshold ( $T_o$ ) so as to limit calculations to temperatures that are relevant to growth.

Currently, little is known as to the implications of  $T_o$  when comparing temperature-corrected growth rates over large spatial scales. To date, a wide range of  $T_o$  values (0–18 °C) have been used in among-population growth studies with as many as four different values (0, 5, 10, and 13.5 °C) applied to a single species (e.g., yellow perch, *Perca flavescens*; Table 1). Among yellow perch studies, it appears that significant evidence for CGG is only apparent when  $T_o$  is  $\geq 10$  °C. This discrepancy suggests that  $T_o$  may bias among-population comparisons of temperature-corrected growth rates such that CGG is observed under some  $T_o$  but not others.

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**Table 1.** A summary of published  $T_o$  values used in comparative growth studies of freshwater fishes over a thermal gradient (i.e., ADD<sub>5</sub> range).

Scientific name	Common name	Location(s)	$T_o$ (°C)	Temperature medium	Justification <sup>a</sup>	ADD <sub>5</sub> range (°C-days)	Reference
<i>Acipenser fulvescens</i>	Lake sturgeon	Canada (Man., Ont., Que., Sask.), USA (Wis.)	5	Air	1	650–2250	Power and McKinley 1997
<i>Esox lucius</i>	Northern pike	Minnesota	10	Air	2	550–4010 <sup>c</sup>	Jacobson 1992
		North America and Eurasia	10	Air	3	1120–2730 <sup>d</sup>	Rypel 2012b
<i>Ictalurus punctatus</i>	Channel catfish	Illinois	10	Air	2	4080–6080 <sup>c</sup>	Shoup et al. 2007
<i>Lepisosteus oculatus</i>	Spotted gar	USA (Ala., Ark., Ill., Ky., La., Mich., Miss., Tex.)	18	Air	1	2240–7570 <sup>e</sup>	David 2012
<i>Lepomis macrochirus</i>	Bluegill	Illinois	10	Air	2	4080–6080 <sup>c</sup>	Shoup et al. 2007
<i>Micropterus dolomieu</i>	Smallmouth bass	Canada and USA	10	Air	4	1160–4660 <sup>c</sup>	Beamesderfer and North 1995
		Canada and USA	10	Air	4	1640–3950 <sup>d</sup>	Dunlop and Shuter 2006
<i>Micropterus salmoides</i>	Largemouth bass	Canada and USA	10	Air	4	1160–4660 <sup>c</sup>	Beamesderfer and North 1995
		Illinois	10	Air	2	4080–6080 <sup>c</sup>	Shoup et al. 2007
		Canada and USA	10	Air	5	1030–7510 <sup>e</sup>	McCauley and Kilgour 1990
<i>Morone saxatilis</i>	Striped bass	Eastern USA and eastern Canada	10	Air	3	1400–5420 <sup>c</sup>	Rypel 2012a
<i>Oncorhynchus clarkii</i>	Cutthroat trout	North Central Colorado	0 <sup>b</sup>	Air	2	900–1010 <sup>c</sup>	Coleman and Fausch 2007
<i>Perca flavescens</i>	Yellow perch	Alberta	0 <sup>b</sup>	Water	2	1020–1120 <sup>c</sup>	Abbey and Mackay 1991
		Ontario	10	Air	1	1030–2330 <sup>c</sup>	Chong 2000
		Ontario	0 <sup>b</sup>	Water	2	660–1910 <sup>c</sup>	Post and McQueen 1994
		Alberta, Manitoba, and Saskatchewan	13.5	Water	6	1050–1710	Power and van den Heuvel 1999
		Ontario	5	Air	2	1160–2070	Purchase et al. 2005
		Ontario	5	Water	7	1160–2070	Rennie et al. 2010
<i>Phoxinus phoxinus</i>	Eurasian minnow	Southern England and Central Finland	5	Air	3	470–710	Mills 1988
<i>Pomoxis nigromaculatus</i>	Black crappie	Southern Minnesota	15.5	Air	8	2630–3500 <sup>e</sup>	McInerney and Cross 1999
<i>Richardsonius balteatus</i>	Redside shiner	Utah, Idaho, Wyoming	8	Air	1	1670–3400 <sup>c</sup>	Houston and Belk 2006
<i>Salvelinus alpinus</i>	Arctic char	Canada and northeastern USA	0	Air	1	30–1960 <sup>d</sup>	Chavarie et al. 2010
<i>Sander vitreus</i>	Walleye	Canada and USA	5	Air	2	970–5680 <sup>c</sup>	Colby and Nepszy 1981
		Canada and USA	5	Air	2	1000–4500	Bozek et al. 2011
		Wisconsin	0	Air	8	1140–1920 <sup>c</sup>	Sass and Kitchell 2005
		Ontario and Quebec	5	Air	1	1200–2300	Venturelli et al. 2010
Multiple species	Multiple species	Michigan	10	Air	3	1420–3120 <sup>d</sup>	Wagner et al. 2007

<sup>a</sup>1 = minimum temperature for physiological process, 2 = none given, 3 = commonly used in plant studies, 4 = cites McCauley and Kilgour (1990), 5 = fit a growth model (e.g., bioenergetics model), 6 = used for European perch (Le Cren 1958), 7 = cites Purchase et al. (2005), 8 = used for Atlantic salmon (*Salmo salar*) egg survival (Ketola et al. 2000).

<sup>b</sup> $T_o$  not reported; assumed to be 0 °C.

<sup>c</sup>ADD<sub>5</sub> estimated using eq. 5 in Chezick et al. (2014).

<sup>d</sup>Not given in original literature. Estimated using the 1971–2000 climate normal from the most northern and southern locations. Normals were collected from the National Climate Data and Information Archive distributed by Environment Canada and the NOAA National Climatic Data Center.

<sup>e</sup>ADD<sub>5</sub> estimated using eq. 5 in Chezick et al. (2014) but beyond the  $T_o$  limit for conversion to  $T_5$ .

