

# Bioenergetic and limnological foundations for using degree-days derived from air temperatures to describe fish growth

Andrew E. Honsey, Paul A. Venturelli, and Nigel P. Lester

**Abstract:** Degree-days (DD) are an effective metric for quantifying the thermal opportunity for ectotherm growth. There is strong empirical evidence to suggest that DD are useful for describing fish growth and that immature growth increases linearly with DD. However, fish ecology lags behind other disciplines in the widespread adoption of DD. We provide (1) a foundation for the observed linear relationship between immature fish growth and DD and (2) justification for using DD derived from air temperatures as a proxy for DD derived from water temperatures in fish science. We use bioenergetics models and both simulated and empirical water temperatures to show that immature annual and interannual fish growth are approximately linear with water DD. We then use simulated and empirical data to show that air and surface water temperatures are often highly correlated and that immature fish growth is also approximately linear with air DD. By connecting the dots among air temperature, water temperature, and fish growth, we lay the foundation for wider adoption of DD in fish science.

**Résumé :** Les degrés-jours (DJ) constituent un paramètre utile pour quantifier l'opportunité thermique de la croissance d'ectothermes. Des observations empiriques convaincantes indiquent que les DJ sont utiles pour décrire la croissance des poissons et que la croissance des poissons immatures est reliée linéairement aux DJ. Le domaine de l'écologie des poissons est toutefois à la traîne d'autres disciplines en ce qui concerne l'adoption de l'utilisation des DJ. Nous présentons (1) les bases de la relation linéaire observée entre la croissance des poissons immatures et les DJ et (2) une justification de l'utilisation en sciences halieutiques de DJ obtenus à partir des températures de l'air comme variable substitutive des DJ tirés de la température de l'eau. Nous utilisons des modèles bioénergétiques et des températures de l'eau simulées et empiriques pour démontrer que les croissances annuelle et interannuelle de poissons immatures sont reliées de manière approximativement linéaire aux DJ de l'eau. Nous utilisons ensuite des données simulées et empiriques pour démontrer que les températures de l'air et de la surface de l'eau sont souvent fortement corrélées, et que la croissance des poissons immatures est aussi corrélée de manière approximativement linéaire avec les DJ de l'air. En établissant les liens entre la température de l'air, la température de l'eau et la croissance des poissons, nous jetons les bases de l'adoption plus large des DJ en sciences halieutiques. [Traduit par la Rédaction]

## Introduction

There is an obvious link between ambient temperatures and physiological processes in ectotherms (Hazel and Prosser 1974; Atkinson 1994; van der Have and de Jong 1996). Less obvious is how one should measure temperature to best understand its influence on ectotherm growth and other metabolic processes. Instantaneous metrics (e.g., mean temperatures over a given time period; Pauly 1980; Doubleday et al. 2015) are often used to explain ectotherm growth. These metrics are easy to calculate but may not adequately index the effect of temperature on ectotherm growth and metabolism (Neuheimer and Taggart 2007).

Degree-days (DD) are a summation of the metabolically relevant thermal energy that is experienced by an individual over time. As such, DD are a useful index of the thermal scope for ectotherm growth (Chezik et al. 2014a). Other fields (e.g., agronomy, entomology) have used DD extensively for decades to centuries (Neuheimer and Taggart 2007), and DD have been shown to outperform calendar time in describing ectotherm growth (e.g., Colby and Nepszy 1981). Moreover, because DD integrate time and temperature, they provide a physiologically valid understanding

of how growth responds to temperature that can be particularly useful when comparing growth rates among populations (e.g., for studies of countergradient variation in growth: Chezik et al. 2014b; Snover et al. 2015).

The application of DD in fish science has become increasingly common, as has the use of DD derived from air temperatures as a surrogate for DD calculated from water temperatures (e.g., Fig. 1.1 in Chezik 2013). In particular, DD have been shown to be useful for describing fish growth, with multiple empirical studies finding strong linear relationships between DD and immature fish growth (e.g., Neuheimer and Taggart 2007; Venturelli et al. 2010; Chezik et al. 2014a). Although fish culturists have used DD for many decades (e.g., Wallich 1901; Soderberg 1992; Dumas et al. 2010), other fish sciences, such as fish ecology, have yet to adopt DD in a widespread manner. Likely reasons for this lack of widespread adoption include the relative scarcity of high-resolution water temperature data compared to air temperature data and insufficient evidence to suggest that DD calculated from air temperatures can serve as an accurate proxy for DD derived from water temperatures. Moreover, researchers who are familiar with

Received 10 February 2018. Accepted 27 June 2018.

A.E. Honsey. Ecology, Evolution, and Behavior Graduate Program, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA.

P.A. Venturelli.\* Department of Biology, Ball State University, 121 Cooper Life Science Building, Muncie, IN 47306, USA.

N.P. Lester.† Science and Research Branch, Ontario Ministry of Natural Resources and Forestry, Peterborough, ON K9J7B8, Canada.

**Corresponding author:** Andrew E. Honsey (email: [honse018@umn.edu](mailto:honse018@umn.edu)).

\*Paul A. Venturelli currently serves as an Associate Editor; peer review and editorial decisions regarding this manuscript were handled by Charles Ramcharan.

†Retired.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.rightslink.com).

**Table 1.** Bioenergetics equations and parameters used for simulation.

Model component	Model species		
	Yellow perch ( <i>Perca flavescens</i> ) <sup>a</sup>	Brown bullhead ( <i>Ameiurus nebulosus</i> ) <sup>b</sup>	Tiger muskellunge ( <i>Esox lucius</i> × <i>Esox masquinongy</i> ) <sup>c</sup>
Consumption equation	2	3	2
CA	0.25	0.12	0.2215
CB	-0.27	-0.225	-0.18
CQ	2.3	15	2.53
CTO	29	24	26
CTM	32	26	34
CTL		30	
CK1		0.473	
CK4		0.55	
Respiration equation	2	1	1
RA	0.0108	0.0007	0.00246
RB	-0.2	-0.271	-0.18
RQ	2.1	0.0915	0.055
RTO	32	0.4055	0
RTM	35	0	0
RTL		0	0
RK1		1	0
RK4		0	0
ACT	Variable	Variable	Variable
BACT		0	0
SDA	0.172	0.172	0.14
Egestion–excretion equation	2	1	1
FA	0.158	0.2	0.13
FB	-0.222		
FG	0.631		
UA	0.0253	0.07	0.07
UB	0.58		
UG	-0.299		
Energy density equation	1	1	1
Predator energy density (J·g <sup>-1</sup> )	4186	6700	3600
Prey energy density (J·g <sup>-1</sup> )	3770 <sup>d</sup>	4392 <sup>e</sup>	3874 <sup>f</sup>

Note: All models follow the Wisconsin bioenergetics framework; see Hanson et al. (1997) for equations and details.

<sup>a</sup>Hanson et al. (1997).

<sup>b</sup>Hartman (2017).

<sup>c</sup>Schoenebeck et al. (2008).

<sup>d</sup>Approximate energy density of *Daphnia* sp. (Luecke and Brandt 1993; Tabor et al. 1996).

<sup>e</sup>Energy density of Chironomidae larvae (Myrvold and Kennedy 2015).

<sup>f</sup>Energy density of fathead minnow (*Pimephales promelas*) (Chipps et al. 2000; Schoenebeck et al. 2008).

conventional, nonlinear fish growth models (e.g., the von Bertalanffy model: von Bertalanffy 1938; Beverton and Holt 1957) may not be convinced by the evidence for linear relationships between immature fish growth and DD (e.g., Malzahn et al. 2003; Neuheimer and Taggart 2007; Chezik et al. 2014a).

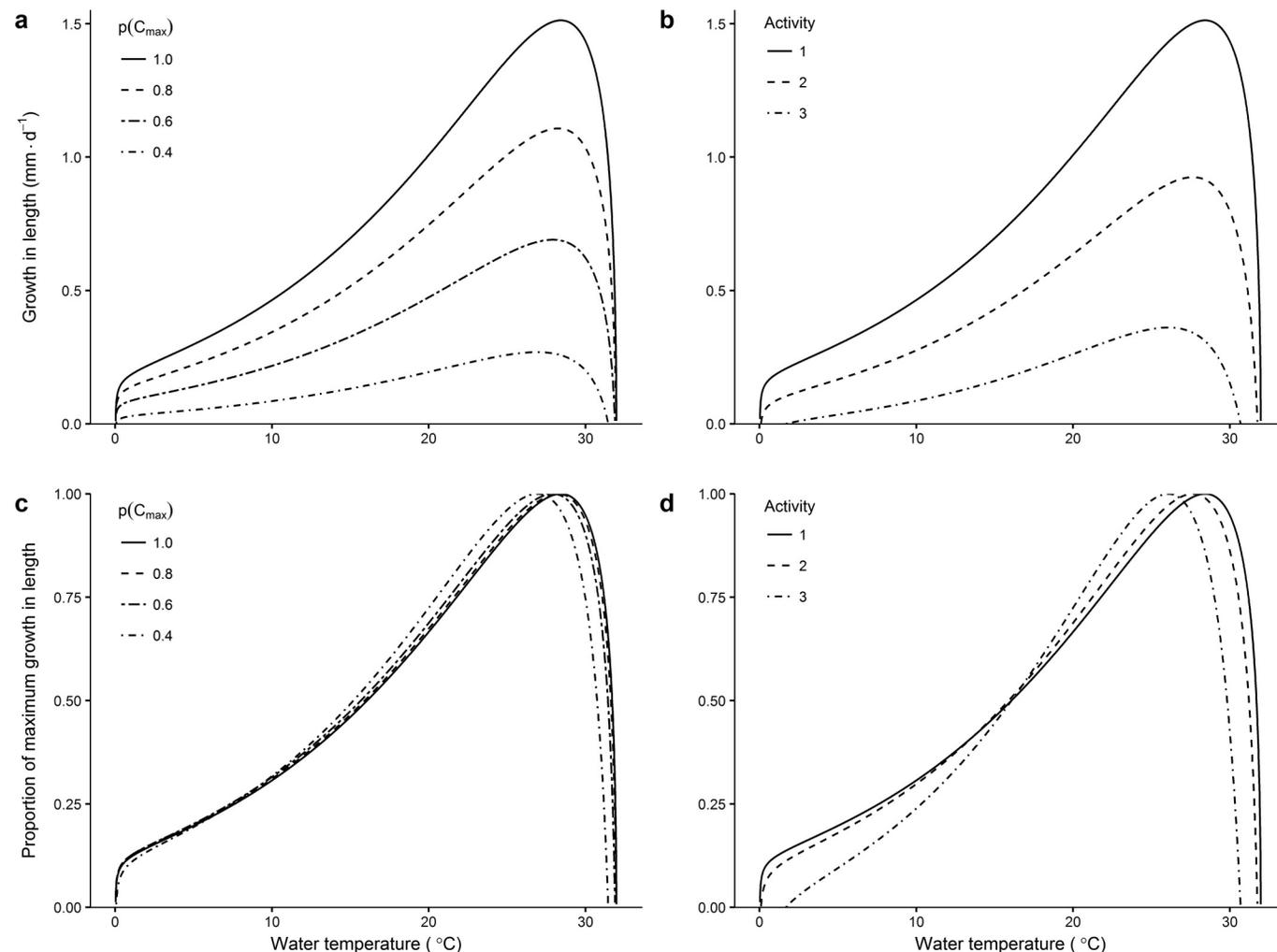
Our objectives were to provide (1) a bioenergetic foundation for the linear relationship between immature fish growth and DD that has been found in multiple empirical studies and (2) justification for using DD derived from air temperatures as a proxy for DD derived from water temperatures. To accomplish these objectives, we review existing knowledge and use simulated and empirical data to connect the dots among air temperature, water temperature, and fish growth. First, we use bioenergetics models to demonstrate the effect of water temperature on fish growth at daily, annual, and interannual time scales. We then examine the relationships between air and surface water temperatures, and we assess whether air-based DD can serve as an accurate proxy for water-based DD. Finally, we compare the performance of air- and water-based DD in describing fish growth, and we discuss the limits of using air-based DD to describe growth (e.g., for coldwater fishes in thermally stratified systems). By providing a theoretically sound and empirically supported basis for the expanded and appropriate use of DD, our analyses promote a more thorough understanding of the growth and physiology of fishes and other aquatic organisms.

## Water temperature and fish growth

In this section, we use bioenergetics models to demonstrate the effects of water temperature on fish growth (Kitchell et al. 1977; Jobling 1995; Hanson et al. 1997). Bioenergetics models are based on an energy balance equation in which the potential for growth is governed by energy acquired via consumption minus metabolism (e.g., respiration, specific dynamic action) and waste. The functions that describe these processes often depend on water temperature. As a result, growth is also temperature-dependent, and the nature of the growth–temperature relationship is shaped by species-specific parameters (e.g., optimum temperature for consumption, upper lethal water temperature: Hanson et al. 1997).

We used bioenergetics models to simulate juvenile growth for three fishes: yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*), and tiger muskellunge (northern pike (*Esox lucius*) × muskellunge (*Esox masquinongy*)). These models encompass diversity in two key areas. First, they use different combinations of model functions (i.e., equations) for the various model processes (Table 1). For instance, the brown bullhead model uses a respiration function that is exponential with temperature, whereas the respiration function used in the other two models accounts for decreased respiration rates at high temperatures. Therefore, any similarities in model results are unlikely to be driven by similar

**Fig. 1.** (a and b) The effect of temperature, activity level, and consumption (as a proportion of maximum consumption,  $p(C_{\max})$ ) on daily growth in length for yellow perch (*Perca flavescens*) based on a bioenergetics model. (c and d) Relative yellow perch growth in length (i.e., growth as a proportion of maximum growth) across levels of temperature, activity, and consumption.



functional response assumptions across model processes. Second, the thermal regimes differ for each model species, with the three models encompassing a fair amount of thermal diversity for cool- and warmwater species (thermal optima for consumption ranging from 24 to 29 °C). Parameters, equations, and sources for these models are given in Table 1. We excluded models for coldwater species because our analytical approaches assumed that the simulated fish experienced epilimnetic temperatures year-round (see below). As such, we chose models for cool- and warmwater fishes so that this assumption would likely not be meaningfully violated.

### Daily growth

We begin by showing how daily growth in length varies with water temperature across levels of prey consumption and activity (a multiplier on respiration, with 1 = resting metabolism). We did this to establish a foundation for how growth responds to these factors over short time scales, which is an important first step in understanding how growth relates to DD at broader time scales. We set initial sizes to 100 mm for yellow perch and brown bullhead and 150 mm for tiger muskellunge. We used geometric mean parameters for the length–mass relationship from FishBase

(Froese and Pauly 2016) for length–mass conversions. We set the energy density of oxygen to 13556 J·g<sup>-1</sup> here and throughout (Elliott and Davison 1975). We conducted these and all additional calculations and simulations in R version 3.4.1 (R Core Team 2017).

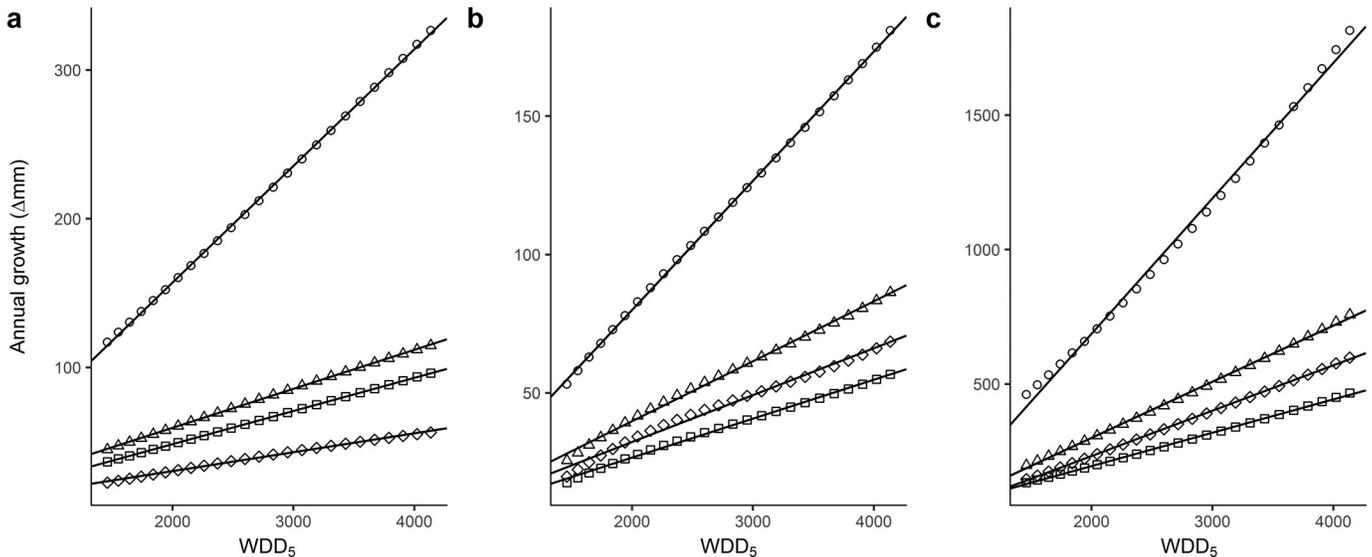
Our bioenergetics simulations produced typical results showing the nonlinear relationship between daily growth in length and temperature (Fig. 1). This relationship is positive for most water temperatures and approximately linear across a midrange of temperatures (e.g., 10–20 °C). The relationships appear to become more linear when either activity is higher than resting metabolism or consumption is below satiation (Figs. 1a and 1b). However, if we consider growth as a proportion of maximum growth for a given activity or consumption level (Figs. 1c and 1d), we see that the relationship is nonlinear for all scenarios examined, and among the most noticeable effects of increased activity or reduced consumption is a decrease in the optimum temperature for growth (see Kitchell et al. 1977). Figure 1 shows results for the yellow perch bioenergetics model; results for the other two models are shown in Supplementary Material, Figs. S1 and S2<sup>1</sup>.

