Ecosystem heating experiment reveals sex-specific growth responses in fish

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Abstract

Size-specific body growth responses to warming are common among animal taxa, but sex-specific responses are poorly known. Here we ask if body growth responses to warming are sex-dependent, and if such sex-specific responses vary with size and age. This was tested with sex-specific data of back-calculated individual growth trajectories, in European perch (*Perca fluviatilis*) from a long-term whole-ecosystem warming experiment (6.3 °C above the surrounding sea). Warming led to both size- and sex-specific differences in growth responses. Warming had a consistent positive effect on body growth of females, but negative effects on male growth at size > 10 cm and age > 2 years. These sex-specific growth responses translate to an increased degree of female-biased sexual size dimorphism (in length-at-age) with warming. Although the exact temperature-mediated effects underlying differential growth responses could not be resolved, results imply global warming may have highly different effects during ontogeny of male and female perch. Such effects should be considered in climate warming scenarios concerning fish growth, population size-structure, and dynamics of aquatic food webs that include fish exhibiting sexual size dimorphism.

Key words: body size, climate change, female, male, fish, temperature

Introduction

Temperature is a key environmental driver of body growth in ectotherms due to strong links with physiological (Brown et al. 2004) and ecological processes (Dell et al. 2011; Gårdmark and Huss 2020). In ectotherms like fish, sex is generally not taken into account when studying impacts of warming or temperature on body growth in natural populations (Thresher et al. 2007; Neuheimer et al. 2011; van Dorst et al. 2019, but see Baudron et al. 2014). However, sexual size dimorphism (SSD), a size difference between adult males and females, is widespread among animals (Shine 1989; Parker 1992), and temperature gradients associated with variation in SSD across latitudes in fish (Estlander et al. 2017) suggest that rising temperatures may affect male and female fishes differently. Potential changes in sex-specific body growth and SSD with warming will likely have consequences for population productivity (Hixon et al. 2014) and size-dependent ecological interactions (Woodward et al. 2005). Nonetheless, combined size- and sex-specific growth responses to warming remain largely unknown.

Temperature affects body growth especially in aquatic ectotherms by influencing rates of metabolism, feeding, and allocation of energy to somatic and gonadal growth (Brown et al. 2004; Kozłowski et al. 2004; Rall et al. 2012), as well as via basal resource densities (Savage et al. 2004; Bernhardt et al. 2018) and oxygen concentrations (Hoefnagel and Verberk 2015) in the water. In fish, standard metabolic rate increases exponentially with temperature, whereas maximum consumption rate (under unlimited food conditions) has a hump-shaped temperature-relationship (Lindmark et al. 2022). Depending on the relative change of these rates with temperature, how they scale with body size (Lindmark et al. 2022), the extent of temperature change, and how other environmental factors vary with temperature, warming may either have a positive or negative effect on growth depending on body size (Lemoine and Burkepile 2012). Small fish individuals usually have a higher optimal growth temperature than larger and older conspecifics (Hokanson 1977; Lindmark et al. 2022), and are therefore more likely to exhibit increased body growth rates with warming (Huss et al. 2019; van Dorst et al. 2019), when resources are not limited. On the other hand, body growth of larger fish is more likely to be negatively affected by warming (van Dorst et al. 2019; Lindmark et al. 2022). Overall, increased temperatures are predicted to

lead to higher growth rates for immature individuals, lower age and size at maturation, and a decrease in maximum body size in ectotherms (Atkinson 1994).

