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**Larger but younger fish when growth compensates for higher mortality in warmed ecosystem**

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**Keywords**: body growth, size-structure, size-spectrum, mortality, climate change

Abstract

Ectotherms are often predicted to “shrink” with global warming due to smaller adult body sizes, in line with the temperature-size rule (TSR). However, the TSR also predicts faster growth rates, hence, the effect of warming on the body size distribution depends on mortality rates. We used data from an artificially heated (+8C) lake to analyze how warming has affected body growth, mortality rates and population size-structure of Eurasian perch (*Perca fluviatilis*). Compared to a reference area, we found that the size was larger for all ages and growth was faster for all sizes, to the extent that the size-spectrum slope was larger (higher proportion of large fish in) – despite the higher mortality. Due to the allometric scaling of ecological functions and the effects of demography on population stability, it is important to move beyond changes in means and evaluate change in size- and age-distributions for predicting the effects of climate change.

Introduction

It is commonly predicted that global warming will cause ectotherm species – which constitute 99% of species globally (Wilson 1992; Atkinson & Sibly 1997) – to shrink (Gardner *et al.* 2011; Sheridan & Bickford 2011; Cheung *et al.* 2013). However, the size-distribution of many species spans several orders of magnitude. A warming-signal in mean size could be therefore be undetected even if the size-distribution changes if e.g. increases in juvenile growth outweigh the decline in growth by adults, as consistent with the temperature size-rule, TSR (Atkinson 1994). It may be more informative to investigate change in the size-distribution and how these emerge (Fritschie & Olden 2016), if the aim is to infer effects of warming on ecosystem properties such as the ecological role of individual species, biomass production, energy fluxes (Yvon‐Durocher *et al.* 2011). This is because key traits such as metabolism, feeding, growth, mortality (Ursin 1973; Pauly 1980; Brown *et al.* 2004; Blanchard *et al.* 2017; Thorson *et al.* 2017; Andersen 2020), scale with size allometrically, and the trait value at the average size is not the same as the average population trait value (Bernhardt *et al.* 2018).

The size-spectrum is the relationship between number of individuals in a body-size class and the average size of that class, and the size-spectrum slope () is the often-linear relationship between the two variables on a log-log scale (Sheldon *et al.* 1973; White *et al.* 2007; Edwards *et al.* 2017). Hence, it implicitly captures temperature-dependent ecological processes such as body growth, mortality and recruitment (Blanchard *et al.* 2017; Heneghan *et al.* 2019). Despite its rich theoretical foundation (Andersen 2019) and usefulness as an ecological indicator, relatively few studies have evaluated warming-effects on the species size-spectrum in larger bodied species (but see (Blanchard *et al.* 2005)). This could be due to a lack of theoretical predictions for how species spectra will change with warming (note that in unicellular multispecies communities, slopes are predicted to decline as smaller-bodied species become more dominant (Daufresne *et al.* 2009; Yvon‐Durocher *et al.* 2011)). Perhaps it is difficult to reconcile the numerous patch by which the species size-spectrum could change with warming (Heneghan *et al.* 2019). For instance, the clearest effect of TSR on the size-spectrum is a decline in the maximum size. However, if the relative abundance of juveniles and adults remains constant, but the same number of adults now accumulate in a smaller size-range, the size-spectrum slope could become less steep. Elevated mortality truncates the age-distribution towards younger individuals (Barnett *et al.* 2017), but increased growth rates (from warming, reduced density dependence or both) can counter the effects of mortality on abundance-at-size – unless only small individuals benefit from warming (Daufresne *et al.* 2009; Lindmark *et al.* 2021). Hence, the effect of warming on the size-spectrum depends on several interlinked processes affecting abundance-at-size and size-at-age.

