

Understanding how lake populations of arctic char are structured and function with special consideration of the potential effects of climate change: a multi-faceted approach

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Abstract Size dimorphism in fish populations, both its causes and consequences, has been an area of considerable focus; however, uncertainty remains whether size dimorphism is dynamic or stabilizing and about the role of exogenous factors. Here, we explored patterns among empirical vital rates, population structure, abundance and trend, and predicted the effects of climate change on populations of arctic char (*Salvelinus alpinus*) in two lakes. Both populations cycle dramatically between dominance by small (≤ 300 mm) and large (>300 mm) char. Apparent survival (Φ) and specific growth rates (SGR) were relatively high (40–96 %; SGR range 0.03–1.5 %) and comparable to those of conspecifics at lower latitudes. Climate change scenarios mimicked observed patterns of warming and resulted in temperatures closer to optimal for char growth (15.15 °C) and a longer growing season. An increase in consumption rates (28–34 %) under climate change scenarios led to much greater growth rates (23–34 %). Higher growth rates predicted under climate change resulted in an even greater predicted amplitude of cycles in population

structure as well as an increase in reproductive output (R_0) and decrease in generation time (G_0). Collectively, these results indicate arctic char populations (not just individuals) are extremely sensitive to small changes in the number of ice-free days. We hypothesize years with a longer growing season, predicted to occur more often under climate change, produce elevated growth rates of small char and act in a manner similar to a “resource pulse,” allowing a subset of small char to “break through,” thus setting the cycle in population structure.

Keywords Temperature · Physiology · Bioenergetics · Food limitation · Fish growth

Introduction

The way populations are structured, both in space and time, is a fundamental focus of population ecology and an inherent component of conservation biology (Murdoch 1994; Hanski 1999). The population structure occurring at any given point in time is determined by the inherent physiology of the organism within a given ecosystem, and by the carrying capacity of the system. In addition, size-dependent competition and predation can determine population structure (e.g., Byström and García-Berthou 1999; Claessen et al. 2002). Fluctuations in the structure and size of the population, its birth rate, death rate, and age structure or size distribution can be used to understand which factors regulate the population (Ebenman and Perrson 1988). Similarly, changes in the ecosystem, its growing season, productivity, or climate, in turn will be manifested in changes in population size and structure (e.g., Persson et al. 1998; Liu et al. 2007). These processes of population regulation and structure are particularly intriguing in fish populations

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of arctic lakes, as productivity and forage diversity is typically very low, many lakes are isolated, closed (e.g., to immigration and emigration) and fish species diversity is typically depauperate, and lakes are ice-covered and <3 °C degrees for 8–9 months of the year (Hershey et al. 1999, 2006a; Sierszen et al. 2003; Luecke et al. 2004).

Native species endemic to these arctic lakes demonstrate a diversity of life history expressions, body sizes and morphologies, and strategies for feeding, survival, and reproduction (e.g., Klemetsen et al. 2003). Polymorphism is common among arctic char (*Salvelinus alpinus*) and their relatives and may be exhibited as different colored or sized morphs and/or morphs occupying different habitats within the same, typically allopatric, population (Klemetsen et al. 2003). Similarly, many populations of char demonstrate strong bimodal size structure characterized by abundant “dwarfs” (approximately <200 mm) and fewer large “giants” (e.g., Finstad et al. 2006).

This bimodal population structure among lake-dwelling char populations is generally thought to be set by strong, early intra-cohort recruitment and competition for resources that subsequently leads to cannibalism (Byström 2006), or similarly by a temporal pulse of abundant resources allowing some individuals to pass through to the larger size-class niche (Griffiths 1994; Claessen et al. 2002). In some of these populations, smaller morphs (i.e., dwarfs) are actually competitively superior until a certain size threshold is reached, after which a larger morph (i.e., giant) maintains greater energy requirements via cannibalism on smaller invertebrate-feeding morphs (reviewed in Finstad et al. 2006). In extreme northern latitudes, winter also represents a survival bottleneck (e.g., Cunjak et al. 1998), and size-selective removal of low-energy, and typically smaller, individuals could also set a bimodal size structure (Finstad et al. 2004; Hurst 2007). Yet uncertainty remains whether this type of population structure in char populations is dynamic or stabilizing in terms of total biomass or abundance (Claessen et al. 2003; Klemetsen et al. 2003; Byström 2006) and to the role of exogenous factors (e.g., duration of ice-free days) in determining annual resource availability, growth rates, and thus recruitment strength (Rose 2000).

Fishes endemic to arctic lakes are well adapted to the extreme conditions of the Arctic and possess an ability to grow and reproduce quickly during the very brief growing season when there is no ice cover [lasting ~ 100 days (Wrona et al. 2006)] and even the potential to forage and grow under complete ice cover (Svenning et al. 2007). As such, even minor changes in the timing and duration of ice-free days and the associated thermal regime should manifest in substantial differences in annual growth (Kristensen et al. 2006) and potentially other vital rates that strongly covary with growth and body size (e.g., survival, fecundity,

timing of spawning; MacDonald et al. 1996; Wedekind and Kung 2010).

Arctic ecosystems are predicted to be particularly sensitive to the effects of global climate change (Reist et al. 2006), and a 2.1 °C increase in air temperature has already been observed over the last 30 years (ACIA 2005). Increased snow pack due to warmer winters appears to be resulting in a later ice-off date, and, mid-summer temperatures at 2-m lake depth are now generally warmer on average as compared to earlier years (MacIntyre et al. 2009). Associated with these changes are concordant increases in zooplankton densities and potentially reduced fish condition (Johnson 2009; Luecke et al. 2014) and over-winter survival (MacDonald et al. 1996). The effects of these environmental changes on arctic fishes are likely non-linear, difficult to predict, and could emerge at many different levels including individual [e.g., physiology and thermoregulation (e.g., Ries and Perry 1995)], population (e.g., structure and life history expression), and beyond.

Our overall goal was to better understand the drivers of arctic char population dynamics in closed arctic lakes with special consideration of the role of climate and climate change. To do this, we linked: (1) a time series of vital rates, information on population structure, abundance and trend; (2) three realistic lake climate change scenarios; (3) bioenergetics trajectories of growth and consumption; and lastly, (4) predicted the effects of climate change on populations of arctic char with a simple matrix model.

Materials and methods

Study sites

This study is part of the Arctic National Science Foundation, Long Term Ecological Research program, centered out of the University of Alaska, Fairbanks, Toolik Lake Field Station, located on the North Slope of the Brooks Range.

We chose two lakes for study of different size, geologic age, and location for study and comparison (Table 1). Both lakes are effectively closed to immigration and emigration of arctic char; and arctic char and slimy sculpin (*Cottus cognatus*) are the only fishes present. Both lakes are low productivity and mean annual summer chlorophyll *a* is usually $1\text{--}2 \mu\text{g L}^{-1}$ (Kling et al. 1992). Lakes in this region are typically ice covered from early October up to and including late May and thermally stratified in summer (June–August).