Sex-specific differences in energy acquisition and allocation over ontogeny can result in variations in body growth rates and maturation between males and females. Variation in body growth and body size between sexes is often driven by sexual selection, commonly favoring large male body size, or by fecundity selection, favoring large female body size (Shine 1989; Rennie et al. 2008). In many fish species there is a selective advantage of large female body size, as females often benefit in terms of fitness from an increasing egg number with body size (Barneche et al. 2018), whereas it can be beneficial for males to mature at a younger age and smaller size to instead spend excess energy on reproductive behavior (Henderson et al. 2003) or cope with reduced food intake to decrease predation risk associated with foraging (Rennie et al. 2008). As there are different fitness consequences of attaining large body size for males and females (Shine 1989) and body growth and size are highly temperature dependent, it is likely that warming will induce sex-specific changes in body growth over ontogeny in fish, especially in species showing strong SSD. However, the degree to which size-specific growth responses to warming also depend on sex remains poorly understood.

In this study, we assess if warming induces size- and sex-specific growth responses in fish using European perch (*Perca fluviatilis*, hereafter perch) as a focal species. Perch is one of the most common and widely distributed freshwater/brackish-water fish species in Europe (Thorpe 1977; Tammi et al. 2003) and displays female-biased SSD (Heibo et al. 2005; Estlander et al. 2017). Age- and length-at-maturity of perch increase with latitude (Heibo et al. 2005), and perch maturation length decreases with warming (Niu et al. 2023). In addition, previous studies show that perch size-specific-body growth is strongly affected by temperature (Huss et al. 2019; van Dorst et al. 2019; Lindmark et al. 2023). A study by Estlander et al. (2017) showed that SSD in perch decreases with latitude, indicating that there likely is an effect of temperature on perch growth and size that may vary with sex. We used data from a 14-year whole-ecosystem warming experiment to evaluate sex-specific growth responses in perch, and study how these vary with size and age. We also assess if these potential size- and sex-specific responses to warming affect the degree of SSD in this population.

Methods

Experimental area and data collection

To examine sex- and size-specific growth responses of perch to warming, we used data from an artificially heated enclosed brackish coastal ecosystem (at 60.4278°N, 18.1898°E, area 1 km², mean depth 2.5 m) in the Baltic Sea, referred to as the Biotest Lake (Fig. S1). The Biotest Lake, finished in 1977, was constructed as an enclosed bay to receive the heated cooling water from the nuclear power plant in Forsmark in Sweden. Fish migration into the Biotest Lake from the sur-

rounding sea was prevented by a grid at the outlet as well as by a strong current (80–100 m³ water/s) through this grid (Adill et al. 2013). In 1980, the first reactor was started and since then the water temperature in the Biotest Lake has been ~5–10 °C above the surrounding sea (Huss et al. 2019). More specifically, during the growing season (May–September) in 1986–1990, the mean temperature was 6.3 °C higher in the Biotest Lake (at 1.9 m depth) than in the surrounding sea (at 2 m depth, for daily means see Fig. S2). No fishing, commercial or recreational, has been allowed in the Biotest Lake since construction was initiated, apart from regular scientific fishing with stationary gears.

Previous studies have reported no differences in salinity (Snoeijs and Wakuru Murasi 2004), light (Huss et al. 2021), or dissolved nutrients (Hillebrand et al. 2010) between the Biotest basin and the adjacent archipelago, although it should be noted that we lack such data for most years. The abundance of benthic invertebrates, which are potential prey for perch, was higher in the Biotest basin after the onset of warming than before (Sandström et al. 1995). Finally, warming seems to have changed the community composition of epilithic algae (Snoeijs and Prentice 1989) and strengthened the trophic cascade from fish to algae, linked to a change in diet, leading to increased macroalgal biomass (at least in more recent years, Svensson et al. 2017).

The fish community in the Biotest Lake has been monitored since the construction of the enclosure. The most abundant species in the Biotest Lake are perch and roach (*Rutilus rutilus*) (Sandström 1990; Huss et al. 2019). About 20 different fish species were regularly observed in the sampling programs during the study period. Total fish biomass and the biomass of perch and roach seemed to increase from 1977 to 1990 (Sandström 1990), but neither perch catch-per-unit-effort (used as a relative abundance metric) nor fish community composition differed between the Biotest lake and the adjacent archipelago before compared to after warming (Huss et al. 2019). Previous studies examining only female perch have shown that their maturation size decreased (Niu et al. 2023) and that their length-at-age increased after the onset of warming, the latter mostly due to an increased body growth of young individuals (Huss et al. 2019).

