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

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Abstract

Ectotherms are often predicted to “shrink” with global warming due to smaller adult body sizes, in line with the temperature-size rule (TSR). Still, TSR predicts faster juvenile growth rates. The net effect of warming on population body size distributions, however, depends also on mortality. We used data from an artificially heated (+8C) bay in comparison with an unheated area, to analyze how warming has affected body growth, mortality rates and population size-structure of Eurasian perch (*Perca fluviatilis*). In the warm bay, body size was larger for all ages and growth faster for all sizes, resulting in larger size-spectrum slope (greater proportion of large fish) – despite higher mortality. Combining temperature effects on growth with those on mortality is necessary for understanding warming-induced changes in size-distributions. Because ecological dynamics emerge from size-dependent processes and functions, addressing how warming affects size-distributions through multiple processes is essential for predicting the effects of climate change.

Introduction

Global warming is commonly predicted to cause ectotherm species, constituting 99% of species globally (Wilson 1992; Atkinson & Sibly 1997), to shrink (Gardner *et al.* 2011; Sheridan & Bickford 2011; Cheung *et al.* 2013). Mean body size responses to temperature may however be uninformative, as the size-distribution of many species spans several orders of magnitude. Warming can even shift size-distributions without altering mean size; for example, if increases in juvenile growth outweigh the decline in growth by adults, as consistent with the temperature size-rule, TSR (Atkinson 1994). Resolving how warming induces changes in population size-distributions may thus be more instructive (Fritschie & Olden 2016), especially for inferring warming effects on species’ ecological role, biomass production, or energy fluxes (Yvon‐Durocher *et al.* 2011). This is because key traits such as metabolism, feeding, growth, mortality scale with body size (Ursin 1973; Pauly 1980; Brown *et al.* 2004; Blanchard *et al.* 2017; Thorson *et al.* 2017; Andersen 2020). The diversity of size within a population thus matters for its dynamics under warming, as the value of these traits at mean body size is not the same as the mean population trait value (Bernhardt *et al.* 2018).

The population size distribution can be represented as a size-spectrum, which is the number of individuals in different body-size classes related to the mean size of each class. The size-spectrum slope () is the often-linear relationship between these variables on a log-log scale (Sheldon *et al.* 1973; White *et al.* 2007; Edwards *et al.* 2017). Hence, the size-spectrum slope 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 (ref), few studies have evaluated warming-effects on the species size-spectrum in larger bodied species (but see (Blanchard *et al.* 2005)). There are numerous ways by which the species size-spectrum could change with warming (Heneghan *et al.* 2019). For instance, the clearest consequence of TSR for the size-spectrum is a decline in maximum size. However, unless warming also alters the relative abundances of juveniles and adults, the same number of adults will accumulate in a smaller size-range, resulting in a less steep slope of the size-spectrum. Warming can also lead to elevated mortality, which truncates the age-distribution towards younger individuals (Barnett *et al.* 2017). Increased growth rates can however counter the effects of mortality on abundance-at-size, unless only small individuals benefit from warming (Daufresne *et al.* 2009; Lindmark *et al.* 2021). Growth rates can increase due to physiological responses to higher temperatures, or reduced density-dependence following warming-induced mortality, or both. Hence, the effect of warming on the size-spectrum depends on several interlinked processes affecting abundance-at-size and size-at-age. Yet, while warming effects on ectotherm body growth has been thoroughly studied (ref, ref, ref), those on mortality in wild populations have not, nor their joint consequences for population size-spectra in warming environments.

We used data from a unique large-scale 23-year-long experiment heating a coastal ecosystem to quantify how warming changed fish body growth, mortality, and the size structure in a unexploited population of Eurasian perch (*Perca fluviatilis*, ‘perch’). We compare fish from this enclosed bay exposed to temperatures 5-10 above normal (‘warm area’) with fish from a reference area (‘cold area’) in the adjacent archipelago (Fig. 1). Using hierarchical Bayesian models, we quantify differences in key individual- and population level parameters, such as body growth, asymptotic size, mortality rates, and size-spectra between the warm and cold coastal area.

Results

Analysis of fish (perch) size-at-age using the von Bertalanffy growth equation (VBGE) revealed that fish cohorts in the warm area both grew faster initially (larger size-at-age and VBGE parameter) and reached larger predicted asymptotic sizes than those in the cold area (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 in both the estimated values for fish asymptotic length () and growth rate () between the warm and cold area (Fig. 2B-E). For instance, the distribution of differences between the warm and cold area of the posterior samples for and only had 11% and 2%, respectively, of the density below 0, illustrating that it is unlikely that the parameters are larger in the cold area or similar in the two areas (Fig. 2C, E). We estimated that fish in the warm area had an asymptotic length that was 16% greater than fish in the cold area (, , given as posterior median with 95% credible interval) and grew with 27% faster growth rate (). Corresponding estimates of the third parameter in the VBGE were , and .

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 (Fig. 3). The best model for growth () had area-specific parameters (Table S2), and we found even stronger support for differences in growth parameters between the areas (Fig. 3). Initial growth was estimated to be 18% faster in the warm than in the cold area (,), and growth of fish in the warm area had a 4% lower decline with length than in the cold area (, ). The distribution of differences of the posterior samples for 𝛼 and *θ* both only had 0.3% of the density below 0 (Fig. 3C, E), indicating that identical growth in the warm and the cold area is highly unlikely.

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). C We estimated to be and to be , which correspond to annual mortality rates of 53% in the warm area and 47% in the cold.