If  $T_o$  can exaggerate differences in temperature-corrected growth rates among populations, then  $T_o$  may have implications for studies that use DDs to describe and compare growth among populations spread over a wide thermal range (e.g., CGG; Table 1). Current methods for identifying  $T_o$  do not consider and have not accounted for any potential effect of  $T_o$  on temperature-corrected growth. In fact, many studies provide little or no justification for their use of  $T_o$ . When justification is provided, it is usually that  $T_o$  is the approximate minimum temperature associated with some physiological process (e.g., growth), which likely accounts for the variety of inter- and intraspecific  $T_o$  values in the literature (Table 1).

In this study, we demonstrate how one's choice of  $T_o$  when calculating the thermal opportunity for growth can bias conclusions as to whether CGG compensation exists. This work is a companion to Chezick et al. (2014), which describes how DDs vary with  $T_o$  and how this variation affects the ability of DDs to account for growth within a single population. Here we explore how the rela-

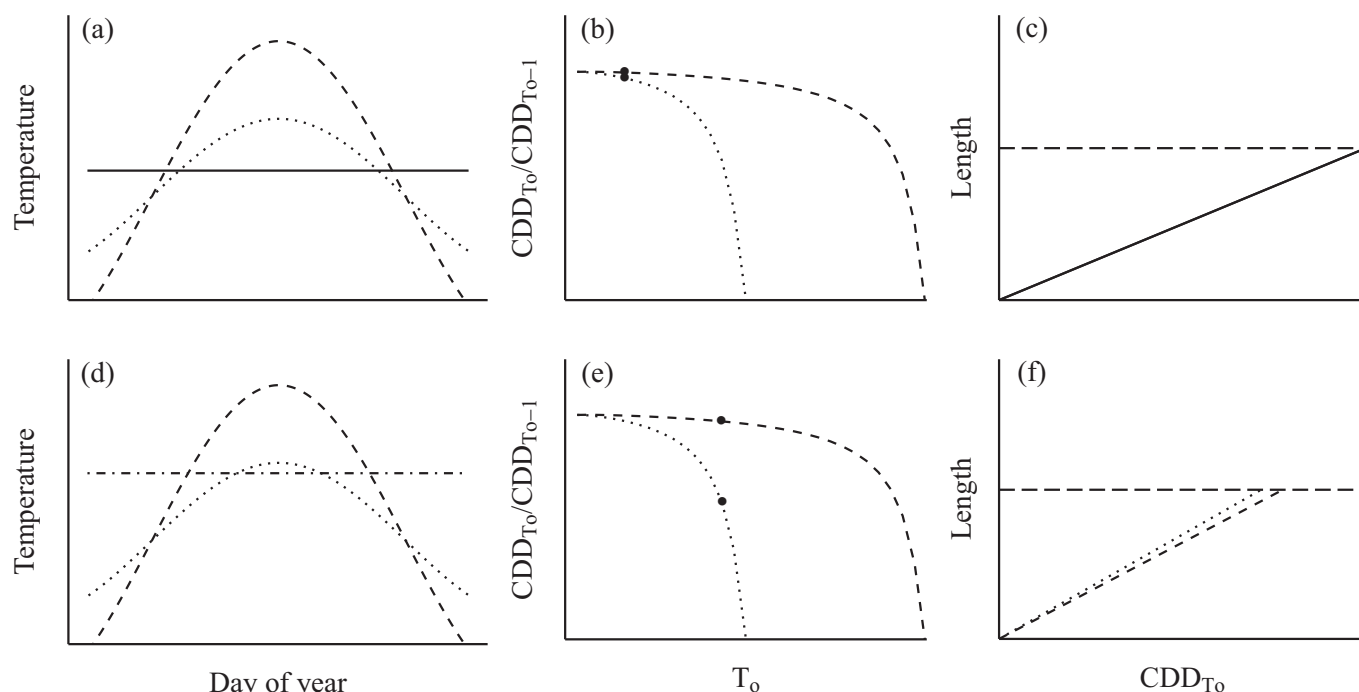
tionship between DDs and  $T_o$  varies among populations in different climates and determine how this variation affects differences in temperature-corrected growth. We explore these relationships by using both theoretical and empirical data to compare growth rates among populations that experience diverse annual temperature regimes (i.e., varied thermal distance) and for different values of  $T_o$ .

### Simulated effects of $T_o$ and thermal distance on apparent CGG

#### A simple thought experiment

To understand how our choice of  $T_o$  may bias observed differences in temperature-corrected growth rates among populations, it is helpful to first consider a simple conceptual scenario in which temperature-corrected growth rates at the thermal extremes of a species' range are identical, but appear to be different as a result of  $T_o$  (Fig. 1). We begin by imagining two annual temperature

**Fig. 1.** Depiction of a hypothetical thought experiment showing the effect of  $T_o$  on temperature-corrected growth rates in two populations from different climates. Panel (a) is the temperature curves experienced by the two populations: one in a cooler climate (dotted line) and one in a warmer climate (dashed line). The horizontal line in panel (a) (solid line) refers to the “true” base temperature ( $T_o$ ) below which fish in these populations do not grow. Panel (b) shows the proportion of cumulative degree-days (CDD; °C·days) retained at a given  $T_o$  relative to the CDD at the previous  $T_o$  for both the cool (dotted line) and warm (dashed line) populations (Chezik et al. 2014). The circles are CDD at “true”  $T_o$ . Panel (c) is the temperature-corrected growth trajectory of immature fish in these populations up to a hypothetical length at maturity (dashed line) as described by CDD at “true”  $T_o$ . Panel (d) depicts the use of an “incorrect”  $T_o$  (dot-dashed line) that is higher than the “true”  $T_o$ . Panel (e) shows the proportion of CDD retained at the “incorrect”  $T_o$  (circles) for each population, and panel (f) shows the resulting temperature-corrected growth rates when using the “incorrect”  $T_o$ . When CDD are calculated using “true”  $T_o$ , immature growth rate is the same for both populations (i.e., panel (c)). When CDD are calculated using an “incorrect”  $T_o$ , it introduces an error in CDD that is larger in the cool population than it is in the warm population. As a result of this error, the immature growth rate in the cool population (dotted line) appears to be greater than the immature growth rate in the warm population (dashed line).



curves that describe the thermal environment at these extremes. We also imagine that fish at these extremes share a growth rate ( $\text{mm} \cdot (\text{°C} \cdot \text{day})^{-1}$ ) and do not grow below some limiting temperature (i.e., “true”  $T_o$ ). If we calculate DDs at “true”  $T_o$  (Figs. 1a, 1b), fish in either environment have identical growth rates (Fig. 1c). However, if we calculate DDs assuming a  $T_o$  above “true”  $T_o$  (Fig. 1d), “true” DDs are underestimated (especially in the cooler environment; Fig. 1e), such that fish in the cooler environment appear to be growing faster (i.e.,  $\text{mm} \cdot (\text{°C} \cdot \text{day})^{-1}$  is greater).