### Annual growth

In fish science and other disciplines, samples are often collected at a relatively coarse temporal resolution (e.g., once per year), and

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0051>.

**Fig. 2.** Simulated annual growth versus degree-days above 5 °C derived from simulated water temperatures (WDD<sub>5</sub>) across levels of activity and consumption for (a) yellow perch (*Perca flavescens*), (b) brown bullhead (*Ameiurus nebulosus*), and (c) tiger muskellunge (*Esox lucius* × *Esox masquinongy*). Circles, satiation at resting metabolism; squares, satiation with activity multiplier = 3; triangles, 50% satiation with resting metabolism; diamonds, 85% satiation with activity multiplier = 2. Adjusted  $R^2 \geq 0.99$  for all linear fits.



individual sizes across ages and (or) sampling events are compared to approximate growth patterns (Lorenzen 2016). Therefore, we were primarily interested in examining the cumulative effect of water temperature on growth at annual and interannual time scales.

For this portion of the analysis, our goal was to examine the effect of varying temperature scenarios on the relationship between annual immature fish growth and DD derived from water temperatures (WDD). We first simulated annual surface water temperature cycles using the Shuter water temperature model and empirical predictors for maximum daily surface water temperature ( $T_{\max}$ ) and the duration of the ice-free season (DR) (Shuter et al. 1983):

$$T_{\max} = 23.5\bar{Z}^{-0.108} e^{0.0437\bar{AT} - 0.002\bar{AT}^2}$$

$$DR = 149\bar{Z}^{0.073} e^{0.06\bar{AT}}$$

$$T_t = 4 + (T_{\max} - 4) \sin\left(\pi \frac{t - (365 - DR)}{DR}\right)$$

where  $\bar{Z}$  is mean lake depth (or mean thermocline depth for stratified systems),  $\bar{AT}$  is mean annual air temperature, and  $T_t$  is mean surface water temperature on day  $t$ . We used simulated rather than empirical water temperatures for this portion of the analysis so that we could encompass a broad range of climatic scenarios in a relatively straightforward and analytically robust manner. We assumed that liquid water temperature did not fall below 4 °C and that the year was 365 days long. Using these equations, the annual water temperature cycle can be defined as a function of  $\bar{Z}$  and  $\bar{AT}$ . We fixed  $\bar{Z}$  at 8 m for the sake of simplicity and because variation in  $\bar{Z}$  generally has a smaller impact than variation in  $\bar{AT}$  on the surface water temperature cycle (Supplementary Material A, Fig. S3). We then simulated annual surface water temperature cycles from 0 to 10 °C  $\bar{AT}$  in increments of 0.5 °C.

We used these simulated daily water temperatures to drive the yellow perch, brown bullhead, and tiger muskellunge bioenergetics models (Table 1). We assumed that fish experienced surface water temperatures, which approximate the temperature of the typically well-mixed epilimnion (e.g., Livingstone and

Lotter 1998), throughout the ice-free season. We then summed daily growth in length throughout the ice-free season, assuming that growth during winter was negligible (Pitcher and Macdonald 1973; García-Berthou et al. 2012). We subtracted initial length from final length to determine annual growth. We then compared annual growth to WDD above 5 °C (WDD<sub>5</sub>), calculated as

$$(1) \quad WDD_5 = \sum_{t=1}^N T_t - 5, \quad T_t > 5$$

where  $N$  is the number of days (in this case, 365) and  $T_t$  is the daily mean surface water temperature on day  $t$ . We used 5 °C as a base temperature because it is highly correlated with the length of the ice-free season (Shuter et al. 1983; Venturelli et al. 2010) and has been used to describe growth in yellow perch and other fishes (e.g., Power and McKinley 1997; Purchase et al. 2005; Rennie et al. 2010).

We first simulated growth under the “ideal” bioenergetic scenario in which individuals achieve satiation at resting metabolism. However, these results are unrealistic because empirical data suggest that activity costs are often higher than resting metabolism (e.g., Rowan and Rasmussen 1996). In addition, consumption can be highly variable (e.g., Schaeffer et al. 1999) and is typically estimated at roughly 40%–60% of satiation in wild populations (Hartman and Margraf 1992; Petersen and Paukert 2005; Hartman and Cox 2008). To explore the nature of the relationship between WDD<sub>5</sub> and annual growth given reduced consumption and (or) increased activity, we repeated the simulations for three additional bioenergetics scenarios: (1) satiation with increased activity (activity multiplier = 3), (2) lower consumption (50% of satiation) with resting metabolism, and (3) lower consumption (85% of satiation) with increased activity (activity multiplier = 2). Our results show that the relationship between annual growth and WDD<sub>5</sub> is approximately linear for all of these bioenergetic scenarios (all  $R^2 \geq 0.99$ ), with the most substantial change in the relationship among scenarios being a change in the slope of the line (Fig. 2).

### Interannual growth

We have shown that annual fish growth in length is roughly linear with  $WDD_5$  across a variety of scenarios. Here, we test whether interannual immature growth (i.e., length-at-age) is also approximately linear with  $WDD_5$  for many bioenergetic scenarios. We focus on immature growth because the linear approximation of the length-at-age versus DD relationship is typically only valid for growth leading up to maturity (Lester et al. 2004), whereas adult length-at-age is often nonlinear due to investment in reproduction and other factors (e.g., increasing activity costs with body size: Ware 1978; Kozłowski 1996; Andersen and Beyer 2015).

We included empirical water temperature in this portion of the analysis by retrieving five years of publicly available daily mean water temperature data (1 m depth) from two lakes: Sparkling Lake, Wisconsin, USA (2000, 2002–2005) and Lake Lacawac, Pennsylvania, USA (2010–2014) (Fig. 3). The Sparkling Lake data were retrieved from the University of Wisconsin's North Temperate Lakes Long Term Ecological Research network (NTL LTER 1991a). These data were continuous apart from eight gaps (mean  $\pm$  SD gap length =  $2.875 \pm 3.23$  days, 1.3% of total sample size), which we filled using linear interpolation. The Lake Lacawac data were retrieved from an electronic database maintained by Lehigh University ([http://www.lehigh.edu/~brh0/pocono\\_mon/](http://www.lehigh.edu/~brh0/pocono_mon/)) and were continuous.

We used the empirical water temperature data to drive multi-annual bioenergetics simulations for each of our model species (Table 1). We summed growth throughout the ice-free seasons (i.e., when water temperatures at 1 m were  $>4$  °C) and defined length-at-age as the length on the last day of each year. We carried out a factorial simulation to determine the effects of varying consumption (10%–100% satiation in increments of 5%), activity (1–4 in increments of 0.2), and initial size (yellow perch = 25, 50, and 75 mm; brown bullhead = 50, 100, and 150 mm; tiger muskellunge = 100, 150, and 200 mm) on interannual growth. We fit a linear model to the length versus  $WDD_5$  relationship and recorded the adjusted  $R^2$  value after each simulation. We focused on  $R^2$  because we were primarily interested in the explanatory power of a metric ( $WDD_5$ ) in describing interannual fish growth in a linear model framework across a wide range of bioenergetic scenarios; we were not interested in, e.g., the relative performance of a given model or whether a particular relationship was statistically significant. We disregarded  $R^2$  values for scenarios in which individuals did not grow across all five years (e.g., fish losing mass from one year to the next) because these scenarios would likely result in death. Figure 4 shows example results from simulations with consumption set at 40% and the activity multiplier set at 1.2. We acknowledge that simulating immature growth across five years may be unrealistic because the model species may mature before age 5 (e.g., Trippel 1995; Feiner et al. 2015); however, we argue that these simulations are valid given our goal of better understanding how immature growth relates to DD, and we note that the relationship should be approximately linear leading up to maturity regardless of age-at-maturity.

Our results suggest that immature interannual growth is highly linear with  $WDD_5$  for most bioenergetic scenarios across species (Fig. 5). The brown bullhead and tiger muskellunge models displayed nearly linear ( $R^2 \geq 0.90$ ) growth for all scenarios examined. Simulated growth for the yellow perch model was less linear ( $R^2 < 0.90$ ) in some cases; however, most of these cases occurred when activity was unrealistically high for immature yellow perch (e.g.,  $ACT \geq 2$ : Rowan and Rasmussen 1996). The yellow perch model was the most sensitive to initial fish size, with fewer cases of highly linear growth at smaller initial sizes. Importantly, growth was approximately linear ( $R^2 \geq 0.90$ ) with  $WDD_5$  for 95% of cases ( $n = 268$ ) for which consumption was similar to empirical estimates (40%–60% of satiation, or  $p(C_{max}) = 0.4$ – $0.6$ : Hartman 2017). This percentage increased to 98% ( $n = 256$ ) for realistic levels of activity ( $ACT \approx 1$ – $2.4$  for

immature fishes: Rowan and Rasmussen 1996). These summaries and Fig. 5 describe the simulations driven by Sparkling Lake water temperatures; results from the simulations driven by Lake Lacawac temperatures were nearly identical (Fig. S4).

### Air temperature and fish growth

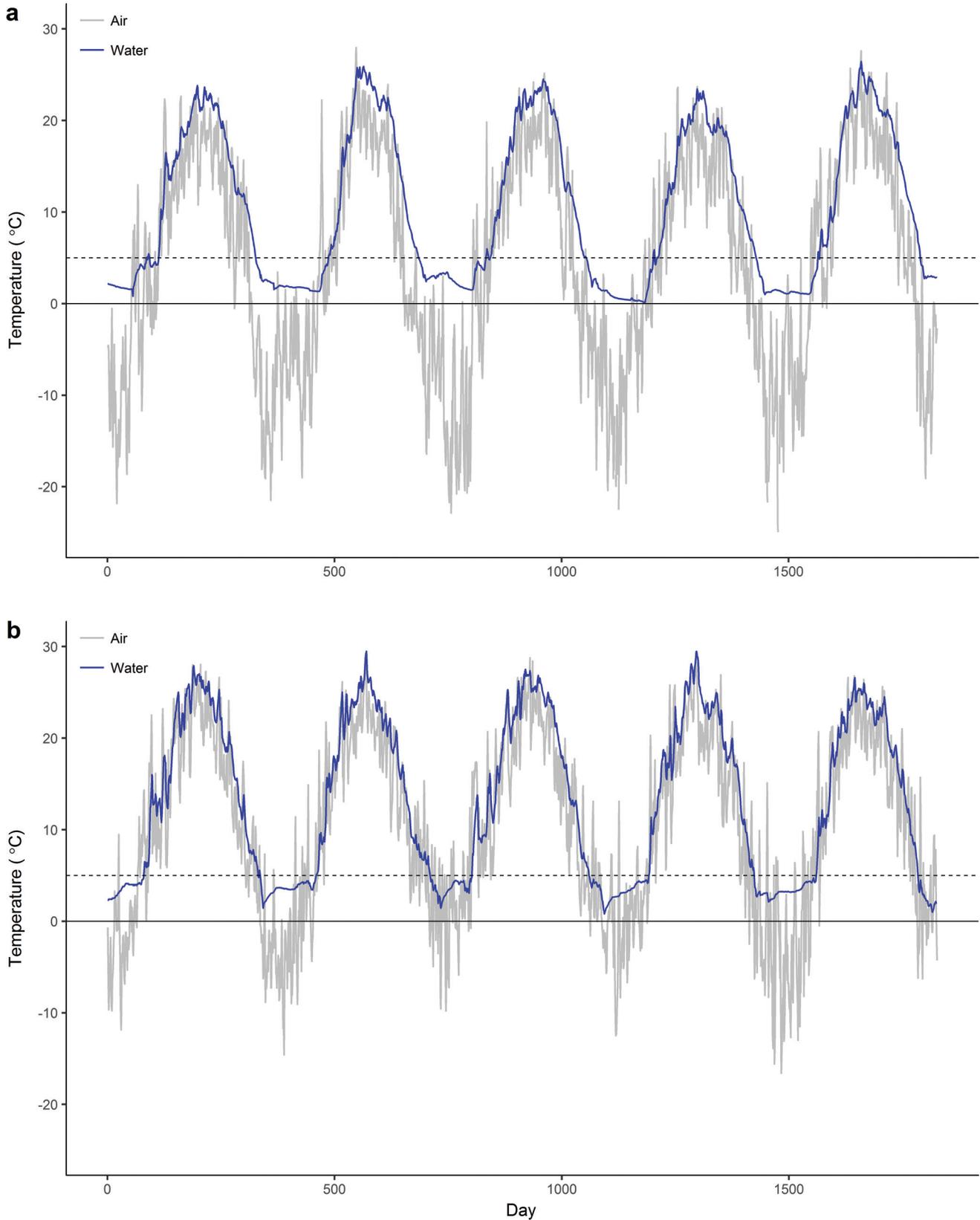
#### Air temperature as a proxy for water temperature

Air temperatures and surface water temperatures are often highly correlated in lacustrine (Macan and Maudsley 1966; Livingstone and Lotter 1998; Livingstone and Dokulil 2001) and riverine (Pilgrim et al. 1998; Mohseni and Stefan 1999; Erickson and Stefan 2000) systems during open water periods. For this reason, air temperatures have been used in place of surface water temperatures in fish science (e.g., Schlesinger and Regier 1982; Rypel 2012; Honsey et al. 2016). Moreover, because heat flux at the air–water interface is a major driver of lake temperatures (e.g., Edinger et al. 1968; Wetzel and Likens 2000; Read et al. 2014), air temperatures are commonly included as drivers in limnological models (e.g., Hondzo and Stefan 1993; Jacobson et al. 2010; Piccolroaz et al. 2018).

