

# Temperature-Driven Regime Shifts in the Dynamics of Size-Structured Populations

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**ABSTRACT:** Global warming impacts virtually all biota and ecosystems. Many of these impacts are mediated through direct effects of temperature on individual vital rates. Yet how this translates from the individual to the population level is still poorly understood, hampering the assessment of global warming impacts on population structure and dynamics. Here, we study the effects of temperature on intraspecific competition and cannibalism and the population dynamical consequences in a size-structured fish population. We use a physiologically structured consumer-resource model in which we explicitly model the temperature dependencies of the consumer vital rates and the resource population growth rate. Our model predicts that increased temperature decreases resource density despite higher resource growth rates, reflecting stronger intraspecific competition among consumers. At a critical temperature, the consumer population dynamics destabilize and shift from a stable equilibrium to competition-driven generation cycles that are dominated by recruits. As a consequence, maximum age decreases and the proportion of younger and smaller-sized fish increases. These model predictions support the hypothesis of decreasing mean body sizes due to increased temperatures. We conclude that in size-structured fish populations, global warming may increase competition, favor smaller size classes, and induce regime shifts that destabilize population and community dynamics.

**Keywords:** cannibalism, competition, global warming, population dynamics, PSPM.

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## Introduction

Understanding and predicting the ecological impacts of climate change has become a major goal of today's science. Climate change is believed to have severe impacts on virtually all ecosystems and biota (Stenseth et al. 2002; Par-

mesan and Yohe 2003; Root et al. 2003), including many freshwater organisms (Schindler 2001; Sharma 2007). The most important and well-known ecological responses to climate change are shifts in species' distribution ranges, changes in the timing of events, and alterations in gene frequencies. Further, climate-driven changes in individual body size have recently been reported in aquatic animals (Millien et al. 2006; Daufresne et al. 2009).

For ectotherms such as freshwater fish that control body temperature through external means, warming is a particularly critical component of climate change. Temperature has profound impacts on most individual-level processes, including development, locomotion, growth, survival, and fitness (Jobling 1994; Wootton 1998; Angilletta 2009). Most of these impacts are mediated through the direct effects of temperature on biochemical and physiological rates that are linked to energetic processes, most importantly, food intake and metabolic costs. For many physiological processes the temperature relationships are well known, but the population-level consequences are poorly understood. Therefore, approaches for investigating population dynamical consequences of temperature change are needed to further advance our understanding of potential impacts of global warming on natural populations.

Most ectothermic animal populations are structured with respect to size. Individual body size is of fundamental importance, since virtually all physiological processes scale with size, including rates of metabolism, foraging, and digestion (Peters 1983; Calder 1984). Body size is directly linked to life-history traits, individual competitive ability, and cannibalistic potential (Fox 1975; Arendt 2007). An approach that has been widely used to link the size-dependent physiology of individuals to population-level processes is that of physiologically structured population models (PSPMs; Metz and Diekmann 1986; de Roos et al. 1992). Theoretical work using PSPMs has shown that the

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dynamics of size-structured populations depend on the strengths and nature of inter-cohort and inter-age-class competition and that changes in the size scaling of physiological rates can alter the dynamics between population oscillations and stability (Persson et al. 1998). Further, the population dynamics depend on the potential for intraspecific predation or cannibalism (Claessen et al. 2000, 2002), a common phenomenon in animals (Fox 1975; Smith and Reay 1991). It has been shown theoretically and empirically that the interplay between these two size-dependent interactions can lead to major shifts in population dynamics (Persson et al. 2003). Although it is known that individual-level processes critically depend on temperature, its effects on size-dependent competition and cannibalism have not been studied before.

In a previous attempt, Vasseur and McCann (2005) used a simple bioenergetics model to determine the influence of temperature on a consumer-resource interaction in order to predict the consequences of temperature changes on the dynamics and persistence of consumer populations. Their results indicate that warming is likely to destabilize consumer-resource interactions and that the qualitative response of a population depends on whether individual metabolic rate increases faster or slower with temperature than ingestion rate. Their model is a first step toward a bioenergetics theory of the impact of climate change on food web dynamics, but it has two critical shortcomings, which are the absence of size structure and the simplifying assumption about the temperature dependence of biological rates that does not allow for a higher metabolic efficiency of large compared to small individuals in cold environments (Kozłowski et al. 2004). Van de Wolfshaar et al. (2008) present the first size-structured population model that accounts explicitly for temperature effects on vital rates. They show that the temperature and size dependence of vital rates may have fatal consequences for winter survival of both individuals and the population as a whole. However, they did not study the effect of changing temperature on population dynamics.

Here we investigate the impact of temperature on intraspecific competition and cannibalism, levels of resource exploitation, and population size structure and dynamics. We calibrate our model to Eurasian perch (*Perca fluviatilis* L., subsequently referred to as “perch”), a common freshwater fish for which abundant physiological data and a validated population model exist. The basic model for our study is described in Claessen et al. (2000) and builds on a model presented in Persson et al. (1998). Their models correctly predicted growth trajectories and population dynamics observed in natural populations (Sanderson et al. 1999; Persson et al. 2000, 2004; Svanbäck and Persson 2009), thereby showing that the studied effects of intraspecific interactions on population dynamics reflect com-

mon characteristics of size-structured populations. To this model we add general temperature dependencies of individual physiological rates. With this study, we aim for a mechanistic understanding of population-level consequences of increasing temperatures due to global warming.

### Model Description

We model the effects of temperature on the dynamics of a cannibalistic consumer population using a physiologically structured population model based on individual-level processes (Metz and Diekmann 1986; de Roos et al. 1992). The individual-level processes are determined by the consumers' physiological state and interactions with their environment (consumer-resource interactions), whereas the population state is the distribution of individuals over all possible individual states. Our model is based on the size-structured consumer-resource model described by Persson et al. (1998), with added cannibalistic interactions among the consumers, as presented by Claessen et al. (2000). This model has been calibrated to perch using empirically derived functions and parameter values to describe the physiological state of an individual fish.

We extend this size-structured model by simulating the effects of temperature on both (i) the consumers' individual physiological state through rates of food intake and metabolism and (ii) the population growth rate of the resource. Data for the effects of temperature on consumption and metabolism as well as the allometric scaling of these processes were taken from a bioenergetics model (Karås and Thoresson 1992) based on experimental data for perch (Lessmark 1983). All model equations and parameters are listed in tables 1 and 2, and a full description is presented in the appendix in the online edition of the *American Naturalist*. The model is simulated with the “escalator boxcar train” method (de Roos et al. 1992) using the software EBTtool (<http://staff.science.uva.nl/~aroes>).