In our thought experiment, the apparent difference in growth rate at  $T_o > \text{“true” } T_o$  stems from differences in annual temperature curves in the cooler and warmer environments. In both environments, “true” DDs are underestimated at high  $T_o$  because DDs decrease with increasing  $T_o$ . As the number of DDs decrease, growth rates ( $\text{mm} \cdot (\text{°C} \cdot \text{day})^{-1}$ ) increase because growth remains constant. However, this effect is exaggerated in the cooler environment because DDs in cooler environments decrease with increasing  $T_o$  more rapidly than in warmer environments (Fig. 1e). Therefore, because  $T_o$  in our thought experiment is greater than “true”  $T_o$ , fish in the cooler environment appear to grow faster than fish in the warmer environment. This thought experiment suggests that  $T_o$  can influence our interpretation of temperature-corrected growth rates among populations that are thermally dissimilar.

### Simulation framework

To build on the thought experiment in Fig. 1, we simulated data from numerous populations across a hypothetical species range

to determine how temperature-corrected growth rates might vary both with  $T_o$  and the degree of thermal distance among populations. The populations in these simulations experienced different mean annual temperatures, but shared (i) a maximum annual air temperature of 35 °C, (ii) a growth rate of  $0.03 \text{ mm} \cdot (\text{°C} \cdot \text{day})^{-1}$  based on  $T_o = 10 \text{ °C}$ , and (iii) no discernable length at hatch. We assumed growth to be well approximated by a linear function, a reasonable assumption for immature growth when described at an annual time step. This approach ignored interactions among growing season, mean annual temperature, and maximum annual temperature in favor of a simplified model for exploring how among-population differences in the availability of thermal energy affect temperature-corrected growth. We used a sine curve (Arnold 1959) to generate annual temperature cycles for each population and then calculated annual degree-days for a range of  $T_o$  ( $\text{ADD}_{T_o}$ ; °C·days) by integrating the area under each curve (Baskerville and Emin 1969; Chezik et al. 2014). We then predicted length-at-age as

$$(1) \quad \hat{L} = \frac{dl}{d\text{DD}_{10}} \cdot [(\text{ADD}_{10} \cdot \text{Age}) + \text{ADD}_{10}]$$

where,  $\frac{dl}{d\text{DD}_{10}}$  is the change in length per DD at a  $T_o$  of 10 °C (i.e.,  $0.03 \text{ mm} \cdot (\text{°C} \cdot \text{day})^{-1}$ ), Age is age in years assuming a common birth-day of 1 January, and  $\text{ADD}_{10}$  is the annual degree-days experienced at a  $T_o$  of 10 °C. This process resulted in each simulation being

made up of thermally unique populations that shared a common temperature-corrected growth rate.

### Simulated effect of $T_o$ on apparent CCG

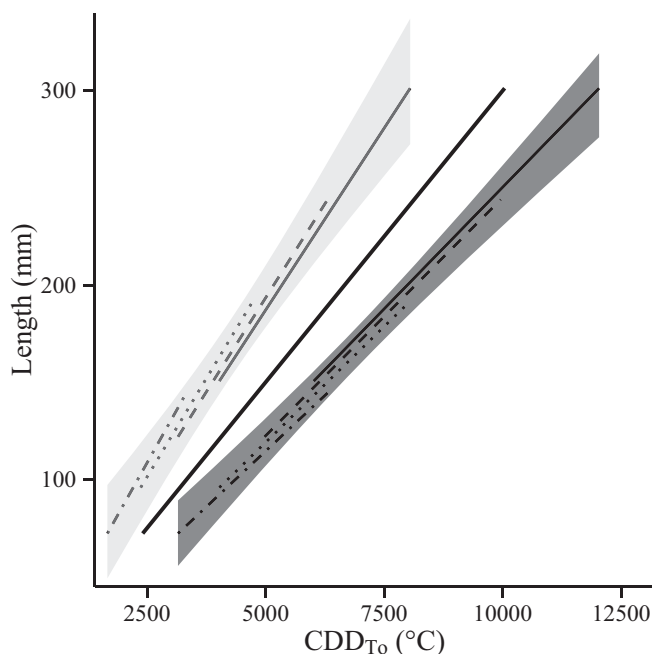
To simulate the effect of  $T_o$  on temperature-corrected growth, we imagined three studies that compared growth in four populations spread over a large thermal range. These four populations experienced mean annual temperatures of 0, 5, 10, and 15 °C. The three studies were identical except that each used a different threshold (i.e.,  $T_o$ ) to calculate DDs (5, 10, and 15 °C). Our simulation results showed that the study that assumed a threshold of 10 °C would have concluded that all populations shared the same growth rate, but that the other studies would have concluded that growth rates either increased ( $T_o = 15$  °C) or decreased ( $T_o = 5$  °C) among populations by mean annual temperature (Fig. 2). Because growth in our simulation began at 10 °C (i.e., “true”  $T_o = 10$  °C), apparent differences in growth were entirely an artifact of incorrectly assigning  $T_o$ . As in our simple thought experiment, these artifacts stem from the interaction between an incorrect  $T_o$  and among-population differences in annual temperature. Specifically, an incorrect  $T_o$  biases DD calculations for all populations, but this bias is smallest in the warmest population and largest in the coolest population. These DD differences translate into apparent differences in the rate at which fish grow in different thermal environments.

