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

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## Abstract

Ectotherms are often predicted to “shrink” with global warming, in line with general growth models and the temperature-size rule (TSR), both predicting smaller adult sizes with warming. However, they also predict faster juvenile growth rates, leading to larger size-at-age. Hence, the result of warming on population size-structure also depends on mortality rates and how much also adult size changes. 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 heated bay, body size was larger for all ages and growth faster for all sizes, resulting in larger size-spectrum exponent (greater proportion of large fish) – despite higher mortality. Hence, to understand how warming alters species size-structure, and thus ecological interactions and dynamics, it is critical to account for warming-induced changes in both mortality and growth rate.

## Introduction

Ectotherm species, constituting 99% of species globally<sup>1,2</sup>, are commonly predicted to shrink in a warming world<sup>3–5</sup>. 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 size-at-age outweigh the decline in size-at-age in adults, which is consistent with the temperature size-rule, TSR<sup>6</sup>. Resolving how warming induces changes in population size-distributions may thus be more instructive<sup>7</sup>, especially for inferring warming effects on species' ecological role, biomass production, or energy fluxes<sup>8</sup>. This is because key traits such as metabolism, feeding, growth, mortality scale with body size<sup>9–14</sup>. Hence, as the value of these traits at mean body size is not the same as the mean population trait value<sup>15</sup>, the size-distribution within a population thus matters for its dynamics under warming,

The population size distribution can be represented as a size-spectrum, which generally is the frequency distribution of individual body sizes<sup>16</sup>. It is often described in terms of the spectrum slope (slope of individuals or biomass of a size class over the mean size of that class on log-log scale<sup>16–18</sup>) or simply the exponent of the power law individual size-distribution<sup>16</sup>. The size-spectrum thus results from temperature-dependent ecological processes such as body growth, mortality and recruitment<sup>10,19</sup>. Despite its rich theoretical foundation<sup>20</sup> and usefulness as an ecological indicator<sup>21</sup>, few studies have evaluated warming-effects on the species size-spectrum in larger bodied species (but see Blanchard *et al.*<sup>21</sup>). There are numerous paths by which the species size-spectrum could change with warming<sup>19</sup>. 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<sup>22</sup>. Increased growth rates can however counter the effects of mortality on abundance-at-size, unless only small individuals benefit from warming<sup>23,24</sup>. 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 have been thoroughly studied<sup>6,24,25</sup>, those on mortality in wild populations have not to the same extent, nor their joint consequences for population size-spectra in warming environments.

We used data from a unique, large-scale 23-year-long heating-experiment of a coastal ecosystem to quantify how warming changed fish body growth, mortality, and the size structure in an unexploited population of Eurasian perch (*Perca fluviatilis*, ‘perch’). We compare fish from this enclosed bay exposed to temperatures 5-10 °C above normal (‘heated area’) with fish from a reference 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 heated and reference coastal area.

## Results

Analysis of fish (perch) size-at-age using the von Bertalanffy growth equation (VBGE) revealed that fish cohorts (year classes) in the heated area both grew faster initially (larger size-at-age and VBGE  $K$  parameter) and reached larger predicted asymptotic sizes than those in the reference area (Fig. 2). The model with area-specific VBGE parameters ( $L_{\infty}$ ,  $K$  and  $t_0$ ) had best out of sample predictive accuracy (the largest expected log pointwise predictive density for a new observation; Table S1), and there is a clear difference in both the estimated values for fish asymptotic length ( $L_{\infty}$ ) and growth rate ( $K$ ) between the heated and reference area (Fig.

2B-E). For instance, the distribution of differences between the heated and reference area of the posterior samples for  $L_\infty$  and  $K$  only had 11% and 2%, respectively, of the density below 0, illustrating that it is unlikely that the parameters are larger in the reference area or similar in the two areas (Fig. 2C, E). We estimated that fish in the heated area had a 16% larger asymptotic length than in the reference area ( $L_{\infty heat} = 45.7[36.8, 56.3]$ ,  $L_{\infty ref} = 39.4[35.4, 43.9]$ , given as posterior median with 95% credible interval) and 27% larger growth coefficient ( $K_{heat} = 0.19[0.15, 0.23]$ ,  $K_{ref} = 0.15[0.12, 0.17]$ ). Corresponding estimates of the third parameter in the VBGE were  $t_{0heat} = -0.16[-0.21, -0.11]$ , and  $t_{0ref} = -0.44[-0.56, -0.33]$ .

In addition, we found that the initial growth rate (at small size) was higher in the heated area and that the decline in growth with length was steeper in the reference area (Fig. 3). The best model for growth ( $G = \alpha L^\theta$ ) 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 heated than in the reference area ( $\alpha_{heat} = 509.7[460.1, 563.5]$ ,  $\alpha_{ref} = 433.5[413.3, 454.1]$ ), and growth of fish in the heated area had a 4% lower decline with length than in the reference area ( $\theta_{heat} = -1.13[-1.16, -1.11]$ ,  $\theta_{ref} = -1.18[-1.19, -1.16]$ ). The distribution of differences of the posterior samples for  $\alpha$  and  $\theta$  both only had 0.3% of the density below 0 (Fig. 3C, E), indicating high probability that growth rates have differentiated between the heated and reference area.