### Individual-Level Processes

Total body mass is composed of two physiological variables: irreversible mass, consisting of structural mass such as bones and vital organs that cannot be starved away, and reversible mass, consisting of energy reserves such as fat, muscle, and gonad tissue. Energy is acquired through food intake, lost through respiration, and converted to reversible and irreversible mass according to previously described allocation rules (Persson et al. 1998). The amount of net energy an individual can allocate to somatic or reproductive growth is the difference between energy acquired from food intake, accounting for conversion efficiency, and energy required for metabolism (fig. 1; tables 1, 2). Perch consumption consists of piscivory (cannibal-

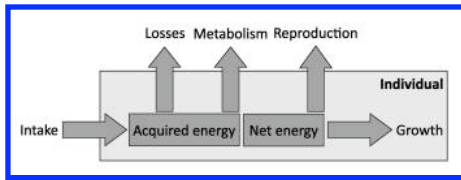
**Table 1:** Variables and parameter values calibrated to Eurasian perch

Symbol	Value	Unit	Interpretation	Reference
<b>Variables:</b>				
$x_i$	...	g	Irreversible mass of cohort $i$	
$y_i$	...	g	Reversible mass of cohort $i$	
$N_i$	...	individuals $L^{-1}$	Abundance of cohort $i$	
$k$	...	...	Number of cohorts	
$R$	...	$L^{-1}$	Resource population density	
<b>Environment:</b>				
$T$	Varied	$^{\circ}C$	Temperature	
$S$	120	days	Length of growing season	Le Cren 1958
<b>Ontogeny and mortality:</b>				
$w_b$	.0018	g	Egg mass	Claessen et al. 2000
$x_r$	4.6	g	Maturation bone mass	Claessen et al. 2000
$q_j$	.74	...	Juvenile maximum condition	Claessen et al. 2000
$q_A$	1.37	...	Adult maximum condition	Claessen et al. 2000
$k_r$	.5	...	Gonad-offspring conversion	Claessen et al. 2000
$\lambda_1$	52.3	mm $g^{-\lambda_2}$	Allometric size scalar	Le Cren 1958
$\lambda_2$	.303	...	Allometric size exponent	Le Cren 1958
$\mu_0$	.01	day $^{-1}$	Background mortality rate	Claessen et al. 2000
$q_s$	.2	...	Starvation condition	Claessen et al. 2000
$s$	.2	day $^{-1}$	Starvation coefficient	Claessen et al. 2000
<b>Consumption:</b>				
$\alpha$	.62	...	Allometric exponent of planktivory	Claessen et al. 2000
$\hat{A}$	3.0E+4	L day $^{-1}$	Maximum zooplankton attack rate	Claessen et al. 2000
$w_{opt}$	8.2	g	Optimal forager size	Claessen et al. 2000
$\sigma$	.6	...	Allometric exponent of piscivory	Claessen et al. 2000
$\beta$	0, 100	L day $^{-1}$ mm $^{\sigma}$	Cannibalistic voracity (with/without)	
$\delta$	.06	mm $^{-1}$	Minimum victim/cannibal ratio	Claessen et al. 2000
$\epsilon$	.45	mm $^{-1}$	Maximum victim/cannibal ratio	Claessen et al. 2000
$\varphi$	.2	mm $^{-1}$	Optimal victim/cannibal ratio	Claessen et al. 2000
$\xi_1$	5.0	day $g^{-(1+\xi_2)}$	Allometric scalar of handling	Claessen et al. 2000
$\xi_2$	-.8	...	Allometric exponent of handling	Claessen et al. 2000
$\vartheta_a$	2.8	...	Allometric scalar of $Q_a$	Karås and Thoresson 1992
$\theta_a$	.072	...	Allometric exponent of $Q_a$	Karås and Thoresson 1992
$\gamma_{a, max}$	32.0	$g^{-\nu_{a, max}} ^{\circ}C$	Allometric scalar of $T_{max}$	Karås and Thoresson 1992
$\nu_{a, max}$	-.029	...	Allometric exponent of $T_{max}$	Karås and Thoresson 1992
$\gamma_{a, opt}$	28.0	$g^{-\nu_{a, opt}} ^{\circ}C$	Allometric scalar of $T_{opt}$	Karås and Thoresson 1992
$\nu_{a, opt}$	-.043	...	Allometric exponent of $T_{opt}$	Karås and Thoresson 1992
<b>Metabolism:</b>				
$\rho_1$	.033	$g^{(1-\rho_2)}$ day $^{-1}$	Allometric scalar of metabolism	Claessen et al. 2000
$\rho_2$	.77	...	Allometric exponent of metabolism	Claessen et al. 2000
$\vartheta_m$	2.0	...	Allometric scalar of $Q_m$	Karås and Thoresson 1992
$\theta_m$	.073	...	Allometric exponent of $Q_m$	Karås and Thoresson 1992
$\gamma_{m, max}$	36.5	$g^{-\nu_{m, max}} ^{\circ}C$	Allometric scalar of $T_{max}$	Karås and Thoresson 1992
$\nu_{m, max}$	-.013	...	Allometric exponent of $T_{max}$	Karås and Thoresson 1992
$\gamma_{m, opt}$	32.0	$g^{-\nu_{m, opt}} ^{\circ}C$	Allometric scalar of $T_{opt}$	Karås and Thoresson 1992
$\nu_{m, opt}$	-.029	...	Allometric exponent of $T_{opt}$	Karås and Thoresson 1992
<b>Resource:</b>				
$K$	100	$L^{-1}$	Carrying capacity	Claessen et al. 2000
$M$	3.0E-5	g	Wet mass of zooplankton	Claessen et al. 2000
$r_z$	.58	day $^{-1}$	Maximum population growth rate	Mitchell et al. 2004
$T_{z, max}$	32.40	$^{\circ}C$	$T_{max}$ for zooplankton growth	Mitchell et al. 2004
$T_{z, opt}$	27.54	$^{\circ}C$	$T_{opt}$ for zooplankton growth	Mitchell et al. 2004
$Q_z$	1.799	...	Slope of zooplankton growth with $T$	Mitchell et al. 2004

