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Stronger effect of temperature on body growth in cool than in warm populations suggests lack of local adaptation

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Body size is a key functional trait that has declined in many biological communities, partly due to changes in individual growth rates in response to climate warming. However, our understanding of growth responses in natural populations is limited by relatively short time series without large temperature contrasts and unknown levels of adaptation to local temperatures across populations within species. In this study, we collated back-calculated length-at-age data for the fish Eurasian perch *Perca fluviatilis* from 10 populations along the Baltic Sea coast between 1953 and 2015 (142 023 length-at-age measurements). We fitted individual growth trajectories using the von Bertalanffy growth equation, and reconstructed local temperature time series using generalized linear mixed models fitted to three data sources. Leveraging a uniquely large temperature contrast due to climate change and artificial heating from nuclear power plants in two of the examined populations, we then estimated population-specific and global (across populations) growth–temperature relationships using Bayesian mixed models, and evaluated whether populations are locally adapted to environmental temperatures. We found little evidence for local adaptation of body growth. Populations did not exhibit unique optimum growth temperatures nor unique growth rates at a common reference temperature. Instead, population-specific curves mapped onto a global curve, resulting in body growth increasing with warming in cold populations but decreasing in one of the warmer populations. Understanding whether the effects of warming on growth are population-specific is critical for generalizing predictions of climate impacts on body size, which affects multiple levels of biological organization from individuals to ecosystem functioning.

Keywords: body growth, climate change, fish, non-linear, perch, spatiotemporal, temperature–size rule, von Bertalanffy

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Introduction

Body growth is an individual-level trait that is relevant to ecology across all levels of biological organisation (Peters 1983, Barneche et al. 2019). In aquatic systems in particular, body growth is sensitive to environmental conditions and is related to individual fitness (Sibly et al. 2018). It determines species interactions and dictates how much energy is transferred between trophic levels (Lindeman 1942, Barneche and Allen 2018). It is also directly related to body size, a key ecological trait (Peters 1983) that is correlated with diet, survival and reproductive success (Barneche et al. 2018) and largely shapes size-dependent species interactions (Ursin 1973, Werner and Gilliam 1984).

In ectotherms such as fish, environmental temperature has a large influence on body growth via the effects on metabolic rate (Jobling 1997, Brown et al. 2004). For species living at temperatures cooler than those maximizing growth, as commonly observed (Tewksbury et al. 2008, Lindmark et al. 2022), a slight increase in temperature is likely to be beneficial to growth. Body growth or size-at-age of fish in natural environments, is commonly observed to correlate positively with temperature, especially for small or young fish (Atkinson and Sibly 1997, Thresher et al. 2007, Baudron et al. 2014, Huss et al. 2019, Oke et al. 2022, Lindmark et al. 2023). The effects on old fish, however, are often smaller or negative (Atkinson and Sibly 1997, Morrongiello et al. 2014, van Dorst et al. 2019, Ikpewe et al. 2020), although there are exceptions (Lindmark et al. 2023) and responses can vary within populations, e.g. with sex (van Dorst et al. 2024). Experimental and modelling studies have pointed out that size-dependent responses of growth and size could be due to optimum growth temperatures being lower for larger fish (Lindmark et al. 2022), or that warming is linked to earlier maturation, after which energy is increasingly allocated to reproduction over somatic growth (Wootton et al. 2022, Niu et al. 2023), or both (Audzijonyte et al. 2022). In natural systems, other factors, such as competition and food limitation, also influence growth directly (Cline et al. 2019, Oke et al. 2020, Ohlberger et al. 2023), and indirectly by reducing the optimal growth temperatures (Brett et al. 1969, Brett 1971, Huey and Kingsolver 2019). To understand fish responses to changing temperatures, it is therefore important to evaluate growth–temperature relationships in natural systems and across gradients of environmental temperature.

The ability to quantify the impacts of temperature change in natural systems on growth and size, or other ecological traits, is often limited by relatively short time series that contain small temperature contrasts (White 2019, Freshwater et al. 2023). As an alternative, studies often use space-for-time approaches (Morrongiello et al. 2014, van Dorst et al. 2019, van Denderen et al. 2020) to estimate the effects of temperature on growth. However, it is difficult to know to what extent we can infer effects of warming in a given location from the temperature effects estimated across locations over a limited time (Perret et al. 2024). Both the estimates (van Denderen et al. 2020) and the form of the growth–temperature relationship may differ. For example, responses to warming tend to be unimodal, whereas they can be more linear or exponential across all populations of a species (van Denderen et al. 2020). For projecting impacts of warming at the species level, another missing piece is to understand the extent of local adaptation to the experienced thermal environments (Eliason et al. 2011). That is, to what extent populations conform to a global, species-wide thermal performance curve, versus having developed local thermal response curves with local temperature optima in order to have higher fitness in their local habitats. In other taxa, such as kelp (Britton et al. 2024), corals (Howells et al. 2013), invertebrates (Sanford and Kelly 2011) and phytoplankton (Thomas et al. 2012), there is growing evidence that local adaptation has led to populations exhibiting different responses in growth (individual or population) to ocean warming. However, studies on fishes are scarcer (Neuheimer and Grønkjær 2012, Beaudry-Sylvestre et al. 2024). Testing this requires time series with large temperature contrasts, both within and between multiple populations in the wild.