In this study, we used perch data from 1977 to 1990, including both sexes. Back-calculated length-at-age throughout each individual's life history was estimated for perch sampled with gillnets and fyke nets (Thoresson 1996). Random subsamples of perch were collected in proportion to the size distribution of the total perch catch (Thoresson 1996). As heating of the Biotest Lake started in 1980, we excluded that year from analyses. Individuals from year-classes 1970–1979 that were caught in 1977–1979 were regarded as fish from the cold period (note that year-classes 1970–1977 were born in the area but not necessarily inside the Biotest Lake, as its construction was not completed at that time), while the year-classes 1981–1990 were regarded as fish from the warm period. Perch subsampled for age determination and growth estimates were measured to the nearest millimeter, weighed to the nearest gram, their sex was determined by gonadal inspection, and opercular bones and otoliths were retrieved. Distances between annual (winter) rings on the opercular

bones were used for back-calculation of length-at-age of 2097 individuals, composed of 345 females and 244 males captured in the cold period and 750 females and 758 males captured in the warm period. For a smaller subset of the individuals for which opercula were taken, age was validated using winter year rings in otoliths (Thoresson 1996). The back-calculated length-at-age for each individual was derived based on the body proportional hypothesis (in our case, a nonlinear version using a power function), which assumes that the ratio of body length to an expected body length given the length of the operculum is maintained throughout life (Francis 1990; Thoresson 1996). The back-calculation procedure included assessment of length–weight and age–length relationships to check for errors.

For all analyses we excluded growth during the catch year, since this did not represent a full year of growth. To ensure enough data points per sex and time period, we only used back-calculated age 1–6 for further analyses.

Growth calculations and sexual dimorphism index

We used back-calculated mean length-at-age and annual length increments before and after onset of warming for males and females separately.

Sex- and length-specific annual body growth of perch individuals before and after the onset of warming was estimated from back-calculated sex-specific length-at-age for each time period. We calculated length-specific annual growth rates for all individuals using

$$(1) \quad G_{L, t-1} = ((L_t - L_{t-1})/L_{t-1}) * 100$$

where $G_{L, t-1}$ is the length-specific annual body growth rate (% per year) at fish length (L) at age $t - 1$ years.

The sexual dimorphism index (SDI) (Lovich and Gibbons 1992) per age and time period was calculated from the mean back-calculated length-at-age (L) per sex (f = female, m = male) and time period (before or after onset of warming) as the ratio difference of how much larger females are than males,

$$(2) \quad \text{SDI}_{\text{period}} = (\text{mean} L_{f,\text{period}}/\text{mean} L_{m,\text{period}}) - 1$$

Statistical analyses

To analyze the effect of sex and warming on length-specific annual individual body growth rate over body length (back-calculated for each individual) we fitted a linear mixed model ($\ln(G_{L, t-1}) \sim$ body length × sex × period) in R 4.2.1 (R Core Team 2022), using the function *lmer* from package lme4 (Bates et al. 2015). The model included fish individual as random effect (1|individual), and only fish of age 5 years and older when caught were included to ensure enough data points (≥ 4 size-at-age) per fish (391 individuals). We used likelihood ratios for model selection by comparing the full model with a model without the three-way interaction, and found that the three-way interaction could not be removed ($\chi^2_{[1]} = 38.49$, $p < 0.001$). A similar linear mixed model was done to analyze the effect of sex and warming on growth increments over age (see supplementary methods and results). We used Analysis

of covariance (ANCOVA) to test the hypothesis that warming (categorical explanatory variable, before and after onset of warming in the experiment) affects the relationship between SDI (response variable) and age (continuous explanatory variable). The interaction term was used to test whether the slope of the relationship between SDI and age differed between the cold and warm period. Given a significant interaction, we fitted linear regression models for each period. Normality of residuals was assessed by visual inspection of Q-Q plots and residual density plots, and homogeneity of variance by visual inspection of fitted versus residuals plots, concluding that assumptions were met. All statistical analyses were performed using R computing program version 4.2.1 (R Core Team 2022).