**Table 2:** Model equations

Name	Equation
Standardized weight	$w = x(1 + q_1)$
Length	$l = \lambda_1 w^{\lambda_2}$
Zooplankton attack rate	$A_z(x, y, T) = \hat{A} \left[ \frac{w}{w_{\text{opt}}} \exp\left(1 - \frac{w}{w_{\text{opt}}}\right) \right]^\alpha r_a(x, y, T)$
Cannibalistic attack rate	$A_c(c, v, x, y, T) = \begin{cases} \beta c^\sigma \frac{v - \delta c}{(\varphi - \delta)c} r_a(x, y, T) & \text{if } \delta c < v < \varphi c \\ \beta c^\sigma \frac{\varepsilon c - v}{(\varepsilon - \varphi)c} r_a(x, y, T) & \text{if } \varphi c < v < \varepsilon c \\ 0 & \text{otherwise} \end{cases}$
Zooplankton encounter	$\eta_z(x_p, y_p, T) = A_z(x_p, y_p, T) R m$
Cannibalistic encounter	$\eta_c(x_p, y_p, T) = \sum_j A_c(c_p, v_p, x_p, y_p, T) (x_j + y_j) N_j$
Total encounter rate	$\eta(x_p, y_p, T) = \eta_z(x_p, y_p, T) + \eta_c(x_p, y_p, T)$
Handling time	$H(x_p, y_p, T) = \xi_1 w_i^{\xi_2} \frac{1}{r_a(x, y, T)}$
Food intake rate	$I(x_p, y_p, T) = \frac{\eta(x_p, y_p, T)}{1 + H(x_p, y_p, T) \eta(x_p, y_p, T)}$
Acquired energy	$E_a(x, y, T) = k_e I(x, y, T)$
Maintenance requirements	$E_m(x, y, T) = \rho_1 (x + y)^{\rho_2} r_m(x, y, T)$
Energy balance	$E_g(x, y, T) = E_a(x, y, T) - E_m(x, y, T)$
Energy allocation rule	$\kappa(x, y) = \begin{cases} \frac{1}{(1 + q_1) q_1} \frac{y}{x} & \text{if } x \leq x_f \\ \frac{1}{(1 + q_\lambda) q_\lambda} \frac{y}{x} & \text{if } x > x_f \end{cases}$
Fecundity	$F(x, y) = \begin{cases} \frac{k_f (y - q_1 x)}{w_b} & \text{if } x > x_f \text{ and } y > q_1 x \\ 0 & \text{otherwise} \end{cases}$
Total mortality	$\mu(x, y, T) = \mu_0 + \mu_s(x, y) + \mu_c(x, y, T)$
Starvation mortality	$\mu_s(x, y) = \begin{cases} s(q_s x / y - 1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$
Cannibalistic mortality	$\mu_c(x_p, y_p, T) = \sum_i \frac{A_c(c_p, v_p, x_p, y_p, T) N_i}{1 + H(x_p, y_p, T) \eta(x_p, y_p, T)}$
Resource dynamics	$\frac{dR}{dt} = r_z(T)(K - R) - R \sum_i \frac{A_z(x_p, y_p, T) N_i}{1 + H(x_p, y_p, T) \eta(x_p, y_p, T)}$
Temperature dependence	$r(x, y, T) = V(x, y, T)^{X(x, y, T)} e^{X(x, y, T)[1 - V(x, y, T)]}$
	$V(x, y, T) = \frac{(T_{\max}(x, y) - T)}{(T_{\max}(x, y) - T_{\text{opt}}(x, y))}$
	$X(x, y, T) = W^2 \left[ 1 + \left( 1 + \frac{40}{Y} \right)^{0.5} \right] \frac{1}{400} \quad \text{a}$
	$W = (T_{\max}(x, y) - T_{\text{opt}}(x, y)) \ln Q(x, y)$
	$Y = (T_{\max}(x, y) - T_{\text{opt}}(x, y) + 2) \ln Q(x, y)$
Acquired energy	$T_{a, \text{opt}}(x, y) = \gamma_{a, \text{opt}} (x + y)^{\gamma_{a, \text{opt}}}$
	$T_{a, \text{max}}(x, y) = \gamma_{a, \text{max}} (x + y)^{\gamma_{a, \text{max}}}$
	$Q_a(x, y) = \vartheta_a (x + y)^{\vartheta_a}$
Metabolism	$T_{m, \text{opt}}(x, y) = \gamma_{m, \text{opt}} (x + y)^{\gamma_{m, \text{opt}}}$
	$T_{m, \text{max}}(x, y) = \gamma_{m, \text{max}} (x + y)^{\gamma_{m, \text{max}}}$
	$Q_m(x, y) = \vartheta_m (x + y)^{\vartheta_m}$
Resource growth	$T_{z, \text{max}}, T_{z, \text{opt}}$ , and $Q_z$ directly estimated (see table 1)

<sup>a</sup> The parameter values 40 and 400 had to be changed to 20 and 200, respectively, in the temperature-dependence term for intake rate according to Karås and Thoresson (1992).



**Figure 1:** Illustration of the energy flow in a physiologically structured population model. The amount of net energy an individual can allocate to somatic or reproductive growth is the difference between energy acquired from food intake, accounting for conversion efficiency (losses), and energy required for metabolism.

ism) and planktivory (an unstructured zooplankton resource). We model the effect of temperature on maintenance rate, cannibalistic and zooplankton attack rates, handling time, and resource growth rate.

### Temperature Dependence

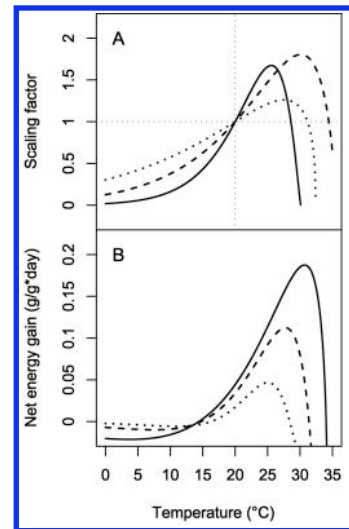
Temperature is constant in our model (i.e., we account only for the average temperature during the growing season, not for daily or seasonal fluctuations). As in previous models, we assume that biological activity outside the growing season is negligible (Person et al. 1998; Claessen et al. 2000). We analyze our model for the temperature range 12°–22°C. This range refers to the average surface temperatures of lakes within the perch distribution range and includes the expected increase in average global surface temperatures during the twenty-first century of ~2°C (IPCC 2007).