In this study, we use data from the unique large-scale semi-natural experiment that is the Biotest lake to quantify changes in body growth, mortality, and the size structure in a non-commercially exploited population of Eurasian perch (*Perca fluviatilis*, henceforth perch) that was enclosed and exposed to temperatures 5-10 above the normal for 23 years, in relation to the reference outside the enclosure. The Biotest lake is a 1 artificial enclosure of Swedish Baltic Sea archipelago (Fig. 1) that since 1980 has received warm cooling water from the nuclear power plant in Forsmark and where all types of fishing is banned (Adill *et al.* 2013; Huss *et al.* 2019). Henceforth, we refer to the Biotest as the warm and the reference as the cold area. Using hierarchical Bayesian models, we quantify key individual-and population level parameters, such as body growth, asymptotic size, mortality rates, and size-spectra between the areas.

Results

Analysis of size-at-age using the von Bertalanffy growth equation (VBGE) revealed that cohorts in the warm area not only grew faster initially (larger size-at-age as well as VBGE parameter), but also reached had larger predicted asymptotic sizes. (Fig. 2). The model with area specific VBGE parameters (, and ) had the largest expected log pointwise predictive density (Table S1), and there is a clear difference between the estimated values for and (Fig. 1). For instance, the distribution of differences of the posterior samples for and (i.e., and ) only had 11% and 2% (respectively) of the density below 0, which illustrates that it is unlikely that the parameters are larger in the cold area (Fig. 2). Specifically, we estimated the following population-level VBGE parameters: , and , and , and , where the estimate is the posterior median and the range in square brackets indicate the 95% credible interval.

In addition, we found that the initial growth rate (at small size) was higher in the warm are and that the decline in growth with length was steeper in the cold area. Also here is the best model one with area-specific parameters (Table S2), and we fond even stronger support for differences in growth parameters between the areas (Fig. 3). We estimated the allometric parameters relating growth to length () to be: , and , . The distribution of differences of the posterior samples for and (i.e., and ) both only had 0.3% of the density below 0.

By analyzing the decline in catch-per-unit-effort over age, we found that the instantaneous mortality rate (rate at which log abundance declines with age) is higher in the warm area (Fig. 4). We estimate to be and to be , which correspond to annual mortality rates of 53% and 0.47%, respectively. The overlap with zero is 0.1% for the distribution of differences of posterior samples of and (Fig. 4).

Lastly, analysis of the size-structure revealed that the faster growth rates for all sizes leading to a larger size-at-age outweigh the higher mortality rates in the warm area, such that the warmer area both have the largest individuals as well as an overall larger proportion of large individuals (Fig. 5D). This is also evident in the analyses of size-spectrum slopes over time, where we found that the intercept is larger in the warm area (where year is centered to such that the intercept corresponds to the first year, i.e., 1987, and the model without an interaction between year and area was favored). The overlap with zero was 2% for the distribution of differences of posterior samples of and (intercept for the warm and cold area, respectively) (Fig. 4).

Discussion

Our study provides strong evidence for differentiation in growth, mortality, and size-structure in a natural population of a non-exploited, temperate fish species exposed 5-10 above normal temperatures for approximately two decades. While it is a study on only a single species, these features make it a unique climate change experiment, as most studies on natural populations of fish to date are on commercially exploited fish species (and fisheries exploitation affects both the size-structure directly but also indirectly by selecting fast growing individuals). It is also rare to have such large temperature contrasts in natural systems. While other factors could have contributed to these differences, it is interesting that our findings contrast with both broader predictions about declining mean body sizes, and, more specifically, intraspecific responses such as the TSR (temperature-size rule) and the GOLT (Gill-Oxygen-Limitation-Theory). The contrasts lie in that both asymptotic size and size-at-age of mature individuals, as well as the proportion of larger individuals are larger and higher in the warm area – despite the elevated mortality rates. Interestingly, these patterns, rules and mechanistic predictions are essentially agnostic about changes in e.g., food levels, which otherwise could confound the effects we attribute to the temperature difference here. Moreover, since optimum growth temperatures decline with size within species generally even under food satiation in experimental studies (Lindmark *et al.* 2021), the finding that the largest individuals inhabited the warmed area was unexpected.