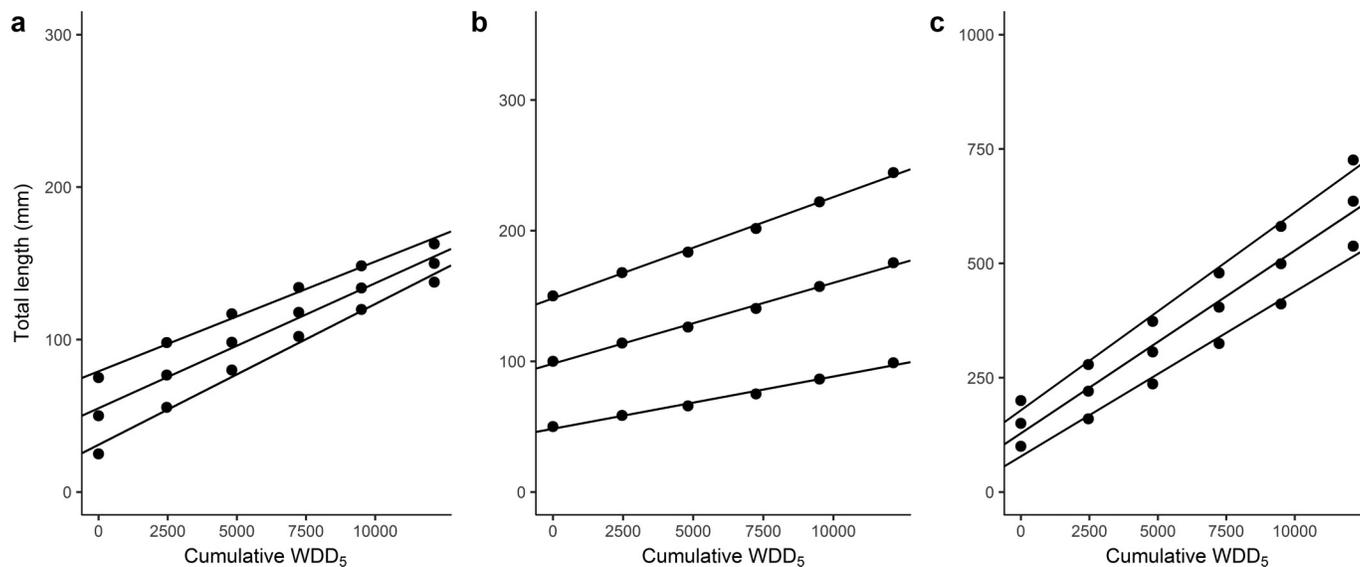
We first demonstrate the correlation between air and surface water temperatures in Sparkling Lake and Lake Lacawac. To do this, we retrieved mean daily air temperature data from weather stations near the two lakes that covered the same time periods as the water temperature data. For Sparkling Lake, we retrieved air temperature data from Woodruff Airport ( $-4.22$  m elevation and 9.11 km from Sparkling Lake: NTL LTER 1991b). These data contained three gaps (mean  $\pm$  SD gap length =  $7.33 \pm 10.12$  days, 1.2% of total sample size). Because one of the gaps in these data was 19 days long and because mean daily air temperature data from other nearby sites were unavailable, we used a linear model to predict the unknown mean daily air temperatures as a function of daily minimum and maximum air temperatures from another nearby weather station (Minocqua Dam,  $-11.32$  m elevation and 6.05 km from Woodruff Airport: Kratz 1983) ( $n = 1805$ ,  $R^2 = 0.994$ ). For Lake Lacawac, we retrieved continuous mean daily air temperature data from the Wilkes Barre Scranton International Airport ( $-160.66$  m elevation and 35.97 km from Lake Lacawac) using the National Oceanic and Atmospheric Administration Climate Data Online tool (<https://www.ncdc.noaa.gov/cdo-web/>). Air and surface water temperatures were highly correlated for both lakes (Pearson's  $\rho = 0.87$  and  $0.91$  for Sparkling and Lacawac, respectively) (Fig. 3), suggesting that mean daily air temperatures can serve as a good proxy for mean daily surface water temperatures.

Our next goals were to examine the relationship between DD derived from air temperatures (ADD) and WDD and to determine whether ADD can serve as an accurate proxy for WDD. Both the degree to which ADD correlates with WDD within lakes and the nature of the ADD versus WDD relationship among lakes have important implications for ADD applications (e.g., using ADD to describe fish growth and physiology within and (or) among lakes, using ADD to drive limnological models, etc.). We used both simulated and empirical data to explore these relationships. For the empirical comparisons, we calculated ADD above 5 °C ( $ADD_5$ ) using eq. 1 and the air temperature data described above. We then calculated the Pearson correlation coefficient between  $ADD_5$  and  $WDD_5$  derived from the empirical water temperature data from each lake at both annual and cumulative (i.e., summed across years) time scales. For the simulations, we once again used the Shuter model (Shuter et al. 1983) to generate annual water temperature cycles across four values of  $Z$  (4, 8, 16, and 32 m) and with  $\overline{AT}$  ranging from  $-10$  to  $15$  °C in increments of  $0.5$  °C. We used these water temperature data and eq. 1 to calculate  $WDD_5$ . We then collected air temperature data from 107 weather stations in the United States and Canada using the National Oceanic and Atmospheric Administration Climate Data Online tool (see

**Fig. 3.** Daily mean surface water (1 m depth, blue line) and air (gray line) temperatures across five years in/near (a) Sparkling Lake, Wisconsin, USA (2000, 2002–2005) and (b) Lake Lacawac, Pennsylvania, USA (2010–2014). Surface water and air temperatures were highly correlated in both cases ( $\rho = 0.87$  and  $0.91$  for Sparkling Lake and Lake Lacawac, respectively). The horizontal dashed line at  $5^{\circ}\text{C}$  indicates the base temperature for degree-day calculations used herein. [Color online.]



**Fig. 4.** Example length-at-age versus cumulative water degree-days above 5 °C (WDD<sub>5</sub>) trajectories for (a) yellow perch (*Perca flavescens*), (b) brown bullhead (*Ameiurus nebulosus*), and (c) tiger muskellunge (*Esox lucius* × *Esox masquinongy*) based on bioenergetics models. In this example, consumption was set at 40% of satiation ( $p(C_{\max}) = 0.4$ ) and the activity multiplier (ACT) was set to 1.2. Each panel shows growth trajectories across three initial sizes (25, 50, and 75 mm for yellow perch, 50, 100, and 150 mm for brown bullhead, and 100, 150, and 200 mm for tiger muskellunge), with linear model fits to each trajectory. Adjusted  $R^2$  values from fits such as these were used to evaluate the linearity of the length-at-age versus degree-day relationship for a variety of bioenergetic scenarios (see Figs. 4, 8, S4, and S8).



Supplementary Material B for details), and we used these data to generate an empirical relationship for predicting ADD<sub>5</sub> from  $\overline{AT}$ :

$$ADD_5 = 1346.8e^{0.0729\overline{AT}}.$$

We used this relationship to estimate ADD<sub>5</sub> for the simulated scenarios, and we compared annual ADD<sub>5</sub> to WDD<sub>5</sub> across simulations.

Our empirical results show that annual ADD<sub>5</sub> and WDD<sub>5</sub> are highly correlated for both the Sparkling Lake and Lake Lacawac data sets ( $\rho = 0.97$  and  $0.87$ , respectively) (Fig. 6). Moreover, although WDD<sub>5</sub> is consistently higher than ADD<sub>5</sub> due to higher average water temperatures (Fig. 3), the two cumulative metrics are almost linearly related for both data sets ( $\rho > 0.99$ ) (Fig. S7). These results suggest that ADD<sub>5</sub> can be an accurate surrogate for WDD<sub>5</sub> both within and across years. Our simulation results indicate that the relationship between WDD<sub>5</sub> and ADD<sub>5</sub> is nonlinear and not proportional (Fig. 6). However, the relationship for a given  $\bar{Z}$  value is approximately linear across relatively broad ranges of temperatures (e.g., ~1300–3000 ADD<sub>5</sub>), suggesting that the slope of the relationship (and therefore the utility of ADD<sub>5</sub> as a proxy for WDD<sub>5</sub>) is not likely to change within a given lake due to annual variation in temperature.

### Annual growth

Our next aim was to investigate the relationship between annual growth and ADD across a variety of temperature scenarios. To do this, we used the Shuter model to generate water temperatures, with  $\bar{Z}$  fixed at 8 m and with  $\overline{AT}$  ranging from 0 to 10 °C in increments of 0.5 °C. We used these simulated temperatures to drive the three bioenergetics models (Table 1), summed daily growth throughout the ice-free season, and subtracted initial length from final length to determine annual growth ( $\Delta$ mm). We calculated ADD<sub>5</sub> using the empirical relationship described above. We then regressed ADD<sub>5</sub> against annual growth for four bioenergetic scenarios: (1) the “ideal” case of satiation at resting metabolism, (2) satiation with activity multiplier = 3, (3) 50% of satiation at resting metabolism, and (4) 85% of satiation with ac-

tivity multiplier = 2. Our results show that annual growth is roughly linear with the empirically derived ADD<sub>5</sub> for all bioenergetic scenarios examined (all  $R^2 \geq 0.98$ ), suggesting that ADD<sub>5</sub> can be as effective as WDD<sub>5</sub> for describing annual growth within lakes (Fig. 7).

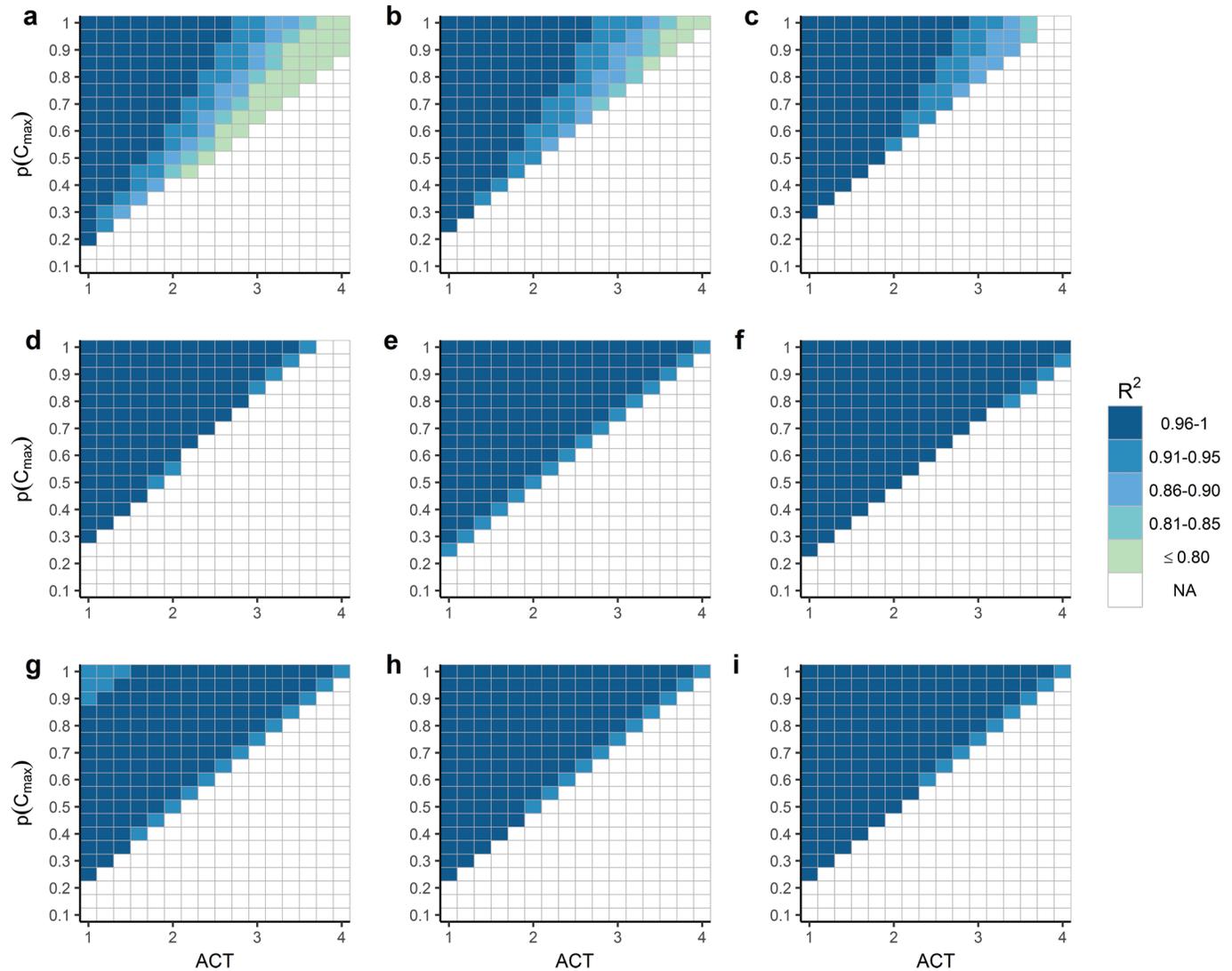
### Interannual growth

We have shown that ADD and WDD have nearly equivalent power in explaining annual fish growth. Our final goal was to compare the performance of ADD to that of WDD in describing interannual growth (i.e., length-at-age). To do this, we again used five years of empirical water temperature data from Sparkling Lake and Lake Lacawac to drive bioenergetics simulations for the three model species (Table 1), and we employed the same factorial design used above to examine the effects of varying consumption, activity, and initial size on the growth versus DD relationship. In this case, we calculated ADD<sub>5</sub> using the empirical air temperature data sets collected near each lake and eq. 1 (substituting ADD<sub>5</sub> for WDD<sub>5</sub>), and we fit linear models to the length versus ADD<sub>5</sub> relationship for each simulation. Our results closely mirrored those of the length versus WDD<sub>5</sub> comparisons for both Sparkling Lake (Fig. 8) and Lake Lacawac (Fig. S8). In some cases, adjusted  $R^2$  values were higher for the length versus ADD<sub>5</sub> regressions than they were for the length versus WDD<sub>5</sub> regressions (e.g., Figs. 8g, 8h, and 8i). These results suggest that immature fish length-at-age is approximately linear with ADD<sub>5</sub> across a wide range of bioenergetic scenarios.

### Discussion

Our analysis provides bioenergetic foundations for the nearly linear relationship between DD and immature fish growth as well as justification for using ADD as a proxy for WDD when describing growth. We show that, although daily growth rates are nonlinear with temperature, the nonlinear increase in DD through time explains the nonlinear nature of growth in a linear manner at annual and interannual time scales (Neuheimer and Taggart 2007). In other words, growth occurs intermittently, but always along a trajectory that is approximately linear with DD at rela-

**Fig. 5.** Coefficients of determination (adjusted  $R^2$ ) from linear model fits to the length versus water-based degree-day ( $WDD_s$ ) relationship from five year growth simulations given various combinations of consumption (proportion of maximum consumption,  $p(C_{max})$ ), activity (ACT), and initial size (columns). (a–c) Results from the yellow perch (*Perca flavescens*) bioenergetics model, with initial sizes of (a) 25, (b) 50, and (c) 75 mm. (d–f) Results from the brown bullhead (*Ameiurus nebulosus*) bioenergetics model, with initial sizes of (d) 50, (e) 100, and (f) 150 mm. (g–i) Results from the tiger muskellunge (*Esox lucius* × *Esox masquinongy*) bioenergetics model, with initial sizes of (g) 100, (h) 150, and (i) 200 mm. Bioenergetics simulations incorporated empirical water temperature data (1 m depth) from Sparkling Lake, Wisconsin, USA. White cells (“NA”) denote cases in which individuals did not grow across all five years. [Color online.]

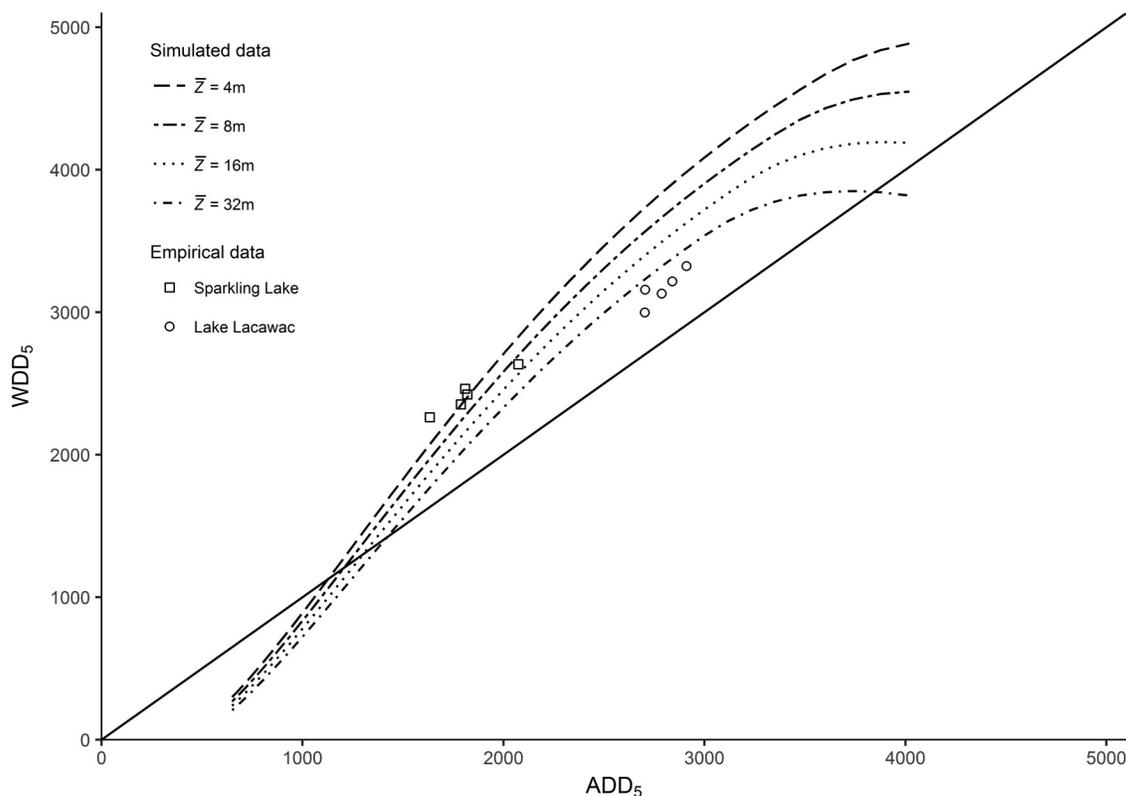


tively coarse (but highly relevant) time scales. The fact that ADD can serve as an accurate proxy for WDD should facilitate the use of DD and promote a more physiologically valid understanding of how the growth of fishes and other aquatic organisms responds to thermal energy.