From 1999 to 2000, in lakes E5 and Fog2 respectively, and up to and including 2009 we marked and recaptured arctic char, primarily through the ice in mid-late May, approximately 1–3 weeks before ice-off. We

Table 1 Lake characteristics and fish population estimates and densities with 95 % confidence intervals (CI) for both study lakes

Lake	Variable (units)	Value	95 % CI
E5	Maximum depth (m)	12	-
Fog2	Maximum depth (m)	20	-
E5	Surface area (m ²)	113,006	-
Fog2	Surface area (m ²)	56,527	-
E5	Volume (m ³)	703,376	-
Fog2	Volume (m ³)	469,114	-
E5	Chlorophyll <i>a</i> (µg L ⁻¹)	2.69	0.38
Fog2	Chlorophyll <i>a</i> (µg L ⁻¹)	0.60	0.08
E5	Secchi depth (m)	3.1	0.4
Fog2	Secchi depth (m)	9.4	0.8
E5	Population estimate	722	568–1,200
Fog2	Population estimate	499	342–921
E5	Density (char m ⁻³)	0.0010	0.0008–0017
Fog2	Density (char m ⁻³)	0.0011	0.0007–0.0020

Chlorophyll *a* and Secchi depth (water transparency) data are from Kling et al. (1992)

weighed (g) and measured (mm) all captured char and tagged all fish >150 mm with a passive integrated transponder (PIT) tag, and removed the adipose fin. On all recaptured fish, we checked for tag loss, weighed, measured, and recorded the unique PIT-tag code. We also collected diet and otolith samples for ageing from all incidental mortalities.

Abundance, density, population structure, and growth

We calculated abundance annually from the mark-recapture data using a Schnabel estimator (Krebs 1999). We calculated specific growth rates (SGR) from all recaptured fish as:

$$SGR = \left[\frac{(\ln W_2 - \ln W_1)}{(t_2 - t_1)} \right] \times 100 \tag{1}$$

where, W_1 and W_2 are body weight at the start and end of the growth period, respectively, and $t_2 - t_1$ is the length of the period in days.

Survival and trends

We estimated apparent survival and population trend using our mark-capture time series using a temporal symmetry model [(Pradel survival and lambda model) Pradel 1996; Nichols and Hines 2002] in program MARK (White and Burnham 1999). Forward-time mark-recapture data is used to estimate apparent survival (Φ) and capture probability (p). Reverse-time mark-recapture data is used to estimate recruitment rate (f), or the per capita recruitment

Table 2 Primary apparent survival (Φ), recapture probability (p) and population trend (λ) results from mark-recapture analysis top models (temporal symmetry Pradel model) of 11 and 10 years of mark-recapture data in lakes E5 and Fog2, respectively

Lake	Parameter	Value	95 % CI
E5	Φ Small (age 3)	0.70	0.52–0.83
	Φ Medium (ages 4–7)	0.74	0.66–0.81
	Φ Large (ages ≥ 8)	0.58	0.48–0.67
	Average p	0.21	0.12–0.36
	λ	0.17–6.34 ^a	0.05–2.23
Fog2	Φ Small (age 3)	0.96	0.87–0.99
	Φ Medium (ages 4–7)	0.49	0.39–0.59
	Φ Large (ages ≥ 8)	0.40	0.16–0.71
	Average p	0.22	0.08–0.43
	λ	0.10–4.44 ^a	0.05–11.66

^a Range shown

probability. Finally, the population growth rate (λ) can be estimated as the net effect of survival and recruitment.

There were 9–10 total years of data for lakes Fog2 and E5, respectively. We allocated data into three size classes of fish: “small” fish ranged in size from 150 to 179 mm and generally represent fish age 3 and less, “medium” fish ranged from 180 to 300 mm and generally represent fish ages 4–7, and “large” fish were all fish >300 mm and generally represent fish ages 8 and older based on otolith ageing analyses. Size classes were coded as groups, there were nine to ten survival intervals, and size at tagging was included as an individual covariate. We constructed models following a standard “step down” approach (Lebreton et al. 1992), and selected models based on Akaike’s information criterion corrected for effective sample size (Burnham and Anderson 2002). λ estimates during the first 2 years and last year within temporal symmetry models are by default confounded (Cooch and White 2008). Apparent survival rates are evaluated independently but are also used as stage (*i*) based inputs in the matrix model (P_i, G_i) described below (Tables 2, 3).

Bioenergetic simulations: current and under future climate change

The modeling approach we used to estimate consumption and growth of arctic char was based on the balanced energy budget of a poikilothermic organism (Hartman and Kitchell 2008), conceptually described as:

$$\text{Growth} = \text{Consumption} - (\text{Respiration} + \text{Wastes} + \text{Digestion}) \tag{2}$$

All physiological rates (e.g., consumption, respiration) are driven by temperature and allometry (Brown et al.

Table 3 Parameters used in the population matrix model, an explanation of their use, and the source

Model parameter	Lake E5	Lake Fog2	Explanation and source
Stage ₃	85 mm	85 mm	Length based on growth estimates from a combination of mark-recapture, size-frequency, and otolith data; this study
Stage ₄	130 mm	130 mm	
Stage ₅	170 mm	170 mm	
Stage ₆	180–245 mm	195–270 mm	
Stage ₇	>300 mm	>300 mm	
F_4	126	126	Relationship between fecundity (y , eggs female ⁻¹) as a function of size [x , length (cm): $y = 0.0889 x^{2.5617}$] (Power et al. 2005)
F_5	146	179	
F_6	248	316	
F_7	322	588	
G_1	0.001	0.003	Back-calculated in matrix, this study
G_2	0.70	0.96	Mark-recapture survival estimates, temporal symmetry model; this study
G_3	0.70	0.96	
G_4	0.70	0.96	
G_5	0.19	0.12	
G_6	0.10	0.07	
P_6	0.56	0.37	
P_7	0.48	0.34	
γ_{2-4}	1.00	1.00	Based on growth and number of years in stage; this study
γ_5	0.25	0.25	
γ_6	0.17	0.17	

For each stage (i), P_i is the probability of surviving (Φ) and staying in the same stage [$\Phi \times (1 - \Upsilon)$], and G_i is the probability of surviving and moving to the next stage ($\Phi_i \times \Upsilon_i$), where Υ_i is the transition probability

2004); for the bioenergetic simulation modeling, these rates are determined in the laboratory. For a cold water fish such as char, rates of consumption, respiration, and other losses increase gradually towards an optimal temperature, then decrease rapidly beyond this point (Fig. 1). Energy ($\text{g g}^{-1} \text{day}^{-1}$) gained via food consumed is then lost due to respiration (active and standard), specific dynamic action (digestion), and wastes (egestion and excretion). What energy remains is available for somatic growth and the development of gonads. Using this approach, if the temperature occupied by the fish, the proportion of the diet composed of different prey items of different energetic densities, and either growth or consumption (g day^{-1}) is known, either of the latter can be estimated. Details of bioenergetic modeling including energetic densities of prey, proportion of diet by wet weight, parameter values, and both arctic char weight inputs and model output are described in detail in Appendix I.