A key question for understanding the implications of warming on ectotherm populations is if larger individuals in a population become rarer or smaller (Ohlberger 2013; Ohlberger *et al.* 2018) – i.e. how the size- and age-distribution change rather than the mean size. Not only for evaluating population-level changes in functions and ecological roles due to the allometric scaling of vital rates (Fritschie & Olden 2016; Audzijonyte *et al.* 2020), but also because age-truncated populations tend to have less stable dynamics (Anderson *et al.* 2008). Our study contributes to the literature revealing large variations across species in terms of the warming effects on life history traits and demographic parameters. A key challenge is to account for this variation into projections on the impacts of climate change on natural populations.

Materials and Methods

*Data*

We use years after the onset of warming (earliest cohort is 1981) to omit transient dynamics and acute responses and to ensure we use cohorts that only experience one of the thermal environments during its life. A grid at the Biotest outlet together with the strong current prevented fish larger than 10 cm from migrating in and out of the area (Adill *et al.* 2013; Huss *et al.* 2019), and genetic studies confirm the reproductive isolation between the two populations during the time period (Björklund *et al.* 2015). However, since the grid removal in 2004, fish growing up in the Biotest lake can easily swim out, meaning we cannot be sure fish in the reference area did not recently arrive from the Biotest lake. Hence, we use data up until 2003. This resulted in 12658 length-at-age measurements from 2426 individuals in 256 nets.

The Biotest lake and the reference bay outside have been scientifically sampled using survey-gillnets since the construction of the enclosure. We use data from fishing events that took place in October in the Biotest lake and in August in the reference area when temperatures are most comparable between the two areas (Huss et al., 2019). The catch was recorded by 2.5 cm length classes during 1987-2000, and into 1 cm length groups between 2001-2003. To express lengths in a common length standard, 1 cm intervals were converted into 2.5 cm intervals. The unit of catch data is hence number of fish caught per 2.5 cm size class per night per net (i.e., a catch-per-unit-effort [CPUE] variable). All data from fishing events with disturbance affecting the catch (e.g., seal damage, strong algal growth on the gears, clogging by drifting algae, boat traffic or other human inference) were removed (this mean removing years 1996 and 1999 from the warm area in the catch data).

Age and length-at-age was reconstructed for a semi-random length-stratified subset of individuals each year. This was done using annuli rings on the operculum bones (with control counts done on otoliths), and an established power-law relationship between the distance of annual rings and fish length: , where is the length of the fish, the operculum radius, the intercept, and the slope of the line for the regression of log-fish length on log-operculum radius (Thoresson 1996). Back-calculated length-at-age were obtained from the relationship , where is the back-calculated body length at length , is the final body length (body length at catch) and is the distance from the centre to the annual ring corresponding to age . Since perch exhibit sexual size-dimorphism, and age-determination and back calculation was only done for males in select years, we only used females for our analyses.

To focus on the long term differentiation between the two areas, and to ensure that we had enough back-calculated length-at-age observation within individual fish born after the onset of heating, we avoided the initial years of warming (when mortality rates increased only to decline again (Sandström *et al.* 1995), and used data from 1987-2003. 2003 corresponds to the year before the populations were no longer reproductively separated, and when the back-calculation parameters potentially changed.

*Statistical Analysis*

The differences in size-at-age, growth, mortality, and size structure between the two areas in the period after the onset of warming and before the removal of the barrier were quantified using hierarchical linear and non-linear regression models fitted in a Bayesian framework. First, we describe each statistical model and then we provide details of model fitting, model diagnostics and comparison.

We fit the von Bertalanffy growth equation (VBGE) on a scale, describing length as a function of age to evaluate differences in size-at-age and asymptotic size: , where is the length at age (, years), is the asymptotic size, is the Brody coefficient (). We used only age-and-size at catch as the response variables (i.e., not back-calculated length-at-age). This was to have a simpler model and not have to account for parameters varying within individuals as well as cohorts (mean sample size per individual was only ~5). We let parameters vary among cohorts rather than year of catch, because individuals within cohorts shares similar environmental conditions and density dependence (Morrongiello & Thresher 2015). Eight models in total were fitted (with area being dummy-coded), with different combinations of shared and area-specific parameters. We evaluated if models with area-specific parameters led to better fit and quantified the differences in area-specific parameters. The model with all area-specific parameter can be written as:

where we lengths are distributed to account for extreme observations, , and represent the degrees of freedom, mean and the scale parameter. Henceforth, subscripts and are used for the warm and cold area, respectively (except in figures where subscripts are spelled out for clarity). and are dummy variables such that and if it is the cold area, and vice versa, and and subscripts indicate area-specific parameters. The multivariate normal distribution in Eq. 3 is the prior for the cohort-varying parameters , ,and (for cohorts …,1997) (note that cohorts extend further back in time than the catch data), with hyper-parameters , , , describing the non-varying population means and a covariance matrix with the between-cohort variation along the diagonal (note we did not model a correlation between the parameters hence off-diagonals are 0). The other seven models include some or all parameters as common parameters, e.g., substituting and with etc. To aid convergence of this non-linear model, we used informative priors chosen after visualizing draws from prior predictive distributions (Wesner & Pomeranz 2021) using probable parameter values (*Supporting Information*, Fig. S1, S6*)*. We used the same prior distribution for each parameter class for both areas to not give introduce any other sources of differences in parameter estimates between areas. We used the following priors for the VBGE model: , , and . *,* , , , were given a prior.

We also compared how growth scales with *size* (in contrast to length vs age) in the two areas, because length-at-age is by fitting allometric growth models describing how specific growth rate scales with length: , where, the specific growth, is defined as: and is the geometric mean weight: . Here we also used back-calculated length-at-age, meaning multiple observations within individuals. As with the VBGE model, we dummy coded area in order to compare models with different combinations of common and shared parameters. We assumed growth rates were distributed, and the full model can be written as:

We assumed only varied across individuals and cohorts, and compared two models, one with a common and one with an area-specific . We used the following priors, after visual exploration of the prior predictive distribution (*Supporting Information*, Fig. S7, S9): , and . , and were all given a prior.

We estimated total mortality by fitting linear models to the natural log of catch (CPUE) as a function of age (catch curve regression), under the assumption that in a closed population, the exponential decline can be described as , where is the population at time , is the initial population size and is the instantaneous mortality rate. This equation can be rewritten as a linear equation: , where is catch-at-age , if catch is assumed proportional to the number of fish (i.e., ). Hence, the negative of the slope of the regression is . To get catch-at-age data, we constructed area-specific age-length keys from the sub-sample of the total catch that was age-determined. Age length-keys describe the age-proportions of each length-category (i.e., a matrix with length category as rows, ages as columns). Age is then estimated for the total catch based on the “probability” of fish in each length-category being a certain age. With fit this model with and without an --interaction, and the former can be written as:

where and are the intercepts for the cold and warm areas, respectively, is the age slope for the cold area for the cold area and is the interaction between and . All parameters vary by cohort (for cohort ) and their correlation is set to 0 (Eq. 12). We use the following (vague) priors: (where is the population-level estimate for and is the population-level estimate for ) and . and were given a prior.

Lastly, we quantified differences in the size-distributions between the areas using size-spectrum slopes. We follow (Edwards *et al.* 2017, 2020) and estimate for each year and area using their likelihood approach for binned data, i.e., the *MLEbin* method in the R package *sizeSpectra* (Edwards 2020). This method explicitly accounts for uncertainty in body masses *within* size-classes (bins) in the data and has been shown to be less biased than regression-based methods or the likelihood method based on bin-midpoints (Edwards *et al.* 2020). We then fit a linear model of the size-spectrum slopes with and (and their interaction) as predictors, after initial exploration revealed clear trends over time. The model with the - interaction for the size-spectrum slopes can be written as:

where the response is assumed to be normally distributed, and represent each areas’ intercept, is the year effect for the cold area and is the difference in slope between the cold and the warm area. We use a prior for the intercepts and , which in this model represent the size-spectrum slopes at the beginning of the time series. is the size-spectrum slope predicted by (Andersen & Beyer 2006) based on individual-level processes under the assumption of size-independent average satiation levels. To include uncertainty around this average we use a large standard deviation. We use a prior for and a prior for and .