### Simulated effect of both $T_o$ and thermal distance on apparent CCG

Given that temperature-corrected growth rates depend on  $T_o$  and among-population differences in annual temperature (Fig. 2), it stands to reason that the effect of an incorrect  $T_o$  on temperature-corrected growth also increases with among-population difference in mean annual temperature. To test this hypothesis, we first created 200 populations with mean annual temperatures that were uniformly spread over a narrow thermal range (8.4–11.6 °C). Each temperature curve was approximated by a sine curve (Baskerville and Emin 1969; Chezik et al. 2014), and ADD values were calculated for each  $T_o$  in the range –5 to 20 °C. We used these temperature curves and eq. 1 (“true”  $T_o = 10$  °C) to generate length-at-age data for each population. We also incorporated temperature-independent variation in length-at-age by randomly sampling normal distributions centered on each calculated length-at-age, assuming a standard deviation of 0.08 mm. This standard deviation was based on observed variation in walleye (*Sander vitreus*) length-at-age (see next section) and was therefore realistic. We incorporated temperature-independent length-at-age variation because growth is rarely exclusively dependent on temperature in natural systems.

For each population, we estimated temperature-corrected growth rates by regressing length onto cumulative degree-days (CDD; °C-days) (i.e., the summation of all experienced ADD <sub>$T_o$</sub> ) at each  $T_o$  value. We then identified the  $T_o$  that minimized the coefficient of variation (CV) in growth rates among populations. Our rationale for using the CV was that whereas temperature-corrected growth rates at “true”  $T_o$  are identical in deterministic simulations (Fig. 2), growth rates at “true”  $T_o$  are likely to be most similar in stochastic simulations. However, because variation in length-at-age can result in the CV being minimized at a  $T_o$  other than “true”  $T_o$ , we allowed the CV method to identify negative  $T_o$  values that are typically biologically irrelevant (Yang et al. 1995; Legg et al. 1998). To determine the distribution of  $T_o$  values at which the CV was likely to be minimized, we generated length-at-age data 1000 times for each population and for each iteration determined the  $T_o$  at which CV was minimized. We then repeated this entire process for 200 simulated populations that had mean annual temperatures spread uniformly between 3.9 and 16.1 °C. The result was two distributions of  $T_o$  values at which the CV of temperature-

**Fig. 2.** Relationship between length and cumulative degree-days at  $T_o$  values of 5 °C (dark grey), 10 °C (solid line), and 15 °C (light grey) for four hypothetical populations that experience mean annual temperatures of 0 °C (dot-dashed line), 5 °C (dotted line), 10 °C (dashed line), and 15 °C (solid line). At  $T_{10}$  (“true”  $T_o$ ), all populations share the same slope (i.e., temperature-corrected growth rate). At  $T_5$  and  $T_{15}$ , each population has a unique slope. Populations appear to grow more quickly when assigned  $T_o > \text{“true” } T_o$  and more slowly when assigned  $T_o < \text{“true” } T_o$ . These biases are smallest in the warmest population and largest in the coldest population.



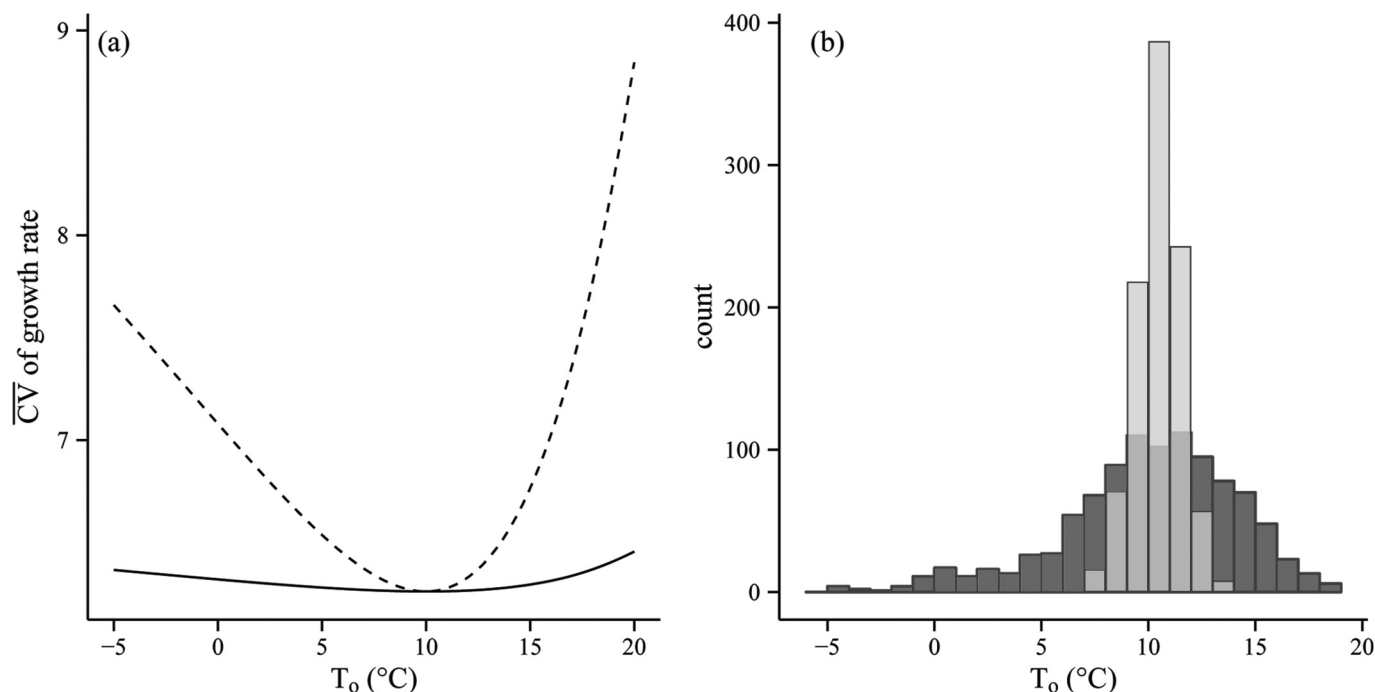
corrected growth was minimized: one for a wide thermal range and one for a narrow thermal range.