We used the Wisconsin bioenergetics model (Hanson et al. 1997; <http://aqua.wisc.edu/publications/ProductDetails.aspx?productID=360>), scaled to arctic char to model growth and consumption; the bioenergetics model has been effectively applied to arctic char by others (Lyytikäinen and Jobling 1998; Guénard et al. 2008). We modeled annual trajectories of growth and consumption based on inputs of diet composition and growth from empirical observations (see above), for the same three size classes. Diet proportions were based on the mean diet proportion for each lake. In lake E5, char consumed 9.2 % Diptera, 12.9 % Trichoptera,

24.4 % Mollusca, 23.7 % unidentifiable aquatic and terrestrial invertebrates, and 29.8 % “other” (mostly vegetation). In contrast, in lake Fog2, char consumed 99.8 % Diptera and 0.2 % other (mostly vegetation). We based diet energy densities (reported in Appendix I) on Cummins and Wuycheck (1971) and Guénard et al. (2008).

For temperature inputs we used an approach commonly used in bioenergetics (e.g., Vatland et al. 2008) and assumed char would behaviorally thermoregulate. We reviewed ambient temperature and dissolved oxygen (DO) profiles and restricted their thermal position to 1.5 m deep or deeper assuming they would not maintain a surface position, and to depths with DO levels above 4 mg L^{-1} . Of the remaining available habitat, we assumed char would occupy waters closest to their optimal temperature for growth [$15.15 \text{ }^\circ\text{C}$ (Lyytikäinen et al. 1997)]. We performed all model simulations for a representative “warm year” and a “coldest” in each of the study lakes. The “coldest” water years in the time series (since 1999) were 2003 and 2001 for lakes E5 and Fog 2, respectively, and the ‘warmest’ water year was 2007 for both lakes (see also Appendix I).

We first ran “base” bioenergetics simulations of growth and consumption using observed temperature data for the coldest and warmest years, for each lake respectively. For the cold year, we fit total consumption to observed end weight (mass on 19 May, day 365) for each size class (small, medium, large), annually (20 May to 19 May). For the warm year, annual consumption was adjusted

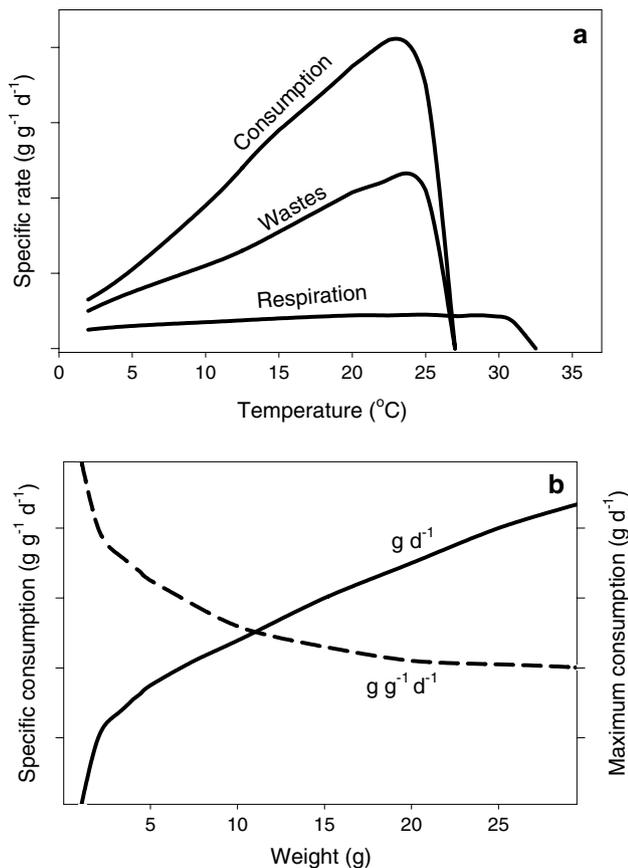


Fig. 1 Conceptual diagram demonstrating the basic metabolic relationship between consumption, respiration, and wastes and temperature (**a**) and the allometric relationship between consumption and fish size (weight, g; **b**) for char, using the basic bioenergetics approach. All rates increase towards the optimal temperature for consumption and growth, and then decline rapidly beyond that temperature. The amount of energy available for growth is the difference between the amount of energy consumed as food and the amount lost due to respiration and wastes. Specific consumption ($\text{g g}^{-1} \text{day}^{-1}$) is greatest for small fish and decreases with increasing mass (g)

by increasing the daily ration by 2 % during the summer growth period (11 June to 2 September), then lowering the ration back to the observed cold water levels during the winter period (3 September to 19 May).

To best capture the range of likely temperature scenarios in the future under continued and elevated climate change, we developed three climate change scenarios based on the literature and available data describing the trajectory of annual warming and cooling in these and other lakes of this region. We bracketed these temperature scenarios with empirical observations, and applied all scenarios relative to the warmest and coldest years on record for each lake (see above). In scenario SC1 we modeled a 2 °C increase over observed temperatures during the ice-free stage of each lake (for both a warm year and a cold year). In scenario SC2 we modeled a 5 °C increase over observed temperatures during

the ice-free stage of each lake. And, in scenario SC3, we modeled both a 5 °C increase during the ice-free stage and an earlier date of ice-off. We estimated the date of ice-off in SC3 by calculating the difference between the observed mean date of ice-off on sentinel lake Toolik Lake (17-Jun) and the range (19 days), for the time series (1999–2000).

As we were interested only in temperature effects on char, we set the ceiling at 15.5 °C, assuming char would thermoregulate and avoid greater surface temperatures greater than this ceiling. For bioenergetic simulations of climate change, we applied the climate change scenario to the base starting size for each size class and lake, and all else was held the same as in the base scenarios above. We report the effect of climate warming in terms of the percent weight and consumption change for each year and lake, for the base relative to the climate change scenario. For simplicity, for most summary graphics we show the results only for SC3 relative to the base scenario for a cold year in each lake. Although SC3 may be the most extreme scenario, this comparison brackets the widest range of possibilities. Trajectories of growth under climate change were evaluated independently and also used to modify transition probabilities (γ) in the matrix model described below.

Population matrix model

We constructed a simple stage-based population matrix model based primarily on the empirical data and parameter estimates described above to better understand the drivers of population structure and to evaluate the population-level effect of predicted climate change. The underlying population matrix models were a birth-pulse, post-breeding model with seven stages, and one model for each lake and population (Fig. 2). Based on field observations of post-spawning condition, we assumed hatching occurred once per year in April or May in our study populations and adults are capable of reproduction in sequential years (1-year time interval). In the absence of gender data for our systems, we assumed a 1:1 sex ratio (Sparholt 1985). Because these char populations sizes were >200 (i.e., they were not demographically small, or $n < 30$) and we were only interested in the effects of climate change relative to a “base” scenario, we did not include demographic stochasticity (Boyce 1992; Morris and Doak 2002).