We model the temperature dependence of physiological rates by multiplying the default value of each rate with a temperature-dependent factor. All temperature factors equal unity for  $T = 20^\circ$  (fig. 2A), such that for this temperature we obtain the default model described in Claessen et al. (2000). We define three functions with asymmetric hump-shaped temperature relationships that apply to the consumer intake rate, the maintenance rate, and the resource population growth rate. This functional form most adequately describes measures of animal performance by considering the temperature tolerance range and optimum temperature for a specific process (Huey and Kingsolver 1989; Angilletta et al. 2009), as opposed to a simple exponential Arrhenius relationship. The temperature-dependence functions for the consumer were taken from a data-based bioenergetics model for perch (fig. 2B; Lessmark 1983; Karås and Thoreson 1992). Two sets of parameter values were used for scaling metabolic and intake rates with size and temperature (see table 1). Figure 2B shows that the net energy gain of an individual increases faster with temperature for smaller-sized individuals. This means that the difference in relative energy gain between size

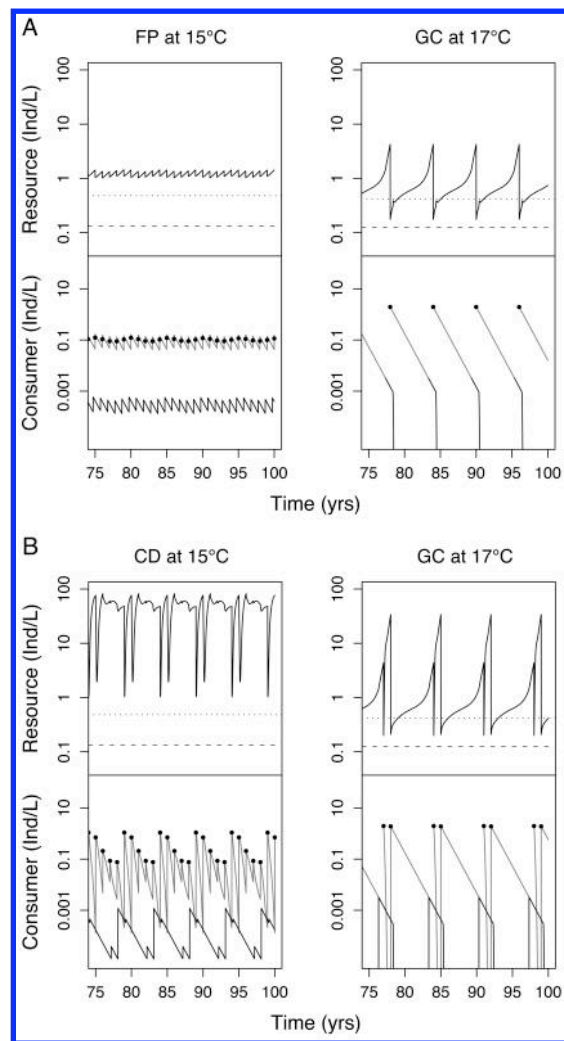
classes changes with temperature. The same functional form as for the consumer rates was applied to describe the temperature dependence of the zooplankton growth rate, which was modeled as an unstructured population (table 1). The parameters were estimated from data on temperature effects on individual and population growth of *Daphnia magna* (fig. 2A; Mitchell et al. 2004).

### Model Behavior and Analysis

For a fixed temperature, our size-structured population model is analogous to the cannibalistic model described by Claessen et al. (2000), and it is analogous to Persson et al.'s (1998) model for the case without cannibalism. Hence, our model exhibits the same types of population dynamics, which we refer to in “Results” (see fig. 3), namely, fixed-point (FP) dynamics, cannibal-driven (CD) dynamics, and recruit-driven generation cycles (GCs). The effect of average summer temperature was analyzed using bifurcation analyses over the temperature range 12°–22°C. A bifurcation plot is constructed as follows: for a large number of fixed temperatures in the specified range, we



**Figure 2:** Temperature-dependence terms (A) for perch consumption (solid lines), perch metabolism (dashed lines), and zooplankton growth rate (dotted lines); and the individual net energy gain (B) as a function of temperature for perch of body weight 0.1 g (solid lines), 1 g (dashed lines), and 10 g (dotted lines). Parameter values were taken from Karås and Thoreson (1992) and Lessmark (1983) for perch and estimated for zooplankton, based on data from Mitchell et al. (2004). Thin dotted lines (A) indicate calibration to a value of 1 at 20°C (see text). The body size of perch was set to 8.2 g, the optimal size for prey attack. The net energy gain for differently sized perch (B) was calculated at a zooplankton density of 2 individuals  $L^{-1}$ , which resembles rather low resource levels where exploitative competition in perch is expected to be high.



**Figure 3:** Daily model output for  $\beta = 0$  (A) and  $\beta = 100$  (B) at 15°C (left) and 17°C (right). *Top*, predicted resource density (solid lines) and critical resource densities (defined as zero-growth resource level) for newborns (dashed lines) and maturing fish (dotted lines). *Bottom*, predicted consumer density of newborns (circles), juveniles (gray lines), and adults (black lines). In the noncannibalistic population (A), the left panel shows fixed-point dynamics (FP), whereas the right panel shows recruit-driven generation cycles (GC), here also referred to as single-cohort cycles. In the cannibalistic population (B), the left panel shows cannibal-driven cycles, whereas the right panel shows a type of generation cycles referred to as “dwarfs-and-giants” cycles. See main text for a detailed description of the dynamics.

run the model for 500 years, sampling the population state yearly during the last 250 years (to omit transient dynamics). The obtained population data are plotted against temperature to obtain the bifurcation plot. This allows one to assess the amplitude and periodicity of population cycles, since a regular cycle at a given temperature will be char-