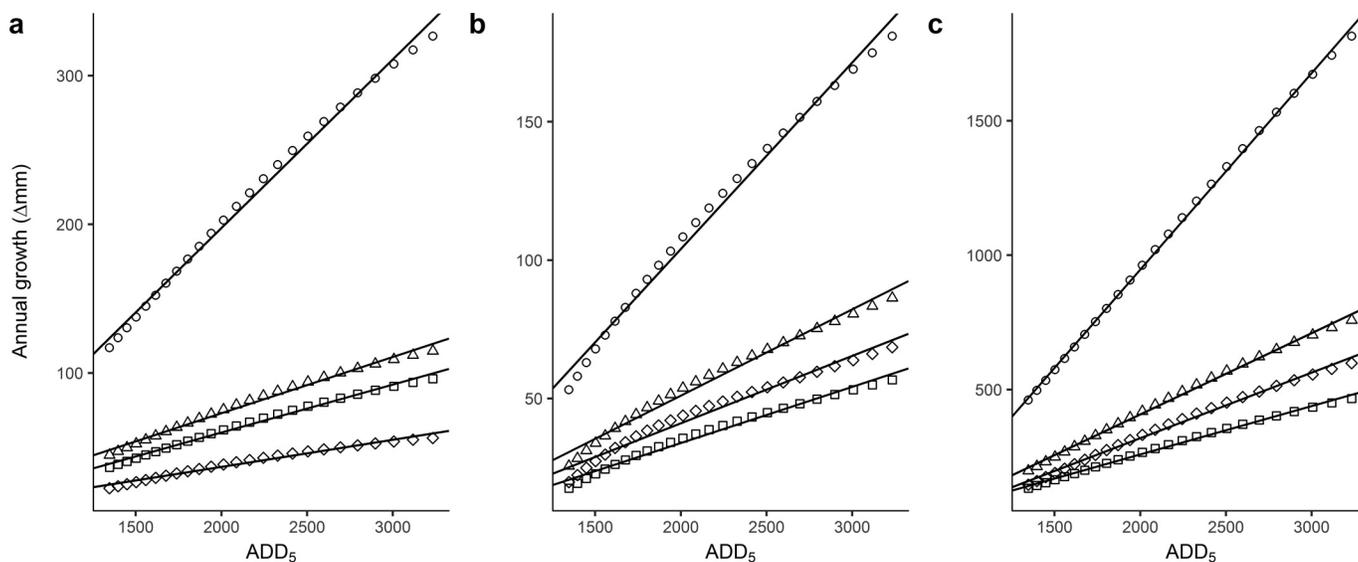
A number of factors can limit the ability of surface WDD or ADD to describe fish growth. For example, the growth versus ADD relationship may be nonlinear if ADD become disentangled from WDD (e.g., due to wind, groundwater, shade, etc.). We also assumed that our simulated fish experienced epilimnetic temperatures throughout the growing season. This assumption was reasonable for our three model species, but coldwater species in many stratified systems spend much of the growing season below the epilimnion. As such, ADD and surface WDD may not provide an adequate description of the thermal environments experienced by these fishes. We note that more adequate DD metrics could be calculated for fishes that do not inhabit the epilimnion year-round but that doing so would require both depth-specific

water temperature data and knowledge of the depths that individuals inhabit throughout the year, which may render the calculation of such a metric impractical or impossible (although more complex water temperature models could facilitate such efforts, e.g., Read et al. 2014). We also note that any shortcomings of ADD in describing growth of coldwater fishes in stratified systems would likely extend to any air-temperature-based metric due to the often poor correlation between air temperatures and meta- or hypolimnetic water temperatures (e.g., Robertson and Ragotzkie 1990). Importantly, Chezick et al. (2014a) showed that ADD can still have a high degree of explanatory power in describing length-at-age for a coldwater species (cisco (*Coregonus artedii*)), albeit a reduced amount compared to cool- and warmwater fishes. Furthermore, if surface water temperatures exceed growth optima and no refugia are present (e.g., in unstratified systems), then the growth versus surface WDD or ADD relationship may become nonlinear; however, we expect that nonlinearities due to this mechanism are relatively rare in nature because species seldom

**Fig. 6.** Relationships between annual degree-days above 5 °C derived from air ( $ADD_5$ ) and water ( $WDD_5$ ) temperatures. Points denote empirical data sets from Sparkling Lake, Wisconsin, USA and Lake Lacawac, Pennsylvania, USA ( $\rho = 0.97$  and  $0.87$ , respectively). Dotted and dashed lines denote simulated data generated using the Shuter water temperature model and an empirically derived relationship between mean annual air temperature and  $ADD_5$  (see text for details). The solid line is a 1:1 line.



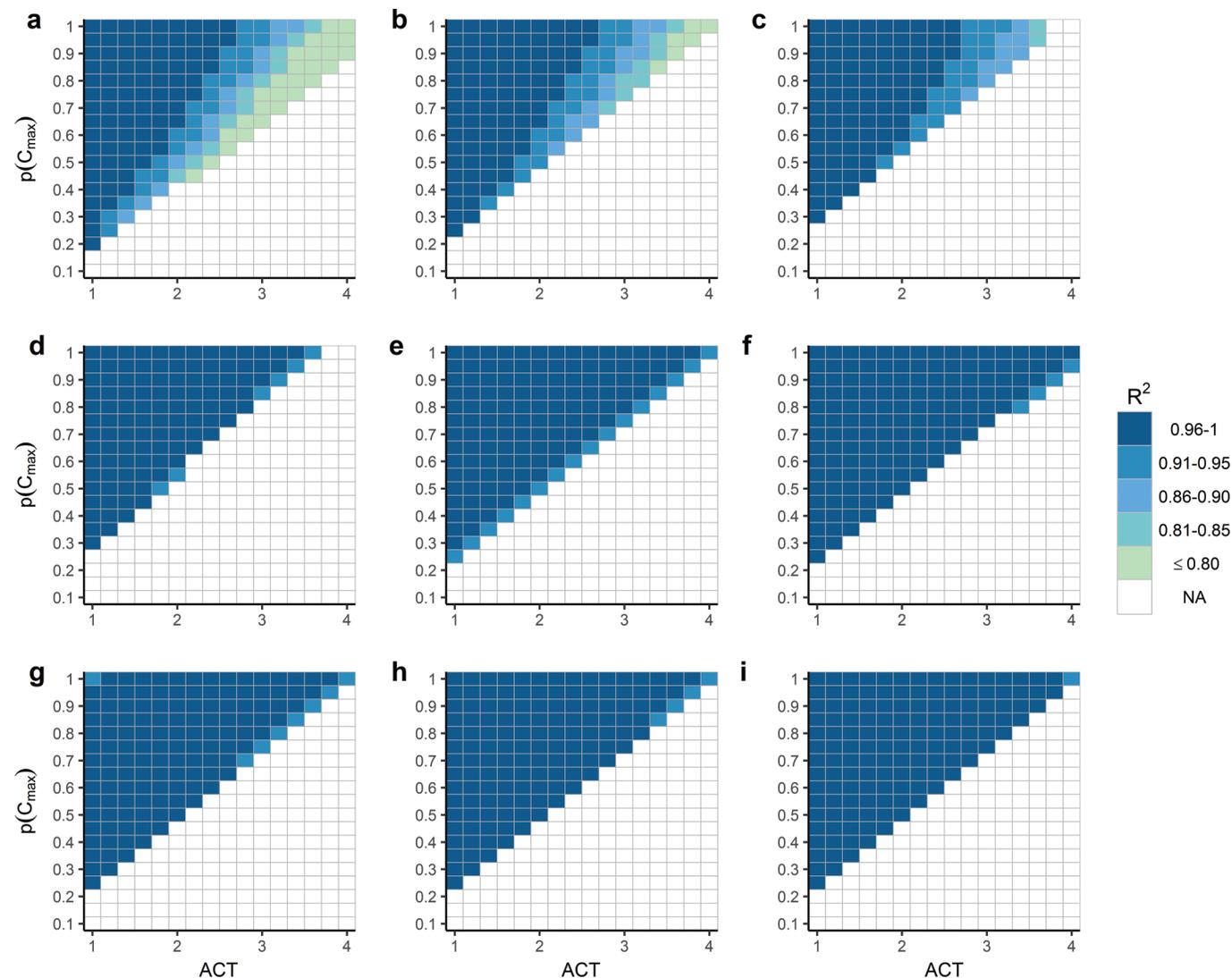
**Fig. 7.** Simulated annual growth versus air degree-days above 5 °C ( $ADD_5$ ) (derived from an empirical relationship between  $ADD_5$  and mean annual air temperature) across levels of activity and consumption for (a) yellow perch (*Perca flavescens*), (b) brown bullhead (*Ameiurus nebulosus*), and (c) tiger muskellunge (*Esox lucius* × *Esox masquinongy*). Circles, satiation at resting metabolism; squares, satiation with activity multiplier = 3; triangles, 50% satiation with resting metabolism; diamonds, 85% satiation with activity multiplier = 2. Adjusted  $R^2 \geq 0.98$  for all linear fits.



persist in systems in which temperatures regularly exceed growth optima and in which no refugia are present (e.g., coldwater species such as lake trout (*Salvelinus namaycush*) do not inhabit warm, unstratified lakes). That being said, individuals may spend some amount of time in temperatures that are above growth optima

(e.g., Sellers et al. 1998), which can reduce the utility of DD metrics in describing growth and other physiological processes. Future work should address this shortcoming, perhaps by introducing an upper temperature limit for calculating DD or incorporating a “penalty” (i.e., reduction in DD) if temperatures exceeded some

**Fig. 8.** Coefficients of determination (adjusted  $R^2$ ) from linear model fits to the length versus air-based degree-day ( $ADD_5$ ) relationship from five year growth simulations given various combinations of consumption (proportion of maximum consumption,  $p(C_{max})$ ), activity (ACT), and initial size (columns). (a–c) Results from the yellow perch (*Perca flavescens*) bioenergetics model, with initial sizes of (a) 25, (b) 50, and (c) 75 mm. (d–f) Results from the brown bullhead (*Ameiurus nebulosus*) bioenergetics model, with initial sizes of (d) 50, (e) 100, and (f) 150 mm. (g–i) Results from the tiger muskellunge (*Esox lucius*) × *Esox masquinongy*) bioenergetics model, with initial sizes of (g) 100, (h) 150, and (i) 200 mm. Bioenergetics simulations incorporated empirical water temperature data (1 m depth) from Sparkling Lake, Wisconsin, USA. White cells (“NA”) denote cases in which individuals did not grow across all five years. [Color online.]



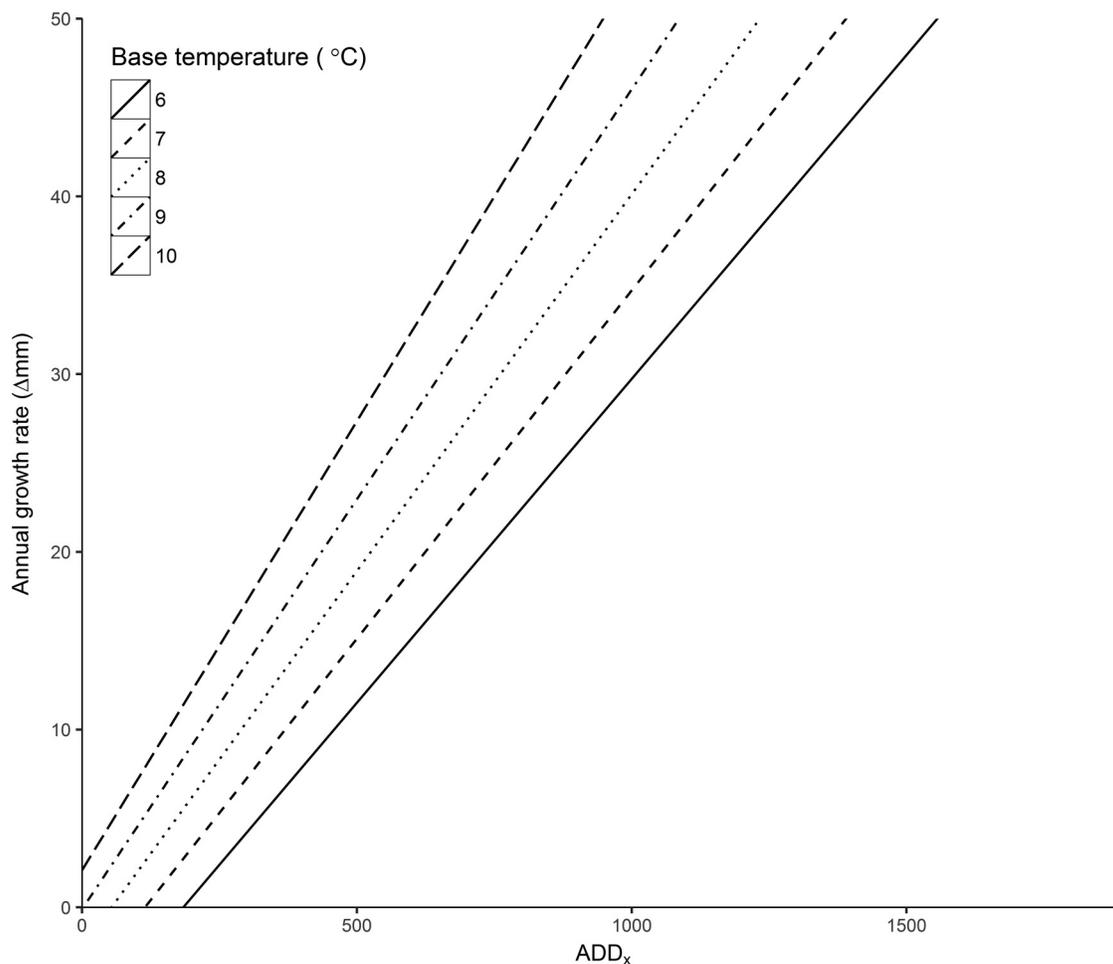
(likely species-specific) value. Finally, growth may be nonlinear due to a variety of other biological factors, including factors that cause large changes in consumption rates or activity costs within or among years (e.g., substantial shifts in prey or predator density; ontogenetic diet shifts, especially in very early life; etc.: Lorenzen and Enberg 2002).

Although the adult fish growth versus DD relationship may be nonlinear due to investment in reproduction and other factors (e.g., Lester et al. 2004; Andersen and Beyer 2015; Honsey et al. 2017); using DD to describe lifetime growth is still useful, particularly when comparing growth among populations that experience different thermal regimes (Chezik et al. 2014b; Lester et al. 2014). That being said, daily growth for adult fishes is often a near-linear function of temperature over a midrange of temperatures, much as it is for immature fishes (see Supplementary Material C). Indeed, many fish bioenergetics models are intended to apply to both juvenile and adult growth for a given species, as is the case for the brown bullhead model used herein (Hartman

2017; see also, e.g., Madon et al. 2001; Pääkkönen et al. 2003). As such, many of our results (particularly the linearity of annual growth versus DD) may also extend to adult fish growth.

Both our simulated and empirical comparisons of ADD and WDD highlight the potential for the ADD versus WDD relationship to vary among lakes. For instance, in Lake Lacawac,  $WDD_5 \approx 1.2 \times ADD_5$ . In contrast,  $WDD_5 \approx 1.3 \times ADD_5$  for Sparkling Lake. This result is intuitive because water temperatures in lakes with different characteristics (e.g., Secchi depth, morphometry) will respond differently to air temperatures (e.g., Rose et al. 2016). These differences are important to consider for a number of applications, including using ADD to (1) describe growth and other physiological processes among lakes and (2) drive limnological models of lake thermal regimes. Future work should examine the degree to which the ADD versus WDD relationship varies among lakes and explore whether that variation introduces substantial error and (or) bias in among-lake comparisons of growth and other physiological processes.