Here, we seek to understand how climate warming has affected the growth of fish across multiple populations, using *Perca fluviatilis* (hereafter perch) as a case study. Perch is a widely distributed freshwater fish, common along the Swedish Baltic Sea coast, that is not commercially exploited and has a fine-scale population structure (< 50 km), likely due to reproductive homing behaviour and limited dispersal (Bergek and Björklund 2009, Hall et al. 2022). These characteristics make it an ideal species for analyzing effects of temperature change on growth across environmental gradients. Specifically, we quantify growth–temperature relationships from 10 populations and evaluate whether there is support for site-specific growth–temperature relationships, and whether or not those are consistent with local adaptation (with respect to optimum growth temperatures and growth rate at reference temperature) (Fig. 1). To address this question, we collated size-at-age data from back-calculated growth trajectories for 23 605 individual fish over seven decades spanning large temperature contrasts due to climate warming and artificial heating from nuclear power plants, and fit statistical models relating cohort-specific growth estimates to reconstructed temperatures.

Material and methods

Data

We compiled individual-level size-at-age data from perch and sea surface temperature data from 10 sites along the Swedish Baltic Sea coast. The longest time series started in 1953 and the shortest in 1985, and the average time series length was 34 years, which can be compared to an average generation time of approximately six years (Fig. 2; Froese and Pauly 2024). The temperature contrast in this data set is considerable both within each site and across sites (Fig. 3), due to long time series and a large latitudinal gradient. Also contributing

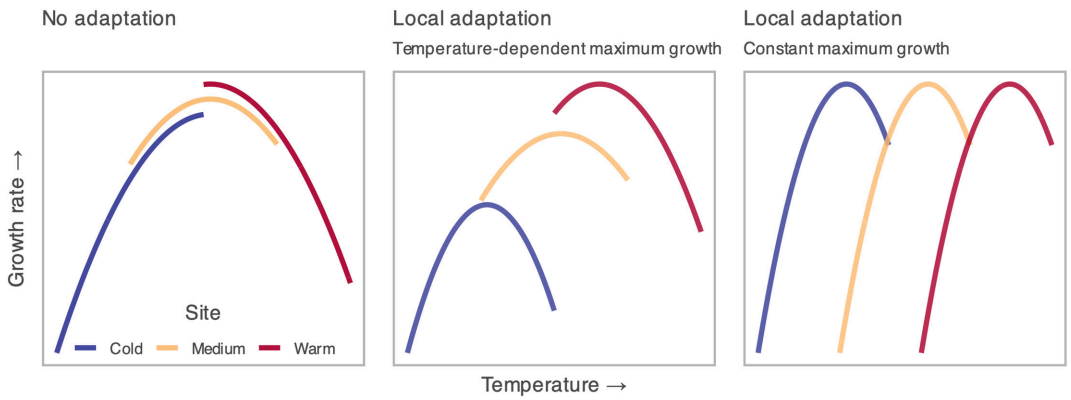

Figure 1. Three examples of hypothetical growth–temperature relationships across isolated populations along a temperature gradient. In all cases, the average growth rate increases with temperature across populations based on metabolic theory. In the left column, there is no local adaptation in optimum growth temperatures, such that growth in cooler (blue) populations increases with warming whereas warmer populations (yellow, red) are the first to show growth declines with warming. Hence, the effect of further warming depends on the population's distance from the global optimum. In the middle and right columns, there is local adaptation (with maximum growth rate increasing (middle) or being constant (right) with temperature across populations), such that responses to warming are similar despite populations experiencing different temperatures.

to the large temperature range is the inclusion of sites artificially heated by warm water discharge from nearby nuclear power plants (sites (SI_HA and BT in Fig. 3). The size-at-age data include information on age (at catch), total length (at catch, in millimeters), sex and back-calculated length-at-age (in millimeters). Back-calculated length-at-age was derived from annuli rings on the operculum bones (part of the gill lid), with control counts of age carried out on otoliths (ear stones). This method is common in fisheries (Morrongiello and Thresher 2015, Essington et al. 2022), and is based on an assumed power-law relationship between the distance of annuli rings and fish length (Thoresson 1996), which allows reconstruction of the individual's body length at each age when annuli rings were formed. Individual-level data originate from different fish monitoring programs using gill-nets. Individuals sampled for age and growth were selected from the total catch from the gill net survey in each site using random or length-stratified sub-sampling of the catch, but information on the stratification method could not be retrieved for all data.

We reconstructed local temperatures at each fishing site using three types of temperature data: automatic temperature loggers deployed near the fishing sites, manually measured temperatures at the time of fishing, and extended reconstructed sea surface temperature, ERSST (Huang et al. 2017). We chose these three types because they are complementary. Logger data provide daily temperatures during the ice-free season but do not go back as far in time as the growth data. Temperatures at the fishing event give a snapshot of temperature at the site, and go back as far in time as we have fishing data. However, temperatures during fishing may not be representative of the whole growth season, and since we are working with back-calculated length-at-age, we also need temperatures for years prior to fishing. Therefore, we also used modelled temperature time series (ERSST), which both provide good seasonal coverage and extend far back in time, but have a much coarser spatial resolution than the other sources. These three temperature data sources overlap in time (Supporting information), which allowed us to standardize the data using a statistical model.