All analyses were done using R (R Core Team 2020) version 4.0.2. The packages within the *tidyverse* (Wickham *et al.* 2019) collection were used to processes and visualize data. Models where fit using the R package *brms* (Bürkner 2017)*.* When priors were not chosen based on the prior predictive distributions, we used the default priors from *brms* as written above. We used 3 chains and 4000 iterations in total per chain. Models were compared by evaluating their expected predictive accuracy (expected log pointwise predictive density) using leave-one-out cross-validation (LOO-CV)(Vehtari *et al.* 2017) while ensuring pareto values < 0.7, in the R package *loo* (Vehtari *et al.* 2020)*.* Results of the model comparison can be found in the *Supporting Information*, Table S1-S4. *bayesplot* (Gabry *et al.* 2019) and *tidybayes* (Kay 2019) were used to process and visualize model diagnostics and posteriors. Model convergence and fit was assessed by ensuring potential scale reduction factors () where <1.1 (suggesting all three chains converged to a common distribution) (Gelman *et al.* 2003), and by visually inspecting trace plots, residuals QQ-plots and with posterior predictive checks (*Supporting Information*, Fig. S2, S8, S10, S12).

Acknowledgements

We thank all staff involved in data collection.

Code and Data Availability

All data and R code can be downloaded from a GitHub repository (<https://github.com/maxlindmark/warm_life_history>) and will be archived on Zenodo upon publication.

Author Contributions

ML conceived the idea and designed the study and the statistical analysis. Data-processing, initial statistical analyses, and initial writing was done by MK and ML. AG contributed critically to all mentioned parts of the paper. All authors contributed to the manuscript writing and gave final approval for publication.

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Figures

A picture containing map

Description automatically generated

**Fig. 1.** Map of the study area, with inset showing the 1 Biotest lake, the reference area, and locations of the cooling water intake and where the warm water outlet enters the Biotest lake.

Chart

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**Fig. 2.** The average length-at-age is larger for all ages in the warm (red) compared to the cold (blue) area. Points in panel (A) depicts individual-level length-at-age and lines show the global posterior prediction (both exponentiated) without group-level effects (i.e., cohort) from the von Bertalanffy model with area-specific coefficients. The shaded areas correspond to 50% and 90% credible intervals. Panel (B) shows the posterior distributions for parameters and and panel (C) shows the distribution of differences. Panel (D) shows the posterior distributions for parameters and , and panel (E) shows the distribution of differences.

Diagram

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**Fig. 3.** The faster growth rates in the warm area are maintained as fish grow. The points illustrate specific growth estimated from back-calculated length-at-age (within individuals) as a function of length (expressed as the geometric mean of the length at the start and end of the time interval). Lines show the global posterior prediction without group-level effects (i.e., individual within cohort) from the allometric growth model with area-specific coefficients. The shaded areas correspond to the 90% credible interval. The equation uses mean parameter estimates. Panel (B) shows the posterior distributions for parameters and , and panel (C) shows the distribution of differences. Panel (D) shows the posterior distributions for parameters and , and panel (E) shows the distribution of differences.

Chart

Description automatically generated

**Fig. 4.** The instantaneous mortality rate is higher in the warm area. Panel (A) shows the as a function of , where the slope corresponds to the global . Lines show the posterior prediction without group-level effects (i.e., cohort) and the shaded areas correspond to the 50% and 90% credible intervals. The equation uses mean parameter estimates. Panel (B) shows the posterior distributions for parameters and , and panel (C) shows the distribution of differences.

Chart

Description automatically generated

**Fig. 5.** The warm area has a larger proportion of large fish, illustrated both as histograms of proportions and the generally smaller size-spectrum slopes (which also increased over time in both areas). Panel (A) shows mean annual size-spectrum slopes as points and their 95% confidence interval, estimated using maximum likelihood. Lines and shaded areas correspond to the median and 90% credible interval. The equation uses mean parameter estimates. Panel (B) shows the posterior distributions for the cold and warm intercepts (i.e., and in the model shown in panel (A) of size-spectrum slopes as a function of year), and panel (C) shows the distribution of differences (). Panel (D) illustrates histograms of length groups as proportions (for all years pooled).