Lastly, analysis of the population size-structures revealed that the faster growth rates for fish of all sizes leading to a larger size-at-age outweigh the higher mortality rates in the warm area, such that the size-spectrum slope is less steep in the warm area (Fig. 5A). As a consequence of this faster growth, the warmer area both has the largest individuals as well as an overall larger proportion of large individuals (Fig. 5D). This is evident in the analyses of size-spectrum slopes over time, where we found that the intercept () is larger in the warm area (Fig. 5B; 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 the size-spectrum intercepts of the warm and the cold area, and (Fig. 5C).

Discussion

Our study provides strong evidence for warming-induced differentiation in growth, mortality, and size-structure in a natural population of a non-exploited, temperate fish species exposed to 5-10 above normal temperatures for more than two decades. While it is a study on only a single species, these features make it a unique climate change experiment, as most warming studies on natural populations of fish to date are on commercially exploited fish species (and fisheries exploitation affects size-structure both directly and indirectly by selecting for fast growing individuals). While factors other than temperature could have contributed to the elevated growth and mortality, the temperature contrast is unusually large for natural systems. Moreover, heating occurred at the scale of a whole ecosystem, which makes the findings highly relevant in the context of global warming. Interestingly, our findings contrast with both broader predictions about declining mean body sizes (ref), and on intraspecific responses such as the TSR (temperature-size rule; ref) and the GOLT (Gill-Oxygen-Limitation-Theory; ref). The contrasts lie in that both asymptotic size and size-at-age of mature individuals, as well as the proportion of larger individuals were larger and higher in the warm area – despite the elevated mortality rates. 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. Our results suggest that organisms respond differently to warming of whole ecosystems than to direct warming of individuals, and that growth (and mortality) changes emerge not only from direct physiological responses to increased temperatures, but also from warming-induced changes in the food web, e.g. prey productivity, diet composition and trophic transfer efficiencies (Gårdmark & Huss 2020).

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 in projections on the impacts of climate change on natural populations.

Materials and Methods

*Data*

We use trait data from perch sampled annually from the heated enclosed bay (‘the Biotest lake’) and its reference area with natural temperatures in the years after the onset of warming (first cohort is 1981 and last catch year is 2003) 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 outlet of the warm area (Fig. 1) prevented fish larger than 10 cm from migrating between the areas (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 heated 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.

We use data from fishing events using survey-gillnets 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), because temperature affect catchability in static gears. 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 the 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) were removed (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 from a large reference data set for perch (Thoresson 1996). Back-calculated length-at-age were obtained from the relationship , where is the back-calculated body length at age , is the final body length (body length at catch), is the distance from the centre to the annual ring corresponding to age and for perch (Thoresson 1996). Since perch exhibits sexual size-dimorphism, and age-determination together with back calculation of growth was not done for males in all years, we only used females for our analyses.

To focus on the long term differentiation in mortality between the heated and reference area 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.

*Statistical Analysis*

The differences in size-at-age, growth, mortality, and size structure between the heated and the reference area were quantified using hierarchical linear and non-linear regression models fitted in a Bayesian framework. First, we describe each statistical model and then 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 () and is the XXXX. 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, as mean sample size per individual was only ~5. We let parameters vary among cohorts rather than year of catch, because individuals within cohorts share 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:

#(1)

#(2)

#(3)

where lengths are distributed to account for extreme observations, , and represent the degrees of freedom, mean and the scale parameter, respectively. Henceforth, subscripts and are used for the warm and cold area, respectively (except in figures and main text 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 parameters common for the two areas, e.g., substituting and with . 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 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, 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 length: . Here we also used back-calculated length-at-age, resulting in multiple observations for each individual. 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:

#(4)

#(5)

#(6)

#(7)

#(8)

#(9)

We assumed only varied across individuals and cohorts, and compared two models, one with common for the warm and cold area, 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 using 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:

#(10)

#(11)

#(12)

where and are the intercepts for the cold and warm areas, respectively, is the age slope 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 the 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:

#(13)

#(14)

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. We used *bayesplot* (Gabry *et al.* 2019) and *tidybayes* (Kay 2019) to process and visualize model diagnostics and posteriors. Model convergence and fit was assessed by ensuring potential scale reduction factors () were less than 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).

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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 area with unique the ecosystem warming experiment from which perch in this study was sampled. Inset shows the 1 enclosed coastal bay that has been artificially heated for 23 years, the adjacent reference area with natural temperatures, and locations of the cooling water intake and where the warm water outlet from nuclear power plants enters the heated coastal area.

Chart

Description automatically generated

**Fig. 2.** The average length-at-age is larger for fish of all ages in the warm (red) compared to the cold (blue) coastal 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 growth model with area-specific coefficients. The shaded areas correspond to 50% and 90% credible intervals. Panel (B) shows the posterior distributions for growth rate (parameters (red) and (blue)) and (C) the distribution of their difference. Panel (D) shows the posterior distributions for asymptotic length (parameters and ), and (E) the distribution of their difference.

Diagram

Description automatically generated with medium confidence

**Fig. 3.** The faster growth rates in the warm area (red) compared to the cold (blue) 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 initial growth ( (red) and (blue)), and (C) the distribution of their difference. Panel (D) shows the posterior distributions for the allometric decline in growth with length ( and ), and (E) the distribution of their difference.

Chart

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**Fig. 4.** The instantaneous mortality rate () is higher in the warm area (red) than in the cold (blue). 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 mortality rate ( and ), and (C) the distribution of their difference.

Chart

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**Fig. 5.** The warm area (red) has a larger proportion of large fish than the cold area (blue), illustrated both as (B) histograms of proportions and (A) 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 (C) the distribution of their difference. Panel (D) illustrates histograms of length groups in the warm and cold area as proportions (for all years pooled).