Statistical analyses

Individual-level growth models

To characterise individual growth rates, we fit von Bertalanffy growth equations (von Bertalanffy 1938) – a special case of a Pütter model (Pütter 1920). The model describes growth rate in weight w as the difference between the rates of energy input (or anabolism) and energy expenditures (or catabolism) (Eq. 1):

$$\frac{dw}{dt} = Aw^n - \kappa w^m, \tag{1}$$

where A and κ are the coefficients for anabolism and catabolism, respectively, and n is the size scaling of anabolism. With the assumption that catabolism is proportional to w ($m=1$) and that $w=aL^3$, where a is a condition factor and L is length, it can be integrated to the following form (Eq. 2) (Essington et al. 2001):

$$L_t = L_\infty(1-e^{-k\times age}), \tag{2}$$

where L_t is the size (mm) at age t (years), L_∞ the asymptotic size (mm), and k is the growth rate coefficient (year^{-1}). It is however not a growth rate per se (which has unit size per time), but is instead related to the time it takes to reach the asymptotic size. Following Andersen (2019) and van Denderen et al. (2020), we further assume that the condition factor a is 0.01 such that we can acquire A from Eq. 1 and 2 as $A=0.65kL_\infty$. A, in contrast to k, can be interpreted as a

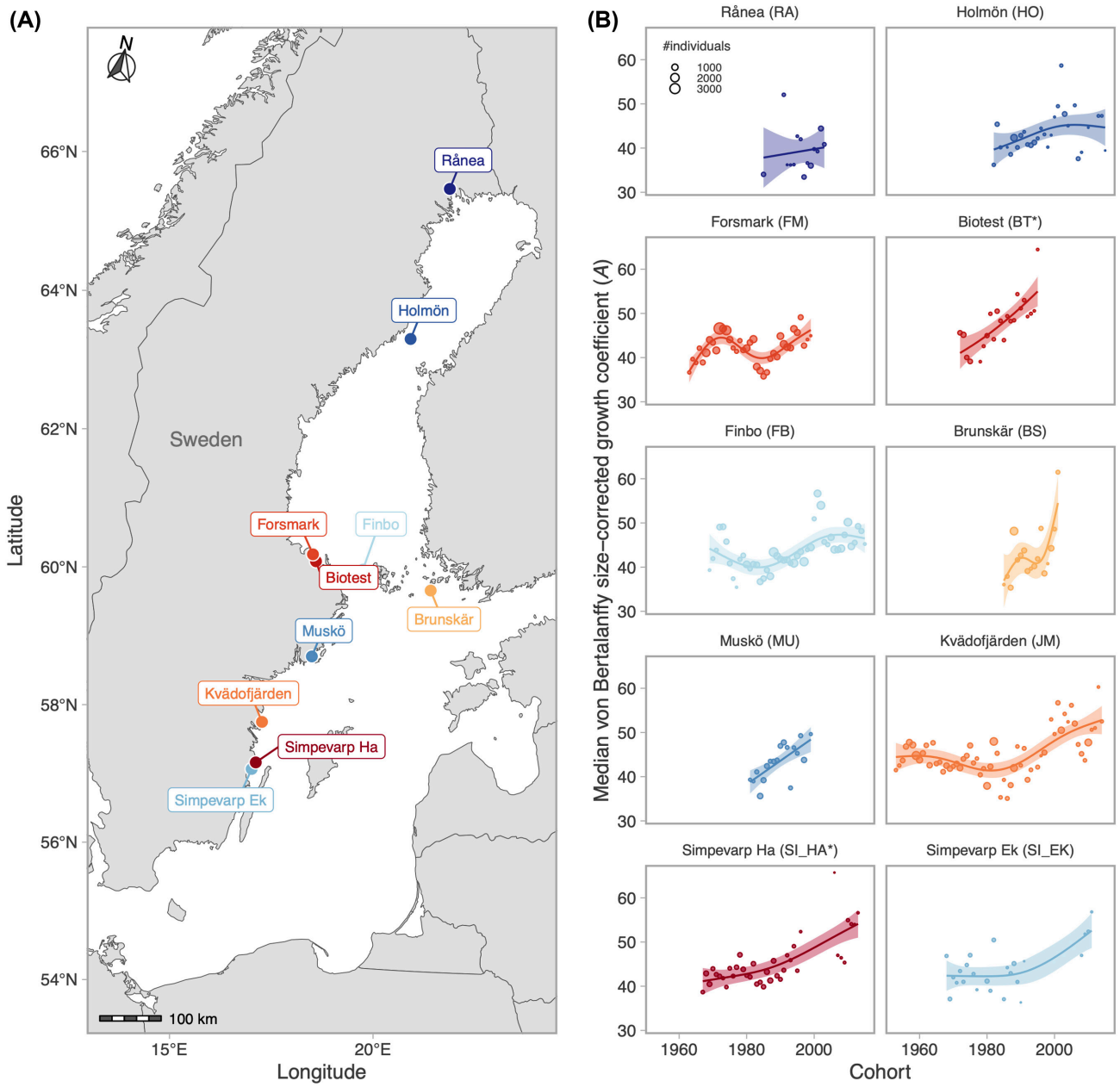

Figure 2. Map of sampling locations (A) and time series of the median von Bertalanffy growth coefficients A by cohort (B), where colours are assigned based on the minimum temperature in the growth time series, ranging from blue (coldest) to red (warmest). Circle size corresponds to the number of individuals in that cohort and site. The lines depict fits from generalized additive models (GAMs) with Gaussian error and basis dimension k = 5, to highlight trends. Asterisk indicates areas heated by warm water discharge.

size-corrected growth coefficient (Gallucci and Quinn 1979, Charnov 2010). Henceforth we refer to A as the growth coefficient, and k in Eq. 2 to simply k.