Results

Annual growth increments (Fig. 1a, Fig. S3, Table S1) and annual body growth as a function of body size (Fig. 1b, Table 1) were affected by both sex and warming. Our predicted values based on the linear mixed model with a three-way interaction ($\ln(G_{L, t-1}) \sim$ body length × sex × period) showed that at small size and young age (<approximately 100 mm and <2 years), both males and females had a slightly higher growth rate after the onset of warming (Fig. 1, Table 1). However, only for females did growth rates increase for all body sizes with warming. For males, growth instead decreased more with length after onset of warming than before (Fig. 1b), such that large males grow slower after warming (Fig. 1a). The difference in growth rates between males and females therefore increased with warming, especially at large size and old age (Fig. 1). This led to larger length-at-age of older females after onset of warming, but not of older males (>4 years, Fig. 2a). As a result, experimental warming led to a higher SDI; the relationship between perch SDI and age differed between the cold and warm period in the warming experiment (ANCOVA: $F_{[1,8]} = 60.15$, $p < 0.001$, Fig. 2b). SDI increased more rapidly with age after (Slope$_{\text{warm}}$ = 0.055, R^2 = 0.97, $p < 0.001$) than before (Slope$_{\text{cold}}$ = 0.015, R^2 = 0.92, $p < 0.01$) the onset of artificial warming of the ecosystem (Fig. 2b).

Discussion

While life-history trait responses to climate warming are increasingly studied, population responses have usually been predicted without taking size- and sex-specific responses into account. Using a whole-ecosystem warming experiment, we showed that ~6 °C warming led to size- and age-specific growth responses in perch that differed between sexes: increased growth of females irrespective of size but decreased growth among large males. Warming thereby increased the degree of female-biased SSD (in length-at-age). This suggests that warming can potentially alter not only overall size distributions (Daufresne et al. 2009; van Dorst et al. 2019), but also the sex-specific size-distributions of fish populations exhibiting female-biased SSD.

Warming increased the growth of both males and females at small size/young age. However, at larger size warming increased the growth of females, but not that of males. A po-