By analyzing the decline in catch-per-unit-effort over age, we found that the instantaneous mortality rate  $Z$  (rate at which log abundance declines with age) is higher in the heated area (Fig. 4). The overlap with zero is 0.1% for the distribution of differences of posterior samples of  $Z_{heat}$  and  $Z_{ref}$  (Fig. 4C). We estimated  $Z_{heat}$  to be  $0.76[0.63, 0.88]$  and  $Z_{ref}$  to be  $0.63[0.58, 0.69]$ , which corresponds to annual mortality rates of 53% in the heated area and 47% in the reference area.

Lastly, analysis of the size-structure in the two areas revealed that the faster growth rates for fish of all sizes, which lead to a larger size-at-age, outweigh the higher mortality rates in the heated area, such that the size-spectrum exponent is larger in the heated area (Fig. 5A). However, in contrast to the results on size-at-age, growth and mortality, the differentiation is not as strong statistically, as the 95% confidence intervals overlap. That said, because of this faster growth, the heated area both has the largest individuals and an overall larger proportion of large individuals (Fig. 5C).

## Discussion

Our study provides strong evidence for warming-induced differentiation in growth, mortality, and size-structure in a natural population of an unexploited, temperate fish species exposed to 5-10 °C 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 experimental studies on fish to date are much shorter and long time series exist mainly for commercially exploited fish species (and fisheries exploitation affects size-structure both directly and indirectly by selecting for fast growing individuals)<sup>26</sup>. While factors other than temperature could have contributed to the elevated growth and mortality, the temperature contrast is unusually large for natural systems (i.e., 5-10 °C, which can be compared to the 1.35 °C change in the Baltic Sea between 1982 and 2006<sup>27</sup>). 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 or adult body sizes based on the GOLT hypothesis<sup>5,28</sup>, and with intraspecific patterns such as the TSR (temperature-size rule; Atkinson<sup>6</sup>). 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 heated area—despite the elevated mortality rates. Since optimum growth

temperatures decline with size within species generally under food satiation in experimental studies<sup>24</sup>, the finding that the largest asymptotic size and the largest individuals were found in the heated area was unexpected. This suggests that growth dynamics under food satiation may not be directly proportional to those under natural feeding conditions<sup>29</sup>. Our results suggest that growth 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<sup>30</sup>. Moreover, it also highlights that we need to focus on gaining understanding to what extent the larger size-at-age for juveniles in warm environments that is commonly observed can be maintained as they grow older.

Our finding that mortality rates were higher in the heated area was expected—warming leads to faster metabolic rates, which in turn is associated with shorter life span<sup>11,31,32</sup> (higher “physiological” mortality). Warming may also increase predation mortality, as predators’ feeding rates increase in order to meet the higher demand of food<sup>12,14,33</sup>. However, most evidence to date of the temperature dependence of mortality rates in natural populations stem from across species studies<sup>12,13,34</sup> (but see<sup>33,35</sup>). Across species relationships are not necessarily determined by the same processes as within species relationships; thus our finding of warming-induced mortality in a heated vs control environment in two nearby con-specific populations is important. Since a key question for understanding the implications of warming on ectotherm populations is if larger individuals in a population become rarer or smaller<sup>36,37</sup>, within-species mortality responses to warming need further study. Importantly, this requires accounting also for effects of warming on growth, and how responses in growth and mortality depend on each other. For instance, higher mortality (predation or natural, physiological mortality) can release intra-specific competition and thus increase growth. Conversely, altered growth and body sizes can lead to changes in size-specific mortality, such as predation or starvation. In conclusion, understanding how the size- and age-distribution change rather than the mean size is critical

for predicting how warming changes species functions and ecological roles<sup>7,30,38</sup>. Key to do this is to acknowledge temperature effects on both growth and mortality and how they interact.

## Materials and Methods

### *Data*

We use size-at-age 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 first and last catch year is 1987 and 2003, respectively) to omit transient dynamics and acute responses, and to ensure we use cohorts that only experienced one of the thermal environments during its life. A grid at the outlet of the heated area (Fig. 1) prevented fish larger than 10 cm from migrating between the areas<sup>39,40</sup>, and genetic studies confirm the reproductive isolation between the two populations during this time-period<sup>41</sup>. 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 net deployments.

We use data from fishing events using survey-gillnets that took place in October in the heated Biotest lake and in August in the reference area when temperatures are most comparable between the two areas<sup>40</sup>, 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 heated area in the catch data).

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:  $L = \kappa R^s$ , where  $L$  is the length of the fish,  $R$  the operculum radius,  $\kappa$  the intercept, and  $s$  the slope of the line for the regression of log-fish length on log-operculum radius from a large reference data set for perch<sup>42</sup>. Back-calculated length-at-age were obtained from the relationship  $L_a = L_s \left(\frac{r_a}{R}\right)^s$ , where  $L_a$  is the back-calculated body length at age  $a$ ,  $L_s$  is the final body length (body length at catch),  $r_a$  is the distance from the center to the annual ring corresponding to age  $a$  and  $s = 0.861$  for perch<sup>42</sup>. 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.