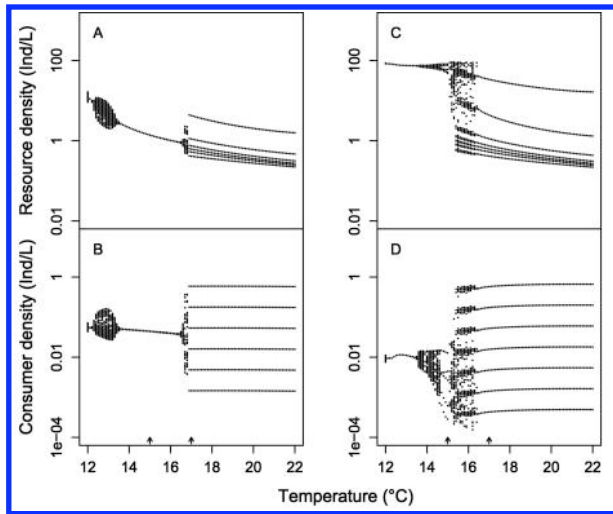
acterized by a fixed number of dots spaced vertically (see figs. 3, 4). We performed bifurcation analyses over temperature for a noncannibalistic population ( $\beta = 0$ ; see eq. [A19] in the appendix) and for various degrees of cannibalism ( $\beta = 0, 5, 10, 25, 50, 100, 300$ ). Complementary bifurcation analyses over the cannibalistic voracity  $\beta$  were performed for discrete temperatures (12°–22°C, in 2°C steps). To further evaluate the model behavior, we used bifurcation analyses of maximum attack rate, digestion rate, and metabolic rate. To analyze the dynamics for a given temperature in detail, we ran our model at a fixed temperature for 100 years with a daily output and sampled during the last 25 years.

### Sensitivity Analysis

First, we analyzed the sensitivity of our results to changes in all parameters specifying the temperature dependence (all parameters new to our model; tables 1, 2), in order to account for the uncertainty in the measured parameters. We did this by performing bifurcation analyses for the cannibalistic and the noncannibalistic populations (see figs. 3, 4), for each parameter value increased or decreased by 10% (60 perturbations in total). We then examined changes in the population dynamics, both qualitatively (types and sequence of dynamics) and quantitatively (temperature at the onset of generation cycles).

Second, we analyzed the effect of changes in the scaling parameter of the attack rate ( $\alpha$ ) on our results for the noncannibalistic population. We did this, because it is known that  $\alpha$  has a strong effect on the population dynamics and the potential for generation cycles because it determines the size dependence of the critical resource density (Persson et al. 1998). Values of  $\alpha$  for freshwater fish preying on zooplankton that are reported in the literature range from 0.47 to 0.68, including for species such as pikeperch (*Stizostedion lucioperca*), roach (*Rutilus rutilus*), bream (*Abramis brama*), bluegill sunfish (*Lepomis macrochirus*), and arctic char (*Salvelinus alpinus*; Persson and de Roos 2006). Hence, we run our model within this range of  $\alpha$  values to mimic the size scaling of attack rates of a variety of other species for which data were available (see table A2).

Third, we analyzed the effects of changes in the “cannibalism window” ( $\delta, \epsilon$ ) on our results for the cannibalistic population. The cannibalism window strongly determines the intraspecific interactions and thus the dynamics of cannibalistic populations (Claessen et al. 2002). Changes in  $\delta$  and  $\epsilon$  were tested at the same time to mimic two other cannibalistic species for which empirical data exist (Persson et al. 2004), yellow perch (*Perca flavescens*), and pike (*Esox lucius*; see table A2).



**Figure 4:** Bifurcation diagrams over the temperature range 12°–22°C for the noncannibalistic ( $\beta = 0$ ; left) and the cannibalistic ( $\beta = 100$ ; right) populations. Shown are population densities of the resource (A, C) and the consumer (B, D). The bistability of the noncannibalistic population is not shown in this plot. The arrows indicate model runs for specific temperature values presented in figure 3.

## Results

Our model predicts that temperature has a major impact on the dynamics of size-structured populations. With increasing temperature, resource density decreases due to increasing food intake and increasing population birth rate in the consumer, which eventually shift the population dynamics from a stable fixed point to competition-driven generation cycles, irrespective of the degree of cannibalism (figs. 3, 4). These shifts in population dynamics are typically associated with an increase in competition (Persson et al. 1998; Claessen et al. 2000). A direct consequence of the different temperature dependencies of the vital rates at the individual level is that energy gain increases faster with temperature for small individuals (fig. 2B). Therefore, cool conditions favor big individuals, while warm conditions favor small ones. Increasing temperature hence reinforces the competitive advantage of small over large individuals, which enhances the mechanism that causes generation cycles (Persson et al. 1998). Below we present a detailed analysis of the model behavior for a cannibalistic and a noncannibalistic population.

### Population Dynamics

The effect of temperature on the consumer and resource dynamics is exemplified in figure 4. It shows the bifurcation plots over temperature for a noncannibalistic (fig.

4A, 4B) and a cannibalistic (fig. 4C, 4D) consumer population and the respective resource densities.

In the noncannibalistic case (fig. 4A, 4B), the population dynamics shift from fixed-point dynamics to recruit-driven generation cycles at  $\sim 16.5^\circ\text{C}$ . The fixed point, or stable equilibrium, at low temperature is characterized by small fluctuations in consumer and resource densities (fig. 3A, left). The pulses of newborns are almost constant over time, and the population consists of multiple coexisting cohorts. At low temperatures, the competitive asymmetry between small and large individuals is reduced and the total population fecundity is relatively low. Consequently, newborn cohorts are never sufficiently numerous to outcompete the adult cohorts, resulting in a uniform consumer age and size structure. Although the fixed point destabilizes slightly in a narrow, low-temperature range ( $12.2^\circ\text{C}$ – $13.5^\circ\text{C}$ ; fig. 4A, 4B), the population dynamics remain qualitatively similar to the FP dynamics in terms of size structure and level of competition. By contrast, as temperature increases, the resource density declines (fig. 4A) and competition among cohorts increases. Up to  $\sim 16.5^\circ\text{C}$ , increasing temperature is associated with a considerable decline in resource density but not in consumer density (fig. 4A, 4B), indicating that the total food intake of the consumer increases. At this threshold temperature, total food intake and, as a consequence, population birth rate have increased sufficiently to allow certain newborn cohorts to deplete the resource to levels where they can still grow at a slow rate but mature individuals starve to death. Consequently, the population dynamics shift to recruit-driven generation cycles in which a single recruit year class dominates the population as it grows slowly throughout the years until it matures, reproduces, and is outcompeted by its offspring, the new dominating cohort (fig. 3A, right). These generation cycles have a 6-year periodicity (“horizontal” lines in fig. 4A, 4B), and they correspond to the recruit-driven single-cohort cycles first described by Persson et al. (1998). Interestingly, in the  $13.5^\circ\text{C}$ – $16.5^\circ\text{C}$  temperature range, the system is bistable, meaning that both types of dynamics (FP and GC) can be observed, depending on the initial conditions. In this range the amplitude of FP dynamics is sufficiently small to prevent the occurrence of high newborn pulses that would cause a shift to generation cycles. Beyond  $\sim 16.5^\circ\text{C}$ , the amplitude of FP dynamics is such that high newborn pulses occur frequently, resulting in a rapid shift to GCs, whereas below  $\sim 13.5^\circ\text{C}$  the GC dynamics are unstable because the newborn pulses are insufficient to outcompete the mature cohorts.