Fig. 1. Whole-ecosystem warming led to size- and sex-specific growth responses. (*a*) Annual growth increments from hatching to age 5 years. Growth of males (turquoise triangles) and females (purple circles) before (open symbols, dashed lines) and after (closed symbols, solid lines) the onset of warming. For the purpose of illustration, the symbols are jittered for each age. (*b*) Annual body growth over body length (excluding growth of the first year), with each symbol representing 1 year of growth for an individual before or after onset of warming. Lines with 95% confidence interval are predicted values of the linear mixed model (conditional $R^2 = 0.81$, marginal $R^2 = 0.76$, Table 1). Note the logarithmic scale of the lower *y*-axis.
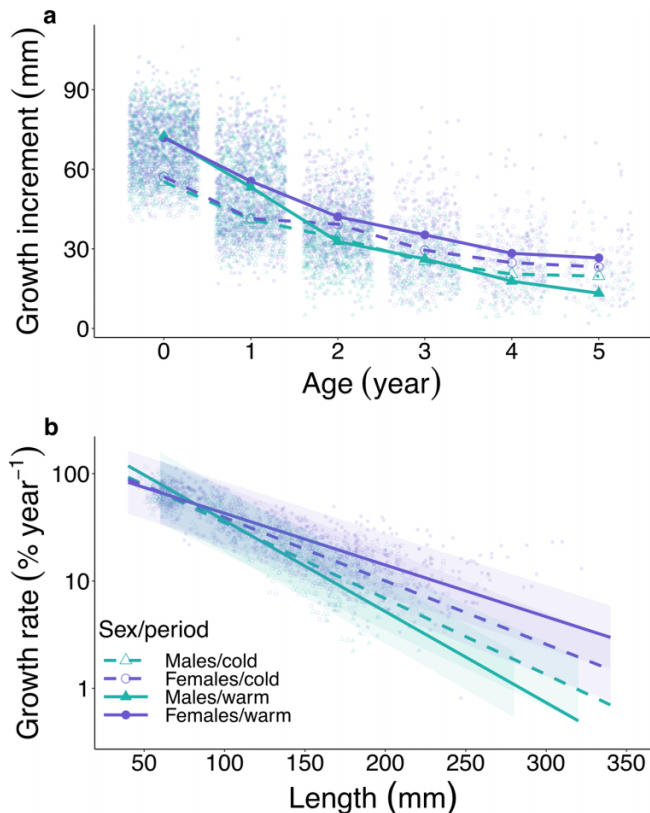
tential explanation for this pattern is that the benefit of increased fecundity with body size (Craig 1987; Barneche et al. 2018) is large enough to offset the increased maintenance costs caused by higher temperatures (Brown et al. 2004; Lindmark et al. 2022) in females but not in males. Thus, females can prioritize high growth rates throughout ontogeny also in warming environments, e.g., by increased feeding rates (Estlander et al. 2015), unless optimum growth temperatures are surpassed (Fig. S2). On the other hand, for males the higher maintenance costs at high temperatures and large body size (Ohlberger et al. 2012) likely outweigh any benefits from increased feeding rates, leading to decreased growth rates, as observed in this study. This probably relates to the much smaller reproductive gain of a larger body size for male than female perch (Craig 1987), making maladaptive effects of increased feeding activity (e.g., risk of predation (Rennie et al. 2008)) more important to avoid for males.

Slower growth in males than in females of other percids was suggested to be caused by higher female feeding rates, food conversion efficiency and metabolic activity in a modeling study by Rennie et al. (2008). Studies addressing warming effects on such physiological parameters (e.g., Lindmark et al. 2022) rarely account for sex; however, and more research on sex-specific temperature effects on feeding and metabolism across body size is thus needed. The observed sex-specific growth responses over ontogeny in our study led to an increased SSD in the population after onset of warming. Female perch of age 5 years, for example, were on average 8% larger than male perch before warming, while after onset of warming these females were 20% larger than males (2.5 times increase in SDI). Overall, the warming experiment demonstrates that temperature, although unclear if via direct physiological responses and/or indirect effects, has sex-specific effects on body growth and size, and thereby strongly amplifies SSD in a wild fish population.

In addition to individual physiological responses, resource availability and strength of competition are likely to change with warming. A decreased basal resource carrying capacity with warming is commonly predicted (Savage et al. 2004; Bernhardt et al. 2018). However, the availability of benthic invertebrate resources in the experimentally heated ecosystem was slightly higher after onset of warming (Sandström et al. 1995), but we have no comprehensive information on resource availability. Nevertheless, a potential increased abundance of nutritional resources with warming may thus be part of the explanation of how female perch were able to increase their growth rates. Males, on the other hand, do not seem to benefit from this increase in benthic resources. One explanation could be that they feed, on other, potentially negatively affected, resources in other (colder) habitats, or that acquired energy is allocated to, for example, maintenance or reproduction, instead of body growth. However, Prchalová et al. 2022 showed that perch males and females do not differ in their thermal habitat use or dietary composition. Yet another explanation could be that males do not increase their feeding with warming to minimize predation risk (Rennie et al. 2008). Further studies in a more controlled setting can potentially shed light on the exact role of resource availability, if any, in the sex-specific growth response to increased temperatures in perch.