Parameterization of matrix stages

We based matrix parameters on the empirical data (i.e., survival, growth, and trend) collected as part of this study and described in detail in Table 3. We represented survival and growth for each stage (i) in the matrix models by P_i [$P_i = \Phi \times (1 - \Upsilon)$], the probability of surviving and staying in the same stage, and G_i ($G_i = \Phi \times \Upsilon$), the probability

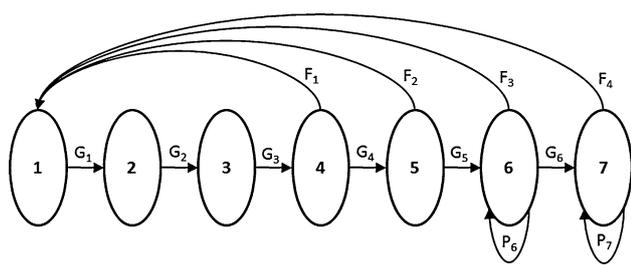
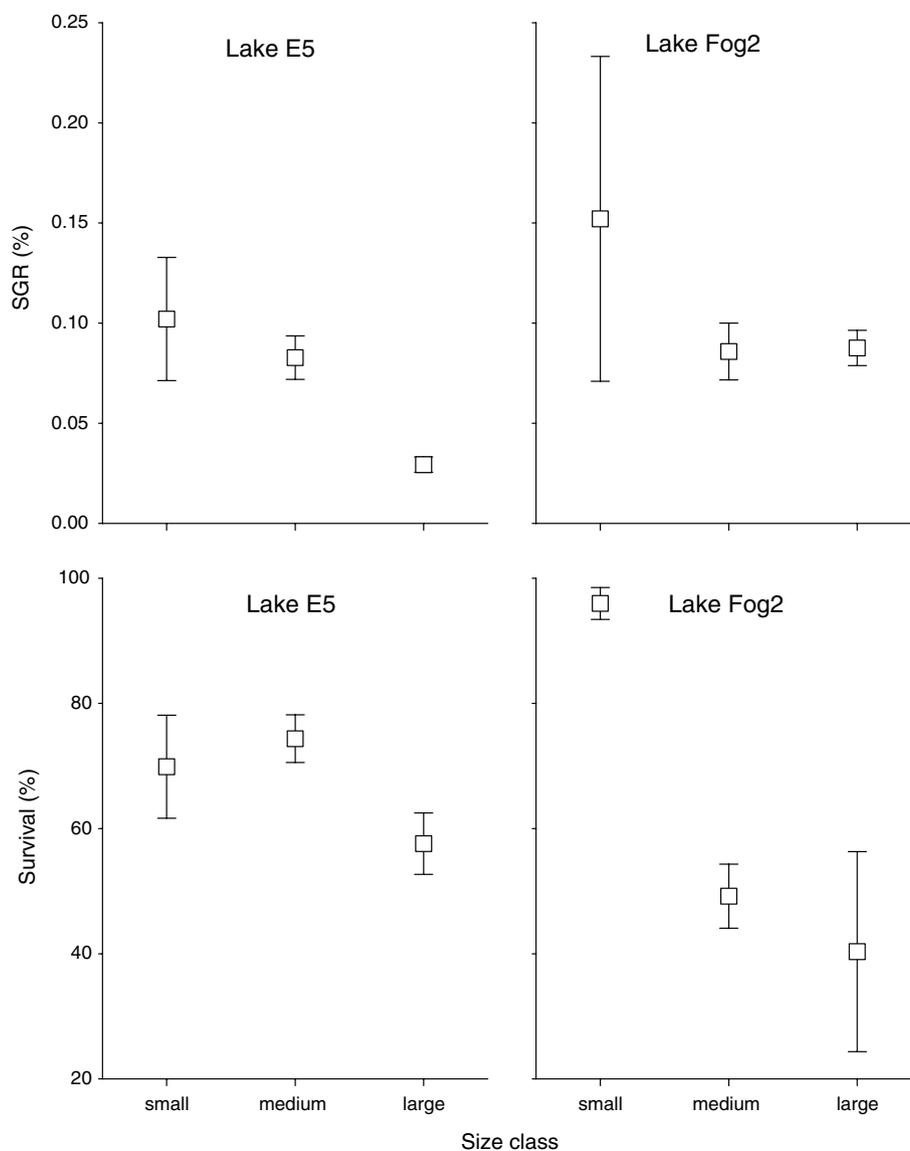


Fig. 2 Life cycle diagram for the population matrix model. The basic model structure is a birth-pulse, post-breeding model with seven stages. Survival and growth for each stage (i) is represented in the matrix models by the probability of surviving and staying in the same stage [P_i ; $\Phi \times (1 - \Upsilon)$], and the probability of surviving and moving to the next stage (G_i ; $\Phi \times \Upsilon$), where Υ is the transition probability. Fecundity (F_i) was based on the relationship between body size (i.e., length) and the number of eggs per female (Table 3)

of surviving and moving to the next stage, where Υ is the transition probability (Fig. 2). We based stage-based apparent survival (Φ) on the mark-recapture analysis described above (Tables 2, 3; Fig. 3, bottom panel) and Υ on observed growth rates (Fig. 3, top panel; Caswell 2001). We calibrated the model annually using independent estimates of population trend (λ) from the Pradel model described above and solving for P_1 , a parameter representing survival from hatch to age 1 (i.e., early recruitment), the only life stage for which there is no or very little empirical data. We based fecundity (F_i) on the relationship between body size (i.e., length) and the number of eggs per female as reported in Power et al. (2005), corroborated by ranges of fecundity data reported in [Jonsson et al. (1988); Table 3]. We initiated base models each year with the observed proportion

Fig. 3 Specific growth rate (mean $SGR \pm SE$, %; top panels) and apparent survival rates (%; mean $\pm SE$; bottom panels) for different size classes (small, medium, large) of arctic char based on mark-recapture data collected in lake E5 (left panels) and lake Fog2 (right panels). Sample sizes (n): lake Fog2 small 8, medium 36, large 4; lake E5 small 3, medium 49, large 30



of fish in each stage (size class), based on the annual abundance data; we later condense this data into the proportion of the population greater than or less than 300 mm to observe dominant cycles in population structure.

Applying predicted climate change effects

To model the effects of climate change in the population matrix model, we assumed fish grew faster (based on bioenergetics predictions) and would thus transition (Υ) into the next stage at a higher rate [i.e., Υ under climate change is adjusted by the ratio of the observed (base) final length of a fish divided by the final length of a fish under the given bioenergetics climate change scenario]. For each population, the climate change scenario matrix models were again run for 9–10 years, initialized with the base (observed) population trend (λ) and the observed proportion of fish in each stage (size class). As above, the size classes were later condensed into the proportion of the population greater than or less than 300 mm to observe dominant cycles in population structure.