We fit Eq. 2 to the multiple observations of back-calculated length-at-age for each individual using non-linear least squares (*nls* function in R ver. 4.3.2; www.r-project.org). We only used length-at-age, meaning only length at a back-calculated integer age (i.e. length at the formation of the age-ring), because sampling has occurred in different times of the year. We fit this model to every individual age five or older to ensure enough data points per individual to reliably fit the model. The filtering resulted in 142 023 data points across 23 605 individuals. We then calculated the median A by cohort and site across individuals (resulting in n = 306 A values) (Fig. 2).

Model-based standardization of local temperatures

In order to relate the site- and cohort-specific growth coefficients to temperature over time, we reconstructed average annual temperature sea surface temperature (sst, °C) for each

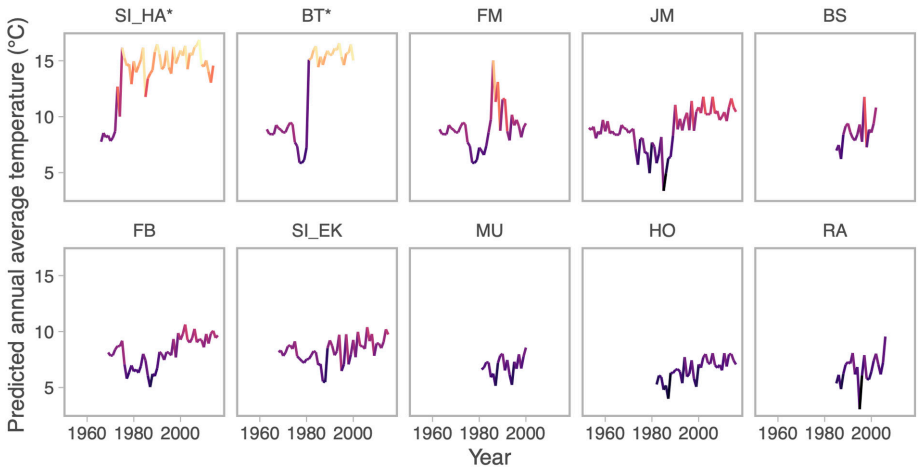

Figure 3. Annual average sea surface temperature as predicted by the GAM model fitted to three temperature sources. Colour indicates temperature. Areas SI_HA* and BT* have been heated by warm water discharge from nuclear power plants since 1972 and 1980, respectively.

site using generalized linear mixed models assuming Student $-t$ distributed residuals to account for extreme observations (Eq. 3–4):

$$\text{sst} \sim \text{Student} - t(\mu_i, \sigma, \nu), \tag{3}$$

$$\mu_i = \alpha_i + f(\text{day}_i) + \text{source}_i, \tag{4}$$

where μ_i is the mean sst, σ is the scale and ν is the degrees of freedom parameter. ν was not estimated within the model, but found by iteratively testing different values and visually inspecting Q–Q plots to see how well the model could capture the heavy tails in the data. We used two sets of values, $\nu = 6$ for sites BS (Brunskär), BT (Biotest), FB (Finbo), FM (Forsmark), MU (Muskö), RA (Råneå) and SI_EK (Simpevark Ekö) and $\nu = 10$ for HO (Holmön), JM (Kvädöfjärden) and SI_HA (Simpevarp Hamnefjärden) (Supporting information). The parameter α_i is the mean sst of year t (included as factor), f(day) is a global smooth implemented as a penalized cyclic spline (i.e. the ends match – in this case 31 December and 1 January) for the effect of day-of-the-year, and source is the mean temperature for each temperature source. We fit the temperature models by site separately, because the presence of artificial heating from nuclear power plants warranted complicated interactions between time, source and site in a global model, and those models did not converge. We fit our models in R using the package 'sdmTMB' ver. 0.6.0.9034 (Anderson et al. 2024), which uses 'mgcv' (Wood 2017) to implement penalized smooths as random effects, and 'TMB' (Kristensen et al. 2016) to estimate parameters via maximum marginal likelihood and the Laplace approximation to integrate over random effects.

We assessed convergence by confirming that the maximum absolute gradient with respect to all fixed effects was < 0.001 and that the Hessian matrix was positive-definite. We evaluated consistency of the model with the data by visually inspecting Q–Q plots of randomized quantile residuals (Dunn and Smyth 1996) with fixed effects held at their maximum likelihood estimates and random effects sampled via a single draw from Markov chain Monte Carlo (MCMC) (Thygesen et al. 2017) using Stan (Carpenter et al. 2017, Stan Development Team 2024a, 2024b) via 'tmbstan' (Monnahan and Kristensen 2018).