### *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 *log* scale, describing length as a function of age to evaluate differences in size-at-age and asymptotic size:  $\log(L_t) = \log(L_\infty(1 - e^{(-K(t-t_0))}))$ , where  $L_t$  is the length at age ( $t$ , years),  $L_\infty$  is the asymptotic size,  $K$  is the Brody coefficient ( $\text{yr}^{-1}$ ) and  $t_0$  is the age when the average length was zero. 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  $\sim 5$ . We let parameters vary among cohorts rather than year of catch, because individuals within cohorts share similar environmental conditions and density dependence<sup>43</sup>. 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:

$$L_i \sim \text{Student-}t(v, \mu_i, \sigma) \quad (1)$$

$$\begin{aligned} \log(\mu_i) = & A_R \log \left[ L_{\infty Rj[i]} \left( 1 - e^{(-K_{Rj[i]}(t-t_{0Rj[i]}))} \right) \right] + \\ & A_H \log \left[ L_{\infty Hj[i]} \left( 1 - e^{(-K_{Hj[i]}(t-t_{0Hj[i]}))} \right) \right] \end{aligned} \quad (2)$$

$$\begin{bmatrix} L_{\infty Rj} \\ L_{\infty Hj} \\ K_{Rj} \\ K_{Hj} \end{bmatrix} \sim \text{MVNormal} \left( \begin{bmatrix} \mu_{L_{\infty R}} \\ \mu_{L_{\infty H}} \\ \mu_{K_R} \\ \mu_{K_H} \end{bmatrix}, \begin{bmatrix} \sigma_{L_{\infty R}} & 0 & 0 & 0 \\ 0 & \sigma_{L_{\infty H}} & 0 & 0 \\ 0 & 0 & \sigma_{K_R} & 0 \\ 0 & 0 & 0 & \sigma_{K_H} \end{bmatrix} \right) \quad (3)$$

where lengths are *Student* – *t* distributed to account for extreme observations,  $v$ ,  $\mu$  and  $\phi$  represent the degrees of freedom, mean and the scale parameter, respectively. Henceforth, subscripts  $H$  and  $R$  are used for the heated and reference area, respectively (except in figures and main text where subscripts are spelled out for clarity).  $A_R$  and  $A_H$  are dummy variables such that  $A_R = 1$  and  $A_H = 0$  if it is the reference area, and vice versa. The multivariate normal distribution in Eq. 3 is the prior for the cohort-varying parameters  $L_{\infty Rj}$ ,  $L_{\infty Hj}$ ,  $K_{Rj}$  and  $K_{Hj}$  (for cohorts  $j = 1981, \dots, 1997$ ) (note that cohorts extend further back in time than the catch data), with hyper-parameters  $\mu_{L_{\infty R}}$ ,  $\mu_{L_{\infty H}}$ ,  $\mu_{K_R}$ ,  $\mu_{K_H}$  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  $L_{\infty Rj}$  and  $L_{\infty Hj}$  with  $L_{\infty j}$ . To aid convergence of this non-linear model, we used

informative priors chosen after visualizing draws from prior predictive distributions<sup>44</sup> using probable parameter values (*Supporting Information*, Fig. S1, S7). 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:  $\mu_{L_{\infty R,H}} \sim N(45, 20)$ ,  $\mu_{K_{R,H}} \sim N(0.2, 0.1)$ ,  $t_{0R,H} \sim N(-0.5, 1)$  and  $v \sim \text{gamma}(2, 0.1)$ .  $\sigma$ ,  $\mu_{L_{\infty R}}$ ,  $\mu_{L_{\infty H}}$ ,  $\mu_{K_R}$ ,  $\mu_{K_H}$  were given a *Student - t*(3, 0, 2.5) prior.

We also compared how growth scales with body size (in contrast to length vs age) in the two areas, by fitting allometric growth models describing how specific growth rate scales with length:  $G = \alpha L^\theta$ , where  $G$ , the specific growth, is defined as:  $G = 100 \times (\log(L_2) - \log(L_1)) / (t_2 - t_1)$  and  $L$  is the geometric mean length:  $L = (L_1 \times L_2)^{0.5}$ . 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 to compare models with different combinations of common and shared parameters. We assumed growth rates were *Student - t* distributed, and the full model can be written as:

$$\begin{aligned}
 L_i &\sim \text{Student} - t(v, \mu_i, \sigma) & (4) \\
 \mu_i &= A_R(\alpha_{Rj[i],k[i]} L^{\theta_R}) + A_H(\alpha_{Hj[i],k[i]} L^{\theta_H}) & (5) \\
 \alpha_{R,Hj} &\sim N(\mu_{\alpha_{R,Hj}}, \sigma_{\alpha_{R,Hj}}) & (6) \\
 \alpha_{R,Hj} &\sim N(\mu_{\alpha_{R,Hj}}, \sigma_{\alpha_{R,Hj}}) & (7) \\
 \theta_{R,Hj} &\sim N(\mu_{\theta_{R,Hj}}, \sigma_{\theta_{R,Hj}}) & (8) \\
 \theta_{R,Hj} &\sim N(\mu_{\theta_{R,Hj}}, \sigma_{\theta_{R,Hj}}) & (9)
 \end{aligned}$$