**Fig. 9.** Air-based degree-days calculated using various base temperatures for growth ( $ADD_x$ ) (base temperatures from 6 to 10 °C) versus annual growth ( $\Delta mm$ ) from a yellow perch bioenergetics model. The growth versus degree-day relationship is roughly proportional when the base temperature is 9 °C, suggesting that this base temperature is most appropriate for among-population studies of yellow perch (*Perca flavescens*) growth. See Supplementary Material D for details.



If DD are an accurate index for the thermal scope for growth, then growth should be proportional to DD given that they are calculated using the correct base temperature for growth, i.e., the temperature below which growth is negligible. This base temperature for growth ( $T_0$ ) is a key parameter for calculating DD; incorrect  $T_0$  values can bias growth rate estimates, which can be particularly problematic for among-population comparisons (Chezik et al. 2014b). Unfortunately,  $T_0$  has not been estimated for most fish species. It may be possible to use bioenergetics models to estimate  $T_0$  by finding the  $T_0$  value for which the growth versus DD relationship is proportional (i.e., passes through the origin). We provide an example of this approach using the yellow perch bioenergetics model in the annual growth simulation framework described above (see Supplementary Material D). Our results indicate that the appropriate  $T_0$  value for yellow perch when using ADD is  $\sim 9$  °C (Fig. 9), which agrees with two other independent estimates for this species (Chezik et al. 2014b).

In our view, DD remain underutilized in fish science (but see, e.g., Rypel and David 2017; Ward et al. 2017). Our results suggest that the empirically observed, linear relationship between DD and immature fish growth is rooted in bioenergetics. As such, DD are an effective metric for quantifying the thermal scope for growth in fishes. In addition, ADD can serve as an accurate proxy for WDD. Given that high-resolution air temperature data are more common than water temperature data, this result provides a foundation for expanding the use of DD in fish science and other

aquatic disciplines. This expanded use of DD should, in turn, promote a better understanding of the growth and physiology of aquatic organisms and may be particularly useful for assessing and predicting the impacts of global change. In addition to the suggestions mentioned above, future work should focus on (1) standardizing DD calculation (e.g., by estimating  $T_0$  for many fishes) and (2) assessing whether ADD can serve as an accurate proxy for WDD in lotic and marine systems.

### Acknowledgements

We thank Jacques Finlay, James Cotner, Przemek Bajer, and the members of the Venturelli lab for their helpful comments and suggestions. We also thank the handling editor and two anonymous reviewers for their helpful comments. Funding for A.E.H. was provided by a University of Minnesota Doctoral Dissertation Fellowship.

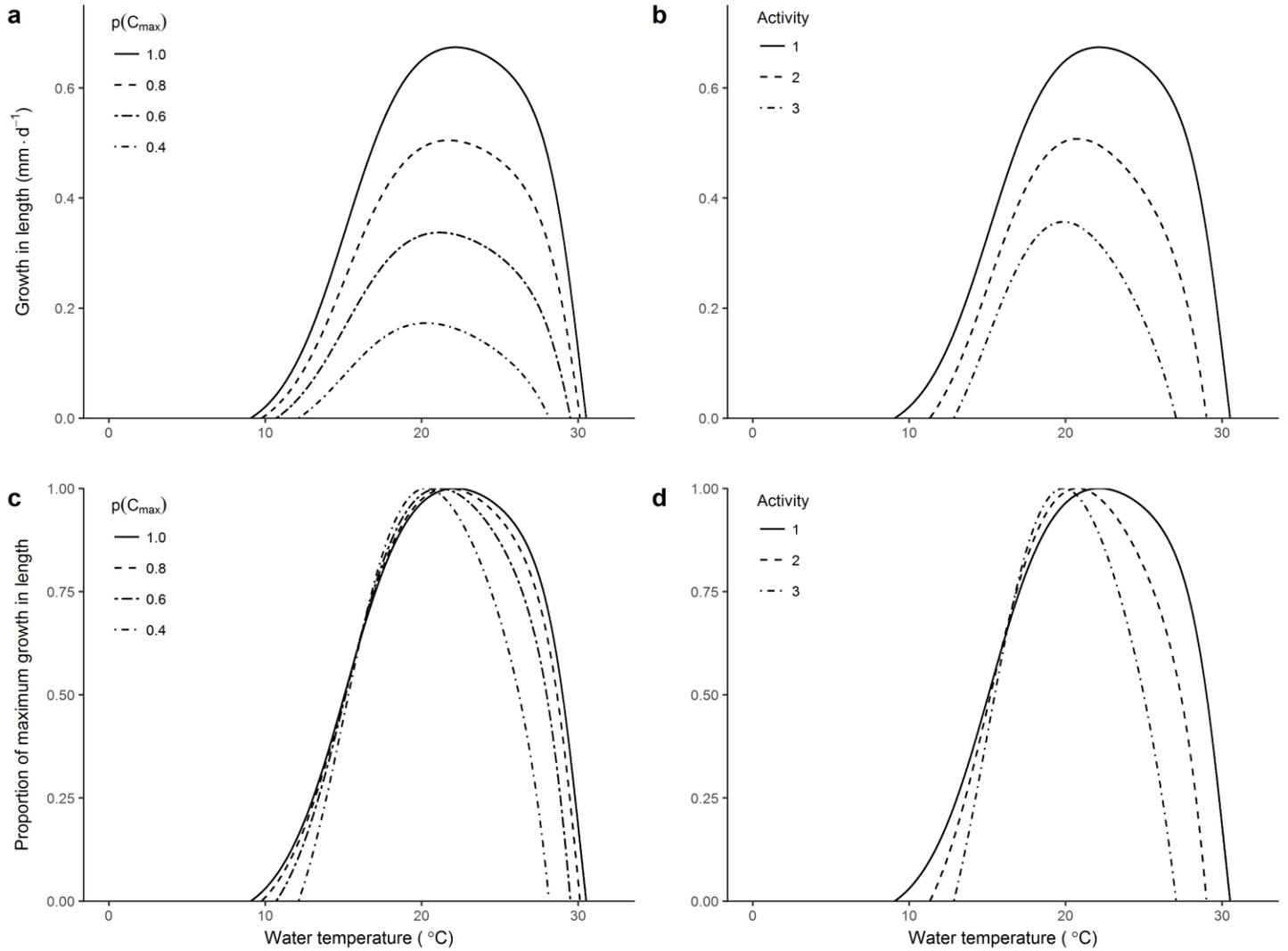
### References

- Andersen, K.H., and Beyer, J.E. 2015. Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish. Fish.* **16**: 1–22. doi:10.1111/faf.12042.
- Atkinson, D. 1994. Temperature and organism size — a biological law for ectotherms? *Adv. Ecol. Res.* **25**: 1–58. doi:10.1016/S0065-2504(08)60212-3.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fish. Investig. Ser. II*, **19**: 1–533. doi:10.1007/978-94-011-2106-4.

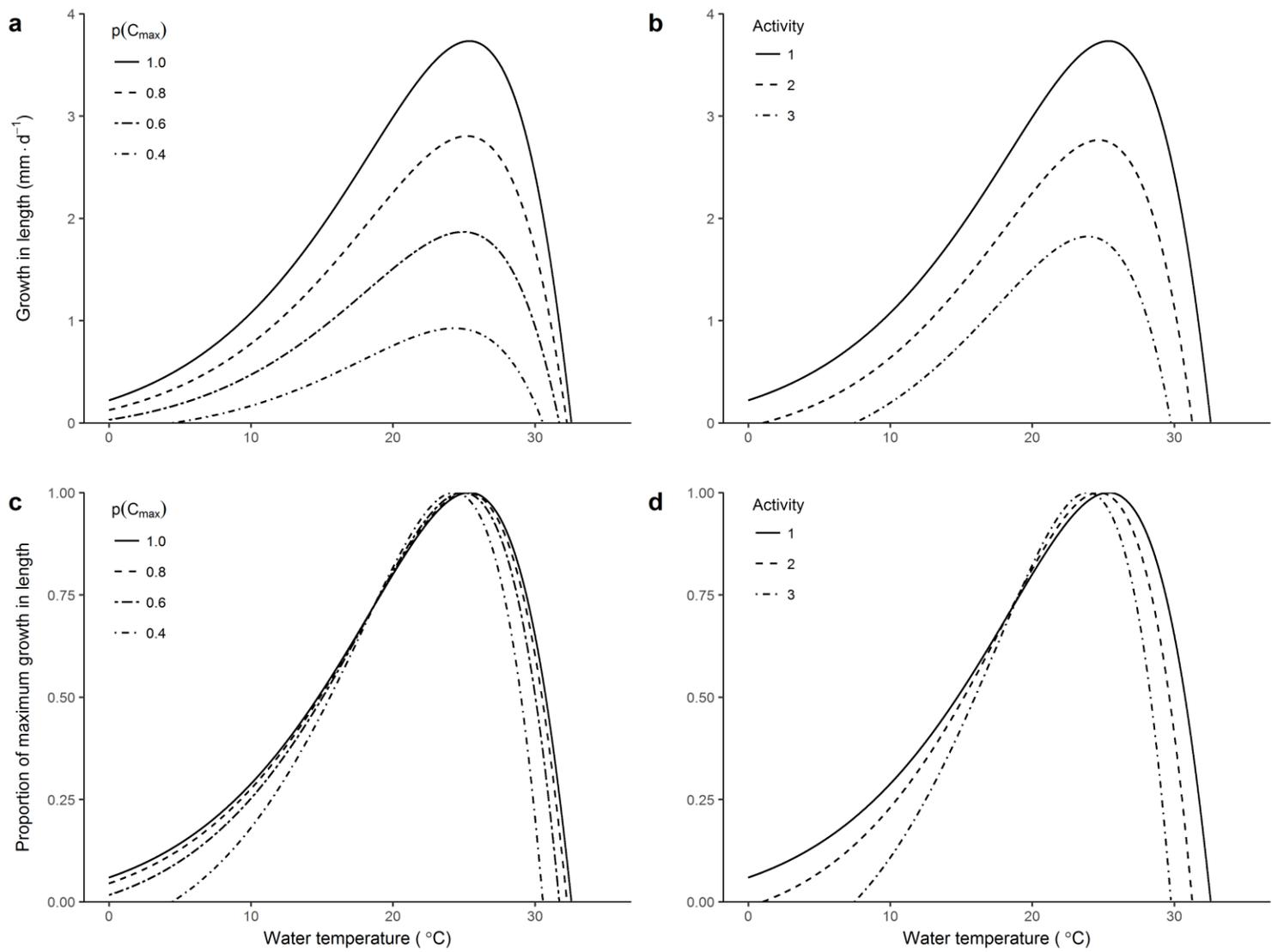
- Chezik, K.A. 2013. Fish growth and degree-days: advice for selecting base temperatures in both within- and among-lake studies. M.Sc. thesis, University of Minnesota, St. Paul, Minn.
- Chezik, K.A., Lester, N.P., and Venturelli, P.A. 2014a. Fish growth and degree-days I: selecting a base temperature for a within-population study. *Can. J. Fish. Aquat. Sci.* **71**(1): 47–55. doi:10.1139/cjfas-2013-0295.
- Chezik, K.A., Lester, N.P., and Venturelli, P.A. 2014b. Fish growth and degree-days II: selecting a base temperature for an among-population study. *Can. J. Fish. Aquat. Sci.* **71**(9): 1303–1311. doi:10.1139/cjfas-2013-0615.
- Chipps, S.R., Einfalt, L.M., and Wahl, D.H. 2000. Growth and food consumption by tiger muskellunge: effects of temperature and ration level on bioenergetic model predictions. *Trans. Am. Fish. Soc.* **129**(1): 186–193. doi:10.1577/1548-8659(2000)129<0186:GAFCBT>2.0.CO;2.
- Colby, P.J., and Nepszy, S.J. 1981. Variation among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. *Can. J. Fish. Aquat. Sci.* **38**(12): 1814–1831. doi:10.1139/f81-228.
- Doubleday, Z.A., Izzo, C., Haddy, J.A., Lyle, J.M., Ye, Q., and Gillanders, B.M. 2015. Long-term patterns in estuarine fish growth across two climatically divergent regions. *Oecologia*, **179**(4): 1079–1090. doi:10.1007/s00442-015-3411-6. PMID:26245148.
- Dumas, A., France, J., and Bureau, D. 2010. Modelling growth and body composition in fish nutrition: where have we been and where are we going? *Aquacult. Res.* **41**(2): 161–181. doi:10.1111/j.1365-2109.2009.02323.x.
- Edinger, J.E., Duttweiler, D.W., and Geyer, J.C. 1968. The response of water temperatures to meteorological conditions. *Water Resour. Res.* **4**(5): 1137–1143. doi:10.1029/WR004i005p01137.
- Elliott, J.M., and Davison, W. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia*, **19**(3): 195–201. doi:10.1007/BF00345305. PMID:28309234.
- Erickson, T.R., and Stefan, H.G. 2000. Linear air/water temperature correlations for streams during open water periods. *J. Hydrol. Eng.* **5**(3): 317–321. doi:10.1061/(ASCE)1084-0699(2000)5:3(317).
- Feiner, Z.S., Chong, S.C., Knight, C.T., Lauer, T.E., Thomas, M.V., Tyson, J.T., and Höök, T.O. 2015. Rapidly shifting maturation schedules following reduced commercial harvest in a freshwater fish. *Evol. Appl.* **8**(7): 724–737. doi:10.1111/eva.12285. PMID:26240608.
- Froese, R., and Pauly, D. (Editors). 2016. FishBase. World wide web electronic publication. [www.fishbase.org](http://www.fishbase.org).
- García-Berthou, E., Carmona-Catot, G., Merciai, R., and Ogle, D.H. 2012. A technical note on seasonal growth models. *Rev. Fish Biol. Fish.* **22**(3): 635–640. doi:10.1007/s11160-012-9262-x.
- Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish Bioenergetics 3.0 for Windows. University of Wisconsin Sea Grant Institute, Madison, Wis.
- Hartman, K.J. 2017. Bioenergetics of Brown Bullhead in a changing climate. *Trans. Am. Fish. Soc.* **146**(4): 634–644. doi:10.1080/00028487.2017.1293563.
- Hartman, K.J., and Cox, M.K. 2008. Refinement and testing of a brook trout bioenergetics model. *Trans. Am. Fish. Soc.* **137**(1): 357–363. doi:10.1577/T05-243.1.
- Hartman, K.J., and Margraf, F.J. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. *Trans. Am. Fish. Soc.* **121**(2): 245–260. doi:10.1577/1548-8659(1992)121<0245:EOPAPA>2.3.CO;2.
- Hazel, J.R., and Prosser, C.L. 1974. Molecular mechanisms of temperature compensation in poikilotherms. *Physiol. Rev.* **54**(3): 620–677. doi:10.1152/physrev.1974.54.3.620. PMID:4366928.
- Hondzo, M., and Stefan, H.G. 1993. Regional water temperature characteristics of lakes subjected to climate change. *Clim. Change*, **24**: 187–211. doi:10.1007/BF01091829.
- Honsey, A.E., Bunnell, D.B., Troy, C.D., Fielder, D.G., Thomas, M.V., Knight, C.T., Chong, S.C., and Höök, T.O. 2016. Recruitment synchrony of yellow perch (*Perca flavescens*, Percidae) in the Great Lakes region, 1966–2008. *Fish. Res.* **181**: 214–221. doi:10.1016/j.fishres.2016.04.021.
- Honsey, A.E., Staples, D.F., and Venturelli, P.A. 2017. Accurate estimates of age-at-maturity from the growth trajectories of fishes and other ectotherms. *Ecol. Appl.* **27**(1): 182–192. doi:10.1002/eap.1421. PMID:27973729.
- Jacobson, P.C., Stefan, H.G., and Pereira, D.L. 2010. Coldwater fish oxythermal habitat in Minnesota lakes: influence of total phosphorus, July air temperature, and relative depth. *Can. J. Fish. Aquat. Sci.* **67**(12): 2002–2013. doi:10.1139/F10-115.
- Jobling, M. 1995. Fish bioenergetics. Chapman and Hall, London.
- Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* **34**: 1922–1935. doi:10.1139/f77-258.
- Kozłowski, J. 1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. *Proc. R. Soc. B Biol. Sci.* **263**: 559–566. doi:10.1098/rspb.1996.0084.
- Kratz, T. 1983. Minocqua Dam Daily Meteorological Data at North Temperate Lakes LTER 1978 — current. Long Term Ecological Research Network. doi:10.6073/pasta/f81f16c816e73c767505b1e9d9792b9b3.
- Lester, N.P., Shuter, B.J., and Abrams, P.A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proc. R. Soc. B Biol. Sci.* **271**(1548): 1625–1631. doi:10.1098/rspb.2004.2778.
- Lester, N.P., Shuter, B.J., Venturelli, P.A., and Nadeau, D. 2014. Life-history plasticity and sustainable exploitation: a theory of growth compensation applied to walleye management. *Ecol. Appl.* **24**(1): 38–54. doi:10.1890/12-2020.1. PMID:24640533.
- Livingstone, D.M., and Dokulil, M.T. 2001. Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. *Limnol. Oceanogr.* **46**(5): 1220–1227. doi:10.4319/lo.2001.46.5.1220.
- Livingstone, D.M., and Lotter, A.F. 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *J. Paleolimnol.* **19**: 181–198. doi:10.1023/A:1007904817619.
- Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: embracing plasticity and its consequences. *Fish. Res.* **180**(January): 4–22. doi:10.1016/j.fishres.2016.01.006.
- Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. B Biol. Sci.* **269**(1486): 49–54. doi:10.1098/rspb.2001.1853.
- Luecke, C., and Brandt, D. 1993. Estimating the energy density of daphnid prey for use with rainbow trout bioenergetics models. *Trans. Am. Fish. Soc.* **122**(3): 386–389. doi:10.1577/1548-8659(1993)122<0386:NETEDO>2.3.CO;2.
- Macan, T.T., and Maudsley, R. 1966. The temperature of a moorland fishpond. *Hydrobiologia*, **27**: 1–22. doi:10.1007/BF00161483.
- Madon, S.P., Williams, G.D., West, J.M., and Zedler, J.B. 2001. The importance of marsh access to growth of the California killifish, *Fundulus parvipinnis*, evaluated through bioenergetics modeling. *Ecol. Modell.* **136**(2–3): 149–165. doi:10.1016/S0304-3800(00)00416-6.
- Malzahn, A.M., Clemmesen, C., and Rosenthal, H. 2003. Temperature effects on growth and nucleic acids in laboratory-reared larval coregonid fish. *Mar. Ecol. Prog. Ser.* **259**: 285–293. doi:10.3354/meps259285.
- Mohseni, O., and Stefan, H.G. 1999. Stream temperature/air temperature relationship: a physical interpretation. *J. Hydrol.* **218**(3–4): 128–141. doi:10.1016/S0022-1694(99)00034-7.
- Myrvold, K.M., and Kennedy, B.P. 2015. Interactions between body mass and water temperature cause energetic bottlenecks in juvenile steelhead. *Ecol. Freshw. Fish.* **24**(3): 373–383. doi:10.1111/eff.12151.
- Neuheimer, A.B., and Taggart, C.T. 2007. The growing degree-day and fish size-at-age: the overlooked metric. *Can. J. Fish. Aquat. Sci.* **64**(2): 375–385. doi:10.1139/f07-003.
- NTL LTER. 1991a. North Temperate Lakes LTER: High Frequency Water Temperature Data — Sparkling Lake Raft 1989 — current. University of Wisconsin Center for Limnology, Long Term Ecological Research Network. <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.5.19>.
- NTL LTER. 1991b. North Temperate Lakes LTER Meteorological Data — Woodruff Airport 1989 — current. University of Wisconsin Center for Limnology, Long Term Ecological Research Network. <https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.1.21>.
- Pääkkönen, J.P., Tikkanen, O., and Karjalainen, J. 2003. Development and validation of a bioenergetics model for juvenile and adult burbot. *J. Fish Biol.* **63**(4): 956–969. doi:10.1046/j.1095-8649.2003.00203.x.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* **39**(2): 175–192. doi:10.1093/icesjms/39.2.175.
- Petersen, J.H., and Paukert, C.P. 2005. Development of a bioenergetics model for humpback chub and evaluation of water temperature changes in the Grand Canyon, Colorado River. *Trans. Am. Fish. Soc.* **134**(4): 960–974. doi:10.1577/T04-090.1.
- Piccolroaz, S., Healey, N.C., Lenters, J.D., Schladow, S.G., Hook, S.J., Sahoo, G.B., and Toffolon, M. 2018. On the predictability of lake surface temperature using air temperature in a changing climate: a case study for Lake Tahoe (U.S.A.). *Limnol. Oceanogr.* **63**(1): 243–261. doi:10.1002/lno.10626.
- Pilgrim, J.M., Fang, X., and Stefan, H.G. 1998. Stream temperature correlations with air temperatures in Minnesota: implications for climate warming. *J. Am. Water Resour. Assoc.* **34**(5): 1109–1121. doi:10.1111/j.1752-1688.1998.tb04158.x.
- Pitcher, T.J., and Macdonald, P.D.M. 1973. Two models for seasonal growth in fishes. *J. Appl. Ecol.* **10**(2): 599–606. doi:10.2307/2402304.
- Power, M., and McKinley, R.S. 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. *Trans. Am. Fish. Soc.* **126**(4): 549–558. doi:10.1577/1548-8659(1997)126<0549:LVLSS>2.3.CO;2.
- Purchase, C.F., Collins, N.C., Morgan, G.E., and Shuter, B.J. 2005. Predicting life history traits of yellow perch from environmental characteristics of lakes. *Trans. Am. Fish. Soc.* **134**: 1369–1381. doi:10.1577/T04-182.1.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Read, J.S., Winslow, L.A., Hansen, G.J.A., Van, Den, Hoek, J., Hanson, P.C., Bruce, L.C., and Markfort, C.D. 2014. Simulating 2368 temperate lakes reveals weak coherence in stratification phenology. *Ecol. Modell.* **291**: 142–150. doi:10.1016/j.ecolmodel.2014.07.029.
- Rennie, M.D., Purchase, C.F., Shuter, B.J., Collins, N.C., Abrams, P.A., and Morgan, G.E. 2010. Prey life-history and bioenergetic responses across a pre-