Results

On average, we sampled ~30–50 arctic char in each lake, each year. Recapture rates were relatively high given the low density of fish (Table 1) and sample method and approached 30 % in most years. Sampled and tagged fish ranged from 150 to 450 mm.

Abundance, density, and growth

Population estimates ranged from 722 to 499 in lakes E5 and Fog2, respectively, and 95 % confidence intervals (CI) were relatively narrow (Table 1). Despite large differences in abundance, surface area, and volume, the density of char in both lakes was similar with overlapping 95 % CI (~0.001 char m⁻³; Table 1).

Population structure, as indicated by the proportion of the population greater than and less than 300 mm, fluctuated dramatically in both lakes but at differing intervals (Fig. 4). In lake E5, the abundance has remained stable but the population structure switched from one strongly dominated by fish <300 mm to one composed of near equal proportions of small and large char twice across the time series (interval of 4–5 years). In contrast, in lake Fog2, small char <300 mm strongly dominated (>80 %) the population for the first 8 years of the time series.

SGRs (%) were generally largest for the small size class and smallest for the largest size class, with the medium fish in-between (Fig. 3, top panel). In addition, the pattern of growth across the life time was generally similar between

lakes E5 and Fog2, but with large fish in lake E5 demonstrating extremely low growth rates.

Survival and trend

Annual estimates of apparent survival (Φ) were high and stable across the time series while model estimates of trend (λ) varied considerably across time (Fig. 3, bottom panel; Table 2). For lake E5, our top model included Φ as a function only of size class (group), p (~ recapture probability) varied with year (time), and λ varied with year (time). Similarly, for lake Fog2, our top model included Φ as a function only of size class (group), p varied with year (time) and length of fish (individual covariate), and λ again varied with year (time).

Annual survival rates in lake E5 ranged from 0.58 to 0.70 and from 0.40 to 0.96 in lake Fog2 and were consistently lowest for the large size class (Fig. 3, bottom panel; Table 2). SEs about survival estimates were narrow in all cases except for the large size class in lake Fog2, where sample size was lowest. The strong effect of year (time) on λ is most likely a result of variable recruitment into the adult population, as these lakes are generally closed to both emigration and immigration. Thus variability in estimates of λ across years likely results from recruitment pulses into the small size class (Table 2).

Bioenergetic simulations: current and under future climate change

Bioenergetics trajectories of annual fish growth demonstrated that char gain weight rapidly from the time of ice-off in late May–June until late September–early October, when the trajectory of growth changes (Fig. 5). Char then slowly lose weight over the winter until ice-off (around mid-May) the following year. Depending on the year and the size class of the fish, their annual net weight gain can be as little as 25 % in a cold year, yet as great as 65 % in a warm year (Fig. 5). The bioenergetic trajectories of growth were within the range of our observations of char growth (Fig. 5).

Climate change temperature scenarios closely mimicked the observed pattern of warming and cooling in both lakes for SC1 and SC2, but with extremely rapid warming demonstrated in SC3, the scenario that also included earlier ice-off (Fig. 6). From the time of ice-off, water temperatures rose rapidly, arriving at 16.0 °C in early July for SC1 and SC2 and early June in SC3. Temperatures remained >8 °C in observed and climate change scenarios until early September, at which time water temperatures cooled rapidly until the lakes froze in October. Water temperatures reach an optimal for char growth (15.15 °C) only under scenarios of climate change. In SC2 and SC3, water temperatures are in the

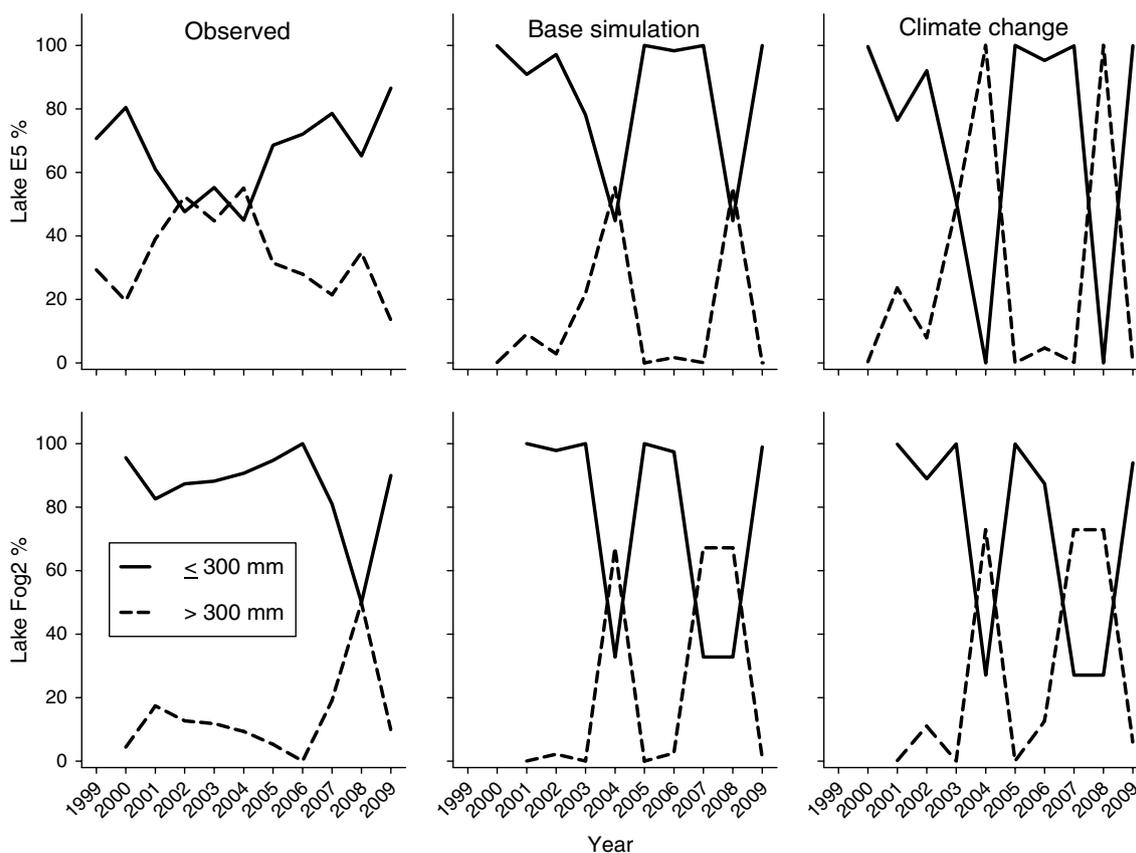


Fig. 4 Population size structure for arctic char ≤ 300 mm and > 300 mm across the time series 1999–2009. Observed (left panels) size-structure, matrix model, predicted size structure of current

conditions (i.e., *Base conditions*; middle panels), and matrix model, future predicted population structure under a warmer climate scenario (*Climate change*; right panels) are shown for each year

range optimal for growth for almost 3 months of the summer growth season. In contrast, in SC1 and SC2, water temperatures only rarely exceed 12°C for the entire summer.