These stochastic simulations show that, on average, CV was minimized when  $T_o$  was equal to “true”  $T_o$  (Fig. 3a). This relationship was especially pronounced for the populations spread over a large thermal range. The large thermal range also resulted in a much narrower distribution of  $T_o$  values over which CV was minimized (Fig. 3b). This inverse relationship between among-population thermal range and the width of the  $T_o$  distribution resulted from the relative importance of among-population thermal variation and variation in length-at-age. When populations were distributed over a small thermal range, among-population variation in growth was primarily a result of stochastic variation in length-at-age such that the CV was minimized over a wide range of positive and negative  $T_o$  values. When populations were distributed over a large thermal range, among-population variation in growth was primarily a result of differences in mean annual temperature such that the CV was minimized at only a few positive  $T_o$  values.

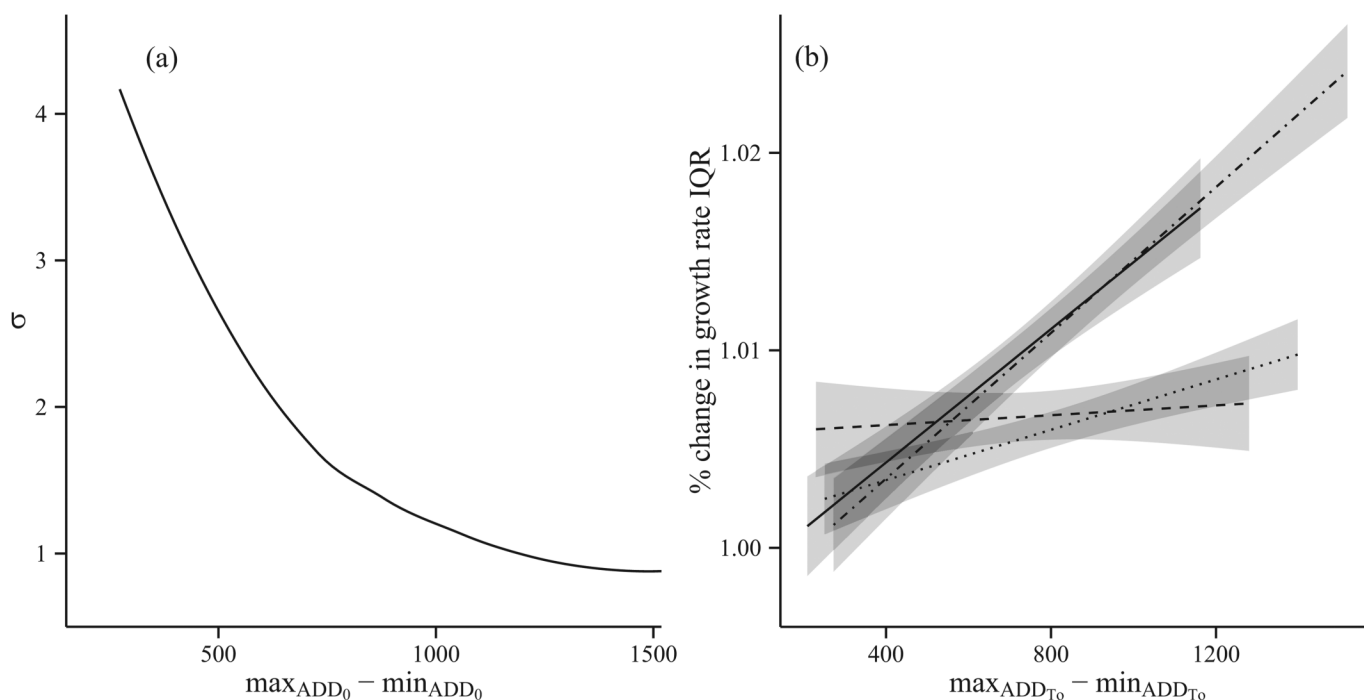
Finally, we created 39 additional thermal ranges that had a median annual temperature of 10 °C and were uniformly distributed in width between the narrowest thermal range (8.56–11.44 °C) and the widest thermal range (2–18 °C). As described above, each thermal range contained 200 populations, and length-at-age in each population was randomly generated 1000 times. When growth was simulated in this way, we found that as thermal range increased, there was a rapid decrease in the distribution of  $T_o$  values at which CV was minimized (Fig. 4a) and a gradual increase in the effect of  $T_o$  on temperature-corrected growth (Fig. 4b). Figure 4b shows clearly that increased differences in growth rates over a wide thermal range were the result of a bias that was



**Fig. 3.** Results of 1000  $T_o$  identification simulations over a small thermal range (8.4–11.6 °C,  $\Delta\text{ADD}_0 = 300$ , solid line) and a large thermal range (3.9–16.1 °C,  $\Delta\text{ADD}_0 = 1150$ , dashed line). Panel (a) shows the mean among-population coefficient of variation (CV) in temperature-corrected growth rate at each  $T_o$  over both thermal ranges. Panel (b) shows the distribution of  $T_o$  at which the CV of growth was minimized for both thermal ranges (represented by shades of grey: darker grey = small thermal range, lighter grey = large thermal range).