- dationgradient.J.FishBiol.77(6):1230–1251.doi:10.1111/j.1095-8649.2010.02735.x.PMID:21039502.
- Robertson, D.M., and Ragotzkie, R.A. 1990. Changes in the thermal structure of moderate to large sized lakes in response to changes in air temperature. *Aquat. Sci.* 52(4): 360–380. doi:10.1007/BF00879763.
- Rose, K.C., Winslow, L.A., Read, J.S., and Hansen, G.J.A. 2016. Climate-induced warming of lakes can be either amplified or suppressed by trends in water clarity. *Limnol. Oceanogr. Lett.* 1(1): 44–53. doi:10.1002/lo2.10027.
- Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (137 Cs). *Can. J. Fish. Aquat. Sci.* 53(4): 734–745. doi:10.1139/f95-046.
- Rypel, A.L. 2012. Meta-analysis of growth rates for a circumpolar fish, the northern pike (*Esox lucius*), with emphasis on effects of continent, climate and latitude. *Ecol. Freshw. Fish*, 21(4): 521–532. doi:10.1111/j.1600-0633.2012.00570.x.
- Rypel, A.L., and David, S.R. 2017. Pattern and scale in latitude–production relationships for freshwater fishes. *Ecosphere*, 8(1): e01660. doi:10.1002/ecs2.1660.
- Schaeffer, J.S., Haas, R.C., Diana, J.S., and Breck, J.E. 1999. Field test of two energetic models for yellow perch. *Trans. Am. Fish. Soc.* 128: 414–435. doi:10.1577/1548-8659(1999)128<0414:FTOTEM>2.0.CO;2.
- Schlesinger, D.A., and Regier, H.A. 1982. Climatic and morphoedaphic indices of fish yields from natural lakes. *Trans. Am. Fish. Soc.* 111: 141–150. doi:10.1577/1548-8659(1982)111<141:CAMIOF>2.0.CO;2.
- Schoenebeck, C.W., Chipps, S.R., and Brown, M.L. 2008. Improvement of an esocid bioenergetics model for juvenile fish. *Trans. Am. Fish. Soc.* 137(6): 1891–1897. doi:10.1577/T07-229.1.
- Sellers, T.J., Parker, B.R., Schindler, D.W., and Tonn, W.M. 1998. Pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light. *Can. J. Fish. Aquat. Sci.* 55(1): 170–179. doi:10.1139/f97-232.
- Shuter, B.J., Schlesinger, D.A., and Zimmerman, A.P. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. *Can. J. Fish. Aquat. Sci.* 40(10): 1838–1845. doi:10.1139/f83-213.
- Snover, M.L., Adams, M.J., Ashton, D.T., Bettaso, J.B., and Welsh, H.H. 2015. Evidence of counter-gradient growth in western pond turtles (*Actinemys marmorata*) across thermal gradients. *Freshw. Biol.* 60(9): 1944–1963. doi:10.1111/fwb.12623.
- Soderberg, R.W. 1992. Linear fish growth models for intensive aquaculture. *Progr. Fish-Cult.* 54(4): 255–258. doi:10.1577/1548-8640(1992)054<0255:LFGMFI>2.3.CO;2.
- Tabor, R., Luecke, C., and Wurtsbaugh, W. 1996. Effects of *Daphnia* availability on growth and food consumption of rainbow trout in two Utah reservoirs. *N. Am. J. Fish. Manage.* 16(3): 591–599. doi:10.1577/1548-8675(1996)016<0591:EODAOG>2.3.CO;2.
- Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. *Bioscience*, 45(11): 759–771. doi:10.2307/1312628.
- van der Have, T.M., and de Jong, G. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. *J. Theor. Biol.* 183: 329–340. doi:10.1006/jtbi.1996.0224.
- Venturelli, P.A., Lester, N.P., Marshall, T.R., and Shuter, B.J. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. *Can. J. Fish. Aquat. Sci.* 67(7): 1057–1067. doi:10.1139/F10-041.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* 10: 181–213.
- Wallich, C. 1901. Method of recording egg development, for use of fish-culturists. *In* Report of Commissioner of Fish and Fisheries. pp. 185–195.
- Ward, H.G.M., Post, J.R., Lester, N.P., Askey, P.J., and Godin, T. 2017. Empirical evidence of plasticity in life-history characteristics across climatic and fish density gradients. *Can. J. Fish. Aquat. Sci.* 74(4): 464–474. doi:10.1139/cjfas-2016-0023.
- Ware, D.M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Board Can.* 35(2): 220–228. doi:10.1139/f78-036.
- Wetzel, R.G., and Likens, G.E. 2000. The heat budget of lakes. *In* Limnological analyses. Springer. pp. 45–56.

Supplementary Material – Additional Analyses and Methodological Details



**Figure S1.** (a-b) The effect of temperature, activity level, and consumption (as a proportion of maximum consumption,  $p(C_{max})$ ) on daily growth in length for brown bullhead *Ameiurus nebulosus*, based on a bioenergetics model. (c-d) Relative brown bullhead growth in length (i.e., growth as a proportion of maximum growth) across levels of temperature, activity, and consumption.

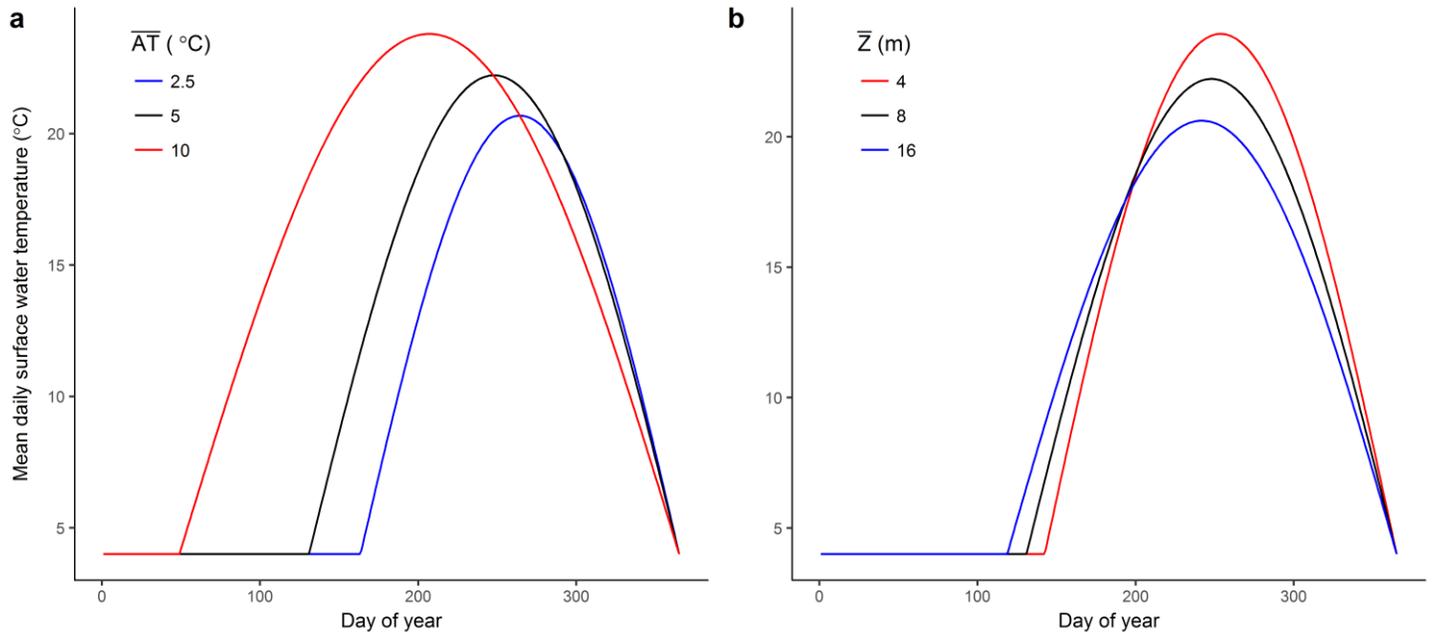


**Figure S2.** (a-b) The effect of temperature, activity level, and consumption (as a proportion of maximum consumption,  $p(C_{max})$ ) on daily growth in length for tiger muskellunge (northern pike *Esox lucius* X muskellunge *Esox masquinongy*), based on a bioenergetics model. (c-d) Relative tiger muskellunge growth in length (i.e., growth as a proportion of maximum growth) across levels of temperature, activity, and consumption.