We assumed only  $\alpha$  varied across individuals  $j$  within cohorts  $k$  and compared two models: one with  $\theta$  common for the heated and reference area, and one with an area-specific  $\theta$ . We used the following priors, after visual exploration of the prior predictive distribution (*Supporting Information*, Fig. S7, S9):  $\alpha_{R,H} \sim N(500, 100)$ ,  $\theta_{R,H} \sim N(-1.2, 0.3)$  and  $v \sim \text{gamma}(2, 0.1)$ .  $\sigma$ ,  $\sigma_{id:cohort}$  and  $\sigma_{cohort}$  were all given a *Student - t*(3, 0, 13.3) 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  $N_t = N_0 e^{-Zt}$ , where  $N_t$  is the population at time  $t$ ,  $N_0$  is the initial population size and  $Z$  is the instantaneous mortality rate. This equation can be rewritten as a linear equation:  $\log(C_t) = \log(vN_0) - Zt$ , where  $C_t$  is catch-at-age  $t$ , if catch is assumed proportional to the number of fish (i.e.,  $C_t = vN_t$ ). Hence, the negative of the slope of the regression is  $Z$ . 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 composition is then estimated for the total catch based on the “probability” of fish in each length-category being a certain age. We fit this model with and without an *age-area*-interaction, and the former can be written as:

$$\log(CPUE_i) \sim \text{Student-}t(v, \mu_i, \sigma) \quad (10)$$

$$\mu_i = \beta_{0j[i]}(area_R) + \beta_{1j[i]}(area_H) + \beta_{2j[i]}age + \beta_{3j[i]}(age \times area_H) \quad (11)$$

$$\begin{bmatrix} \beta_{0j} \\ \beta_{1j} \\ \beta_{2j} \\ \beta_{3j} \end{bmatrix} \sim \text{MVNormal} \left( \begin{bmatrix} \mu_{\beta_0} \\ \mu_{\beta_1} \\ \mu_{\beta_2} \\ \mu_{\beta_3} \end{bmatrix}, \begin{bmatrix} \sigma_{\beta_0} & 0 & 0 & 0 \\ 0 & \sigma_{\beta_1} & 0 & 0 \\ 0 & 0 & \sigma_{\beta_2} & 0 \\ 0 & 0 & 0 & \sigma_{\beta_3} \end{bmatrix} \right) \quad (12)$$

where  $\beta_{0j}$  and  $\beta_{1j}$  are the intercepts for the reference and heated areas, respectively,  $\beta_{2j}$  is the age slope for the reference area and  $\beta_{3j}$  is the interaction between *age* and *area*. All parameters vary by cohort (for cohort  $j = 1981, \dots, 2000$ ) and their correlation is set to 0 (Eq. 12). We use the following (vague) priors:  $\mu_{\beta_0, \dots, \beta_3} \sim N(0, 10)$  (where  $\mu_{\beta_2}$  is the population-level estimate for  $-Z_R$  and  $\mu_{\beta_2} + \mu_{\beta_3}$  is the population-level estimate for  $-Z_H$ ) and  $v \sim \text{gamma}(2, 0.1)$ .  $\sigma$  and  $\sigma_{\beta_0, \dots, \beta_3}$  were given a *Student - t*(3, 0, 2.5) prior.

Lastly, we quantified differences in the size-distributions between the areas using size-spectrum exponents. We estimate the biomass size-spectrum exponent  $\gamma$  directly, using the

likelihood approach for binned data, i.e., the *MLEbin* method in the R package *sizeSpectra*<sup>16,45,46</sup>. 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<sup>16,45</sup>. We pooled all years to ensure negative relationships between biomass and size in the size-classes (as the sign of the relationship varied between years).

All analyses were done using R<sup>47</sup> version 4.0.2 with R Studio (2021.09.1). The packages within the *tidyverse*<sup>48</sup> collection were used to process and visualize data. Models were fit using the R package *brms*<sup>49</sup>. 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)<sup>50</sup> while ensuring pareto  $k$  values  $< 0.7$ , in the R package *loo*<sup>51</sup>. Results of the model comparison can be found in the *Supporting Information*, Table S1-S4. We used *bayesplot*<sup>52</sup> and *tidybayes*<sup>53</sup> to process and visualize model diagnostics and posteriors. Model convergence and fit was assessed by ensuring potential scale reduction factors ( $\hat{R}$ ) were less than 1.1, suggesting all three chains converged to a common distribution)<sup>54</sup>, and by visually inspecting trace plots, residuals QQ-plots and with posterior predictive checks (*Supporting Information*, Fig. S2, S8, S10).

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## Code and Data Availability