Effects of temperature on growth coefficients

To estimate how von Bertalanffy growth parameters (growth coefficient A, k and L_∞) were related to temperature we fit Bayesian generalized mixed models with site-varying and correlated intercepts and slopes and Student $-t$ distributed residuals to account for extreme observations (Eq. 5–16):

$$y_i \sim \text{Student} - t(\mu_i, \sigma, \nu), \tag{5}$$

$$\mu_i = \alpha_{\text{site}[i]} + \beta_{1,\text{site}[i]} T_i + \beta_{2,\text{site}[i]} T_i^2, \tag{6}$$

$$\begin{bmatrix} \alpha_{\text{site}} \\ \beta_{1,\text{site}} \\ \beta_{2,\text{site}} \end{bmatrix} \sim \text{MVNormal}\left(\begin{bmatrix} \alpha \\ \beta_1 \\ \beta_2 \end{bmatrix}, \text{S} \right), \tag{7}$$

$$\text{S} = \begin{pmatrix} \sigma_\alpha^2 & 0 & 0 \\ 0 & \sigma_\beta^2 & 0 \\ 0 & 0 & \sigma_\beta^2 \end{pmatrix} \text{R} \begin{pmatrix} \sigma_\alpha^2 & 0 & 0 \\ 0 & \sigma_\beta^2 & 0 \\ 0 & 0 & \sigma_\beta^2 \end{pmatrix}, \tag{8}$$

$$\alpha \sim \text{Student} - t(3, 43.4, 4.4), \tag{9}$$

$$\beta_1 \sim \text{Normal}(0, 5), \tag{10}$$

$$\beta_2 \sim \text{Normal}(0, 5), \tag{11}$$

$$\nu \sim \text{Gamma}(2, 0.1), \quad (12)$$

$$\sigma \sim \text{Student} - t(3, 0, 4.4), \quad (13)$$

$$\sigma_\alpha \sim \text{Student} - t(3, 0, 4.4), \quad (14)$$

$$\sigma_\beta \sim \text{Student} - t(3, 0, 4.4), \quad (15)$$

$$R \sim \text{LKJcorr}(1), \quad (16)$$

where y_i represents the response variable, μ is the mean, σ is the scale and ν is the degrees of freedom parameter. We scaled temperature, T, by subtracting the mean and dividing by the standard deviation before squaring to reduce the correlation between the two variables (Schielzeth 2010). The intercept is denoted α, and β_1 and β_2 are the coefficients for temperature and temperature squared. The covariance matrix is denoted S, with the correlation matrix, R, of site random effects and their correlations, factored out. We used the default prior specification for the overall intercept as implemented in the 'brms' R package, and a Normal(0,5) for regression coefficients. The σ priors had a lower bound of 0. The prior for the correlation matrix R is a LKJcorr(1), which is flat and puts similar probability on all possible correlation values (correlation between random effects), ρ (McElreath 2016). We fit alternative models with other fixed and random effects (e.g. only random intercepts and linear temperature effects only). A full overview of the alternative models and their expected predictive accuracy (expected log pointwise predictive density, elpd) using Pareto smoothed importance sampling to approximate leave-one-out cross-validation (Vehtari et al. 2017) can be found in the Supporting information. The model presented here (Eq. 5–16) was selected because it has a good fit to data, and its elpd was not substantially different from the model with the highest elpd, and is complex enough to allow site-specific and non-linear temperature responses (Gelman et al. 2021). We fit the same model to von Bertalanffy growth coefficients k and L_∞, with the modification that the prior for the intercept α was Student – t(3,0.2,2.5) and Student – t(3,340.9,80), respectively.

We quantify the temperature sensitivity of A using Q_{10}, which describes the relative increase in the rate of growth for each 10°C increase and is calculated as $Q_{10} = \frac{A_2^{10/(T_2-T_1)}}{A_1}$. Here, A_1 and A_2 are the predicted global growth coefficients from the model in Eqs 5–16, and T_1 and T_2 is temperature in °C.

We fit the model using Stan (Carpenter et al. 2017, Stan Development Team 2024a, 2024b) via the R package 'brms' ver. 2.20.4 (Bürkner 2017, 2018). We sampled from the models with 4000 iterations each on four chains, discarding the first 2000 as warmup. Model convergence and fit were assessed by ensuring potential scale reduction factors were smaller than 1.01, which suggests all four chains converged to a common distribution (Gelman et al. 2003), as well as by visually inspecting posterior predictive checks (Supporting information). Bayesian R^2 values were calculated using the R package 'performance' (Lüdecke et al. 2021), which implements the method described in Gelman et al. (2019). We made conditional predictions and manipulated posterior draws with the R package 'tidybayes' (Kay 2023).

Results

We find large inter-annual fluctuations in annual average temperatures between sites, and increasing trends over time in some sites (Fig. 3). Due to the spatial and temporal range of data, and the artificial heating from nuclear power plant water discharges (sites BT* and SI_HA*), we observe large contrasts in average temperatures, which were not clearly related to latitude (Fig. 2). Across all sites, mean annual average temperatures range from 3 to 17°C, and the largest range within a site (over time) is 6–16°C (site BT). Individual growth trajectories of fish showed large variation within and across sites (Fig. 4). Site-specific growth coefficients (A) generally increased over time, but not always linearly and not synchronously across all sites, indicating that local drivers shape variation in growth between cohorts (Fig. 2).