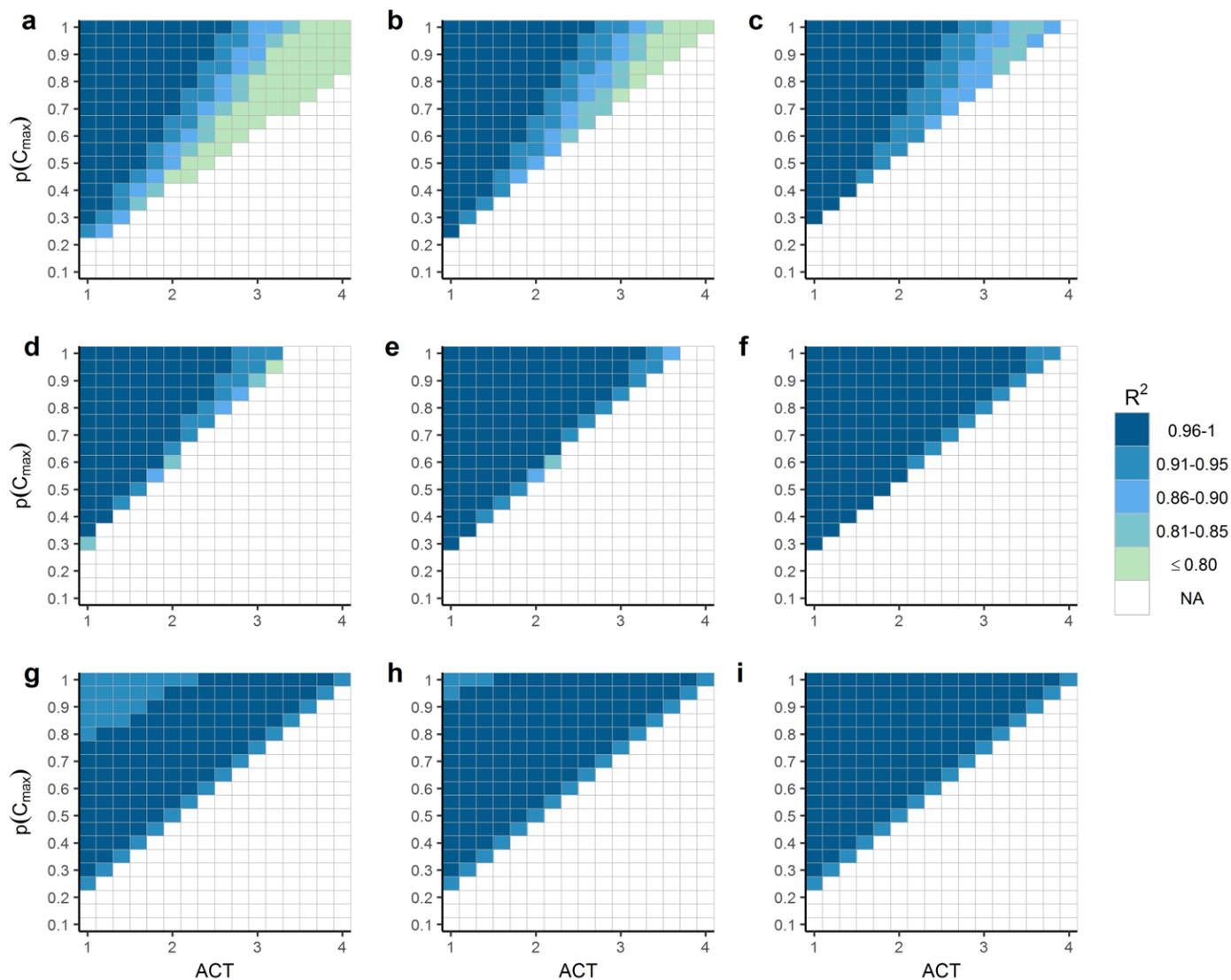
### Supplementary Material A – Influence of mean annual air temperature and mean lake depth on the surface water temperature cycle

We used the Shuter et al. (1983) water temperature model (see text for details) to demonstrate the effect of varying mean annual air temperature ( $\overline{AT}$ ) and mean lake/thermocline depth ( $\overline{Z}$ ) on the surface water temperature cycle. We first simulated annual water temperature cycles with  $\overline{Z}$  fixed at 8 m and  $\overline{AT}$  at 2.5, 5, and 10 °C. We then repeated the simulation with  $\overline{AT}$  fixed at 5 °C and  $\overline{Z}$  at 4, 8, and 16 m. These values cover a range of scenarios that is realistic for many lakes in North America.

Our results suggest that variation in  $\overline{AT}$  generally has a larger impact on the surface water temperature cycle than variation in  $\overline{Z}$  across the range of values that we investigated (Fig. S3). In particular, variation in  $\overline{AT}$  has a much larger impact on the duration of the ice-free season than variation in  $\overline{Z}$ .



**Figure S3.** Effect of (a) mean annual air temperature ( $\overline{AT}$ ) and (b) mean lake/thermocline depth ( $\overline{Z}$ ) on the annual surface water temperature cycle, based on the Shuter et al. (1983) model. In these simulations, day 0 is the first day on which the surface of the simulated lake is frozen.

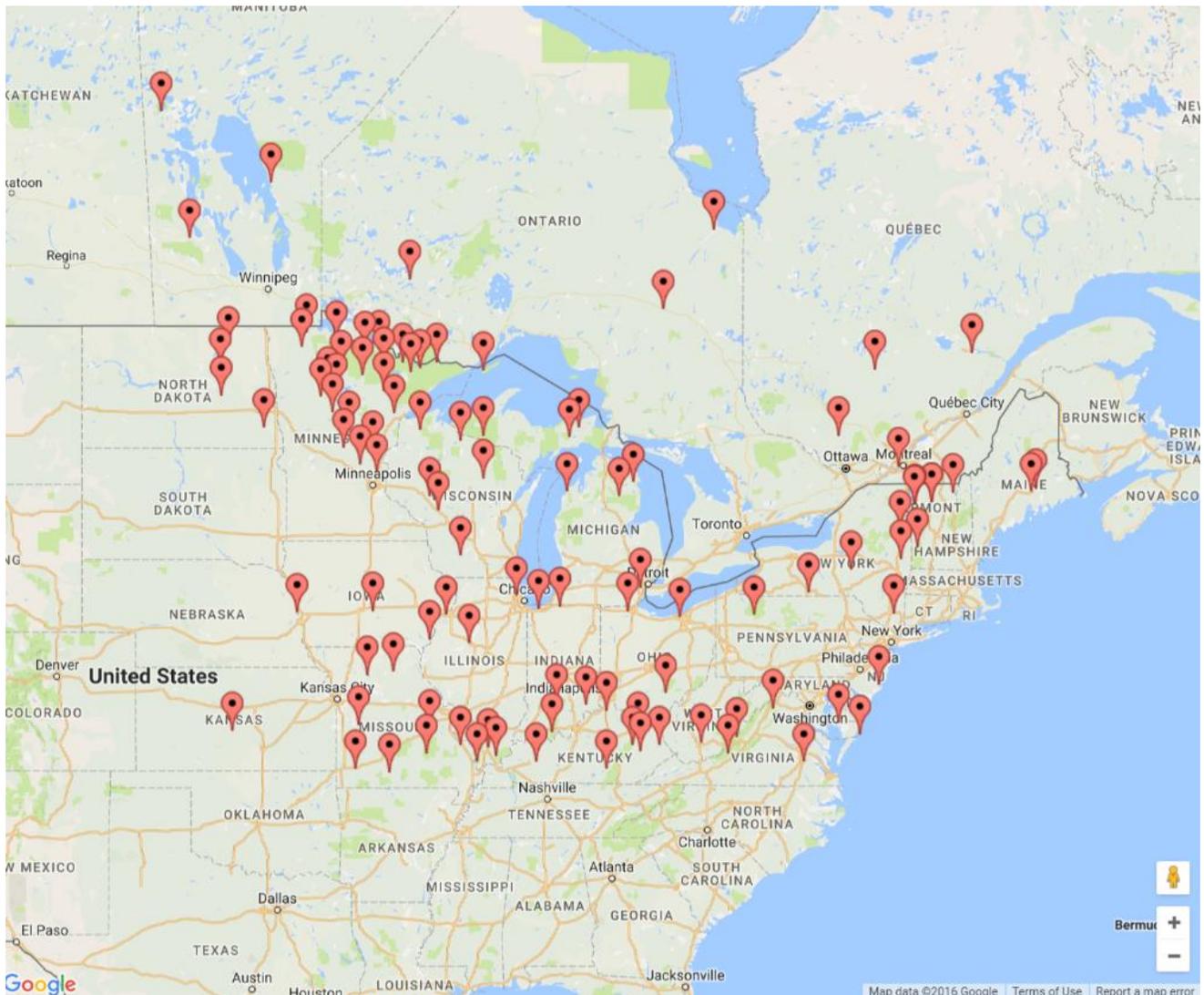


**Figure S4.** Coefficients of determination (adjusted  $R^2$ ) from linear model fits to the length vs. water-based degree-day ( $WDD_5$ ) relationship from five year growth simulations given various combinations of consumption (proportion of maximum consumption,  $p(C_{max})$ ), activity (ACT), and initial size (columns). (a-c) Results from the yellow perch *Perca flavescens* bioenergetics model, with initial sizes of (a) 25 mm, (b) 50 mm, and (c) 75 mm. (d-f) Results from the brown bullhead *Ameiurus nebulosus* bioenergetics model, with initial sizes of (d) 50 mm, (e) 100 mm, and (f) 150 mm. (g-i) Results from the tiger muskellunge (northern pike *Esox lucius* X muskellunge *Esox masquinongy*) bioenergetics model, with initial sizes of (g) 100 mm, (h) 150 mm, and (i) 200 mm. Bioenergetics simulations incorporated empirical water temperature data (1 m depth) from Lake Lacawac, PA. White cells (“NA”) denote cases in which individuals did not grow across all five years.

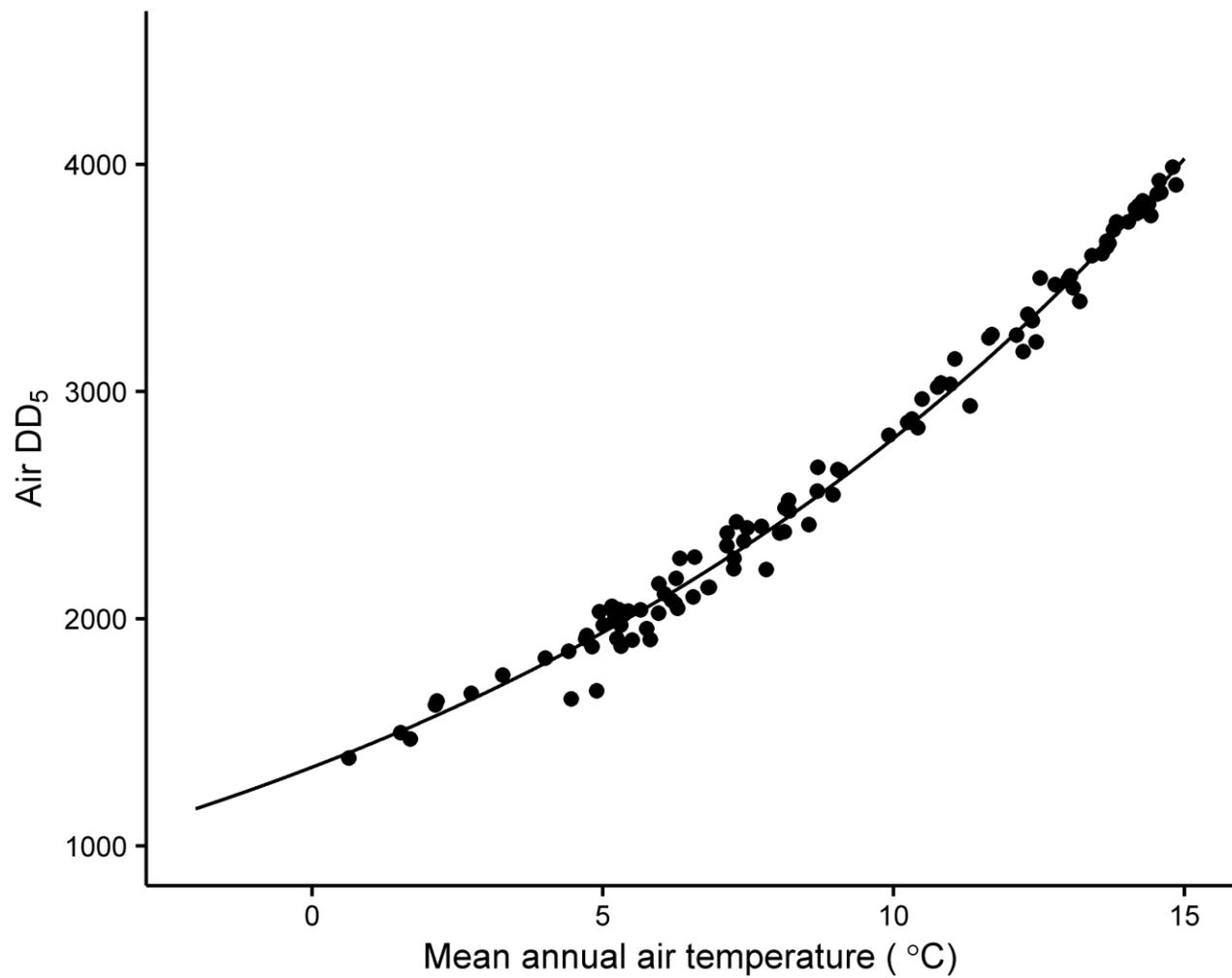
### Supplementary Material B – Empirical relationship for predicting air-based degree-days from mean annual air temperatures

To predict air-based degree-days above 5 °C ( $ADD_5$ ) from mean annual air temperatures ( $\overline{AT}$ ), we collected empirical air temperature data from 107 weather stations in the United States and Canada using the National Oceanic and Atmospheric Administration Climate Data Online tool (<https://www.ncdc.noaa.gov/cdo-web/>). The locations of these 107 weather stations are shown in Fig. S5. The data described mean daily air temperatures from 1 January through 31 December 2015, and all datasets were continuous. We used these data to calculate both  $\overline{AT}$  and  $ADD_5$ , and we constructed a relationship to predict  $ADD_5$  from  $\overline{AT}$  (Fig. S6):

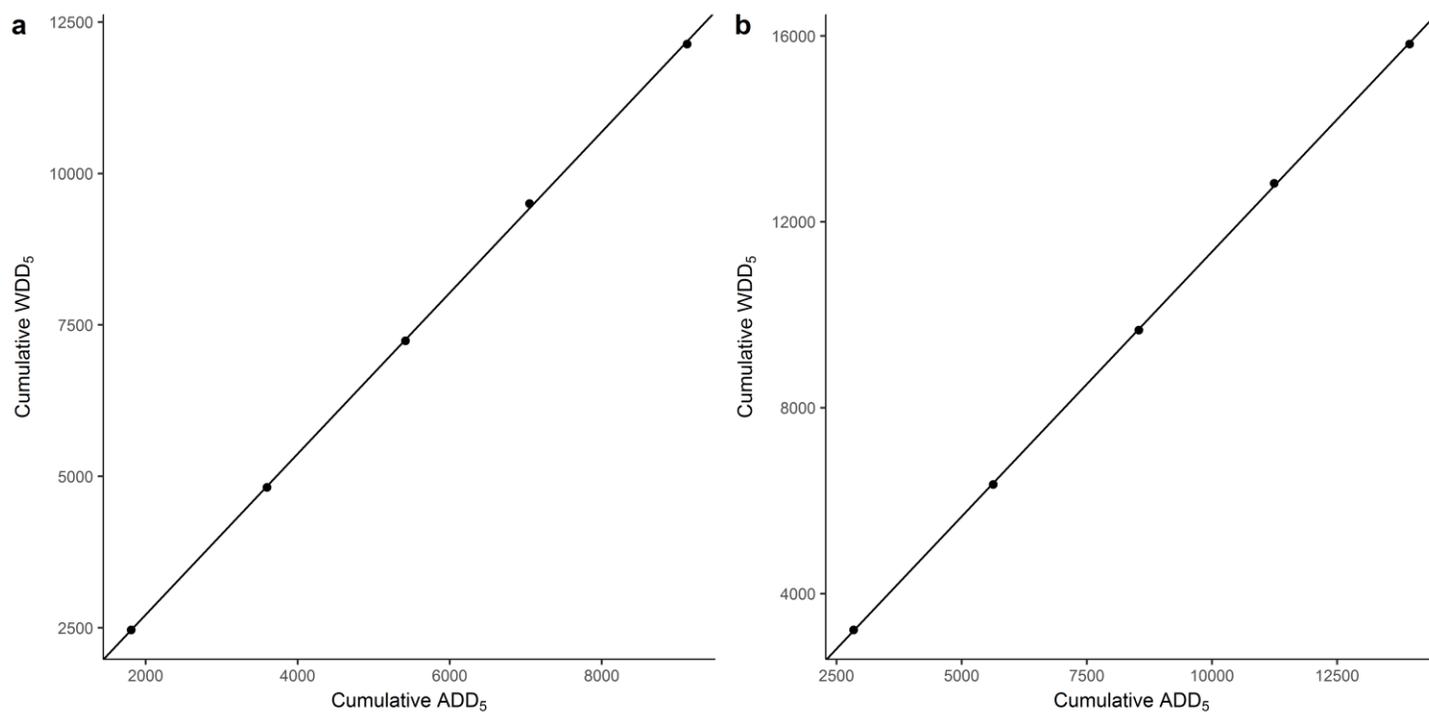
$$ADD_5 = 1346.8 \cdot e^{0.0729 \cdot \overline{AT}}.$$