All data and R code to reproduce the analyses can be downloaded from a GitHub repository ([https://github.com/maxlindmark/warm\\_life\\_history](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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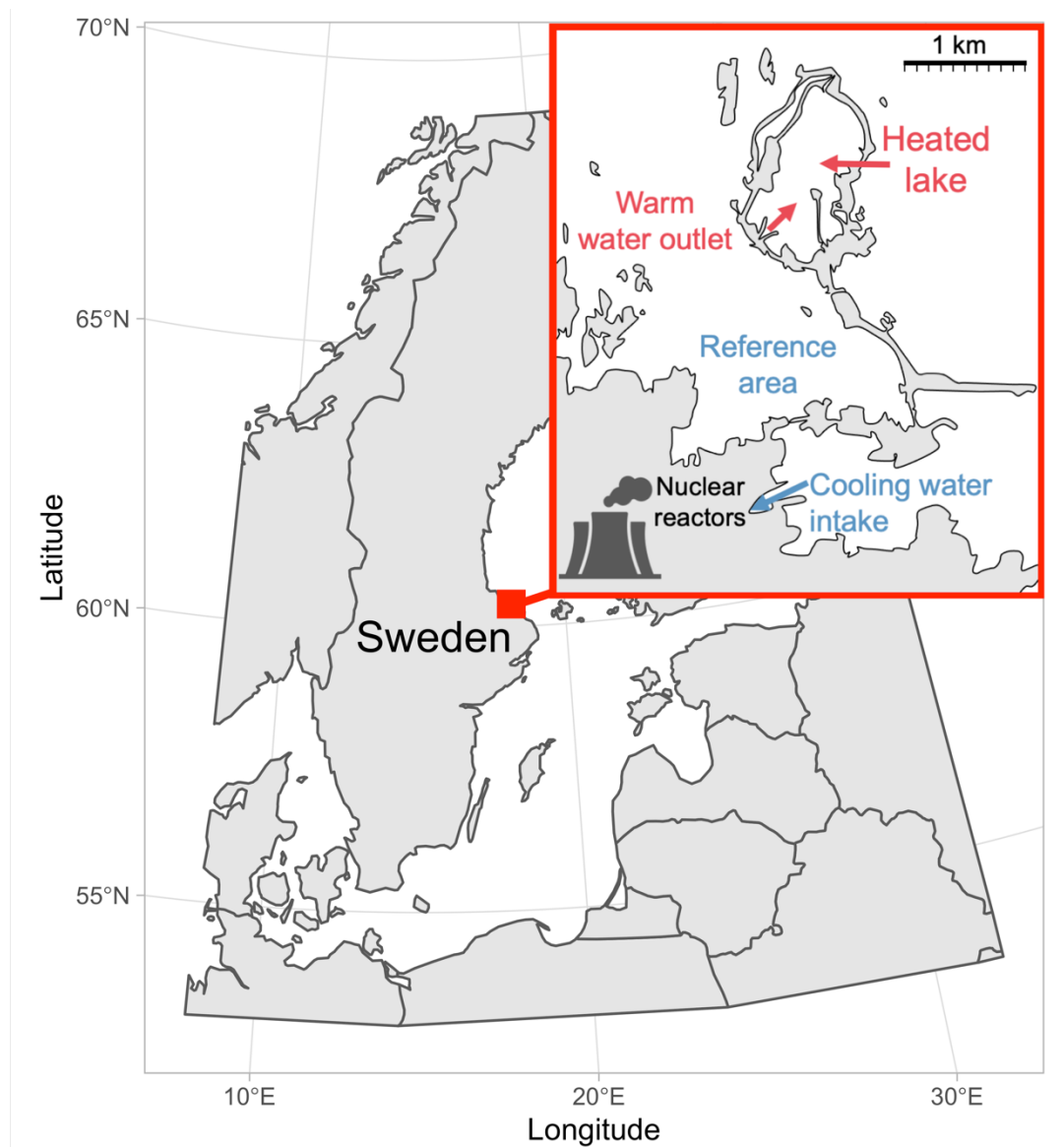