Models relating the growth coefficient A to temperature that allowed for site-specific estimates (as temperature–site interactions or site-varying parameters) were indistinguishable based on the leave-one-out cross-validation, as the expected log predictive density ($\Delta elpd$) was less than four (Supporting information; Sivula et al. 2023). We therefore used the model with site-varying intercepts and site-varying effects of temperature and allowed for non-linear temperature relationships by using linear and quadratic temperature terms. The variance explained by the model (Bayesian conditional R^2) with fixed and random effects was 0.27 (95% credible interval 0.20–0.34). The distribution of cohort and site-specific growth coefficients A was characterized by heavy tails compared to a Gaussian distribution, and the ν parameter (Eq. 5) was estimated to 5.9.

Predictions from the full model revealed that growth coefficients increased with temperature initially in all sites. We estimated Q_{10} of A to be 1.25 (95% credible interval 1.07–1.48), based on draws from the expectation of the posterior predictive distribution of the global A predicted at 5 and 15°C. However, the growth coefficients in two of the three warmest sites either plateaued or declined with warming at high temperatures (sites FM and SI_HA in Fig. 5). Site-specific growth coefficients (random intercepts) were not significantly related to the average site temperature (Fig. 6) ($p = 0.235$). Taken together, these findings indicate that population-specific growth–temperature curves largely mapped onto a pooled 'global' growth–temperature curve across all populations without clear evidence of local adaptation in growth. This pattern was also found for the von Bertalanffy growth parameters k and L_∞ (Supporting information).

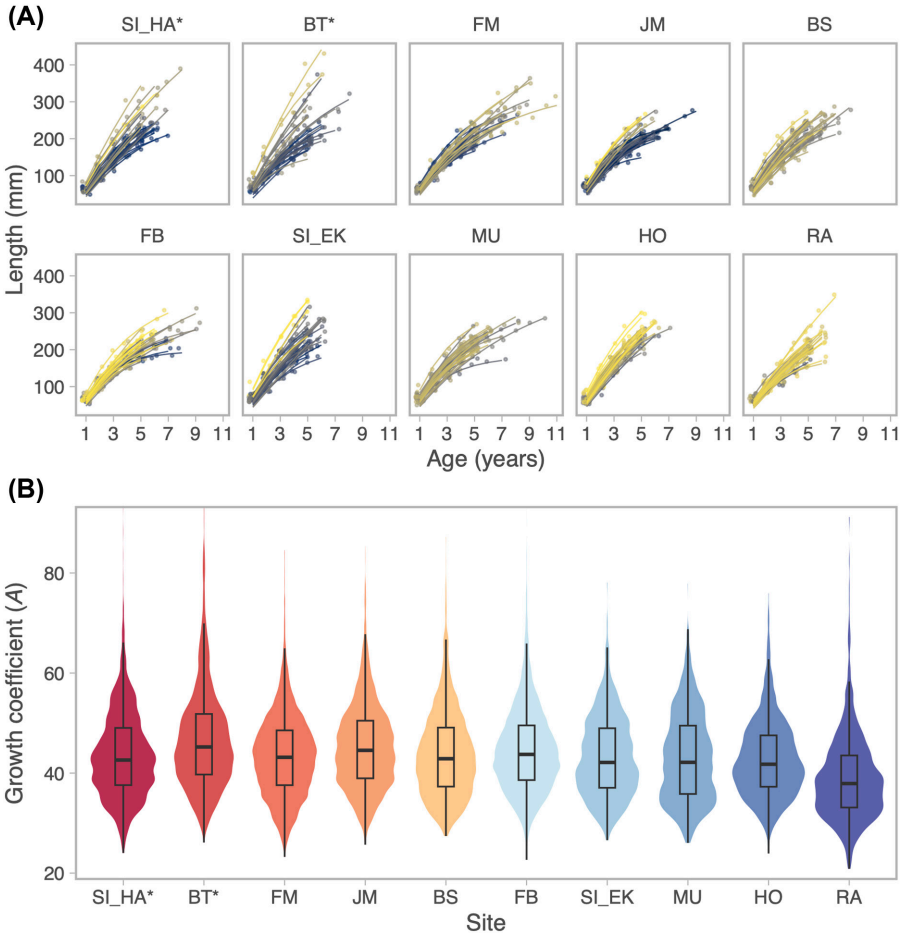

Figure 4. (A) Length plotted against age for all sites. Points are data for 30 randomly selected individuals (indicated by colour) in each site, and lines are the predicted von Bertalanffy growth curve. (B) depicts the distribution of von Bertalanffy growth coefficients *A*, where colours are based on the mean temperature across all years, as violins, and boxplots depicting quantiles. Asterisk indicates areas heated by warm water discharge.