Apart from being caused by sex-specific growth responses in adults, SSD could also increase with warming through temperature effects (sex-specific) on size at maturation and on juvenile developmental rates. A recent study shows that female perch mature at a smaller size in the heated experimental area compared to the surrounding archipelago (Niu et al. 2023). SSD in fish mainly manifests at or after maturation (Parker 1992; Stamps 1993). In percids, this is due to growth of percid males slowing down more than growth of females after maturation, likely because of differences in energy allocation to growth versus reproduction (Rennie et al. 2008), which leads to an increase in SSD over age and size. In populations with a lower age and smaller size at maturation (in warmer waters) the difference between male and female body size, and thus the degree of SSD, will be more prominent at a given adult age than in populations with a higher age and size

Table 1. Linear mixed model on the effects of sex and warming on annual growth rate over body size, back-calculated for each individual (In(annual growth rate) ~ body length × sex × period, $n = 1711$).

Explanatory variables	Estimate	SE	CI low	CI high	t	p
Intercept	5.0250	0.0379	4.950	5.0990	132.74	<0.001***
Sex-male	0.1576	0.0717	0.0173	0.2980	2.20	0.028*
Period-warm	−0.1604	0.0603	−0.2795	−0.0424	−2.66	0.008**
Body length	−0.0136	0.0003	−0.0141	−0.0131	−52.16	<0.001***
Sex-male:period-warm	0.5331	0.1349	0.2694	0.7981	3.95	<0.001***
Sex-male:body length	−0.0027	0.0005	−0.0037	−0.0017	−5.17	<0.001***
Period-warm:body length	0.0025	0.0004	0.0018	0.0033	6.64	<0.001***
Sex-male:period-warm:body length	−0.0058	0.0009	−0.0076	−0.0039	−6.22	<0.001***

Note: The conditional $R^2 = 0.81$, marginal $R^2 = 0.76$. SE, standard error. CI low and high are 95% confidence interval minimum and maximum, respectively. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Fig. 2. Whole-ecosystem warming led to size- and sex-specific changes in body lengths and an increase in sexual dimorphism index (SDI). (*a*) Mean with 95% CI length-at-age (mm) of male (turquoise triangles and line) and female (purple dots and line) perch of ages 1–6 before (dashed line) and after (solid line) onset of warming. (*b*) The relationships between the sexual dimorphism index (SDI$_{period}$) and age of perch before (dashed) and after (solid) the onset of artificial warming (Slope$_{cold}$ = 0.015, Slope$_{warm}$ = 0.054), with lines representing significant linear regression lines with 95% confidence interval. The *y*-axis shows how much larger the average female is than the average male at a specific age. At SDI = 0, males and females of a certain age have the same mean size.
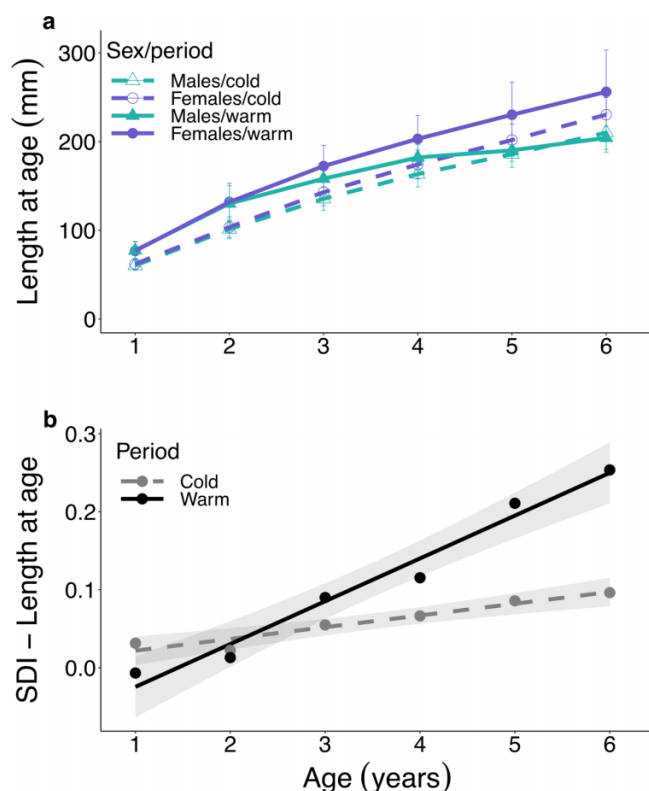
the difference in body size between males and females at age 5 will be larger in the early maturing (warm) population. The earlier maturation of female perch in the heated area induced by warming (Niu et al. 2023; data on male maturation is lacking for their study period) could thus likely have contributed to the growth patterns and degree of SSD we find in our study.