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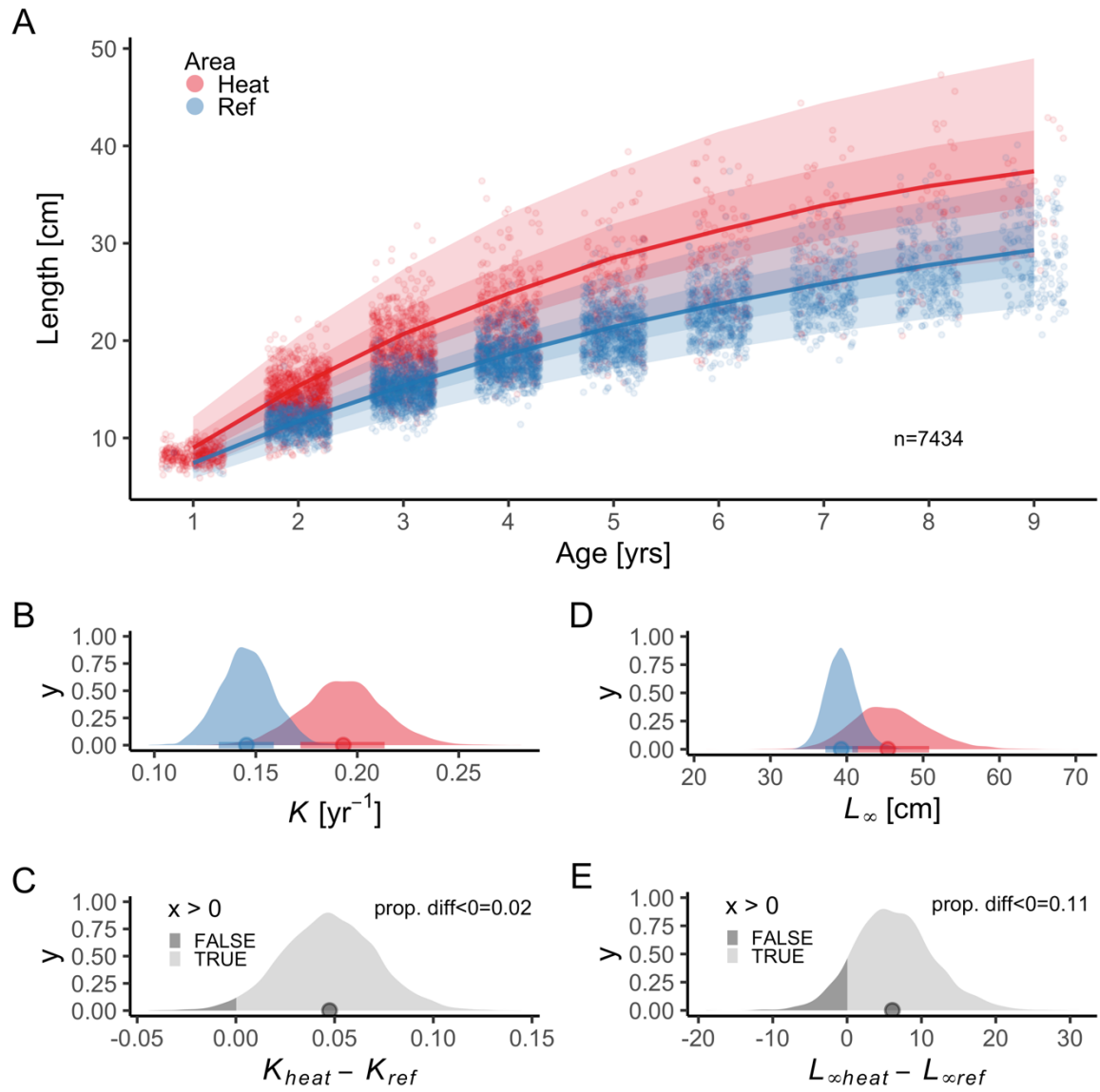
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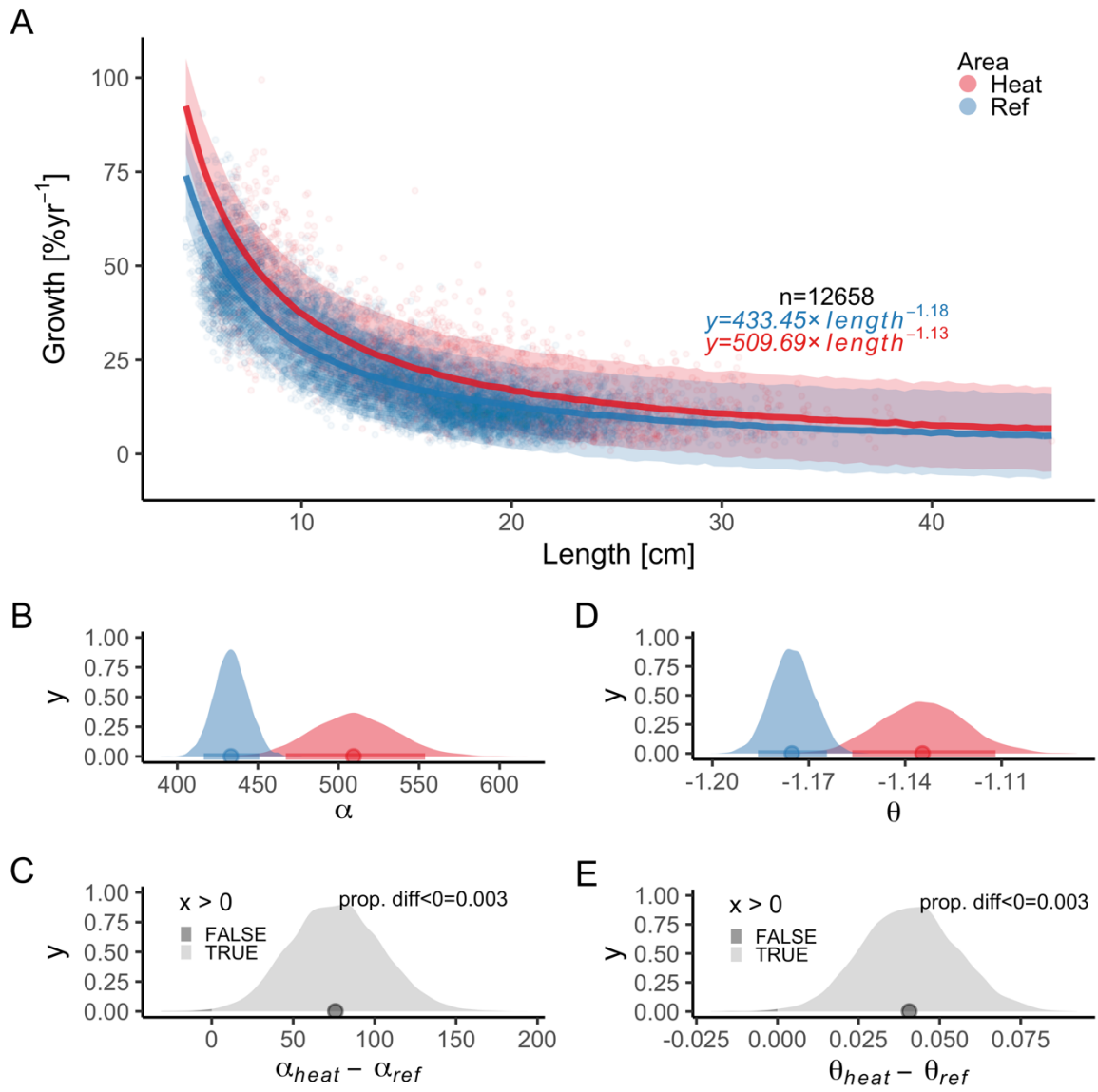
## Figures