Under all climate change scenarios consumption rates increased dramatically and resulted in concordant increases in growth. Compared to the observed cold year, and for all size classes and in both lakes, annual growth (char weight; g) increased 23–34 % and annual consumption (g) increased 28–34 % across all three climate change scenarios (Fig. 7). In contrast, compared to the observed warm year, the increase in growth and consumption predicted under climate change was less but still ranged from 4 to 7 % and 10 to 13 % for annual growth and consumption, respectively (Fig. 7). In both cases, the increase was greatest for the small size class and smallest for the large size class.

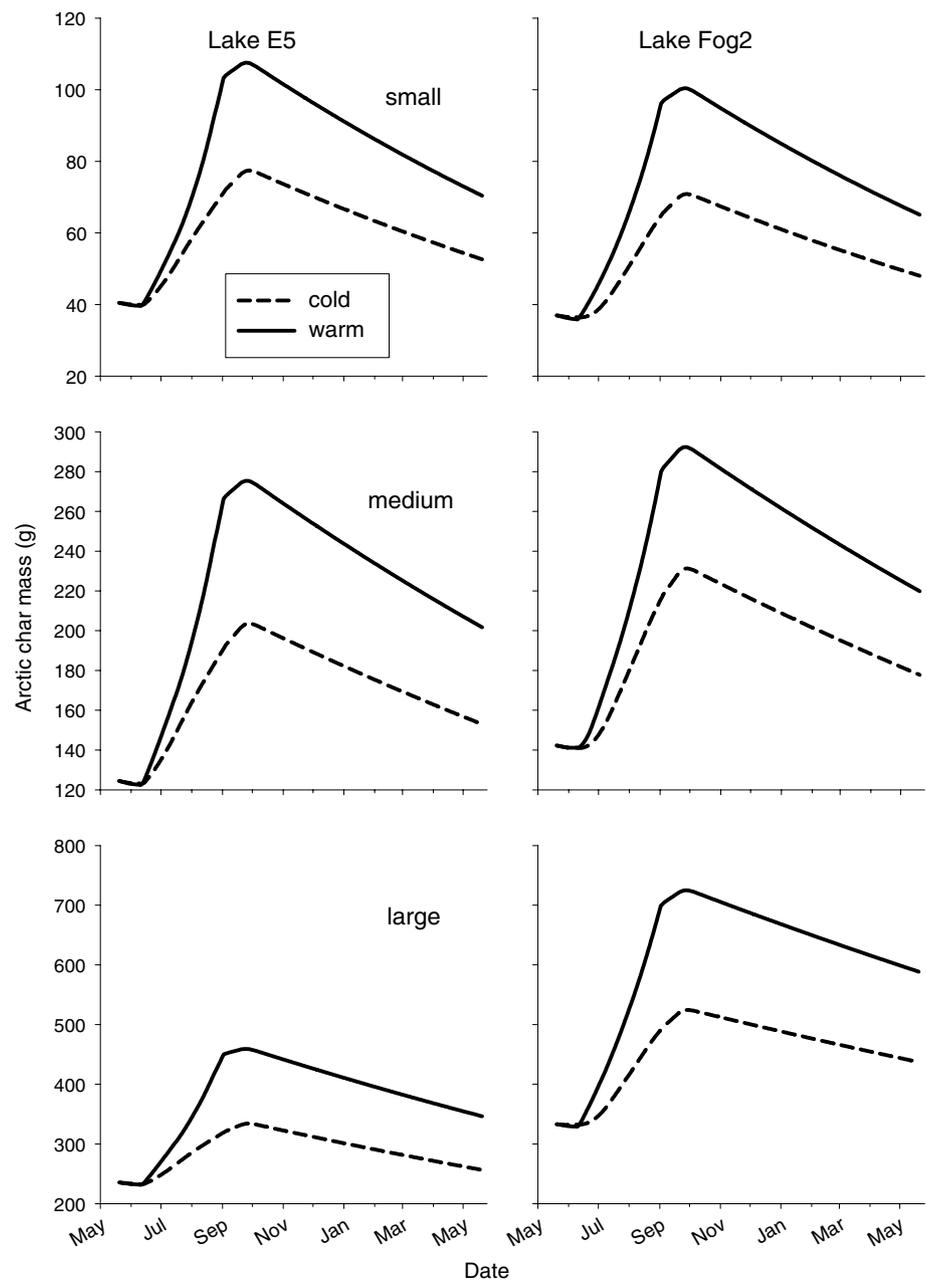
Population matrix model

Our population matrix model generally captured the cycle in population structure in lakes E5 and Fog2 but with

slightly greater amplitude in cycles and a few notable exceptions (Fig. 4, middle and right panels). The greater amplitude of the cycle is unsurprising and results from strong (and likely over-estimated) recruitment signals arising from λ (Table 3). In lake E5, the cycles between small and large char were accurately timed (Fig. 4). In lake Fog2, the observed cycle in 2008 was accurately timed, but the population model added an additional cycle in 2004 not observed in the size frequency and abundance data alone. This additional cycle similarly arises from a strong recruitment signal in the mark-recapture data (and thus high λ ; Table 3).

The effect of faster growth rates in adult fish as a result of climate warming included both much greater amplitude of cycles and duration of cycles. In lake E5, cycles remained accurately timed; however, the fluctuation in proportions between small and large fish was much more dramatic, and large char dominated the population to a greater extreme and for a longer time than observed in the population (Fig. 4, top right panel). The model predicted the same relative differences in lake Fog2 under climate change but

Fig. 5 Trajectory of growth (body mass; g) over the year based on bioenergetics calculations for three size classes in both study lakes in a representative “cold” and “warm” year. Note difference in y-axis scales



to a lesser degree (Fig. 4, bottom right panel). In addition, under scenarios of climate change, on average (R_0) increased by 55 % and generation time (T) decreased 36 %.