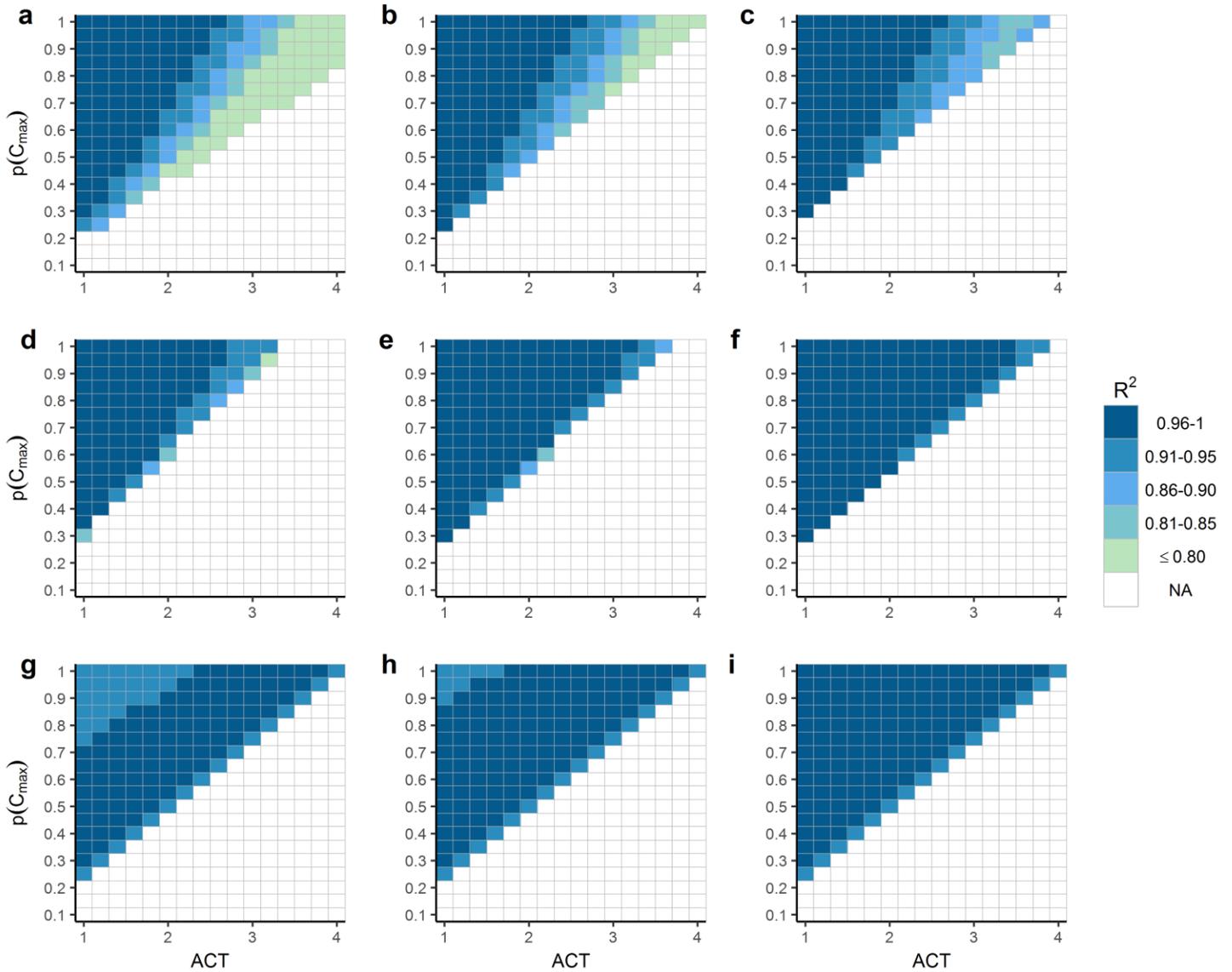
**Figure S5.** Locations of air temperature stations used to generate the empirical relationship for predicting air-based degree-days above 5 °C from mean annual air temperatures. Image ©2016 Google.



**Figure S6.** Empirical relationship between mean annual air temperature (°C) and air-based degree-days above 5 °C (Air DD<sub>5</sub>) constructed using data from 107 weather stations in the United States and Canada.



**Figure S7.** Cumulative air-based degree-days above 5 °C (ADD<sub>5</sub>) vs. cumulative water-based degree-days above 5 °C (WDD<sub>5</sub>) for (a) Sparkling Lake, WI, USA and (b) Lake Lacawac, PA, USA across five years. Empirical air and water temperature data sources used to calculate these metrics are described in the text. Pearson's  $\rho > 0.99$  for both comparisons.



**Figure S8.** Coefficients of determination (adjusted  $R^2$ ) from linear model fits to the length vs. air-based degree-day ( $ADD_5$ ) relationship from five year growth simulations given various combinations of consumption (proportion of maximum consumption,  $p(C_{max})$ ), activity (ACT), and initial size (columns). (a-c) Results from the yellow perch *Perca flavescens* bioenergetics model, with initial sizes of (a) 25 mm, (b) 50 mm, and (c) 75 mm. (d-f) Results from the brown bullhead *Ameiurus nebulosus* bioenergetics model, with initial sizes of (d) 50 mm, (e) 100 mm, and (f) 150 mm. (g-i) Results from the tiger muskellunge (northern pike *Esox lucius* X muskellunge *Esox masquinongy*) bioenergetics model, with initial sizes of (g) 100 mm, (h) 150 mm, and (i) 200 mm. Bioenergetics simulations incorporated empirical water temperature data (1 m depth) from Lake Lacawac, PA. White cells (“NA”) denote cases in which individuals did not grow across all five years.

### Supplementary Material C – Daily growth across water temperatures for adult fishes

In the main text, we focus on immature fish growth because the linear approximation of the length-at-age vs. DD relationship is typically only valid for growth leading up to maturity (Lester *et al.* 2004; Andersen and Beyer 2015; Honsey *et al.* 2017). However, much like with immature growth, the response of adult growth to water temperature is often nearly linear over a midrange of temperatures. For this reason, some of our results (e.g., the linearity of annual growth vs DD) may also extend to adult growth.

To demonstrate the nearly linear response of adult growth in length to water temperature across middling water temperatures, we conducted brief simulations of daily fish growth using bioenergetics models that were parameterized for adults of three species: white crappie *Pomoxis annularis* (Bajer *et al.* 2004), steelhead *Oncorhynchus mykiss* (Rand *et al.* 1993), and rainbow smelt *Osmerus mordax* (Lantry and Stewart 1993). Parameters and equations for these models are given in Table S1. We assumed that individuals achieved satiation and set the activity multiplier to the suggested number (Table S1). We used geometric mean parameters for the length-weight relationship from FishBase (Froese and Pauly 2016) for length-weight conversions, and we set the energy density of oxygen at  $13556 \text{ J}\cdot\text{g}^{-1}$  (Elliott and Davison 1975). We set initial fish sizes at 253 mm (250 g), 453 mm (1 kg), and 197 mm (60 g) for adult white crappie, steelhead, and rainbow smelt, respectively. Our results show that, although the shapes of the relationships differ, daily growth is nearly linear with water temperature across a midrange of temperatures for these adult fish models, much like it is for immature fishes (Fig. S9).

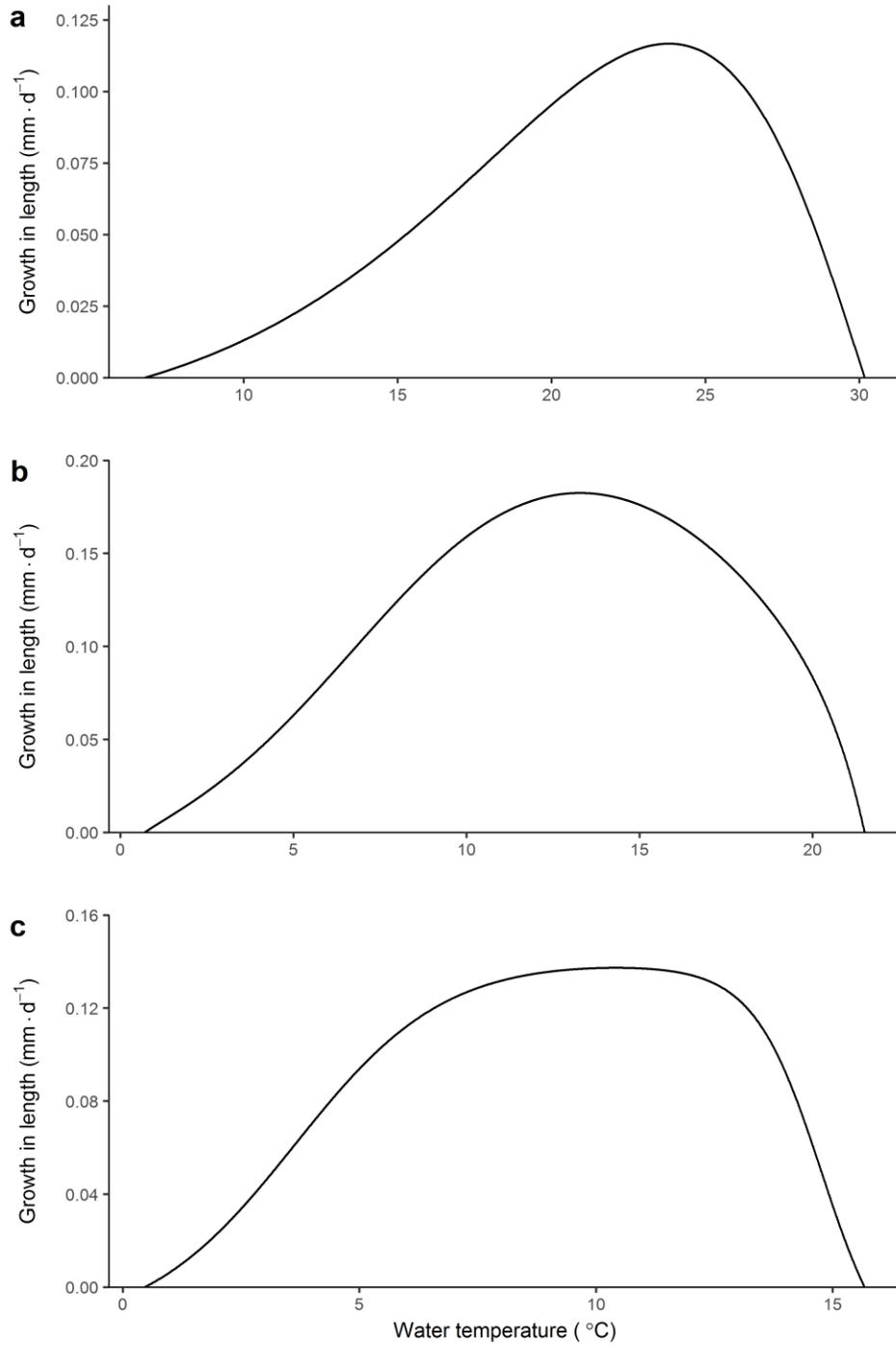
**Table S1.** Bioenergetics equations and parameters used for supplemental simulations. All models follow the Wisconsin bioenergetics framework; see Hanson *et al.* (1997) for equations and details. Sources are listed in footnotes.

Model component	Model species		
	White crappie <sup>1</sup>	Steelhead <sup>2</sup>	Rainbow smelt <sup>3</sup>
Consumption equation	2	3	3
CA	1.2589	0.628	0.18
CB	-0.661	-0.3	-0.275
CQ	2.945	5	3
CTO	24	20	10
CTM	32	20	12
CTL	-	24	18
CK1	-	0.33	0.4
CK4	-	0.2	0.01
Respiration equation	1	1	1
RA	0.02366	0.00264	0.0027
RB	-0.623	-0.217	-0.216
RQ	0.0237	0.06818	0.036
RTO	0	0.0234	0
RTM	0	0	0
RTL	0	25	0
RK1	1	1	0
RK4	0	0.13	0
ACT	1	9.7	1
BACT	0	0.0405	0
SDA	0.16	0.172	0.175
Egestion-excretion equation	1	3	1
FA	0.104	0.212	0.16
FB	0	-0.222	0
FG	0	0.631	0
UA	0.068	0.0314	0.1
UB	0	0.58	0
UG	0	-0.299	0
Energy density equation	1	2	1
Predator energy density (J·g <sup>-1</sup> )	4186	-	4814
Alpha <sub>1</sub>	-	5764	-
Beta <sub>1</sub>	-	0.9862	-
Cutoff (g)	-	4000	-
Alpha <sub>2</sub>	-	7602	-
Beta <sub>2</sub>	-	0.5266	-
Prey energy density (J·g <sup>-1</sup> )	3500	3500	3500

<sup>1</sup>Bajer et al. (2004)

<sup>2</sup>Rand et al. (1993)

<sup>3</sup>Lantry and Stewart (1993)



**Figure S9.** Daily growth in length (assuming satiation) across water temperatures for adult (a) white crappie *Pomoxis annularis*, (b) steelhead *Oncorhynchus mykiss*, and (c) rainbow smelt *Osmerus mordax*, based on bioenergetics models (Table S1).

## Supplementary Material D – Estimating the base temperature for growth using annual growth simulations

If degree-days (DD) are an accurate index for the thermal scope for growth, then growth should be proportional to DD provided that DD are calculated using the correct base temperature for growth ( $T_0$ ; the temperature below which growth is assumed to be negligible). Using this logic, one can estimate  $T_0$  for a given species by finding the  $T_0$  value for which the growth vs. DD relationship is proportional (i.e., passes through the origin).

Here, we demonstrate this approach using the juvenile yellow perch bioenergetics model (Table 1) and the annual growth simulation framework described in the text (see the two subsections entitled 'Annual growth'). We chose to estimate  $T_0$  for air-based degree-days (ADD) in order to further promote their application. We used the approach and empirical data described in Appendix B to construct relationships between mean annual air temperatures and ADD at  $T_0$  values ranging from 0-15 °C. The parameters for these relationships are given in Table S2. We then used these relationships to estimate ADD from the hypothetical mean annual air temperatures used in the simulations, and we compared annual growth to ADD at various  $T_0$  values. Our results suggest that the juvenile yellow perch annual growth vs ADD relationship passes through the origin when  $T_0$  is roughly 9 °C (Fig. 9 in main text).

**Table S2.** Parameters for relationships between mean annual air temperatures and air-based degree-days at various base temperature values (derived from empirical air temperature data; see Appendix B). Equations take the following form:  $ADD_{T_0} = \alpha e^{\beta \cdot \overline{AT}}$ , where  $ADD_{T_0}$  is air-based degree-days at base temperature  $T_0$ ,  $\overline{AT}$  is mean annual air temperature, and  $\alpha$  and  $\beta$  are parameters.

Base temperature ( $T_0$ ; °C)	$\alpha$	$\beta$
0	2244.83	0.0613
1	2044.76	0.0635
2	1855.44	0.0657
3	1676.31	0.0680
4	1506.71	0.0704
5	1346.80	0.0729
6	1196.23	0.0757
7	1054.94	0.0786
8	922.88	0.0817
9	800.67	0.0851
10	687.39	0.0887
11	583.10	0.0927
12	486.54	0.0974
13	396.94	0.1032
14	315.02	0.1104
15	241.93	0.1193

## Supplemental References

- Andersen, K.H., and Beyer, J.E. 2015. Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish Fish.* **16**: 1–22.
- Bajer, P.G., Hayward, R.S., Whitledge, G.W., and Zweifel, R.D. 2004. Simultaneous identification and correction of systematic error in bioenergetics models: demonstration with a white crappie (*Pomoxis annularis*) model. *Can. J. Fish. Aquat. Sci.* **61**: 2168–2182. doi:10.1139/F04-160.
- Elliott, J.M., and Davison, W. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia* **19**(3): 195–201. doi:10.1007/BF00345305.
- Froese, R., and Pauly, D. (Editors). 2016. FishBase. World wide web electronic publication. [www.fishbase.org](http://www.fishbase.org).
- Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish Bioenergetics 3.0 for Windows. University of Wisconsin Sea Grant Institute, Madison, WI.
- Honsey, A.E., Staples, D.F., and Venturelli, P.A. 2017. Accurate estimates of age-at-maturity from the growth trajectories of fishes and other ectotherms. *Ecol. Appl.* **27**(July): 182–192. doi:10.1002/eap.1421.
- Lantry, B.F., and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. *Trans. Am. Fish. Soc.* **122**(5): 951–976. doi:10.1577/1548-8659(1993)122<0951:EEORSI>2.3.CO;2.
- Lester, N.P., Shuter, B.J., and Abrams, P.A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proc. R. Soc. London B* **271**(1548): 1625–1631. doi:10.1098/rspb.2004.2778.
- Rand, P.S., Stewart, D.J., Seelbach, P.W., Jones, M.L., and Wedge, L.R. 1993. Modeling Steelhead Population Energetics in Lakes Michigan and Ontario. *Trans. Am. Fish. Soc.* **122**(5): 977–1001. doi:10.1577/1548-8659(1993)122<0977.
- Shuter, B.J., Schlesinger, D.A., and Zimmerman, A.P. 1983. Empirical predictors of annual surface water temperature cycles in North American Lakes. *Can. J. Fish. Aquat. Sci.* **40**(10): 1838–1845. doi:10.1139/f83-213.