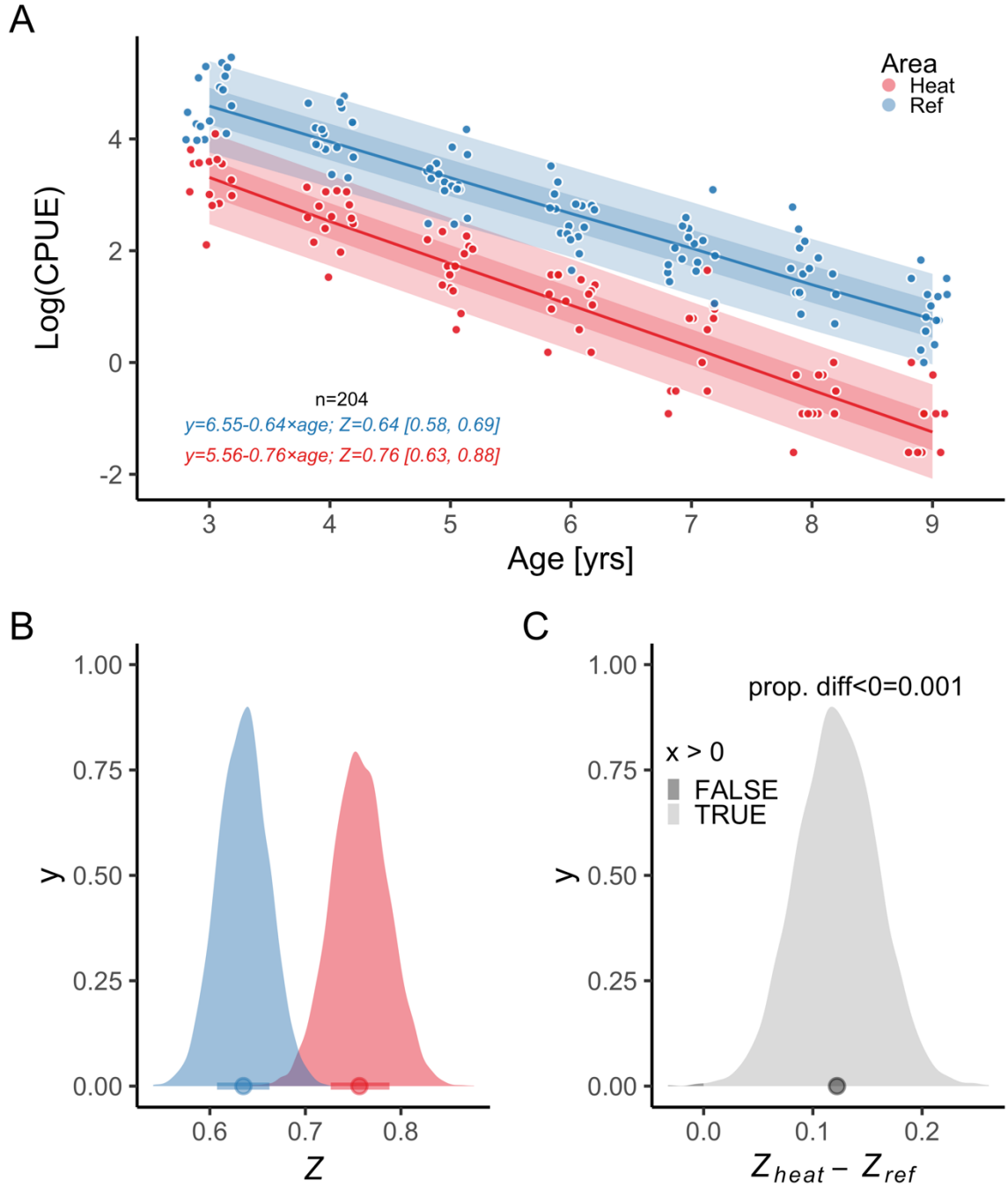
**Fig. 1.** Map of the area with the unique whole-ecosystem warming experiment from which perch in this study was sampled. Inset shows the 1 km<sup>2</sup> enclosed coastal bay that has been artificially heated for 23 years, the adjacent reference area with natural temperatures, and locations of the cooling water intake and where the heated water outlet from nuclear power plants enters the heated coastal area.