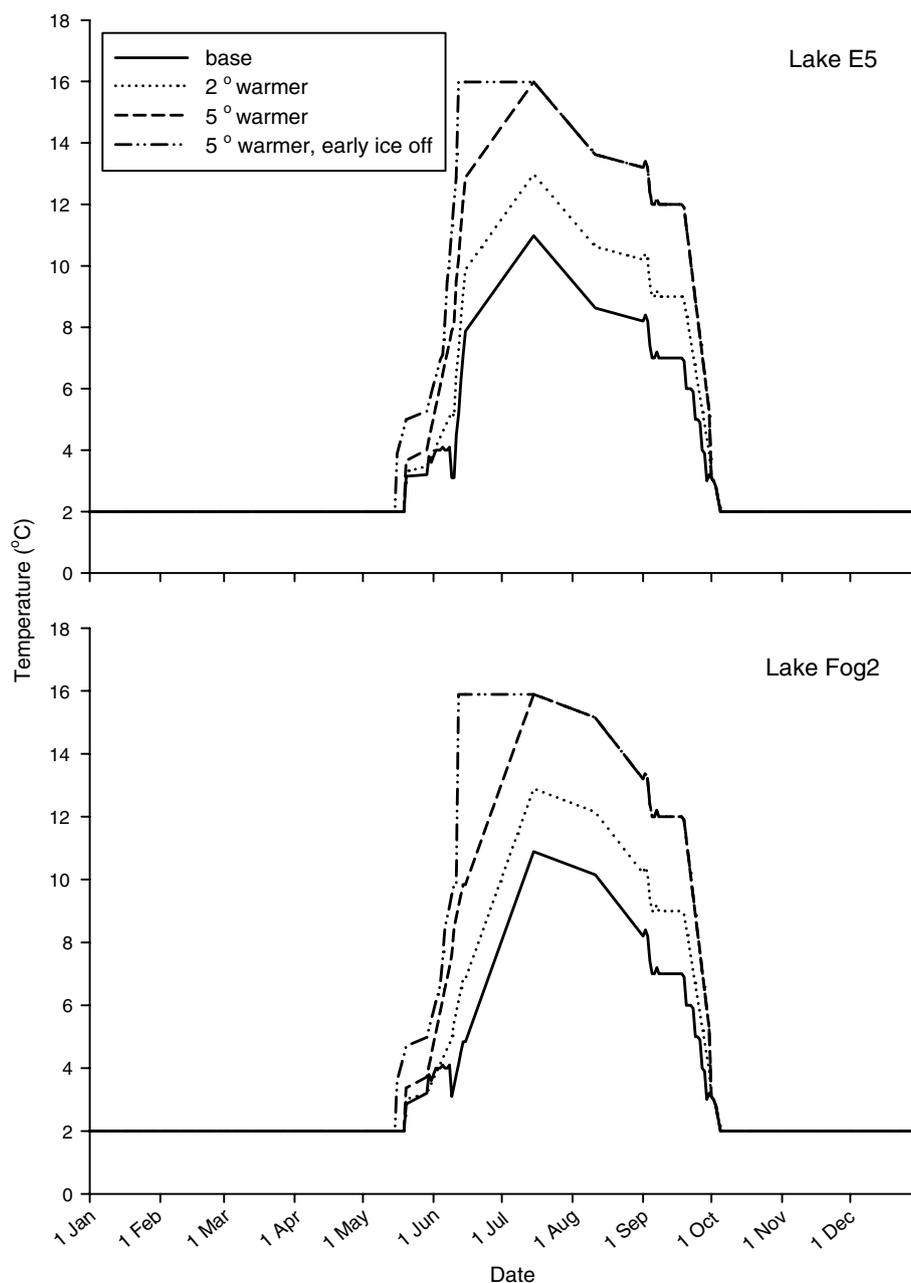
Discussion

Polymorphisms (trophic, ontogenetic, and genetic), cohort organization, and intraspecific interactions are common and frequently strong regulators of population structure in lentic systems in northern latitudes of low productivity and fish diversity (reviewed in Klemetsen et al. 2003). In this study, although overall abundance did not vary dramatically across

years, both populations demonstrated a cycle in population structure between small (≤ 300 mm) and large (> 300 mm) char. In many char systems, population regulation occurs via cannibalism, whereby a strong cohort “breaks through” and becomes piscivorous on smaller char (e.g., Klemetsen et al. 2003; Byström et al. 2004; Finstad et al. 2006).

The emergence of a cohort of giants can also arise from size-based competition for preferred habitat (Byström 2006), size-based competition for an exclusive resource (Claessen et al. 2002), or a “resource pulse” in general (Griffiths 1994), all of which can be linked strongly to cannibalism. Similar to our results, Sparholt (1985) observed populations of char in Greenland lakes composed of many

Fig. 6 Lake temperature profiles observed (“base” scenario) and predicted under the three climate change scenarios over a year. Temperatures represent the temperature closest to optimal for arctic char, 15.15 °C available on that day, but not including surface waters



small (<140 mm), few intermediate sized (140–260 mm) and many large (380–610 mm) char, with recruitment to the large char component occurring between ages 3 and 10, a pattern they attribute to differential growth patterns among the two morphs. Based on our results, rare warm years of a longer, ice-free growing season result in a strong cohort of small char, many of which die before reaching large sizes. Once char reach large sizes (>250 mm), their survival can be high and their lifespan long (25 years). Thus, the presence of the two coexisting morphs, albeit fluctuating in dominance, may be a stabilizing factor in population regulation (Klemetsen et al. 2002; Byström 2006).

In our study lakes, survival was not only relatively high on average for older fish (mean of 65 %) but also varied little across time. In unexploited Greenland lakes, adult char survival was similar (about 77 %) and nearly constant from age 3 to age 20 (Sparholt 1985), a pattern the authors attribute, in part, to a population structure characterized by low production and high standing stock. Svenning and Borgstrøm (1995) also estimated survival rates ranging from 70 to 95 % in allopatric, landlocked char populations in Norway. We detected no signal of year in our top survival and trend models, indicating adult survival varied little across this time series. In contrast, given that these lakes are

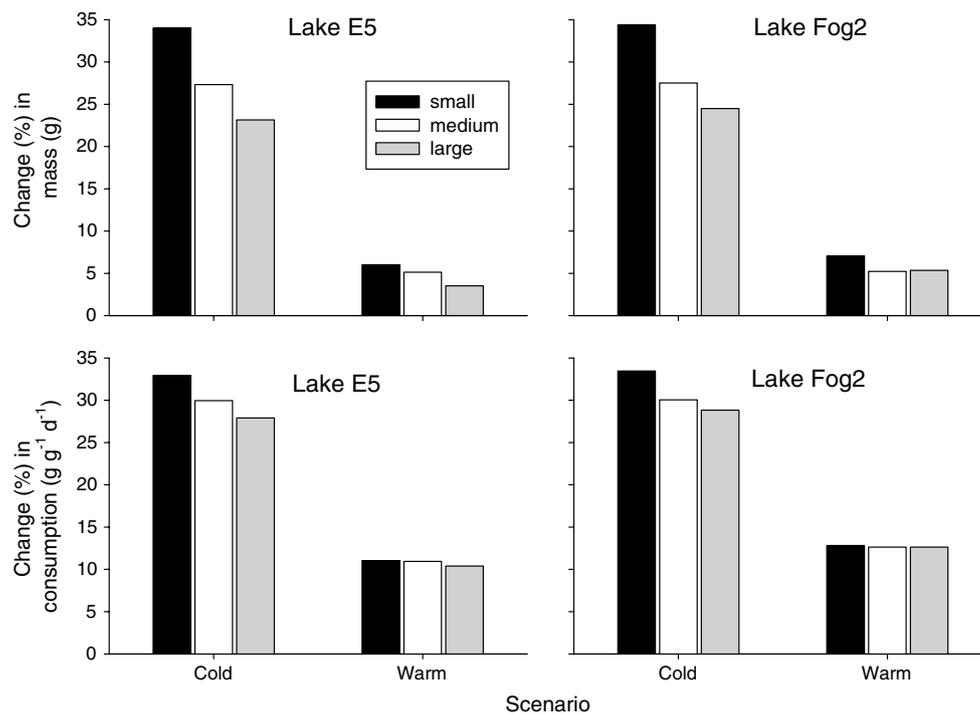


Fig. 7 Bioenergetic predictions of the relative change (%) in body mass (g; upper panels) and consumption ($\text{g g}^{-1} \text{d}^{-1}$; lower panels) for arctic char under the SC3 (5 °C warmer, early ice off) climate change scenario. Values are relative to the observed data in a