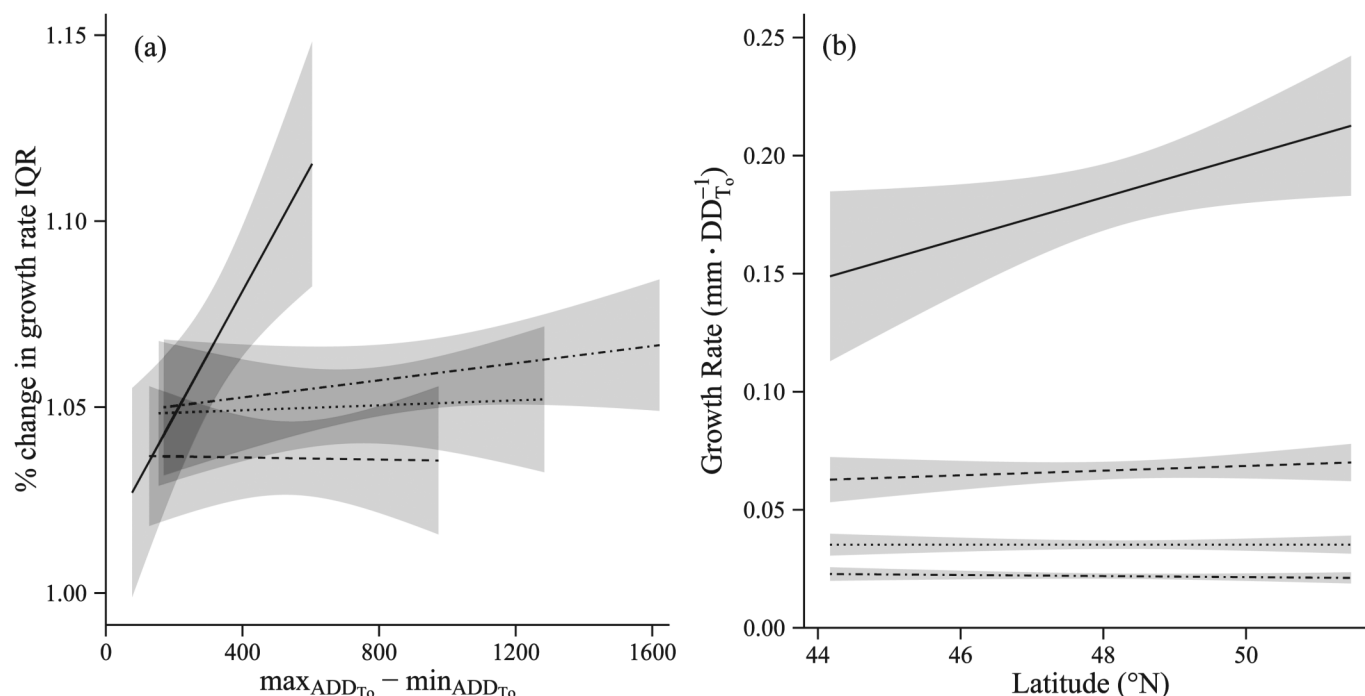
**Fig. 4.** Simulation results along a continuum of thermal ranges. Panel (a) shows how the standard deviation ( $\sigma$ ) of 1000  $T_o$  estimates change with increasing thermal range. Thermal range is described by ADD values at  $T_o = 0$  °C but results were the same for all  $T_o$ . Panel (b) shows how the growth rate interquartile range (IQR) changes with increasing thermal range when using  $T_o$  values of 0 °C (dot-dashed line), 5 °C (dotted line), 10 °C (dashed line), and 15 °C (solid line). Shaded areas are 95% confidence intervals.



introduced by selecting an incorrect  $T_o$ . This bias increased with the magnitude of the difference between incorrect  $T_o$  and “true”  $T_o$ . The results of this simulation suggest that evidence for CGG can be a result of  $T_o$  rather than a biological phenomenon.

For instance, in this simulation, using a  $T_o = 15$  °C rather than the “true” value of 10 °C inflated the among-population differences in temperature-corrected growth rates by 2.4% over a thermal range of 1115 °C·days ( $T_o = 15$  °C).

**Fig. 5.** Temperature-corrected growth rates as a function of thermal difference (a) and latitude (b) among walleye populations in Minnesota and Ontario. Panel (a) shows how the growth rate interquartile range (IQR) changes with thermal difference among populations when using  $T_o$  values of 0 °C (dot-dashed line), 5 °C (dotted line), 10 °C (dashed line), and 15 °C (solid line). Panel (b) shows how the temperature-corrected growth rates change with latitude given the same  $T_o$  values. Shaded areas are 95% confidence intervals.



### Observed effects of $T_o$ and thermal distance on apparent CGG

Although our simulations show that an incorrect threshold (i.e.,  $T_o$ ) can artificially generate among-population differences in temperature-corrected growth rate, especially when populations are distributed over a large thermal range, unknown is the extent to which this effect is observable in nature. To determine if apparent CGG is sensitive to  $T_o$  and thermal distance, we analyzed immature length-at-age and air temperature data from 81 water bodies throughout Minnesota, USA, and Ontario, Canada.

### Data

See [Chezik et al. \(2014\)](#) for a detailed description of the data that we used in this study. In brief, walleye were collected by the Minnesota Department of Natural Resources (2001–2011) and the Ontario Ministry of Natural Resources (1993–2008). Fish records included water body, sample date (day, month, year), age (years), total length ( $L$ ; mm), and maturity. For water bodies in Minnesota, air temperature data ( $T_{\max}$  and  $T_{\min}$ ) were kriging-interpolated to the centroid of each lake. DDs were calculated at a range of  $T_o$  (0, 5, 10, and 15 °C), and positive values were summed to produce annual degree-days ( $ADD_{T_o}$ ) for each year of interest. For water bodies in Ontario,  $ADD_{T_o}$  values were obtained using the Historic Climate Analysis Tool ([Cross et al. 2012](#)). We assigned  $CDD_{T_o}$  values to each fish by summing water-body-specific ADDs experienced prior to capture.

### Methods

Our analysis of observed length-at-age data was similar to our analysis of simulated length-at-age data that included variation in both  $T_o$  and thermal distance. For each water body, we regressed mean length-at-age onto CDDs that were estimated for each assigned value of  $T_o$  and determined growth rates (mm · (°C · day) $^{-1}$ ) using ordinary least squares. We used a simple linear model because linear immature growth is predicted by theory ([Shuter et al. 2005](#)) and was observed in this dataset ([Chezik et al. 2014](#)). We

then defined 17 unique thermal ranges, each containing  $\geq 15$  water bodies. To define these thermal ranges, we first determined the thermal character of each water body by (i) identifying all unique years experienced by the cohorts in a given water body and (ii) calculating mean  $ADD_o$  across these years. We then identified the 15 water bodies that had mean  $ADD_o$  values that were closest to the median  $ADD_o$  (2645 °C · days) across all water bodies in the dataset. This step established a narrow thermal range (2550–2720 °C · days) that included a “thermal group” of 15 water bodies. We began with 15 water bodies to ensure a large enough sample to meet the needs of all statistical methods. We then increased the thermal limits of the initial range in increments of 100 °C · days. Additional thermal groups were identified as the number of included water bodies increased. This process resulted in 17 thermal ranges, the largest of which spanned from 2090 to 3710 °C · days at  $T_o$  of 0 °C and included all water bodies. This procedure was nearly identical to that of our thermal distance and  $T_o$  error simulation, except that the number of water bodies (i.e., growth rates) in each thermal group was variable and water bodies were unevenly distributed within each thermal range.