In the cannibalistic case (fig. 4C, 4D), population dynamics shift from a fixed point at temperatures below  $13.5^\circ\text{C}$  to irregular cannibal-driven dynamics at  $13.5^\circ\text{C}$ – $15^\circ\text{C}$ , to a mixture of cannibal-driven dynamics and generation cycles (CD-GC) around  $15.5^\circ\text{C}$ , and finally to sta-



ble generation cycles above 16.5°C. The temperatures at which these shifts occur depend on the degree of cannibalism in the population. Here we illustrate the dynamics for a cannibalistic voracity of  $\beta = 100$  (see Claessen et al. 2000). At very low temperatures, we see fixed-point dynamics, but as temperature increases above 13.5°C, the fixed point destabilizes. At this point, juveniles can grow sufficiently quickly to cannibalize the recruits and thereby dominate the dynamics, which leads to the occurrence of cannibal-driven cycles at temperatures around 15°C. Figure 3B (left) shows an example of a 5-year CD cycle. The cycle is initiated by two high pulses of newborns that deplete the resource momentarily before being decimated quickly by cannibals. The resource level is thus relatively high throughout the cycle, indicating the absence of strong competition. The two abundant year classes nevertheless dominate the population structure, in particular by their strong cannibalistic impact on the survival of subsequent cohorts. Once background mortality has sufficiently reduced the abundance of the dominant year classes, new dominant year classes can arise. CD dynamics are thus driven not by competition for the resource but instead by cannibalism, which strongly reduces the abundance of the newborns, enabling the coexistence of many age classes. As temperature increases further (above 16.5°C), the population dynamics shift to stable generation cycles with a 7-year periodicity (“horizontal” lines in fig. 4C, 4D), which correspond to dwarfs-and-giants cycles (Claessen et al. 2000). These cycles are mainly driven by competition, in the same way as the GCs occur without cannibalism. The difference is that the first offspring cohort (fig. 3B), produced by the slowly growing “dwarf” cohort, is almost entirely cannibalized by its parental cohort. As a consequence, the resource level recovers quickly after the first offspring pulse (fig. 3B), ensuring the survival of the dwarf cohort, which subsequently reproduces a second offspring cohort the following year. This time, however, the dwarfs have become too big to consume the newborns, and the old dwarfs are thus outcompeted by this new dwarf cohort. The first offspring cohort, meanwhile, has reached a body size that allows them to cannibalize the new dwarf cohort and thereby grow to giant sizes (up to 800 mm; fig. 5) by the end of the cycle. The temperature range 15.5°–16.5°C represents mixed dynamics, in which CD dynamics and GC dynamics are both unstable and the system alternates between them (Claessen et al. 2000).

In both the cannibalistic and the noncannibalistic cases, increasing temperature is associated with a decreasing average zooplankton density with increasing variability (fig. 5A, 5B) despite a higher population growth rate. These changes reflect the above-described increased food consumption and thus competition within the consumer pop-

ulation as well as the onset of generation cycles at high temperatures.

#### *Individual Life-History Traits*

As a consequence of increased competition and the shift to generation cycles at high temperatures, average perch body size tends to decrease with temperature (fig. 5C). The trend is continuous and monotonic without cannibalism but discontinuous and oscillatory with cannibalism due to the occasional occurrence of giants at intermediate to high temperatures. Consequently, the relationship between maximum and average size and temperature is hump shaped in cannibalistic populations, and the variation in body size increases (fig. 5D). The lower temperature threshold for the occurrence of giants (length >250 mm) is ~14.5°C. Without cannibalism, growth is limited by planktivory and the fish never reach sizes above 200 mm, but as cannibalism becomes stronger, the fish grow larger and reach sizes of up to 800 mm within the 15.5°–20°C temperature range. Moreover, the number of coexisting year classes and the maximum age in the population decrease with temperature, most dramatically in the range 14°–16°C with cannibalism and around 16°C without cannibalism (fig. 6A).

#### *Sensitivity Analysis*

Our sensitivity analysis of the parameters in the temperature-dependence term shows that the model is qualitatively robust with respect to types and sequence of the dynamics for most parameters and that the onset temperature for generation cycles is more sensitive to perturbations in the noncannibalistic compared to the cannibalistic case (table A1). In the cannibalistic case, all but two of the possible perturbations result in the same sequence and types of dynamics (FP, CD, GC) as in the nonperturbed model, and in all but one case, the onset of generation cycles occurs within a similar temperature range of 15.5°–17°C. In the noncannibalistic case, all but one of the perturbations result in the same sequence of dynamics as in the nonperturbed model (FP, GC). However, the threshold for the onset of generation cycles appears to be more variable, with values ranging from 12.5° to 18°C. In both cases, four perturbations result in the population becoming extinct at relatively low temperatures (12.5°–15°C). Changes in those parameters related to the resource growth rate have virtually no effect on the population dynamics of the consumer. The perturbations slightly alter the population numbers but never shift the onset temperature for GCs by more than ~0.2°C. Interestingly, the strongest effects come from changes in the parameters related to consumption. Some of the pertur-



bations remove the FP dynamics at low temperatures, but they never remove the generation cycles at high temperatures within the 12°–22°C range.

The sensitivity analysis of the scaling parameter of the attack rate ( $\alpha$ ) indicates that, in the noncannibalistic case, the dynamics do not change qualitatively when using known  $\alpha$  values for other freshwater fish but that the temperature threshold above which the GCs are predicted varies between the mimicked species. It should be noted that, similar to the Eurasian perch parameterization, these systems are bistable, meaning that the types of dynamics at intermediate temperatures depend on the initial conditions. According to these tests, a lower  $\alpha$  (as reported for pikeperch) results in lower onset temperatures, whereas a slightly higher  $\alpha$  (as reported for arctic char and bluegill sunfish) results in higher onset temperatures for GCs. However, at even higher  $\alpha$  (as reported for bream and roach), the FP dynamics first destabilize to multicohort, small-amplitude GCs and then to single-cohort GCs at intermediate temperatures, around 12.5°–15°C (see table A2).