representative cold and warm year type for lake E5 (left panels) and lake Fog2 (right panels) and for all three size classes (small, medium, large) of arctic char

closed to immigration or emigration, a strong year effect on trend (λ) estimates indicates highly variable recruitment before age 3 (Pradel 1996). These results, in combination with observations of others, indicate that once char recruit into the adult age classes (i.e., \geq age 3), survival rates are typically quite high and constant (Sparholt 1985; Svenning and Borgström 1995).

Arctic fishes are well adapted for rapid growth over the short, ice-free period of their harsh arctic environments (Reist et al. 2006). In this study, despite the extremely short growing season and cold temperatures, adult growth rates were comparable to those observed for lentic char species at lower latitudes [e.g. bull trout *Salvelinus confluentus*; Flathead Lake (Fraley and Shepard 1989)]. In Swedish arctic char lakes, char growth efficiency is comparable or even higher than that observed in other salmonids and was remarkably similar across lakes (Larsson and Berglund 2005). Furthermore, Helland et al. (2011) demonstrated that char perform better (i.e., less energy loss) than other salmonids under simulated ice-cover. Low densities of char, maintained through strong internal population regulation, can also contribute to their exceptional growth rates (Rubin 1993).

Despite the relatively high growth rates exhibited over the growing season, char in this study lost on average

25 % of their summer growth over the subsequent winter, depending on the length of the growing season (duration of ice-free days). These trajectories of growth indicate that even small increases in summer water temperature, resulting primarily from the duration of the ice-free time period, have large effects on seasonal fish growth and annual net weight gain and loss. Based on our results, an arctic char experiencing a series of years of longer ice cover could remain the same size or even lose weight, demonstrating no increase in body size with age. Due to the chronic stress, these fish would likely not reproduce, and smaller fish may even lose enough mass to starve to death (MacDonald et al. 1996), a source of mortality determining recruitment dynamics and population structure over longer time periods (reviewed in Hurst 2007).

The effect of a warmer climate and longer growing season on aquatic biota can be difficult to predict and can have impacts at multiple levels of biological organization (Reist et al. 2006; Keith et al. 2008). Our climate change scenarios mimicked the pattern of warming and cooling observed in nature yet anticipated in the future (e.g., Hobbie et al. 1999), and resulted in temperatures much closer to optimal for char growth and for a longer duration, compared to both a typical warm or cold year in either lake. The optimal temperature for char growth is thought to be around 15 °C

(Lyytikäinen et al. 1997), an optimal temperature only rarely observed in our time series and only in warm years of an exceptionally longer period of ice-free days. Therefore, it is safe to assume that in most years, char consumption is temperature limited in these systems. An increase in predicted consumption rates (28–34 %) under climate change scenarios led to much higher predicted growth rates (23–34 %). Using a similar bioenergetic approach, MacDonald et al. (1996) similarly predicted an even greater (more than eightfold increase) required consumption rate of young-of-year lake trout (*Salvelinus namaycush*) under scenarios of warmer climate in the Arctic and predicted that if lake productivity (e.g., food availability) did not also increase, these fish would not survive their first winter. Furthermore, Ries and Perry (1995) similarly predicted an increase in consumption of 15–20 % for brook trout (*Salvelinus fontinalis*) under scenarios of a warmer climate, concluding 30–40 % more food would be required to maintain present rates of growth in streams of West Virginia, USA.

In this study, our predictions of greater growth rates under future climate scenarios assume fish will not be food limited and consumption can, in fact, increase to meet elevated metabolic capacity. This area remains one of the most important sources of uncertainty in predicting the physiological response of many fishes to climate warming and is worthy of future exploration (ACIA 2005; Reist et al. 2006). Despite this uncertainty, if the increased metabolic demand predicted herein under scenarios of climate change is not met by a significant associated increase in food availability (e.g., Chironomidae, zooplankton), the char will quickly deplete the available food supply, and metabolic demand will exceed consumption rates (Finstad et al. 2006). The depletion of available food will lead to starvation and ultimately mortality (Hurst 2007). Notably there are other negative physiological effects of increased temperatures with the potential to counteract the predicted increase in fish growth including loss of appetite (Larsson and Berglund 2005), decreased ovulation (Gillet 1991), and quality of eggs (Jungwirth and Winkler 1984). In contrast to our approach, however, most predictions of fish response to climate change to date have focused on changes in range, reduction and expansion, resulting from altered thermal tolerances (e.g., reviewed in Reist et al. 2006) and not mechanistic effects on individual physiology and vital rates. As such, our empirically driven and bioenergetic model predictions of fish growth under a warmer climate are noteworthy.

Synthesizing our vital rates in a simple population model allowed us to better understand population structure of these populations as well as to explore the effects of climate variability and change on population process, currently a somewhat depauperate focus of research (Keith et al. 2008; Molnar et al. 2010). The population model generally captured the cycle in population structure from

dominance of small versus large char, but with greater amplitude in cycles. This difference likely resulted from recruitment signals captured in the mark-recapture data that were not obvious in the size proportion data alone. Increased growth rates under climate change resulted in an even greater predicted amplitude of cycles in population structure, an increase in the duration of the cycle, and a shift to populations with decreased generation time and higher reproductive output. These changes in population vital rates and structure are predicted to lead to a population dominated by a smaller morph, but also a less stable one (Byström 2006). Thus when considered collectively, our results indicate that char populations (not just individuals), are extremely sensitive to small changes in summer water temperature and the duration of ice-free days.

In the Arctic, years of significantly longer growing season are predicted to occur more often under climate change and will likely provide elevated growth and reproductive rates of small char, similar to the resource pulse (Griffiths 1994) discussed above. This shift in vital rates may then allow a sub-set of small char to break through into the large char morph or cohort, thus setting the cycle in population structure (Sparholt 1985). Further, given that arctic winters represent an energetic bottleneck whereby larger individuals have a higher probability of survival (Finstad et al. 2004; this study), a shorter winter, as predicted under climate change, may minimize one of the advantages of being “large” and thus further shift the population structure towards the smaller morph. Although the authors speculate the signal could get buried in the background noise of an inherently variable arctic climate, Reist et al. (2006) similarly suggest a hallmark of climate change may be an increase in the variability of good and poor year classes of arctic fishes.

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