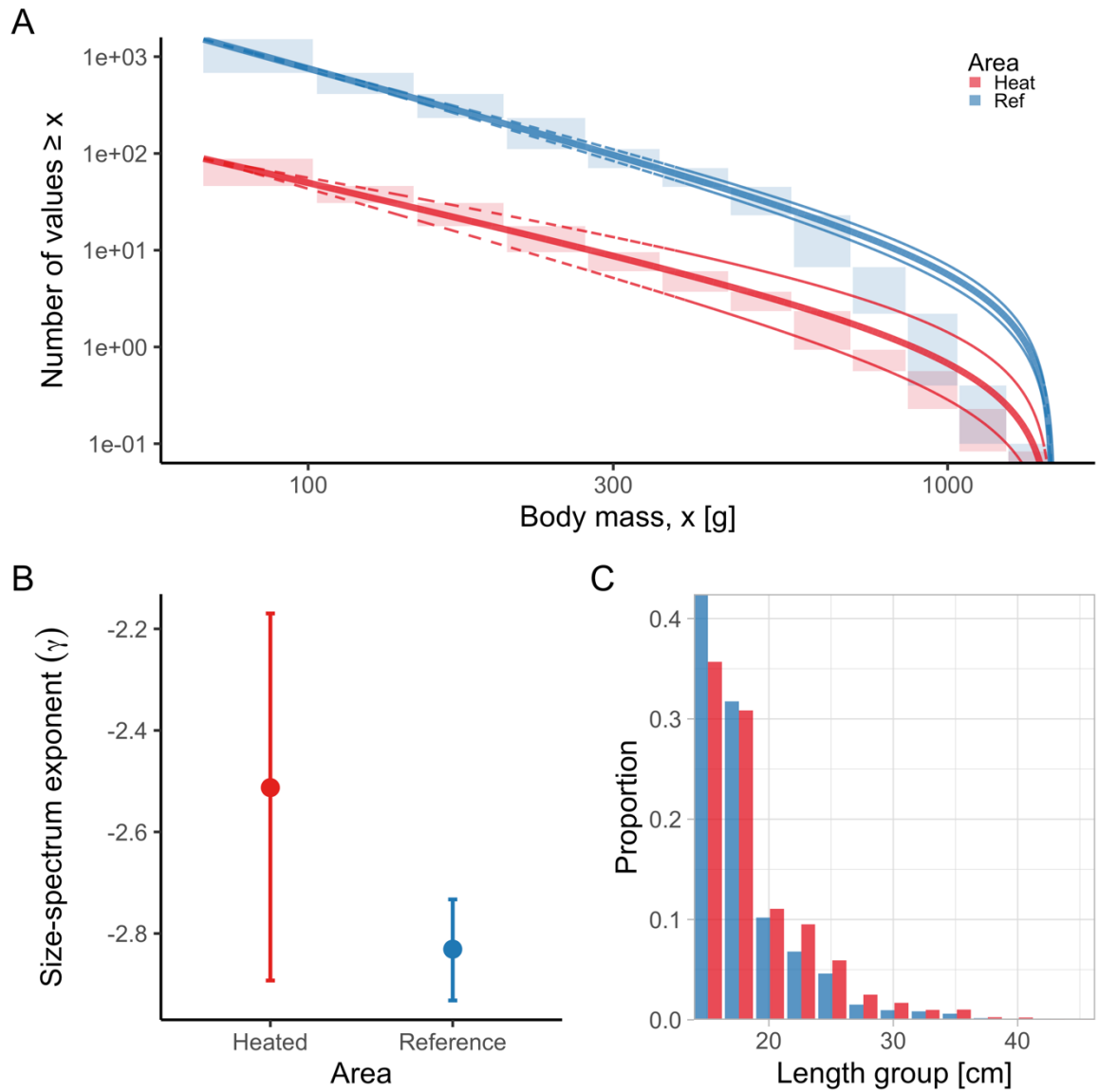
**Fig. 2.** The average length-at-age is larger for fish of all ages in the heated (red) compared to the reference (blue) coastal area. Points in panel (A) depict individual-level length-at-age and lines show the global posterior prediction (both exponentiated) without group-level effects (i.e., cohort) 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 coefficient (parameters  $K_{\text{heat}}$  (red) and  $K_{\text{ref}}$  (blue)) and (C) the distribution of their difference. Panel (D) shows the posterior distributions for asymptotic length (parameters  $L_{\infty\text{heat}}$  and  $L_{\infty\text{ref}}$ ), and (E) the distribution of their difference.



**Fig. 3.** The faster growth rates in the heated area (red) compared to the reference (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 ( $\alpha_{heat}$  (red) and  $\alpha_{ref}$  (blue)), and (C) the distribution of their difference. Panel (D) shows the posterior distributions for the allometric decline in growth with length ( $\theta_{heat}$  and  $\theta_{ref}$ ), and (E) the distribution of their difference.



**Fig. 4.** The instantaneous mortality rate ( $Z$ ) is higher in the heated area (red) than in the reference (blue). Panel (A) shows the  $\log(\text{CPUE})$  as a function of  $\text{age}$ , where the slope corresponds to the global  $-Z$ . 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 ( $Z_{\text{heat}}$  and  $Z_{\text{ref}}$ ), and (C) the distribution of their difference.



**Fig. 5.** The heated area (red) has a larger proportion of large fish than the reference area (blue), illustrated both in terms of the biomass size-spectrum (A-B), and histograms of proportions (C). Panel (A) shows the size distribution and MLEbins fit (red and blue solid curve for the heated and reference area, respectively) with 95% confidence intervals indicated by dashed lines. The vertical span of rectangles illustrates the possible range of the number of individuals with body mass  $\geq$  the body mass of individuals in that bin. Panel (B) shows the estimate of the size-spectrum exponent,  $\gamma$ , and vertical lines depict the 95% confidence interval. Panel (C) illustrates histograms of length groups in the heated and reference area as proportions (for all years pooled).