Finally, the sensitivity analysis of the cannibalism window shows that the values of the minimum and maximum victim/cannibal ratios ( $\delta$  and  $\epsilon$ ) known for yellow perch result in the same dynamics as and a slightly lower onset temperature than in Eurasian perch, whereas when using the values for pike, the dynamics are similar but clear generation cycles never emerge (see table A2).

### Discussion

Our model predicts that a temperature increase can induce regime shifts in the dynamics of size-structured populations and that global warming might destabilize ecosystems. As temperature increases, the consumer population shifts from stable dynamics with several coexisting year classes to competition-driven generation cycles in which population numbers fluctuate more severely in both frequency and amplitude. Additionally, our model predicts that warming increases the proportion of younger, smaller individuals. The driving force behind these changes is size-dependent, intraspecific competition for food, which changes with temperature.

#### *Temperature and Size Effects on the Individual Level*

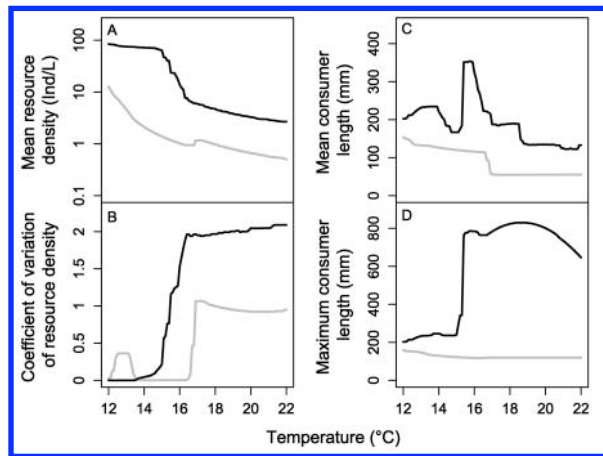
Smaller individuals are generally competitively superior to larger ones because metabolic rate increases faster than foraging ability with body size (Persson 1987; Werner 1988). As a consequence of the different scaling relationships of the physiological rates, critical resource densities generally increase with increasing size, resulting in asymmetrical intraspecific competition (Persson et al. 1998).

Thus, small individuals can usually grow at resource levels where large individuals starve to death. Indeed, this seems to be the case for all freshwater fish species for which the respective data exist (Persson and de Roos 2006). The size dependence of intraspecific competition, however, changes with temperature. The net energy gain of an individual increases faster with temperature at smaller sizes (fig. 2B), thereby magnifying the competitive advantage of small over large individuals. This effect is reflected in the general observation that optimum growth temperatures (which for immature fish can be assumed to be equal to those of the net energy gain) decrease with increasing body size (Kozłowski et al. 2004). This has been reported for several fish species (e.g., Karås and Thoresson 1992; Björnsson and Steinarsson 2002; Imsland et al. 2006) and other ectotherms (e.g., amphipods; Panov and McQueen 1998). Thus, this functional form of the temperature-size relationships can be assumed to be valid for other fish species and possibly ectotherms in general.

#### *Temperature-Driven Regime Shifts in Population Dynamics*

In line with the expected temperature effects on the individual level, we find more stable dynamics with several coexisting cohorts and a constant size distribution at lower temperatures where the difference between the size-dependent scaling of metabolic rate and intake rate, that is, the net energy gain, is smaller. At high temperatures, where the metabolic advantage of small individuals increases, recruit-driven single-cohort cycles appear in populations without cannibalism (Persson et al. 1998), and dwarfs-and-giants cycles appear in cannibalistic populations (Claessen et al. 2000). Thus, generation cycles consistently occur within our modeled populations at temperatures above ~16.5°C. Their onset is ultimately caused by an increase in total fecundity and thus population birth rate (fig. 6B), which results in stronger recruit year classes that deplete the resource to levels below the critical resource density for mature fish, which consequently starve to death (figs. 3, 4).

The impact of temperature on size-structured population dynamics are mediated through changes in physiological rates at the individual level that alter density-dependent interactions (competition and cannibalism) at the population level. However, abrupt transitions in population dynamics from stable to unstable states, as observed in our model, cannot be entirely understood based on individual-level processes that change with temperature in a continuous manner. The observed regime shifts in population dynamics within a few tenths of a degree suggest the existence of temperature thresholds, reflecting complex feedbacks between physiological rates, resource



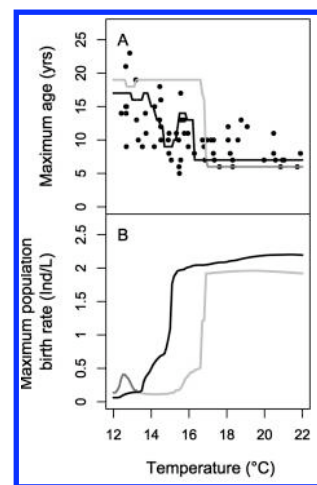
**Figure 5:** Model output for average resource density (A) and coefficient of variation (standard deviation to mean ratio) for the resource density (B), as well as perch mean body length (C) and maximum body length (D) over the temperature range 12°–22°C. Results are shown for populations with cannibalism ( $\beta = 100$ ; black lines) and without cannibalism ( $\beta = 0$ ; gray lines).

levels, population fecundity, and density-dependent processes. Such transitions might be less abrupt in natural systems due to the use of alternative food sources, interactions with other abiotic factors, or the spatial variation of competition between age classes within different microhabitats. Nonetheless, destabilization due to increasing temperature is a robust pattern that has also been predicted for unstructured populations (Vasseur and McCann 2005), and that is in agreement with field data on latitudinal effects on life-history variation (see next section). Our results thus suggest that the impact of global warming on the stability of size-structured populations is qualitatively predictable, provided that the different temperature dependencies of the vital rates are known (see Vasseur and McCann 2005), but that abrupt shifts may occur that cannot be inferred from individual-level processes alone. An important next step for future research will be to evaluate the effects of seasonal temperature cycles and interannual variation in temperatures as compared to the average seasonal temperature used in this study.