### Results

Our results show that the difference in growth rate between the first and third quartiles was only related to among-water-body thermal distance ([Fig. 5a](#)) and latitude ([Fig. 5b](#)) when  $T_o$  was 15 °C. Furthermore, the difference in the growth rate interquartile range was as much as 0.12 mm · (°C · day) $^{-1}$  higher than the smallest thermal group. When all lakes were included in the analysis, variation in among-population growth rates was minimized at a  $T_o$  of 3 °C.

### Discussion

Our results show that the effect of  $T_o$  on temperature-corrected growth rates varies with the degree of  $T_o$  error and thermal range among water bodies ([Fig. 4](#)) and that these effects are observable

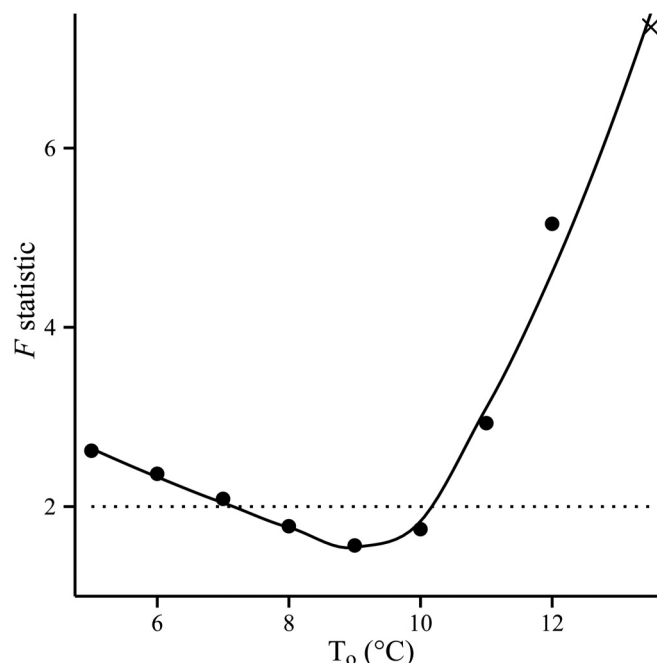
in empirical data (Fig. 5). The apparent variability in temperature-corrected growth rate increased as assigned  $T_o$  deviated from the  $T_o$  that minimizes the among-water-body variation in temperature-corrected growth rate (presumably “true”  $T_o$ ), and this effect became more pronounced as the thermal range among water bodies increased. For instance, we found that variation in the temperature-corrected growth rates of immature walleye increased with thermal range when  $T_o$  was 15 °C but not when  $T_o$  was 0, 5, or 10 °C. This result suggests that a study that used a  $T_o = 15$  °C to correct growth rates of populations living in different climates would have concluded that walleye are latitudinally adapted to differences in temperature and exhibit CGG. Given the results of our simulation (Fig. 4b) and the absence of CGG at lower thresholds (i.e.,  $T_o = 0, 5, 10$  °C; Fig. 5), it is possible that this conclusion would be false.

Although the  $T_o$  that minimized the CV in growth rates among populations does not provide evidence for CGG in walleye, this does not suggest that walleye are not locally adapted to temperature. It is possible that local adaption exists (e.g., Zhao et al. 2008) but is simply obscured by temperature-independent variability in growth. For instance,  $T_o$  (and growth–temperature curves in general) may be locally adapted but so similar among populations that the CGG signal is obscured by local density-dependent, food web, or stochastic processes (e.g., measurement error), especially when thermal distances are short. Given that our empirical analysis was limited to Minnesota and Ontario, it is possible that walleye exhibit CGG over their full range (Bozek et al. 2011). Overall, our analyses suggest that it is possible to falsely detect CGG and that care must be taken to select an appropriate temperature threshold.

The effect of assigned  $T_o$  on temperature-corrected growth rates is greater when assigned  $T_o$  is overestimated than when assigned  $T_o$  is underestimated (Fig. 3a). In our simulations, the effect of  $T_o$  on temperature-corrected growth stemmed from both error in  $T_o$  and among-water-body differences in temperature curves. When both of these conditions were met, they resulted in water-body-specific biases in temperature-corrected growth. However, because ADDs become more similar as  $T_o$  decreases (Chezik et al. 2014), biases in DDs, and therefore the bias in temperature-corrected growth, were larger when  $T_o$  was overestimated than when  $T_o$  was underestimated by the same degree.

Given that the effect of assigned  $T_o$  on temperature-corrected growth rates is greater when assigned  $T_o$  is larger than “true”  $T_o$ , a risk-averse strategy is to err low when selecting a  $T_o$  for an among-population study. This strategy will reduce the risk of introducing bias that may otherwise result when simply relying on precedent or convention. For example, Power and van den Heuvel (1999) compared the growth of yellow perch in northern Alberta to a population in southern Manitoba using a  $T_o$  of 13.5 °C. This  $T_o$  is routinely used to describe European perch (*Perca fluviatilis*) growth in Lake Windermere (Le Cren 1958), but may be sufficiently high to introduce a bias when comparing growth in populations spread over a wide thermal range ( $\Delta\text{ADD}_0 \sim 1060$  °C-days). To test for such a bias, we repeated the Power and van den Heuvel (1999) analysis for a range of  $T_o$  values (5–12 °C and 13.5 °C). Our results show that the difference between temperature-corrected growth models (i.e., temperature-corrected growth rates) is greatest at 13.5 °C and statistically insignificant when  $T_o$  is 8, 9, or 10 °C (Fig. 6). Power and van den Heuvel (1999) attributed the evidence for CGG at  $T_o = 13.5$  °C to “latitudinal or trophic factors”; however, our re-analysis suggests that this evidence is either exaggerated or solely a result of an incorrect threshold when correcting for temperature. Although Power and van den Heuvel (1999) may be an example of  $T_o$  detecting growth differences when none exist, it is encouraging that many comparative growth studies tend to use low values of  $T_o$  that are less prone to artificially inflating temperature-corrected growth rates (Table 1). However, we suspect that 18 °C (the minimum temperature for growth of larval