Discussion

Our findings indicate a lack of local adaptation in growth to local temperatures, despite differences in experienced environmental temperatures and reproductive isolation among populations. Populations are expected to grow similarly at the average temperature irrespective of origin (Fig. 6), i.e. populations grow similarly where their experienced temperature ranges overlap (at approximately 8°C) (Fig. 5). If populations had adapted to local temperatures, we would expect similar effects of warming across populations, assuming they occupy temperatures slightly below the local optimum temperature (Ohlberger 2013). Instead, we expect that populations in relatively cold environments will benefit from climate warming via increased body growth rates up to a certain 'global' temperature optimum, whereas populations in relatively warm environments will experience reduced growth due to the negative effects of warming beyond their optimum growth temperature.

In line with our results, Neuheimer et al. (2011) found that for populations of banded morwong *Cheilodactylus spectabilis*, increasing temperatures were associated with reduced growth rates for the population at the warm edge of the species' distribution (New Zealand) but higher growth rates for populations at the colder edge of the range (Tasmania). Similarly, Morrongiello and Thresher (2015) found that body growth of tiger flathead in populations off southeast Australia increased with temperature but not in the warmest area. In terms of body size, Beaudry-Sylvestre et al. (2024) recently found that the size of four-year-old Atlantic herring *Clupea harengus* in the Northwest Atlantic followed a similar pattern – populations in warmer regions tended to have negative associations with warming. Analogously, English et al. (2022) found that groundfish species in the Northeast Pacific often responded positively to warming if they were in cool locations, and negatively if they were in warm locations (where both biomass and temperature change were expressed as velocities). Collectively, these and our findings are in contrast to the common finding in invertebrate species that exhibit local adaptation in growth to temperature, even over small spatial scales (Sanford and Kelly 2011). These results illustrate the importance of testing for population-specific temperature

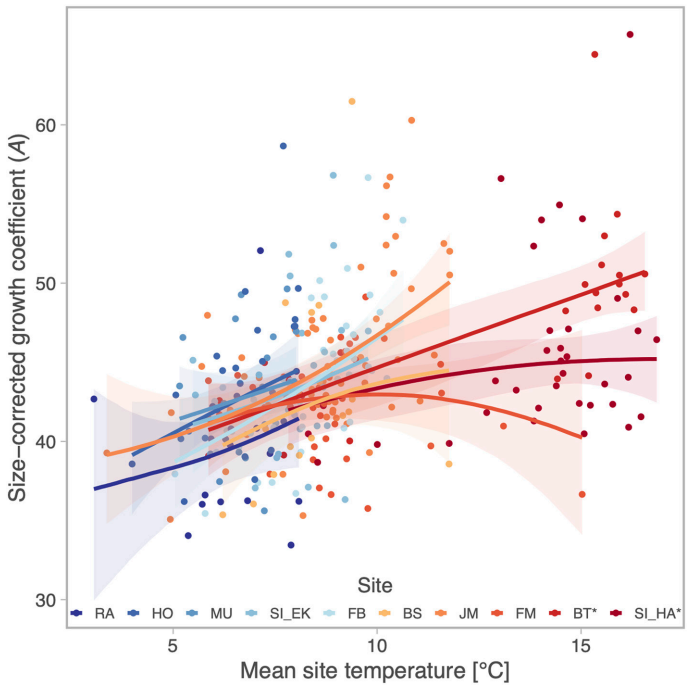

Figure 5. von Bertalanffy growth coefficients *A* as a function of temperature. Each point depicts the median growth coefficient for a cohort and site, and the coloured lines depict the median of draws from the expectation of the posterior predictive distribution and ribbons the 90% credible interval, from the generalized linear mixed effect model for each site. Asterisk indicates areas heated by warm water discharge.

sensitivities when studying species responses to warming, and of accounting for both the rate of climate change and baseline temperature conditions.

The ability to adapt to local environmental conditions allows populations to expand their range and better cope with spatially varying environmental conditions (Kirkpatrick and Barton 1997). Changes in trait–temperature relationships due to thermal adaptation in natural populations are expected in response to climate warming (Angilletta 2009), and previous studies have shown that local adaptation in physiological traits can facilitate different thermal optima among populations (e.g. Atlantic cod (Righton et al. 2010), kelp (Britton et al. 2024), corals (Howells et al. 2013) and invertebrates (Sanford and Kelly 2011)). However, adaptive capacities and the pace of thermal adaptation differ among species (Martin et al. 2023) and depend on life-history trade-offs, underlying genetic variation, the potential for gene flow (Kirkpatrick and Barton 1997) and environmental conditions. The apparent lack of contemporary thermal adaptation in Baltic Sea perch, despite low gene flow between populations due to reproductive homing behaviour (Hall et al. 2022), limited dispersal and movement (Bergek and Björklund 2009), indicates limitations in evolutionary changes to local temperature. This suggests that similar factors may also limit future thermal adaptation that would allow local populations to better withstand changing temperatures. A low adaptive capacity implies that body growth rates in populations already experiencing temperatures around or above their thermal optimum will decline with further warming. This will likely result in lower biomass production in warm environments, as observed, for example, across spatial temperature gradients (van Dorst et al. 2019).