We studied the fish for the first 10 years after onset of warming (i.e., maximum five generations, Sandström et al. 1995), and the observed responses of perch are therefore most likely plastic. A more long-term (24 year) gradual growth response of female perch to the warming (Huss et al. 2019, no males sampled in later years), suggests that also local adaptation or gradual ecological change could be important components of warming-induced changes in body growth. The temperature increase in our experiment (~6 °C) is likely higher than what has been predicted to be realized in the Baltic Sea in the next decades (HELCOM 2013), but the results show the direction of change with increasing temperatures. Potential evolutionary responses in sex-specific growth responses and SSD to warming therefore remain an important topic for future studies.

Our finding of negative effects of warming on body growth of large males, but positive effects on female body growth and size can, in turn, have a number of ecosystem consequences. For many fish species, including perch, large females are essential for population productivity, due to their high egg production (Olin et al. 2012). Sustained high body growth of females in warm environments may thus dampen negative influences of warming on population regeneration rates. Ecological interactions and processes often depend on both body size (Woodward et al. 2005) and temperature (Dell et al. 2011; Gårdmark and Huss 2020). Fish feeding rates, for example, often increase with warming (Lindmark et al. 2022) and may alongside shifts in body size, potentially increase top-down regulation of prey. Such warming-induced changes in size-dependent interactions have the potential to both alter community dynamics and lead to sudden shifts in food web structure (e.g., collapses of predatory fish (Lindmark et al. 2019; Thunell et al. 2021)). For perch, diet composition may change indirectly with temperature, as rates of piscivory increase with body size (Hjelm et al. 2000), and a warming-induced increase in female body size may thus lead to an increase in piscivory. Increased body size differences between males

at maturity (in colder waters), as there is a longer time since maturity for females to outgrow males. For example, if fish mature at age 2 in warm water, but at age 4 in cold water—

and females may therefore also reduce diet overlap and alter competitive interactions between the sexes. In summary, warming-induced changes in sex-specific body growth and SSD thus have the potential to change both predator–prey and competitive interactions, as well as population productivity and overall food web dynamics.

Evidence is accumulating that global warming and high temperatures affect growth rates of fish (van Rijn et al. 2017; van Dorst et al. 2019; Lindmark et al. 2023). Our results reveal that warming can also lead to sex-specific body growth responses and an increase in SSD in perch, a common, often numerically dominant and widely distributed European fish species (Thorpe 1977; Tammi et al. 2003). This calls for further studies to assess the generality of the relationships between warming, sex-specific growth responses and SSD across other fish species. In addition, there is need to further disentangle the exact mechanisms by which temperature can affect life history traits in wild fish populations. Importantly, our results imply that because growth responses over individual life history to warming can vary between sexes, mean population responses are likely insufficient for predicting body growth and thus ecological interactions in a warmer future.

Article information

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Data availability

Data analyzed during this study are openly available in the Zenodo repository at https://doi.org/10.5281/zenodo.8367178.

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Formal analysis: RMvD
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Methodology: RMvD, AG, KKK, LN, SE, HH, MO, MR, MH
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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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