Fig. 6. The effect of  $T_o$  on significance (Chow test) when comparing growth model coefficient estimates of yellow perch in northern Alberta, Canada (three populations), with West Blue Lake in southern Manitoba, Canada. Fish and temperature data for West Blue Lake were obtained from Wong (1972), and data from northern Alberta were digitized from Power and van den Heuvel (1999). Missing temperature data from Sucker Lake were predicted using data from Kimowin Lake. The trend line (solid) is via a LOESS smoother ( $\alpha = 0.85$ ), and the horizontal line (dotted) indicates the significance threshold. This re-analysis of Power and van den Heuvel (1999) shows that a significant difference in growth is detected at  $T_o > 10$  °C and  $< 8$  °C and that these differences are more likely to be detected at high  $T_o$ . The original  $T_o$  used in Power and van den Heuvel (1999) was 13.5 °C (x).

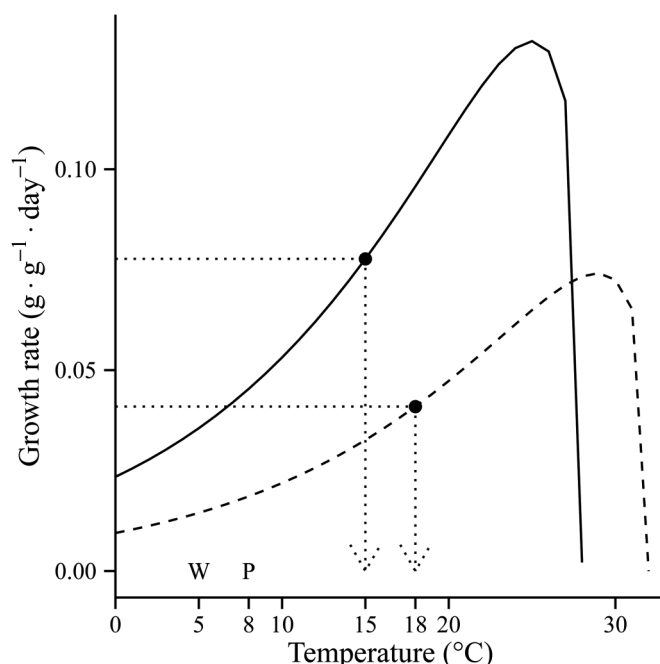


gar, *Lepidosteus oculatus*) is too high for comparing growth of individuals age 0–16 over 2240–7570 ADD<sub>5</sub> (David 2012).

If error in threshold assignment can bias among-population growth studies, especially when populations are spread over a wide thermal range, it follows that threshold assignment should be done with care. Unfortunately, many  $T_o$  values currently in use are rarely justified (Table 1) and others may bias results and conclusions (e.g., Power and van den Heuvel 1999). Our results suggest that  $T_o$  can be estimated as the  $T_o$  that minimizes the CV in growth rate among populations spread over a large thermal range; however, data may not be available to perform such an analysis. Similarly, although there are methods for estimating  $T_o$  in single populations, results often vary among methods and populations (reviewed by Chezik et al. 2014).

A relatively simple approach of estimating  $T_o$  is to determine the mean developmental temperature and subtract 10 °C (Charnov and Gillooly 2003). In the context of our study, the mean developmental temperature is the temperature associated with the mean growth rate experienced over a range of biologically valid temperatures. To demonstrate this approach, we used the Wisconsin Bioenergetics model (Hanson et al. 1997) to describe how walleye and yellow perch growth change with temperature when food is not limiting (Fig. 7). This model suggests that mean developmental temperature in walleye and yellow perch occurs at 15 and 18 °C, respectively. Therefore, the “10 °C rule” predicts that  $T_o$  is 5 and 8 °C, respectively. These results are consistent with our analysis of walleye data (among-water-body variation in growth minimized

**Fig. 7.** Application of the “10 °C rule” for estimating  $T_0$  (Charnov and Gillooly 2003) to growth rates of juvenile walleye (solid line) and yellow perch (dashed line) as predicted by the Wisconsin Bioenergetics model (Hanson et al. 1997), assuming ad libitum feeding. Dots are mean developmental temperatures (15 and 18 °C for walleye and yellow perch, respectively), and letters (W and P) are estimated  $T_0$  values (5 and 8 °C, respectively). Mean developmental temperatures were identified by averaging each species maximum and minimum growth rate and identifying the temperature that governs these values (dotted lines and arrows).



at 3 °C) and with our re-analysis of yellow perch data (among-water-body variation in growth minimized at 9 °C). Although this approach needs to be explored further, it does show promise as a means of assigning a species to one of the  $T_0$  standards (0, 5, 10, and 15 °C) advocated by Chezik et al. (2014). Assigning species to a standard  $T_0$  (e.g., 5 °C for walleye and 10 °C for yellow perch) is important because it minimizes the risk of using  $T_0$  values that bias growth rate comparisons, simplifies comparisons among datasets and studies, and facilitates the use of DDs in future studies.

Ideally, CGG should be assessed in common-garden experiments, but opportunities to conduct such experiments are constrained by time and cost. A common substitute is to compare temperature-corrected growth rates via readily available field data. In this study, we have shown that an incorrect  $T_0$  can bias growth comparisons among water bodies. This bias leads to apparent differences in growth rates among populations that are solely an artifact of  $T_0$ . This effect of  $T_0$  on temperature-corrected growth is exaggerated by large thermal differences among water bodies. Because these thermal differences are predominately observed over a latitudinal gradient, an incorrect  $T_0$  can result in the appearance of CGG. To minimize the risk of introduced bias, we suggest first estimating  $T_0$  (e.g., via the minimum CV method or “10 °C rule”) and then setting  $T_0$  to the nearest standard value proposed by Chezik et al. (2014). Doing so will limit the introduction of a bias that may enhance differences among populations and both simplify and encourage the use of DDs in future studies.

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