Our study also illustrates the importance of accounting for unimodal temperature dependencies. Often simpler models like the exponential Arrhenius equation are used to model biological and ecological processes (Savage et al. 2004, Vasseur and McCann 2005, Lindmark et al. 2018), under the assumption that the 'biologically relevant temperature range' which species occupy is below their optimum. Growth rates are only exponentially related to temperature even further from the optimum, i.e. below the inflection point of the unimodal curve. We find this supra-linear temperature curve in only two of the cooler sites. Across the full temperature range, the temperature curves tend to flatten, even though a true optimum curve is only found in one population (Fig. 5); hence, temperatures close to or above the optimum are therefore biologically relevant, in which case models other than the Arrhenius equation are more appropriate.

We find that our estimate of the sensitivity of growth (Q_{10} = 1.25) is lower than both predictions from the interspecific metabolic theory of ecology (MTE; Brown et al. 2004) and experimental data on growth from fish fed ad libitum (Lindmark et al. 2022). The MTE assumes growth scales with a Q_{10} of 2.5, as does individual metabolism, and our estimate of Q_{10} of specific growth rate (in unit % mass day^{-1}) based on a re-analysis of Lindmark et al. (2022) is even higher (Q_{10} = 2.9) (see the Supporting information for details). Instead, our results are in line with the findings of van Denderen et al. (2020), who reported an average intraspecific Q_{10} of 1.14 (1.05, 1.26) across fish species. These

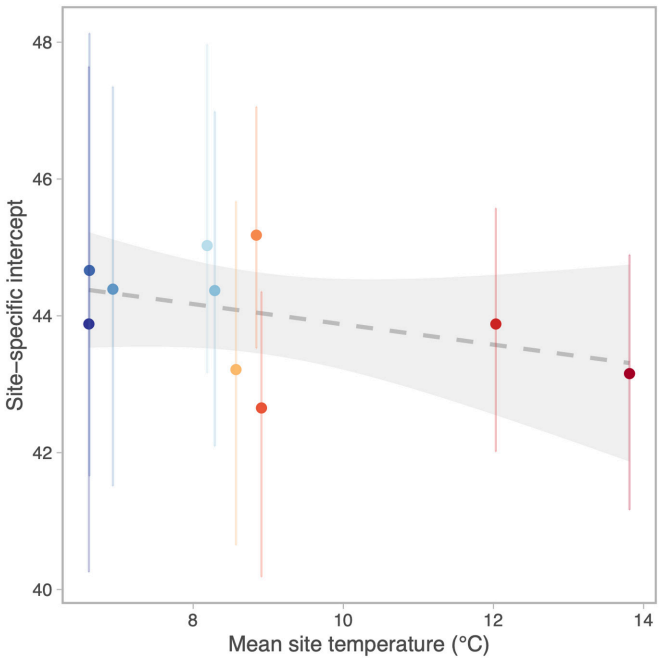

Figure 6. Site-specific intercepts, which correspond to the growth coefficient at average cohort temperature across all sites, as a function of the mean site temperature, from the generalized linear mixed model. Vertical lines correspond to the 90% credible interval. The line and ribbon depict the fit of a linear regression (slope is not significant).

results suggest species do not fulfill the metabolic growth potential, possibly due to constraints on food availability (van Denderen et al. 2020).

There are a number of limitations to our analysis. For instance, growth in temperate regions varies over the year and no single temperature metric can fully reflect thermal conditions that determine cohort-specific growth rates. Given that growing season lengths differ in our data set due to different light conditions, we opted to use a simple annual average (but note these are highly correlated with our predicted summer temperatures; Supporting information). Degree days (the integral of time above a certain temperature threshold) is an often-recommended metric (Neuheimer and Grønkjær 2012), but there is some uncertainty in temperatures below which growth does not occur, even for a well-studied species like perch (Karås and Thoresson 1992), how starvation during cold periods affects growth trajectories, and whether that varies between sites. In our analysis of growth coefficients over temperature, each data point represents a cohort's growth and temperature by site. Hence, the temperature contrast is due to both spatial and temporal variation, and we are unable to isolate these two sources of variation. Lastly, it is not straightforward to formally test for differences in thermal optima between populations because populations generally occupy temperatures below their optimum. In addition, the warmer part of the temperature gradient is due to the inclusion of sites impacted by warm-water pollution from power plants. Future studies could test whether these results hold when comparing similar temperature gradients but from sites across the entire biogeographic range of the species.

Conclusion

Our findings suggest that mean environmental temperatures during warm years have reached or surpassed the optimum growth temperature for two of the examined populations (Fig. 5), but that most populations have a positive, linear relationship with temperature. Our ability to detect this pattern relies heavily on the length of the time series as well as the unusually large temperature contrasts due to warm water pollution from nuclear power plants, which highlights the importance of long-term environmental monitoring across environmental gradients. Considering the lack of evidence for local adaptation to temperature, we expect that adverse effects of continued warming on Baltic Sea perch will accumulate and decrease individual growth rates in the warmest populations. Similar constraints on adaptive capacities in response to warming can be expected for other species of fish, and ectotherms more generally (Pawar et al. 2024).

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Author contributions

Max Lindmark and **Jan Ohlberger** contributed equally to this publication. **Max Lindmark**: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Jan Ohlberger**: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Anna Gårdmark**: Conceptualization (lead); Data curation (equal); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data and code available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15166961 (Lindmark et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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