#### *Generality of the Observed Dynamics*

Theoretical models of varying complexity, from stage-structured to fully size-structured consumer-resource models, suggest that single-generation cycles are to be expected whenever intraspecific competition is asymmetric, with small individuals being competitively superior over large ones in exploiting the common resource (de Roos and Persson 2003). Accordingly, recruit- or juvenile-driven

generation cycles have been observed in fish species, including roach (*Rutilus rutilus*) and vendace (*Coregonus albula*; Persson and de Roos 2006), as well as in *Daphnia* (McCauley et al. 1999; Nilsson et al. 2010). The similarity between different types of population models as well as the corresponding empirical data suggests that these effects of intraspecific competition on population dynamics reflect a general characteristic of size-structured populations. However, whether the occurrence of generation cycles depends on environmental temperature has never been studied empirically or theoretically. Similar to these size-structured consumer-resource models, theoretical models of cannibalism in size-structured populations yield some general predictions about the effects of cannibalistic interactions (Claessen et al. 2003). When cannibals and victims share a common resource, two mechanisms of size-dependent interaction may arise: either the cannibals control the victims or the victims control the cannibals. In the former case many cannibals of relatively small sizes cannibalize most of the victims, whereas in the latter case the victims can outcompete the cannibals so that most of them die and only a few can grow to giant sizes. Data from several fish species support these predictions, and it has been shown empirically that perch populations may actually switch between these two types of dynamics (Persson et al. 2003).



**Figure 6:** Comparison of maximum age from model output with data on perch populations (A) as well as maximum population birth rate (B) over the simulated temperature range 12°–22°C. Model results are shown for populations with cannibalism ( $\beta = 100$ ; black lines) and without cannibalism ( $\beta = 0$ ; gray lines). Data on maximum age versus latitude (A) were taken from Heibo et al. (2005) and converted to temperature values using a latitude to mean summer surface temperatures relationship (in Lewis 1987). Note that the steep increases in maximum population birth rate in both cases (bottom) coincide with the onset of the generation cycles (fig. 4).

### Sensitivity Analysis

The observed bifurcations in the noncannibalistic population are qualitatively robust to perturbations of the temperature-related parameters, but the onset temperature for generation cycles varies considerably. In contrast, the bifurcations for the cannibalistic population are qualitatively and quantitatively robust to parametric perturbations. The higher sensitivity in the noncannibalistic population may be explained by its bistability over a wide temperature range, as this means that the transition to GCs takes place whenever the fixed point is sufficiently perturbed. A slight increase in the bifurcation parameter may then be enough to trigger an attractor change, even if the FP attractor is still stable (but has a small basin of attraction).

Our sensitivity analysis of the bifurcations shows that our model generally yields the same results and conclusions if we mimic the size scaling of the attack rate or the cannibalism window of other fish species for which data exist. The types of dynamics that occur with increasing temperature are consistent for the different parameter values tested, with fixed-point dynamics at low and generation cycles at high temperatures. Nonetheless, the thresholds at which the dynamics shift vary depending on parameter value or mimicked species. That, however, does not challenge the conclusions drawn from our model results.

### Temperature Effects on Age and Size Structure

The observed increase in competition and the destabilization of the population dynamics result in a higher proportion of smaller-sized fish and thus reduced average body size at high temperatures. This trend is continuous in the noncannibalistic population but discontinuous in the cannibalistic population (fig. 5C). These findings support the age-structure shift hypothesis according to which global warming might increase the proportion of young age classes and thus lead to a reduction in average body size in aquatic animals (Millien et al. 2006; Daufresne et al. 2009). Our model provides a mechanistic explanation for these findings by showing that increased temperature increases a metabolism-associated competitive advantage of small individuals over large ones. Warming-induced shifts towards smaller-sized populations represent a threat to population persistence since smaller size decreases diet breadth and fecundity but increases competitive ability and often predation risk (Arendt 2007). Therefore, warming might destabilize not only population dynamics but also whole ecosystems. It should be noted, however, that such ecological effects might be altered by evolutionary re-

sponses, since changes in size structure may also cause genetic changes related to life-history traits (Roff 2002).

The predictions of our model match well with observed changes in perch life-history traits with latitude. Size-dependent competition and cannibalism are barely considered in studies on life-history variation over latitudinal or temperature ranges (e.g., Bergmann's rule; Ray 1960; Atkinson and Sibly 1997). However, both interactions control individual growth and body size (Fox 1975; Claessen et al. 2000) and may change with environmental temperature. In perch, various life-history traits have been shown to correlate with latitude and most likely temperature (Belk and Houston 2002; Heibo et al. 2005). For instance, Heibo et al. (2005) found a latitudinal cline for maximum age in perch that could be attributed to either an accelerated growth rate or a longer growing season at low latitudes and high temperatures (fig. 6A). This decline corresponds well to our model predictions of reduced maximum age and number of coexisting cohorts in the population due to the shift toward competition-driven, recruit-dominated dynamics. Since perch populations are potentially cannibalistic, the model performs well in predicting the general decline in maximum age. The cannibalistic case describes the smooth decline as seen in the data much better than the noncannibalistic case (fig. 6A).

Interestingly, maximum body size does not seem to correlate with latitude in perch (Belk and Houston 2002; Heibo et al. 2005). Instead, the biggest perch are found in lakes at intermediate degrees of latitude, thus corresponding to intermediate water temperatures (Heibo et al. 2005). This also matches with our model prediction of maximum body sizes for a cannibalistic population at intermediate temperatures (fig. 5D), whereas maximum size decreases continuously with temperature in the noncannibalistic population. Hence, cannibalism may invalidate the temperature to maximum size relationship. Since most families of freshwater teleosts have been described as at least partly cannibalistic (Smith and Reay 1991), this could explain why Bergmann's rule does not apply to most freshwater fish (Belk and Houston 2002). Our results suggest that maximum body size in size-structured populations is determined by a combined effect of temperature and size-dependent competition and cannibalism. Our study suggests that the ecological mechanism causing the decline in mean body size and age at high temperatures is change in size-dependent intraspecific competition, whereas the mechanism explaining the occurrence of the largest individuals at intermediate temperatures is change in the cannibalistic interactions.

### Conclusions

Due to the generality of both the size and the temperature dependence of the individual physiological rates that we

use in our model, we suggest that the predictions presented broadly apply to size-structured fish populations that are highly dependent on environmental temperature and possibly to aquatic ectotherms in general. We conclude from our model analysis that global warming might destabilize aquatic ecosystems through the onset of generation cycles that are characterized by strong recruit year classes with high intraspecific competition.

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